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Precipitation and habitat degradation influence the occurrence of the common green grasshopper Omocestus viridulus in southeastern England

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Abstract

Insects of mesic and hydric habitats may be affected by increased frequency of summer droughts brought about by climate change, in addition to habitat degradation caused by scrub encroachment. The common green grasshopper *Omocestus viridulus* prefers moist grassland and is relatively rare in the County of Essex, perhaps being limited by low precipitation in southeastern England. The abundance and distribution of *O. viridulus* populations were compared for high- (Epping Forest) and low-precipitation areas using Geographic Information Systems (GIS) software. Populations were aggregated in Epping Forest (population isolation: 1 km), a high precipitation area (*ca* 69 cm precipitation/yr), and present on both well and poorly drained soils where acid grassland/wet heathland occurred. Outside of the Forest, where precipitation was generally lower (*ca* 58 cm/yr), populations of this grasshopper were highly isolated (isolation: 4 km) and more often present on clay soils with high water retention in winter/early summer than on well-drained soils. However, there was no significant difference in the abundance of this grasshopper within Epping Forest or outside it, and there has likely been an overall decline of 50% since 1997 for this insect in Essex Co.

The decline has partly occurred due to unmanaged scrub encroachment and loss of favorable open grassland/wet heathland habitat. Intensive grazing (particularly by large numbers of rabbits *Oryctoloagus cuniculus*), regular mowing, and trampling by walkers, led to the creation of short swards (< 10 cm in height) in midsummer, effectively extirpating this tall-grassland grasshopper from many of its former sites not threatened by natural succession to woodland.

Unfortunately, the predicted decline in summer rainfall may lead to this grasshopper becoming scarce in southeastern England, outside of relatively high precipitation areas such as Epping Forest. Given concern about this grasshopper it may be important to prevent further drainage of ecologically valuable wetlands and to promote appropriate conservation management of the remaining sites (such as cattle grazing in Epping Forest). Large-scale wetland creation should allow populations of this declining grasshopper to exist in a changing climate.

Key words

Acrididae, climate change, grazing, GIS, Orthoptera, scrub encroachment, wetlands

Introduction

The common green grasshopper *Omocestus viridulus* (Orthoptera: Acrididae) is a widespread insect in the UK (Haes & Harding 1997); it is found from northern Scotland to the south coast of England at altitudes up to 1000 m above sea level in Scotland (Marshall & Haes 1988), 500 m in Wales (Gardiner & Gardiner 2008), and 400 m in England (Horsfield 2010). It inhabits primarily tall grasslands (Berner 2005), which are often unimproved (swards which have never been agriculturally altered through ploughing or spraying of herbicides for example) in nature (Marshall & Haes 1988), although this grasshopper was found in a recent survey (2002-2004) in pastures that were ploughed and cropped in the late 1800s in northwest Devon, UK (Gardiner *et al*. 2005b). Its large size (1-2 cm adult body length) suggests it may be intolerant of short (< 10 cm high) grassland swards, where the near-ground air temperatures (microclimate) may be very 'hot' (40 to 50^{o}C; Gardiner & Hassall 2009), as it cannot cool down quickly and may overheat (Willott 1997). Therefore, it avoids those habitats and prefers to live in tall grassland, often dominated by tussock-forming grasses such as purple moor-grass *Molinia caerulea* (Wake 1997, Gardiner *et al*. 2005b). In Culm grassland in northwest Devon, densities of *O. viridulus* in *M. caerulea* pastures were relatively low (21-119 adults/ha; Gardiner *et al*. 2005b), however, this may reflect the difficulty in detecting them visually on transects in very tall vegetation.

In Essex County, in southeastern England, *O. viridulus* is relatively rare (Wake 1997) and has been added to the Essex Red Data List (ERDL, Gardiner & Harvey 2004). The landscape of the County is dominated by intensive agriculture: 52% of the land area is cropped and 22% is pasture or mown grassland (Essex County Council 1996), habitats unlikely to be favorable for *O. viridulus*. Only 10,800 ha (3% of land cover) of rough grassland remain as habitat for this grasshopper (ECC 1996). In Essex Co. *O. viridulus* is mainly recorded from calcareous grassland, commons, wet heaths, as well as disused quarries and sand pits (see Table 1 for a description of the main habitats mentioned in this paper).

O. viridulus is a sedentary grasshopper; mark-recapture studies showed that males moved 6.7 m and females 4.3 m on average over the course of a week in an experiment by Southwood & Waloff (1967). Therefore, this species may have difficulty colonizing newly created habitats (particularly on farmland) and is a good 'indicator' of long-existing unimproved grassland (Marshall & Haes 1988). However, adult males fly rapidly and are particularly active in warm weather; the larger females do not fly as readily (Marshall & Haes 1988). *Omocestus viridulus* is herbivorous, feeding mainly on grasses, with no preference for particular species (a generalist) (Richards & Waloff 1954).

The main threats to this grasshopper in Essex Co. appear to be from habitat destruction through improvement of pastures and old grassland, scrub encroachment on commons/wet heathland (Gardiner & Gardiner 2009), summer droughts, and urban development. Small, isolated insect populations are most vulnerable to habitat change, and are easily extirpated (Gardiner *et al*. 2003). Highly isolated sites are unlikely to be recolonized by this grasshopper after local extinction. Therefore, extensive patches of wet heath and unimproved grassland are likely to be important for the continued existence of this insect, particularly in the agricultural landscape of southeastern England.

