

Orthoptera response to grazing: an introduction to the special issue

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Grazing is a global driver of vegetation dynamics and exerts far-reaching effects on plant traits such as promoting the growth of annual over perennial plants, short plants over tall plants, and procumbent plant architectures (Díaz et al. 2007). Since approximately one quarter (26%) of Earth's non-ice surface is utilized as wildland or pastures for grazing of livestock and wild ungulates (FAO 2006), grazing is responsible for shaping much of the world around us, both directly and indirectly. Orthoptera, which largely co-occur with mammalian grazers in pasturelands and meadows worldwide, are more vulnerable to the effects of trampling and grazing than most.

The order Orthoptera includes many herbivorous species which are specifically adapted to play an important nutrient cycling role in grassland environments and compete with ungulates for the same forage. All Orthoptera, herbivores and non-herbivores alike, are sensitive to meso- and micro-climatic conditions (Gardiner and Dover 2008) brought about, at least in part, by structural aspects of their grazed habitats. With few exceptions (but see Gardiner et al. 2002), the diversity and abundance of grassland orthopterans correlate with vegetation structure rather than species composition of the plant community (Hochkirch and Adorf 2007, Gardiner and Hassall 2009, Bazelet and Samways 2011a), making Orthoptera particularly vulnerable to habitat changes caused by grazing.

The effects of grazing on Orthoptera are multi-faceted and depend on many biotic and abiotic factors relating to both the grazing animal, the orthopteran, their surrounding environment, and its management. In this issue, co-editor Gardiner (2018) provides a detailed review of these factors which include, among others, grazing intensity, type of grazing animal, and season of grazing; as well as life stage of the orthopteran, its movement capability, and resource requirements. Furthermore, in many environments grazing is used as a defoliation technique in combination with fire and/or mowing, all of which can have synergistic, complementary, neutral, or opposing effects on local Orthoptera (Joern 2005, Bazelet and Samways 2011b, Kati et al. 2012, Joubert et al. 2016). For these reasons, the effect of grazing on Orthoptera can be either positive, negative or neutral. For instance, heavy livestock grazing led indirectly to increased abundance of locusts in China (*Oedaleus asiaticus*: Cease et al. 2012) and pest grasshoppers in

American rangelands (*Aulocara elliotti*: O'Neill et al. 2003). On the other hand, in multi-species studies, total grasshopper density decreased in heavily grazed plots in Mediterranean pastures (Fonderflick et al. 2014), and for most species in the American rangeland community (O'Neill et al. 2003).

The idea for this special issue originated from an International Union of Nature Conservation (IUCN) Grasshopper Specialist Group (GSG) email discussion in 2015, as the group discussed possible monitoring targets and their implementation. As members of the GSG described the monitoring needs for their particular regions, and for species of conservation interest in their areas, the impacts of grazing arose several times. Participants debated whether grazing impacts were net positive or negative for Orthoptera, as well as logistical, political, and biological differences which were particular to their region. It became clear that the impacts of grazing are localized and specific to individual habitats and species.

In this special issue, we address the diversity of grazing impacts on Orthoptera in two principal sections. First, we present four papers from South Africa, North America, and Europe which describe the effects of grazing at the habitat-scale and on Orthoptera communities. Joubert-van der Merwe and Pryke (2018) investigate the interaction of burning and grazing practices on a South African grasshopper community, as well as on the subset of the community which is endemic and rare. Kenyeres (2018), working in a Hungarian grassland, investigates the effects of grazing intensity, including the abandonment of grazing, on his local Orthoptera community. Lightfoot (2018) conducts a long-term study in a North American semi-arid grassland to assess the interaction of grazing and climate variation on the plant and Orthoptera communities. Finally, Fargeaud and Gardiner (2018) review the effects of grazing sea walls (i.e. dikes) throughout Europe on the resident orthopteran communities and suggest measures to improve these practices.

In the second group of articles, each study focuses on the effects of grazing on an individual Orthoptera species which is of conservation concern. All four of these species are found in Europe and were included in the recently published Red List of European species (Hochkirch et al. 2016). Two of the species, the Criti-

cally Endangered Crau Plain grasshopper, *Prionotropis rhodanica* (Pamphagidae), and the Near Threatened saltmarsh band-winged grasshopper, *Mioscirtus wagneri* (Acrididae: Oedipodinae), are found in Mediterranean regions of Europe, in France and Spain, respectively. Both the Crau Plain grasshopper and the saltmarsh band-winged grasshopper are rare habitat specialists which are confined to very narrow niches. Piry et al. (2018) investigate whether the population density and gene flow of the Crau Plain grasshopper correlates with habitat quality as an indication of sheep grazing. Aguirre et al. (2018) relate the presence and abundance of the saltmarsh band-winged grasshopper to the presence and abundance of goat and sheep droppings.

The two final articles discuss the British populations of species which were assessed as Least Concern globally (Hochkirch et al. 2016), but which have experienced significant range reductions in Britain in recent years. Selman and Cherrill (2018) investigate the effects of grazing on the lesser mottled grasshopper, *Stenobothrus stigmaticus* (Acrididae: Gomphocerinae), at its last remaining site in Britain. Miller and Gardiner (2018) review the interactive effects of mowing and grazing on the large marsh grasshopper, *Stethophyma grossum* (Acrididae: Oedipodinae), which is confined to wet habitats in two regions of Britain. Both studies make recommendations for mitigating measures to help conserve their species.

The articles presented here contribute significant evidence to the growing body of work investigating the effects of ungulate grazing on Orthoptera. This relationship is not straight-forward, and our hope is that this synthesis will assist in identifying general, common principles that can be used to improve management decision-making for the benefit of healthy ecosystems and the survival of threatened Orthoptera species.

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Grazing and Orthoptera: a review

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Abstract

Orthoptera are an important biological component of grasslands as a crucial link in the food chain. Grazing, either by wild animals or livestock for human food production, exerts considerable influence on the Orthoptera of grasslands. For example, grazing prevents succession of open grasslands to scrub and forest, creates heterogeneity in sward height, and provides patches of bare earth through the action of livestock hooves breaking the vegetative cover. Grazing may also interact with other forms of grassland management such as burning to produce quite complex interactions which vary greatly between regions and Orthoptera species. Threats to grassland Orthoptera include overgrazing; conversely, abandonment of grazing can lead to the loss of open habitats vital to many species. It is important to have ungrazed areas to provide refuges for species negatively affected by grazing. Rotational management – moving domestic livestock between different pastures – will also allow a range of sward structures to develop over a landscape. The over-arching principle for grazing management should be to establish a heterogeneous sward with a range of sward heights and bare earth for oviposition/basking. In more extensive systems, patches of scrub can form habitat of woody vegetation for species such as bush crickets. The greatest diversity of habitats should provide the highest species richness.

Key words

conservation, ecosystem, grassland, habitat, management

Introduction

Grasslands are one of the most extensive and important ecosystems. Grasses originated in the late Cretaceous period and, by the Miocene, grasslands were a prominent component of the earth's vegetation (de Wet 1981). It is estimated that grasslands now cover approximately 40% of the earth's land surface (White et al. 2000) and co-evolved with the grazing animals which maintain them in an early successional stage (Singh et al. 1983). Grasslands are a source of grass crop plants (grains) and herbivore products (fibre and meat), essential for the earth's expanding human population (Foley et al. 2011). Many grassland ecosystems have been altered by human activities and as such are considered 'semi-natural'. Grasslands are threatened by conversion to arable cropping

(Suttie et al. 2005) and the pressures on those remaining from intensive agricultural practices such as overgrazing or, conversely, from a lack of grazing management leading to woodland encroachment, are great.

Grasslands are found in temperate and tropical regions on all continents except Antarctica, and can be classified into many different types including chalk downland, tallgrass prairie, savanna and shrubland steppe. In this review, grasslands are defined as "land on which the vegetation is dominated by grasses" (FGTC 1991) and no distinction is made between the types. Orthoptera form an important part of grassland ecosystems across the earth, consuming between 0.3–8% of net primary production (Köhler et al. 1987), although they are particularly wasteful feeders (e.g. *Chorthippus parallelus* consumes 2% of net primary production, but wastes 8%; Ingrisch and Köhler 1998). Orthoptera are also particularly important in food chains (Latchininsky et al. 2011), as prey for spiders and avian predators, for example. From an assessment of the status of European Orthoptera, 555 species (51.3%) were found in grassland, underlying the importance of the habitat (Hochkirch et al. 2016).

While Orthoptera can be used as indicators of healthy grassland ecosystems (Kati et al. 2004, Gardiner et al. 2005, Bazelet and Samways 2011), locusts are also an abundant pest in the rangelands of the USA and the arid grasslands of Africa, for example. Significant time and expense is invested in the control of locust outbreaks (Latchininsky et al. 2011) which can have negative effects on other fauna in the grassland ecosystem.

Grazing (by both domesticated and wild animals) effects properties of grasslands which are crucial for grasshopper life history processes. Intensity of grazing, type of grazer, rotational or seasonal aspects of the grazing regime, and the interaction of grazing with other grassland management practices, has an impact on characteristics of grasslands such as vegetation height, biomass, and plant species. In turn, these factors can influence oviposition, dispersal and feeding behaviors of grasshoppers, thereby affecting the dynamics within Orthoptera assemblages and communities. The aim of this paper is to provide a short introduction to grazing and its effects on Orthoptera, setting the scene for the more focused papers that follow.

Ecology of Orthoptera in grazed grasslands

Habitat preferences of Orthoptera may relate to choice of oviposition site, food preferences, vegetation height and biomass, and grassland management regimes (Clarke 1948). Waloff (1950) stated that the egg-pods of *Chorthippus albomarginatus* are oviposited into the base of grass lamina, while *Chorthippus brunneus* and *Chorthippus parallelus* lay their egg-pods in the superficial layers of the soil. Bare earth (often exposed in ant hills) is the usual egg-laying site for *C. parallelus*, although this species and *Omocestus viridulus* have been found to oviposit into grass-covered soil (Waloff 1950). All these oviposition niches are influenced by grazing, either for agricultural production or of wild animals.

An important distinction was made by Waloff (1950) in characterizing grasshopper species as either hygrophilous (egg-pods in vegetation just above soil: e.g. *O. viridulus*) or mesophilous (egg-pods laid in soil: e.g. *C. brunneus*). Grassland management such as heavy grazing may remove or damage egg-pods of hygrophilous species laid in the vegetation while leaving those of mesophilous species in the soil undamaged.

Choudhuri (1958) investigated the oviposition habits of *C. brunneus* and *C. parallelus*, concluding that *C. parallelus* preferred to oviposit in moist sand, while *C. brunneus* mostly laid eggs into dry sand. Compaction, temperature, moisture content and particle size of the soil were also found to influence the choice of oviposition site (Choudhuri 1958). 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. Trampling of the soil surface by grazing animals can create suitable oviposition sites for a range of species, and the type of livestock is important. For example, on sea walls cattle can produce a sward with a higher amount of bare earth than sheep due to their heavier nature (Gardiner et al. 2015), providing suitable niches for oviposition (Fig. 1).

The food preferences of *C. brunneus* and *C. parallelus* have been examined in some depth by Clarke (1948), Richards and Waloff (1954) and Bernays and Chapman (1970a, b). Clarke (1948) and Richards and Waloff (1954) suggest that the availability of suitable food (in respect of nutrient availability and palatability) may not be a limiting factor for British grasshoppers. However, Bernays and Chapman (1970a) found that *C. parallelus* selected grasses in preference to herbs for feeding. This selection could be due to a natural chemical on the leaf surface of grasses which induces biting. Bernays and Chapman (1970b) noted that fine-leaved grasses of the genera *Agrostis* and *Festuca* were often selected in preference to *Holcus*, *Cynosurus* and *Dactylis* by *C. parallelus* (Bernays and Chapman 1970b). Gardiner and Hill (2004), however, found a preference for coarse grasses such as *Dactylis glomerata* and *Lolium perenne* over the fine-leaved *Festuca rubra* and *Cynosurus cristatus*. Both *D. glomerata* and *L. perenne* are grass species that are commonly sown for agricultural purposes in pastures due to their high nutritive value to grazing livestock (Spedding and Diekmahns 1972, Hubbard 1984), 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* because of their superior nutritive value and palatability.

Vegetation structure is an important factor for grassland fauna (Duffey et al. 1974, Morris 2000), particularly for grasshoppers. Clarke (1948) and Gardiner and Hassall (2009) noted that vegetation height and density are the most important habitat factors for grasshoppers, particularly in respect to their influence on microclimate.



Fig. 1. Cattle trampled ground with an abundance of bare earth, credit T. Gardiner.

Vegetation which is dense and tall is not readily warmed by the sun or cooled by free circulation of air, in contrast to sparser vegetation which provides better conditions for diurnal activity (Clarke 1948, Gardiner and Hassall 2009). Dense vegetation with high percentage cover, however, provides abundant food sources. Therefore, grasshoppers may be abundant in habitats which possess both dense vegetation and areas of sparser vegetation, and such local differentiation of vegetation structure may be important (Clarke 1948, Gardiner et al. 2002). Heterogeneity of sward structure may be important for other invertebrates such as butterflies (Ausden and Treweek 1995) and can be produced through rotational mowing, which creates a mosaic of cut and uncut areas (English Nature 1992), or extensive grazing regimes (Crofts 1999). Grazing that creates the small-scale patchwork of bare ground, low, herb-rich turf, and taller, tussocky grassland occurring in close proximity, is necessary for the conservation of the bush cricket *Decticus verrucivorus*, which can be easily lost due to even slight changes in management.

Gardiner et al. (2002) in a survey of grasslands in the Chelmsford area of Essex in the UK identified the optimum sward height and vegetation composition for three *Chorthippus* species. Grasshoppers were most abundant between vegetation heights of 100–200 mm (Gardiner et al. 2002), and in grasslands dominated by fine-leaved grass species such as *Agrostis stolonifera*. The findings detailed in Gardiner et al. (2002) agree with the conceptual model outlined in van Wingerden et al. (1991a) which visually displayed the relationship between grasshopper abundance and quantity of vegetation as an optimum curve.

Vegetation structure may influence egg development (van Wingerden et al. 1991a). Tall vegetation could lead to lower maximum temperatures in the soil surface and consequently delay hatching of eggs laid in the soil, resulting in a loss of some mesophilous grasshopper species (van Wingerden et al. 1991b). Such tall grasslands may be described as 'cold', while those with shorter, sparse vegetation are 'warm' (van Wingerden et al. 1991b).

Clarke (1948) suggested that vegetation height and density may be related to the following three factors: growth form of component plant species, properties of the soil, and grazing and other biotic factors such as trampling.

Factors influencing the abundance and behavior of Orthoptera in a grassland sward are complex and inter-related. To reflect this

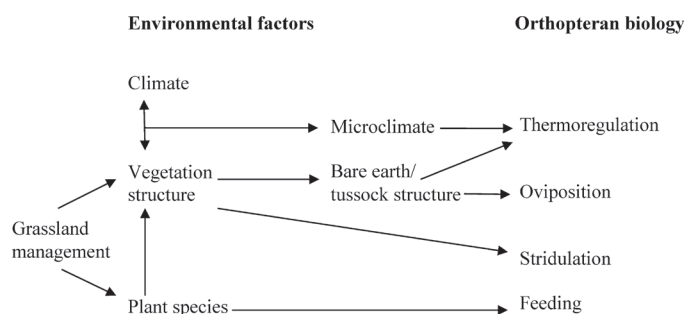


Fig. 2. Relationships between environmental parameters and the main behavioral activities of Orthoptera in a grassland sward (after Gardiner 2009).

complexity, Fig. 2 shows how the behavioral activities of Orthoptera may be affected by environmental parameters in a grassland sward (Gardiner 2009). Many of the environmental parameters presented in Fig. 2 are altered by grassland management such as grazing; therefore, in the field, Orthoptera will be affected by the interaction between management and environmental factors. For example, grazing will remove large quantities of herbage biomass and reduce sward height in the short-term, which may create a warmer microclimate which is more conducive to basking. Additionally, grazing may create patches of bare earth (through trampling of the soil by hooves) that provides a better environment for oviposition and basking purposes. I suggest that sward height and biomass are pivotal in determining suitability of grassland for Orthoptera due to their influence on many other environmental parameters such as microclimate, behavioral activities of individuals, and the abundance of grasshoppers (Gardiner 2009). Grassland management such as grazing is concerned mainly with the removal of the harvestable standing crop (Hopkins 1999) and is therefore crucial in determining the habitat preferences of Orthoptera.

Behavior and dispersal in grazed environments

Narisu et al. (1999) suggested that directional movements of grasshoppers in rangeland habitats may be related to the direction of the prevailing wind. In their study, adults moved predominantly into the prevailing north-westerly wind and it was suggested that the movement upwind may have reflected the search for resources such as feeding sites or mates. In the study reported by Gardiner and Hill (2004), both nymphs and adults of *C. parallelus* displayed directional dispersal within a small area of extensively-grazed pasture and a high proportion of adults and nymphs were re-observed in pasture north-west of the release site which was neither into or with the prevailing wind. The release area had been heavily grazed by sheep and the sward height in this area was below 50 mm (Gardiner and Hill 2004). Gardiner et al. (2002) suggested that *C. parallelus* is less abundant in short (<100 mm) vegetation. Therefore, the release circle was unsuitable for this species, having a short sward that provides no cover from avian predators or inclement weather conditions. This heavily grazed environment was 'spatially hostile' (Rogers 1984) for both *C. parallelus* nymphs and adults. Both life stages would therefore have a greater chance of survival and breeding success in a more suitable environment, and dispersal away from the release circle was a necessity for large proportions of the marked population in this heavily grazed pasture.

Horn (1984) suggested that the dispersal of grasshoppers is favored when the local environment is deteriorating, especially

if more suitable conditions exist in other adjacent areas. Furthermore, patches that form in areas contaminated by feces or in latrines are avoided by most grazing livestock and have taller vegetation (Duffey et al. 1974, Ausden and Treweek 1995). Grasshoppers may actively seek out these areas for shelter and breeding sites in particularly unfavorable pastures. However, these patches of tall grass are only a temporary habitat and may be removed at any time if grazing pressure increases, which may lead to frequent movements of grasshoppers between favorable areas of tall grass and potentially unfavorable areas in relation to the rate of defoliation by the grazing animal (Gardiner 2015).

For successful migration, grasshoppers must have had some indication of the favorable habitat in the direction of travel. The compound eyes of orthopteroids are quite efficient at detecting movement (Marshall and Haes 1988) and it is reasonable to suggest grasshoppers can detect the long grass by its movement in the wind. Grasshoppers can judge the distance of long grass and singing perches by undertaking peering movements while assessing the suitability of a patch of vegetation (Chapman 1998). Nymphs and adults may be able to quickly assess distance and direction of suitable ungrazed patches of grass using their extensive 360° vision (Chapman 1998), particularly as peering movements would be unobscured by tall vegetation structures in heavily grazed habitats. Further neurobiological and behavioral research is needed to determine whether Orthoptera can see patches of suitable habitat and orientate towards them.

Other factors may also play a role in the dispersal of Orthoptera in grazed habitats. For example, sheep grazing may disturb nymphs and adults, leading to greater dispersal in a particular direction, or they may act as a transportation mechanism (Fischer et al. 1996). Grazing animals such as cattle could also 'flush' grasshoppers into pools within grasslands or heathlands, initiating swimming or drowning (Gardiner 2009).

The effect of grazing

Grazing intensity.—Grazing and trampling exert important influences on vegetation structure (Clarke 1948). Heavy grazing by cattle and sheep on fertile soils can produce a short, dense sward of neutral grassland species such as *Lolium perenne*, which is unsuitable for grasshoppers (Gardiner et al. 2002). However, Clarke (1948) suggested that excessive grazing by rabbits on chalk grassland and heaths promoted sparser vegetation, comprised of less vigorous species such as *Festuca ovina*, which was consequently more favorable to grasshoppers.

In another study on a heavily rabbit-grazed calcareous grassland, *C. brunneus* was more abundant within an enclosure than on the surrounding grazed grassland (Grayson and Hassall 1985). The authors suggested that the taller vegetation in the enclosure provided better cover from vertebrate predators and better quality food resources for grasshopper nymphs than the shorter grazed vegetation. In coastal pastures which have been ungrazed for many decades on Skipper's Island in southern England, the species richness of orthopteroids is higher than in mainland habitats such as sea wall flood defenses where mowing management is undertaken (Gardiner and Ringwood 2010). These ungrazed pastures have developed a mosaic of tussocky, rank grassland and scrub which is suitable for grasshoppers and bush crickets.

A large mesa in South Africa acted as a refuge for Orthoptera in comparison to the heavily grazed flatlands which surrounded it (Gebeyehu and Samways 2006). The summit, which was inaccessible to grazing livestock, was an important conservation refuge for one grasshopper species, *Orthochtha dasyncemis*.

Across Europe, overgrazing (particularly by cattle) is the greatest threat to Orthoptera (affecting 262 species; Hochkirch et al. 2016). In the UK, concerns have been raised about the negative effect of pony overgrazing upon the orthopteran assemblages of the New Forest (Tubbs 1986, Pinchen 2000, Denton 2006). Denton (2006) outlines the importance of exclosures, from which grazing ponies are largely excluded, for Orthoptera in the forest. For example, both the nationally scarce *Omocystus rufipes* and *Nemobius sylvestris* are found in exclosures, the varied and taller vegetation structure created in the absence of excessive grazing being particularly important. Surveys along the Mardyke River Valley in the UK also showed that Orthoptera were extremely scarce in intensively grazed horse pastures and that species richness was lower than in ungrazed grassland (Gardiner and Haines 2008). The horses grazed continuously throughout the year on the south side of the Mardyke and this led to an extremely short sward (<100 mm in height) that may have provided insufficient cover from inclement weather and predators (particularly birds) for Orthoptera (Gardiner et al. 2002).

A study of rangeland grasshoppers in the USA found that most grasshopper species were more abundant on ungrazed treatments when compared to heavily grazed areas (O'Neill et al. 2003). However, one species, *Aulocara elliotti*, a serious pest of rangelands, preferred the heavily grazed plots, perhaps due to its exclusion from densely vegetated pasture. Conflicting evidence is provided in Holmes et al. (1979) who stated that some grasshopper species were more abundant in heavily grazed fields when compared with lightly grazed fields, while other species exhibited the opposite preference for infrequently grazed pastures with tall and dense vegetation. Cease et al. (2012) also demonstrated that abundance of the locust *Oedaleus asiaticus* was promoted by heavy grazing in north Asian steppe grasslands by the lowering of plant nitrogen (N).

In savannah grassland in South Africa, abundance and guild structure of grasshoppers varied between lightly and heavily grazed areas (Prendini et al. 1996). The heavily grazed areas characterized by short vegetation were dominated by grasshopper species associated with short grass and/or bare earth, whereas the lightly grazed grassland with taller and thicker grass had mainly grasshoppers of taller vegetation which were mixed feeders or tough grass feeders (Prendini et al. 1996).

Interaction with burning.—Fire and grazing are two of the main methods of grassland management, and in many areas they interact to influence populations or assemblages of Orthoptera. In Afriomontane grasslands in South Africa, grasshopper abundance benefited greatly from burning and cattle grazing (Joubert et al. 2016). Most grasshoppers favored recently grazed or burned grassland, although some did not, further highlighting the species-specific response to grazing management observed in other studies.

In the UK, traditional Culm grassland management, such as grazing and burning, has been undertaken to restore neglected sites (Wolton 1991). Grazing of pastures usually occurs between late May and late September, at a stocking rate of approximately 1 suckler cow per ha over a period of 20 weeks, leading to a diverse sward about 150 mm in height (Wolton 1991). Winter burning (known as swaling) during January or February is also practiced and has traditionally been used after particularly wet summers when it is impossible to graze livestock. This burning reduces the quantity of leaf litter, therefore providing a more open sward (Ausden and Treweek 1995). The complex interaction between weather and grassland management has important effects on Orthoptera populations.

In a small-scale study of formerly grazed Culm grasslands subjected to burning, there was increased Orthoptera abundance (density 29X greater on burned plots than on unburned replicates) in the post-burn year (Gardiner et al. 2005), as in the studies of Samways (1994) and Bieringer (2002). It is likely that mesophilous species such as *C. parallelus*, which overwinter as egg pods in the soil, may escape the main destructive impact of winter burning. The reduced sward height/biomass and increased light penetration on winter-burned swards in April/May could lead to enhanced post-diapause development and basking opportunities for hatched nymphs. Recently-burned ground could also be attractive to melanid groundhoppers (*Tetrix undulata*; Gardiner 2012) and grasshoppers (*Myrmeleotettix maculatus*; Gardiner 2014). Grazing in the post-burn year could keep the vegetation open and prevent development of a tall, tussocky *Molinia caerulea* sward.

Hochkirch et al. (2016) suggest that wildfires are a significant threat to 173 European Orthoptera species, with bush crickets (Tettigoniidae) more threatened than grasshoppers (Acrididae), perhaps due to many bush cricket species being flightless and unable to escape from the flames.

Abandonment of grazing.—As most grassland exists at a relatively early stage of succession, abandonment of grazing can be particularly harmful to the Orthoptera assemblages reliant on the open sward, with 148 European species affected (Hochkirch et al. 2016). In Epping Forest in the UK, the locally-scarce grasshopper *O. viridulus* was significantly more abundant on cattle-grazed sites than in ungrazed grassland and heathland (Gardiner 2010). The absence of grazing in particular, led to scrub encroachment and natural woodland succession throughout the open plains in the forest, causing major declines in floristic and thermophilous insect diversity in the 20th century (Rackham 1986). Despite these losses, Epping Forest is still considered one of the most important areas for Orthoptera in Essex County (Wake 1997), with new species such as *Stenobothrus lineatus* colonizing the open plains (Wilde 2009), perhaps in response to climate change (Gardiner 2009).

Rare species in the UK, such as *D. verrucivorus*, which are on the edge of their range, have very specific micro-habitat requirements (Cherrill and Brown 1990, 1992). *D. verrucivorus* was formerly found on several heathland sites in southern England, but with the loss of these populations, it is now restricted to ancient calcareous grassland (Fig. 3). *D. verrucivorus* disappears very quickly if winter-cattle-grazing ceases and tall rank grasses such as *Brachypodium pinnatum* encroach onto the bare ground. These rank grasses replace the low, herb-rich turf that *D. verrucivorus* requires for oviposition and which its early nymphal stages require for quick development in the warm microclimate provided by the open niches of this turf (Sutton 2015).

Conversely, abandonment of cattle livestock grazing in Spanish grasslands had an immediate positive effect on density, diversity and species richness of Orthoptera, although the effects were species-specific (Isern-Vallverdu and Pedrocchi 1994). The ungrazed pastures had taller grasses which were generally more favorable for Orthoptera because they had more refuges than the formerly grazed habitats. Species which benefitted from abandonment of grazing in Isern-Vallverdu and Pedrocchi's (1994) study included *S. lineatus* and large species such as *Platycleis tessellata* which needed the cover from avian predation. One species which was associated with short grassland and bare ground, *M. maculatus*, disappeared with the abandonment of cattle grazing. This may explain its extirpation from Epping Forest in the UK where cattle grazing ceased



Fig. 3. Grazed chalk downland in Sussex, UK, habitat for the rare *Decticus verrucivorus*, credit T. Gardiner.



Fig. 4. Cattle grazed wet grassland in Epping Forest, UK, habitat for *Omocestus viridulus*, credit T. Gardiner.

in the 20th century, although cattle grazing was reintroduced in 2002 and has since been linked to an increase in abundance of *O. viridulus* (Gardiner 2010; Fig. 4).

Type of grazing animal.—The type of grazing animal has widely differing impacts on the sward structure of grassland. Large-scale cattle grazing in Georgia led to a mosaic of grassland, scrub, and trees, offering habitats for several highly specialized species of Orthoptera (Bontjer and Plachter 2002). However, contradictory evidence is provided by a study of vegetated sea wall flood defenses in the UK (Gardiner et al. 2015). On two cattle-grazed sea walls which had fairly short swards (<10 cm in height) with few grass tussocks, abundance of grasshoppers was lower than on the ungrazed sea walls which had higher densities and more variation in sward height (10–40 cm). This suggests that the impact of heavy cattle grazing, which leads to very uniformly short swards, is not favorable for *Chorthippus* grasshoppers which require tussocks of tall grass for shelter and feeding. However, on the sheep-grazed sea walls, which had greater variation in sward height (10–30 cm) than the cattle-grazed sections, abundance of grasshoppers was

higher than in the ungrazed control swards which were quite uniformly tall and rank in nature (>40 cm in height). Therefore, the impact of grazing on grasshoppers is likely to be through the establishment of suitable sward heights at appropriate stocking rates, with light sheep grazing producing more variation in vegetation height than cattle grazing where swards can be uniformly short due to high stocking rates (Gardiner et al. 2015).

Fonderflick et al. (2014) found that the impact of sheep grazing exerted a species-specific influence on the grasshopper assemblage, which varied greatly over the season in Mediterranean steppe-like 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. Fonderflick et al. (2014) suggested that rotational grazing systems could conserve Orthoptera at a farm scale by promoting heterogeneity in sward structure. Irregular grazing, likely to produce a sward with greater sward heterogeneity, was also found to have significantly higher species richness of Orthoptera (28 species) than plots with mown grass (17 species) or permanent sheep pens (14 species) (Fabriciusová et al. 2011). Species-specific responses to grazing were also noted in submontane pastures in the Hrubý Jeseník Mountains in the Czech Republic, where the abundance of *Gomphocerippus rufus* increased substantially with grazing, which contrasted with *G. rufus*' negative response to mowing (Rada et al. 2014).

In subalpine pastures in the Swiss Alps, Spalinger et al. (2012) found no direct effect of wild ungulate grazing (red deer and chamois). However, they did observe the small-scale alteration of habitats and plant N content by ungulates, which in turn affected Orthoptera abundance and diversity.

Intensive grazing by unmanaged wild rabbit, *Oryctolagus cuniculus*, populations in Epping Forest in the UK, led to the extirpation of *O. viridulus*, a grasshopper with a preference for tall grassland (Gardiner 2010). The grazing created a very homogenously short grassland sward resembling a 'lawn' which consequently did not provide the necessary shelter or 'cool' microclimate for *O. viridulus*.

In Europe generally, there has been a move away from traditional sheep and goat farming to cattle grazing, leading to fewer and larger farms, with overgrazing a significant issue (Hochkirch et al. 2016). While this process was well underway during the middle of the 20th century in north-west Europe, it has now spread to Mediterranean areas and the new Member States of the eastern European Union.

Agricultural improvement of pastures – Orthoptera in decline?—The effect of agricultural improvement of grasslands on Orthoptera has received little attention when compared to other aspects of farmland management in Europe in particular. One study detailed the effects of fertilization on the species composition and abundance of grasshoppers in the Netherlands (van Wingerden et al. 1992). In this study, overall grasshopper density and species richness decreased with increased fertilization, perhaps due to the higher herbage biomass and denser structure of the sward in the fertilized plots which created a 'cold' sward, unsuitable for diurnal activities such as basking of nymphs/adults or egg development.

The studies conducted by van Wingerden et al. (1991a, b, 1992) in the Netherlands, and research in the UK by Clarke (1948) and Gardiner et al. (2002), would seem to suggest that herbage height and biomass are important factors that regulate the abundance of grasshoppers in grasslands. Based on these studies, we would expect management which reduces herbage biomass to affect grasshopper abundance as outlined in the simple conceptual model in Fig. 5. The model attempts to portray the highly complex relation-

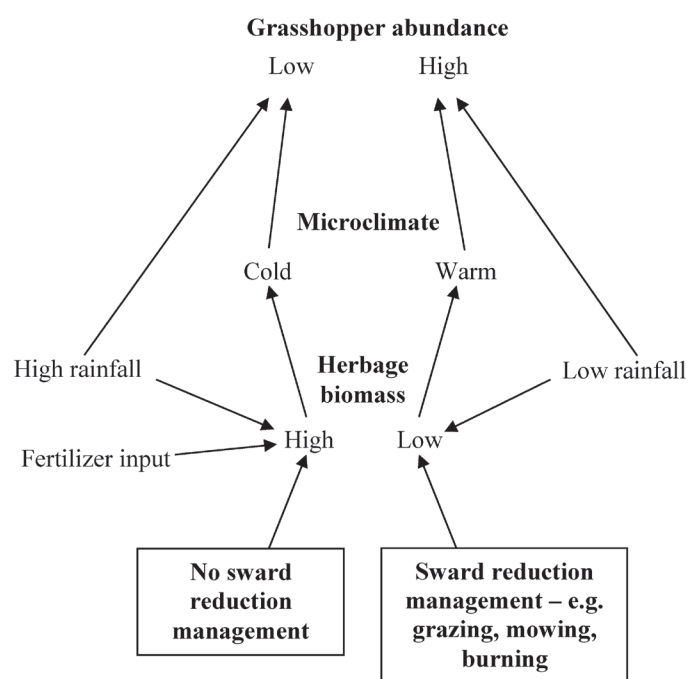


Fig. 5. A simplified conceptual model of the possible effects of management to remove herbage biomass and lack of management on grasshopper abundance (the effects of fertilizer input and rainfall are added to provide a more holistic approach) (after Gardiner 2009).

ship between management which reduces the standing crop, and grasshopper abundance, in a simplified manner.

This model illustrates that lack of sward reduction management leads to higher herbage biomass, which, in turn, leads to a 'cold' microclimate and lower grasshopper abundance. This trend can be exacerbated by fertilizer input and high rainfall, which would both contribute to an increase in herbage biomass. Alternatively, sward reduction management actions such as grazing, mowing, and burning, can be expected to lead to low herbage biomass, a warmer microclimate, and higher grasshopper abundance. This, in turn, can be exacerbated by low rainfall in a certain year (Fig. 5).

Any research into the temporal changes in Orthoptera communities in agricultural habitats should consider the economic constraints of agricultural management. The primary objective of grassland farming, which accounts for approximately 66% of land use in the UK, is to produce high livestock yield to serve the consumer food chain (McInerney 1995). This is often produced through optimizing grass yields with the application of nitrogen fertilizer which may be detrimental to grasshopper abundance (Fig. 5).

Pasture intensification – a case study from the UK.—A study of intensive and extensive pasture in the UK (Gardiner 2009) showed that unfertilized extensive pastures led to enhanced species richness, assemblage diversity and increased nymphal and adult abundance of Orthoptera, particularly of the grasshopper species *C. albomarginatus* and *C. parallelus*. These results supported those of Krüss and Tschardt (2002) and van Wingerden et al. (1991a) who concluded that species richness and abundance of Orthoptera, respectively, were higher on extensively-grazed pastures compared with intensively-managed grassland. Contradictory evidence was provided by Batáry et al. (2007), who found only marginally

significant differences in the abundance of Orthoptera between intensively and extensively grazed grasslands in the Hungarian Great Plain. Other studies on the impact of extensive grazing on grasshoppers in Europe concluded that grasshopper diversity and abundance were higher at grazed sites compared with mown grasslands (van Wingerden et al. 1991a, Wettstein and Schmid 1999).

The intensively managed pasture in Gardiner (2009) may have been unfavorable for Orthoptera due to silage cutting during June and intensive (high stocking rate) grazing. Inorganic fertilization led to tall vegetation height in May which can create a 'cold' microclimate (low temperatures in intensive pasture) that is unsuitable for nymphal development or post-diapause development in the egg stage.

Assemblage diversity of Orthoptera was higher in the extensive, unfertilized pastures perhaps due to the presence of tussocky patches of grass in rejected areas created where dung was deposited (Gibson 1997). Rejected areas were not necessarily present in the intensive pasture due to the removal of most vegetation above 70 mm during silage cutting and subsequent heavy grazing. In the extensive pastures, rejected areas supported small populations of bush crickets (*Conocephalus discolor* and *Metrioptera roeselii*) and grasshoppers (*C. albomarginatus* and *C. parallelus*). The short vegetation between tussocks provided ideal 'warm' conditions for basking and development of nymphs, while the tall vegetation offered shelter from inclement weather and avian predation as well as feeding resources. It is possible that grasshopper species such as *C. parallelus* actively seek out these nutrient rich niches in extensive patches (Gardiner and Hill 2004, Gardiner 2015), and may have to move between tussocks in a season due to disturbance by cattle or sheep and subsequent removal of tussocks through defoliation (Gibson 1997).

Examination of the stocking rate in the extensively managed pastures showed they were continuously grazed at approximately 2–4 cows per ha. The stocking rate suggested by Crofts (1999) as favorable for conservation objectives is 2 cows per ha for a similar grazing duration (24 weeks). Gardiner (2009) decided on a higher intensity stocking rate than is indicated by the literature to test whether a more economically viable grazing system with a higher number of livestock per unit area could provide biodiversity benefits. Although both extensive pastures provided better habitat for Orthoptera than intensively managed grassland, the suboptimal sward heights (<100 mm) led to low orthopteran densities, particularly of grasshopper species such as *C. albomarginatus* and *C. parallelus*. A lower stocking rate (2 cows per ha) would have led to a relaxation in the grazing pressure (Frame 1992) and taller sward height, particularly in July and August. These swards may have provided a greater chance of refuge for adult grasshoppers and bush crickets. However, a trade-off must be considered between economic viability of the grazing system and biodiversity benefits. Since the extensive pastures provided larger numbers of Orthoptera and higher assemblage diversity than the intensive sward, the moderate-intensity stocking rate and grazing pressure were justified on financial grounds. The stocking rate of 2–4 cows per ha is only slightly lower than that suggested by Frame (1992) as the proper management of improved swards for optimal agricultural production (5–8 cows per ha). Pastures are often assessed by using target sward heights and, for improved grassland managed by continuous grazing, the target sward height is 60–80 mm for cattle (Frame 1992). In all years the extensive pastures had a mean sward height that was predominantly 60–90 mm, suggesting that they were managed at stocking rates which produced swards of acceptable height for good agricultural management.

The absence of inorganic fertilizer input on these swards may impact upon yields but not necessarily economic viability. For example, under silage cutting, inorganic fertilizer input may substantially increase dry matter (DM) production in grass/swards (Frame 1992, Tallowin et al. 2002) but beef cattle output on low input systems (restricted N input) and fertilized pastures (moderate N input) has been found to be very similar, suggesting that low input systems may not affect the economic viability of grazing, particularly in clover-rich swards [such as the extensive pasture in Gardiner's (2009) study] with high rates of nitrogen fixation (Frame 1992). Other studies confirm that absence of fertilizer input may not necessarily affect animal liveweight gain and may be comparable to conventional farming systems with a high nitrogen input (296 kg N per ha; Lawes et al. 1995). However, lack of inorganic fertilizer usage in the study of Lawes et al. (1995) did significantly reduce the quantity of herbage conserved, suggesting that silage cutting may not be viable on extensive pastures. The absence of silage cutting and fertilizer input on pastures would seem to be a key requirement for maintaining populations of Orthoptera, and we suggest that where conservation of insects such as grasshoppers and bush crickets is desired, then pastures should be managed by continuous, low-input grazing at a moderate stocking density (2–4 cows per ha) which produces a sward of 60–80 mm in height. A study of extensive pastures by Marriott et al. (2002) concluded that unfertilized herbage at a height of 80 mm with a high quantity of dead leaf material may not pose problems for livestock diet due to preferential grazing of green leaves.

Of course, the stocking rates and choice of livestock are greatly influenced by subsidies provided by governments or the Common Agricultural Policy (CAP) in Europe, for example. Many farmers in the EU receive payments to farm more sustainably.

Conclusions

It is not the purpose of this paper to provide a comprehensive overview of the effects of grazing on Orthoptera; this will be provided by the other contributions to this special issue. However, from this brief review of the literature, the following are key issues to be considered when determining the impact of grazing management on Orthoptera:

1. Response of Orthoptera assemblages and species to grazing differs depending on the region and type of grassland.
2. The effect of grazing on Orthoptera is largely species-specific.
3. The type of grazing animal influences Orthoptera abundance and assemblage diversity. Cattle and sheep can be important domestic grazing animals, but both have their advantages and disadvantages for Orthoptera conservation and pest management. Wild animals may also have an important impact on Orthoptera (e.g. rabbits and ungulates).
4. Agricultural improvement (inorganic fertilizer input, heavy grazing and ploughing) of many lowland temperate pastures has led to a decrease in their suitability for Orthoptera due to unfavorable sward structure and height.
5. Grazing can interact with other forms of management such as mowing and burning, producing complex effects on assemblages of Orthoptera.
6. It is important to have ungrazed areas to provide refuges for Orthoptera species negatively affected by grazing. This can be accomplished through fencing off grassland or open woodland to form exclosures, where practical.
7. Rotational management – moving domestic livestock between different pastures – allows a range of sward structures to develop over a landscape.
8. Latrines can be refuges for Orthoptera in pastures, providing tall grassland avoided by grazing animals. These may be actively sought out by grasshoppers dispersing through pastures to find favorable feeding patches.
9. Abandonment of grazing, leading to the development of rank grassland and, ultimately, woodland, can have devastating effects on species of early successional stages, such as the rare *Decticus verrucivorus*.

The over-arching principle for grazing management should be to establish a heterogeneous sward with a range of sward heights and bare earth for oviposition/basking. In more extensive systems, patches of scrub can form habitat for Orthoptera species associated with woody vegetation, such as bush crickets. The greatest diversity of habitats should provide the highest species richness at a landscape scale.

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Is cattle grazing more important than landscape heterogeneity for grasshoppers in Afromontane grassland?

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Abstract

Overgrazing is a major driver of habitat degradation, especially in southern Africa. Although grasshoppers are adapted to and benefit from natural disturbances, such as grazing by indigenous game and burning, we do not know how they respond to heavy cattle grazing, and how this response interacts with different fire regimes. We also do not know whether grasshoppers respond principally to these disturbances, to changes in the vegetation layer, or to larger landscape attributes (e.g. elevation). We addressed these questions in the topographically heterogeneous Central Midlands of KwaZulu-Natal Province, South Africa. We compared grasshopper assemblages among sites differing in grazing intensity (light, moderate and heavy), fire regime, rocky outcrops and vegetation structure, and attributes of landscape heterogeneity. The local environment (rocky outcrops, bare ground cover, grass height and total vegetation cover) was more important than landscape attributes for all measures of diversity. Grasshopper species richness was best explained by grazing intensity, with the specific response determined by fire regime. Greatest species richness was consistently recorded in heavily-grazed grassland. Thus, we found no evidence in support of the Intermediate Disturbance Hypothesis. Grasshopper assemblage composition of areas with light grazing was different from those with heavy grazing, but areas with light grazing were similar to those with moderate grazing under all fire regimes. Different suites of grasshopper species were adapted to changes in the local environment, with greatest diversity (Shannon H') associated with elevated levels of bare ground and sparse vegetation cover. The greatest proportion of rare, endemic and sensitive grasshoppers (incl. *Lentula minuta*, *Machaeridia conspersa* and *Qachasia fastigiata*) was associated with a greater proportion of vegetation cover. The sensitivity of grasshopper assemblages to fire-grazing interactions, and the habitat requirements of different suites of species necessitates consideration of different types (fire and grazing) as well as levels of disturbances when adjusting management practices. We recommend that conservation of rare, endemic and sensitive grasshoppers should be prioritized, as these are most vulnerable to local extirpation.

Key words

assemblage composition, burning regime, elevation, Grasshopper Conservation Index (GCI), grazing intensity, indicators, landscape heterogeneity, plants, Shannon diversity (H'), species richness, topographic position, vegetation structure

Introduction

Fire and grazing by indigenous large ruminant mammals are natural disturbances in Afromontane grassland, which is one of several consumer-controlled grasslands in the world (Bond et al. 2003, Bond and Keeley 2005). Natural disturbances maintain favorable conditions for species coexistence of stationary taxa, such as plants (Chesson 2000). The exclusion of fire causes grassland plant assemblages to change in composition and become species-poor (Pausas and Ribeiro 2017), especially in an African context (Kirkman et al. 2014). Grazing interacts with fire to change the richness and structure of the vegetation layer (Burkepile et al. 2016, Joubert et al. 2017), which then influences arthropod assemblages (Joern and Laws 2013). Superimposed upon these effects of disturbances and disturbance interactions on biodiversity are large-scale spatial and temporal phenomena, such as landscape fragmentation (Stoner and Joern 2004, Krauss et al. 2010), landscape heterogeneity (Batáry et al. 2007), seasonal changes (Fonderlick et al. 2014) and weather cycles (Jonas and Joern 2007). It is necessary to identify drivers with large effects on biodiversity, and to understand how they relate with one another in natural landscapes in order to implement appropriate and effective conservation interventions.

Not all of biodiversity responds similarly to drivers of natural landscapes. Patterns in plant assemblages often show a lag in response to changes in the landscape, but respond quite rapidly to changes in the local environment (Krauss et al. 2010, Joubert et al. 2016a). Herbivorous arthropods respond more frequently and consistently to local changes in the vegetation layer than to changes in the landscape, while predatory arthropods respond more frequently to landscape than to local changes in vegetation structure (Collinge et al. 2003, Stoner and Joern 2004, Torma et al. 2014). Due to the taxonomic challenge and sheer numbers of insects (Cardoso et al. 2011), especially in sub-tropical grasslands, it is important to select indicators to represent biodiversity's response to ecosystem and environmental change (McGeoch 1998, Gerlach et al. 2013).

Grasshoppers are often used as indicators of grassland quality (Gerlach et al. 2013). This is because they are taxonomically well-

known and ecologically sensitive, they respond reliably to changes in their local environment (Bazelet and Samways 2011a) and they mimic the response of other invertebrate groups, e.g. butterflies (Marini et al. 2009, Bazelet and Samways 2012). As primary consumers, grasshoppers show greater response to local attributes than to changes in the landscape (Marini et al. 2007, Bazelet and Samways 2011b), but this may vary (Batáry et al. 2007). Grazing influences grasshoppers directly (e.g. mortality due to trampling or unintentional ingestion) and indirectly via the effect of cattle grazing on vegetation structure and specific plant assemblage (Joern 2005, Marini et al. 2009, Joubert et al. 2016b). In a global review of arthropod response to large grazing mammals, it was concluded that arthropod diversity only increases in grazed ecosystems if increased heterogeneity of the biotic and abiotic environment outweigh loss of resources and increased mortality (Van Klink et al. 2015).

Afromontane grassland is conserved in formally protected areas as well as Ecological Networks (ENs) among forestry plantations in South Africa (Samways and Pryke 2016). The conservation and management of heterogeneity at the local and landscape spatial scale is central to the success of grassland ENs (Pryke et al. 2013). Design of ENs should incorporate the typical landscape heterogeneity found in the region (Pryke and Samways 2015), while management should avoid homogenization of grassland habitat by incorporating a patch mosaic burning regime (Bazelet and Samways 2011b, Joubert et al. 2016b) and encouraging grazing by indigenous game (Pryke et al. 2016). However, in ENs where domestic cattle replaced indigenous animals as dominant grazers, it is not clear how grasshoppers respond to different intensities of grazing. We also do not know whether grasshoppers respond primarily to these natural disturbances, to changes in the local biotic environment caused by these disturbances, or landscape heterogeneity.

The aim of this paper is to determine the main drivers of grasshopper assemblage composition, diversity and species richness in Afromontane grasslands. Are grasshoppers influenced mostly by grazing intensity, or phenomena at the local or landscape spatial scale? We hypothesize that grazing intensity and the local environment will have a larger effect than larger scale phenomena, because these small herbivores are sensitive to local changes in microclimatic niches, oviposition sites, and shelter from predators. Secondly, we hypothesize that grasshopper diversity will peak at intermediate levels of disturbance, as observed in the literature (Van Klink et al. 2015). Here, we also wish to identify indicator species of different grazing regimes. Thirdly, we expect different measures of grasshopper diversity to correlate with one another, as they correlated with other taxonomic groups (Bazelet and Samways 2012). Answering these questions will help us decide upon conservation action, specifically where it involves grasshoppers in ENs within transformed landscapes.

Methods

Description of study area.—The study took place in the mid-elevation grasslands (1168–1573 m a.s.l.) east of the Drakensberg mountain range in KwaZulu-Natal Province, South Africa. It is a summer rainfall area, with precipitation mostly in the form of thunderstorms and mist in summer, with mean annual precipitation of ~1120 mm. The topography is variable, and so are the vegetation patterns. Grasslands co-occur with natural wetlands in depressions and indigenous forest patches in steep valleys.

Anthropogenic changes to the disturbance regime.—Fire and grazing are natural disturbances in these landscapes (Bond et al. 2003), but their frequency and intensity have changed greatly in response to change in anthropogenic land uses. Domestic livestock replaced indigenous game as dominant grazers, following the introduction of husbandry practices ~2000 years BP, and the influx of European settlers since the early 19th century (Deacon and Deacon 1999). Concurrently, the intensity of grazing increased (Rowe-Rowe and Scotcher 1986), impacting upon fuel load and spread of fire. Changes in land use from natural grasslands to agricultural crops (e.g. maize) and alien tree plantations further drove changes in the fire regime, as land users adapted fire as a tool for managing these novel landscapes. The current fire regime is more homogeneous than in the past due to legislative and organizational constraints that attempt to balance risks and benefits to commercial enterprises and remaining natural habitat.

Site selection and classifications.—Sites ($n = 68$) were in a large-scale EN in the Mt Shannon and Good Hope Forestry Estates, as well as in the adjacent Protected Area (PA), iMpendle Nature Reserve (Fig. 1). The variability in topography and disturbance regimes (found among sites) is representative of the variability found in the larger landscape. There were differences in abiotic landscape attributes (topographic position, elevation and aspect), or the local environment (rocky outcrops and vegetation structure).

Fire frequency was classified as either annual burning (AB) or longer fire rotations (LFR). Time since last fire at LFR sites were classified as recently-burned (RB) i.e. burned <12 months prior to sampling vs. unburned (UB) i.e. burned >12 months prior to sampling (Table 1). Grazing intensity at each site was categorized as light (reference sites in the PA), and moderate or heavy in the EN. Classification of sites was based on indicators of historical grazing (dominant grass composition and aerial cover by poisonous forbs - *Senecio isatideus* or *S. retrorsus*) and current grazing (grass height, bare ground due to trampling, and occurrence of cattle) (Joubert et al. 2017).

Sampling procedure.—Sites were >400 m apart to allow for independence of sampling. Except for annually-burned sites in narrow (<50 m) corridors, all sites were >30 m from forestry compartment edges in the interior of wider (>150 m) corridors. At each site, we sampled the grasshoppers three times: late spring (November 2012), mid-summer (January 2013), and early autumn (March 2013) with sweep nets. This involved sweeping a net (diameter: 400 mm; mesh size: 2 mm) back and forth in an 180° arch. There was one sweep with each step along four 100 m long transects that were spaced parallel to one another and 5 m apart; thus, 400 sweeps per sampling season and 1200 sweeps per site. Data from the three sampling seasons were pooled for analyses. Nets were emptied after every 25–30 sweeps to prevent escape of agile species. Grasshoppers were frozen, sorted and identified to the lowest possible taxonomic level (Dirsh 1965, Johnsen 1984, Johnsen 1991, Cigliano et al. 2017).

For the local environment, we recorded vegetation attributes at each site. Plant assemblage composition outperforms vegetation structure at predicting response of different functional groups of arthropods (Schaffers et al. 2008), including grasshoppers (Kemp et al. 1990). However, vegetation structure and host plant diversity hinges upon the contribution of individual plant species (Joern and Laws 2013), especially in an African context (Gandar 1982). Therefore, using plant species richness and measures of vegetation structure as a proxy for change in the vegetation layer is justified.

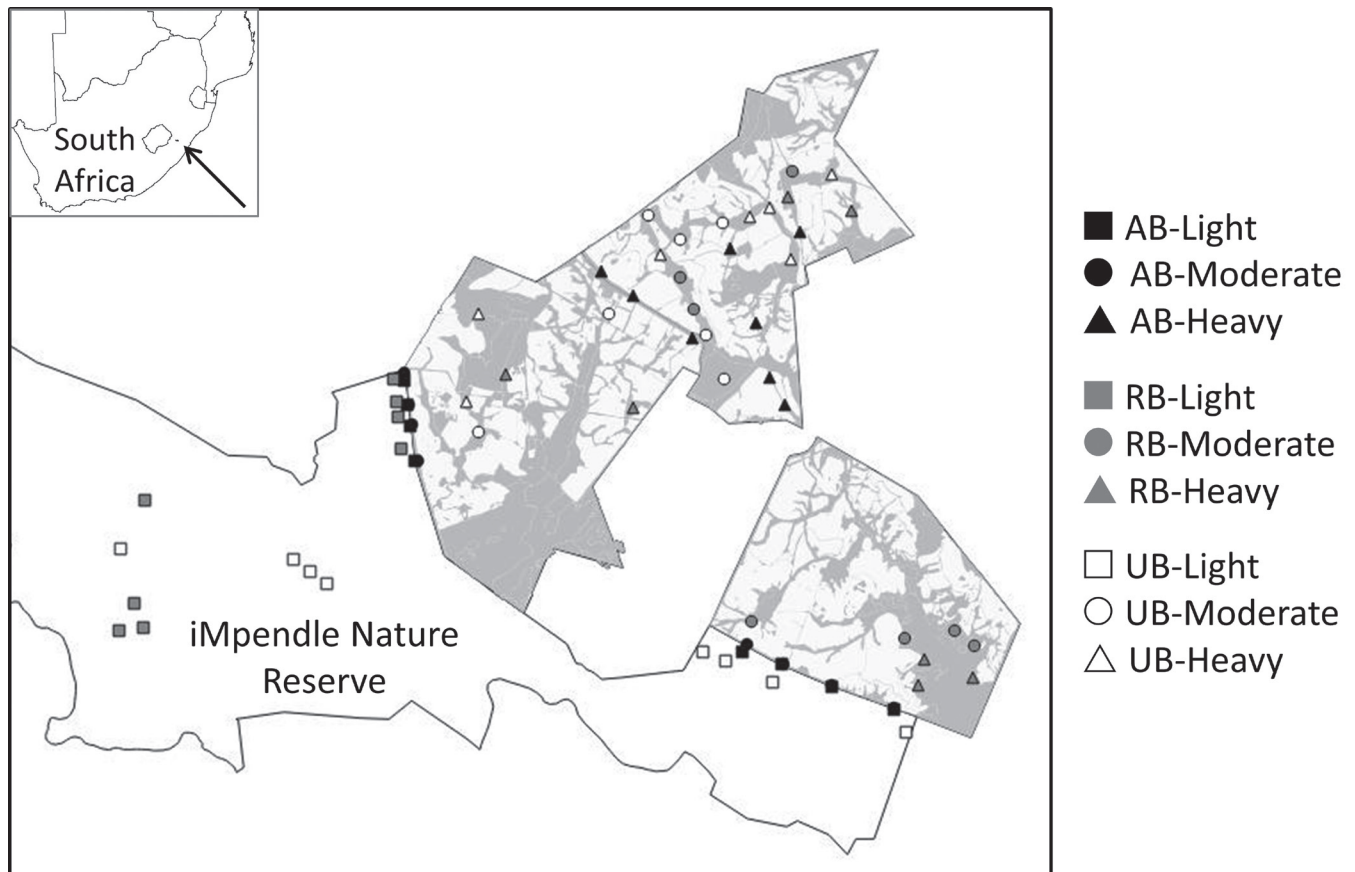


Fig. 1. Map of study sites in the KwaZulu-Natal Midlands. Abbreviations for grazing intensity: light in iMpendle Nature Reserve (square symbols), and moderate (circular symbols) or heavy (triangular symbols) in the ecological network. Abbreviations for fire regime: annual burning (AB, solid black symbols), grasslands with longer fire rotation that were recently-burned (RB, solid grey symbols) i.e. burned < 12 months prior to sampling and unburned (UB, open symbols) i.e. burned > 12 months prior to sampling.

Table 1. Description of the grazing and fire regime in each group of sites. Abbreviations for grazing intensity: light in the protected area (PA), and moderate or heavy in the ecological network. Abbreviations for fire regime: annual burning, grasslands with longer fire rotation that were recently-burned (i.e. burned < 12 months prior to sampling) and unburned (i.e. burned > 12 months prior to sampling).

| Fire frequency | Time since last fire | Fire abbreviation | Grazing intensity | Sample size (n) |
|-----------------------|----------------------|-------------------|-------------------|-----------------|
| Annual burning | Recently-burned | AB | Light (PA) | 8 |
| Annual burning | Recently-burned | AB | Moderate | 8 |
| Annual burning | Recently-burned | AB | Heavy | 8 |
| Longer fire rotations | Recently-burned | RB | Light (PA) | 8 |
| Longer fire rotations | Recently-burned | RB | Moderate | 7 |
| Longer fire rotations | Recently-burned | RB | Heavy | 7 |
| Longer fire rotations | Unburned | UB | Light (PA) | 8 |
| Longer fire rotations | Unburned | UB | Moderate | 7 |
| Longer fire rotations | Unburned | UB | Heavy | 7 |

At each site (~1000 m²), we recorded vegetation attributes in 24 discontinuous vegetation quadrats (1 m²) and six transects (i.e. six transects × 30 m = 180 measurements) (Joubert et al. 2017). In quadrats, we recorded vegetation cover of all plants (i.e. total veg-

etation cover), vegetation cover by only grasses (i.e. only grass cover), bare ground cover, rocky outcrop cover, and cumulative plant species richness in vegetation quadrats. The cumulative plant species richness of 24 discontinuous vegetation quadrats was used as a proxy for plant species richness of the whole site (1000 m²) (Güler et al. 2016). Vegetation quadrats were spaced evenly along vegetation transects. Along transects, we recorded vegetation height and basal distance at 1 m intervals. Basal distance serves as a proxy for trampling and erosion potential, especially on steep slopes, and measured as the distance from the bottom of a vertical rod (diameter: 15 mm) to where the nearest plant was rooted. Table 2 summarizes the differences in vegetation structure for each grazing intensity class. Transects were connected end-to-end, with orientation of each transect determined randomly. Averages were calculated for all attributes of the vegetation layer, except for cumulative plant species richness. Lastly, we recorded the following landscape parameters for each site: topographic position (foot-slope/valley bottom, midslope, and crest/ridge/escarpment), elevation and aspect.

Calculation of the Grasshopper Conservation Index.—The Grasshopper Conservation Index (GCI) estimates conservation value of a site based on occurrence of grasshopper species with specific traits related to extinction risk and sensitivity to habitat change. The standardized GCI site score (GCI_{in}) is the sum of all GCI scores of spe-

Table 2. Vegetation structure in each disturbance category. Abbreviations for grazing intensity: light (L) in the protected area, and moderate (M) or heavy (H) in the ecological network. Abbreviations for fire regime: annual burning (AB), grasslands with longer fire rotation that were recently burned (RB; i.e. burned <12 months prior to sampling) and unburned (UB; i.e. burned >12 months prior to sampling).

| | Bare ground cover (%) | Vegetation cover (%) | Only grass cover (%) | Rock cover (%) | Vegetation height (cm) | Basal distance (cm) |
|------|-----------------------|----------------------|----------------------|----------------|------------------------|---------------------|
| AB-L | 3.50 ± 0.85 | 95.75 ± 1.03 | 65.50 ± 2.04 | 0.75 ± 0.47 | 38.13 ± 2.97 | 0.58 ± 0.04 |
| AB-M | 5.25 ± 1.11 | 93.88 ± 1.04 | 65.13 ± 1.42 | 1.15 ± 0.84 | 28.38 ± 2.65 | 0.53 ± 0.04 |
| AB-H | 16.13 ± 3.38 | 81.75 ± 2.95 | 60.50 ± 2.72 | 2.00 ± 1.94 | 28.38 ± 3.20 | 0.94 ± 0.09 |
| RB-L | 5.50 ± 0.98 | 87.75 ± 2.38 | 57.13 ± 1.46 | 7.08 ± 2.29 | 36.13 ± 1.84 | 0.98 ± 0.1 |
| RB-M | 4.29 ± 1.69 | 89.29 ± 3.96 | 57.57 ± 4.49 | 6.61 ± 4.21 | 47.14 ± 8.20 | 0.90 ± 0.11 |
| RB-H | 10.86 ± 3.25 | 86.57 ± 3.11 | 59.86 ± 3.00 | 2.60 ± 1.94 | 30.00 ± 4.35 | 0.82 ± 0.1 |
| UB-L | 1.00 ± 0.76 | 91.88 ± 2.99 | 70.75 ± 3.50 | 1.38 ± 0.72 | 45.88 ± 1.65 | 2.58 ± 1.64 |
| UB-M | 1.43 ± 0.81 | 94.29 ± 1.6 | 63.71 ± 1.51 | 3.99 ± 1.96 | 40.00 ± 1.72 | 0.79 ± 0.05 |
| UB-H | 5.86 ± 2.16 | 92.29 ± 2.86 | 69.14 ± 3.37 | 1.27 ± 0.85 | 38.57 ± 6.69 | 0.83 ± 0.11 |

cies present at that site divided by grasshopper species richness for that site. GCI species scores were calculated for each grasshopper species by adding up the values of individual criteria: geographic distribution, mobility and rarity (Matenaar et al. 2015). Scores for geographic distribution were: 1) occurrence outside of South Africa, 2) endemic to South Africa, and 3) endemic to one province. Scores for dispersal capacity were: 1) fully capable of flight, 2) wings dimorphic, and 3) flightless. Scores for rarity were: 1) common (i.e. present in >15 sites), 2) intermediate (i.e. present in 8–15 sites), and 3) rare (i.e. present in ≤7 sites). Values for species were taken from published literature (Bazelet and Samways 2012, Adu-Acheampong et al. 2016). Where grasshoppers in our dataset were not identified to species-level, the geographic distribution was recorded as one (= 1). All analyses were conducted on the standardized GCI site score.

Data analyses.—We determined whether grasshopper assemblages were influenced by 1) landscape parameters, 2) the local environment, or 3) grazing intensity when viewed within the context of a certain fire regime (from here onwards referred to as just ‘grazing intensity’). Landscape parameters were elevation, topographic position and aspect. The local environment comprised of rocky outcrops, total vegetation cover, only grass cover, vegetation height, basal distance, and bare ground cover.

We tested for the effect of these variables on grasshopper species richness, Shannon H' diversity, the standardized grasshopper conservation index (GCI_n) (Matenaar et al. 2015) and grasshopper assemblage composition. We calculated Shannon H' diversity using the vegan package in R statistical software (version 3.2.5).

Grasshopper species richness, Shannon H' diversity, and GCI_n data were normally distributed. Hence, data were analyzed with General Linear Models using the lme4 package in R statistical software (version 3.2.5). We used the automatic model selection function glmulti in the package glmulti to select the best model (Calcagno and Mazancourt 2010). Model selection was based on grazing intensity, all local attributes and landscape parameters. Where grazing intensity was included in the best model, we used Tukey post-hoc tests to conduct pairwise comparisons among grazing intensity classes. Lastly, we used Spearman's rank coefficient (ρ) to test for relationships among attributes of vegetation structure, rock cover and elevation, as existence of such relationships influences interpretation of research findings.

Good indicators need to represent biodiversity's response to ecosystem and environmental change (McGeoch 1998, Gerlach et al. 2013). Using Spearman's rank coefficient (ρ) in the hmisc package in R statistical software, we tested whether any of the measures of grasshopper diversity (species richness, Shannon H'

diversity, and GCI_n) represented changes in plant species richness. Then, we tested for any correlations among different measures of grasshopper diversity using the same method, because we did not want to assume a linear relationship among variables (Hauke and Kossowski 2011). Finally, we used the indicator value (IndVal) method in the labdsv package of R (Dufrene and Legendre 1997) to identify grasshopper indicators of grazing intensity.

Grasshopper assemblage composition was analyzed in PRIMER 6.0 software. Grasshopper data were standardized, and abundances were square root transformed to reduce the effect of dominant species. Then, a resemblance matrix was compiled based on the Bray-Curtis similarity index. We used canonical analysis of principal coordinates (CAP) to visualize patterns in grasshopper assemblage composition, i.e. how it responds to grazing intensity, vegetation structure and landscape attributes. This ordination method displays sites in a multivariate space based on the calculated similarity indices, i.e. sites grouped closely together are similar, whereas widely dispersed sites are different from one another (Anderson and Willis 2003). Then, we used two statistical tests – DistLM for continuous landscape and local variables, and permutational analyses of variance (PERMANOVA) for grazing intensity (i.e. categorical data) – to determine their effects on grasshopper assemblage composition. All continuous variables were imported as environmental data. Bare ground cover, basal distance and rock cover were log transformed. Continuous environmental variables that best describe grasshopper assemblage composition were identified using DistLM with a stepwise selection procedure and AICc selection criterion. We used PERMANOVA in the same software to test for the main effect of grazing intensity, and then to conduct pairwise comparisons among grazing intensity classes.

Results

Grasshopper species richness, Shannon H' diversity and Grasshopper Conservation Index (GCI_n).—In the first model with all variables, grasshopper species richness was best explained by only grazing intensity (AICc = 342.44; Adjusted R^2 = 0.535, and LM, F = 10.15, P < 0.001). The greatest number of species was recorded in annually-burned areas with heavy cattle grazing, while the lowest number of species was recorded in unburned grassland with light grazing (Fig. 2). In annually-burned and unburned grassland, grasshopper species richness increased with increasing grazing intensity (light < moderate < heavy). For these fire regimes, we found significant differences between areas with light and heavy grazing (annual burning: light < heavy, t = -4.16, P = 0.003; unburned: light < heavy, t = -3.94, P = 0.006). In contrast, grasshopper species richness of recently-burned areas showed a unimodal response (light

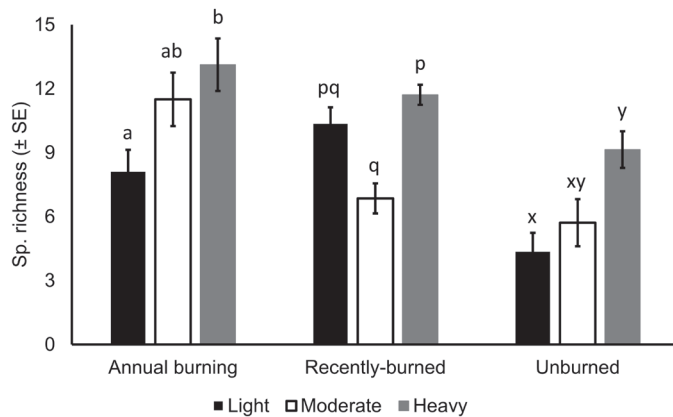


Fig. 2. Grasshopper species richness responds to grazing intensity under different fire regimes. Pairwise comparisons among grazing intensity classes (light, moderate and heavy) for annually-burned firebreaks and grasslands with longer fire rotations that were recently-burned i.e. <12 months prior to sampling and unburned i.e. burned >12 months prior to sampling. Bars with the same letters are not significantly different from one another.

> moderate < heavy) to increasing grazing intensity. For recently-burned areas, species richness of moderate-grazed areas was significantly less than in heavily-grazed areas ($t = -3.46$, $P = 0.026$).

Out of all variables, Shannon H' diversity was best explained by the local environment (Shannon's diversity index, $AICc = 53.07$; Adjusted $R^2 = 0.175$, and LM, $F = 5.66$, $P = 0.001$), but not grazing intensity. There were significant increases in Shannon H' diversity, as rocky outcrops ($F = 7.66$, $P = 0.007$) and bare ground cover ($F = 5.58$, $P = 0.02$) increased, and a near-significant increase as vegetation cover decreased ($F = 3.74$, $P = 0.058$).

The standardized GCI score per site (GCI_n) was indicative of the proportion of rare, sensitive or range-restricted grasshopper species in the assemblage. Out of all variables, GCI_n was best explained by total vegetation cover ($AICc = 525.37$, Adjusted $R^2 = 0.113$, and LM, $F = 9.57$, $P = 0.003$). The greatest GCI_n score was 7 and recorded in an unburned site with light grazing in the PA. This site had only four grasshopper individuals representing three species (*Lentula minuta*, *Machaeridia conspersa* and *Qachasia fastigiat*), which each had a score of 7.

Relationships among diversity measures and environmental variables.—We found a significant positive correlation between grasshopper species richness and Shannon H' diversity (Spearman, $Rho = 0.741$, $P < 0.001$). However, the standardized grasshopper conservation index (GCI_n) was not significantly correlated with either grasshopper species richness (Spearman, $Rho = -0.031$, $P = 0.800$) or Shannon H' diversity (Spearman, $Rho = -0.055$, $P = 0.658$). Also, plant species richness was not significantly correlated with grasshopper species richness (Spearman, $Rho = -0.154$, $P = 0.210$), Shannon H' diversity (Spearman, $Rho = -0.045$, $P = 0.720$), or the GCI_n (Spearman, $Rho = 0.012$, $P = 0.921$).

Environmental variables in this study were not independent of one another. There were significant correlations among several attributes of the local environment as well as larger landscape (Table 3). Elevation was significantly correlated with the local environment, i.e. rocky outcrops, bare ground cover and vegetation height (Table 3). Proportion of rocky outcrops was significantly correlated with most variables of the local environment:

Table 3. Spearman's correlation coefficient (ρ) test for relationships among environmental variables. The variables were elevation, rocky outcrop cover, bare ground cover, grass cover, total vegetation cover, vegetation height and basal distance. Rho-values are listed (range: -1 to 1), with P-values in parentheses. Significant correlations in bold.

| | Rocky outcrops | Bare ground cover | Basal distance | Grass cover | Vegetation cover | Vegetation height |
|------------------|----------------|-------------------|----------------|------------------|------------------|-------------------|
| Elevation | 0.276 (0.023) | -0.291 (0.016) | -0.146 (0.236) | 0.027 (0.826) | 0.081 (0.514) | -0.350 (0.004) |
| Rocky outcrops | | -0.291 (0.016) | 0.430 (0.001) | -0.346 (0.004) | -0.328 (0.006) | 0.047 (0.701) |
| Bare ground | | | 0.040 (0.744) | -0.243 (0.043) | -0.543 (< 0.001) | -0.317 (0.009) |
| Basal distance | | | | -0.481 (< 0.001) | -0.547 (0.001) | 0.360 (0.003) |
| Grass cover | | | | | 0.573 (0.001) | 0.137 (0.265) |
| Vegetation cover | | | | | | 0.261 (0.032) |

Table 4. Grasshopper assemblage composition response to grazing intensity under different fire regimes. Pairwise comparisons among grazing intensity classes (light, moderate and heavy) for annually-burned (AB) firebreaks and grasslands with longer fire rotations (LFR) that were recently-burned (RB) (i.e. < 12 months prior to sampling) and unburned (UB) (i.e. burned >12 months prior to sampling).

| Fire regime | Comparison | t-value | P-value |
|-------------|--------------------|---------|---------|
| AB | Light vs. Moderate | 1.211 | 0.139 |
| AB | Moderate vs. Heavy | 1.152 | 0.190 |
| AB | Heavy vs. Light | 1.777 | < 0.001 |
| RB | Light vs. Moderate | 1.207 | 0.134 |
| RB | Moderate vs. Heavy | 1.439 | 0.019 |
| RB | Heavy vs. Light | 1.742 | 0.003 |
| UB | Light vs. Moderate | 0.802 | 0.814 |
| UB | Moderate vs. Heavy | 1.047 | 0.369 |
| UB | Heavy vs. Light | 1.666 | < 0.001 |

bare ground, basal distance, grass cover and total vegetation cover. Most variables of the local environment were correlated with one another (Table 3).

Grasshopper assemblage composition.—Sites arranged along a continuum of disturbance intensity, with annually-burned and heavily-grazed sites to the left of the ordination space and unburned sites to the right (Fig. 3). Sites with heavy grazing grouped separately from sites with either light or moderate grazing. The bare ground: total vegetation cover gradient explained horizontal spread of sites along the first axis, while variation in rock and grass cover explained the vertical spread of sites along the second axis (Fig. 3). The two axes explained 15.5% and 11.5% of total variation in the dataset, respectively.

Grasshopper assemblage composition was best explained by the local environment ($AICc = 531.02$; Adjusted $R^2 = 0.157$; Table 4). Specific variables with a significant effect were total vegetation cover (Pseudo- $F = 2.59$, $P < 0.001$), grass height (Pseudo- $F = 3.13$, $P < 0.001$), bare ground cover (Pseudo- $F = 4.33$, $P < 0.001$), and rock cover (Pseudo- $F = 2.02$, $P = 0.015$).

Grazing intensity had a significant effect on grasshopper assemblage composition (Pseudo- $F = 2.19$, $P < 0.001$), with heavily grazed areas differing significantly from lightly grazed areas under

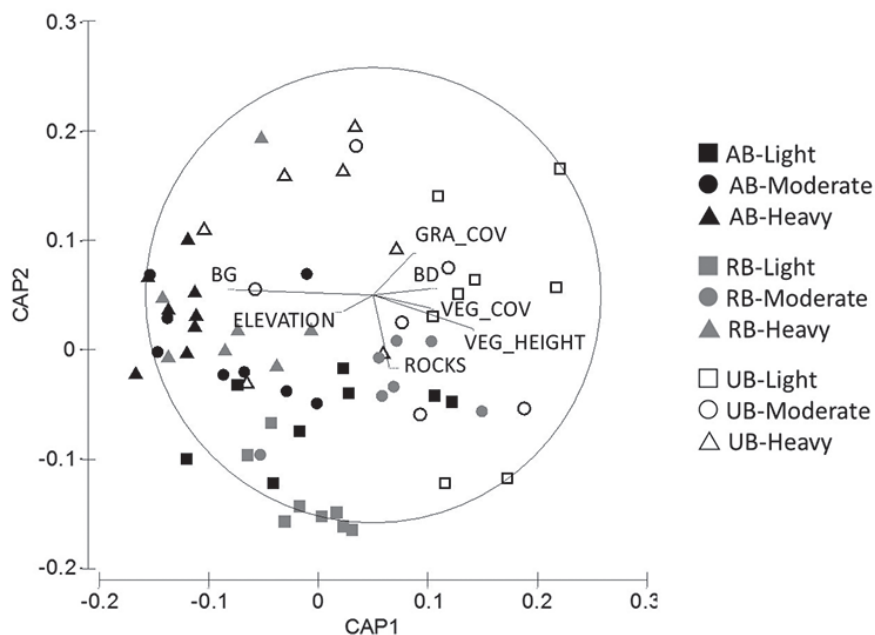


Fig. 3. Canonical analysis of principal coordinates ordination (CAP) of grasshopper assemblage composition to display patterns in the data. Abbreviations for grazing intensity: light in the protected area (square symbols), and moderate (circular symbols) or heavy (triangular symbols) in the ecological network. Abbreviations for fire regime: annual burning (AB, solid black symbols), grasslands with longer fire rotation that were recently-burned (RB, solid grey symbols) i.e. burned < 12 months prior to sampling and unburned (UB, open symbols) i.e. burned > 12 months prior to sampling. Significance values for pairwise comparisons are in Table 4.

Table 5. Indicator species of grazing intensity, fire frequency, and time since last fire. Abbreviations for grazing intensity: light in the protected area, and moderate or heavy in the ecological network. Abbreviations for fire regime: annual burning (AB), grasslands with longer fire rotation that were recently-burned (RB) (i.e. burned < 12 months prior to sampling) and unburned (UB) (i.e. burned > 12 months prior to sampling). The GCI values of individual species, Indicator values and P-values were included.

| Species | Disturbance | GCI | Ind Val | P-value |
|--------------------------------------------------------|-------------|-----|---------|---------|
| <i>Anablepia pilosa</i> | RB-Light | 6 | 0.74 | 0.001 |
| <i>Eyprepocnemis calceata</i> | RB-Light | 4 | 0.21 | 0.058 |
| <i>Pseudocercopoda cephalica</i> | RB-Light | 6 | 0.27 | 0.017 |
| <i>Dnopherula callosa</i> | AB-Moderate | 4 | 0.27 | 0.013 |
| Tetrigid sp. 3 | AB-Moderate | 7 | 0.26 | 0.031 |
| <i>Acorypha ferriifer</i> | AB-Heavy | 4 | 0.27 | 0.025 |
| <i>Catantops ochtheophilus</i> | AB-Heavy | 5 | 0.38 | 0.003 |
| Tetrigid sp. 1 | AB-Heavy | 5 | 0.35 | 0.009 |
| <i>Coryphosima stenoptera</i> subsp. <i>stenoptera</i> | RB-Heavy | 4 | 0.33 | 0.015 |
| <i>Lentula obtusifrons</i> | RB-Heavy | 7 | 0.30 | 0.065 |
| <i>Vitticatantops maculatus</i> | RB-Heavy | 4 | 0.28 | 0.013 |
| <i>Orthochtha</i> sp. 2 | UB-Heavy | 3 | 0.33 | 0.078 |
| <i>Spathosternum nigrotaeniatum</i> | UB-Heavy | 6 | 0.49 | 0.001 |

all fire regimes (Table 4). In addition, there were significant differences between moderately and heavily grazed areas that were burned recently. Under no fire regime did we find differences in composition between areas with light and moderate grazing.

We identified 13 species that were indicative of grazing intensity, of which eight species were associated with heavy grazing (Table 5). The GCI scores of two individual indicator

species (*Lentula obtusifrons* and *Spathosternum nigrotaeniatum*) in heavily grazed areas were high (≥ 6).

Discussion

Local versus landscape attributes.—Grasshopper assemblages responded primarily to changes in their local environment and not to larger landscape attributes. This was surprising, because earlier studies found large and significant effects of elevation and aspect on grasshopper assemblages in these mid-to-high elevational grasslands (Samways 1990, Gebeyehu and Samways 2006, Crous et al. 2013, 2014). In Afromontane grassland, grasshopper assemblage composition changed, and species richness increased with an increase in elevation (900–2200 m a.s.l.) (Crous et al. 2013). However, in Swaziland, grasshopper species richness showed the opposite response, as it declined with an increase in elevation (800–1400 m a.s.l.) (Wettstein and Schmid 1999). It is possible that the 400 m range in elevation in our study was not sufficient to detect this major ecological gradient. Alternatively, the effect of elevation might be explained by covariation among local and landscape attributes. There were significant correlations among landscape and local environmental attributes in our study. Our study is not unique. In the Succulent Karoo, there was sparser vegetation cover and greater grasshopper diversity on small hills (Gebeyehu and Samways 2006). Grasshopper assemblages in North America respond to large-scale and long-term environmental gradients (e.g. elevation and precipitation), but these variables are also known to correlate with changes in the local environment (Kemp et al. 1990, Jonas and Joern 2007). This is the case for calcareous and steppe grasslands in Germany (Fartmann et al. 2012, Weiss et al. 2013). Such relationships among environmental variables at the local and landscape spatial scale are a natural part of the landscape, and the reason

why many arthropods respond indirectly to major drivers in the landscape (Joern and Laws 2013).

The effect of grazing intensity.—Grazing intensity was the most important determinant of grasshopper species richness in our study. However, the specific response of grasshopper species richness to grazing intensity (light < or > moderate < heavy) depended on fire regime. This is because each fire regime exerts its own selection pressure on the grasshopper species assemblage (Joubert et al. 2016b), especially during the first year after fire (Little et al. 2013). The observed effect of grazing intensity is therefore on a subset of the complete species pool in these mesic grasslands. A case in point is recently-burned grassland where we found a significant response in assemblage composition and species richness when comparing moderately- and heavily-grazed areas. Such differences between moderately- and heavily-grazed areas did not exist in either annually-burned or unburned grassland. This scenario differs from a case where fire frequency and time since last fire had no such effect on grasshopper assemblage composition, causing grasshoppers to respond primarily to grazing and not to a fire-grazing interaction (Joern 2005). Because grasshoppers respond to a fire-grazing interaction in our study area, it is necessary to consider both types and different levels of these disturbances when making management adjustments.

Grasshopper assemblages in heavily-grazed areas were unique in composition and more species-rich than areas with light or moderate grazing. The shift towards a more species-rich grasshopper assemblage illustrates that grasshoppers are relatively tolerant of disturbance. This includes at least one flightless, narrow-range endemic species (*Lentula obtusifrons*) that was an indicator of heavily-grazed areas. The high degree of tolerance to heavy cattle grazing came as a surprise, although we knew beforehand that grasshoppers are adapted to and benefit from grazing by domestic livestock (Prendini et al. 1996) and indigenous game (Pryke et al. 2016). In North American tallgrass prairies, an increasing level of recent grazing by bison also increased grasshopper species richness (Joern 2005). In a global assessment of arthropod response to grazing, it was concluded that grazing can only increase the richness of grasshopper assemblages if it increases heterogeneity of the local environment, and if this increase in heterogeneity is large enough to make up for the loss of resources and increased mortality (Van Klink et al. 2015). This was expected to occur at moderate levels of grazing, and so lend support to the Intermediate Disturbance Hypothesis (Connell 1978). However, because greatest richness was documented in areas with heavy grazing, our findings did not meet these expectations. Grazing and its interaction with fire indeed increases the heterogeneity of vegetation layers across the landscape, with bare patches interspersed with patches of tall grass and grazing lawns (Archibald et al. 2005). These less disturbed vegetation patches are of great value for grasshoppers in an African savanna, especially in a disturbed mosaic (e.g. around a waterhole) where elevated levels of bare ground leaves insufficient cover for grasshoppers to escape predators and intense heat (Samways and Kreuzinger 2001, Gebeyehu and Samways 2003). Management for heterogeneity should be prioritized to provide in the habitat requirements of different taxa – disturbance-tolerant species that benefit from heavy grazing, and less disturbed patches for other more sensitive species.

The effect of vegetation structure.—Full vegetation cover indicative of low levels of disturbance was most important for a suite of sensitive, rare and range-restricted grasshopper species that were of great conservation importance. This contrasts with the majority of grass-

hopper species that were more tolerant of disturbance, as indicated by the rich suite of species associated with elevated levels of bare ground, shorter grass, and sparser vegetation cover. Different grasshopper species are also associated with differences in bare ground cover and grass height in African subtropical grassland (Bazelet and Samways 2011a) and savanna (Prendini et al. 1996). Shorter grass benefitted grasshopper species richness in the Swiss Alps (Marini et al. 2009). Although a unique and rich suite of species were associated with greater levels of disturbance, the conservation of sensitive and range-restricted grasshopper species should be prioritized, as they are most vulnerable to local extirpation, especially when considering the large-scale occurrence of heavy grazing.

The effect of rocky outcrops.—Grasslands with more rocky outcrops supported a different and more diverse grasshopper assemblage than grasslands with less rocky outcrops. This concurs with an earlier study, which found surface rockiness to be a good abiotic indicator of grasshopper species richness in a nearby mesic grassland (Crous et al. 2013). Grasshoppers are very sensitive to changes in their local environment, and may use rocky crevices for shelter to escape large temperature fluctuations (Samways 1990). In the United Kingdom, sensitivity of grasshoppers to microclimate was illustrated by their movement away from prevailing winds relative to the direction of a footpath (Gardiner and Dover 2008). Grasshoppers also avoided excessively warm microhabitats devoid of sufficient vegetation cover to prevent them from overheating (Gardiner and Hassall 2009). In the temperate Cape Floristic Region in South Africa, behavior of small, endemic *Betiscoides* species was influenced by wind intensity, temperature and vegetation height (Matenaar et al. 2014). We argue that rocky outcrops might add to the heterogeneity of microclimatic niches available in the landscape, directly by providing shelter and basking sites, and indirectly by altering the vegetation layer (Crous et al. 2014).

Surrogates of grassland diversity.—Apart from the significant, positive correlation between grasshopper species richness and Shannon H' diversity, we found no meaningful relationships among measures of plant and grasshopper diversity. The proportion of rare, sensitive or range-restricted grasshoppers (GCI_n) was not correlated with either grasshopper species richness or Shannon H' diversity. This contrasts with the findings in another study where small grasshopper species with localized distributions were good indicators of species richness in another arthropod group i.e. butterflies (Bazelet and Samways 2012). Also, we found no relationship among plant and grasshopper species richness. In fact, the greatest number of grasshopper species in this study was documented in annually-burned areas with heavy grazing, while this management practice was absolutely detrimental to indigenous plant conservation (Joubert et al. 2014). Non-congruence between plant and grasshopper species richness concurs with findings of a regional study conducted in Inner Mongolia (Hao et al. 2015). In contrast, there was a significant positive relationship between grasshopper and plant species richness in North American tallgrass prairie (Joern 2005) as well as in the Italian Alps (Marini et al. 2009). The absence of significant relationships among measures of plant and grasshopper diversity emphasizes the need to use multiple taxa and multiple measures of diversity to monitor change in grasslands, particularly since the same level of disturbance can cause gains in one taxonomic group and losses in another.

Management recommendations.—Afromontane grassland management should be cognizant of the individual and interactive effects of grazing and fire, as they each uniquely influence the richness and

composition of grasshopper assemblages. The majority of species are adapted to high levels of disturbance causing them to persist well in grazed landscapes typical for large parts of the African continent. As such, they do not require special conservation measures to be put in place, provided these grasslands are grazed or burned. However, to also conserve the smaller, more sensitive suite of grasshopper species, patches of minimally disturbed grassland (i.e. areas where grazing or burning is difficult, such as rocky outcrops) should be left. Creating a mosaic of patches with different levels of disturbance is necessary to provide habitat for taxa with diverse requirements.

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Effects of grazing on orthopteran assemblages of Central-European sand grasslands

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Abstract

The effect of grazing on Orthoptera assemblages has long been the focus of research worldwide due to the high sensitivity of orthopterans to changes in vegetation structure. According to previous studies, grazing has individual, spatially-different effects on orthopteran assemblages. The current case study was carried out between 2012 and 2016 in a subarea dominated by open sandy grasslands in the Carpathian Basin. The ~70 ha study area was grazed by 250–300 sheep in 2012. In the beginning of 2014, the overgrazing pressure was overall reduced, for the most part, in the examined grassland patches. The study aimed to answer how the complete abandonment of grazing and moderate grazing influences the species richness, diversity and density of the orthopteran assemblages. Investigations in Central European sand steppes confirmed that both intense grazing and the abandonment of grazing have a detrimental effect on the structure of orthopteran assemblages: (a) the Shannon diversity index was higher on moderately grazed sites than on grazed and ungrazed ones; (b) the number of habitat specialists of sandy grasslands was higher on moderately grazed patches than in grazed habitats; and (c) the frequency of geophilic species was higher on grazed patches than on moderately grazed and grazing-abandoned ones.

Key words

density, diversity, Hungary, land use intensity, sheep, vegetation structure

Introduction

The structure of habitats and their insect communities exposed to direct and indirect human impact usually can be considered a transient state (Pickett et al. 1992). This phenomenon can be well observed in grazed grasslands where current vegetation structure, as a background factor to the insect communities, is highly influenced by the intensity, spatial and temporal characteristics and abandonment of grazing (Carboni et al. 2015, Török et al. 2016). Both the vertical and horizontal structure of vegetation, through the removal of the biomass and through trampling, are changed by grazing (Asner et al. 2004). Intensive grazing (~overgrazing) in grasslands usually results in decreased plant diversity, the invasion of some grazing-tolerant plant species, and the overall degradation

of the habitat-structure (Metera et al. 2010). Nutrient-poor habitats seem to be the most sensitive to grazing intensity (Kruess and Tschamntke 2002). When the grazing pressure decreases or is abandoned in the grasslands of a temperate climate zone, the coverage of the dominant, narrow-leaved perennial monocotyledons of the associated plants increases (Critchley et al. 2008), while the coverage of annual plant species becomes reduced (Matus et al. 2003). In addition to the favorable changes for the vegetation-dependent insect communities, the abandonment of grazing can also cause the invasion of weeds in the grasslands (Sedláková and Fiala 2001). This usually greatly decreases the presence of rare and threatened Orthoptera (Fonderflick et al. 2014). Therefore, in the habitats grazed traditionally, the maintenance of extensive grazing is a prerequisite for preserving biodiversity (Dolek and Geyer 2002) and seems to be far more suitable than mowing (Weiss et al. 2013).

The high sensitivity of orthopterans to a change in vegetation structure is well known (Báldi and Kisbenedek 1997, Samways 1997, Gardiner et al. 2002, Bazelet and Samways 2011, Weiss et al. 2013). Based on this, the effect of grazing on orthopteran assemblages has been the focus of research worldwide and for a long time (e.g. White 1975, Jepson-Innes and Bock 1989, Prendini et al. 1996, Kruess and Tschamntke 2002, Jauregui et al. 2008, Gardiner and Haines 2008, Zhu et al. 2015). Grazing results in individual, spatially different effects on the orthopterans. Some studies, for example, revealed lower orthopteran density in grazed grasslands than in ungrazed ones (Welch et al. 1991, Onsager 2000), while in other cases the opposite was found (Wingerden et al. 1991). These differences are likely to be due to not only the habitat-dependent effects of the grazing, but also to species-specific responses (O'Neill et al. 2003, Jauregui et al. 2008) of orthopterans to intensity (Kruess and Tschamntke 2002, Cease et al. 2012), timing (Fonderflick et al. 2014) and livestock type (Dolek and Geyer 2002) of grazing. Most of the results of the assessment of the impact of grazing suggest that, according to the intermediate-disturbance hypothesis of Connell (1978), orthopteran assemblages show the largest diversity in moderately grazed grasslands (Batáry et al. 2007, Fabricsusová et al. 2011, Jerrentrup et al. 2014).

My study area is situated between the Danube and the Tisza rivers in the Carpathian Basin in the eastern half of Central-Europe,

where the dominant vegetation type is the Pannonian sand steppe occurring in Europe only in the Pannonian biogeographical region (6260 Pannonian sand steppes, 2002/83/EC Habitat Directive). Due to the conditions of the almost humus-less bedrock (sand), the structure and species composition of the habitats could remain potentially unchanged even for centuries in the absence of any interventions. However, grazing has been present in the area since, most likely, the Neolithic (Molnár et al. 2008), so for several thousand years. Thus, large herbivores played a role in the development of the actual state of the grasslands (Máté 2014). In the 16–17th century, extensive grazing was carried out on a large area of the region – mainly with cattle and, to a lesser extent, with sheep (Frisnyák et al. 2015). After the beginning of the 18th century, afforestation was carried out for the purpose of impeding erosion and for utilizing areas unsuitable for agricultural use (mainly *Pinus sylvestris* and *Robinia pseudo-acacia* were planted). As a result, the extent of areas covered by forests increased from 3.5% to 60% (Molnár 2003). However, some hills covered by open sandy grasslands remained, and until the middle of the 20th century they were grazed by the sheep of small farmers (Kun 1998). In the past decades and even now, grazing, especially sheep-grazing, was concentrated in small areas. The dominance of sheep grazing affected, among other things, the Fabaceae plant species of the sandstone pastures and their associated animal species, resulting in the decline or extinction of a number of plant species at the beginning of the 19th century (Máté 2014).

In addition to the above historical landscape characteristics, responses of the orthopteran assemblages associated with the typical habitats of the Central European sand steppes were affected by several local and global factors. From a local point of view, it can be said that the orthopteran assemblages of Central European habitats grazed with different intensity have not yet been sufficiently investigated. Certainly, in regards to the long-term effects of the various types of grazing, and the long-term effects of the abandonment of grazing, there are several questions to be answered. Several further questions remain to be answered both locally and globally with regards to quality and intensity of grazing being adequate for the most diverse and dense orthopteran assemblages (Jerrentrup et al. 2014).

The main questions of the present investigation were the following: 1) How does the complete abandonment of grazing or moderate grazing influence the species richness, diversity and density of orthopteran assemblages in grasslands that were heavily overgrazed at the beginning of the study? 2) Is the span of the study (from 2012 to 2016) enough to detect changes in the structure of orthopteran assemblages occurring in sandy grasslands characterized by low plant production? 3) How does the drastic decrease of grazing pressure impact the density of local populations of habitat-specific species?

Material and methods

Study area.—The study area is part of the Natura 2000 site Kék-hegyi lőtér (HUKN22037; southern Hungary) (Fig. 1). It is located at an altitude of ~160 m a.s.l. and is characterized by flat, low sandy hills and flatlands. The average total duration of annual insolation in the region is 2,055 hours. Mean annual temperature is around 10.6°C. The mean values of absolute maximum and minimum temperatures are 34.7°C and -16.4°C. The average annual precipitation is 570 mm (330 mm in the growing season) (Dövényi 2010). The study area is characterized by sandy soils. Based on analyses of Szilard Szabó (pers. comm.), mean of the main soil parameters of the local grasslands are the following: CaCO₃

content: 8.5%; humus content: 2.9%; pH-H₂O: 7.2; percentages of the soil fractions: rough: 0.2%; middle-class: 9.7%; small: 80.6%; mud: 7.1%; loam: 2.3%.

Land use.—Based on the first known detailed map of the study area, in the 18th century the typical land use of the open sandy grasslands studied was grazing (<http://mapire.eu/hu/map/firstsurvey>). In the 19th and 20th centuries some places in the area were afforested, but the main form of land use on the grasslands was still grazing (see <http://mapire.eu/hu/map/secondsurvey>; http://mapire.eu/hu/map/hkf_25e; <http://mapire.eu/hu/map/hungary1941>). After World War II the area was used as a closed military base, but the grazing of sheep continued. When military operations ceased in 1990, the grazing of sheep became increasingly intense. The ~70 ha study area was grazed by 250–300 sheep in 2012. The overgrazing pressure was overall reduced in the majority of the study area in the beginning of 2014 in order to conserve nature.