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Table 1. Description of habitats and their main plant species mentioned in this paper.

Habitat	Typical soil pH	Typical plant species	Description
Acid grassland	4-5	*Agrostis capillaris/Festuca rubra*	Short, open sparse grassland on acid soil with scattered *Ulex europaeus* and *Calluna vulgaris*.
Neutral grassland	7	*Holcus lanatus/Lolium perenne*	Short and tall swards, often on agricultural land and managed intensively (*e.g.*, heavily grazed). Can be unimproved and cut annually for hay.
Calcareous grassland	>7	*F. rubra*, very floristically diverse sward with herbs such as *Anacamptis pyramidalis*	Short and sparse swards with patches of bare earth, as well as tall herb-rich grassland cut annually for hay.
Heathland	4-5	*C. vulgaris/U. europaeu*s have > 25% ground cover, where soil is wetter *Erica tetralix* may occur as dominant undershrub and *Molinia caerulea* is the main grass species	Acid substrate (*e.g.*, gravel/sand) with coverage of heathy undershrubs, can be interspersed with acid grassland. Wet heathland often occurs on damp, poorly drained soils (*e.g.*, peat).
Fen	>7	*Carex* spp. and tall herbs (often *Filipendula ulmaria*)	Very tall and dense sward on peaty soil which is precipitation and groundwater fed.
Quarry	>7	Herb-rich, orchids plentiful (*e.g.*, *A. pyramidalis*)	A type of open-pit from which rock or minerals are extracted. Quarries are generally used for extracting building materials, such as dimension stone, construction aggregate, and gravel.
Green lane	4-8	Herb-rich including *Primula vulgaris*, *P. veris* and *Orchis mascula*	Old highway with hedgerow on either side of central track, green lanes have sheltered microclimate and are often > 500 y old.
Woodland ride	4-8	Often herb-rich, with *M. caerulea* the dominant grass in this study	Linear, treeless open space between blocks of dense woodland, often have footpaths or horse rides along them.
Marsh	> 6	Often dominated by neutral grassland plants of damp habitats (*e.g.*, *Caltha palustris* and *Mentha aquatica*)	Low-lying poorly drained land that is sometimes flooded and often lies at the edge of lakes and rivers.

Epping Forest in Essex Co. comprises 2,476 ha of continuously wooded medieval hunting forest (Rackham 1986) with open, heathy plains often dominated by *M. caerulea*. Open habitats such as acid grassland, wet heathland and scrub, cover 560 ha (*ca* 23% of Forest, Woodhouse *et al*. 2007). At least 11 Orthoptera species have been recorded in Epping Forest, including the locally rare mottled grasshopper *Myrmeleotettix maculatus* (ERDL), great green bush-cricket *Tettigonia viridissima* (ERDL); the dusky cockroach *Ectobius lapponicus* (ERDL, Nationally Scarce) is recorded from the allied Dictyoptera (Hanson 1992). But it is doubtful whether any of these insects still persist in the area, due to the loss of many open plains in the Forest in the 1900s after cessation of traditional tree pollarding and cattle grazing management (Leutscher 1974). 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 (Rackham 1986). Despite these losses, Epping Forest is still considered one of the most important areas for Orthoptera in Essex Co. (Wake 1997), with new species such as the striped-winged grasshopper *Stenobothrus lineatus* (ERDL) colonizing the open plains in response to climate change (Gardiner 2009b, Wilde 2009).

Wake (1997) suggested Epping Forest as a stronghold for *O. viridulus* in Essex Co. and the species was described as one of the commonest grasshoppers in the Forest in the 1950s (Payne 1958); it prefers the tall swards present on the clay soils occurring in association with patches of heath bedstraw *Galium saxatile* (W. Broughton pers. comm. to A. Wake). Fortunately, the Forest is protected by an extensive Site of Special Scientific Interest (SSSI) and a Special Area of Conservation (SAC) (Woodhouse *et al*. 2007). The Epping Forest Act (1878) prevented the Forest from being destroyed (Rackham 1986) and should avert further encroachment by urban development due to its close proximity to the center of London (*ca* 20 km) (Leutscher 1974). However, scrub encroachment of the open plains remains a serious threat to Orthoptera of early successional stages, and free-roaming cattle grazing (rare breed English Longhorns) was re-introduced into the Forest in 2002 by the City of London Corporation (management organisation) to try to maintain the wet heathlands in particular (Dagley 2008).

This grasshopper tolerates high precipitation, and it prefers the tall, damp grassland of upland areas in the UK (Marshall & Haes 1988). It is less abundant in the drier climate of southeast England and is not commonly found on the east coast where precipitation is lower (Haes & Harding 1997). Its apparent absence from coastal areas in Essex Co. may be due to any number of factors, including low precipitation, but there is no conclusive evidence to relate its distribution in the county to precipitation levels.

Climate models predict that climate change may lead to a 35-50% decrease in summer precipitation in low and high-emission scenarios respectively, in eastern England, with a predicted increase in winter precipitation of 20-30% (ECC 2002). There will therefore be greater differences between wet winters and dry summers in eastern England, with a predicted 10% decrease in summer relative humidity by 2080 (ECC 2002). Woodhouse *et al*. (2007) have concerns that the wetlands of Epping Forest may suffer from these droughts, with dry summers leading to severe soil moisture deficits.

Wetlands such as *Sphagnum* bogs are in decline in Essex Co. often due to encroachment by scrub and woodland from a lack of active conservation management (Jermyn 1974). Once trees become established on bogs and wet heathland, they absorb large quantities of water from the soil, leading to the loss of *Sphagnum* mosses and other wetland plants. Droughts may make wetlands more susceptible to encroachment of trees from drier habitats (*e.g.*, silver birch *Betula*

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pendula), and once established these woody species contribute to the problem further due to their large water intake. It seems that a lack of appropriate habitat management and climate change may interact to form a serious future threat to our wetlands, particularly those in Epping Forest that are important for *O. viridulus*.

In this paper, I use Geographic Information Systems (GIS) software to assess the extent of the isolation of *O. viridulus* in Epping Forest, a high precipitation area in Essex Co., and outside the Forest in the wider Essex countryside, where precipitation is generally lower. This will allow a determination of the importance of precipitation for this grasshopper in Essex Co., which may be particularly relevant if summer droughts become more frequent due to climate change.

Due to the likely importance of active habitat management (*e.g.*, cattle grazing) in preventing degradation of wetlands and unimproved damp grasslands (the preferred habitats of this grasshopper in Essex Co.), this paper also contains an assessment of the abundance (*e.g.*, density) of *O. viridulus* within Epping Forest and outside it in the agricultural countryside. The abundance data are assessed in relation to habitat composition (*e.g.*, dominant vegetation species) and management (*e.g.*, grazing or cutting). It is hoped to assess the relative importance of precipitation and habitat degradation in determining the occurrence of *O. viridulus* in Essex Co. and to discuss this in relation to future climate change.

Methods

Orthoptera surveying (distribution).—An in-depth survey of the Orthoptera of Essex Co. was initiated by Alan Wake in 1980. Some 5000 records were accumulated from 1980-1995 of 16 different species and led to the publication of the first County atlas in 1997 (Wake 1997). Approximately 3000 records have been collected since 1995 and have been entered into a database. Interactive distribution maps for these Orthoptera (and many other insect orders) are available online from the Essex Field Club website (www.essexfieldclub.og.uk). During Wake's survey, every 5 × 5-km Ordnance Survey (OS) grid square in Essex Co. was visited (N = 192) and at least five Orthoptera species were found in each 10 x 10-km grid square (N = 57) to ensure even recording coverage of the County. No special effort was made to sample for *O. viridulus*, and the dearth of records (< 1% of the total number of Orthoptera records collected were of this grasshopper) reflects its genuine scarcity in Essex Co. (Wake 1997), particularly as it has a loud stridulation and is not easily overlooked (Richmond 2001). Only adults were recorded in Wake's survey.

Female adults of *O. viridulus* could be confused with the woodland grasshopper *Omocestus rufipes* and with *S. lineatus*. *O. rufipes* was described as fairly well distributed, but in small numbers, in Essex Co. in the Victoria County History (VCH) of 1903 (Harwood 1903), whereas there was no mention of *O. viridulus* (currently recorded in the County) and it is difficult to believe *viridulus* was not present in the early 1900s (Gardiner 2009b).

This leads to the possibility that *O. viridulus* had been misidentified as *O. rufipes* by Victorian orthopterists. This is certainly possible as mistakes were easily made in the early days of Orthoptera recording (Marshall & Haes 1988). The only other record of *O. rufipes* in the County was in 1974 in Writtle Forest, although the reliability of this sighting has been called into question by Wake (1997) due to the possible confusion with *O. viridulus*. *O. rufipes* has not been refound in Writtle Forest, despite extensive searches by orthopterists, suggesting it had become extinct in the County before Wake's survey commenced in 1980. Therefore, it is very unlikely that confusion arose in the identification of the two *Omocestus* grasshopper species in Wake's survey, and all adults reported in this paper can confidently be assumed to be *O. viridulus*. There is also the remote possibility that S. *lineatus* females could be confused with those of *O. viridulus*, however, the former species was only recorded in Essex Co. for the first time in 2009 (Gardiner 2009b, Wilde 2009), before the collection of most of the *Omocestus* records reported in this paper.

Transect surveys (relative abundance).—To ascertain the density of *O. viridulus* at sites from which it had been recorded since 1997, transect surveys were undertaken in July 2010. Transect surveys are an effective method of determining the relative abundance of grasshoppers (Gardiner *et al.* 2005a, Gardiner & Hill 2006), and have been used to measure the density of *O. viridulus* in northwest Devon, UK (Gardiner *et al.* 2005b). However, the detection rate of the grasshopper was poor in the Devon surveys, giving a low estimate of numbers per unit area (*e.g.*, 21-119 adults/ha; Gardiner *et al.* 2005b). To try to increase the detection rate of this grasshopper at Essex sites, a transect method was developed where adults were counted within a 1-m band in front of the surveyor (an increase on the 0.5 m width used by Gardiner *et al.* 2005b), combined with recording the number of stridulating adult males heard whilst the observer was moving at a slow strolling pace (2 km/h). Combined together, the total number of visual and auditory recordings formed an index of abundance for each site. All transect surveys were undertaken in similar weather conditions which were suitable for Orthoptera activity such as stridulation (*e.g.*, air temperature > 17°C, sunny).