Experimental design.—Six sampling sites were established, as 50×50 m sized quadrats. Data collection was carried out from 2012 to 2016. One site was on a place ungrazed during the study (Ungrazed – U-G), three sites were located in places on which grazing pressure was reduced to zero at the beginning of 2014 (Grazing Abandoned – G-A), two sites were located in places on which grazing pressure was reduced to a moderate level (Moderately Grazed – M-G) (Fig. 1). Sites were considered to be “grazed” (Grazed – G) prior to 2014 and the reduction of grazing pressure.

Vegetation and landscape structure.—Measurements of the vegetation parameters were carried out on 3 plots in each sampling site of each orthopteran sampling. The following parameters were recorded: total vegetation cover (%), average height of the vegetation (cm), and bare soil (%). Height of the vegetation was measured in cm with the use of a 30 cm wide and 100 cm high white card. Total cover of the vegetation was measured in a square meter quadrat occurring around the spot. Related to each orthopteran sampling, percentage cover of plant species was estimated. Annual means of the measured parameters per sampling sites were calculated.

Orthoptera.—During each of the five study years, sampling of the Orthoptera took place in June, July, and August. In every period, 2 samplings were carried out by sweep-netting on random patches of each sampling site (altogether 180 samples). Within the 50 × 50 m sized sites, the samplings took place at least 30 m from each other. Densities were recorded in 10 × 10 m quadrats with 300 sweeps per sample and were completed by direct observations. To the samples collected by sweep netting I added a simple count of the number of adult specimens which were detected by direct observation/collection. Sweep-netted samples were identified to species level using the works of Harz (1969, 1975). *Acrida ungarica* (Herbst), *Acrotylus insubricus* (Scopoli), *Acrotylus longipes* (Charpentier), *Calliptamus barbarus* (Costa), *Celes variabilis* (Pallas), *Dociostaurus brevicollis* (Eversmann), *Euchorthippus pulvinatus* (Fischer de Waldheim), *Gampsocleis glabra* (Herbst), *Montana montana* (Kollar), *Myrmeleotettix maculatus* (Thunberg), *Oedaleus decorus* (Germar), *Omocestus minutus* (Brullé), *Platycleis affinis* Fieber, *Sphingonotus caeruleus* (Linnaeus), *Stenobothrus fischeri* (Eversmann) were classified as habitat specialists of local sandy grasslands. Scientific nomenclature follows Cigliano et al. (2017).

Categories of Uvarov (1977), Ingrisch and Köhler (1998) and Krištín et al. (2009) were used for classification of life forms (arboricol: species found in habitats dominated by tree-sized elements; ar-

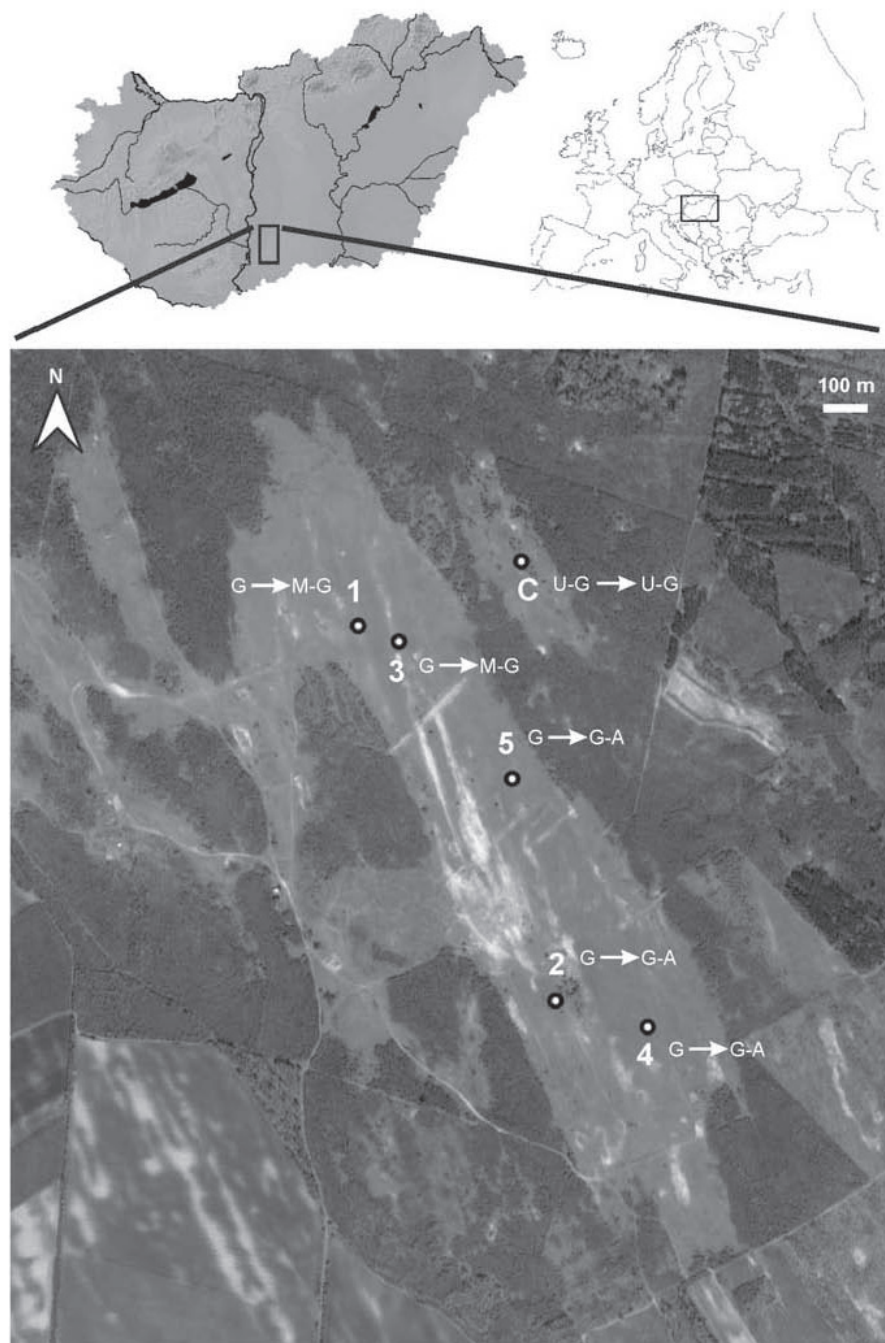


Fig. 1. Location and land use-changes of the studied sites (G: grazed; G-A: grazing-abandoned; M-G: moderately grazed; U-G: ungrazed). Letters to the left of the arrow indicate land use in 2012 and 2013; letters to the right of the arrow indicate land use in 2014, 2015 and 2016.

busticol: species found in habitats dominated by shrub-sized items; silvicol: species found in forest habitats with a grass understory; pratnicol: species found in grasslands of tall grass; graminicol: species found in grasslands of short grass; geophilic: species found in grasslands characterized by a high percentage of bare soil; psammophilic: species found in sandy grasslands; pseudo-psammophilic: species found mainly in sandy grasslands, but also in grasslands occurring on soil very similar to sand, e.g. dolomite rendzina).

Characterization of climatic requirements of the species as thermophilic, moderately-thermophilic, mesophilic, moderately-

hygrophilic, and hygrophilic were assigned based on the works of Varga (1997), Rácz (1998), and Ingrisch and Köhler (1998).

Statistical analysis.—Samples collected in the same sampling sites in the same year were pooled (number of pooled samples was 30: Ungrazed – U-G $n = 5$; Grazing Abandoned – G-A $n = 9$; Moderately Grazed – M-G $n = 6$; Grazed – G $n = 10$). Pooled samples were used for calculating assemblage variables and statistical analyses. Shannon diversity index, species richness, density (individual/10 m²), species number and relative frequencies

of habitat specialist species, relative frequencies of geophilic and graminicol/pratinicol species were calculated and used as Orthoptera response variables in statistical analyses. Mean values (\pm SE) of Orthoptera response variables were calculated for comparison of structure of orthopteran assemblages exposed to different grazing pressure. Mann-Whitney U test was used to evaluate statistical differences among the derived orthopteran variables. Orthoptera samples were ordered by PCoA (similarity index: correlation, relative frequency data of species were used and subtract mean transformed). Generalized linear models (Poisson distribution; response variables: relative frequencies of geophilic and graminicol/pratinicol species; predictor variables: total vegetation cover, average height of the grass, bare soil) were performed. CCA ordination based on Orthoptera species data and environmental parameters (total vegetation cover, percentage of bare soil, height of the vegetation) were also compiled. All statistical analyses were performed by using Past 3.14. software package (Hammer et al. 2001).

Results

Orthoptera diversity and density.—Thirty-five Orthoptera species (Appendix 1) comprising 2,655 individuals were recorded on 6 sampling sites. The most prevalent species was *Calliptamus barbarus* with 580 individuals (24%), followed by *Acrida ungarica* with 514 individuals (19%), *Euchorthippus declivus* (Brisout de Barneville) with 302 individuals (11%), *Oedaleus decorus* with 279 individuals (10%), *Oedipoda caerulescens* (Linnaeus) with 210 individuals (8%), *Myrmeleotettix maculatus* with 185 individuals (7%), *Docostaurus brevicollis* with 117 individuals (4%), *Euchorthippus pulvinatus* with 54 individuals (2%) and *Omocestus petraeus* (Brisout de Barneville) with 52 individuals (2%). Shannon diversity, more sensitive to rare species (Magurran 2004), was highest on moderately grazed sampling sites, and this parameter was lower and similar to each other on grazed, grazing-abandoned and ungrazed sampling sites (Mann-Whitney test: $U_{G-MG} = 7$, $p = 0.014$; $U_{MG-UG} = 0$, $p = 0.008$; Fig. 2). Species richness was non-significantly higher in moderately grazed and grazing-abandoned grasslands, than on grazed and ungrazed patches (Fig. 2). Overall, Orthoptera density was higher on the ungrazed patches than on moderately grazed and grazing-abandoned ones ($U_{MG-UG} = 1$, $p = 0.013$; $U_{GA-UG} = 5$, $p = 0.023$) and non-significantly higher than on grazed ones (Fig. 2).

Composition of Orthoptera assemblages.—PCoA ordination showed separation of orthopteran assemblages under different grazing pressure. Sites grouped according to whether they were ungrazed, grazing-abandoned/moderately-grazed or grazed (Fig. 3). The number of habitat specialist species was significantly higher on moderately-grazed patches than on grazed ones ($U_{MG-G} = 13.5$, $p = 0.05$) and that parameter was non-significantly higher on grazing-abandoned and ungrazed patches than on grazed sites (Fig. 4). The number of habitat specialist species was as high on grazing-abandoned sites than on the ungrazed site. The frequency of habitat specialist species did not show decided differences related to grazing pressure (Fig. 4). The frequency of geophilic species was significantly higher on grazed sites than on moderately-grazed and grazing-abandoned ones ($U_{G-MG} = 9$, $p = 0.026$; $U_{G-GA} = 15$, $p = 0.015$). Furthermore, the above mentioned parameter was significantly higher on ungrazed sites than on moderately-grazed ones ($U_{UG-MG} = 4$, $p = 0.050$) (Fig. 5). Parallel to the latter results, the frequency of graminicol/pratinicol species was significantly lower on grazed sites than on moderately-grazed and grazing-abandoned

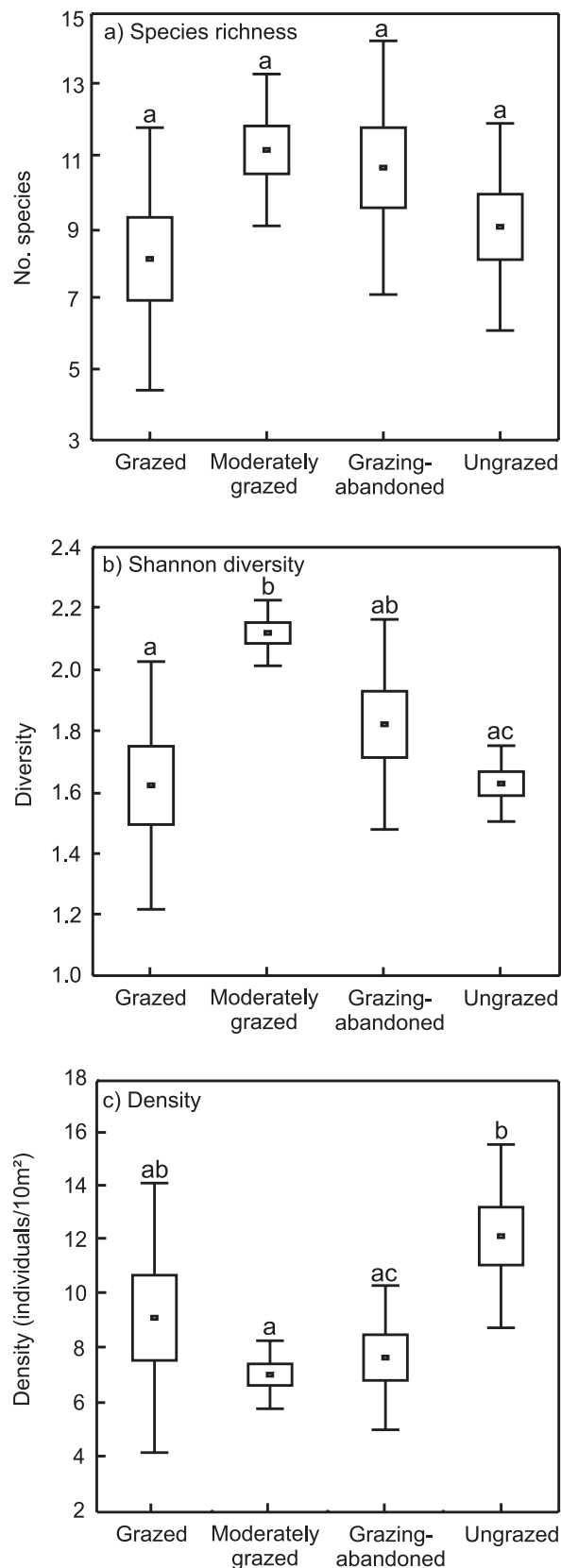


Fig. 2. Mean values (min-max and \pm SE) of main parameters of orthopteran assemblages under different grazing pressure. Significant ($p < 0.05$) differences detected by Mann-Whitney U test are indicated by different letters.

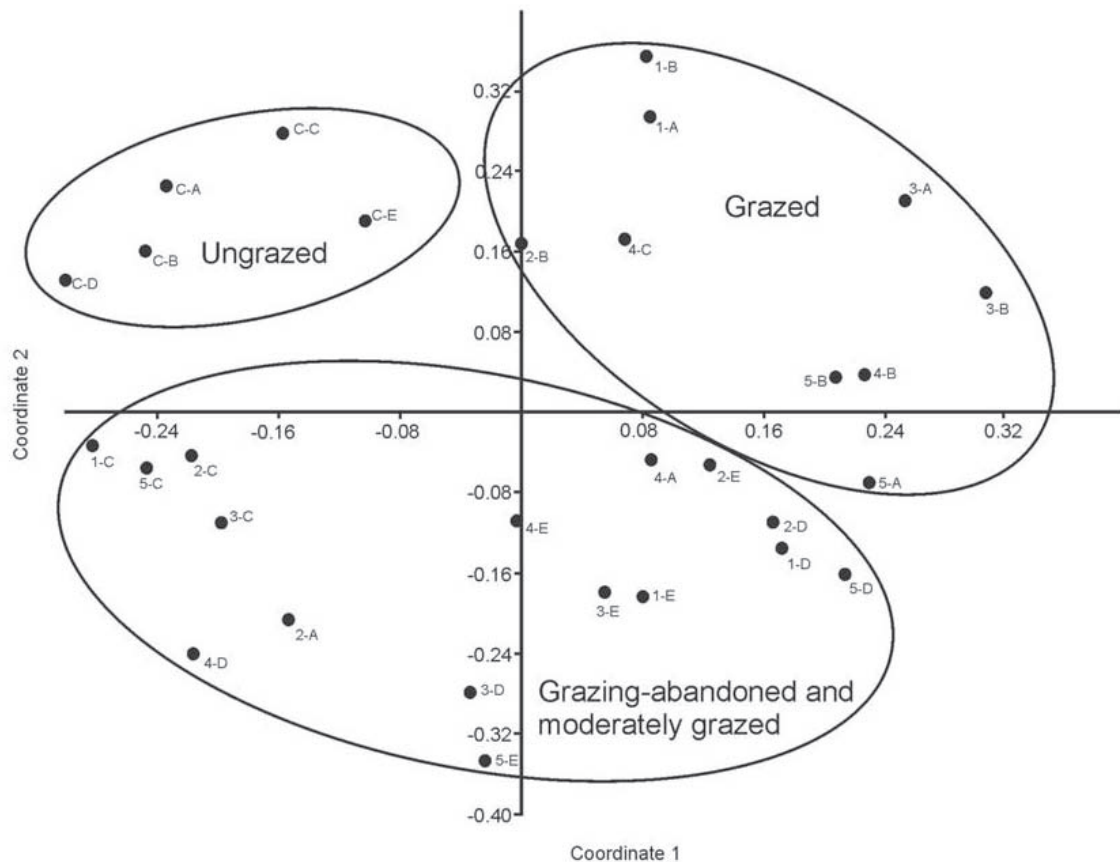


Fig. 3. PCoA ordination (sum of all eigenvalues: 20.008, similarity index: correlation) based on Orthoptera data. The different years are marked by A, B, C, D and E (A: 2012, B: 2013, C: 2014, D: 2015 and E: 2016; e.g. 1-A: site 1 in 2012, 2-B: site 2 in 2013, C-C: control site in 2014).

Table 1. Main vegetation characteristics of the sampling sites (mean values (\pm SE) of the measured data in June, July and August).

| | Grazed (June–August) | Grazing-abandoned (June–August) | Moderately grazed (June–August) | Ungrazed (June–August) |
|------------------------|-------------------------|------------------------------------|------------------------------------|---------------------------|
| Vegetation height (cm) | 3.3 \pm 0.4 | 11.7 \pm 1.3 | 18.3 \pm 3.5 | 26.0 \pm 1.8 |
| Vegetation cover (%) | 44.0 \pm 4.8 | 78.8 \pm 1.8 | 82.5 \pm 1.1 | 72.0 \pm 3.4 |

ones ($U_{G-MG} = 9$, $p = 0.026$; $U_{G-GA} = 15$, $p = 0.015$) and the relative frequency of graminicol/pratinicol species was significantly lower on ungrazed sites than on moderately grazed sites ($U_{MG-UG} = 4$, $p = 0.050$) (Fig. 5).

Effects of environmental parameters.—Based on the results of generalized linear models, total vegetation cover (VCOV), vegetation height (VH) and percentage of bare soil (BSOIL) were found as significant predictors of the frequency of geophilic species and, parallel to this, the frequency of graminicol/pratinicol species (VCOV/Geo_freq: -0.0055; SE: 0.125; $p = 0.002$; VCOV/Gra_prat_freq: 0.0055; SE: 0.018; $p = 0.002$; VH/Geo_freq: -0.0097; SE: 0.003; $p = 0.012$; VH/Gra_prat_freq: 0.0097; SE: 0.003; $p = 0.012$; BSOIL/Geo_freq: 0.0056; SE: 0.001; $p = 0.001$; BSOIL/Gra_prat_freq: -0.0056; SE: 0.001; $p = 0.001$). Total vegetation cover (VCOV) and vegetation height (VH) (Table 1, Fig. 6) were negatively related to the frequency of geophilic species, while the percentage of bare soil (BSOIL) was positively related. The total vegetation cover (VCOV) and vegetation height (VH) were positively related to the

frequency of graminicol/pratinicol species, and the percentage of bare soil (BSOIL) was negatively related.

Three predictor variables contributed significantly to the CCA ordination. Relative frequency of geophilic species, such as *Acrida ungarica*, *Acrotylus insubricus*, *Aiolopus thalassinus* (Fabricius), *Calliptamus barbarus*, *Calliptamus italicus* (Linnaeus), *Celex variabilis*, *Oedaleus decorus*, and *Oedipoda caerulescens*, was positively correlated with a high percentage of bare soil (BSOIL) (Fig. 7). On the other hand, relative frequency of graminicol/pratinicol species, such as *Gampsocleis glabra*, *Montana montana*, *Platycleis albopunctata* (Goeze), *Stenobothrus fischeri*, and *Stenobothrus lineatus* (Panzer) was positively related to a high total cover of vegetation and vertically structured grasslands (Fig. 7).

Discussion

Grazing intensity or abandonment of grazing has a detrimental effect on the structure of orthopteran assemblages (Kruess and Tschamntke 2002, WallisDeVries et al. 2007, Eschen et al. 2012).

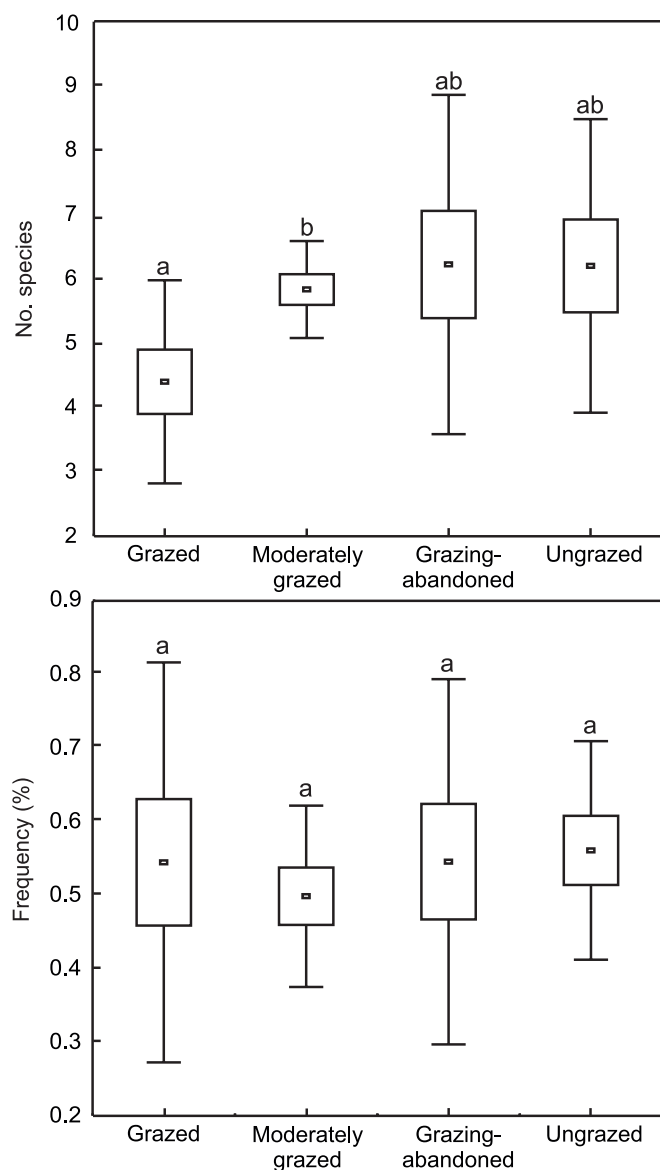


Fig. 4. Mean values (min-max and \pm SE) of species number and frequency of habitat specialist species under different grazing pressure. Significant ($p < 0.05$) differences detected by Mann-Whitney U test are indicated by different letters.

Studied grasshopper assemblages of the Central-European sand grasslands showed the greatest diversity on patches affected by extensive grazing (Quinn and Walgenbach 1990, Enyedi et al. 2008). This result is similar to those of Batáry et al. (2007) and Fabriciusová et al. (2011) from other grassland types of the Carpathian Basin. In addition to the species with a positive correlation to open soil surfaces, these patches provide for the conservation of xero-thermophilic habitat specialists (Fonderflick et al. 2014) related to heterogeneous vegetation (Batáry et al. 2007) such as the European Red-Listed *Gampsocleis glabra* and *Montana montana* (Hochkirch et al. 2016). Extensive grazing therefore results in higher species richness of habitat specialist orthopterans in the moderately grazed patches than in grazed ones (Fig. 4). Overall density of the orthopteran assemblages

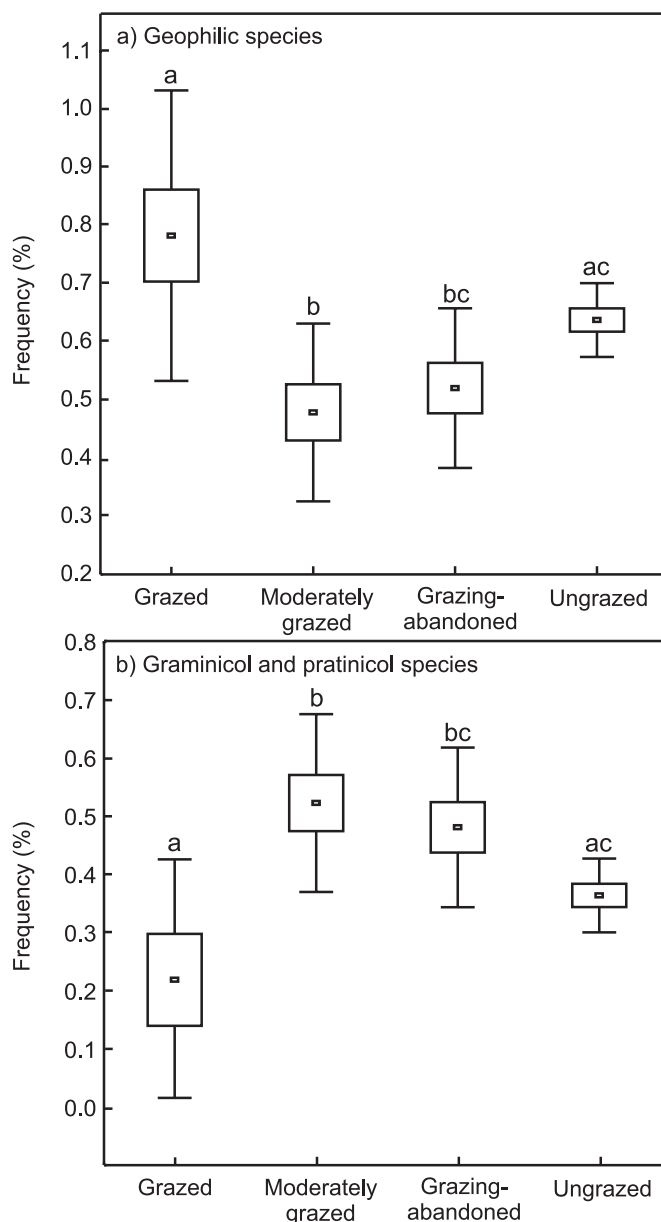


Fig. 5. Mean values (min-max and \pm SE) of relative frequency of geophilic and vegetation structure-dependent species under different grazing pressure. Significant ($p < 0.05$) differences detected by Mann-Whitney U test are indicated by different letters.

was high on several grazed patches. This is probably explained by the species-specific response of the orthopterans to grazing (O'Neill et al. 2003, Jauregui et al. 2008). For example, *Chorthippus biguttulus* (Linnaeus) (Fonderflick et al. 2014) and *Stenobothrus stigmaticus* (Rambur) (Jauregui et al. 2008) reach high density in intensively grazed grasslands. In the present study, *Acrida ungarica*, *Calliptamus barbarus* and *Oedaleus decorus* have proved to be species preferring habitat-structure transformed by grazing. The latter species, according to their energy requirements (Fielding and Brusven 1995), reached much higher abundance on the grazed patches characterized by short vegetation and fragmented by open sandy surfaces, than on the grazing-abandoned habitats. The decline in prevalence of the geophilic lifestyle due to the abandonment of grazing (Fig.

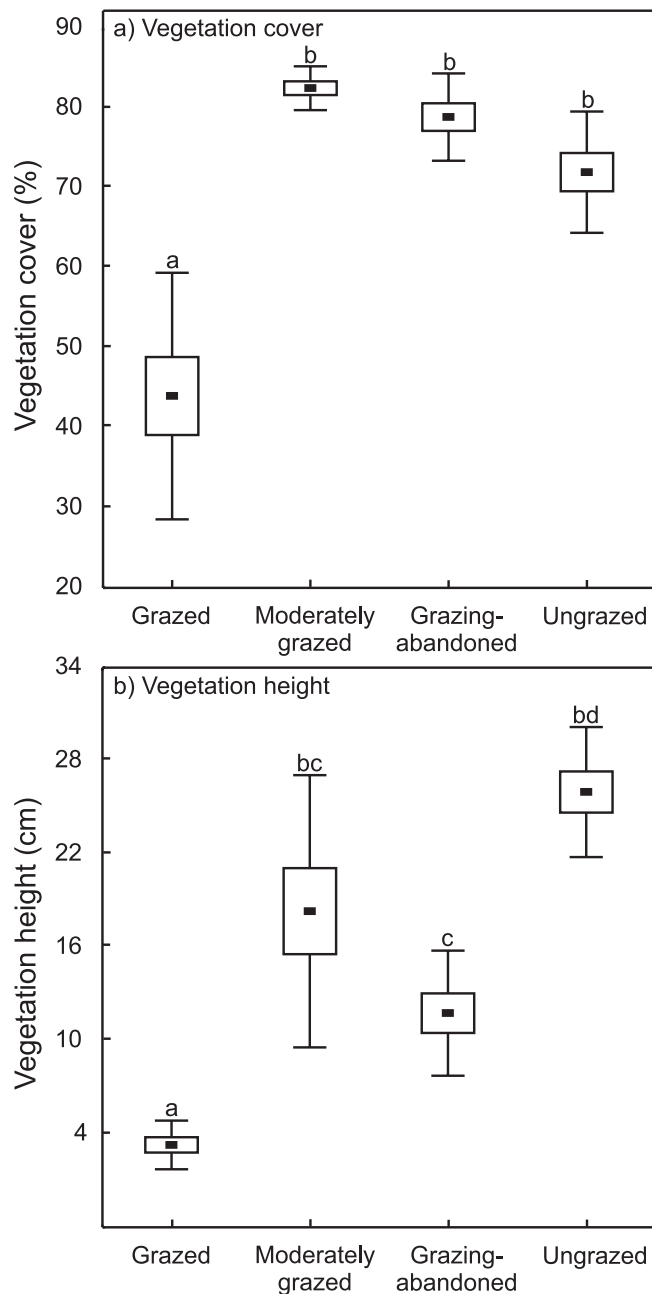


Fig. 6. Mean values (min-max and \pm SE) of vegetation cover and vegetation height on the studied sites. Significant ($p < 0.05$) differences detected by Mann-Whitney U test are indicated by different letters.

5) has also been proven by revealing a sharp difference between the habitat requirements of species related to open patches with short grasses and to closed patches with structured spatial composition (Fig. 7). The fact that the density of pratinicol and graminicol species, as an inverse trend, was significantly low until the abandonment of grazing, is explained by the fact that the vegetation structure was simplified due to the effect of grazing, which is unfavourable for pratinicol and graminicol species in terms of a nutritional base, microclimate, egg-laying possibilities and exposure to predators (Krüss and Tschardtke 2002, Gardiner and Haines 2008).

Following from the results and suggestions by Jerrentrup et al. (2014) and Joubert et al. (2016), the conservation of species rich-

ness and diversity of the studied orthopteran assemblages can best be ensured by moderate grazing. The definition of moderate vs. extensive grazing is not possible in general, but only in relation to the given habitats. Jerrentrup et al. (2014) estimated that grazing intensity of ~ 1 Livestock Units/ha can still be considered moderate, resulting in habitat structure rich in microhabitats that ensure the presence of diverse orthopteran assemblages. However, the assemblages of dry steppe grasslands are more sensitive to grazing pressure. According to the results of Fonderflick et al. (2014), in the case of extensive grazing of dry steppe grasslands with sheep (0.24 Livestock Units/ha), the abundance of orthopterans is significantly higher in the ungrazed spots than in the post-grazed areas. According to Gardiner and Haines (2008), in the case of grazing by horses, reduction of intensity from 3.5 horse/ha to 2 horse/ha can lead to an increase in the diversity and abundance of the orthopteran assemblage. The grasslands examined in the current study belong to the extremely low grass-producing habitats that are highly sensitive to treading. Thus, for the largest species richness, diversity and density of the local orthopteran assemblages, the extensive grazing system proposed by Máté (2014) should be used: 1) Grazing pressure should be set between 0.1–0.2 Livestock Units/ha; 2) Ungrazed patches should be left in the grasslands concerned each year. The desirable extent of the latter should be set as 10–50% of the grazed parcels. The greater the precipitation in a year, the smaller the percentage of the grasslands that has to be spared from grazing. Ungrazed areas should be designated at several isolated spots, and the grazed and ungrazed patches should be changed from year to year (on large pastures designated subareas should be used in every 1st, 3rd, 6th, and 10th year); 3) the land use must be controlled by the shepherd, ensuring the spread of the grazing animals.

In the examined habitats the annual grazing schedule is also important. In this respect, it has to be taken into account that the changing of vegetation structure affects orthopterans the most dramatically in the period when the number of adults in the assemblages is at its highest (August in Europe) (Fonderflick et al. 2014). During this period, the concentration of grazing on smaller, less natural, weedy patches is also acceptable in order to protect the valuable vegetation patches and their orthopteran assemblages. The conservation potential is strongly influenced by habitat conditions (Weiss et al. 2013). This is particularly true for habitats as sensitive as the Central European sandy steppes, where the grazing method should always be chosen by taking the weather conditions into consideration: during dry periods grazing must be moderated, or abandoned completely on the patches most sensitive to treading (Máté 2014).

On a global or historical scale, it is odd that we consider the development and use of different grazing systems for habitats that have been under continuous grazing pressure for hundreds or thousands of years, in order to preserve their biodiversity. This is not unjustified, however, given that from the end of the nineteenth century, in a significant part of Europe, habitats resulting from moderately disturbing and selective effects of extensive land management have disappeared, degraded and fragmented to the greatest extent (Bakker and Berendse 1999). As a result, the remaining habitat fragments became biodiversity hotspots (Steffan-Dewenter and Tschardtke 2002), the possible disappearance of which would be an irreversible loss. The preservation of the latter must therefore be given priority. As demonstrated by the present case study, changing the grazing patterns toward nature conservation-based land use can have positive results in terms of the protection of diverse orthopteran assemblages. However, for successful conserva-

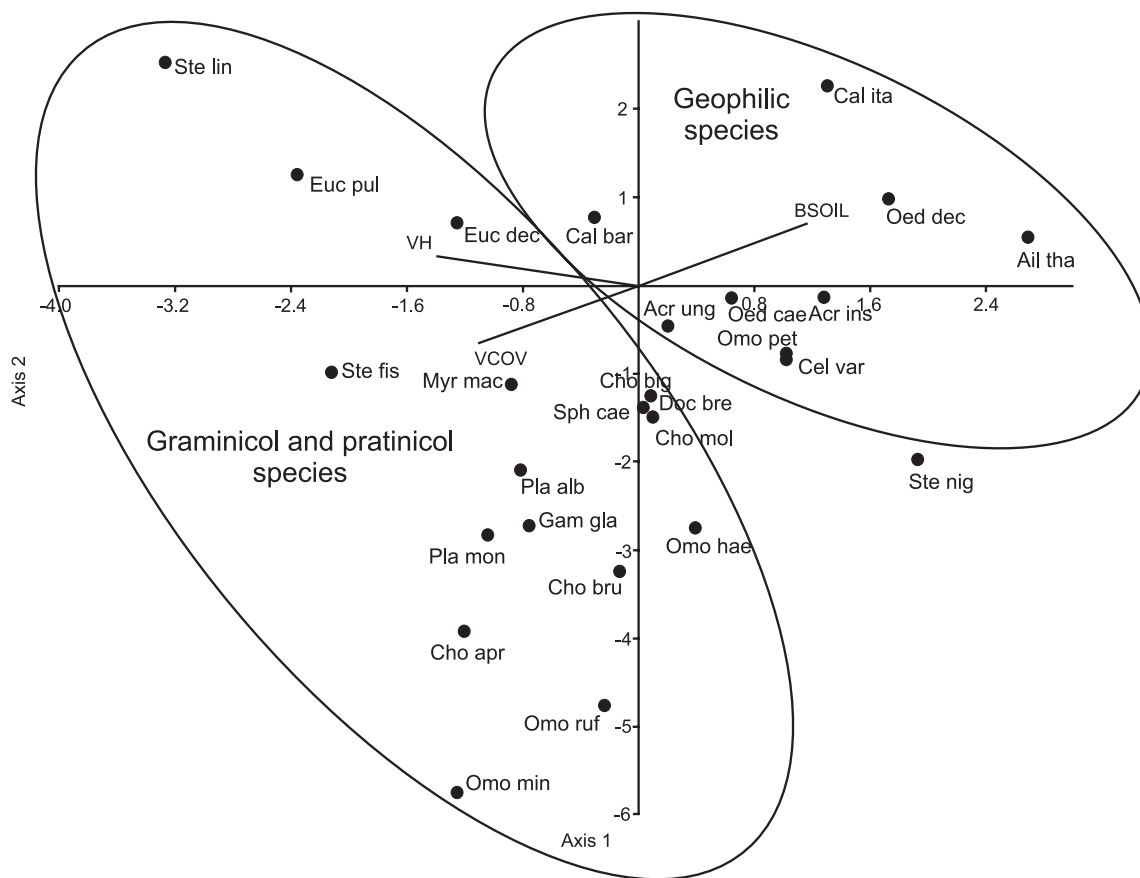


Fig. 7. CCA ordination based on Orthoptera data and environmental parameters (VCOV: total vegetation cover; BSOIL: percentage of bare soil; VH: height of the vegetation). Abbreviations of species names: Acr ins: *Acrotylus insubricus*; Acr ung: *Acrida ungarica*; Ail tha: *Aiolopus thalassinus*; Cal bar: *Calliptamus barbarus*; Cal ita: *Calliptamus italicus*; Cel var: *Celes variabilis*; Cho apr: *Chorthippus apricarius*; Cho big: *Chorthippus biguttulus*; Cho bru: *Chorthippus brunneus*; Cho mol: *Chorthippus mollis*; Doc bre: *Dociostaurus brevicollis*; Euc dec: *Euchorthippus declivus*; Euc pul: *Euchorthippus pulvinatus*; Gam gla: *Gampsocleis glabra*; Mon mon: *Montana montana*; Myr mac: *Myrmeleotettix maculatus*; Oed cae: *Oedipoda caerulescens*; Oed dec: *Oedaleus decorus*; Omo hae: *Omocestus haemorrhoidalis*; Omo min: *Omocestus minutus*; Omo pet: *Omocestus petraeus*; Omo ruf: *Omocestus rufipes*; Pla alb: *Platycleis albopunctata*; Sph cae: *Sphingonotus caerulans*; Ste fis: *Stenobothrus fischeri*; Ste lin: *Stenobothrus lineatus*; Ste nig: *Stenobothrus nigromaculatus*.

tion strategies for sensitive communities requiring moderate disturbance, it is important to conduct further, preferably long-term, studies on the response of orthopteran assemblages as bioindicators (Bazelet and Samways 2011) to the direct and indirect effects of grazing systems linked to fragmented habitats.

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Appendix 1

Species composition and abundance of the pooled samples of different grazing pressure (LF: life form; EF: ecotype form; G: grazed, MG: moderately grazed, GA: grazing-abandoned, UG: ungrazed; arbu: arbusticol; geo: geophilic; gra: graminicol; pra: pratinicol; ps: psammophilic; psp: pseudo-psammophilic; mes: mesophilic; m-ther: moderately-thermophilic; ther: thermophilic)

| Taxon | LF | EF | G | MG | GA | UG |
|-------------------------------------------------------------|------|--------|-----|-----|----|-----|
| Caelifera | | | | | | |
| Acridoidea | | | | | | |
| Acridomorpha | | | | | | |
| Acrididae | | | | | | |
| Acridinae | | | | | | |
| <i>Acrida ungarica</i> (Herbst, 1786) | psps | ther | 172 | 186 | 77 | 79 |
| Calliptaminae | | | | | | |
| <i>Calliptamus barbarus</i> (Costa, 1836) | ps | ther | 203 | 116 | 69 | 241 |
| <i>Calliptamus italicus</i> (Linnaeus, 1758) | gra | ther | 6 | 0 | 4 | 0 |
| Gomphocerinae | | | | | | |
| <i>Euchorthippus declivus</i> (Brisout de Barneville, 1848) | gra | ther | 18 | 89 | 60 | 135 |
| <i>Euchorthippus pulvinatus</i> (Fischer de Waldheim, 1846) | gra | ther | 0 | 8 | 18 | 28 |
| <i>Euthystira brachyptera</i> (Ocskay, 1826) | pra | mes | 0 | 0 | 2 | 0 |
| <i>Dociostaurus brevicollis</i> (Eversmann, 1848) | psps | ther | 32 | 48 | 15 | 22 |
| <i>Chorthippus apricarius</i> (Linnaeus, 1758) | pra | mes | 0 | 1 | 1 | 0 |
| <i>Chorthippus biguttulus</i> (Linnaeus, 1758) | pra | m-ther | 6 | 6 | 12 | 0 |
| <i>Chorthippus brunneus</i> (Thunberg, 1815) | pra | m-ther | 10 | 17 | 11 | 1 |
| <i>Chorthippus dichrous</i> (Eversmann, 1859) | pra | mes | 0 | 0 | 6 | 0 |
| <i>Chorthippus mollis</i> (Charpentier, 1825) | pra | mes | 11 | 11 | 13 | 0 |
| <i>Myrmeleotettix maculatus</i> (Thunberg, 1815) | gra | ther | 22 | 99 | 37 | 27 |
| <i>Pseudochorthippus parallelus</i> (Zetterstedt, 1821) | pra | mes | 3 | 0 | 0 | 0 |
| <i>Omocestus haemorrhoidalis</i> (Charpentier, 1825) | pra | ther | 5 | 0 | 1 | 0 |
| <i>Omocestus minutus</i> (Brullé, 1832) | psps | ther | 0 | 4 | 0 | 0 |
| <i>Omocestus petraeus</i> (Brisout de Barneville, 1856) | gra | ther | 30 | 16 | 4 | 2 |
| <i>Omocestus rufipes</i> (Zetterstedt, 1821) | pra | mes | 1 | 3 | 1 | 0 |
| <i>Stenobothrus fischeri</i> (Eversmann, 1848) | pra | ther | 0 | 9 | 33 | 2 |
| <i>Stenobothrus lineatus</i> (Panzer, 1796) | pra | m-ther | 0 | 0 | 8 | 0 |
| <i>Stenobothrus nigromaculatus</i> (Herrich-Schäffer, 1840) | gra | ther | 31 | 0 | 0 | 0 |
| <i>Stenobothrus stigmaticus</i> (Rambur, 1838) | pra | m-ther | 1 | 0 | 0 | 0 |

| Taxon | LF | EF | G | MG | GA | UG |
|------------------------------------------------|------|--------|-----|----|----|----|
| Oedipodinae | | | | | | |
| <i>Acrotylus insubricus</i> (Scopoli, 1786) | ps | ther | 30 | 5 | 2 | 6 |
| <i>Acrotylus longipes</i> (Charpentier, 1845) | psps | ther | 0 | 1 | 0 | 0 |
| <i>Aiolopus thalassinus</i> (Fabricius, 1781) | gra | m-ther | 21 | 2 | 0 | 0 |
| <i>Celes variabilis</i> (Pallas, 1771) | gra | ther | 4 | 0 | 0 | 1 |
| <i>Oedaleus decorus</i> (Germar, 1826) | psps | ther | 213 | 18 | 21 | 27 |
| <i>Oedipoda caerulescens</i> (Linnaeus, 1758) | geo | ther | 98 | 48 | 27 | 37 |
| <i>Sphingonotus caerulans</i> (Linnaeus, 1767) | psps | ther | 2 | 1 | 0 | 1 |
| Pezotettiginae | | | | | | |
| <i>Pezotettix giornae</i> (Rossi, 1794) | gra | ther | 1 | 0 | 0 | 0 |
| Ensifera | | | | | | |
| Tettigoniioidea | | | | | | |
| Tettigoniidae | | | | | | |
| Tettigoniinae | | | | | | |
| <i>Gampsocleis glabra</i> (Herbst, 1786) | psps | ther | 0 | 2 | 1 | 0 |
| <i>Montana montana</i> (Kollar, 1833) | psps | ther | 0 | 3 | 0 | 0 |
| <i>Platycleis affinis</i> Fieber, 1853 | psps | ther | 0 | 0 | 2 | 0 |
| <i>Platycleis albopunctata</i> (Goeze, 1778) | pra | ther | 1 | 3 | 1 | 1 |
| Phaneropteridae | | | | | | |
| Phaneropterinae | | | | | | |
| <i>Leptophyes albobittata</i> (Kollar, 1833) | arbu | ther | 0 | 0 | 0 | 2 |

The effects of livestock grazing and climate variation on vegetation and grasshopper communities in the northern Chihuahuan Desert

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Abstract

Grasshoppers are important herbivores of North American semi-arid grasslands and shrublands, and vegetation and climate are key factors controlling their species compositions and population dynamics. Domestic livestock grazing is a historic and a current landscape-scale ecological perturbation that has caused reductions of perennial grasses and increases in woody shrubs and weedy annual herbs in desert grassland communities. Climate variation also affects vegetation and grasshopper production, and the combined effects of livestock grazing and climate variation on vegetation and grasshoppers have not been adequately studied in the American Southwest. I measured vegetation and grasshoppers for five years at a series of five semi-arid sites in the northern Chihuahuan Desert to evaluate the interactive effects of short-term livestock grazing and climate variation on plant and grasshopper community structure and species abundances. The study sites ranged from shrub dominated to grass dominated landscapes, with livestock fence lines separating land that was grazed at 30% annual forage utilization, and lands on the other sides of the fences excluded from grazing for at least 20 years. I assigned grasshopper species to life-form guilds based on their ecomorphologies and their microhabitat substrate uses that I observed. A wet spring/dry summer El Niño event occurred at the beginning of the study, and a dry spring/wet summer La Niña event occurred at the end of the study. Livestock grazing changed plant and grasshopper species compositions and abundances significantly during those wet years, further favoring annual forbs, annual grasses and non-graminicole grasshoppers on grazed lands during wet years, while favoring perennial grasses and graminicoles on non-grazed lands also during wet years. The biotic communities at all sites probably supported more perennial grasses and more graminicoles prior to European settlement and livestock grazing that began over a century before this study.