At each of 10 sites in Epping Forest and 10 sites outside of the Forest (see Table 2 for details of each survey site), a 300-m transect was walked once in July 2010 to determine the abundance of *O. viridulus*. Each site was known to have had at least one sighting of this grasshopper since 1997. The management of each site was noted (*e.g.*, cut, grazed, or not managed); additionally the main threats to each habitat were also recorded (*e.g.*, overgrazing, scrub encroachment *etc.*). The dominant vegetation species were recorded for each site: these were mainly grasses. The transect surveys will also allow a determination of the likely decline of the grasshopper since 1997, as nondetection on the transect walks, coupled with deteriorating habitat, may mean the species has become extirpated in the last decade from former sites.

Reliance on visual sightings of this grasshopper may lead to an underestimation of its occurrence in the County. There were only eight visual sightings of *O. viridulus* on the transect surveys (6% of 133 adults counted), with most detections being of stridulating adult males (125 individuals counted, 94% of total number). This underlines the importance of using appropriate sampling methods to maximize detection of Orthoptera (Gardiner *et al.* 2005a); bat detectors (a Magenta detector (available from Magenta Electronics Ltd., 135 Hunter Street, Burton on Trent, Staffs, UK, DE14 2ST) set at 28 kHz could be used) can be particularly useful for locating stridulating males of this grasshopper in dense tussocks of grass.

Geographic Information Systems (GIS) analysis.—For this study, I plotted *O. viridulus* distribution at a 1 × 1-km grid square level (monad) on a map of Essex Co., using MapInfo Version 8.0 software. On this map, I drew a series of expanding concentric circles, centered at the Robin Hood roundabout (traffic circle) in the heart of Epping Forest (Gunton 2008), and drawn at 10-km distances. These circles represented concentric zones, and allowed me to determine which populations fell within each 10-km increment from the center of the Forest. The method also allowed me to determine both the location of populations and their relative isolation, which was measured as the distance from an occupied monad to the nearest adjacent oc-

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Table 2. Description of transect sites within Epping Forest and sites outside the Forest.

Transect site	OS grid reference	Description	Dominant grass species	Management
Inside Epping Forest				
Long Running	TQ437997	Wet heathland	*Molinia caerulea*	Cattle grazing
Sunshine Plain South	TQ422992	Wet heathland	*M. caerulea*	Cattle grazing
Sunshine Plain North	TQ422994	Wet heathland	*M. caerulea*	Cattle grazing
Fairmead Bottom	TQ410967	Acid grassland	*Holcus lanatus*	Cattle grazing
Swaines Green	TL452024	Acid grassland	*H. lanatus*	Mowing
Deershelter Plain	TQ426988	Wet heathland	*M. caerulea*	Cattle grazing
Lippitts Hill	TQ398977	Acid grassland	*Agrostis capillaris*	No management on hill, horse grazed in part
Woodredon Farm Lane	TQ419998	Roadside verge	*Arrhenatherum elatius*	Mowing
Honey Lane Plain	TQ417992	Dry heathland	*A. capillaris*	Mowing
Pillow Mounds	TQ411983	Acid grassland	*A. capillaris*	No management
Outside Epping Forest				
Danbury Common	TL781041	Dry heathland	*H. lanatus*	Mowing
Takeley Meadow	TL526216	Unimproved grassland	*A. elatius*	Mowing
Start Hill	TL527213	Unimproved grassland	*A. elatius*	No management
Hatfield Forest	TL536197	Unimproved grassland	*H. lanatus*	Cattle grazing
Aubrey Buxton Nature Reserve	TL521263	Unimproved grassland	*H. lanatus*	Mowing
Aubrey Buxton arable field margin	TL522261	Grass field margin	*Lolium perenne*	Mowing
Good Easter Fen	TL618121	Unimproved grassland	*H. lanatus*	No management
Mill Green Common	TL638012	Heathland	*M. caerulea*	No management
Stanway Pit	TL947236	Quarry (disused)	*Agrostis stolonifera*	No management
Basildon Rugby Club	TQ716904	Unimproved grassland	*A. elatius*	Mowing

cupied monad (nearest-neighbor distance), using the MapInfo ruler tool. The center of each monad was taken as the measuring point. If a recorded monad was adjacent to another occupied monad, then a measurement of 1 km was given as the extent of isolation. This may give a slightly false impression of population isolation, but as the study was comparative, the error should be the same both within the Forest and outside it.

Precipitation data.—Long-term precipitation (rainfall, sleet and snow) data from two weather stations were analyzed. The Writtle College Weather Station (WCWS) is situated in mid Essex Co. (OS grid ref: TL 6707) and has collected climate data since 1943 (Writtle College 2002). Standardized meteorological methods recorded daily precipitation in millimetres at 0900 h (Overton 2007). The WCWS is approximately 25 km from the center of Epping Forest and *O. viridulus* is very rare in the area. Indeed, only one grasshopper population has been recorded within 10 km of Writtle College: that population is located in Writtle Forest (Mill Green Common), approximately 7 km southeast of the College.

The Epping Weather Station (EWS, OS grid ref: TL 4500) is situated just north of Epping Forest and 107 m above sea level. Data collection is similar to WCWS and is summarized on www.eppingweather.co.uk/. *O. viridulus* is frequent in Epping Forest to the south of the weather station (15 recorded populations within 10 km of EWS).

Statistical analysis

Omocestus viridulus distribution analysis.—To determine if *O. viridulus* had habitat preferences, the frequency of recorded populations in four different habitats within Epping Forest and for the same four habitats outside it, were compared using a Chi-square χ^2 test (Heath 1995). Chi-square analysis was also used to assess whether *O. viridulus* populations were randomly distributed on four different soil types within Epping Forest and outside it, or whether there was a preference for particular soils. Chi-square analysis was used to determine whether *O. viridulus* populations (recorded monads) were randomly distributed among the six concentric zones from the center of Epping Forest (see Fig. 1). To allow for the greater land area within each concentric circle, the number of populations in each zone was standardized to 100 ha. In the calculation of the area of each zone, large waterbodies (*e.g.*, Hanningfield and Abberton Reservoirs) that provide no habitat for *O. viridulus* were excluded from the analysis.

To determine the extent of population isolation, the median nearest-neighbor distance for Epping Forest populations was compared to that from outside the Forest (*e.g.*, Epping Forest *vs* outside Epping Forest, two medians compared), using a Mann Whitney U test (Heath 1995). All data were analyzed using SPSS Version 16.0 (SPSS 2007).

Precipitation data analysis.—A Mann-Whitney U test was used to compare the median annual precipitation between Epping and Writtle College Weather Stations for 1980-2007 data (28 y). The EWS records climate in the area containing the highest-frequency of *O. viridulus* populations, whereas the WCWS, at 25 km from the center of Epping Forest, records from a low-frequency *O. viridulus* area. Mann-Whitney U tests were also used to compare differences in median annual summer (April-September inclusive) and winter (October-March inclusive) precipitation between Epping and Writtle. Summer precipitation may directly affect *O. viridulus* feeding stages; nymphs hatch from underground pods in April and adults may survive until early October (Marshall & Haes 1988). In comparison, winter precipitation will affect the species in its overwintering egg stage.

Trends in annual, summer and winter precipitation for Epping and Writtle were correlated with year, using Spearman's Rank Correlation (Heath 1995). These analyses should detect any significant increases or decreases in precipitation. The data were analyzed using SPSS Version 16.0 (SPSS 2007).

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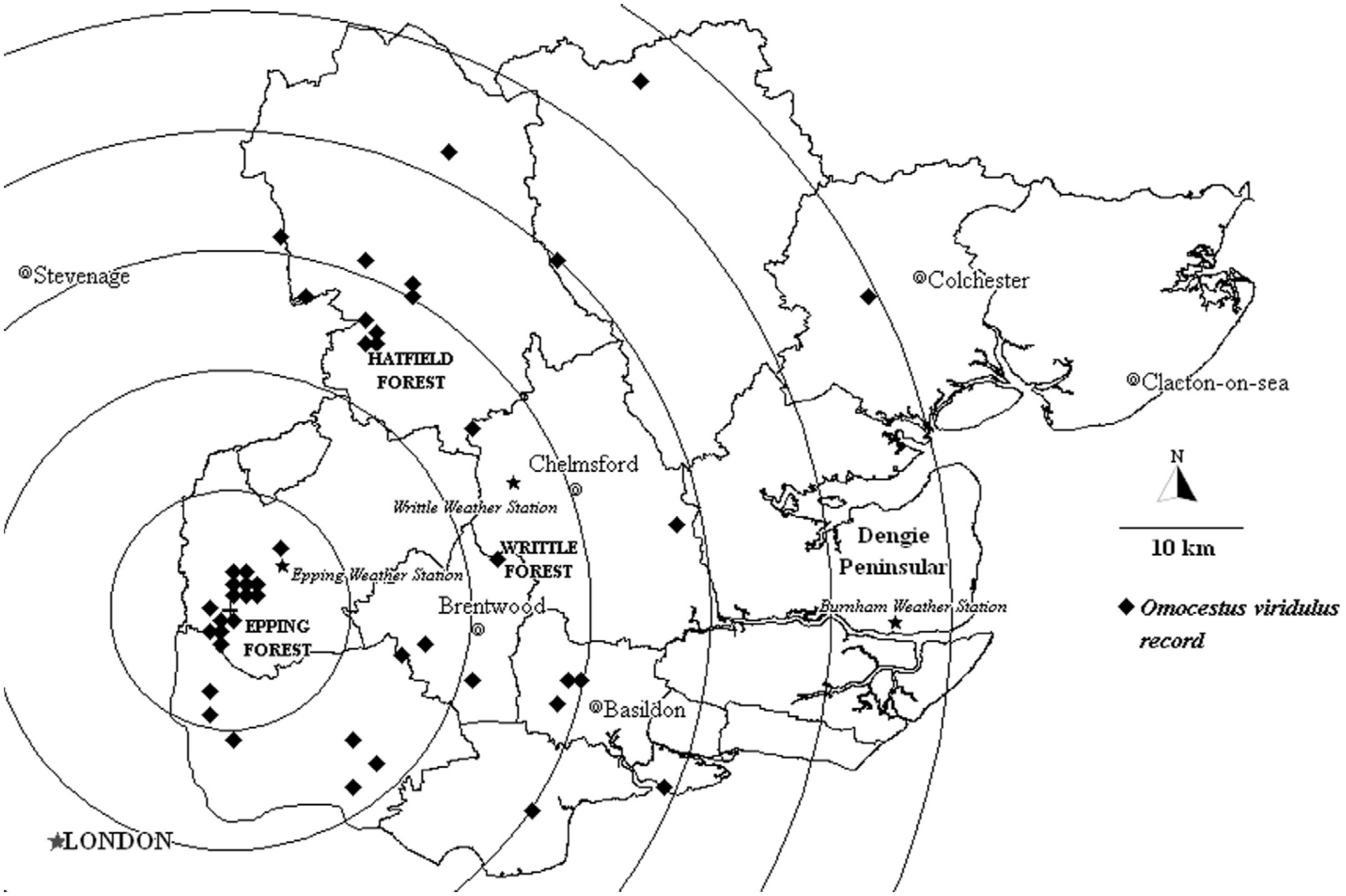