Key words

Acrididae, desertification, ecological disturbance, guilds, life-forms

Introduction

Grasshoppers are important primary consumers in semi-arid regions throughout the world (Uvarov 1977), and grasshopper species compositions are determined largely by geographic proximity to evolutionary source regions (Key 1959, Otte 1976) and

by species adaptations to local soils and vegetation composition and structure (e.g. Anderson 1964, Mulkern 1967, 1982, Otte and Joern 1977, Joern 1979, 1982, Kang et al. 1989, Fielding and Brusven 1995a, Torrusio et al. 2002, Cigliano et al. 2010, Savitsky 2010). Population densities of many grasshopper species fluctuate widely over time, apparently largely due to bottom-up changes in food plant availability and quality, caused not only by variation in precipitation, but also by physiological responses to variation in temperature and moisture conditions (Rodel 1977, Capinera 1987, Fielding and Brusven 1990, Joern and Gaines 1990, Belovsky and Joern 1995). Density-dependent effects of other grasshoppers, predators, parasitoids, and disease also interact to affect grasshopper populations (Dempster 1963, Street and McGuire 1990). How grasshopper communities and populations respond to environmental disturbance such as domestic livestock grazing and climate change depends to what extent soil, vegetation and weather conditions change in magnitude, space and time, and to what extent different grasshopper species with variable environmental tolerances are affected by the changes. Some species are likely to respond in certain ways, while other species may show different responses (Fielding and Brusven 1996).

Convergence or divergence in grasshopper species ecologies and specializations are likely driven by the evolution of ecological traits (e.g. Van der Plas et al. 2012). Grasshoppers that occur in particular types of habitats and feed on particular types of plants have morphological, physiological and behavioral adaptations, or ecological traits that maximize evolutionary fitness for those species in their particular environments. Grasshopper species that share similar ecological traits for morphology, diet and behavior are ecological guilds; groups of species that exploit the same class of environmental resources in a similar way (Root 1967, Diamond 1975). How one chooses to describe grasshopper community structure, including guilds, depends upon the purpose for such description (Lockwood 2011), and the guild concept is useful for understanding higher level ecological structure that may show patterns beyond taxonomically constrained species, tribes, subfamily and family ranks. The grasshopper community guild concept has been used to describe grasshopper community structure for specific assemblages and locations in North America (e.g. Joern and

Lawlor 1981), China (Hong-Shi 1991, Sun et al. 2013) and Africa (Prendini et al. 1996). Those studies assigned grasshopper species from local assemblages to guilds based on microhabitat and food resource use, which provided good descriptions of the ecological structures of those grasshopper communities.

Uvarov (1977) described grasshopper life-forms that occur globally, and that correspond to ecological/morphological traits of grasshoppers that live in particular types of microhabitats, such as open bare soil, grass, forbs and shrubs and trees. I previously applied Uvarov's life-form concept to describe grasshopper guild structure in the North American desert grasshopper communities in the cool-temperate Great Basin Desert and in the warm subtropical Chihuahuan Desert, based on substrate use by individual grasshoppers (Lightfoot 1985). I found that life-forms reflected the ecological traits of grasshopper species: 1) terricoles live on bare soil or rock surfaces and feed on grasses and forbs, 2) herbi-coles live and feed on forbs, 3) graminicoles live on and feed on grasses, and 4) arbusticoles live on and feed on woody shrubs (a subset of arboricoles). The life-form guild structure was similar in both deserts, while the species were not. Grasshopper species within life-form guilds should exhibit similar responses to changes in vegetation resources, relative to other responses of species in other guilds. Grasshopper life-form guilds have also proved useful for documenting the effects of burrowing rodents (*Cynomys* spp.) and livestock grazing on plant and grasshopper communities in the northern Chihuahuan Desert (Davidson and Lightfoot 2008, Davidson et al. 2010). Just as grasshopper species with different ecologies can serve as species indicators of environmental change in local geographic regions (Bazelet and Samways 2011), grasshopper life-form guilds transcend regional taxonomic constraints of species (Uvarov 1977), and have the potential to serve globally as grasshopper life-form guild indicators to environmental change.

Desertification is the anthropogenic environmental degradation of semi-arid grasslands from long-term excessive and unsustainable domestic livestock grazing, that has occurred extensively throughout the semi-arid regions of the world, including the semi-arid regions of North America (Nelson 1988). The most intense desertification in North America has taken place in the northern Chihuahuan Desert (Dregne 1986), largely the result of excessive domestic livestock grazing and droughts (York and Dick-Peddie 1969, Dick-Peddie 1993). Unlike more mesic grassland and savanna environments where vegetation and animals are adapted to grazing, domestic livestock are a substantial and unnatural perturbation to semi-arid desert grassland biotic communities that did not evolve with large ungulate grazers (Pieper 1994, Young 1994). Desertification in the Chihuahuan Desert has resulted in a dramatic reduction in the abundance of perennial grasses, and an increase in woody shrubs (Buffington and Herbel 1965, Archer 1994, Pieper 1994). Attempts to better understand and manage natural resources of desertified landscapes are evolving toward better applications of science and ecology to address the problem (Peters et al. 2015). Vegetation changes on North American rangelands associated with domestic livestock grazing and desertification continue to have disruptive impacts on the species composition, diversity, and stability of rangeland grasshopper assemblages and populations (Fleischer 1994, Laycock 1994, Jones 2006). Understanding both the short-term and long-term ecological implications of livestock impacts to grasshoppers (e.g. Fielding and Brusven 1996) will contribute to more sustainable natural resource management.

Livestock grazing typically causes changes to herbaceous vegetation composition and structure that in turn cause shifts in

grasshopper species compositions and population densities in savanna, shrub-steppe and desert grassland environments (e.g. Capinera and Sechrist 1982, Jepsen-Innes and Bock 1989, Quinn and Walgenbach 1990, Fielding and Brusven 1993, 1995b, 1996, Prendini et al. 1996, Gebeyehu and Samways 2003, Debano 2006, Kang and Chen 2008, Branson and Sword 2010). Results of studies vary, especially between grasslands/savanna and desert grasslands, but grasshoppers that prefer more open microhabitats with sparser and lower stature vegetation tend to respond more favorably to livestock grazing than those that prefer taller and denser herbaceous vegetation (e.g. Prendini et al. 1996). Livestock grazing also can reduce grasshopper diversity, and favor fewer ecological generalist grasshopper species (e.g. Fielding and Brusven 1993) that can shift the temporal stabilities of such communities, making them more sensitive to changes in climate.

Fielding and Brusven (1996) provided a literature review of livestock grazing effects on semi-arid region grasshoppers of North America. They concluded that there is no one answer to the question of how livestock grazing effects grasshoppers; each situation is different, and each depends upon current and historic grazing regimes, local environments, grasshopper species ecologies, and ecological, temporal, spatial and functional characteristics of the system studied. Of particular importance is the differentiation of short-term (< 10 years) vs. long-term (decades to centuries) effects of grazing on soils, vegetation and grasshoppers. Long-term grazing can permanently change soils, vegetation and grasshoppers, while the impacts of short-term grazing may revert back to original conditions within a few years if grazing ceases (Fielding and Brusven 1996).

Variation in weather or long-term climate is known to be a key factor affecting grasshopper populations (Edwards 1960, Gage and Mukerji 1977, Begon 1983, Capinera and Horton 1989, Fielding and Brusven 1990, Jonas and Joern 2007, Nufio et al. 2010). Therefore, anthropogenic global climate change likely is and will have a significant influence on grasshopper communities, just as it is predicted to have on all biota globally (Parmesan 2006, Rosenzweig et al. 2008). Climate change will not only directly affect grasshopper physiological responses and phenologies (Nufio et al. 2010), but also will interact with other anthropogenic disturbances such as livestock grazing to cumulatively affect grasshoppers (Fielding and Brusven 1995b, 1996, Jonas and Joern 2007, Branson and Sword 2010). As global warming continues to accelerate, the climate of the American Southwest is becoming warmer, drier and the timing and intensity of precipitation more variable (Seager et al. 2008, Gutzler and Robbins 2011, Gutzler 2013), likely intensifying adverse impacts of livestock grazing to vegetation and grasshoppers.

Given that grasshoppers are key primary consumers in semi-arid ecosystems across the Southwest, and given that grasshoppers are known to be affected by variation in vegetation caused by livestock grazing and variation in climate, what effects do domestic livestock and climate have on vegetation and grasshoppers in the Southwest? I conducted this research project to address the following questions: 1) Does short-term livestock grazing alter the species compositions, plant life-form (i.e. grass, forb, shrub, tree) and grasshopper life-form guild structures, and abundances of rangeland plants and grasshoppers? 2) Does annual and seasonal variation in precipitation interact with livestock grazing to affect plant and grasshopper species assemblages and grasshopper guild structure? 3) Which grasshopper species and guilds are most sensitive to the impacts of short-term livestock grazing and climate variation?

This research was conducted as part of the U.S. Department of Interior (USDI), Bureau of Land Management (BLM), Global

Change Research Projects program, 1991–1996, which was intended to support long-term research on the ecological impacts of global climate change to natural resources. However, in 1996, the program was terminated due to politically motivated USDI administrative research program changes. This article presents the findings of the five-year vegetation and grasshopper grazing response research that was conducted from 1992–1996 as part of the Chihuahuan Desert Subproject. This research was intended to be a long-term (decades) study to document biotic community responses to climate change, but the entire Global Change Research Program was terminated, so the long-term goals were not accomplished.

Methods

Study sites and sampling design.—Study sites for this research were subjectively located where BLM lands within the Chihuahuan Desert in southern New Mexico were adjacent to lands under other ownership and/or management that excluded livestock grazing, and shared a common boundary with a standard 5 strand barbed-wire livestock fence. Livestock grazing was present on the BLM side of the fence, but not on the other side. From those potential locations, site selection then depended upon obtaining permission from the other landowner/agency to conduct the study, and then depended upon finding a 1 km long section of the boundary fence that had relatively homogeneous topography, soils, and vegetation, so that the presence of livestock grazing on the BLM side of the fence, but not on the other side, was the only primary factor that differed along the potential fence line. The grazed side of each fence line was BLM public land that was currently grazed by domestic cattle, and had been historically grazed for at least 20 years. The non-grazed side of the fences had been excluded from cattle for at least 20 years. Grazing intensity at all sites was year-round, approximately 30% utilization of available plant foliage by domestic livestock, the standard stocking rate for BLM public rangelands in the region. Each site consisted of semi-arid grassland or shrubland that was grazed by domestic cattle, and adjacent non-grazed land on the other side of the barbed-wire livestock fence line. All sites were further chosen to be situated at the same approximate elevation (~1,500 m above sea level), and all on similar topographic landscapes; lower piedmont slopes with silty to sandy loamy soils. All sites supported Chihuahuan Desert grassland or shrubland vegetation communities. Sites ranged from shrub-dominated to grass-dominated, but all sites had both grass and shrub elements.

The study sites were located in the northern Chihuahuan Desert (Chihuahuan Deserts Level III Ecoregion, Griffith et al. 2006), in south-central New Mexico, USA. The Sevilleta Site was located along the north boundary of the Sevilleta National Wildlife Refuge, Socorro County, and the vegetation was desert grassland dominated by black grama (*Bouteloua eriopoda*) and blue grama (*B. gracilis*); the Bosque Site was located along the east boundary fence of Bosque del Apache National Wildlife Refuge, Socorro County, and the vegetation was mixed desert grassland and shrubland dominated by sacaton grasses (*Sporobolus* spp.) and sand sage (*Artemisia filifolia*); the Jornada Site was located along the southwest boundary fence of the US Department of Agriculture, Jornada Experimental Range, Doña Ana County, and the vegetation was creosote bush (*Larrea tridentata*) shrubland; the Phillips Site was located along the east boundary fence of the US Army, White Sands Missile Range at the Phillips Hills, Lincoln County, and the vegetation was creosote bush shrubland; all four sites above were within the

Chihuahuan Basins and Playas Level IV Ecoregion; and the Otero Site was located on the northwestern side of Otero Mesa along the boundary fence of a BLM grazing enclosure, Otero County, and the vegetation was desert grassland dominated by black grama and blue grama, and within the Chihuahuan Desert Grasslands Level IV ecoregion. See Dick-Peddie (1993) for detailed descriptions of the vegetation of those ecoregions in New Mexico. Table 1 provides location information for each site.

Sampling at each site was systematic, not random or subjective. Two 600 m, paired, grazed and non-grazed sampling transects were permanently installed at each of the five study sites. Each of the paired 600 m measurement transects were located parallel to, and each 20 m from the fence line between the two, to avoid roads and/or livestock trails along some of the fence lines. Each 600 m transect was partitioned into thirty, 20 m segments. All transects and segments were permanently marked and labeled with 0.5 m steel rods that were hammered into the soil.

Weather.—Weather data were obtained from the nearest long-term U.S. National Weather Service weather station to each of the five study sites. Monthly precipitation amounts and ambient temperatures were summed and averaged respectively over each year of this study. Table 2 presents the name and location of each of the weather stations.

Vegetation.—Vegetation was measured from a 1 m² quadrat located at the start (north or west end) of each of the thirty, 20 m segments per transect. The same permanent quadrats were repeatedly sampled over the five-year study period. A 1 m² vegetation measurement frame made of 0.5 inch PVC pipe with an internal string 10 by 10 grid of 100, 1 decimeter² subunits, was used to measure vegeta-

Table 1. Study site information based on center of each site.

| Study site name | Location | Elevation | Level IV Ecoregion* |
|--------------------------------------------|---------------------|-----------|----------------------------------|
| Bosque del Apache National Wildlife Refuge | N33° 24', W106° 45' | 1,520 m | Chihuahuan Basins and Playas 24a |
| Jornada Experimental Range | N32° 28', W106° | 1,340 m | Chihuahuan Basins and Playas 24a |
| Otero Mesa | N32° 29', W105° 46' | 1,540 m | Chihuahuan Desert Grasslands 24b |
| Phillips Hills, White Sands Missile Range | N32° 27', W106° 06' | 1,490 m | Chihuahuan Basins and Playas 24a |
| Sevilleta National Wildlife Refuge | N34° 24', W106° 36' | 1,610 m | Chihuahuan Desert Grasslands 24b |

*Griffith et al. 2006

Table 2. U.S. National Weather Service weather stations that provided weather data for this study. Each of the five study sites was represented by one nearest weather station.

| Study site name | Weather station name | Location | Elevation |
|--------------------------------------------|----------------------------|---------------------|-----------|
| Bosque del Apache National Wildlife Refuge | Bosque del Apache | N33° 46', W106° 54' | 1,445 m |
| Jornada Experimental Range | Jornada Experimental Range | N32° 37', W106° 44' | 1,440 m |
| Otero Mesa | Orogrande | N32° 23', W106° 06' | 1,270 m |
| Phillips Hills, White Sands Missile Range | Carrizozo | N33° 39', W105° 53' | 1,650 m |
| Sevilleta National Wildlife Refuge | Bernardo | N34° 25', W106° 50' | 1,085 m |

tion canopy cover by species. The PVC frame was attached to 1 m tall legs with height adjustments on each corner to keep it elevated immediately above the plant foliage canopies. The total foliage canopy cover of each plant species, and the maximum foliage height of each plant species per quadrat were recorded. Vegetation was sampled twice each year, at the end of the spring growing season in late May (especially for spring annual C3-photosynthetic pathway plants), and at the end of the summer growing season in late September for most other largely C4 plants. Vegetation was measured over a period of five years; 1992, 1993, 1994, 1995, and 1996. Plant species classification, common names and Latin names, life-histories and growth-forms follows USDA PLANTS Database (2017).

Grasshoppers.—Many different field sampling methods have been utilized to count grasshoppers (Onsager 1977). Most physical sampling methods are biased toward grasshopper species that are either less active than others, or more active than others, depending on the method and the environment. Physical sampling methods also capture and remove grasshoppers from study sites. I chose to use visual transect sampling instead, by slowly walking each of the thirty, 20 m by 1 m segments or strips of each transect. All grasshoppers observed in each 20 m strip transect along each segment were recorded. I walked slowly along each 20 m strip transect segment, tapping the ground and vegetation with a 1m long white 13 mm diameter PVC pipe to flush all grasshoppers ahead of me as I slowly walked forward. I recorded species, sex, age class, and substrate (physical surface that the individual flushed from) of each grasshopper observed on a voice-activated micro-audio recorder. I had ten years of prior experience visually identifying the regional grasshopper species in the field, and I was the only observer/recorder for this study. Resulting data were the absolute density of each grasshopper species per each 20 m by 1 m, or 20 m² transect segment, per sampling period.

The substrate was the physical surface that each grasshopper was first observed on, including soil surfaces, and different species of plants. I watched grasshoppers as they hopped and/or flew ahead of me and did not recount any individuals that I had already counted. Grasshoppers were sampled twice each year during the five-year study period, at the same time that vegetation was measured. Several species of grasshoppers in the region hatch from eggs in the late summer/fall, over-winter as juveniles and become adults in the late spring (e.g. *Psoloessa* spp., *Cibolacris parviceps*, *Arphia conspersa*, *Xanthippus* spp.). Also, one of the most common grasshoppers in the region, *Trimerotropis pallidipennis* has two distinct generations each summer in the region of this study, one early and one late (Richman et al. 1993). Most other grasshopper species hatch from eggs in the mid-summer, and become adults in the late summer/fall. Grasshopper sampling was conducted during the late morning to early afternoon hours when grasshoppers tend to be most active. Grasshopper sampling was conducted only when winds were less than 10 miles per hour, the sun was shining, and the soil surface and vegetation were dry. Grasshopper species classification, common names and scientific names follows Cigliano et al. (2017).

I assigned grasshopper species to ecological life-forms following the morphological descriptions of Uvarov (1977). I used multivariate cluster analysis (see McCune and Grace 2002) to evaluate groupings of grasshopper species in this study based on similarities in observed substrate use (see Results) to provide additional ecological information to evaluate grasshopper assemblage guild structure based on resource use (as indicated by substrate use) and morphology (as described by Uvarov 1977).

Data management and analysis.—Vegetation data were entered on field data forms and then transferred to a Microsoft Excel spreadsheet for management and error checking, then converted to a text file for analysis. Grasshopper data were entered from field audio-recordings to an Excel spreadsheet and converted to a text file for analysis. All data were quality checked and verified. The vegetation, grasshopper, and climate data resulting from this study were summarized and analyzed using SAS analytical software (Version 9.4, SAS Institute, Cary, North Carolina, USA). I used hierarchical group-average cluster analysis (SAS; PROC CLUSTER, PROC TREE) utilizing Euclidean distance for similarity measures of species composition or grasshopper substrate use to evaluate entire assemblages of species from different locations, each year and season. Vegetation data were mean canopy covers and heights of each species/quadrat over all 30 quadrats per site, by control and treatment sides of the fence (control vs. grazed; 30 quadrats each). I used paired t-tests (SAS; PROC TTEST) to test for significant differences in vegetation canopy cover and heights between grazed and non-grazed paired fence side locations within sites. I used Chi-square goodness of fit tests (SAS; PROC FREQ) to test for differences in grasshopper counts, summed by species, and categorized by life-forms, from each paired 600 m transect (non-grazed vs. grazed) at each site and year/season. I used a standard statistical test level of alpha (p) = 0.05. The relationships between grasshopper life-form counts from individual grasshopper species counts, and available plant life-form and bare soil cover values that were measured from the 1 m² quadrats, were evaluated with non-parametric Spearman-rank correlation analysis (SAS; PROC CORR).

Results

Weather.—Annual total precipitation summed over 12 months of each year from 1992–1996 across all five sites, ranged from 10 cm/year to 40 cm/year, with an overall decline trend over time, especially in 1995 (Fig. 1). El Niño / Southern Oscillation Events (ENSO) occurred in 1992 and in 1996. A moderate El Niño event occurred in 1991/1992, with above average rainfall during the winter and spring of that period, and weak El Niño events occurred in 1993 and in 1995, followed by a weak La Niña event in 1996, with above average late summer rains (NOAA 2016). The Phillips site had the most precipitation over the 5 year study, except in 1995, followed by the Otero site (both in the Tularosa Basin, adjacent to the Sacramento Mountains), while the Jornada, Bosque, and Sevilleta sites (all in the Rio Grande valley) tended to be drier over the 5 year study period. Annual average ambient temperatures, averaged over 12 months of each year from 1992–1996 across all 5 sites, ranged from 13.0°C to 17.5°C across the sites, with an overall increase of one degree centigrade over all 5 sites over the 5 year period, with particularly warm temperatures in 1994 (Fig. 2).

Vegetation.—A listing of all 151 plant species observed, their life-histories, and life-forms is presented in Suppl. material 2: Table S1. The majority of plant species sampled from all five study sites over the five-year period were herbaceous forbs, followed by grasses, shrubs, and cacti.

Plant species counts or richness ranged from about 15 to 30 species over the study sites and years, with most sites showing declines in 1994 and increases in 1995, and slightly more species were present during late summer/fall sampling than during the early summer/spring (Suppl. material 1: Fig. S1). Some sites like the Bosque and Jornada had slightly greater species richness

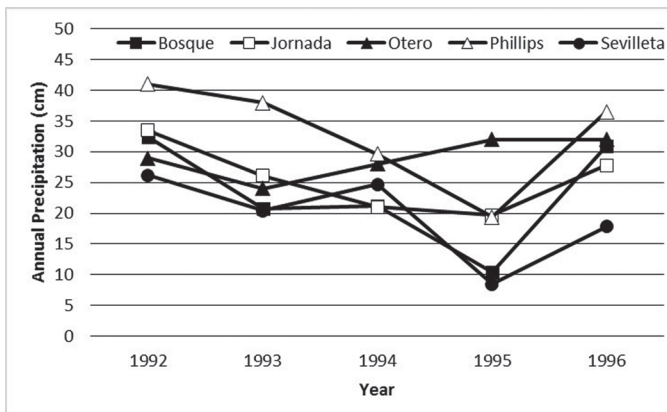


Fig. 1. Total annual precipitation (January-December) at each of the study sites over the five-year study period.

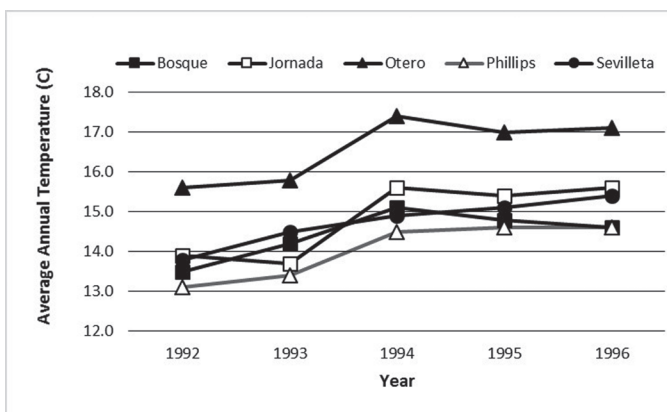


Fig. 2. Annual average (12 months/year) temperatures at each of the study sites over the five-year study period.

on grazed quadrats than on non-grazed quadrats, while the other sites showed greater richness on the non-grazed quadrats.

Cluster analysis of the five study sites and their control vs. grazed sides of the fences, and based on similarities of plant species compositions summed over the five-year period, revealed that each of the sites supported very distinct plant species compositions both in the spring and fall (Fig. 3). The branch or stem lengths of the dendrograms in Fig. 3 demonstrate much more similarity across grazed and non-grazed quadrats within each site, than between sites, and similarities between sites were greater during the spring seasons (Fig. 3A) than in the fall (Fig. 3B) based on cluster branch or stem lengths. Higher level groupings revealed that the Sevilleta, Bosque, and Phillips sites were more similar to each other than the Jornada or Otero sites in the spring, but that the Bosque, Sevilleta and Otero sites were more similar to each other than to the Jornada and Phillips sites in the fall over all five years. The Jornada and Phillips sites were creosote bush dominated shrublands on gravelly alluvial soils, while the Sevilleta, Bosque and Otero sites were black and blue grama grass, and burro (*Scleropogon brevifolius*) and sacaton grass dominated desert grasslands on finer alluvial and aeolian soils. The Sevilleta site was primarily grassland, the Bosque site also had considerable amounts of sand sage (*Artemisia filifolia*), and the Otero site had creosote bush but not as dominant as at the Jornada and Phillips sites.

Analysis of the major plant life-forms forbs, grasses, and shrubs, revealed that livestock grazing primarily affected grasses and forbs,

but not shrubs (except for broom snakeweed). Across all five sites, forbs and grasses tended to have significantly more cover on the non-grazed sides of the fences than on the grazed sides, especially in association with the 1991/1992 El Niño event, and the 1996 La Niña event (Suppl. material 1: Fig. S2 and Suppl. material 2: Table S2). Spring and summer annual forbs at the Bosque and Otero sites increased significantly on the non-grazed side of the fences in 1995, only spring annual forbs increased in 1995 and on the non-grazed sides of the fences at the Jornada and Sevilleta sites, while annual forbs increased significantly on the grazed side of the fence at the Otero site in 1996 (Suppl. material 1: Fig. S2, Suppl. material 2: Table S2). Grass cover increased significantly in the fall of 1996 on the grazed areas at the Otero and Sevilleta sites, dominated by the annual grass sixweeks threeawn (*Aristida adscensionis*). Otherwise, grass cover at Otero and Sevilleta sites was dominated by the perennial grama grasses (*Bouteloua* spp.), and at the Jornada site where perennial bush muhly (*Muhlenbergia porteri*) was abundant, grass cover was generally significantly greater on the non-grazed areas over the five-year study (Suppl. material 1: Fig. S2). Plant height measurement data also revealed that perennial grasses were not significantly different, or were significantly taller on non-grazed vs. grazed areas at all sites across all years, except for Bosque and Sevilleta sites in 1996, where again, annual sixweeks threeawn created significantly taller grass on the grazed areas (Suppl. material 2: Table S2). Shrub canopy cover and heights tended to vary little over space and time (Suppl. material 1: Fig. S2, Suppl. material 2: Table S2). The only dynamic shrub species was broom snakeweed (*Gutierrezia sarothrae*) which increased significantly in the spring of 1992 and in the fall of 1996 on grazed areas at the Sevilleta site.

Overall, the canopy cover and abundance of annual forbs and annual grasses varied considerably in response to variation in rainfall over the five sites and five years, especially the late summer of 1996 when annual sixweeks threeawn grass had higher cover and height than perennial grasses at two of the five sites. Perennial grasses tended to be less variable in cover and height over time, but typically with consistently greater cover and height in non-grazed vs. grazed areas over the five years. Forb and grass canopy cover and height either did not significantly differ between grazed and non-grazed areas, or was significantly greater in non-grazed areas than grazed areas. Shrub cover tended to vary little over time, and generally was not significantly different between grazed and non-grazed locations, except for the small, short-lived shrub broom snakeweed that had greater cover in grazed areas following wet periods at the Sevilleta site. The only common exotic weed species, prickly Russian thistle (*Salsola tragus*), was typically more abundant on grazed than non-grazed lands.

Grasshoppers.—A total of 54 grasshopper species were observed across the sites and years; their names, life-form and life-history status are presented in Table 3. The majority of grasshopper species belonged to the family Acrididae (52), along with two species of Romaleidae. The subfamily Gomphocerinae was represented by 21 species, followed by 16 Oedipodinae, 14 Melanoplinae and one Cyrtacanthacridinae. The majority (45) of grasshopper species were late summer season species, 7 species were spring season, and two species had both spring and fall cohorts (Table 3). Summed numbers of individuals of each grasshopper species across all sites, treatments, years and seasons is presented in Suppl. material 3. Observed substrate use by all grasshopper species over all sites, treatments, years and seasons is presented in Suppl. material 4. Those same substrate use values also provide counts of each grasshopper species summed over the five-year study, and were used

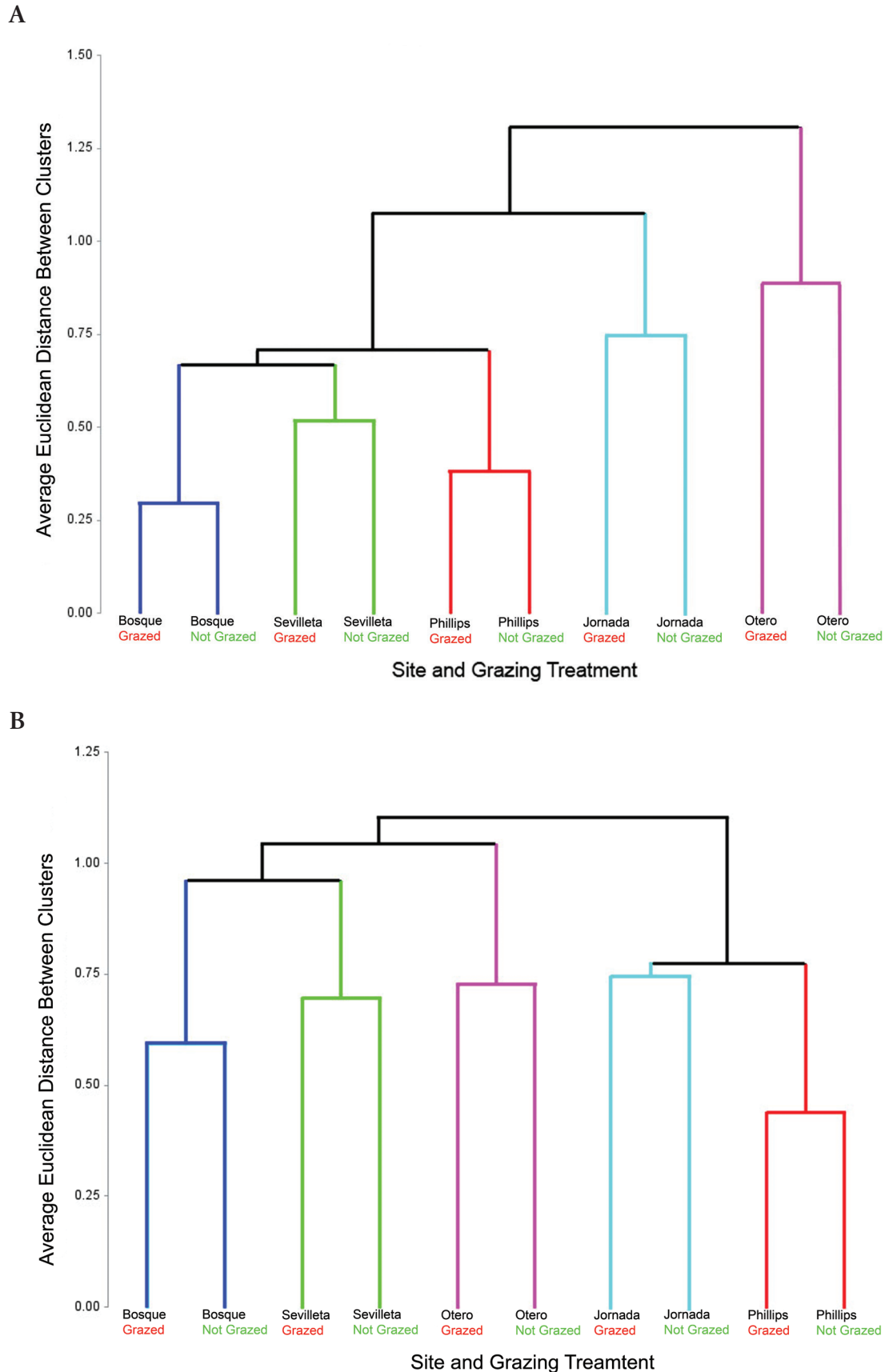


Fig. 3. Cluster analysis dendrogram showing the similarities of plant species compositions at sites and grazed and not grazed transects within sites, from annual canopy cover/m² averaged over all years and seasons; A. Spring; B. Fall.

Table 3. Grasshopper species observed across the 5 study sites. Taxonomic classification and names follow Cigliano et al. (2017). Table is sorted in alphabetical order.

| Species | Family | Subfamily | Code | Life-form | Life history |
|-------------------------------------|------------|---------------------|-------|-----------|--------------|
| <i>Acantherus piperatus</i> | Acrididae | Gomphocerinae | ACPI | G | SU |
| <i>Acrolophitus maculipennis</i> | Acrididae | Gomphocerinae | ACHI | T | SU |
| <i>Ageneotettix deorum</i> | Acrididae | Gomphocerinae | AGDE | TG | SU |
| <i>Amphitornus coloradus</i> | Acrididae | Gomphocerinae | AMCO | G | SU |
| <i>Arphia conspersa</i> | Acrididae | Oedipodinae | ARCO | T | SP |
| <i>Arphia pseudonietana</i> | Acrididae | Oedipodinae | ARPS | T | SU |
| <i>Aulocara ellioti</i> | Acrididae | Gomphocerinae | AUEL | TG | SU |
| <i>Aulocara femoratum</i> | Acrididae | Gomphocerinae | AUFE | TG | SU |
| <i>Boettettix argentatus</i> | Acrididae | Gomphocerinae | BOAR | A | SU |
| <i>Brachystola magna</i> | Romaleidae | Romaleinae | BRMA | H | SU |
| <i>Campylacantha olivacea</i> | Acrididae | Melanoplinae | CAOL | A | SU |
| <i>Cibolacris parviceps</i> | Acrididae | Gomphocerinae | CIPA | T | SP |
| <i>Conozoa texana</i> | Acrididae | Gomphocerinae | COTE | T | SU |
| <i>Cordillacris crenulata</i> | Acrididae | Gomphocerinae | COCR | TG | SU |
| <i>Cordillacris occipitalis</i> | Acrididae | Gomphocerinae | COOC | TG | SU |
| <i>Dactylotum bicolor</i> | Acrididae | Melanoplinae | DABI | H | SU |
| <i>Eritettix simplex</i> | Acrididae | Gomphocerinae | ERSI | G | SU |
| <i>Hadrotettix trifasciatus</i> | Acrididae | Oedipodinae | HATR | T | SU |
| <i>Heliaula rufa</i> | Acrididae | Gomphocerinae | HERU | T | SU |
| <i>Hesperotettix viridis</i> | Acrididae | Melanoplinae | HEVI | A | SU |
| <i>Hippopodon capito</i> | Acrididae | Oedipodinae | HICA | T | SU |
| <i>Hypochlora alba</i> | Acrididae | Melanoplinae | HYAL | A | SU |
| <i>Lactista azteca</i> | Acrididae | Oedipodinae | LAAZ | T | SU |
| <i>Leprus wheeleri</i> | Acrididae | Oedipodinae | LEWH | T | SU |
| <i>Ligurotettix planum</i> | Acrididae | Gomphocerinae | LIPL | A | SU |
| <i>Melanoplus regalis</i> | Acrididae | Melanoplinae | MERE | H | SU |
| <i>Melanoplus aridus</i> | Acrididae | Melanoplinae | MEAR | A | SU |
| <i>Melanoplus arizonae</i> | Acrididae | Melanoplinae | MEAR2 | H | SU |
| <i>Melanoplus bowditchi</i> | Acrididae | Melanoplinae | MEBO | A | SU |
| <i>Melanoplus flavidus</i> | Acrididae | Melanoplinae | MEFL | H | SU |
| <i>Melanoplus gladstoni</i> | Acrididae | Melanoplinae | MEGL | H | SU |
| <i>Melanoplus lakinus</i> | Acrididae | Melanoplinae | MELA | H | SU |
| <i>Melanoplus occidentalis</i> | Acrididae | Melanoplinae | MEOC | H | SU |
| <i>Melanoplus sanguinipes</i> | Acrididae | Melanoplinae | MESA | H | SP, SU |
| <i>Melanoplus thomasi</i> | Acrididae | Melanoplinae | METH | H | SU |
| <i>Mermiria texana</i> | Acrididae | Gomphocerinae | METE | G | SU |
| <i>Mestobregma terricolor</i> | Acrididae | Oedipodinae | METE2 | T | SU |
| <i>Opeia obscura</i> | Acrididae | Gomphocerinae | OPOB | G | SU |
| <i>Paropomala pallida</i> | Acrididae | Gomphocerinae | PAPA | G | SU |
| <i>Phlibostroma quadrimaculatum</i> | Acrididae | Gomphocerinae | PHQU | TG | SU |
| <i>Phrynotettix robustus</i> | Romaleidae | Romaleinae | PHRO | T | SP |
| <i>Psoloessa delicatula</i> | Acrididae | Gomphocerinae | PSDE | TG | SP |
| <i>Psoloessa texana</i> | Acrididae | Gomphocerinae | PSTE | TG | SP |
| <i>Schistocerca nitens</i> | Acrididae | Cyrtacanthacridinae | SCNI | A | SU |
| <i>Syrbula montezuma</i> | Acrididae | Gomphocerinae | SYMO | G | SU |
| <i>Trachyrhachys aspera</i> | Acrididae | Oedipodinae | TRAS | T | SU |
| <i>Trachyrhachys kiowa</i> | Acrididae | Oedipodinae | TRKI | T | SU |
| <i>Trimerotropis californica</i> | Acrididae | Oedipodinae | TRCA | T | SU |
| <i>Trimerotropis pallidipennis</i> | Acrididae | Oedipodinae | TRPA | T | SP, SU |
| <i>Trimerotropis pistrinaria</i> | Acrididae | Oedipodinae | TRPI | T | SU |
| <i>Trimerotropis latifasciata</i> | Acrididae | Oedipodinae | TRLA | T | SU |
| <i>Tropidolophus formosus</i> | Acrididae | Oedipodinae | TRFO | H | SU |
| <i>Xanthippus corallipes</i> | Acrididae | Oedipodinae | XACO | T | SP |
| <i>Xanthippus montanus</i> | Acrididae | Oedipodinae | XAMO | T | SP |

* Life-form codes: A=arbusticole, G=graminicole, TG=terri-graminicole, H=herbicole, T=terricole.

** Life history codes: SP=spring/early summer, SU=late summer/fall.



Fig. 4. Examples of each grasshopper life-form type; A. Arbusticole; *Boottettix argentatus* on *Larrea tridentata*; B. Graminicole; *Paropomala pallida* on *Bouteloua eriopoda*; C. Terri-graminicole; *Phlibostroma quadrimaculatum*; D. Herbicole; *Tropidolophus formosus* on *Spharalcea hastulata*; E. Terricole; *Trimerotropis pallidipennis*.

for cluster analysis to evaluate similarities of substrate use across all grasshopper species. Based on morphology and substrate use, the resulting life-form guild terricoles, were the largest life-form group with 20 species, followed by 11 herbicoles, 8 arbusticoles, and 7 graminicoles (Table 3). Additionally, a group of species (*Ageneotettix deorum*, *Aulocara* spp., *Cordillacris* spp., *Phlibostroma quadrimaculatum*, *Psoloessa* spp.) used bare soil and low-growing grasses as their substrates, and had morphologies intermediate between graminicoles and terricoles. Uvarov (1977) called such intermediate life-forms terri-graminicoles, and I categorized those 8 species as terri-graminicoles: species that use both bare soil and low stature grasses as microhabitat substrates, and are known to

feed largely on grasses. Examples of grasshopper life-forms represented by species observed in this study are presented in Fig. 4. Note that the determination of a species' substrate use in this study is relative to the number of observations made for each species; determinations for species with many observations are more likely to reflect the species actual substrate uses more accurately than for species with few observations (see Suppl. material 3 and Suppl. material 4).

Examination of the morphology of each species relative to Uvarov's (1977) life-form descriptions revealed high correspondence between substrate use groupings and life-form morphologies, except for some grasshopper species in the subfamily Melanopli-

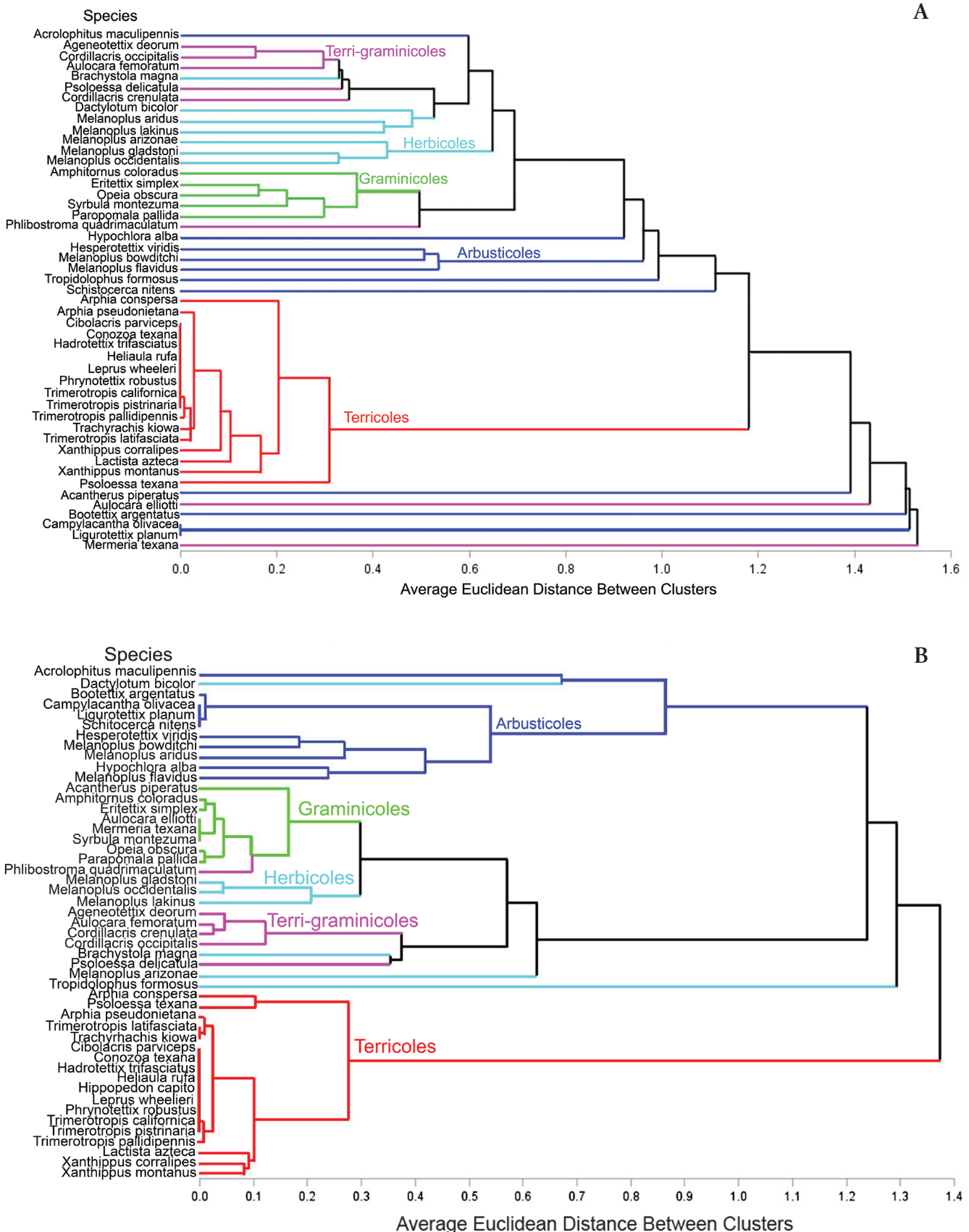


Fig. 5. Cluster analysis dendrograms of grasshopper species similarities based on substrate use among all grasshopper species over all sites, years and seasons; **A**. Based on specific substrate use to the plant species level and bare soil; **B**. Based on substrates categorized to forbs, grasses, shrubs and bare soil.

nae, which separated into both herbicoles and arbusticoles based on substrate use, while sharing similar ecomorphologies (Suppl. material 4). Some species that had herbicole life-form morphologies used shrubs (e.g. *Campylacantha olivacea*, *Hypochlora alba*, *Melanoplus aridus*, *M. bowditchi*, and *M. flavidus*), while others such as *Brachystola magna* and *M. arizonae* used forb, grass, and soil substrates. *Tropidolophus formosus* had the morphology of a herbicole but was distinct from other herbicoles based on primary substrate use of *Spharalcea* species forbs. *Acantherus piperatus* had the morphology of a graminicole, and occurred primarily on bush muhly grass, which grew inside of shrub canopies, and individuals often rested on shrub branches mixed with bush muhly. *Acrolophus maculipennis* (Gomphocerinae) was associated primarily with the small shrub, hairy crinkle mat (*Tiquilia hispidissima*), and individuals were usually on their host plants, but also often on bare rocky gypsum soil in association with hairy crinkle mat plants. Overall substrate use did correspond well with grasshopper species life-form guild morphologies for most grasshopper species.

Cluster analysis of each grasshopper species based on observed specific substrate use by all individuals of each grasshopper species, over all five sites and all five years, revealed distinct groupings of species based on specific observed substrate use (Fig. 5A). Arbusticoles that were host plant specific, such as *Boottettix argentinatus*, *Campylacantha olivacea*, *Ligurotettix planum*, *Hypochlora alba*, *Melanoplus bowditchi*, *Melanoplus flavidus*, *Schistocerca nitens* and *Hesperotettix viridis* were distinct from all other species. Terricoles such as *Arphia* spp., *Cibolacris parviceps*, *Conozoa texana*, *Hadrotettix trifasciatus*, *Heliaula rufa*, *Hippopedon capito*, *Leprus wheelerii*, *Phrynotettix robustus*, *Lactista azteca*, *Psoloessa texana*, *Trimerotropis* spp., *Trachyrhachys kiowa*, and *Xanthippus* spp., formed a large distinct group. Graminicoles such as *Amphitornus coloradus*, *Eritettix simplex*, *Syrbula montezuma*, *Opeia obscura* and *Paropomala pallida* grouped together. Terri-graminicoles such as *Ageneotettix deorum*, *Cordillacris* spp., *Aulocara femoratum*, and *Psoloessa delicatula*, grouped together, and all had mandible morphologies of grass-feeders. Herbicoles such as *Dactylotum bicolor* and all *Melanoplus* spp., except *M. bowditchi* and *M. flavidus*, grouped together.

I further examined the relationships between grasshopper life-forms, plant-life forms, and bare soil, by performing a second cluster analysis of observed grasshopper species substrate use, with plant species specific substrates pooled into the plant life-form categories instead of plant species; forbs, grasses or shrubs, along with bare soil. The resulting dendrogram (Fig. 5B) revealed similar but more pronounced substrate category use groupings to Fig. 5A. Arbusticole and herbicole grasshoppers formed more pronounced groups rather than separating as disparate species in Fig. 5A. All arbusticoles grouped together with the herbicole *Dactylotum bicolor*, which was observed on forbs, soil and shrubs. All graminicoles grouped together along with the terri-graminicole *Phlibostroma quadrimaculatum* and the herbicoles *Melanoplus gladstoni*, *M. occidentalis*, and *M. lakinus*, all of which were usually on forbs but also on grasses. The terri-graminicoles grouped together with the herbicole *Brachystola magna* which occurred on forbs, grasses and bare soil. Terricoles grouped together in a distinct cluster from all other clusters. One herbicole species, *Tropidolophus formosus*, did not group with any other herbicoles due to its primary association with forbs in the genus *Spharalcea*.