Fig. 1. Location of recorded populations (monads marked by a diamond symbol) of *O. viridulus* in Essex County, England and their distribution within 10-km wide concentric zones from the center of Epping Forest (map created using MapInfo software).

Transect survey analysis.—To determine whether Epping Forest had a higher abundance of *O. viridulus*, the total number of detections of this grasshopper from each site (*e.g.*, visual and auditory combined) were compared against those outside of the Forest (*e.g.*, Epping Forest *vs* outside Epping Forest, two medians compared), using a Mann Whitney U test (Heath 1995). Further analysis was conducted to ascertain the importance of cattle grazing in Epping Forest (five grazed and five ungrazed sites). The total number of detections of this grasshopper from each grazed and ungrazed site were compared (two medians compared), using a Mann Whitney U test (Heath 1995). All data were analyzed using SPSS Version 16.0 (SPSS 2007).

Results

Grasshopper distribution.—*O. viridulus* was found in 45 monads (1 × 1-km grid squares, *ca* 1% of County total of 3958), situated within 23 10 × 10-km grid squares (40% of the County total of 57), indicating that it is not a common insect in Essex Co., England. In Epping Forest there were 18 occupied monads (40% of the total number of occupied monads in Essex Co.), compared to 27 occupied monads outside of the physical Forest boundaries (Fig. 1). Within Epping Forest, populations of this grasshopper were recorded mainly within open (treeless) wet heathland areas such as Deershelter Plain, Long Running, and Sunshine Plain, all of which were within the boundaries of the SSSI designation in the Great Monk Wood and High Beach areas of the heart of the Forest. The grasshopper was also found in the south of Epping Forest at Leyton and Wanstead Flats. The distribution of populations followed the crescent shape of Epping Forest and its buffer lands very closely (Fig. 1). The phenology of the grasshopper is shown in Fig. 2; adults were mainly present from mid-July until the end of August.

O. viridulus was found primarily in acid grassland/wet heathland in Epping Forest and unimproved neutral grassland outside of it, Chi-square analysis revealed definite habitat preferences (Table 3). The grasshopper was occasionally encountered within marshes and fens, and disturbed habitats such as quarries/pits. *O. viridulus* had no significant preference for clay or sandy soils in Epping Forest, but did have definitive preferences outside of the Forest, being more frequently recorded on clay soils than on any other type (Table 4). From the transect survey data, *O. viridulus* was most abundant in *M. caerulea* swards in Epping Forest (73 adults detected, 96% of total

Table 3. Frequency of recorded habitats for *O. viridulus* in Epping Forest and outside its boundaries, in Essex County, England.

Habitats	Epping Forest	Outside Epping Forest	Total
Acid grassland/heath	10	2	12
Grassland (unimproved)	6	20	26
Marsh/fen	2	3	5
Quarry (disused)	0	2	2
Total	18	27	45
χ^2	5.33	20.22**	30.47**
df	3	3	3

** Significant at P<0.01

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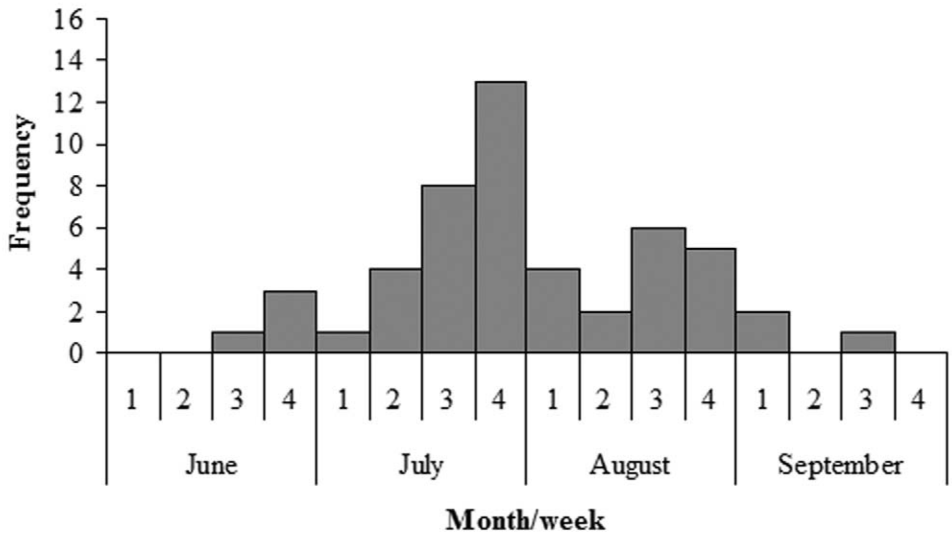

Fig. 2. Frequency of sightings of adult *O. viridulus* during the summer in southeast England in Essex County (N = 50 sightings total).

number counted in the Forest), with only three adults recorded from Yorkshire fog, *Holcus lanatus*-dominated vegetation. Conversely, outside of the Forest in the wider agricultural countryside on clay soils, there was a distinct preference for *H. lanatus* grassland (53 adults detected in these swards, 93% of total number counted outside of Forest), with only four adults being recorded from false-oat grass *Arrhenatherum elatius*-dominated vegetation. No adults were detected at transect sites with common bent, *Agrostis capillaris*, creeping bent, *Agrostis stolonifera*, or perennial rye grass, *Lolium perenne*.

The importance of Epping Forest for this grasshopper is illustrated by examining its presence in the concentric 10-km increments from the center of the Forest (Fig. 3). There was an aggregation of populations within 10 km of the center of Epping Forest (Fig. 1), and a decrease in the frequency of occupied monads at greater distances from the center of the Forest (Fig. 3). Indeed, occupied monads were not randomly distributed among zones (χ^2 = 11.67, d.f. 5, $P<0.05$), indicating the importance of Epping Forest for this grasshopper.

The median distance between a population and its nearest occupied monad was significantly different ($Z = -3.83$, $P<0.001$) within Epping Forest (median distance: 1.0 km, min/max: 1.0-3.6 km) and outside it (median distance: 4.1 km, min/max: 1.0-24.8 km).

However, there was no significant difference in abundance ($Z = -0.69$, $P>0.05$) in comparing the transect surveys between sites inside Epping Forest with those outside the Forest (Table 5). *O. viridulus* was only detected at 6 sites (out of 10) in Epping Forest where it had previously been recorded, this compared with just four sites (out of 10) outside the Forest. This suggested that the grasshopper was either in low abundance and difficult to detect, or had generally been extirpated from the transect areas. In total, only 10 out of the 20 (50%) previously recorded sites, had *O. viridulus* detected on the transect walks. Assuming these data are reliable, it can be inferred that this grasshopper has declined by approximately 50% in Essex Co. since 1997.

The highest abundance in Epping Forest was recorded at Long Running and Sunshine Plain North, both wet heathlands grazed by English Longhorn cattle. Indeed, there was significantly higher

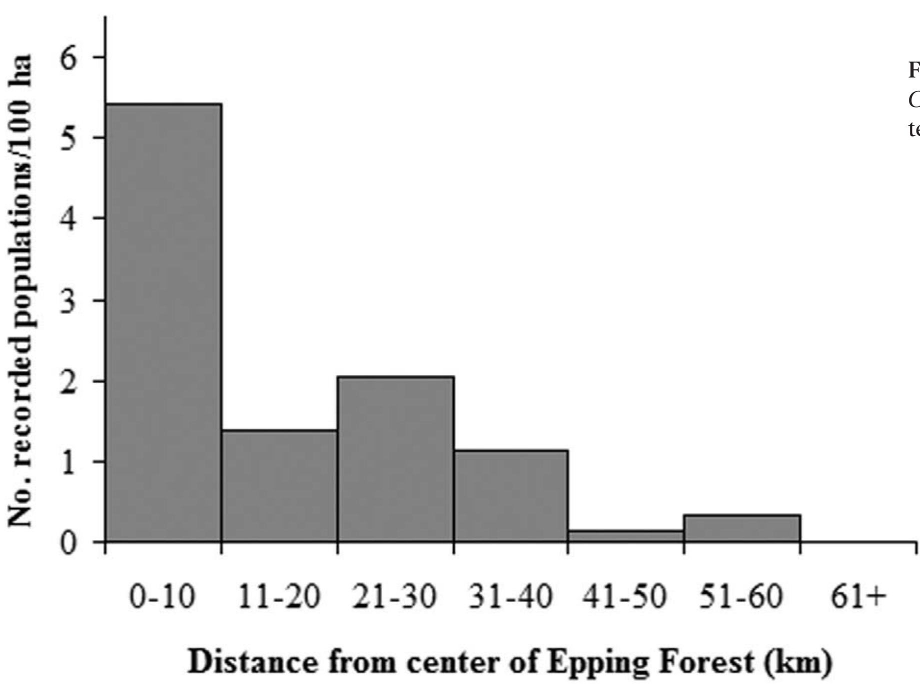

Fig. 3. Frequency of recorded populations of *O. viridulus* at 10-km increments from the center of Epping Forest (N = 45 populations).