Spearman rank correlation analysis compared the total numbers of individual grasshoppers observed across all species, and assigned to grasshopper life-forms, with available plant life-form and bare soil cover measured from 1 m² quadrats and averaged over all sites, transects, years and seasons. Correlation analysis

Table 4. Spearman-rank correlation coefficients (r_s) and significance values (P) from testing relationships between grasshopper life-forms and the available cover of substrate categories measured on the grasshopper and vegetation transects at each study site, over all years and seasons. Correlation coefficients are listed first, above significance values within each life-form by substrate set of cells. Significant ($P < 0.05$) correlations are in bold text, positive correlations are in regular font and negative correlations are in italic font. Sample size for all tests was 96.

| Grasshopper life-forms | Substrate Categories | | | |
|------------------------|----------------------|----------|---------|----------|
| | Bare Soil | Grasses | Forbs | Shrubs |
| Arbusticoles | -0.24058 | -0.24703 | 0.14819 | 0.61254 |
| | 0.0182 | 0.0153 | 0.1496 | <.0001 |
| Graminicoles | -0.31407 | 0.57682 | 0.12125 | -0.26054 |
| | 0.0018 | <.0001 | 0.2393 | 0.0104 |
| Terri-graminicoles | 0.13191 | 0.47328 | -0.1248 | -0.57136 |
| | 0.2002 | <.0001 | 0.2257 | <.0001 |
| Herbicoles | -0.13658 | 0.23129 | 0.38279 | -0.26019 |
| | 0.1845 | 0.0234 | 0.0001 | 0.0105 |
| Terricoles | -0.28696 | 0.44601 | 0.17449 | -0.18596 |
| | 0.0046 | <.0001 | 0.0891 | 0.0697 |

revealed significant relationships between grasshopper life-forms and substrate availability (Table 4). Arbusticoles were positively correlated with shrub canopy cover, while they were negatively correlated with bare soil and grass cover. Graminicoles were positively correlated with grass cover, and negatively correlated with bare soil and shrub cover. Terri-graminicoles were positively correlated with grass cover, and negatively correlated with shrub cover. Herbicoles were positively correlated with both forb and grass cover, and negatively correlated with shrub cover. However, terricoles were positively correlated with available grass cover, and negatively correlated with available bare soil.

Cluster analysis of grazed vs. non-grazed sites in the spring and in the fall over all years revealed that, like vegetation, grasshopper species assemblages were unique to each site. Branch lengths in the dendrograms were not as long as for plant assemblages, demonstrating the site to site variation and differences in grazed vs. non-grazed in grasshopper assemblages was less than it was for plant assemblages (Fig. 3 vs. Fig. 6). Grasshopper species assemblages at the Bosque, Jornada and Phillips sites were more similar to each other than species assemblages at the Otero and Sevilleta sites (Fig. 6). The Otero site grazed area was unique from all other sites/treatments, in both spring and fall seasons. Grasshopper species richness ranged from about five species to about 20 species across the study sites, years and seasons. Overall grasshopper species richness generally ranged from five to 15 species at each site over the five-year period, averaging around 10 species at any given time, and more grasshopper species were typically present in the fall than in the spring of each year (Suppl. material 1: Fig. S3). The Jornada and Otero sites generally had the most grasshopper species, followed by the Bosque and Phillips sites. The grazed areas tended to support less grasshopper species than the non-grazed areas at all five sites over the five-year period, but that pattern was inconsistent (Suppl. material 1: Fig. S3). Overall, the non-grazed sides of the fences across all sites, years and seasons tended to support the highest grasshopper species richness.

Analysis of the grasshopper life-form guilds revealed that livestock grazing primarily affected graminicoles and terri-graminicoles.

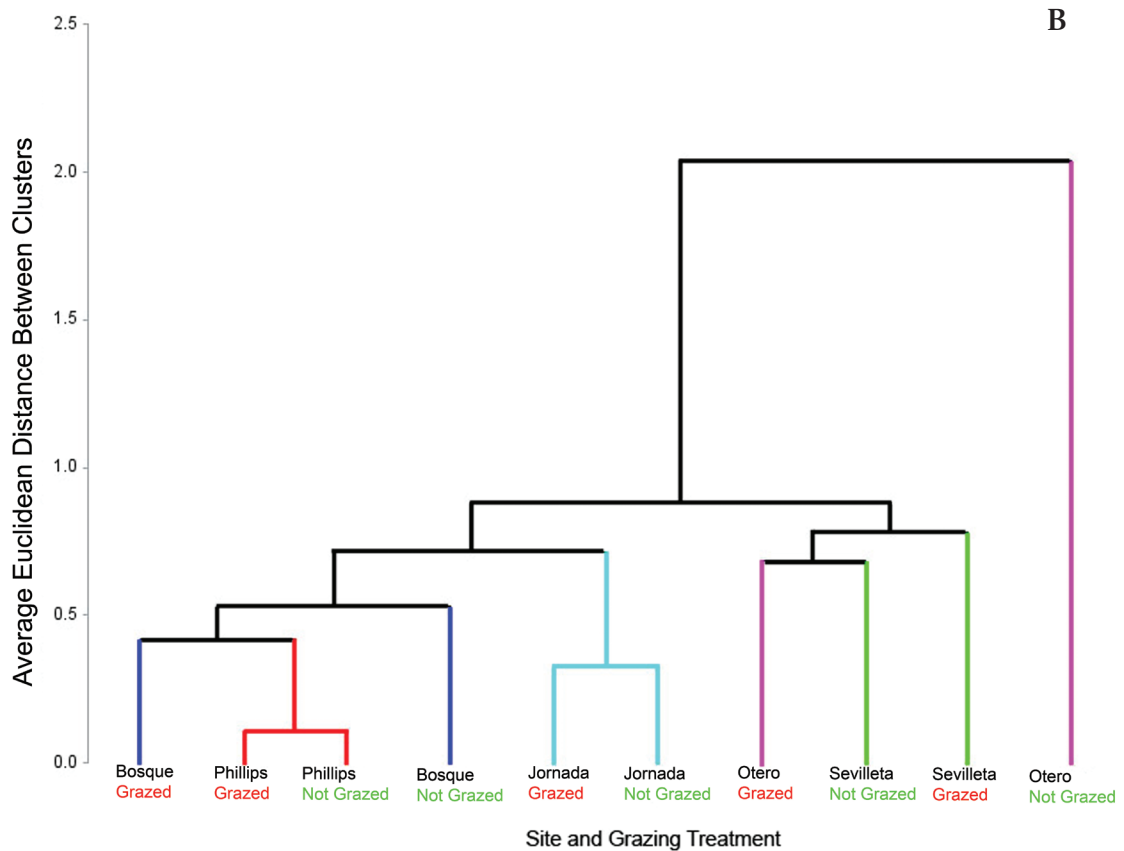
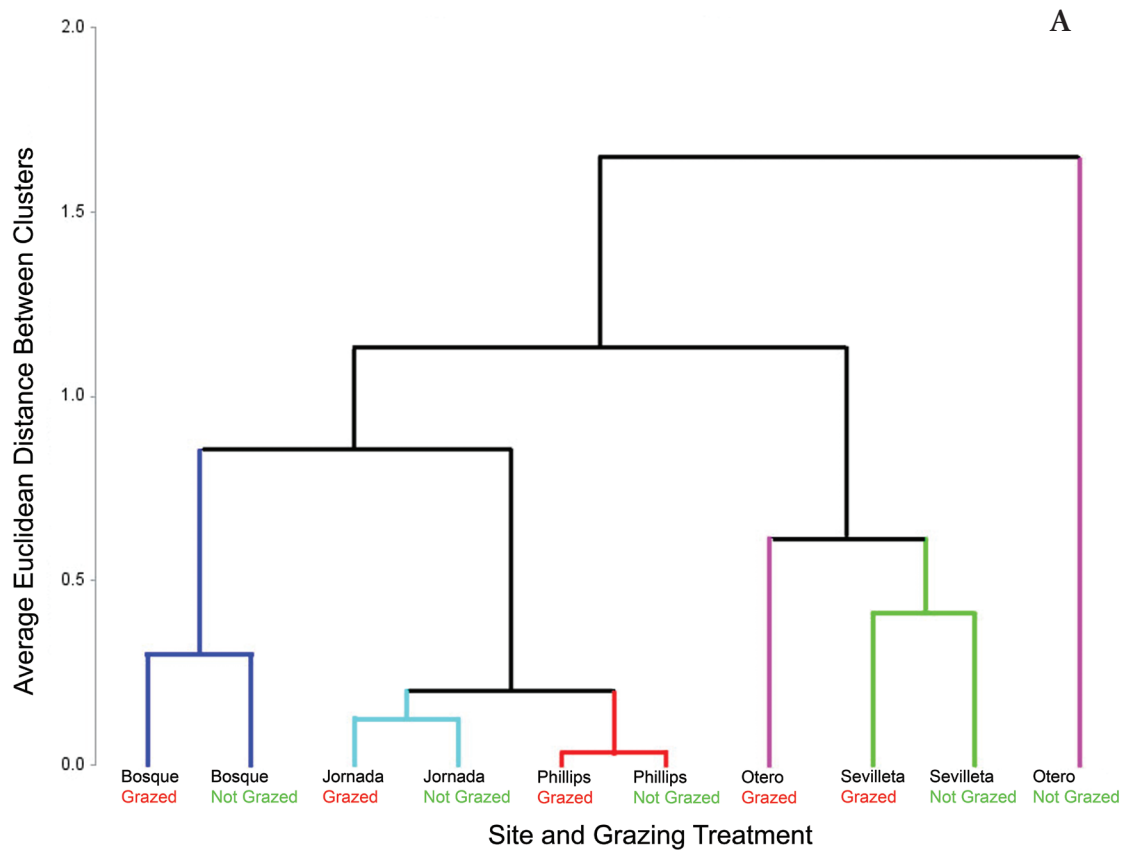


Fig. 6. Cluster analysis dendrograms showing site and grazing treatment similarities of grasshopper species compositions; A. Spring; B. Fall.

coles, which tended to be significantly more abundant on non-grazed than grazed areas, and especially at the Bosque, Otero, and Sevilleta sites, both in the spring and in the fall seasons (Suppl. material 1: Fig. S4, Suppl. material 2: Table S5). That pattern was especially pronounced in high precipitation years with high grasshopper abundance. Herbicoles followed a similar but less pronounced pattern of greater abundance on non-grazed sides of the fences across the same sites, especially in wet years. In contrast, terricoles tended to be significantly more abundant on grazed areas than non-grazed areas at the same sites and years as graminicoles and terri-graminicoles were more abundant on the non-grazed sides of the fences (Suppl. material 1: Fig. S4, Suppl. material 2: Table S5). Arbusticoles were generally less abundant than other grasshopper guilds, and were significantly more abundant on the non-grazed area at the Bosque site in fall 1993, but significantly more abundant on the grazed area at the Jornada site in fall of 1992 and 1993 (Suppl. material 2: Table S5, Suppl. material 1: Fig. S4).

Arbusticoles were mostly associated with one or a few species of perennial woody shrubs. *Boottettix argentatus* (Gomphocerinae) was associated only with creosote bush at the Jornada, Otero, and rarely at the Phillips sites. *Campylacantha olivacea* (Melanoplinae) and *Ligurotettix planum* (Gomphocerinae) were found only on tarbush (*Flourensia cernua*) at the Jornada and the Phillips sites, and *Hesperotettix viridis* (Melanoplinae) was only associated with broom snakeweed across the sites. *Hypochlora alba* (Melanoplinae) was associated primarily with sand sage (*Artemisia filifolia*), but also some forbs at the Bosque site (Suppl. material 3, Suppl. material 4). *Melanoplus aridus* and *M. bowditchi* (Melanoplinae) were associated primarily with shrubs in the family Asteraceae at the Jornada and Phillips sites, and *Schistocerca nitens* (Cyrtacanthacridinae) was associated with honey mesquite and tarbush shrubs at the Jornada site. Arbusticoles were consistently associated with woody shrubs, usually one or a few species of shrubs, but the grasshopper species belonged to different subfamilies.

The most abundant graminicoles were species in the subfamily Gomphocerinae; *Paropomala pallida* which was highly associated with black grama grass on the non-grazed side of the fences at the Bosque, Otero and Sevilleta sites, and less associated with bush muhly grass along with *Acantherus piperatus*, at the Jornada and Phillips sites, and *Eritettix simplex* and *Opeia obscura* that tended to be associated with galleta and tabosa grasses (*Pleuraphis* spp.) and burro grass (*Scelopogon brevifolius*) across all of the sites (Suppl. material 3, Suppl. material 4). Graminicoles all belonged to the same subfamily, and all were associated with grasses, but different species were associated with different grass species, and most species were most abundant on the non-grazed areas at the Bosque, Otero, and Sevilleta sites.

Abundant terri-graminicoles also were mostly in the subfamily Gomphocerinae; including *Aulocara femoratum*, *Cordillacris occipitalis*, *Ageneotettix deorum*, and *Phlibostroma quadrimaculatum* that were associated with blue grama and burrow grasses at the Otero and Sevilleta sites in the fall. *Psoloessa delicatula* was a terri-graminicole associated with fine soils and grasses at the Sevilleta, Bosque and Otero sites, while *P. texana* was a terricole associated with coarse gravelly soils at the Jornada and Phillips sites (Suppl. material 3, Suppl. material 4). Like graminicoles, terri-graminicoles were associated with grasses, but all were most associated with low-profile perennial grasses such as blue grama and burro grass.

The most abundant herbicoles were species in the family Melanoplinae; the fall species *Melanoplus arizonae*, *M. lakinus*, and *M.*

gladstoni at the Otero and Sevilleta sites, *M. flavidus* at the Bosque site, and *M. aridus* at the Jornada and Phillips sites (Table S3, Table S4). Most herbicoles were melanoplines associated with a variety of plant species, but included *Brachystola magna* (Romaleidae) a generalist, and *Tropidolophus formosus* (Oedipodinae) a plant specialist which was associated with mallows (*Spharalcea* spp.: Malvaceae). As stated above, Melanoplinae had the ecomorphologies of herbicoles, but also were common on grasses, bare soils, and some on shrubs.

Terricoles were mostly in the subfamily Oedipodinae; the most abundant terricole was *Trimerotropis pallidipennis* across all sites and years, especially in the fall of 1995 and 1996 at the Sevilleta site, and *T. pallidipennis* was represented by two cohorts each year, one in the spring, and another in the fall; the spring cohort was affected positively by the El Niño event in 1992 and the fall cohort by the La Niña event in 1996 (Table S3). Other abundant terricoles included *Trachyrhachys kiowa*, *Trimerotropis californica*, and *Arphia pseudonietana* in the fall, and *Psoloessa texana*, *Xanthippus corallipes* and *Arphia conspersa* in the spring. The common terricole *Cibolacris parviceps* belonged to the subfamily Gomphocerinae, and the rare terricole *Phrynotettix robustus* to the family Romaleidae: Romaleinae. Most terricole species appeared to be more closely associated with specific soil surface types – clay, silt, sand, gravel – than to any particular plant species.

Discussion

The findings from this study demonstrate that short-term domestic cattle grazing and short-term climate variation did affect the species and life-form compositions and foliage canopy cover and height of vegetation, and the species and life-form guild compositions and abundances of grasshopper communities across a series of five study sites over five years. Grazing effects on vegetation and grasshoppers were significant during years with high rainfall, plant production and grasshopper abundance, but not years when rainfall, plant production and grasshopper abundance were all low. These results were similar to the findings of other research in North America (Jepsen-Innes and Bock 1989, Quinn and Walgenbach 1990, Fielding and Brusven 1993, 1995, Jones 2006), in Africa (Prendini et al. 1996, Gebeyehu and Samways 2003) and in China (Kang and Chen 2008). Grasshoppers in this study responded to grazing much as Fielding and Brusven (1996) reported for grasshopper communities from similar semi-arid desert grasslands and shrublands elsewhere in North America. Short-term livestock grazing reduced perennial grass cover and heights, increased annual grasses following periods of increased rainfall, and enhanced populations of terricole grasshopper species (reported as Oedipodinae by Fielding and Brusven 1996). This study demonstrates that short-term livestock grazing did alter the vegetation and grasshopper species and life-form compositions, annual variation in precipitation did interact with grazing to affect both plant and grasshopper species assemblages and grasshopper guild structure, and terricole, terri-graminicole, graminicole and herbicole grasshopper life-form guilds and their most abundant component species were most sensitive to livestock grazing and climate variation, while arbusticoles were not. The effects of livestock grazing on vegetation and grasshoppers were significant during an El Niño event in 1992 that produced high winter and spring rainfall, and during a La Niña event in 1996 that produced high summer rainfall, each affecting vegetation and grasshoppers differently during those different seasons.

The effects of livestock grazing on grasshoppers in this study were more pronounced in desert grassland environments than in

desert shrubland environments. The Bosque, Otero and Sevilleta sites were desert grassland or shrub steppe and supported relatively high perennial grass cover on the non-grazed sides of the fences. The Jornada and Phillips sites were creosote bush shrublands, and most of the perennial grass at those sites was bush muhly which grew within the shrub canopies, while the soil surfaces between shrubs were primarily bare and gravelly. Livestock grazing at the desert grassland sites reduced the canopy cover and heights of perennial grasses on the grazed sides of the fences, while relatively higher perennial grass cover and canopy heights were present on the non-grazed sides of the fences. In spring 1992 and in fall 1996 grasshopper densities were high, and terricoles and terri-graminicoles were abundant along with annual grasses and forbs on the more open bare grazed fence sides, while graminicoles were more abundant on the denser perennial grasses on the non-grazed sides of the fences. Arbusticoles showed relatively little response to livestock grazing, because the perennial shrubs that they lived and fed on also did not change much over the five-year period.

Climate variation resulting primarily from opposing ENSO events over a five-year period further interacted with livestock grazing to amplify or reduce the effects of livestock grazing on vegetation and grasshoppers. Increased winter and spring precipitation from an El Niño event in 1992 positively affected both annual herbaceous vegetation and grasshoppers in the spring of 1992 and 1993, more so on grazed areas than non-grazed areas. The La Niña event of 1996 positively affected annual herbaceous vegetation and grasshoppers in the late summer of 1996, but not in the spring of that year, and that effect was more pronounced on grazed lands than non-grazed lands. Grasshopper responses to annual and season variation in precipitation were similar to the findings of Edwards (1960), Gage and Mukerji (1977), Begon (1983), Capinera and Horton (1989) and Fielding and Brusven (1990). While Jonas and Joern (2007) emphasized the importance of both the previous year's grasshopper population densities and winter precipitation on subsequent populations, the five-year temporal data from this study were not extensive enough nor partitioned into small enough periods to determine if time-lag effects were present, or how such lag effects may have resulted from previous grasshopper density and environmental conditions. Fielding and Brusven (1996) found that over a 27 year period, the previous November precipitation and mean April temperatures were the best predictors of variation in annual grasshopper densities, while cold winter temperatures reduced grasshopper densities. These findings all indicate that ongoing climate change will likely influence the interactive dynamics of grasshoppers, vegetation, livestock grazing and weather.

Grasshopper species and life-form guilds that were affected positively by livestock grazing and climate variation were those that preferred bare soil microhabitats, and also responded to increases in rainfall and annual forb and grass production on bare soils disturbed by livestock. Oedipodinae and Gomphocerinae species that tend to be terricole or terri-graminicole species also tend to be mixed grass and forb feeders with relatively broad diets (Mulkern 1967, Uvarov 1977, Joern 1985, Chapman 1990). Fielding and Brusven (1996) discussed how substrate matching camouflage is important for many grasshopper species, especially Oedipodinae that live on bare soils (i.e. terricoles), and that reduced vegetation cover from grazing favors such ground-dwelling terricole grasshopper species. Capinera and Sechrist (1982) also found that Oedipodinae (i.e. terricoles), were most abundant in heavily grazed areas compared to lightly grazed areas in short-grass prairie.

In this study, terricoles that preferred bare soil tended to show the greatest responses to increased production of annual herba-

ceous vegetation in disturbed grazed areas that also had bare soil substrates, especially *Trimerotropis pallidipennis*, *Trimerotropis californica*, and *Trachyrachis kiowa*. Although terricoles used bare soil surfaces almost exclusively as substrates, and are known to utilize bare ground as a microhabitat, correlation analysis revealed that they were negatively associated with available bare ground across locations, years and seasons, but were positively correlated with spatially and temporally variable annual grass cover. These results indicate that while terricoles require long-term availability of bare soil for a microhabitat substrate, over time and space, their densities vary positively over the short-term with the availability of annual grass and forb canopy cover as a food resource.

Terri-graminicoles also preferred microhabitats with sparse, low-growing grasses such as blue grama and burro grass, and spent much of their time on bare ground substrates (bare soil), and responded to increases in grasses as correlation analysis revealed. Those terri-graminicoles included the Gomphocerinae species *Aulocara femoratum*, *Ageneotettix deorum*, *Psoloessa delicatula*, *Psoloessa texana*, *Cordillacris occipitalis* and *Phlibostroma quadrimaculatum*, most of which were more abundant on the grazed sides of fencelines, but primarily at the Otero and Sevilleta sites that had short and patchy perennial grasses like blue grama and burrow grass. Quinn and Walgenbach (1990) also found that some of the same Gomphocerinae grasshopper species were more abundant in grazed areas with more bare soil and short sparse grasses, where those species were better camouflaged from predators. Also similar to these findings, Prendini et al. (1996) found grasshopper species in savanna environments that preferred sparse and low-profile vegetation were more abundant in heavily grazed areas, while those species that preferred tall and dense grass more abundant in non-grazed and lightly grazed areas.

Graminicoles were affected negatively by livestock grazing, apparently due to the reduced cover and heights of the perennial grasses that they lived and fed on, which were often significantly taller and had greater canopy cover on the non-grazed sides of fencelines at the grasslands Sevilleta and Otero sites. Graminicoles increased with increased rainfall and perennial grass production which occurred mostly in non-grazed areas where perennial grass cover was higher and not affected by current livestock grazing. Graminicoles primarily used grass plants as substrates, and were positively correlated only to available grass canopy cover over space and time. Common graminicoles such as *Paropomala pallida* and *Acantherus piperatus* were highly associated with black grama and bush muhly grasses respectively, which experienced reduced canopy cover when grazed, and increased canopy cover and height under high precipitation conditions. Other graminicoles appeared to be less associated with particular grass species, but *Eritettix simplex*, *Amphitornus coloradus*, *Syrbula montezuma* and *Opeia obscura* were associated with dense, tall perennial grasses that provided adequate structural microhabitats in ungrazed areas, compared to structurally less robust annual grasses (e.g. sixweeks threeawn) that dominated grazed areas. Unlike terri-graminicoles that also feed on and are associated with grasses, but are adapted to live on bare soil, graminicoles have morphological adaptations (elongate bodies and antennae and short legs with grasping tarsi and arolia and camouflage patterns and colors) for living on the stems and leaves of tall dense grasses as resting and feeding substrates (Uvarov 1977, Lightfoot 1985).

Herbicoles were composed largely of Melanoplineae, including several species of *Melanoplus*, and most appeared to be host-plant generalists except for the oedipodine *Tropidolophus formosus* that specialized on *Spharalcea* plants. Many of the common *Melanoplus*

such as *M. arizonae*, *M. lakinus* and *M. sanguinipes* are known to have broad diets and have not evolved to specialize on any particular plants. Such generalization on leafy forbs may be attributed to low plant apparency in space and time, and the diversity of acutely toxic plant secondary chemical defenses such as flavonoids and glycosides that limit herbivores from specializing on those plants as food resources (Otte 1976, Otte and Joern 1977, Chapman 1990). Other research also has shown that melanoplines tend to have broad diets and are ecological generalists, especially agricultural pest species such as *M. sanguinipes*. Such generalist species also tend to have dynamic populations that vary considerably with weather and plant production (Fielding and Brusven 1990, Jonas and Joern 2007). In this study herbivores did increase with increased rainfall and plant production, however the increases occurred both under grazed and non-grazed areas, apparently overriding grazing effects alone.

The arbusticoles also were strongly associated with plants, not soil; all were host-shrub specific species except for the shrub generalist *Schistocerca nitens*. Each arbusticole species was strictly associated with its host shrub species, and unlike the other grasshopper guilds that shared grasshopper species across sites, arbusticoles tended to be site-specific based on shrub species distributions. *Boottettix argentatus* only occurred at the Jornada, Otero and Phillips sites where creosote bush was present, and was not affected by grazing. *Campylacantha olivacea* and *Liguotettix planum* were restricted to tarbush, which only occurred at those same three sites, while *Hypochlora alba* was restricted to sand sage at the Bosque site, the only site where sand sage occurred, along with the more generalist *Melanoplus flavidus*. Broom snakeweed occurred at all sites, and supported not only *Hesperotettix viridis* which is monophagous on broom snakeweed, but also *Melanoplus bowditchi* and *M. aridus* which occurred on a variety of shrubs in the plant family Asteraceae. While terricoles, terri-graminicoles and graminicoles were more closely associated with the microhabitat structure than particular plant species, arbusticoles also were associated with particular plant microhabitats, but those present on particular shrub species with particular morphologies and chemistries. For example *Boottettix argentatus* is a leaf and small stem mimic of creosote bush foliage, and *Liguotettix planum* is a stem mimic on tarbush. Each shrub species also has unique foliage chemistry, apparently driving the evolution of monophagy in arbusticoles as the result of plant apparency and the evolution of specialization on highly apparent host plants with different secondary plant chemistries and different substrates for camouflage from predators (Otte 1976, Otte and Joern 1977, Chapman 1990).

The application of life-form guilds as grasshopper indicators to environmental change has world-wide utility and allows for global comparisons of grasshopper life-form guild structure across continents in relation to landscape features and ecological patterns and processes. As with any attempt by humans to classify species into ecological categories, not all species fit well into grasshopper life-form guilds such as some mentioned above. However, most grasshopper species addressed in this study did correspond to particular life-form guilds, or some combination of more than one guild (e.g. terri-graminicoles). Based on these findings, the grasshopper life-form guild concept does have merit for understanding resource use and structure of semi-arid and arid environment grasshopper communities.

Livestock grazing is prevalent and often ecologically unsustainable across semi-arid regions around the world, as is desertification, the long-term result of unsustainable livestock grazing (Dregne 1986, Nelson 1988). Based on the findings of this study, one may assume that the desertified semi-arid landscapes of the

world, and those studied here, now have different grasshopper community compositions than they did prior to desertification. Desertified landscapes that were formerly dominated by relatively stable desert grasslands, and likely corresponding graminicoles and terri-graminicoles, are likely now dominated by shrublands, and/or bare soil, and annual grasses and forbs that fluctuate with rainfall. Such desertified landscapes also are likely now dominated by terricoles, arbusticoles and herbicoles as in this study. As landscape vegetation changes, so too should the grasshopper species and life-form guild compositions and associated diets and resource uses. Shifts in grasshopper community life-form guild compositions also should have cascading effects on ecosystem processes such as energy flow and nutrient cycling. If desert grasslands shift from a dominance of perennial grass and grass-feeding graminicoles, to a dominance of annual grasses and forbs, woody shrubs, and mixed-diet terricoles, herbicoles and plant specific arbusticoles, the consumer roles of grasshoppers feeding on those different types of plants should also shift. Additionally, a number of independent research studies have demonstrated that soil and vegetation disturbance caused by heavy livestock grazing in semi-arid regions of North America leads to ecological instability and outbreaks of ecological generalist agricultural pest grasshopper species such as *Melanoplus sanguinipes* (Padft 1982, Quinn and Walgenbach 1990, Fielding and Brusven 1995b, 1996, Rambo and Faeth 1999, and Debano 2006). This same pattern may occur globally in other systems with other grasshopper pest species.

Given the global extent of semi-arid landscapes that have been and continue to be negatively impacted by livestock grazing (see Introduction), understanding the effects of grazing on vegetation and grasshoppers is key to understanding how to manage natural resources of such lands (Laycock 1994). Such knowledge of changes to grasshopper community composition and structure will contribute to guiding better management of the natural resources on desertified landscapes (e.g. Peters et al. 2015). Anthropogenic climate change is a serious environmental issue globally, and increasing global temperatures and increasing variation and reductions in precipitation across semi-arid regions is intensifying the negative effects of livestock grazing on soils, native plants and native animals. More research like this study is needed on a global-scale to better understand how livestock grazing and climate change are interacting in different world regions with different environments, plant and grasshopper species, human cultures and associated natural resource uses.

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Supplementary material 1

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The response of Orthoptera to grazing on flood defense embankments in Europe

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Abstract

European flood defense embankments form an excellent habitat for Orthoptera. To be effective against storms, these vegetated earth embankments have to be managed by grazing or mowing. However, grazing can impact invertebrates such as grasshoppers and crickets (Orthoptera). This management can lead to dispersal toward undisturbed grassland and reductions in the quality of habitat, food resources and oviposition sites. In most cases, orthopteran insects require heterogeneous vegetation patches with swards of varying height. The impact of grazing depends on the type of livestock; it is very important to choose appropriate animals, timing and intensity. Sheep grazing in late summer (September–October) at a moderate intensity seems to be favorable for Orthoptera. If grazing is carefully monitored, it can promote Orthoptera conservation while maintaining flood defense integrity.

Key words

biodiversity, bush-cricket, coast, conservation, dike, engineering, fluvial, grasshopper, sea wall

Introduction

In Europe, coastlands are protected from tidal flooding by vegetated earth embankments known as ‘dikes’ or ‘dykes’ (Verheij et al. 1997, Sprangers 1999). In the UK, they are referred to as ‘sea walls’ (Gardiner et al. 2015). There are 259 km of dikes on the Dutch coast (van Loon-Steensma 2015), 970 km in Germany (Rohde 1988), and 900 km in Denmark (Danish Coastal Authority 2015). In the UK, there are approximately 2100 km of sea wall (450 km in the county of Essex alone; Gardiner et al. 2015), which matches the total of the aforementioned three countries combined. A fluvial flood defense can also be required in flood-prone areas; alongside Hungarian rivers for example. In Hungary, 4000 km of dikes protect land from fluvial flooding (IUCN 1995). In England and Wales, there are 35000 km of tidal and fluvial embankments (Dyer 2004).

Significant changes have occurred in the way many vegetated sea walls around the coasts and estuaries of England are managed, not least through increasing efforts to meet common standards

with respect to flood prevention (Environment Agency 2012). The main changes relate to increased removal of woody vegetation, changes in the frequency of mowing, and a reduction in grazing of sea walls. The growth of woody vegetation can undermine the structural integrity of sea walls and promote the activity of burrowing mammals such as badgers *Meles meles* L., 1758 (Carnivora: Mustelidae; Gardiner 2014). Woody vegetation and tall, unmown grassland make it difficult for engineers to inspect the condition of sea walls as a defense against tidal flooding, which is their main function (Environment Agency 2012). In the event of overtopping, water pouring over the crest and down the landward face could rip grass tussocks and trees out of the earth, leaving holes in the surface and damaging the sea wall (Gardiner et al. 2015).

A sea wall, or dike, is typically composed of several distinct habitats (Fig. 1). Sea walls have a complex mosaic of microhabitats which Orthoptera utilize (Gardiner et al. 2015) along with adjacent grazing marshes (Gardiner et al. 2017). When combined, these habitats represent a corridor for the dispersal of orthopteroid insects such as bush-crickets (Tettigoniidae), crickets (Gryllidae) and grasshoppers (Acrididae). Orthoptera are key species in many trophic levels but can be influenced by environmental stresses such as grazing (Gardiner et al. 2015). To be fully effective, embankments need to be managed; grazing by livestock is one of the solutions to maintain a healthy ecosystem and flood defense (Davis et al. 2014). Grazing can also occur naturally, for example where rabbits *Oryctolagus cuniculus* L., 1758 (Lagomorpha: Leporidae) and hares *Lepus europaeus* Pallas, 1778 (Lagomorpha: Leporidae) occur (Gardiner et al. 2015). According to Gardiner (2018), ‘grazing prevents succession of open grasslands to scrub and forest, creates heterogeneity in sward height, and provides patches of bare earth through the action of livestock hooves breaking the vegetative cover.’

In European semi-natural grasslands, livestock grazing is a common practice which maintains a high floristic species richness (van Klink et al. 2016). However, grazing can alter habitat quality and negatively affect invertebrates (Ma et al. 2017) by reducing food abundance and influencing microclimate and oviposition sites (O’Neill et al. 2003). Development of vegetation in grassland varies in response to habitat factors and management (Sprangers 1999). It is therefore very important to choose the appropriate



Fig. 1. The typical composition of a sea wall (Brightlingsea, Essex); credit K. Fargeaud.

kind of livestock for grazing dikes and sea walls (Gardiner et al. 2015). In this paper, we investigate how flood defense management (dikes and sea walls) and Orthoptera conservation can be balanced in Europe by collating the available literature and assessing its implications.

Orthoptera on flood defense embankments

The English coastline can be rich in grasshoppers, bush-crickets and groundhoppers (Gardiner et al. 2015). In the county of Essex, as in the Wadden Sea (Netherlands and Germany) and Tisza Basin (Hungary), flood defense embankments provide an important habitat for a range of common and scarce Orthoptera (Table 1). The species richness of the tidal Essex ($n = 13$) and Wadden Sea ($n = 12$) flood defense embankments was low in comparison to the fluvial walls of the Tisza Basin ($n = 31$). The species assemblages of the embankments were markedly different, with only four species common to all three areas: lesser marsh grasshopper *Chorthippus albomarginatus* De Geer, 1773 (Orthoptera: Acrididae), field grasshopper *Chorthippus brunneus* Thunberg, 1815 (Orthoptera: Acrididae), short-winged conehead *Conocephalus dorsalis* Latreille, 1804 (Orthoptera: Tettigoniidae) and *Tetrix subulata* L., 1761 (Orthoptera: Tettigoniidae). For the Essex sea walls, two species were locally scarce: grey bush-cricket *Platycleis albopunctata* Goeze, 1778 (Orthoptera: Tettigoniidae) and great green bush-cricket *Tettigonia viridissima* L. 1758 (Orthoptera: Tettigoniidae), compared to four scarce species on the Tisza Basin embankment: crested grasshopper *Acrida ungarica* Herbst, 1786 (Orthoptera: Acrididae), heath bush-cricket *Gampsocleis glabra* Herbst, 1786 (Orthoptera: Tettigoniidae), *Tesselana veyseli* Kocak, 1984 (Orthoptera: Tettigoniidae) and large conehead *Ruspolia nitidula* Scopoli, 1786 (Orthoptera: Tettigoniidae), and four scarce species on the Wadden Sea embankment: bow-winged grasshopper *Chorthippus biguttulus* L. 1758 (Orthoptera: Acrididae), lesser grasshopper *Chorthippus mollis* Charpentier, 1825 (Orthoptera: Acrididae), Cepero's groundhopper *Tetrix ceperoi* Bolivar, 1887 (Orthoptera: Tettigoniidae) and *T. subulata* (Sprangers 1999, Verheij et al. 1997). The only embankment species on the IUCN Red Data List for Europe was *G. glabra* which is Near Threatened (Hochkirch et al. 2016) and found on the Tisza Basin embankment.

From 1980 to 2009 in the UK, major changes occurred in climate and land use. Beckmann et al. (2015) studied the changes in distribution of some grasshoppers and crickets. They concluded that habitat generalism, southerly distribution and oviposition

Table 1. Species of Orthoptera recorded from earth embankments in three areas of Europe.

| Species | Essex Coast (EC) | Wadden Sea (WS) | Tisza Basin (TB) |
|---------------------------------------------|------------------|-----------------|------------------|
| <i>Acrida ungarica</i> ³ | | | X |
| <i>Adreppus nutans</i> | | | X |
| <i>Aiolopus thalassinus</i> | | | X |
| <i>Calliptamus italicus</i> | | | X |
| <i>Chorthippus albomarginatus</i> | X | X | X |
| <i>Chorthippus biguttulus</i> ² | | X | |
| <i>Chorthippus brunneus</i> | X | X | X |
| <i>Chorthippus dichrous</i> | | | X |
| <i>Chorthippus dorsatus</i> | | | X |
| <i>Chorthippus mollis</i> ² | | X | |
| <i>Chorthippus oschei</i> | | | X |
| <i>Chorthippus parallelus</i> | X | | X |
| <i>Conocephalus dorsalis</i> | X | X | X |
| <i>Conocephalus fuscus</i> | X | | X |
| <i>Docostaurus brevicollis</i> | | | X |
| <i>Euchorthippus declivus</i> | | | X |
| <i>Gampsocleis glabra</i> ³ | | | X |
| <i>Gryllus campestris</i> | | | X |
| <i>Leptophyes albobittata</i> | | | X |
| <i>Leptophyes bosci</i> | | | X |
| <i>Leptophyes punctatissima</i> | X | X | |
| <i>Meconema meridionale</i> | | X | |
| <i>Meconema thalassinum</i> | X | X | |
| <i>Mecostethus parapleurus</i> | | | X |
| <i>Metrioptera bicolor</i> | | | X |
| <i>Metrioptera roeselii</i> | X | | X |
| <i>Oecanthus pellucens</i> | | | X |
| <i>Omocestus haemorrhoidalis</i> | | | X |
| <i>Omocestus rufipes</i> | | | X |
| <i>Pezotettix giornae</i> | | | X |
| <i>Phaneroptera falcata</i> | | X | |
| <i>Phaneroptera nana</i> | | | X |
| <i>Pholidoptera griseoptera</i> | X | | |
| <i>Platycleis affinis</i> | | | X |
| <i>Platycleis albopunctata</i> ¹ | X | | |
| <i>Ruspolia nitidula</i> ³ | | | X |
| <i>Stenobothrus stigmaticus</i> | | | X |
| <i>Tesselana veyseli</i> ³ | | | X |
| <i>Tetrix ceperoi</i> ² | | X | |
| <i>Tetrix subulata</i> ² | X | X | X |
| <i>Tetrix undulata</i> | X | | |
| <i>Tettigonia viridissima</i> ¹ | X | X | |
| Number of species | 13 | 12 | 31 |

X indicates presence.

¹Essex Red Data List species (Gardiner and Harvey 2004).

²Wadden Sea Red Data Book species (Holst et al. 1996).

³Endangered or protected species in Tisza Basin (Torma and Bozsó 2016).

above ground in vegetation positively influenced range changes. Two species commonly found on sea walls significantly increased: *C. fuscus* and Roesel's bush-cricket *Metrioptera roeselii* Hagenbach, 1822 (Orthoptera: Tettigoniidae) made use of these flood defense corridors during their range expansions. A study in Hun-

gary showed that insect groups respond differently to habitat and landscape characteristics and Orthoptera are generally influenced by landscape more than habitat features (Torma and Bozsó 2016). Krausz et al. (1995) found that the distance between habitats was correlated with a difference in orthopteran assemblages. They also highlighted the lack of knowledge in the role of population isolation and of habitat corridors such as sea walls and dikes in structuring Orthoptera assemblages. A small-scale study in Essex suggested that the absence of intensive agriculture and livestock grazing on an island with sea wall flood defenses created important refuges for Orthoptera (Gardiner and Ringwood 2010).

Therefore, flood defense embankments seem to be an important corridor habitat for Orthoptera across Europe and grazing management should seek to enhance their value without compromising flood risk.

General grazing effects

Timing.—Year-round grazing can be a useful tool for maintaining the insect assemblages of large grassland areas (Fleischer and Hölzel 2013). This management can maintain the characteristic biodiversity of semi-natural heathlands and grasslands (WallisDeVries et al. 2016). In lowland heathland in the Netherlands, grazing seems more beneficial to early successional species than late successional species which are negatively affected (WallisDeVries et al. 2016). In grasslands in southwest Montana (USA), Davis et al. (2014) showed that herbivory affected many plants and arthropod characteristics in a similar manner: early grazing (June) can negatively affect species which need forage in the early growing season. Davis et al. (2014) suggest that the timing of grazing can have big effects on the biodiversity of multiple trophic levels and effects can depend on the grassland habitat type. However, they found that Orthoptera were unaffected by grazing and that plant height was greater with early grazing (late June) than late grazing (July and August). In the Netherlands, a continuous pasturing lasts for the entire grass growing season (mid-April to mid-October) with a low density of livestock (Muijs 1999). In Essex, sea walls are often grazed with sheep through September and October (Gardiner et al. 2015). Indeed, sheep grazing can be the best method if it includes rest periods in areas where plants need to germinate. The grassland should be mown twice a year to reduce the nutrient content of the soil; if not, once a year in mid-July may be sufficient (Sprangers 1999).

Patch formation.—Orthoptera are influenced by the formation of grass patches in grazed habitats (Gardiner and Hill 2004). Heavy grazing can create a homogeneous sward of consistently short vegetation with little cover from avian predation or inclement weather (Fig. 2). In Germany, the interaction between fodder quality and grazing intensity can lead to cattle adjusting their grazing pattern according to the vegetation biomass, which leads to the establishment of heterogeneous patches (Fleischer and Hölzel 2013). On the Wadden Sea coastline, the choice of livestock type has smaller effects on trophic levels than stocking intensity (van Klink et al. 2016). Invertebrates, such as *C. brunneus*, sometimes opt for patches of short turf and bare ground as habitat because it provides ideal oviposition and basking sites (Gardiner et al. 2015).

Soil disturbance.—Orthoptera may also be affected by the soil disturbance associated with grazing. Grasshoppers, such as the mot-



Fig. 2. Sheep grazed sea wall with a homogeneous, short sward; credit T. Gardiner.

tled grasshopper *Myrmeleotettix maculatus* Thunberg, 1815 (Orthoptera: Acrididae), require exposed soil and sparse grassland (good egg-laying and basking conditions) which can be created by associated cattle trampling of the vegetation. However, cattle grazing can lead to a sward with uniformly short grass with reduced grasshopper suitability overall (Gardiner 2012).

Applying livestock

Sea wall and dike vegetation is often maintained by grazing animals. Herbivores grazing on grasslands stimulate grass productivity (Nolte et al. 2014). A study in the Netherlands found that canopy height is affected by two variables: livestock species and livestock density (Nolte et al. 2014). The livestock species (including wild herbivores like rabbits) can also affect plant abundance and assemblage diversity, which are correlated with Orthoptera conservation and pest management (Gardiner 2018). Herbivore species and densities should therefore be chosen depending on their impacts.

Moderate intensity sheep grazing (c. 10 sheep/ha) in Essex can create a high sward heterogeneity which is generally favorable for Orthoptera (Figs 3, 4). Like rabbits, sheep can easily reach inaccessible areas, which can be desirable or undesirable depending on the flood defense management objectives (Gardiner et al. 2015).

Less selective grazers such as cattle can create a relatively uniform sward height by removing long and coarse grass where many invertebrates like *M. roeselii* or *C. albomarginatus* occur (Gardiner et al. 2015). However, intense cattle grazing can damage the soil surface (Fig. 5) and the flood defense requiring costly repairs. For this reason, these grazers are not generally recommended for grazing dikes or sea walls (Gardiner et al. 2015).

Horses can also be used to graze dikes and sea walls. If their stocking intensity is heavy, a very homogeneous, short sward will be created (Fig. 6). Nevertheless, low stocking densities of equines in large areas can provide a varied mosaic with shortly grazed lawns and taller undisturbed vegetation. Ungrazed latrines (dunging areas) form an excellent tall-grass habitat for many species of Orthoptera such as the bush-cricket *C. fuscus* and *M. roeselii* (Gardiner et al. 2015).

To create heterogeneous, small-scale vegetation mosaics, Nolte et al. (2014) recommended cattle rather than horses, but at a



Fig. 3. Light sheep grazing on a sea wall creating a heterogeneous, patchy sward favorable for Orthoptera (Little Oakley, Essex, UK); credit T. Gardiner.



Fig. 5. Post-grazing cattle damage; credit T. Gardiner.



Fig. 4. Sheep grazing on a sea wall folding creating a heterogeneous, patchy sward favorable for Orthoptera (Brightlingsea, Essex, UK); credit T. Gardiner.



Fig. 6. Horse grazed area (left) vs. ungrazed area (right); credit T. Gardiner.

low intensity. However, cattle and horses contribute to very poor erosion-resistant revetments (Muijs 1999).

Of the Dutch dikes, 85% are grazed, and 15% have species-poor grassland used for haymaking (Sprangers 1999). Sprangers (1999) adds that the 'Frysian system' is very efficient. The principle of the system is that grazing a small dike parcel with a large number of livestock during a short period is better than grazing a large parcel with few livestock continuously. This results in periodical heavy grazing of small areas with 35 to 40 ewes and lambs per hectare, corresponding to 15 sheep per hectare per year. These livestock numbers reflect the 60% of sea dikes which were traditionally heavily grazed and fertilized. Moreover, Sprangers (1999) affirms that around 85% of the aforementioned heavily grazed dikes are managed using sheep. This is exactly the opposite in Essex where 86% of sea walls are mown and only 14% are grazed or unmown (Gardiner et al. 2016). This results in a taller vegetation on the Essex sea walls due to the late summer mowing in August and September (Fig. 7).

Livestock effects on Orthoptera

Grazing by livestock affects vegetation, and therefore Orthoptera. Kruss and Tschardtke (2002) suggested that insect diversity increases in the following order: '*intensively grazed* (5.5 cattle/ha) > *extensively grazed* (1.4 cattle/ha) > *short-term ungrazed* (ungrazed for 3 years) > *long-term ungrazed* (ungrazed for more than 5 years)'. In Montana (USA), grazing and trampling encroach upon grasshoppers' food and influence the physical structure of vegetation and the soil surface which, in turn, impacts the thermal environment and oviposition sites (O'Neill et al. 2003). O'Neill et al. (2003) conclude that most grasshoppers are negatively influenced by these stresses. Herbivores frequently disturb Orthoptera, leading to dispersal of species such as the meadow grasshopper *Chorthippus parallelus* Zetterstedt, 1821 (Orthoptera: Acrididae) to undisturbed grasslands (Gardiner et al. 2015). In the long-term, reducing sward height and increasing disturbance through heavy grazing can lead to dispersal through undisturbed and infrequently cut



Fig. 7. Uncut grassland and scrub on a sea wall folding (Brightlingsea, Essex, UK); credit T. Gardiner.



Fig. 8. Sheep-grazed area (left) vs. undisturbed area (right); credit T. Gardiner.

areas (Fig. 8) (Gardiner et al. 2015). Moreover, the linear nature of grassland dikes promotes migration (Krausz et al. 1995).

The response of Orthoptera to a physical disturbance is to jump (Ben-Ari and Inbar 2013). However, this escape mechanism leads to an important energy expense. In Israel, Ben-Ari and Inbar (2013) studied the dropping mechanism of insects in response to mammalian breath. They found a direct influence of mammalian herbivores on plant-dwelling insects.

In the grasslands of the Eastern Eurasian steppe, Ma et al. (2017) recommended avoiding continuous years of intense sheep grazing. They found a significant cumulative effect; an increase in sheep grazing intensity caused decreases in insect abundance, diversity and species richness. Regarding cattle, their presence on sea walls can create very short, homogeneous grassland swards (uniformly <10 cm height) which reduces suitability for Orthoptera (Gardiner et al. 2015). Eventually, modifying grassland ecosystems with domestic livestock grazing can lead to a significant loss of biodiversity (Evans et al. 2015). On Essex sea walls in Eastern England, Orthoptera were recorded from 2 x 2 m quadrats (5 quadrats per plot) in cattle, sheep and rabbit grazed grassland plots and compared to mown plots using a one-way analysis of variance (ANOVA) after square-root transformation of count data to normalize it. A post-hoc Tukey test was performed to determine the differences between the plot means in the four differently-managed grassland types.

The statistical analysis revealed that significantly higher densities of Orthoptera were recorded in sheep and rabbit grazed grassland compared to mown swards (Table 2). Densities of Orthoptera could exceed 3 adults/m² on some grazed sea walls. The greater heterogeneity in sward height on the sheep and rabbit grazed sea walls was particularly favorable for grasshoppers such as *C. albomarginatus*. The mosaic of grass heights provided patches of short vegetation for basking and oviposition, and tall vegetation for shelter from avian predation and excessively hot microclimatic temperatures (Gardiner and Hassall 2009). Species richness did not differ between the sea walls (Table 2).

A German study found a bottom-up effect in heavy cattle grazing impacting plant-insect interactions (Kruess and Tschamtk 2002). Increasing grazing intensity may affect trophic levels

by negatively affecting both primary and secondary consumers (Ma et al. 2017). Removal of vegetation biomass by grazing negatively affects herbivorous arthropod abundance and consequently reduces predator numbers, especially of the field vole *Microtus agrestis* L., 1761 (Rodentia: Cricetidae; Evans et al. 2015). In a ten-year experiment, Evans et al. (2015) suggested that intense long-term ungulate grazing can have an important impact on trophic levels but not on plant diversity. Kruess and Tschamtk (2002) found that decreasing grazing intensity improved insect diversity but not plant diversity, which was low in intensively grazed pastures and high in abandoned areas. In intensively modified vegetation, even if the diversity is not impacted, Orthoptera and their predators are negatively impacted. Evans et al. (2015) also detected a strong positive effect of vegetation biomass on arthropod abundance.

The effect of grazing is usually species-specific because the response of species and assemblages differs in accordance with the region and the grassland type (Gardiner 2018). Both phytophagous and entomophagous insects are affected by grazing intensity (Kruess and Tschamtk 2002). However, not all groups are negatively impacted, such as some larvae and soil-dwelling insects (Evans et al. 2015). Kruess and Tschamtk (2002) consider that grazing or abandoning of grassland does not affect habitat specialist or generalist insects.

Table 2. Density and species richness of Orthoptera on Essex sea walls (UK) with differing management (Gardiner unpublished data, 2011).

| Management (n) | Density/m ² | No. species/plot |
|----------------|------------------------|------------------|
| Rabbits (4) | 2.9 ± 0.4 | 2.0 ± 0.0 |
| Sheep (4) | 2.6 ± 0.8 | 2.5 ± 0.3 |
| Cattle (4) | 1.4 ± 0.1 | 3.3 ± 0.9 |
| Mown (12) | 0.7 ± 0.2 | 2.4 ± 0.4 |

One-way ANOVA:

Density: $F = 9.05$, d.f. 3, sheep vs. mown sig. $P < 0.05$, rabbits vs. mown sig. $P < 0.01$.

Species: $F = 0.74$, d.f. 3, $P = 0.54$.

Mixed management

Grazing can alternate with other kinds of management such as mowing or occasional burning. Sometimes, mowing may be the only solution in areas hardly accessible to domestic livestock such as remote sea walls. A rotational management strategy produces complex effects on orthopteran assemblages and develops a diverse range of vegetation structures (Gardiner 2018). A combination of grazing and mowing is possible on dikes and sea walls. Alternate periods of grazing and mowing on a dike or sea wall can increase biodiversity while ensuring flood defense integrity is maintained (Gardiner et al. 2015). The use of rotational sheep grazing on English sea walls develops suitable conditions for large populations of grasshoppers, especially *C. albomarginatus* (1.7 adults/m²; Gardiner and Charlton 2012). In the Netherlands, grassland needs to be managed by grazing and mowing to prevent irregular grass (Muijs 1999). In Germany, some dikes were frequently mown and grazed, so no impacts were found on already impoverished grasshopper populations (Batáry et al. 2009). In Hungary, grasshopper abundance was higher on extensive fields, and all arthropods (including grasshoppers) were impacted in their community structure (Batáry et al. 2009). The relatively high species richness on some Hungarian dike sides is probably due to the infrequent mowing disturbance (Krausz et al. 1995).

Benefits of unmanaged sites

The structure of grassland provides an excellent habitat for Orthoptera when it is uncut (ungrazed and unmown; Gardiner et al. 2015). In undisturbed patches on Essex sea walls (Fig. 9), locally scarce species such as *T. viridissima* can be abundant. Ungrazed pastures with tall grassland provide important refuges, like latrines, for Orthoptera (Gardiner 2018). Indeed, an experiment showed that *C. parallelus* nymphs and adults released in a heavily grazed area dispersed to tall grass (Gardiner and Hill 2004). Gardiner and



Fig. 9. Undisturbed grassland on a sea wall folding; credit T. Gardiner.

Hill (2004) concluded that these directional movements reflected a preference for ungrazed grass as a more favorable breeding habitat.

Grassland undisturbed for many years provided an important habitat for large populations of Orthoptera, especially for *M. roeselii* (Gardiner et al. 2015). On a sea wall, the uncut and ungrazed folding next to the borrowdyke is the most important habitat in terms of Orthoptera distribution (Fig. 9, Table 3). Bush-crickets (*Conocephalus* spp. and *M. roeselii*) preferred tall vegetation patches on the uncut folding and the landward slope. Grasshoppers (especially *C. brunneus* and *C. parallelus*) preferred the track disturbed by vehicle wheels because of the frequent patches of bare earth probably used as basking and oviposition sites. Soil disturbance is a key consideration in the conservation of flood defense embankment Orthoptera, with trampling live-

Table 3. Orthoptera abundances recorded from five sections of a seawall (Brightlingsea, UK) using quadrat sampling (Gardiner et al. 2015).

| Orthoptera species | Folding (uncut) | Folding (track) | Landward Slope | Crest | Seaward slope | TOTAL (%) |
|-----------------------------------|-----------------|-----------------|----------------|-----------|---------------|------------------|
| <i>Conocephalus</i> spp. | 52 | 0 | 35 | 0 | 7 | 94 (13) |
| <i>Pholidoptera griseoaptera</i> | 6 | 0 | 0 | 0 | 0 | 6 (1) |
| <i>Chorthippus brunneus</i> | 1 | 31 | 12 | 9 | 10 | 63 (9) |
| <i>Chorthippus parallelus</i> | 15 | 32 | 15 | 0 | 3 | 65 (9) |
| <i>Chorthippus albomarginatus</i> | 5 | 4 | 35 | 6 | 41 | 91 (12) |
| <i>Metrioptera roeselii</i> | 236 | 1 | 170 | 1 | 7 | 415 (57) |
| TOTAL | 315 | 68 | 267 | 16 | 68 | 734 (100) |

Table 4. Advantages and disadvantages of three different grazing animals for grassland Orthoptera conservation and maintaining flood defense integrity.

| | Sheep | Cattle | Horses |
|---------------|-----------------------------------------------------------|------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------|
| Advantages | Heterogeneous sward height ¹ Control scrub | Heterogeneous sward height ¹ Poaching creates bare ground Control scrub | Heterogeneous sward height ¹ Poaching creates bare ground Latrine areas Control scrub |
| Disadvantages | Homogeneous, short sward ² Limited poaching | Homogeneous, short sward ² Damage to flood defense from poaching | Homogeneous, short sward ² Damage to flood defense from poaching |

¹At low-medium stocking intensity.

²At high stocking intensity.

stock hooves providing the necessary disturbance in the absence of vehicles (Table 4).

Dike habitats provide diverse resources, completely or incompletely fulfilling resource requirements depending on the species of Orthoptera (Gardiner et al. 2015). The main grazing animal on European sea walls is sheep, which can be favorable for Orthoptera when the stocking intensity is light-moderate establishing a heterogeneous sward (Table 4). However, Orthoptera may also be negatively impacted at high stocking intensities due to the creation of a uniformly short sward with few tall grass refuges (Table 4). It is advisable to alternate grazing with mowing and to prefer sheep over cattle and horses to minimize soil damage on the flood defense.

Conclusion

Flood defense embankments in Europe are commonly rich in Orthoptera. In some cases, grazing can promote plant species richness and favorable habitat for Orthoptera, including scarce species such as *G. glabra* and *T. ceperoi*. Where high flood risk exists, dikes and sea walls are sometimes over-managed by heavy grazing and/or mowing. Controlled management should aim to establish a heterogeneous sward with varying grass heights. The main criteria when deciding on the appropriate flood defense embankment management for Orthoptera are: grazing duration, stocking intensity (numbers of animals per hectare) and type of livestock (Table 5). Without compromising the effectiveness of the defense, a balance can be applied between management intensity and conservation of the Orthoptera. Further research is needed into the precise influence of sheep grazing on sea wall Orthoptera throughout Europe, but particularly where there is a high proportion of scarce and endangered species such as the Wadden Sea.

Table 5. Matrix to enable appropriate grazing and mowing regimes to be chosen in relation to Orthoptera abundance and maintaining flood defense integrity.

| | Low flood risk (farmland) | High flood risk (properties) |
|---------------------------------------------------|-------------------------------|---------------------------------|
| Low Orthoptera abundance (<3/m ²) | Rabbits* Sheep- Mowing- | Sheep+ Mowing+ |
| High Orthoptera abundance (>3/m ²) | Rabbits* Sheep- | Sheep+ |

Key: - low intensity grazing (≤10 sheep/ha) or mowing (1-2 cuts/yr)

+ high intensity grazing (>10 sheep/ha) or mowing (>2 cuts/yr)

* naturally occurring rabbits, not stocked

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Fine-scale interactions between habitat quality and genetic variation suggest an impact of grazing on the critically endangered Crau Plain grasshopper (Pamphagidae: *Prionotropis rhodanica*)

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Abstract

The Crau Plain grasshopper, *Prionotropis rhodanica* Uvarov, 1923 (Orthoptera: Pamphagidae: Thrinchinae), is a rare grasshopper species endemic to the Crau Plain, a steppic habitat in France with unique floristic and faunistic communities. During recent decades, the area covered by these steppic grasslands has been highly reduced and fragmented due to the development of irrigation-based agriculture, roads, as well as industrial and military complexes. The restricted distribution, low population density and poor dispersal ability of *P. rhodanica*, combined with the destruction of its habitat, has led to the classification of this species as critically endangered in the IUCN Red List of Threatened Species. Decreases in habitat quality due to intensive grazing in the remnant grassland patches constitute an additional threat for *P. rhodanica* that can impact population dynamics at a relatively small-scale. In this work, we focused on a small area of about 3 km² occupied by one of the largest subpopulations observed in 2000–2001. We conducted a single-time snapshot intensive survey of grasshopper density and genetic variation at 11 microsatellite markers. We used a recent method, MAPI, to visualize the spatial genetic structure as a continuous surface and to determine, with the simultaneous use of spatial cross-correlograms, whether the normalized difference vegetation index, which informs on the balance between vegetation productivity and grazing intensity, can explain grasshopper population structure at such a fine scale. We found that both population density and gene flow were strongly and positively correlated to habitat quality (higher productivity of grasslands and/or lower sheep grazing). The spatial scales of interaction between these variables were estimated to be highly similar, in the range of 812–880 meters. This result suggests that *P. rhodanica* is very sensitive to the quality of the grasslands it inhabits.

Key words

conservation, grazing, landscape genetics, MAPI, NDVI

Introduction

The Crau Plain (Bouches du Rhône, France; Fig. 1A–B), the ancient delta of the Durance River, is the last arid steppe in France with a unique fauna and flora (Cheylan 1975, Devaux et al. 1983, Wolff et al. 2001, 2002, Romermann et al. 2005, Tatin et al. 2013). The characteristic vegetation of this steppe is called Coussoul and is mainly composed of *Brachypodium retusum* and *Thymus vulgaris* in association with *Asphodelus fistulosus* and *Stipa capillata*. This unique ecosystem has been maintained over 3,000–4,000 years by extensive sheep grazing (Buisson and Dutoit 2006, Tatin et al. 2013). Since the sixteenth century, and more intensely within recent decades, the plain has been highly modified by intensive irrigation-based agriculture (Devaux et al. 1983). The contraction of the Coussoul from ~600 km² to less than 100 km² (Wolff et al. 2002) and its fragmentation by agricultural fields (orchards and hay meadows), irrigation channels and other artificial structures (roads, industrial and military complexes) threaten the natural habitat and its fauna. Since 2001, 7,400 ha of the Crau Plain have been protected as a national nature reserve and since 2010 a management plan has been implemented with conservation actions for its remarkable species. Among them, *P. rhodanica* (Fig. 2) is a large (between 30 and 50 mm) grasshopper species endemic to the Crau Plain and protected in France (Anonyme 1979). This species has been classified as Critically Endangered in the IUCN Red List of Threatened Species (Hochkirch and Tatin 2016) as well as on the European Red List (Hochkirch et al. 2016) and the national Red List of France (Sardet and Defaut 2004). *P. rhodanica* is only known from the Crau Plain, though surrounding areas have been intensively surveyed. The species is generally considered as rare, ex-

* equal contribution

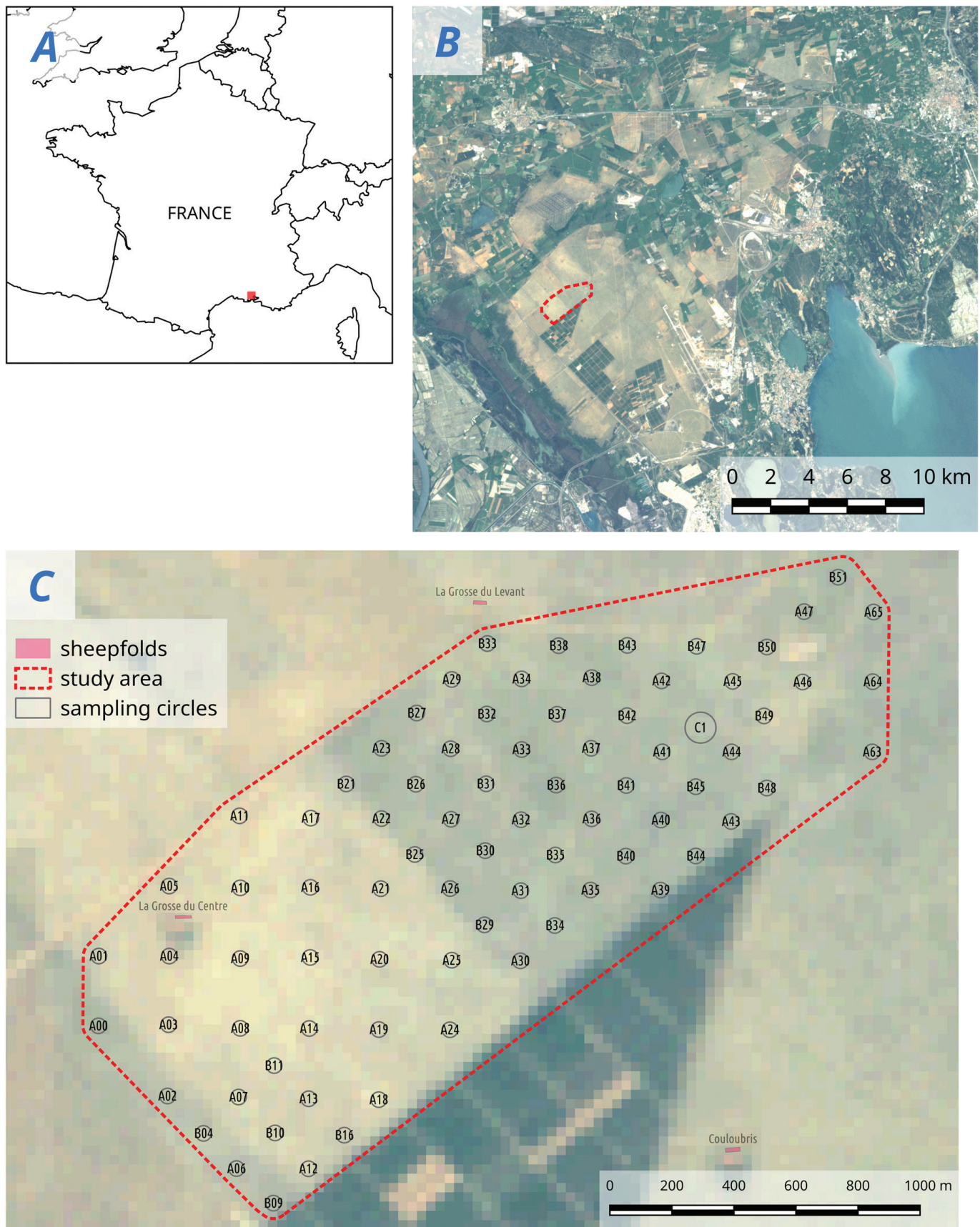


Fig. 1. Map of France and location of A. the plain of Crau (Bouches-du-Rhône, France), B. the sampling site located between the sheepfolds 'La Grosse du Levant' and 'La Grosse du Centre', and C. the circles surveyed to detect and sample *P. rhodanica*. A00-A65: names of circles of the grid A; B01-B51: names of circles of the grid B; C1: additional circle of 100 m diameter (see Material and methods).



Fig. 2. Adult of *Prionotropis rhodanica*.

cept for some atypical years, and observations over the last fifteen years revealed an extreme decline in population densities along with local extinctions (Foucart and Lecoq 1996, Foucart et al. 1999, Hochkirch et al. 2014). In 2014, a conservation strategy for the species was developed under the guidance of the Species Conservation Planning Sub-Committee (SCPSC) and the Invertebrate Conservation Sub-Committee (ICSC) of the International Union for Conservation of Nature (IUCN) (Hochkirch et al. 2014). One main aim of the strategic conservation plan was to identify the reasons for the population decline.

Orthoptera are known to be highly sensitive to landscape alterations, such as those associated with farming, in terms of genetic diversity and structure (Ortego et al. 2012, Gauffre et al. 2015, Ortego et al. 2015) as well as population decline or extinction risk (Barker 2004, Reinhardt et al. 2005). However, demographic responses and evolutionary trajectories differ among species, and some species are more susceptible than others regarding the negative effects of habitat perturbations (Ortego et al. 2015). Thus, conservation practices in protected areas require detailed ecological and evolutionary information to target species that require particular attention and guide their management (Ortego et al. 2015). A capture-mark-recapture study conducted on *P. rhodanica* at a fine scale (8,000 m²) over a two-month period (May-June) in 2000 showed that individual movements occur over very short distances (mean distance between two captures < 20 m) and suggested that adults are more mobile than nymphs (Berthier 2000, see also Besnard et al. 2007). These very limited dispersal abilities of *P. rhodanica* were expected as adults of both sexes are brachypterous

and thus incapable of flight (Fig. 2; Foucart 1995, Foucart et al. 1999). Furthermore, studies of the genetic structure of *P. rhodanica* conducted on a small number of sample sites (2–5) and microsatellite loci (5) revealed that subpopulations are strongly differentiated even when located a few hundred meters apart (Berthier 2000, Streiff et al. 2005). These results suggest that *P. rhodanica* subpopulations are isolated with dispersal events among them being rare, confirming that biological and ecological characteristics of the species result in low demographic and genetic connectivity between isolated subpopulations. Isolation effects depend on the sizes of habitat elements, the distances between them and the quality of the surrounding matrix (Prevedello and Vieira 2010). Their quantification would thus be important to assess the species vulnerability to the reduction and fragmentation of its habitat and would require an intensive sampling of remnant subpopulations at a large scale (e.g. the complete geographic range of the species).

An additional threat for *P. rhodanica* might result from livestock grazing pressure (Hochkirch et al. 2014). While the available surface of Coussoul has continuously been decreasing for centuries, flock sizes fluctuate from one year to the next and can reach 1,600 sheep on average (Wolff et al. 2013). Moreover, the size of flocks can strongly increase when sheep are gathered to prepare for the transhumance in June-July, coinciding with the breeding period of *P. rhodanica* (Foucart and Lecoq 1996). For example, during the capture-mark-recapture study conducted in 2000, the size of the flock grazing the 3 km² land plot within which our study site of 8,000 m² was localized increased from 250 to 1,200 individuals in two months (Berthier 2000). Generally, such successive peri-



Fig. 3. Illustrations of the Coussoul habitat of *Prionotropis rhodanica* with A. sheep accompanied by cattle egrets and B. researchers surveying the species using a circle-based method.

ods of intensive grazing can be detrimental because they reduce primary productivity, impede plant growth and alter vegetation cover that provides the grasshopper with food and shelter. In *P. rhodanica*, the highest observed abundances were associated with a vegetation cover above 70% (Tatin et al. 2013). In addition to competition for resources, negative impacts of intensive grazing include trampling and predation by birds associated with sheep flocks (Hochkirch et al. 2014). In particular, the cattle egret, *Bubulcus ibis* L., often accompanies sheep flocks (Fig. 3A) and catches insect and small vertebrate prey disturbed by sheep (personal observation). Since pasture boundaries delineate plots less than 550 ha (min of 30 ha and mean of 168 ha), grazing pressure and consequently grasshopper habitat quality may vary at a relatively small scale in the Crau Plain, even within apparently continuous and favorable areas of Coussoul. Information on fine-scale spatial genetic structure would allow an assessment of the role of habitat quality, rather than that of unsuitable elements that isolate habitat patches, on contemporary dispersal patterns. However, a sampling scheme at a fine scale has never been attempted in *P. rhodanica*.

MAPI (Mapping Averaged Pairwise Information; Piry et al. 2016) is a new method for spatial visualization of population structure and investigating landscape effects. MAPI is essentially a smoothing procedure for spatial genetic networks, useful for large sample sets for which usual representations (i.e. nodes and edges) are often unreadable. MAPI can be applied to genetic differentiation measures computed from neutral markers (e.g. microsatellites) to detect areas of high genetic continuity and/or discontinuity that reflect areas where gene flow is the highest and/or the lowest, respectively. MAPI allows visualizing the spatial genetic structure as a geographic map that provides information on the average intensity of the genetic relationships, and can be exported simultaneously with landscape layers and density data for further statistical analyses. This exploratory approach may thus provide information on which environmental variables are potential candidates to explain observed genetic patterns. A central feature of MAPI is its low sensitivity to confounding effects resulting from isolation-by-distance (IBD). This is especially true in an ideal situation, with perfect regular sampling and no edge effects (Piry et al. 2016). However, when

sampling is highly irregular, the insensitivity to IBD still holds relatively to clustering methods (Guillot and Santos 2009, Bradburd et al. 2013, Piry et al. 2016). This is a critical issue when assessing the impact of landscape heterogeneity on population genetic structure, which also depends on geographic distance (Bradburd et al. 2013). This may be of high relevance to *P. rhodanica* since significant IBD patterns have been reported at fine spatial scale (2–10 km) in other orthopteran species that are flightless (Lange et al. 2010, Keller et al. 2013, Gauffre et al. 2015), or considered to be sedentary (Ortego et al. 2011, Blanchet et al. 2012).

In this study, we focused on a small area of 2.87 km² within which direct gene flow was likely to occur while potential effects of the physical landscape (i.e. barriers to dispersal, presence of inhospitable patches) were expected to be minimal. Our target study site was a suitable habitat for *P. rhodanica* but with potential variation in quality in particular due to sheep grazing regime. It was located in a large patch of Coussoul where the largest subpopulation of *P. rhodanica* was observed at the end of the nineties (Foucart et al. 1999). In spring 2001, we carried out a single-time snapshot intensive survey of grasshopper density and genetic variation at eleven microsatellite loci. The sampled subpopulation was composed of 266 individuals of a single cohort since *P. rhodanica* is univoltine with discrete generations (eggs hatch in early April and all adults die by mid-July; Foucart and Lecoq 1996). We investigated contemporary patterns of dispersal by first testing whether there is non-random spatial structure due to relatedness among individuals at the scale of the sampling unit (i.e. ≤ 50 m) and/or isolation-by-distance at the scale of the study area. We then used MAPI to produce a continuous variation surface of the genetic relationships between individuals. Finally, we used spatial cross-correlograms to quantify the spatial scales of interactions between this genetic pattern and variations in grasshopper density and habitat quality. To quantify small-scale variation in habitat quality in our study site, we used the normalized difference vegetation index (NDVI) as a proxy of the balance between vegetation productivity and vegetation degradation partly due to grazing. Remotely sensed vegetation indices are commonly used to monitor changes in vegetation and land cover, and their correlation with grazing intensity has been demonstrated in other parts of the world (e.g. Raynolds et al. 2015), including in semi-arid environments (Blanco et al. 2008, Karnieli et al. 2013). Here, the validity of the relationship between vegetation productivity, NDVI and grazing effect was evaluated in the specific area of the Crau Plain using data from a recent experiment (i.e. conducted in 2015).

Material and methods

Sampling and grasshopper densities.—*P. rhodanica* is particularly difficult to detect in the field (less than 10% detection probability) due to its low mobility, cryptic coloration and crypsis behavior (Streiff et al. 2005, Besnard et al. 2007, Tatin et al. 2013). Therefore, we determined a sampling area of 2.87 km² to focus on the zone where densities were relatively large in 2001 (Fig. 1B–C). Within the study area, circles with 50 m diameter were regularly distributed to create two completely overlapping grids (A and B), so that circles from grid A alternate with those from grid B every 160 meters (Fig. 1C). All circle centers were positioned using Global Positioning System (GPS). Grid A was entirely surveyed between the 21st and 29th of June 2001 to ensure a complete coverage of the study area. In grid B, only the circles located in zones where the species was detected in grid A were surveyed between the 27th to the 31st of June 2001. In addition to the 50 m circles of grid A

and B, a circle with 100 m diameter located within the zone with the highest *P. rhodanica* density was also surveyed between the 21st and 29th of May 2001.

All circles were divided in 8 adjacent sectors (16 for the 100 m diameter circle), physically delimited in the field, and each sector was explored by three persons walking abreast and passing at least twice on a same path (Fig. 3B). For each insect observed, polar coordinates to the center were recorded, and then converted in latitude and longitude. Sex and developmental stage (nymph/adult) were recorded. A non-destructive sampling method was used for further genetic analyses (a small piece of elytra or tarsus was collected and the insect released at its capture position). From the 82 surveyed circles, a total of 266 individuals (213 nymphs, 53 adults, 132 females and 134 males) were sampled. More than 50% of the circles (i.e. 44) did not contain grasshoppers and densities varied from 5.1 to 133.3 individuals per hectare within the 38 remaining circles (Suppl. material 1: Table S1). Accordingly, an analysis of the spatial distribution using Ripley's *K* function revealed a patchy distribution of the individuals within the study area (Suppl. material 1: Fig. S1).

Microsatellite genotyping and basic genetic indices.—Genomic DNA was extracted following the CTAB protocol (Doyle and Doyle 1987). DNA concentration was determined using a Nano-drop spectrophotometer (NanoDrop Technologies, Wilmington, USA) and extracts were normalized to a concentration of ca. 5 ng/ μ L. Eleven microsatellite loci were used, ten of which were previously described in Streiff et al. (2002) and Streiff et al. (2005) and one additional locus was developed for this study (see primer sequences in Suppl. material 1: Table S2). We genotyped the 266 individuals at the 11 microsatellites using an ABI PRISM 310 DNA sequencer (Applied Biosystems) using conditions described in Suppl. material 1: Table S2. Alleles were scored using GeneMapper 4.0 (Applied Biosystems).

The level of polymorphism and allelic distribution were estimated with GENEPOP v.4 (Rousset 2008). We first tested for linkage disequilibrium between each pair of loci and within each circle by using G-exact tests (keeping the 22 circles out of 38 non-empty circles with sampling size ≥ 3 individuals). Over the sampling site, and for each locus, we tested for Hardy–Weinberg equilibrium using G-exact tests and estimated the number of alleles, observed and expected heterozygosities of Nei (1987) and Wright's *F*-statistic F_{IS} according to Weir and Cockerham (1984). We also tested for genotypic differentiation among circles by using the exact G-test of heterogeneity of genotypic frequencies (keeping the 22 circles with sampling size ≥ 3 individuals).

Kinship and isolation-by-distance patterns.—In order to analyze the relatedness structure at the circle scale, we calculated the kinship coefficient of Loiselle et al. (1995) between pairs of individuals belonging to a same circle, using SPAGeDI v.1.4 (Hardy and Vekemans 2002). We then used Spearman rank correlation to test whether there is an association between grasshopper density measures and mean values of kinship coefficient within circles.

We assessed whether dispersal was restricted with distance, using GENEPOP v.4 (Rousset 2008). We computed for each pair of sampled individuals, and over all loci, the statistics \hat{a} (Rousset 2000), which is considered as an unbiased estimator of genetic distance (Watts et al. 2007). We used a Mantel test between the matrices of genetic distances (\hat{a}) and the logarithm of geographical Euclidean distances to test for a positive linear relationship as expected under an IBD model. We excluded pairwise comparisons between individuals separated by less than 75 m to exclude intra-circle measures. This would limit the impact of siblings on the es-

timization of the relationship between genetic and geographic distances. Confidence interval and significance of regression slope was calculated by bootstrapping over loci using 10,000 permutations. We also performed the same IBD analysis for each sex separately.

NDVI computation.—As suggested by Gan et al. (2014), we computed rescaled NDVI values by building fine-scale NDVI raster from Landsat images and calibrating the results using a coarse-resolution MODIS raster. The LANDSAT 7/8 ETM+ raster (30 m resolution) and NDVI MODIS raster, all courtesy of the U.S. Geological Survey, were downloaded from <https://earthexplorer.usgs.gov>. The MODIS NDVI is a 16-day composite of MODIS data at a spatial resolution of 250 m. First, NDVI values were computed at the spatial resolution of the Landsat raster (30 m) using an updated version of the python script provided by Dr. J. Degener and available from <https://www.uni-goettingen.de/en/524379.html>. Second, the Landsat NDVI raster and the MODIS NDVI raster were clipped over the area of interest (projection UTM 31 / WGS84). Third, the MODIS NDVI raster was aligned on the Landsat NDVI raster using the nearest value. Both rasters were then loaded in the statistical software R (R Core Team 2015) using the packages “rgdal” and “raster” and, finally, the pixel values from both rasters were bound into a single dataframe. Pixels with missing MODIS values (-3,000) were discarded from the dataset. MODIS NDVI values were divided by 10,000 to be within the range of the Landsat NDVI values. Landsat NDVI values were then normalized by performing a pixel-to-pixel regression of the MODIS NDVI values against the Landsat NDVI values (see Suppl. material 1: Figs S2, S3 for an illustration).

Relationship between NDVI, habitat quality and grazing.—We analyzed the relationship between rescaled NDVI, vegetation productivity and grazing using data from a recent experiment. In 2015–2016, an enclosure of 8.56 ha, located in the same area as our study site (Suppl. material 1: Fig. S4), was fenced between April and August to exclude sheep. One hundred plots (of 30 cm diameter each) were randomly selected to measure vegetation productivity indices within (50 plots) and outside (50 plots) this enclosure. Vegetation productivity indices included: vegetation height, coverage in forbs, coverage in dry vegetation and coverage in bare ground (i.e. no vegetation). We tested whether our four productivity indices reflected the impact of sheep grazing on vegetation using Wilcoxon tests to compare the measures between plots located inside and outside the enclosure. Rescaled NDVI values were computed from Landsat and MODIS images captured in May 2014 (before fencing) and May 2016 (after fencing). Each vegetation plot received the rescaled NDVI value of the 30 m pixel to which it belonged. We analyzed the relationship between 2016-rescaled NDVI values (after fencing) and the four vegetation productivity indices using Spearman rank correlations. Finally, we used Wilcoxon tests to verify that after fencing (2016) the rescaled NDVI values were, on average, significantly lower for the plots located inside the enclosure than outside, while no differences were expected for 2014-rescaled NDVI values (before fencing). In other words we tested that our rescaled NDVI was an appropriate proxy to assess grazing impact on grasshopper habitat quality. Statistical analyses were done using R (R Core Team 2015).

Spatial association between grasshopper density, habitat quality and genetic variation.—We used the MAPI program (Piry et al. 2016), freely available at <https://www1.montpellier.inra.fr/CBGP/software/MAPI/>. We produced a geographical map of the spatial vari-

ation of the mean genetic differentiation between individuals and then interpolated, within the cells of the map grid, grasshopper density and habitat quality (rescaled NDVI) to test for correlations between variables. The successive three steps of this analysis are detailed below.

Map of genetic differentiation.—We attributed the values of the statistics \hat{a} of Rousset (2000) to ellipses that spatially materialize the connections between the pairs of individuals. A grid of hexagonal cells with a half-width of 20 m was superimposed on the study area (cell's area = 1,040 m²; see ‘Grid of cells’ section in Piry et al. (2016) for details). Each cell received the weighted arithmetic mean of the ellipses intercepting its geographical extent. This mean was weighted using the inverse of the ellipse areas to limit long distance effects. MAPI values for the eccentricity of ellipses that controls the smoothing intensity was set by default (i.e. *eccentricity* = 0.975). However, additional analyses were run with *eccentricity* values from 0.800 to 0.999 to assess robustness of MAPI results to the shape of ellipses (i.e. from inflated to narrow). The radius of the error circle that controls for uncertainty on sample polar coordinates (*error_circle_radius*) was set to 2 m. An interesting feature of MAPI is the optional parameters that limit the analysis to a given range of between-sample distances. We used a minimum distance between samples (*min_distance*) of 75 m in order to exclude pairwise comparisons between individuals from a same circle. Details on parameters can be found in Table 1 and Suppl. material 1 from Piry et al. (2016) and in pp. 29–31 from the MAPI manual. Finally, to ensure that MAPI results were not biased by the patchy distribution of individuals (higher number of individuals sampled in high density areas), we ran the analysis on 100 independent resampled datasets with a maximum of three individuals from each circle and checked for consistency of results.

Density and NDVI spatial interpolation.—Grasshopper densities measured within circles and rescaled NDVI values from Landsat (captured the 18 of May 2001: LE07_L1TP_196030_20010518_20170205_01_T1.tar.gz) and MODIS (captured the first 16 days of May 2001: MOD13Q1.A2001129.h18v04.006.2015142065654.hdf) images were first interpolated into a raster (5 m resolution) using the function “using v.surf.rst” of the GRASS software (GRASS Development Team 2012) with parameter values set as follows: maximum number of points in a segment (*segmax*) = 120, minimum number of points for approximation in a segment (*npmin*) = 60 and maximum distance between points on isoline (*dmax*) = 25. Values interpolated below 0 were reset to 0 using the GRASS function “r.mapcalc”. Second, raster pixels were clipped to MAPI grid cells and interpolated density values from pixels belonging to the same MAPI cell were averaged using the ST_SummaryStats function of the PostgreSQL 9.3 with the PostGIS 2.1.2 extension (1996–2016, The PostgreSQL Global Development Group: <http://www.postgresql.org/> – <http://postgis.net/>).

Spatial scales of association between variables.—Spatial cross-correlograms allow investigation of how two variables co-vary with geographic distance. We used the non-parametric spline-correlogram approach implemented in the R package “ncf” (Bjørnstad and Falck 2001) to analyze the spatial scale of association (S_p) between interpolated values of: 1) grasshopper density and rescaled NDVI, 2) grasshopper density and mean genetic differentiation between individuals (i.e. MAPI cell values) and, 3) rescaled NDVI and mean genetic differentiation between individuals (i.e. MAPI cell values).

Confidence envelopes at 95% ($CE_{95\%}$) for the estimated correlograms were calculated using bootstrapping (500 replicates). We also computed Spearman rank correlation coefficients (Rho) between all pairs of variables.

Results and discussion

Thirty-four of the 1,210 tests for linkage disequilibrium between the 11 loci were significant after false discovery rate correction (Storey and Tibshirani 2003). Because these pairs of loci were never significant in more than two circles, all microsatellite loci were considered unlinked. We found significant deviations from Hardy–Weinberg equilibrium at the global scale for most loci and the F_{IS} value averaged to 0.072 across loci (Table 1). Heterozygote deficits can be partly related to presence of null alleles for the few loci that show highest values (i.e. Phr7178 and Phr756 with a $F_{IS} > 0.3$). Prevalence of null alleles has commonly been reported in studies documenting microsatellite variation in orthopteran populations (Zhang et al. 2003, Chapuis et al. 2005, Hamill et al. 2006, Berthier et al. 2008, Chapuis et al. 2008). However, the heterozygote deficit concerns most loci, which suggests that it primarily results from spatial structure (i.e. Wahlund effect) rather than presence of null alleles. As a matter of fact, global genetic differentiation between circles was highly significant ($P < 0.0001$) and all pairs of circles were significantly differentiated ($P \leq 0.001$). Moreover, most of the Loiselle kinship coefficient values averaged within circles were positive. Thus, pairs of individuals within circles were more related than expected under random distribution of genotypes. This pattern at a scale of 50 m confirmed the limited dispersal capacities of this flightless grasshopper species, at least at the nymphal stage.

The levels of genetic diversity were high, with a mean expected heterozygosity of 0.813 and an average of 16.18 alleles for our sample size of 266 individuals (Table 1). They are similar to the levels of genetic diversity observed by Berthier (2000) and Streiff et al. (2005) within subpopulations of the same species. The (apparent) lack of impact of habitat modifications on the level of genetic diversity may be explained by their recentness in the Crau Plain (Streiff et al. 2005). Changes in genetic diversity after a perturbation are related to the total effective population size, and show slow dynamics with non-equilibrium states over large temporal scales. This result may also account for the limited dispersal in the fragmented population of *P. rhodanica*, which allows for strong differentiation between subpopulations and thereby a high level of total genetic diversity (Nei 1973). Beside population demography and history, this outcome may also result from the high microsatellite loci mutation rate, which has been confirmed for the Orthoptera (Chapuis et al. 2012). Overall, *P. rhodanica* did not seem to be affected by a low level of genetic diversity, which is widely recognized as a major impediment for the adaptation of a population to environmental changes. However, this does not preclude that the species may have a low total population size, which would make it vulnerable to demographic stochasticity that can lead to local extinctions (Frankham 2005). Indeed, during a standardized survey conducted in 2012–2013, *P. rhodanica* was not detected in our study site anymore and this subpopulation is now assumed to be extinct (Hochkirch et al. 2014).

We detected a significant negative relationship between the Loiselle kinship coefficient and density within circles (Rho = -0.59; p-value = 0.0012; Fig. 4A), i.e. the lower the grasshopper density, the higher the genetic relatedness. Since we did not find any evidence for lower levels of genetic diversity within lower

Table 1. Genetic diversity indices for each of the 11 loci from *P. rhodanica*. Number of alleles (Na), Wright's F_{IS} and observed (H_o) and expected (H_e) heterozygosities were averaged over the 266 individual samples.

| Locus | Na | F_{IS} | H_o | H_e | HW test P value |
|----------------------|--------------|--------------|--------------|--------------|--------------------|
| Phr1C7 | 23 | 0.034 | 0.865 | 0.895 | < 0.0001 |
| Phr228 | 9 | 0.028 | 0.545 | 0.561 | 0.1770 |
| Phr2C3 | 10 | 0.015 | 0.816 | 0.828 | < 0.0001 |
| Phr2T | 12 | -0.021 | 0.774 | 0.758 | 0.0279 |
| Phr3B3 | 23 | 0.031 | 0.857 | 0.884 | 0.0238 |
| Phr4A10 | 34 | 0.005 | 0.936 | 0.941 | < 0.0001 |
| Phr4G1 | 17 | 0.142 | 0.774 | 0.901 | < 0.0001 |
| Phr7178 | 5 | 0.316 | 0.432 | 0.632 | < 0.0001 |
| Phr756 | 9 | 0.306 | 0.510 | 0.734 | < 0.0001 |
| Phr880 | 19 | -0.037 | 0.940 | 0.906 | 0.1331 |
| Phr4H3b | 17 | 0.059 | 0.853 | 0.907 | < 0.0001 |
| Over all loci | 16.18 | 0.072 | 0.755 | 0.813 | < 0.0001 |

density circles, we can exclude the effects of genetic drift under random mating as cause (Rho = +0.14; p-value = 0.506; Fig. 4B). Moreover, negative F_{IS} values were associated with the lowest grasshopper density conditions and thereby with the highest genetic relatedness values (Rho = +0.62; p-value = 0.0019; Fig. 4C). Theoretical studies demonstrate that excess heterozygosity is expected when allelic frequencies differ in fathers and mothers (e.g. Rousset and Raymond 1995). For example, in social species negative values of F_{IS} may be indicative of complicated breeding tactics rather than classical outbreeding (Van Staaden 1995) as exemplified in some populations of elephants, bats and finches (Tarr et al. 2000, Nyakana et al. 2001, Storz et al. 2001). Since grasshoppers are often polyandrous, our result can hence be explained by the fact that most of the nymphs sampled from the lowest density circles may have emerged from a single egg-pod, where half-siblings are from a same mother but several unrelated fathers.

We detected a significant positive linear relationship between the differentiation coefficient (d) and the logarithm of geographical distance at a scale $\leq 2,500$ m ($P < 0.0001$; Fig. 5). The value of the regression slope suggests that dispersal decreased strongly with geographical distance in this species (estimate [95% confidence interval] = 0.017 [0.008–0.033]). Significant IBD patterns were still found when analyzing males and females separately and overlapping confidence intervals for slope estimates did not support sex-biased dispersal, at least at the nymphal stage (Fig. S5 in the Suppl. material 1). Overall, this result indicates that dispersal is seriously restricted in space at the sampled scale. This dispersal pattern is likely to limit the ability of the species to colonize new areas and can ultimately reduce the long-term persistence of the isolated populations. This is in agreement with local extinctions observed since 1996 in areas that have never been recolonized since (Foucart and Lecoq 1996, Foucart et al. 1999).

The map of the interpolated densities visually confirmed the result of the Ripley's K statistics with a clear occurrence of two main high density nuclei in the northern half of the study site, while the density was very low in the southern half (Fig. 6A). An equivalent pattern was observed from the rescaled NDVI map, with highest values occurring in the northern half of the study site (Fig. 6B). The MAPI analysis also revealed a strong spatial structure, with the lowest levels of genetic differentiation observed between individu-

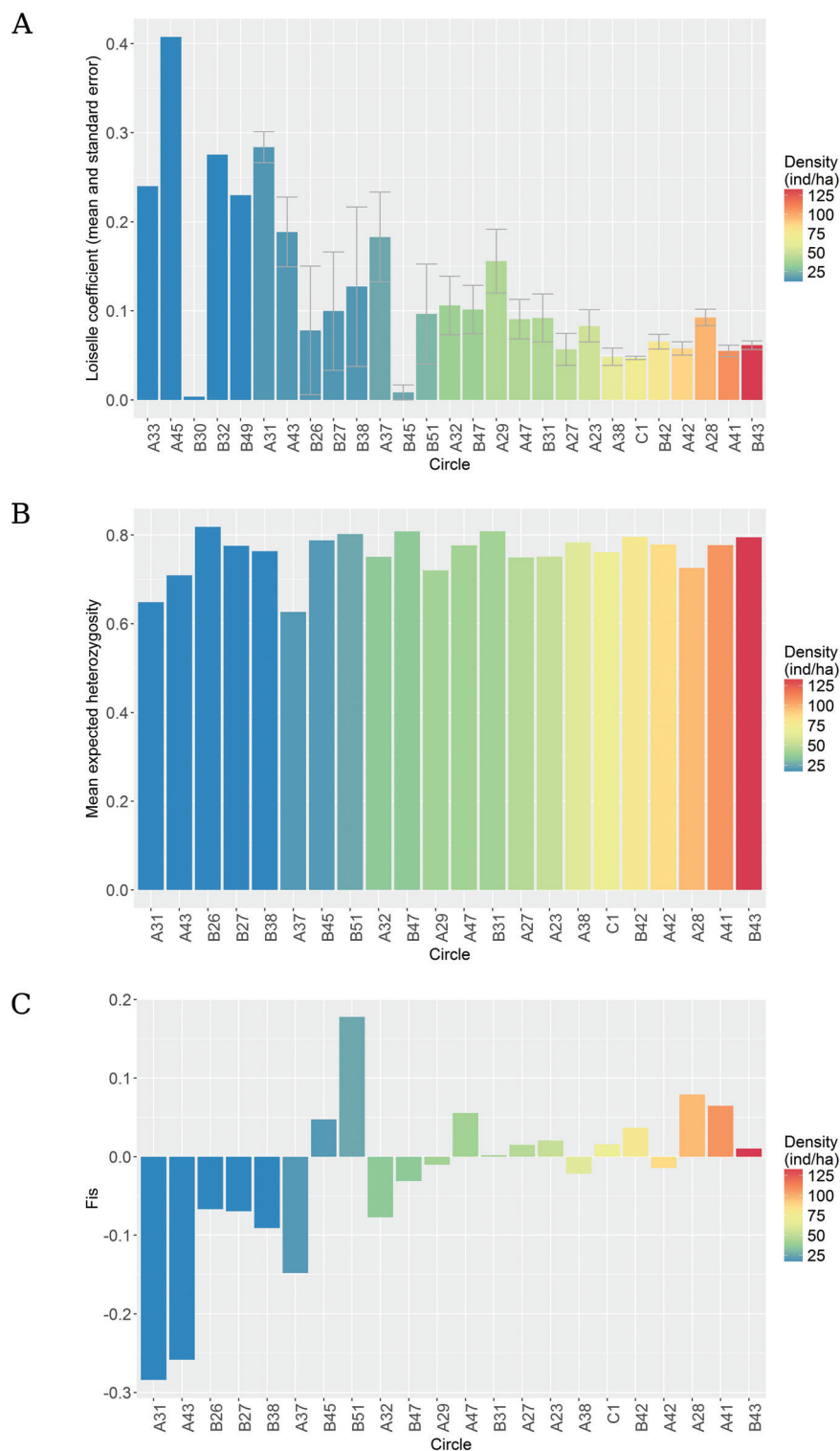


Fig. 4. Relationships between intra-circle grasshopper density and A. Loiselle kinship coefficient, B. expected heterozygosity and C. F_{IS} .

als located within the high density nuclei (Fig. 6C). Individuals located in lower density areas (extreme southern and northern parts of the study area) were not only differentiated from the density nuclei but also exhibited a relatively high level of differentiation across short distances. It is worth noting here that these results are expected to be robust to the observed pattern of strong IBD, even

under our irregular sampling data (Piry et al. 2016). In addition, the optional parameter of minimum distance between samples in MAPI allowed us to eliminate the potential impact of the inferred presence of siblings within circles of low grasshopper density on the assessment of the surface of genetic variation. MAPI results from resampled datasets (of a maximum of 3 individuals within

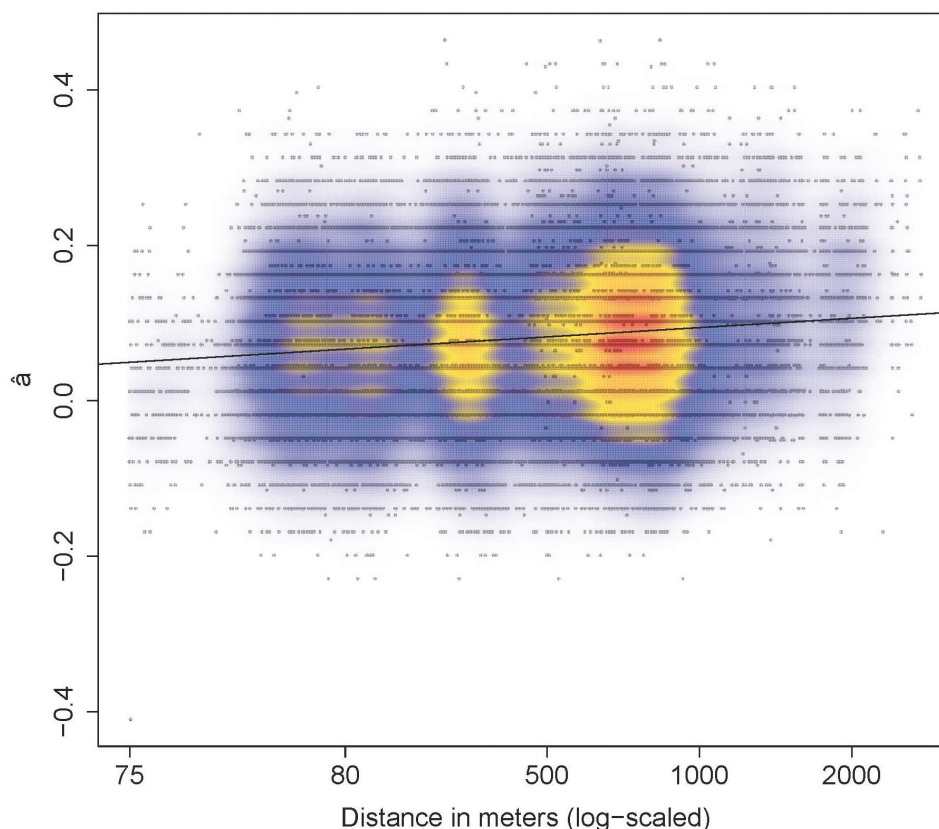


Fig. 5. Linear regression between genetic distance \hat{a} and geographical distances computed between pairs of individuals. Variation in point density is represented by colors, from blue (low density) to red (high density).

circles) were highly consistent with those obtained from the complete dataset (Suppl. material 1: Fig. S8).

Finally, Spearman coefficients showed that grasshopper density and rescaled NDVI values were positively correlated ($Rho = 0.51$; $p\text{-value} < 2.2e^{-16}$) but both negatively correlated to MAPI cell values ($Rho = -0.42$ and -0.34 , respectively; $p\text{-value} < 2.2e^{-16}$ for both). The three cross-correlograms showed that the spatial scales of association between variables were highly similar and quite small (Fig. 7): rescaled NDVI and density values, $Sp = 880m$ ($CE_{95\%} = [855-902]$); density and MAPI cell values, $Sp = 859$ ($CE_{95\%} = [680-927]$); rescaled NDVI and MAPI cell values, $Sp = 812m$ ($CE_{95\%} = [781-850]$). The strong association between values of grasshopper density, rescaled NDVI and genetic differentiation in our target site suggest that relatively subtle alterations in habitat quality can strongly impact local population dynamics by decreasing individual numbers and disrupting gene flow at a very fine scale, independently of barriers that isolate habitats. As our study area was grazed by two different flocks (see Fig. 17 in Hochkirch et al. 2014), the observed demographic and genetic patterns may be the result of a difference in grazing pressure.

This hypothesis was supported by the results of the analysis of vegetation productivity indices and NDVI in relationship with grazing treatment. Indeed, we found that three out of the four measured vegetation indices were significantly different between plots located inside and outside the fenced enclosure (Suppl. material 1: Fig. S6). The mean vegetation height and the coverage in forbs were significantly higher within the fenced enclosure (Wilcoxon test $p\text{-value} = 6.3e^{-07}$ and 0.0002 , respectively) while the coverage in bare ground was significantly lower within the

fenced enclosure (Wilcoxon test $p\text{-values} = 0.0001$). No difference was observed for the coverage in dry vegetation (Wilcoxon test $p\text{-values} = 0.2302$). The 2016-rescaled NDVI values were significantly correlated to the three productivity indices that responded to grazing. A positive correlation was found for the mean vegetation height ($Rho = 0.44$; $p\text{-value} = 6.4e^{-06}$) and the coverage in forbs ($Rho = 0.33$; $p\text{-value} = 0.0008$) while a negative correlation was found with the coverage in bare ground ($Rho = -0.29$; $p\text{-value} = 0.004$). Finally, the temporal analysis of the rescaled NDVI values revealed much higher values for the vegetation plots located within than outside the enclosure in May 2016, after the fencing (Wilcoxon test $p\text{-value} < 2.2e^{-16}$), while a slight opposite trend was found in May 2014, before the fencing (Wilcoxon test $p\text{-value} = 0.0563$) (Suppl. material 1: Fig. S7). Within the area delineated by the fenced enclosure, rescaled NDVI values associated to vegetation plots were also higher in 2016 than in 2014 (Wilcoxon test $p\text{-value} < 2.2e^{-16}$).

Altogether, this study suggests that *P. rhodanica* is sensitive to habitat quality and complements previous findings of a low dispersal capability at the scale of the fragmented landscape. This may explain why some subpopulations are no longer detected in the Crau Plain and imply that the few remaining ones may become extinct in the long-term as they are unlikely to be rescued through immigration. This finding emphasizes the need for managing the *P. rhodanica* population at a local scale by considering the quality of the relict habitat patches, in addition to habitat fragmentation at a larger scale (i.e. sizes of and distances between Coussoul patches). Although this study did not identify clearly the processes driving this critically endangered species to extinction, the MAPI correlative approach

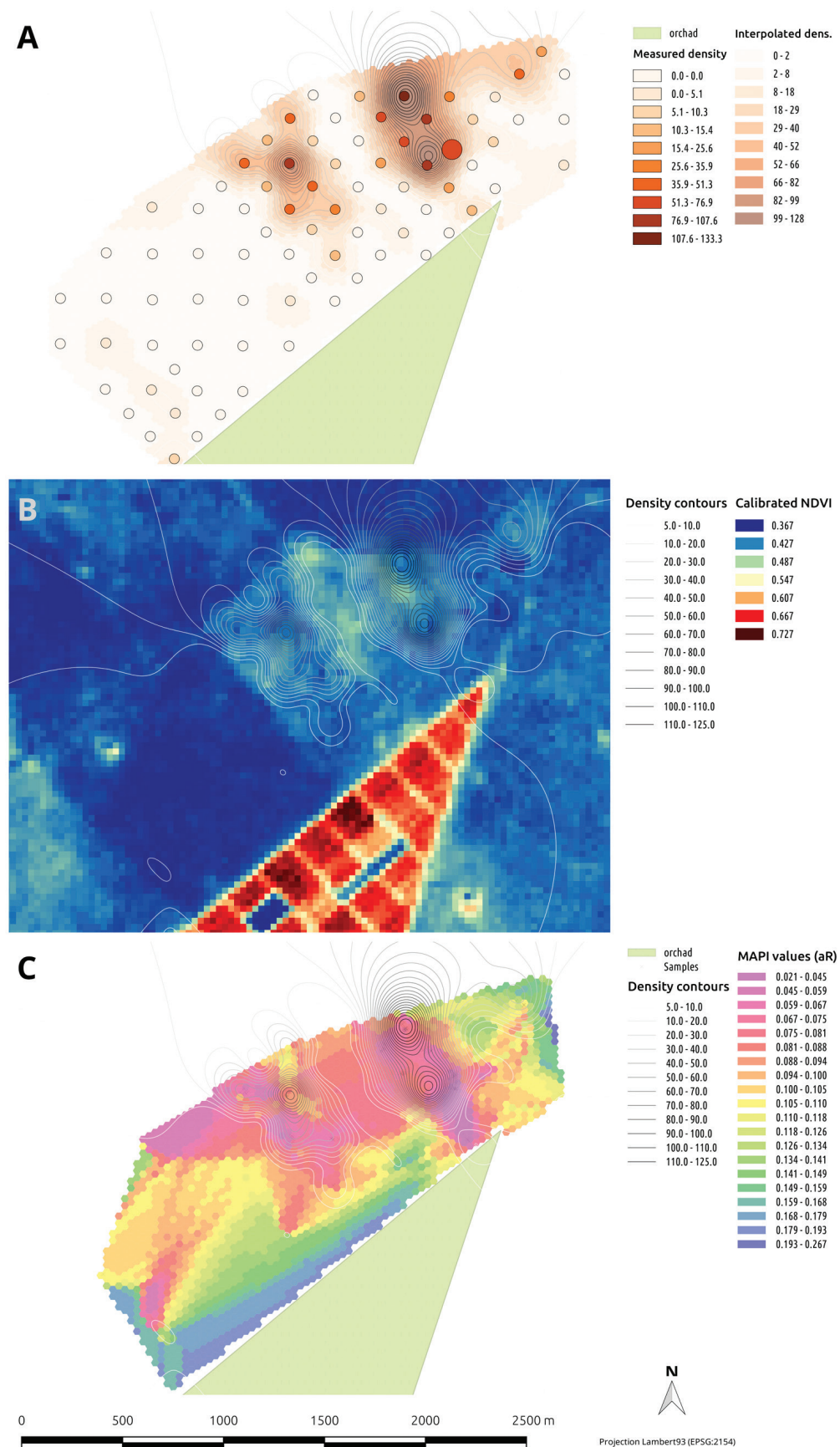


Fig. 6. Maps of A. density of grasshopper in number of individuals per hectare, B. rescale NDVI values and C. mean genetic differentiation between individuals resulting from the MAPI analysis.

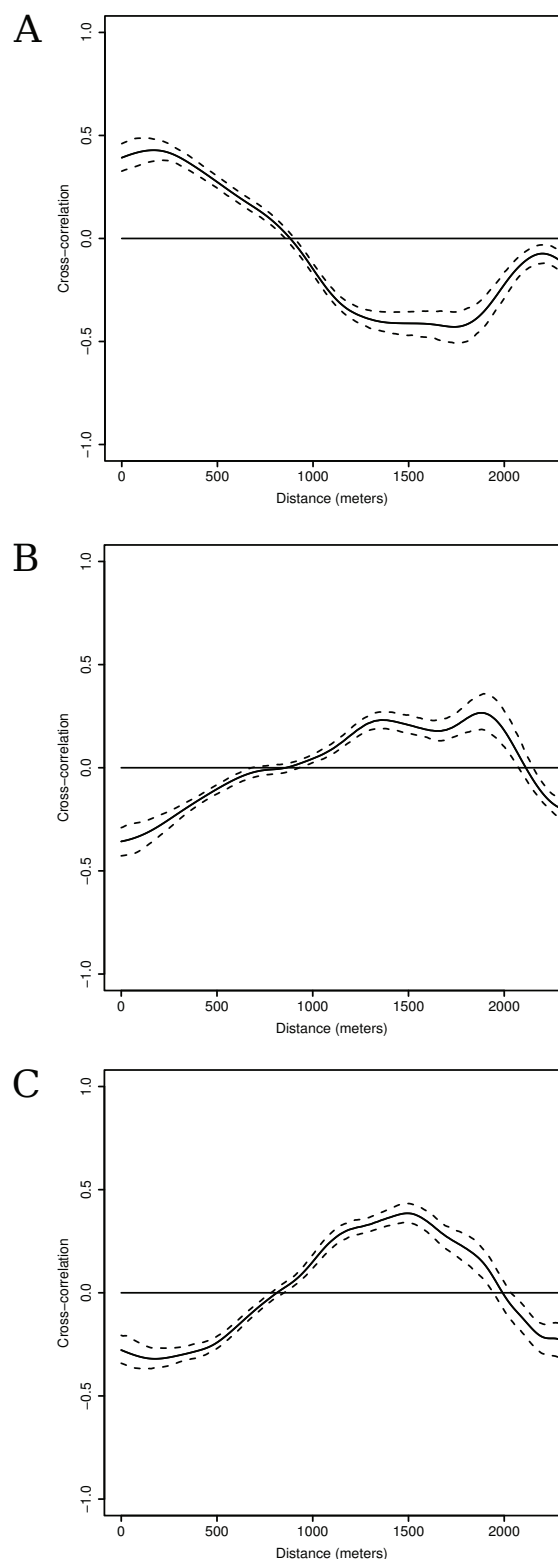


Fig. 7. Spatial cross-correlograms between **A.** grasshopper density and NDVI, **B.** grasshopper density and the mean genetic differentiation between individuals (MAPI cell values) and, **C.** NDVI and the mean genetic differentiation between individuals. The x-intercept of the spline-correlogram is the estimate of the distance at which the correlation between variables is not different than expected by chance alone. Dotted lines represent the 95% confidence envelope based on 500 bootstrap resamples.

helped us identify sheep grazing as a candidate landscape feature that may decrease grasshopper density and restrict gene flow within habitat patches. As our study was limited to a single sampling site, generalizing our results to the entire *P. rhodanica* population should be done with caution. Nonetheless, now that our indirect data-driven exploratory approach identified grazing pressure as a potential candidate driver of population decline, further work is needed in order to test for its population effects in a more direct way, draw firm conclusions and guide management actions. Above all, further fine monitoring of habitat quality (e.g. vegetation cover, structure and composition) in relation to direct measures of grazing pressure is critical. If the negative role of intense grazing is confirmed, implementing an adaptive management of pastoralism in the Crau Plain could help to sustain a higher number of reproductive grasshoppers and potential dispersers.

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Supplementary material 1

Authors: Sylvain Piry, Karine Berthier, Réjane Streiff, Sandrine Cros-Arteil, Antoine Foucart, Laurent Tatin, Linda Bröder, Axel Hochkirch, Marie-Pierre Chapuis

Data type: MS Word document

Explanation note: Supplementary tables and figures.

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Influence of grazing on populations of the specialist grasshopper *Mioscirtus wagneri* inhabiting hypersaline habitats in La Mancha Region, Central Spain

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Abstract

Grazing is an influential land use that has introduced profound changes in worldwide landscapes, ecosystems and their species. In this paper, we analysed the influence of grazing on the presence and abundance of the endangered *Mioscirtus wagneri*, a monophagous grasshopper inhabiting inland hypersaline ecosystems in Spain and showing a marked spatial and genetic fragmentation. Using count transects, we analyzed the presence and abundance of this grasshopper in relation to specific vegetation cover and the abundance of goat and sheep droppings, considering this variable as a surrogate of livestock activity and grazing impact. We found that both the presence and abundance of *M. wagneri* were positively related to the cover of its host plant *Suaeda vera* and negatively associated with the abundance of droppings. We conclude that dropping abundance is a useful parameter to assess livestock impact and evaluate habitat quality and the conservation status of *M. wagneri* and many other singular species of macroinvertebrates inhabiting inland hypersaline ecosystems. We highly recommend the use of electric shepherd fencing around all sensitive and protected areas where inland hypersaline ecosystems are present in order to deter livestock. We also suggest intensive educational campaigns for farmers and shepherds, revealing the ecological importance of these singular and unique habitats for rare and exclusive species like *M. wagneri* and many other coexisting plants and invertebrates.

Key words

Castilla-La Mancha, conservation, grazing management, inland hypersaline ecosystems, livestock droppings, *Suaeda vera*

Introduction

Historical and current grazing activities are an important influence on the landscape and, thus, on plant and animal community composition (González Bernaldez 1981, Blondel and Aronson 1999). However, intense grazing activities may alter the soil, exerting a negative impact on species biodiversity (Fleischer 1994). Intensive browsing, trampling, and resting on the ground can have a negative impact on the vegetation cover, increasing the proportion of bare soil and aggravating the effects of periods of drought

(Ledesma 2000, Gardiner and Haines 2008). However, other studies have found an opposite effect (Kisbenedek 1995, Pocco et al. 2010). In fact, grazing activities can have opposite effects on the biodiversity of both plant and animal communities depending on grazing management, intensity and the characteristics of the affected area (e.g. Rook and Tallwin 2003, Cingolani et al. 2005, Branson et al. 2006, Deban 2006, Dumont et al. 2009, Krausman et al. 2009, Báldi et al. 2013). Grazing contributes to habitat heterogeneity for Orthoptera when moderate (Fartmann et al. 2012). However, the influence of grazing on the abundance of orthopterans varies with grazing management and season (Gebeyehu and Samways 2003). Different studies have found that rotational grazing may be beneficial for orthopteran communities whereas total absence of grazing may be negative for orthopteran populations in other cases (Gebeyehu and Samways 2003, Fonderflick et al. 2014). It is worth mentioning that within a particular area, grazing may also have positive or negative effects on orthopteran populations depending on the species (Jepson-Innes and Bock 1989, Fielding and Brusven 1995, O'Neill et al. 2003).

To test the impact of grazing on grasshopper abundance, we focused on the populations of a specialist species, *Mioscirtus wagneri* (Kittary, 1859) (Orthoptera: Acrididae) inhabiting continental hypersaline habitats both around hypersaline lagoons and in salted ground prairies of the plant association *Suaedetum brevifoliae* (Cirujano-Bracamonte 1981). The species feeds and obtains shelter from alkali seepweed (*Suaeda vera*) bushes (Cordero et al. 2007b, Ortego et al. 2010). Because of its specialized host plant dependence, we predict that grazing has a profound impact on the habitat of *M. wagneri* and provokes a significant negative effect on its populations.

Here, we aim to provide information on threats related to livestock activity on *M. wagneri* and its sensitive and exclusive hypersaline habitat. The aim of this study is to determine, 1) the association of *M. wagneri* with its host plant (*S. vera*, alkali seepweed) and 2) how grazing activity is related to the presence and abundance of this grasshopper in two localities, including grazed and ungrazed plots around hypersaline lagoons of La Mancha Region (Central

Spain). To attain this, we analysed the relationship between the abundance and presence of *M. wagneri* obtained from count transects and the cover of different species of plants, the type of soil, and the abundance of livestock droppings, used as a surrogate of the intensity of livestock activity.

Methods

Study area.—The study area includes two inland salted lagoons in the center of Iberian Peninsula: Peña Hueca ($3^{\circ}20'29''\text{W}$, $39^{\circ}30'50''\text{N}$) and Tirez ($3^{\circ}21'27''\text{W}$, $39^{\circ}32'21''\text{N}$) (Villacañas, Toledo Province, Central Spain) (Fig. 1). The lagoons present shallow waters, strong summer drought, and a high degree of salinity (Camacho et al. 2009). They constitute natural microreserves with karst sedimentation and endorheism (Peinado 1994). These lagoons are within the Biosphere Reserve of “La Mancha Wetlands” belonging to the European entity “LIC Wetlands of La Mancha” (Annex I of Directive 79/409 / EEC and Annex I and II of Directive 92/43 / EEC) (Bartolome et al. 2005). However, in spite of such a protection status, current legislation is not always adequate and livestock may graze, rest or pass through the protected areas around the lagoons. The halophilous vegetation present around these lagoons has been extensively studied (Cirujano-Bracamonte 1981) and is under the protection of European directives (Martín-Herrero et al. 2003). *Suaeda vera* is one of the main plant species present in these habitats, with a woody and perennial existence on saline and hypersaline soils around inland salted lagoons (Fig. 2).

The grasshopper.—The study species is *Mioscirtus wagneri*, a monophagous and specialist grasshopper with a disjunct distribution and high genetic fragmentation of its populations (Cordero et al. 2007b, Ortego et al. 2009, 2010, 2011) (Fig. 3). It has been suggested that this species is particularly sensitive to habitat destruction because of its specialist nature and strong dependence on its host plant *S. vera* (Cordero et al. 2007b, Ortego et al. 2010). *Mioscirtus wagneri* is endangered within Western Europe (Hochkirch et al. 2016). The only populations of this species in Western Europe are found in Spain. Other grasshopper species usually accompanying *M. wagneri* include *Aiolopus strepens* (Latreille, 1804), *Oedaleus decorus* (Germar, 1826), *Oedipoda charpentieri* Fieber, 1853, *Ramburiella hispanica* (Rambur, 1838), *Calephorus compressicornis* (Latreille, 1804), *Dociostaurus crassiusculus* (Pantel, 1886), *Dociostaurus jagoi occidentalis* Soltani 1978, *Calliptamus wattenwylanus* (Pantel, 1896), *Calliptamus italicus* (Linnaeus, 1758), and *Sphingonotus morini* (Defaut, 2005) (personal observation; see also Cordero et al. 2007b, Ortego et al. 2015).

Transects and variables.—To measure *M. wagneri* presence/abundance, plant species and soil type cover, we used transects in areas with different influences from grazing but within the local distribution of the grasshopper. Transects were 20 m in length, and 0.5 m on each side of the observer were surveyed (a total area of 20×1 m per transect = 20 m^2). On transects we collected data on *M. wagneri* presence and abundance, soil type, cover and species of plants and number of droppings of sheep and goats. Transects were chosen

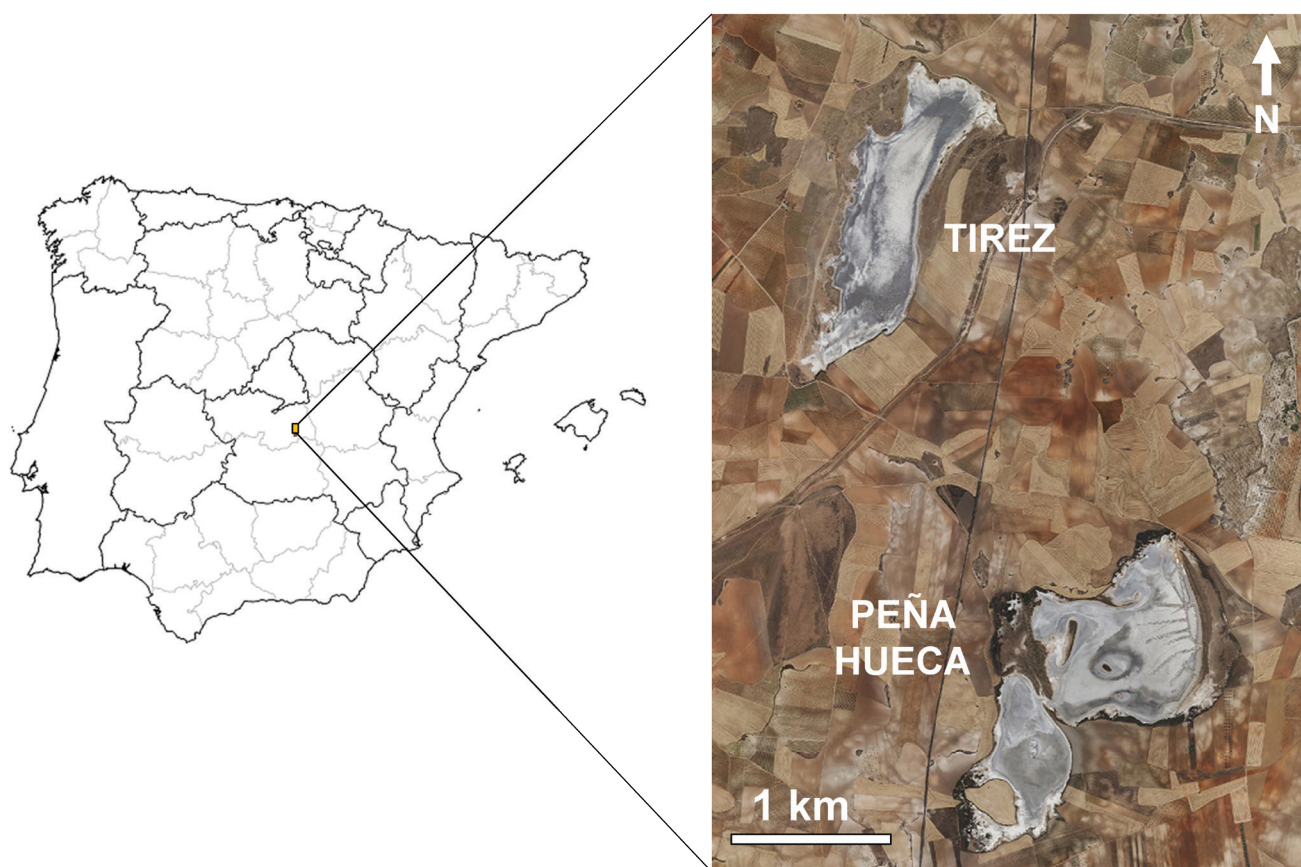


Fig. 1. Map of the study area (Villacañas, Toledo Province, Central Spain) showing the location of the hypersaline lagoons Tirez and Peña Hueca.



Fig. 2. Alkali seepweed prairie (*Suaeda vera*) without grazing, typical habitat of *Mioscirtus wagneri* in the study area (Peña Hueca lagoon, Villacañas, Toledo province, Spain). Photo by P.J. Cordero.



Fig. 3. Male *Mioscirtus wagneri* on alkali seepweed host plant, *Suaeda vera*. Photo by P.J. Cordero.

taking into account the presence/absence of sheep and goat droppings and trying to include areas that have been differentially impacted by grazing. Transects were chosen at random in these areas although we tried to include those with homogeneous vegetation structure along their entire length. Grasshoppers were counted excluding possible repetitions of individuals. Transects were walked as slowly as necessary (2 km/hr) to accurately record the presence and abundance of grasshoppers. Finally, we took pictures of each transect to check plant and soil type cover. As we previously knew the orthopteran communities in these hypersaline areas, and because of the low number of grasshoppers living in salted grounds, we only took into account censuses of *M. wagneri*, discarding other species for analyses. The area and orthopteran communities have been studied since 2005 (P.J. Cordero unpublished). Further, *M. wagneri* is easy to identify *de visu* due to its external appearance, color and hind wing markings. Only *Aiolopus strepens* could be confused with *M. wagneri* beyond a certain distance, but we always took into account this possibility and misidentification was minimal. Capture by hand or netting was unnecessary for identification. Our census of Orthoptera was repeatable and efficient, particularly because the species is well known in the orthopteran community and is easily identifiable (e.g. Gardiner et al. 2005).

We carried out 65 transects in Tirez and 100 transects in Peña Hueca lagoons between 10 and 17 h, during August 2009, the month in which *M. wagneri* is present with 100% adult forms (Cordero et al. 2007b). The data for *M. wagneri* along each transect is summarized by two variables: PRESENCE (presence/absence, 1/0) and ABUNDANCE (number of individuals/m²).

Three percentages of bare soil were considered: brown clay soil not affected by high salt concentration (CLAYED), hypersaline white/grey soil (SALT) and plowed land (PLOWED). Other variables included the percentage cover of the main plant associations in the area. SEEPWEED: formed by the community *Suaeda brevifoliae* described above, with *S. vera* as its most abundant plant species. This small bush is scattered and rarely exceeded 70% ground cover in the study area. It is often associated with other smaller herbaceous species such as *Hordeum marinum*, *Puccinella fasciculata* and, sometimes, *Frankenia thymifolia* and *F. pulverulenta*. HALOPHYTES: heterogeneous grassland associations belonging to halophilic communities, excluding *S. vera*, with plants such as *Sarcocornia perennis*, *Salicornia ramosissima*, *Arthrocnemum coralloides*, *Spergularia media*, *Limonium* spp., *Plantago maritima*, *Suaeda maritima* and some grasses such as *Hordeum marinum*, *Polypogon maritimus*, *Aeluropus litoralis* or *Puccinella fasciculata* (maximum vegetation cover = 79%). SALSOLA: *Salsola vermiculata* association. The distribution of this plant species is similar to that presented by *S. vera*, however the salinity of the soil may be lower, interspersed with various ruderal species such as *Scolymus* sp., *Bromus* sp., *Centaurea* sp., *Chamaemelum* sp., *Frankenia* sp., etc. (maximum vegetation cover = 80%). ESPARTO: includes formations of *Lygum spartum* (esparto grass) characterized by dense cover when it is present as the only species (maximum cover = 100%). The accompanying species is usually *Limonium* sp. in moist areas. WHEATGRASS: mainly composed of *Thinopyrum curvifolius* (wheatgrass), of size and structural characteristics similar to ESPARTO, with high ground covering, often with *Juncus* sp. in small amounts (maximum vegetation cover = 80%). HERBACEOUS: several non-halophile ruderal plants including *Phragmites* sp. among others (maximum vegetation cover = 85%). STUBBLE: mown fields of wheat and barley, very close to halophile vegetation plots and rarely including any other ruderal plant species (maximum vegetation

cover = 100%). DROPPINGS: number of individual cylindrical droppings of ovine-goat livestock. We assigned large clusters of faeces composed of a certain number of dropping units (5 to 10 each) according to their size. We used this variable as a surrogate of livestock influence/presence (i.e. grazing impact) and, thus, it is related to cumulative livestock presence in the area (range of droppings abundance between 0 and 7/m²). For analysis, we also recorded the hour (HOUR) when each transect was performed.

Statistical analyses.—We performed a forward stepwise logistic regression in order to analyze the presence of *M. wagneri* (PRESENCE, dependent or response variable) in relation to the cover of the different types of plant species (SEEWEEED, HALOPHYTES, SALSOLA, ESPARTO, WHEATGRASS, HERBACEOUS, and STUBBLE), cover of the different types of bare soil (CLAYED, SALT, and PLOWED) and the number of droppings per transect (DROPPINGS). We also included in the model the hour (HOUR) and the lagoon (LAGOON) of sampling transects. To analyse the abundance of *M. wagneri* (ABUNDANCE), we performed a forward stepwise multiple regression considering the same independent variables as indicated above. Analyses were performed using SPSS v11 (IBM Corp. 2011).

Results

The average abundance of *M. wagneri* in transects with a presence of the species was 0.3 individuals/m² (range 0.05–1.3 individuals/m²). We found that the presence of *M. wagneri* (PRESENCE) was positively related to the cover of *S. vera* (SEEPWEED) (Wald = 40.65, df = 1, $P < 0.0001$; Fig. 4A) but there was no significant association with any other plant community. In turn, dropping abundance (DROPPINGS), the variable indicative of grazing activity, was negatively related to the presence of the grasshopper (Wald = 8.02, df = 1, $P = 0.005$) (Table 1; Fig. 4B). Fig. 4 shows that the probability of the presence of *M. wagneri* in areas with low values of *S. vera* cover is higher without the influence of droppings. For example, at a cover of *S. vera* near 50%, the probability of finding *M. wagneri* without droppings is high (>0.9) whereas with a density of droppings around 7/m² this probability falls down to 0.7. Seemingly, the number of *M. wagneri* per square meter (ABUNDANCE) was also positively related with the cover of *S. vera* (SEEPWEED) ($F = 147.67$, df = 1, $P < 0.001$; Table 2 and Fig. 5A) and sampling time (HOUR) ($F = 8.64$, df = 1, $P = 0.04$). As in the previous analysis, the abundance of *M. wagneri* was negatively associated with the variable indicative of livestock activity (DROPPINGS) ($F = 13.55$, df = 1, $P < 0.001$; Table 2 and Fig. 5B).

Discussion

Our results show the dependence of *M. wagneri* on alkali seepweed formations as expected from a previous observational study (Cordero et al. 2007b). This is coincident with observations from other parts of the species distributional range like North Africa (personal observation). The species feeds and shelters on *S. vera* and mates and buries its oothecae in salted bare soils around the plant. This dependence on a specific microhabitat is probably the reason why *M. wagneri* is particularly sensitive to livestock activity. We found a negative relationship between the presence and abundance of *M. wagneri* in relation to the amount of sheep and goat droppings, and considered this variable as a surrogate of cumulative livestock activities in a particular area. Within the

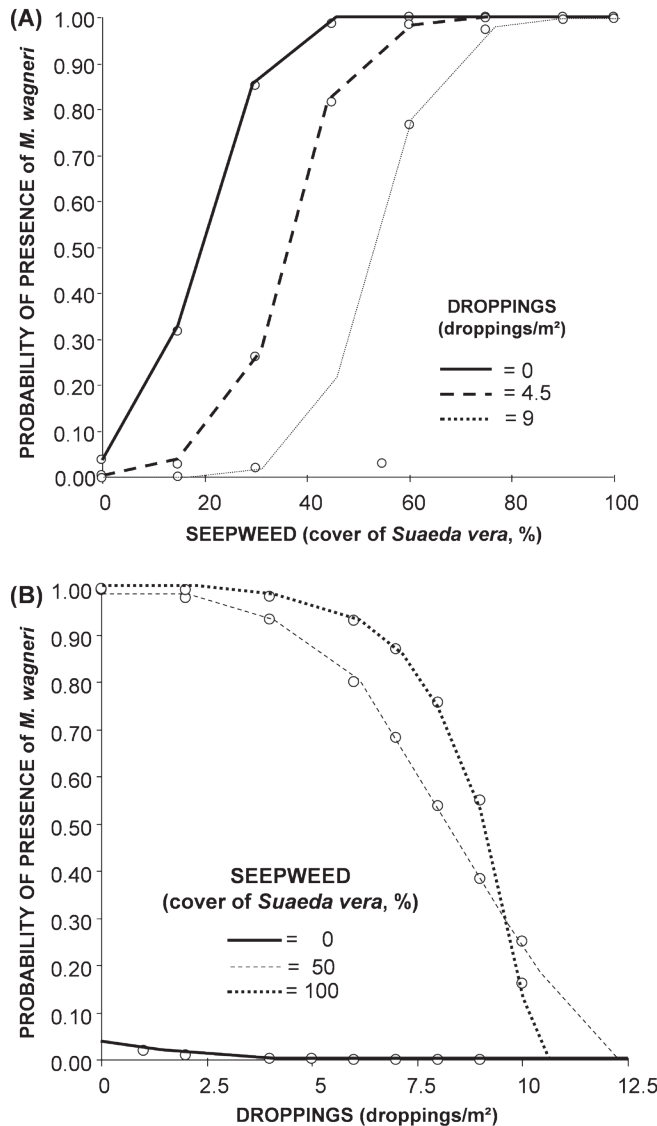


Fig. 4. Relationship between probability of presence of *Mioscirtus wagneri* in the transects (PRESENCE) and A. Cover (%) of *Suaeda vera* (SEEPWEED) for extreme values of livestock droppings per square meter (DROPPINGS), and B. Livestock droppings per square meter (DROPPINGS) for extreme values of cover (%) of *S. vera* (SEEPWEED).

species distributional range, our model predicts the presence and abundance of *M. wagneri* in hypersaline habitats according to different degrees of livestock impact measured as droppings/m². Alkali seepweed plants may coexist with livestock presence, however evident changes occur on a small scale with respect to *M. wagneri* microhabitat (Fig. 2). Alkali seepweed does not seem to be very palatable to sheep and goats, however, under a high concentration of droppings, plants are of lower quality with frequent defoliation and broken branches. This may occur because of livestock activities (trampling, resting over the vegetation, manure, urine or even direct browsing). Abundance of droppings and urine is frequently associated with eutrophic soils. A higher proportion of herbaceous plants like *Hordeum* sp. and *Chenopodium* sp., and

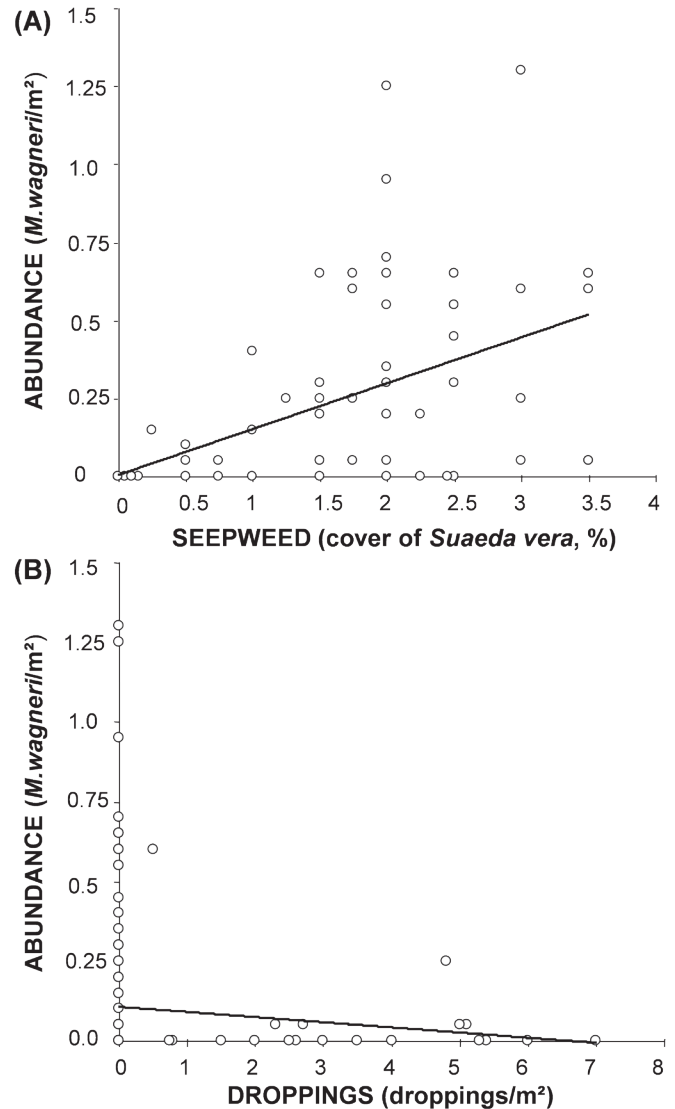


Fig. 5. Relationship between number of *Mioscirtus wagneri* per square meter (ABUNDANCE) and A. Cover (%) of *Suaeda vera* (SEEPWEED), and B. Livestock droppings per square meter (DROPPINGS). Open circles may correspond to one or more overlapping data points.

changes in vegetation composition may increase susceptibility to predation (Joern 2004). Livestock footprints may sink a couple of centimeters into moist salted soils, compacting the ground, modifying its texture, and altering the thin layer of soil above the oothecae, which could compromise egg laying or survival.

Irrespective of the mechanisms involved in the negative relationship between the abundance of droppings and the presence and abundance of *M. wagneri*, our analyses indicate that we can use information on dropping counts as a surrogate of habitat quality for *M. wagneri*. Dropping counts seem to be a measurable and straightforward tool for determining the conservation status and for implementing management measures for preserving the populations of *M. wagneri* and the sensitive hypersaline habitat

Table 1. Results of the forward stepwise logistic regression analysis for presence of *Mioscirtus wagneri* (PRESENCE) in relation to the different explanatory variables analyzed.

| | Estimator \pm S.E. | Wald | P |
|---------------------------|----------------------|-------|--------|
| <i>Variables included</i> | | | |
| Constant | -3.29 \pm 0.49 | 45.55 | <0.001 |
| SEEPWEED | 0.17 \pm 0.30 | 40.65 | <0.001 |
| DROPPINGS | -0.30 \pm 0.11 | 8.02 | <0.005 |
| <i>Variables excluded</i> | | | |
| HALOPHITES | | 2.26 | 0.100 |
| SALSOLA | | 2.56 | 0.110 |
| ESPARTO | | 0.00 | 0.972 |
| WEATGRASS | | 0.00 | 0.996 |
| HERBACEUS | | 0.74 | 0.390 |
| CLAYED | | 3.65 | 0.056 |
| PLOWED | | 0.00 | 0.999 |
| SALT | | 1.65 | 0.199 |
| STUBBLE | | 0.00 | 0.999 |
| HOOR | | 1.47 | 0.225 |
| LAGOON | | 0.01 | 0.801 |

Table 2. Results of the forward stepwise multiple regression analysis for number of *Mioscirtus wagneri*/m² (ABUNDANCE) in relation to the different explanatory variables analyzed.

| | Estimator \pm S.E. | F | P |
|---------------------------|----------------------|--------|--------|
| <i>Variables included</i> | | | |
| Constant | -4.56 \pm 1.67 | 7.46 | <0.007 |
| SEEPWEED | 0.15 \pm 0.13 | 147.67 | <0.001 |
| DROPPINGS | -0.40 \pm 0.11 | 13.55 | <0.001 |
| HOOR | 9.80 \pm 3.32 | 8.64 | <0.004 |
| <i>Variables excluded</i> | | | |
| HALOPHITES | | 0.04 | 0.823 |
| SALSOLA | | 0.08 | 0.782 |
| ESPARTO | | 0.89 | 0.347 |
| WEATGRASS | | 0.05 | 0.817 |
| HERBACEUS | | 0.17 | 0.670 |
| CLAYED | | 2.67 | 0.104 |
| PLOWED | | 0.12 | 0.729 |
| SALT | | 0.00 | 0.988 |
| STUBBLE | | 0.14 | 0.705 |
| LAGOON | | 0.69 | 0.406 |

where this grasshopper occurs. Dropping counts could help to improve management decisions related to compliance with legislation regarding livestock activities and habitat and species conservation. The estimate of droppings is even more important in our study if we consider that inland hypersaline habitats of *M. wagneri* are, by extension, shared by many macroinvertebrate species of great conservation interest within territories of high conservation concern. These include rare and fragmented taxa adapted to salinity, endemics dependent on salted soils, halophilous vegetation, or terrestrial steppic macroinvertebrates that find refuge from agriculture in these hypersaline ecosystems (Williams 1973, Ribera and Blasco-Zumeta 1998, Ribera 2000, Martín-Herrero et al. 2003, Abellán et al. 2005, Cordero et al. 2007a, Cordero and Llorente 2008, Pichaco-García and Ramos 2016).

We highly recommend the use of electric shepherd fencing around all sensitive and protected areas where inland hypersaline ecosystems are present in order to deter livestock. We also recommend intensive educational campaigns for farm owners and shepherds, showing the ecological importance of these singular and unique habitats for rare and exclusive species of plants and invertebrates.

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The lesser mottled grasshopper, *Stenobothrus stigmaticus*: lessons from habitat management at its only site in the British Isles

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Abstract

The lesser mottled grasshopper, *Stenobothrus stigmaticus*, occurs at a single site in the British Isles. This paper describes the history of site protection and management over 30 years including the introduction of conservation grazing management. Successes have been limited, but this has been due largely to issues around recreational access and stakeholder engagement rather than lack of ecological understanding. Despite severe challenges, sufficient experience has been gained to be confident that grazing by sheep can assist in re-establishing the grasshopper over areas of a protected site from which it is now absent or present in only scattered colonies. The grasshopper requires a short, open grassland and pockets of such vegetation occur naturally because of rabbit-grazing and thin, nutrient poor, free-draining soils around rocky outcrops. These small areas have proved to be critical to the species persistence and provide a nucleus from which spread can occur. Grazing management has involved complex negotiations with multiple stakeholders, including landowners, their agents, the landowners' tenants, and the tenants' graziers. Public access, cases of dogs worrying grazing livestock, and objections over the introduction of fencing in a once open landscape have made negotiations more difficult. Future success requires that these issues be addressed. Observations on a golf course within the site, with a remnant population of the grasshopper, suggest that winter-cutting of grassland may be a useful supplement to grazing management while such difficulties remain.

Key words

dogs, golf course, grazing, heathland, Isle of Man, mowing, protected area, recreation pressure, sheep worrying

Introduction

The lesser mottled grasshopper *Stenobothrus stigmaticus* (Rambur) (Orthoptera: Acrididae: Gomphocerinae) is widespread in western, central and eastern Europe, but is often locally uncommon and declining because of habitat loss and abandonment of grazing on its favored agriculturally marginal habitats (Detzel 1998, Benton 2012). In common with many threatened species, there is a body of evidence describing the species distribution, but limited autecological information, and even less practical knowledge on how its habitat should be managed. In this paper, we review the species habitat

requirements with a focus on central and north-west Europe, and provide a detailed case study of the successes and failures of conservation grazing management at the species only known site in the British Isles (Ragge 1965, Cherrill 1994, Benton 2012). We aim to provide an informed basis for future conservation management of the species here and elsewhere in north-west Europe.

Habitat associations

Throughout its range, *S. stigmaticus* is restricted to semi-natural habitats which have not been subjected to agricultural improvement through re-seeding or addition of artificial fertilizers (van Wingerden et al. 1992, Detzel 1998). Consistent features of sites occupied by *S. stigmaticus* are that they are warm and dry, with nutrient poor, free-draining soils supporting short open vegetation (van Wingerden and Dimmers 1993, Detzel 1998). The geology appears unimportant since the species occurs on sites with acidic and calcareous soils.

The habitat of *S. stigmaticus* has been described variously as heath and dry grassland (Harz 1975, Detzel 1998, Behrens and Fartmann 2004), chalk grassland (Hoffmans et al. 1989), moorland and clearings in planted woods (Holst 1986), warm, dry places with very short grass (Bellman 1988, Johannesen et al. 1999), *Deschampsia flexuosa* grasslands (van Wingerden et al. 1991a), inland sand dunes (Detzel 1998), *Carex arenaria* river dunes (van Wingerden and Dimmers 1993), dry acidic *Nardus* pastures with a mosaic of dwarf scrub heath, and dry base-rich *Bromopsis* grasslands (Detzel 1998).

The habitat of *S. stigmaticus* on the Isle of Man accords with that reported elsewhere in Europe. The population occurs at greatest densities in areas with short grassland, heath, and well-drained maritime grassland on rocky cliff tops (Cherrill 1994, Cherrill and Selman 2002) (Figs 1, 2). Highest densities occur in areas of short grass-dominated turf (less than 15 cm tall). Inter-specific comparison of species' microhabitat selection is useful to place the requirements of *S. stigmaticus* in context. On the Isle of Man, *S. stigmaticus* co-occurs with *Myrmeleotettix maculatus* (Thunberg) (Orthoptera: Acrididae: Gomphocerinae) in areas with short turf (< 5cm) and bare ground, but also extends into taller sparsely tus-

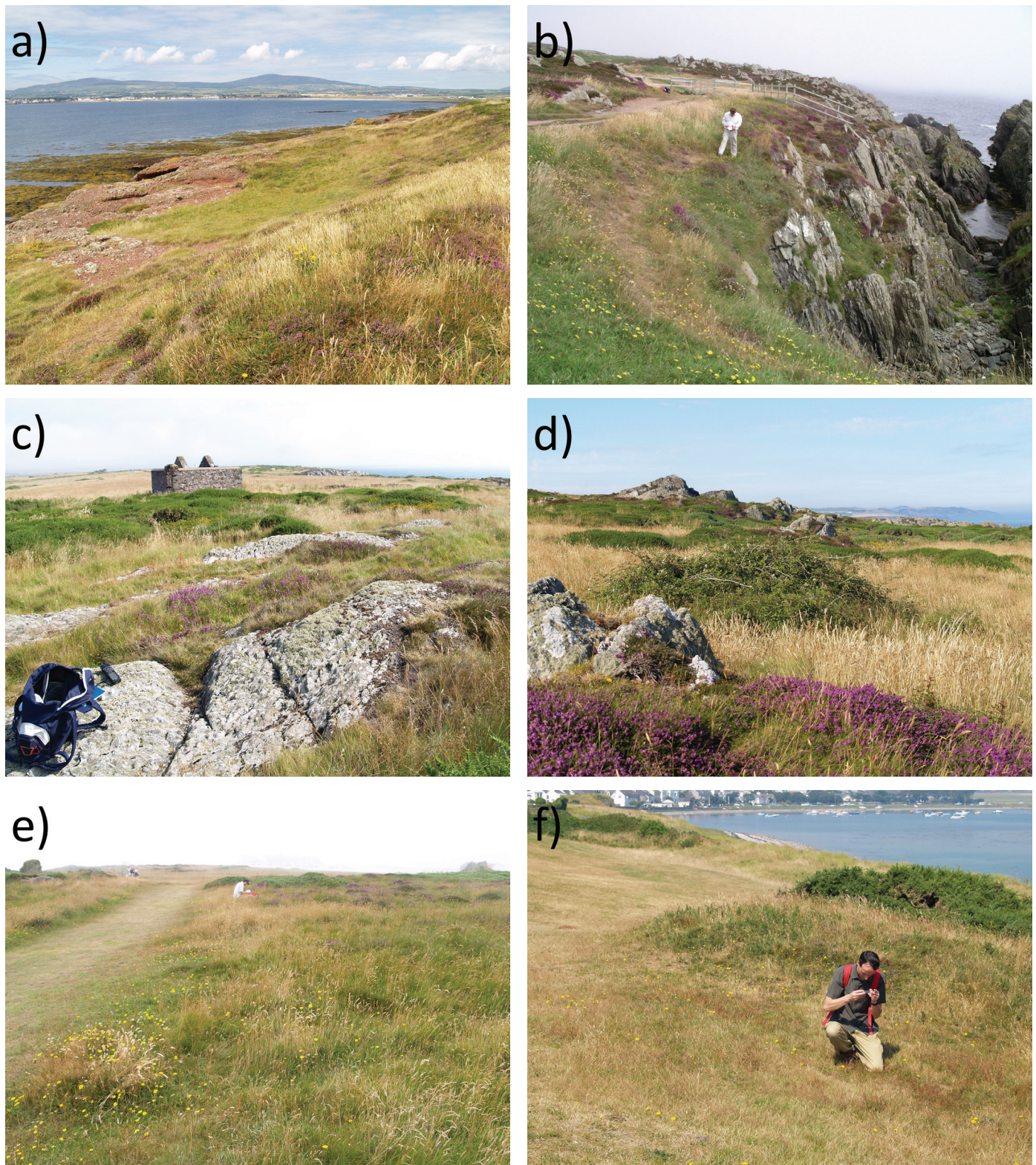


Fig. 1. Langness Peninsula in July 2006: A. and B. Short grassland supporting *S. stigmaticus*, *M. maculatus* and *C. brunneus* around rocky outcrops above the shore (with AJC taking notes); C. short grassy heath supporting *S. stigmaticus* near the mid-line of the peninsula; D. tall grassland and gorse near the mid-line of the peninsula with scarce *S. stigmaticus* restricted to short grass close to rocks and *C. brunneus* throughout; E. a path with *S. stigmaticus* occurring immediately adjacent and *C. brunneus* extending into the taller grassland beyond; and F. a patch of semi-rough (with RGS inspecting a grasshopper) and a grassy mound supporting *S. stigmaticus* and *C. brunneus* within the golf course.

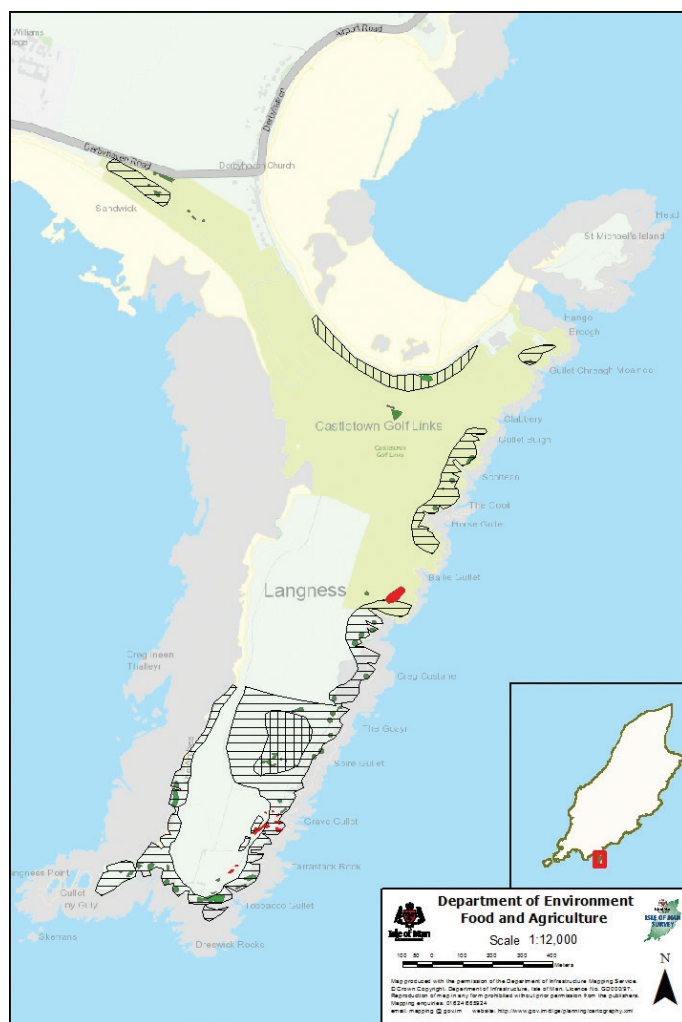


Fig. 2. Aerial photograph of Langness, showing the area covered by the golf course (light green), the distribution of *S. stigmaticus* in August 1964 (vertical hatching), 1990 (horizontal hatching), and sites occupied from 2002 in the absence of grazing (dark green) and sites occupied from 2002 where grazing had been reintroduced (red) (based on mapping by Mr. J. F. Burton reported in RPS Clouston (1990), Cherrill (1990, 1994) and subsequent observations by the authors).

socky vegetation (up to approximately 15 cm) occupied by *Chorithippus brunneus* (Thunberg) (Orthoptera: Acrididae: Gomphocerinae) from which *M. maculatus* is absent. Moreover, while *M. maculatus* is strictly associated with patches of bare ground, this is not the case for *S. stigmaticus*, and of the three species, only *C. brunneus* occurs in the tallest grassland (>15cm). Thus, compared with the two species with which it coexists, *S. stigmaticus* typically occurs in grass of short to intermediate height, and is often but not exclusively associated with patches of bare ground. A similar situation is reported by Behrens and Fartmann (2004) in Germany. The habitat requirements of *S. stigmaticus* appear to be linked to the warm, dry conditions needed for egg development, feeding on fine-bladed grasses such as *Festuca rubra* L., and thermoregulation of nymphs and adults (van Wingerden et al. 1991b, Isern-Vallverdu et al. 1995, van Wingerden and Hereen 1998, Länder 2000).

Livestock grazing is important in maintaining habitat for *S. stigmaticus*, although at some sites grazing by wild deer and rab-

bits appears to be sufficient (van Wingerden and Dimmers 1993, Detzel 1998). Sheep grazing is a common form of management in many areas with *S. stigmaticus* and extensive sheep grazing is therefore a recommended form of vegetation management for this species in Germany (NLWKN 2011), although cattle, horses and goats can also produce a suitable sward (van Wingerden et al. 1991a, Jauregui et al. 2008, Elligsen et al. 2010, Werkgroep Saltabel 2017).

The lesser mottled grasshopper on the Isle of Man

The population of *S. stigmaticus* on the Langness Peninsula represents the species' northernmost outpost in Europe and is the species' only known location in the British Isles (Ragge 1963, Benton 2012). The population provides an example of a thermophilous species at the northern edge of its distribution. Such populations are often susceptible to extinction through degradation of habitat quality (Benton 2012).

The Langness Peninsula is approximately 2.5km long and 0.5km wide, and is formed from a rocky islet connected to the main island by a sand tombolo (Fig. 2). The landward section of the peninsula is dominated by a golf course laid out in the early 1900s and redesigned in the late 1940s. The original vegetation is thought to have been a maritime grassy heath (Radcliffe and Garrad 1990). Semi-natural grassland and dwarf shrubs still occur, particularly along rocky outcrops above the eastern shoreline, and dune-like vegetation occurs on blown sand in limited areas on the western shore and within the golf course. The golf course is thought to have been grazed by sheep over winter in the 1940s and 50s but has since been ungrazed. The golf course is currently managed by mowing. The semi-roughs and roughs include small areas of remnant or recreated semi-natural vegetation.

The southern (seaward) end of the peninsula has a rocky shoreline on all aspects. Maritime grassland, with scattered heath, occurs near the shore. Inland is unimproved grassland, heathland around scattered rock outcrops, and a ploughed field (which has been cultivated in recent years for cereals grown under organic principles and to promote rare arable weeds after many years of abandonment). Until 1987 the southern end of the peninsula was grazed by sheep and cattle on an extensive basis (Selman 2012).

The grasshopper was present at a small number of scattered locations within the golf course in 1964 and this has remained the case, but since discovery its main distribution has always been in the less intensively managed southern part of the peninsula (Burton 1965, RPS Clouston 1990, Cherrill 1994) (Fig. 2). In the 1980s, attention was focused on the grasshopper as a result of a plan to extend the golf course into the southern part of the peninsula. This culminated in a Public Inquiry, rejection of the planning application and ultimately contributed to the decision to designate Langness Peninsula as the Langness, Sandwick and Derbyhaven Area of Special Scientific Interest (ASSI) under the Wildlife Act (1990) in 2000. The grasshopper, *S. stigmaticus*, had previously been listed in Schedule 5 of the Act, prohibiting intentional (and more recently, reckless) damage to the species or its habitat. These developments facilitated the reintroduction of grazing to the southern end of the peninsula in 2003 as part of a Management Agreement between the owner and the Department of Agriculture, Fisheries and Forestry (DAFF) (which in 2010 was absorbed into the new Department of Environment, Food and Agriculture (DEFA)).

The following sections focus primarily on grazing management in the southern half of the peninsula, although lessons arising from mowing within the golf course are summarized. The article is based mainly on unpublished reports (Cherrill 1990,

Cherrill and Selman 2002, 2006, Selman 2009, 2012, 2014, 2017), material recorded in the site management files and based on ongoing discussions with stakeholders variously involved with the site. Recording of the species distribution and abundance was semi-quantitative and undertaken by walk surveys in warm, sunny weather when nymphs and adults were active. Photographs taken in July 2006 are included to illustrate key habitat features (Fig. 1).

Fifteen years without grazing: 1987–2002.—Following limited survey work in the early 1960s (Burton 1965), there were no further searches for *S. stigmaticus* at Langness until the Public Inquiry stimulated an investigation in 1990 (Cherrill 1990, 1994) (Fig. 2). This revealed that *S. stigmaticus* was abundant in maritime heath and grassland along the rocky shores in both the north and south halves of the peninsula (Fig. 1A, B). It was also abundant on a block of heath and around rocky outcrops in areas of the unimproved grassland in the center of the southern part of the peninsula (Fig. 1C). Twelve years later, and after 15 years without livestock grazing, a new survey confirmed the presence of *S. stigmaticus* in the same general areas identified in 1990. The grasshopper had, however, become less abundant and its distribution was more fragmented than that described in 1990 (Cherrill and Selman 2002) (Fig. 2). The co-occurring species, *M. maculatus*, had also become less common, supporting observations of a reduction in area of the short turf required by both species. Whereas in 1990, *S. stigmaticus* occurred in almost an unbroken ribbon in grassy heath above rocky shores, by the early 2000s small colonies were isolated on south-facing slopes, particularly at the heads of rocky gullies leading down to the sea where wind exposure, thin soils on steep slopes, salt spray and rabbit grazing limited grass growth (Cherrill and Selman 2002, 2006) (Fig. 2). These areas have been critical for the persistence of *S. stigmaticus* in the absence of livestock grazing.

Away from the shore, *S. stigmaticus* appeared to be even more dependent on localized rabbit grazing and the presence of thin, free-draining soils around rock outcrops. The species had declined more sharply than seen near the shore, and was restricted to patches of short grassland associated with rock outcrops (Fig. 1C) and along the edges of heavily trampled footpaths (Fig. 1E). Grassland, between rock outcrops and on deeper soils and with little grazing by rabbits or trampling by walkers, was knee-high with a thick layer of dead litter (Fig. 1D), whereas it had been only ankle-high with patches of bare ground in 1990. Paths crossing gorse heath in the center of the peninsula had also become impassable to walkers by the early 2000s. Many such areas occupied by *S. stigmaticus* in 1990 did not support the species in 2002 because of the taller vegetation and accumulation of leaf litter.

Grazing reintroduced under a Management Agreement: 2001–2012.—By 2000, and the designation of the ASSI, it was already apparent that a re-introduction of grazing was desirable. DAFF established a Management Agreement with the owners of land in the south of the peninsula to run from 2001. A key aim was to bring habitat back to suitable condition for *S. stigmaticus*. This was facilitated with an annual payment to compensate for the challenges of conservation grazing and payment of the costs of fencing.

The fencing was put up in 2002/3, but there was outrage reported in local newspapers against the aesthetic impact, and because fences blocked the routes of some of the paths used by local people for recreation, though access was retained across the area (except the arable field) (Cannan et al. 2008). Access had been allowed previously by permission of the landowners and had become expected by local residents, though the only designated

rights of way were along the highways. The matter came to a head in 2005 when the south-western point was closed to public access by the landowners, utilizing new fences, in an effort to protect their privacy in adjacent buildings. A campaign group was set up and demanded the designation of rights of way, including access across this area. This led to negotiation via a political delegation (Cannan et al. 2008), and when that failed, another Public Inquiry. A legal determination in the High Court resulted in the designation of a network of footpaths in 2012. Throughout this period, the grazing management of the land was hampered because the issues of access, grazing and fencing became entangled. It became particularly difficult to achieve consistent grazing due to instances of walkers' dogs worrying the sheep, which dissuaded the tenant from stocking the land. Another unintended consequence of fencing was that a few paths, previously kept open by trampling, were cut off by the fences and rapidly became overgrown. The mid-lines of footpaths were never suitable for *S. stigmaticus*, but where short trampled turf graded into taller vegetation, suitable habitat resulted (Fig. 1E).

There was sheep grazing from 2002 to 2004, but then a change of land ownership necessitated renegotiation of the Management Agreement and sheep worrying issues started in 2005, which made this more challenging and added to the access discussions. As a result, grazing was not re-established until 2007, when a Management Agreement was made with the new owners specifying stocking rates equivalent to approximately 4 to 5 sheep per ha for a minimum of eight months per year. The agreement permitted the use of cattle as an alternative, but it was sheep grazing that was taken up. Grazing by sheep then continued until 2009, but because of the dog attacks the full eight-month prescription was achieved in only one of those three years. Between 2005 and 2009, around a dozen lambs and ewes were killed outright, chased over cliff edges to their deaths, or had to be euthanized after being mauled by dogs or injured on the rocks.

Despite these problems, grazing had some positive impacts on the grassland structure. Surveys in 2006 and 2009, showed the extension of *S. stigmaticus* from remnant colonies at the heads of gullies above the shore, into grassland towards the center of the peninsula where the species had been recorded in 1990 but not in 2002. In 2006, this was evident in one area even though the area had been ungrazed for the two years previous, but having received sheep grazing for two years before (Selman 2009).

In limited areas, grazing created a structure that allowed the spread of *S. stigmaticus* from isolated remnant colonies, but this never reached the level necessary to have an impact on the distribution of *S. stigmaticus* across the whole site. Fundamentally, there were too few sheep for too short a period each year.

With continued problems around public access and dog attacks, there was again no grazing in 2010 and only brief grazing by a couple of horses in 2011, with little effect on the habitat. From the start of the dog issues there had been discussions regarding the need for livestock that would accept rough herbage, be robust against dogs, yet be safe around walkers. Highland cattle were favored but unfortunately were not available. Some provisions for cattle grazing had been provided in the Management Agreement from the start of the project, but cattle were eventually brought to the site as an alternative to sheep grazing, when four 8-month old heifers of modern breeding were introduced in 2012–2013. Survey in 2014 found *S. stigmaticus* in the center of the field, away from the coastal remnant colonies, but not across large areas of it, due to the grazing intensity remaining too low (Selman 2014). Subsequently with the end of the Management Agreement in 2012 there has been only very limited consented grazing by sheep and ponies

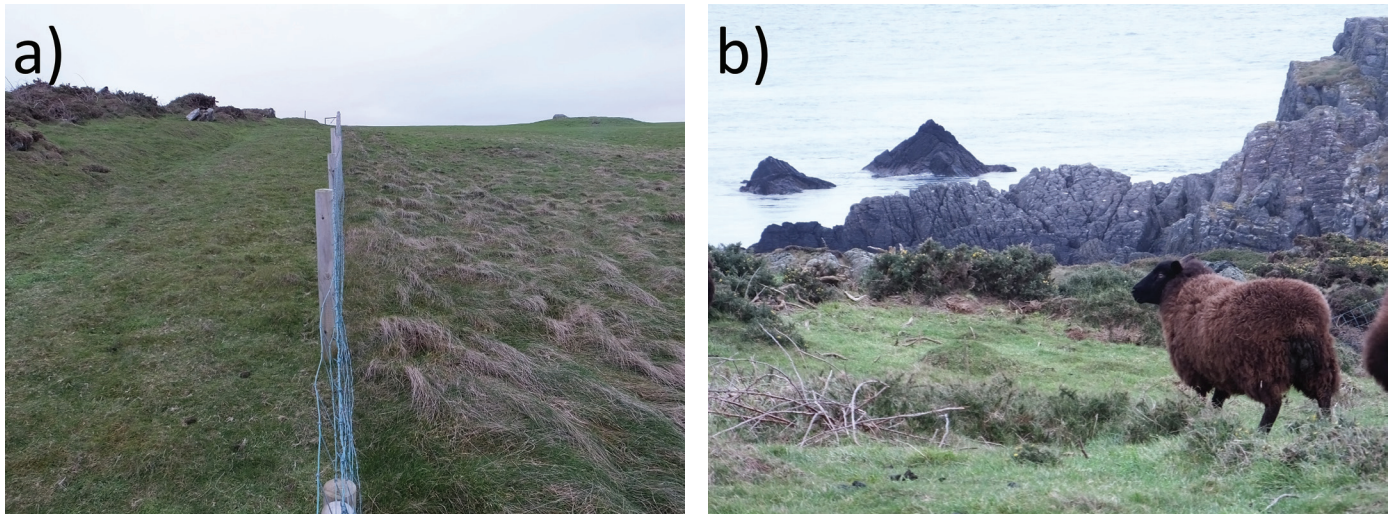


Fig. 3. The impact of targeted grazing in January 2017 after clearance of gorse two years earlier, A. vegetation either side of fencing; B. hardy Welsh Mountain- Texel cross sheep grazing on-site.

at levels insufficient to maintain habitat suitable for *S. stigmaticus*. A new Management Agreement is being negotiated with the landowner, who wishes to introduce Highland cattle.

As with discussions around the access issue, progress with grazing has been hindered by long lines of communication between the officers of DEFA, the landowners, their agents, the tenant, and the tenant's grazier. This produced complex and slow negotiations around issues arising. Moreover, no one lives permanently on the peninsula who can address issues as they occur.

Overall, the Management Agreement failed to deliver the desired outcomes at a large scale due to the prescription not being delivered fully, but did demonstrate that improvement in habitat suitability and population size of *S. stigmaticus* are achievable if grazing is managed effectively.

Small scale mitigation works and targeted gorse clearance.—In 2015, the relocation of a golf course fairway was accompanied by ecological mitigation work agreed with DEFA as part of planning consent. An area of 2.5 ha was targeted for the clearance of gorse from around rocky outcrops known to have supported a single *S. stigmaticus* on a tiny rabbit-grazed patch in 2002. After gorse was removed the area was fenced off and grazed with barren ewes at a stocking rate of approximately 13 ewes per ha for several months in spring, and then again in the autumn. These were then replaced with similar numbers of yearlings (born that year and just weaned) which have grazed each year from September/October to May/early June in both 2016 and 2017. By the summer of 2017, the site was looking ideal for *S. stigmaticus* with short grass, outcropping rocks and a south-facing slope at the head of a gully leading down to the shore (Fig. 3). A small number of *S. stigmaticus* were found in July 2017, within grassland and heath on a short headland in an area that was occupied by *S. stigmaticus* in 1990, but not in the early 2000s, demonstrating the potential for successful habitat restoration through targeted gorse clearance and grazing when the opportunity arises (Selman 2017).

Management within the golf course

Preliminary observations suggest that on the course, *S. stigmaticus* is restricted to grassland similar in structure to its habitat

elsewhere on the peninsula. In the summer, fairways and the semi-roughs (between fairways and roughs) are cut weekly to about 10 mm and 16 mm respectively. *S. stigmaticus* is absent from fairways, but occurs in some areas of semi-rough. It is unclear whether *S. stigmaticus* survives mowing or if semi-rough represents a sink-habitat for grasshoppers dispersing from adjacent rough where scattered colonies occur. In the roughs, *S. stigmaticus* is found on mown areas, and on unmown but dry free-draining mounds of semi-natural grass (Fig. 1F). Cutting of roughs occurs once a year in winter with a flail mower, and some areas are also slot-tined to improve drainage. Adjacent unmown roughs, away from mounds, have damper, thicker grassland and these areas always lack *S. stigmaticus*.

Mowing in summer can be highly damaging for nymphs and adult grasshoppers (Gardiner and Hill 2006, Humbert et al. 2010), but our observations suggest that an autumn or winter cut, while the grasshopper is in the egg stage, can help maintain suitable habitat (Selman 2009, 2014). Research on the effects of mowing would be useful. The effects on grasshopper eggs of chemical, biological and physical methods to control leatherjackets (the subterranean larvae of Tipulid flies) (Christians et al. 2016) also warrant investigation. Areas of rough, some supporting *S. stigmaticus*, were previously treated with the insecticide chlorpyrifos during winter with unknown consequences for grasshopper eggs (Selman 2012).

Overview of grazing impacts and future prospects

Over 25 years of observations at Langness suggest that re-introducing grazing will allow *S. stigmaticus* to spread beyond its current strong-holds around rocky outcrops where grass is naturally short and sparse as a result of thin soils, salt spray and rabbit grazing. Overall, these observations accord with those from elsewhere in Europe. In the Netherlands, the population density of *S. stigmaticus* was found to increase in response to grazing of tall grasslands by cattle (van Wingerden et al. 1991a), and Jauregui et al. (2008) found a similar result using goats to graze a dwarf-shrub heath in north-west Spain. The need to carefully monitor grazing has been demonstrated at some continental sites, however, because heavy grazing in nutrient poor dry grasslands with very short turf can suppress densities of *S. stigmaticus* (van Wingerden and Dimmers 1993).

Since 2002 there have been some beneficial changes in management for *S. stigmaticus* at Langness, and an improved local recognition of the areas of importance for this species and its requirements, but there have also been some challenges and the beneficial effects have mostly been localized. The major management problems encountered have been socio-economic, resulting from difficulties in sourcing suitable livestock and the unintended consequences of fencing and recreational activity, rather than shortfalls in ecological knowledge. Grazing remains the preferred solution for achieving suitable habitat, but mowing in winter may need greater consideration because of continued problems in integrating livestock with public access.

Conclusions

Conservation action for *S. stigmaticus* has, in summary, now included species protection (1990), site protection (2000), distribution mapping (1964 onwards), management agreements for fenced grazing funded through agri-environment payments (2001–2012), consented grazing (discussion ongoing post-2012), and gorse clearance with fenced grazing facilitated as mitigation for development (2014 onwards). This has achieved a level of confidence that key areas can be retained in future and has had success in improving *S. stigmaticus* habitat in some areas, but not on the scale hoped for.

Key lessons are to: a) minimize restrictions on grazing, stating what habitat structure we need rather than prescriptive management techniques, as we have not experienced overgrazing but have frequently encountered undergrazing, so a flexible approach to grazing opportunities may be necessary; b) attempt the simplest agreement and communication route between the paying organization and the grazier; c) consider setting up a public forum for management discussions, if the landowners are happy to do this, with the benefits of encouraging public buy-in to a management strategy and the potential for minimizing problems arising from recreational access with dogs; d) consider winter cutting techniques outside of the golf course, that avoid significant risks to grasshoppers but which might allow management in areas where grazing is not currently possible; and e) continue to explore opportunities for small-scale targeted scrub control, particularly around rock outcrops, followed by grazing, where practicable, though rabbits can also help control scrub following cutting.

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The effects of grazing and mowing on large marsh grasshopper, *Stethophyma grossum* (Orthoptera: Acrididae), populations in Western Europe: a review

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Abstract

The large marsh grasshopper, *Stethophyma grossum* L. (Orthoptera: Acrididae), has undergone a significant range contraction in the UK and is now restricted to the bogs and mires of the New Forest and Dorset Heaths. In other parts of Western Europe, the species makes use of a wider range of wetland habitat types. Traditionally, many of these habitats would be managed through low intensity grazing, mowing, or both, and these measures are now often employed in the conservation management of wet grassland habitats. This paper reviews the effects of mowing and grazing on *S. grossum* populations, through looking at the potential impacts (both positive and negative) on different life stages of the grasshopper. Both techniques are valuable in the maintenance of an open and varied vegetation structure which is known to benefit *S. grossum* in all its life stages. However, grazing on very wet sites or at high intensity can result in trampling of vegetation and *S. grossum* eggs, and mowing which is too frequent may negatively affect populations through repeated losses of nymphs. Recommendations are given regarding the suitability of mowing and grazing for different habitats and intensity of management to generate the required vegetation structure. Measures are also outlined, such as the provision of unmown or ungrazed refuge areas, which can help reduce negative effects.

Key words

adults, biodiversity conservation, bog, eggs, grassland, management, mire, nymphs, vegetation structure, wetland

Introduction

Grazing and mowing exert important influences on vegetation structure and are therefore key factors affecting grasshopper populations (Clarke 1948, Gardiner et al. 2002, Humbert et al. 2009, Kenyeres and Szentirmai 2017). Rare and localized species, such as the large marsh grasshopper, *Stethophyma grossum* L. (Orthoptera: Acrididae), have very specific micro-habitat requirements which can be influenced by grazing and mowing. In the UK *S. grossum* is a priority species under the NERC Act 2006 and has a GB IUCN status of Near Threatened (Sutton 2015). It has undergone the largest range contraction of all the UK Orthoptera between the

1980s and 2000s (Beckmann et al. 2015), and is currently confined to the Dorset Heaths and New Forest. In Europe, it is locally distributed with an IUCN status of Least Concern (Hochkirch et al. 2016), however, in Switzerland and Austria it is listed as Vulnerable (Berg et al. 2005, Monnerat et al. 2007) and in Denmark it is considered Near Threatened (Wind and Pihl 2010). It is the aim of this paper to describe what is known about the links between the life cycle and habitat requirements of *S. grossum* and provide a discussion of the benefits and disadvantages of mowing and grazing for the management of this species in Western Europe.

Stethophyma grossum distribution and life history

Stethophyma grossum (Figs 1, 2) is locally distributed across Europe and found from Ireland in the west, northern Spain and Italy in the south, east to Siberia and north as far as parts of Scandinavia (JNCC 2010, Benton 2012). In the UK, its former distribution was in suitable habitat south of a line from the Bristol Channel to the Wash, although it has experienced a sharp contraction in its range and is now confined to the *Sphagnum*-dominated bogs and mires of east Dorset and the New Forest (Benton 2012). Populations are thought to have been relatively stable in the New Forest over the last 20 years, and there is potential for the species to benefit from mire restoration projects underway in the Forest (Harvey and Brock 2017). In Ireland, the species is found primarily in bogs and mires, with some records from more grassy habitats, and it is locally distributed across the west, south-west and central parts of the country (Sutton 2017).

S. grossum is herbivorous, feeding on the stems and seed heads of grasses, rushes and sedges (Benton 2012). Adults can be seen from late July through to October or even early November (Haes and Harding 1997, Benton 2012). They lay up to 14 eggs in the late summer in an elongated pod at the base of grass stems (Benton 2012). The nymphs usually emerge in late May and early June the following year and pass through four or five instars before reaching the adult stage in late summer (Evans and Edmondson 2007, Benton 2012).



Fig. 1. Female *Stethophyma grossum* purple form; credit P. Brock.



Fig. 2. Male *Stethophyma grossum*; credit P. Brock.

Habitat types used by *S. grossum*

In the UK, *S. grossum* is typically found on quaking acid bogs with purple moor-grass, *Molinia caerulea* (L.) Moench, bog myrtle, *Myrica gale* L., cross-leaved heath, *Erica tetralix* L., broad-leaved cotton grass, *Eriophorum latifolium* Hoppe, and white beak-sedge, *Rhynchospora alba* (L.) Vahl (Haes and Harding 1997, Edwards 2002,



Fig. 3. *Sphagnum*-dominated mire in the New Forest, UK; habitat for *Stethophyma grossum*; credit T. Gardiner.



Fig. 4. *Metrioptera brachyptera*; credit T. Gardiner.

Benton 2012). In the New Forest in southern England (Fig. 3), it shows a preference for *Sphagnum*-dominated mires with open water and wet areas indicated by cotton grass, and often coexists with the bog bush-cricket, *Metrioptera brachyptera* L. (Orthoptera: Tettigoniidae; Fig. 4) (Benton 2012, Harvey and Brock 2017). Similarly, Cheesman and Brown (1998) report that *S. grossum* occurrence shows a positive correlation with area of surface water, cover of *Sphagnum* and white beak-sedge and a negative correlation with ericoids and sub-shrubs. The species typically inhabits the wettest parts of such habitats (Ragge 1965), and has even been observed swimming across bog pools in the New Forest (Gardiner 2013).

Its former distribution in the UK and current distribution in the rest of Western Europe shows a wider habitat usage, including areas of fenland, moorland, wet meadow and riverside (Benton 2012). Lucas (1920) noted a record of the species from Norfolk in 1892 occurring in tall rank grass close to a river bank and Marshall and Haes (1988) suggested that the few remaining fenland populations in England at that time were found in very wet conditions among sedge and grass tussocks.

Malkus (1997) noted that vegetation structure appeared to be particularly important in determining distribution of *S. grossum*, with nymphs being predominantly found in areas with patchy and medium-high vegetation. An open habitat structure (determined by vegetation height and density) is thought to be beneficial in allowing sufficient warming of the ground and the base of the vegetation to promote egg development and hatching (Malkus 1997, Marzelli 1997, Maas et al. 2002). A study by Krause (1996) in Germany found that tufted hair grass, *Deschampsia cespitosa* (L.) P. Beauv., held high densities of early instar nymphs and postulated that the growth form of this plant was favorable at the time of hatching, being lower and less dense than other vegetation in the study area. Decler et al. (2000) and Thorens and Nadig (1997) also recognize a link between periodic/winter flooding and *S. grossum* occurrence, which may be due to the high humidity requirements of *S. grossum* eggs and their sensitivity to dehydration (Detzel 1998, Maas et al. 2002).

Table 1 summarizes the general habitat types currently used by *S. grossum* in Western Europe. A wide variety of wet habitats are used, some of which will provide the required vegetation structure through management by mowing and/or grazing.

Effects of mowing and grazing on life stages of *S. grossum*

The traditional management of wet hay meadows and flood-plain grasslands in Western and Central Europe centered on hay cutting and the grazing of livestock. Many wet areas were grazed by livestock at low intensities. This was sometimes combined with cutting for hay, with one early cut followed by grazing of the remnant sward. Alternatively, on some sites, hay cutting was carried out once or twice a year, typically in May-June and/or August-September (Grootjans and Verbeek 2002, Kenyeres and Szentirmai 2017).

The wet heath, mire and bog habitats of *S. grossum* in the UK and Ireland typically have a naturally open and patchy vegetation structure with areas of open water. The wettest parts of these habitats are not suitable for management by mowing or grazing, either in terms of the potential impacts on the habitat, or safety and accessibility for animals and machinery. Around the drier margins of these hab-

itats, low intensity grazing by ponies or cattle during the summer may be used to help reduce the dominance of purple moor grass and reduce encroachment of scrub (Symes and Day 2003, Lake and Underhill-Day 2004, Groome and Shaw 2015). However, grazing of the wettest areas (mires or bogs) can be detrimental through trampling damage, particularly to bog mosses, and the creation of a more homogeneous vegetation structure (Symes and Day 2003, Groome and Shaw 2015). In the New Forest, Pinchen and Ward (2010) attribute a general decline in Orthoptera to increased grazing pressure since the 1960s, with trampling and changes to vegetation structure likely to negatively affect many invertebrate species. While mires and bogs are less likely to be affected by overgrazing due to inaccessibility of the habitat, the effects of heavy grazing pressure were observed at two *S. grossum* sites in the New Forest during a recent survey (Harvey and Brock 2017).

In wet grassland habitats, sensitive management by mowing and/or grazing is considered beneficial overall to *S. grossum*. The following section discusses considerations relating to mowing and grazing of wet grassland habitats and the requirements and characteristics of *S. grossum* eggs, nymphs and adults.

Eggs.—*S. grossum* eggs require high humidity levels for successful development and are very sensitive to dehydration (Detzel 1998, Maas et al. 2002). Because of this, soils which are saturated or flooded during the winter are preferred (Malkus 1997). While *S. grossum* has relatively low temperature requirements compared to other Orthoptera (Marzelli 1997), a sufficiently open habitat structure will promote egg development and hatching (Malkus 1997, Marzelli 1997, Maas et al. 2002).

Grazing while *S. grossum* is at the egg stage may result in the direct destruction of eggs by trampling, particularly on the wettest sites (Malkus 1997), but grazing or mowing of less wet sites can help provide the necessary open vegetation structure if carried out at low intensity and avoiding very wet areas.

Nymphs.—The distribution of early instar nymphs is thought to be a product of the female choice of habitat for oviposition, as

Table 1. Habitats of *S. grossum* in Western Europe.

| Country | Habitat types | References |
|----------------|---------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------|
| Netherlands | Wet grasslands and meadows, floodplains, ditches and margins of waterbodies, fens, swamp, wet heath. | Kleukers et al. (2004), Bakker et al. (2015) |
| Belgium | Wet grasslands and meadows, swamp, bogs, ditches, wet heath. Land that is wet in winter. | Decler et al. (2000), Sardet et al. (2015) |
| France | Wetlands: marshes, reedbeds, flooded meadows, peat bogs, ditches. In the Alps, up to 2400-2700 m in altitude. | Voisin (2003), Sardet et al. (2015) |
| Luxembourg | Wet meadows, marshes, peat bogs, ditches. | Sardet et al. (2015) |
| Switzerland | Near open water or periodically flooded vegetation, wet meadows and pasture, peat bogs, ditches. Up to 2450-2700 m in altitude. | Thorens and Nadig (1997), Sardet et al. (2015) |
| Austria | Peat bogs, fens, floodplains, ridges of raised bogs. | Ortner and Lechner (2015) |
| Germany | Marshes, edges of lakes, streams and ditches, wet meadows. Up to 1300 m in altitude. | Detzel (1998), Maas et al. (2002), Fischer et al. (2016) |
| Northern Italy | Lake margins, swamps, alpine fens, wet meadows. | Galvagni (2001), Fontana and Kleukers (2002), Kranebitter (2008) |
| Northern Spain | Wet peaty meadows, peat bog, wet mown meadows, margins of ponds and rivers. | Lüders (2009) |
| England, UK | Bogs and mires in the Dorset and New Forest heaths. | Haes and Harding (1997), Benton (2012) |
| Ireland | Mire, wet heath, blanket and raised bogs, <i>Molinia</i> -dominated grassland. By rivers and lakes. | Benton (2012), Sutton et al. (2017) |
| Denmark | Raised bogs, wet meadows, nutrient-poor fen. | Hansen and Jørgensen (2010) |
| Fennoscandia | Bogs, meadows, by lakes and streams. | Holst (1986) |

young nymphs have limited mobility and therefore do not tend to disperse from their hatching location (Marzelli 1997). Malkus (1997) found that patchy vegetation with a heterogeneous structure was preferred by nymphs. As above, low intensity grazing may provide the necessary diversity in sward structure.

Mowing can have a significant effect on the density of nymphs. If mowing takes place during the early summer, the density of early instar nymphs is likely to drop significantly afterwards (Krause 1996, Malkus 1997, Marzelli 1997, Detzel 1998). Due to the limited mobility of young nymphs, they are not able to take evasive action, and may either be directly killed, removed with the hay crop or made more vulnerable to dehydration and predation (Krause 1996, Malkus 1997). Malkus (1997) observed a collapse in nymph numbers after mowing in mid-June, however, after 1-2 weeks, numbers recovered as further hatching occurred, possibly promoted by the increased levels of solar radiation reaching the ground. Krause (1996) noted detrimental effects on populations affected by mowing at an early stage in nymph development. Later instar nymphs may be more able to escape mowed areas – Krause (1996) noted an increase in late instar nymph densities around ditch edges following mowing.

Adults.—Adult *S. grossum* also tend to be found in locations with relatively high soil moisture levels, perhaps due to their need to oviposit in wetter areas. Sonneck et al. (2008) propose that adults also benefit from a heterogeneous vegetation structure as this allows the adults to withstand fluctuating temperatures. Similarly, a variety of soil moisture levels within a site may allow adults to cope with varying weather conditions (Detzel 1998, Kleukers et al. 2004).

Malkus (1997) reports that mowing later in the summer (mid-July onwards) tends to displace adult *S. grossum* to neighboring areas until the vegetation regrows, when repopulation will occur. Grazing during this period has similar effects. Population effects as a result of mowing are unlikely unless the mowing is too frequent, takes place in cool weather when the grasshoppers are less active and therefore less able to take evasive action, or where unmown refuge areas are not available (Malkus 1997). Malkus (1997) also observed adults flying up in front of a mower and moving to the as yet unmown center of the field. It is therefore possible that *S. grossum* could benefit from mowing that works from the inside of the field outwards (as is sometimes employed for certain bird species, e.g. corncrake *Crex crex* L.), as animals may then be more likely to reach safe habitat outside the mown area.

Recommendations relating to mowing and grazing for *S. grossum* conservation

The following recommendations are derived from the studies of *S. grossum* populations in Western Europe and are relevant to the management of wet grasslands including wet meadows and pasture, floodplain grassland and fens. As discussed above, *S. grossum* is currently only found in valley mires and bogs in the UK (and predominantly so in Ireland), therefore many of these recommendations will not be directly applicable to UK and most Irish populations. In mire and bog habitats, management should focus on protecting sites from activities likely to cause drying, although removal of encroaching scrub and/or management of dominant grasses or bog myrtle may occasionally be required on the drier margins of such sites.

Mowing.—A sensitive mowing regime can be beneficial for the management of wet meadows for *S. grossum* (Krause 1996, Sörensen 1996, Marzelli 1997, Malkus 1997, Detzel 1998). While it

may cause short-term reductions in the numbers of grasshoppers (particularly early stage nymphs), if carried out with regard to their lifecycle, careful mowing can have positive effects on egg and nymph development by maintaining a more open vegetation structure, thus raising ground temperatures. Insufficient, irregular, or mowing only in the late summer may have negative effects through matting of the turf (Malkus 1997, Detzel 1998). However, there are some differences of opinion as to the optimum time for mowing. Krause (1996) recommends one late cut in August, by which point most individuals should be adults and able to move to an adjacent area. Marzelli (1997) recommends two cuts – one at the beginning of June before the eggs hatch and one in mid-September after oviposition. She also notes that mowing in July was particularly damaging to populations. Malkus (1997) recommends that mowing should take place once and, at most, twice a year. He points out that the timing may also need to take other grassland species into account – if amphibians or ground-nesting birds are present, early cuts should not take place before mid/end June and the late cut should be after mid-September.

It would therefore appear that wet grasslands managed for *S. grossum* should be cut at least once (though no more than twice) a year, depending on site-specific habitat needs, and with the aim of avoiding the vulnerable early nymph stage. If an early cut is required, ideally this should be before *S. grossum* has hatched, but the needs of other species present should also be considered. If a late summer cut is required, this should be after mid-September when most of the egg-laying is complete. In order to minimize mortality of grasshoppers (and other invertebrates), the use of a bar mower (rather than a rotary or flail mower) set to a minimum height of 10 cm is recommended (Humbert et al. 2009, Kenyeres and Szentirmai 2017). Malkus (1997) also makes further recommendations to reduce mortality of *S. grossum* during mowing: mowing should only take place in warm, sunny weather, to allow grasshoppers to escape; retain the hay on the surface for a few days following the cut, again to allow grasshoppers to escape; and unmown areas should be retained close to the mown area, to provide a refuge.

Grazing.—Low intensity grazing is a useful method for managing vegetation height and density and tends to create a more varied vegetation structure than mowing alone (Lake and Underhill-Day 2004). Grazing can also help prevent scrub encroachment and reduce cover of dominant species (Symes and Day 2003, Lake and Underhill-Day 2004, Groome and Shaw 2015), thus helping to maintain the open vegetation structure required by *S. grossum*. As well as having similar displacement effects to mowing, grazing has the potential to cause damage to habitats and destruction of *S. grossum* eggs through trampling (Malkus 1997, Groome and Shaw 2015). It is therefore important to select an appropriate livestock type and stocking rate for the habitat type; ponies will tend to create a more homogeneous sward than cattle (particularly if grazed at high stocking rates), although cattle may be more likely to cause trampling damage (English Nature 2005). Malkus (1997) recommended that grazing in general should be carried out at a low stocking density and on a temporary basis and avoided completely on very wet habitats due to the risk of trampling damage. The potential negative effects of displacement of grasshoppers can be reduced by the retention of ungrazed refuge areas.

A summary of the advantages and disadvantages of mowing and grazing are presented in Table 2.

Table 2. Advantages and disadvantages of mowing and grazing for *S. grossum*.

| | Mowing | Grazing |
|---------------|--------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Advantages | Creates an open sward structure. Restricts scrub encroachment. | Creates a varied sward structure. Reduces cover of dominant grasses. Restricts scrub encroachment. |
| Disadvantages | Mortality of nymphs. Displacement of adults. Potential effects on other species (e.g. ground-nesting birds). | Poaching of wet habitats. Displacement of adults. Trampling of eggs. Overgrazing possible. Potential effects on other species (e.g. ground-nesting birds). |

Conclusions

The following recommendations for mowing and grazing as part of the management of wet grassland habitats occupied by *S. grossum* can be derived from this review:

- Grazing and/or mowing (dependent on habitat type) are valuable management techniques for the maintenance of the open and varied vegetation structure required by *S. grossum*.
- Grazing should be at a low stocking density (and, where necessary, for a limited time-period), and nearby ungrazed refuge areas should be maintained.
- Grazing of very wet areas should be avoided.
- Wet grasslands should be cut once a year, or twice at the most, depending on the vegetation type.
- If early mowing is used, this should be before the main hatching period from mid-June onwards where possible (depending on the needs of other species) and late mowing should be after the main oviposition period from mid-September onwards.

- Use a bar mower set to a minimum height of 10 cm to minimize mortality.
- Grasshoppers should be allowed to escape mowing by carrying out operations only on warm, sunny days when grasshoppers are active, retaining unmown refuge areas nearby and leaving the hay crop on the surface for a few days before removal.

The following recommendations relate to the management of wet heath, mire and bog habitats, such as those used by *S. grossum* in the UK and Ireland:

- Protect sites from activities likely to cause drying of habitats.
- Grazing (and mowing) should be avoided in the wettest areas, particularly in mires and bogs.
- If necessary, low intensity grazing could be used on the drier margins of such sites during the summer months to reduce dominance by grasses or encroachment of scrub.

Recommended management measures for habitat types used by *S. grossum* in the UK and Western Europe are summarized in Table 3.

Table 3. Appropriate management options for *S. grossum* in Western Europe.

| Habitat | Management | Frequency | Additional measures |
|----------------|----------------------------|-----------------|--------------------------------------------------------------------|
| Alpine pasture | Light grazing ¹ | 2-3 months/year | Livestock moved to valleys in winter. |
| Ditch banks | Mowing | 1-2 cuts/year | Unmown refuges (exclosures). |
| Fen | Sedge cutting | 1 cut/year | Uncut refuges (exclosures). |
| Mire/bog* | Avoid grazing | n/a | Protect from drying. May need to manage scrub encroachment. |
| Reedbed | Reed cutting | 1 cut/year | Uncut refuges (exclosures). |
| Wet heath* | Light grazing | Summer/all year | Ungrazed refuges (exclosures). Avoid grazing of very wet areas. |
| Wet grassland | Mowing | 1-2 cuts/year | Unmown refuges (exclosures). |

¹Typical stocking density: 0.1 cows/ha (Homburger et al. 2015).

*Only habitats left for *S. grossum* in the UK (Dorset, New Forest).

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