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Table 4. Frequency of *O. viridulus* populations on differing soil types in Essex County, England.

Soil type	Epping Forest	Outside Epping Forest	Total
Sand/gravel	10	5	15
Clay	8	18	26
Alluvial	0	3	3
Chalk	0	1	1
Total	18	27	45
χ^2	0.22	26.19**	35.98**
df	3	3	3

** Significant at P<0.01.

abundance of *O. viridulus* at cattle-grazed sites than those without intentional livestock grazing (Z = -2.6, P<0.01). The grasshopper appeared to be absent from sites where scrub encroachment was a serious threat (*e.g.*, trees covered a significant proportion, > 25% ground cover, of formerly open habitat) to the open grassland/heathland and where intensive trampling of habitat by walkers, mowing, and uncontrolled grazing rabbits, *Oryctoloagus cuniculus*, created short swards (< 10 cm in height, Table 5) in midsummer (June-August).

Outside of the Forest, high abundance was detected at Danbury Common, but at no other site (Table 5). As in Epping Forest, the grasshopper appeared to be absent from sites where trampling, mowing, and rabbit grazing created short swards in midsummer (June-August).

Even those sites where *O. viridulus* was detected in high abundance (*e.g.*, Long Running and Danbury Common) were still threatened by scrub encroachment (Table 5). Several threats were present on many sites, indicating the precarious nature of the persistence of this insect in Essex Co. For example, at Woodredon Farm Lane in Epping Forest, *O. viridulus* was found on grassy roadside verges in 2006; however, a 1-m wide strip is mown in midsummer next to the road to improve visibility for vehicles, and blackthorn *Prunus spinosa* scrub is encroaching onto the unmown verge from the hedgerow (*ca* 1-m width of scrub in places), leaving a very narrow band of tall-grass habitat for this grasshopper on the 3-m wide verges. Consequently, in 2010 no grasshoppers were detected.

The apparent decline of this grasshopper may also be due to uncontrolled intensive rabbit grazing at Pillow Mounds in the Forest, which when combined with high numbers of trampling feet from walkers (the site is a popular part of the Forest to visit), produces a very short sward (< 10 cm in height) in midsummer, not favorable for *O. viridulus*. I recall much taller vegetation at Pillow Mounds in 2002 when the species was last detected at the site, suggesting deterioration in the quality of the habitat.

Precipitation data.—There were significantly (Z = 2.56, p<0.01) higher annual precipitation totals in Epping Forest (median annual precipitation: 69 cm, min/max: 49/97 cm) than outside it at Writtle (median annual precipitation: 58 cm, min/max: 40/81 cm). Summer (Z = 2.11, P<0.05) and winter precipitation (Z = 2.16, P<0.05) were both significantly higher in Epping Forest (median annual summer precipitation: 35 cm, min/max: 17/52 cm, median annual winter precipitation: 34 cm, min/max: 15/52 cm) than at Writtle (median annual summer precipitation: 29 cm, min/max: 16/41 cm, median annual winter precipitation: 29 cm, min/max: 21/44 cm).

There was no noticeable trend for an increase or decrease in annual precipitation in Epping Forest (r_s = 0.15) or Writtle (r_s = -0.10) (Fig. 4). There was also no significant trend for summer or winter precipitation in Epping Forest (summer r_s = 0.04, winter r_s = 0.13) or Writtle (summer r_s = -0.08, winter r_s = -0.10).

Table 5. Abundance of *O. viridulus* (number of detections) from 300-m transect walks at sites within Epping Forest and outside the Forest; threats to the persistence of each population are listed.

Transect site	Abundance	Threats
Epping Forest		
Long Running*	54	Scrub encroachment
Sunshine Plain North*	15	Scrub encroachment
Sunshine Plain South*	3	Scrub encroachment
Fairmead Bottom*	2	Intensive cattle grazing
Deershelter Plain*	1	Scrub encroachment
Swaines Green	1	Intensive rabbit grazing, recreation (trampling), scrub encroachment
Honey Lane Plain	0	Mowing in midsummer
Lippitts Hill	0	Intensive horse grazing, scrub encroachment
Pillow Mounds	0	Intensive rabbit grazing, recreation (trampling)
Woodredon Farm Lane	0	Mowing in midsummer, scrub encroachment
Outside Epping Forest		
Danbury Common	49	Mowing in midsummer, recreation (trampling), scrub encroachment
Hatfield Forest*	4	Intensive cattle grazing, recreation (trampling), scrub encroachment
Takeley Meadow	3	Mowing in midsummer
Start Hill	1	Scrub encroachment
Aubrey Buxton arable field margin	0	Mowing in midsummer, intensive rabbit grazing
Aubrey Buxton Nature Reserve	0	Intensive rabbit grazing, scrub encroachment
Basildon Rugby Club	0	Mowing in midsummer, recreation (trampling)
Good Easter Fen	0	Ploughing, agricultural improvement
Mill Green Common	0	Scrub encroachment
Stanway Pit	0	Building development

* Indicates site is cattle-grazed

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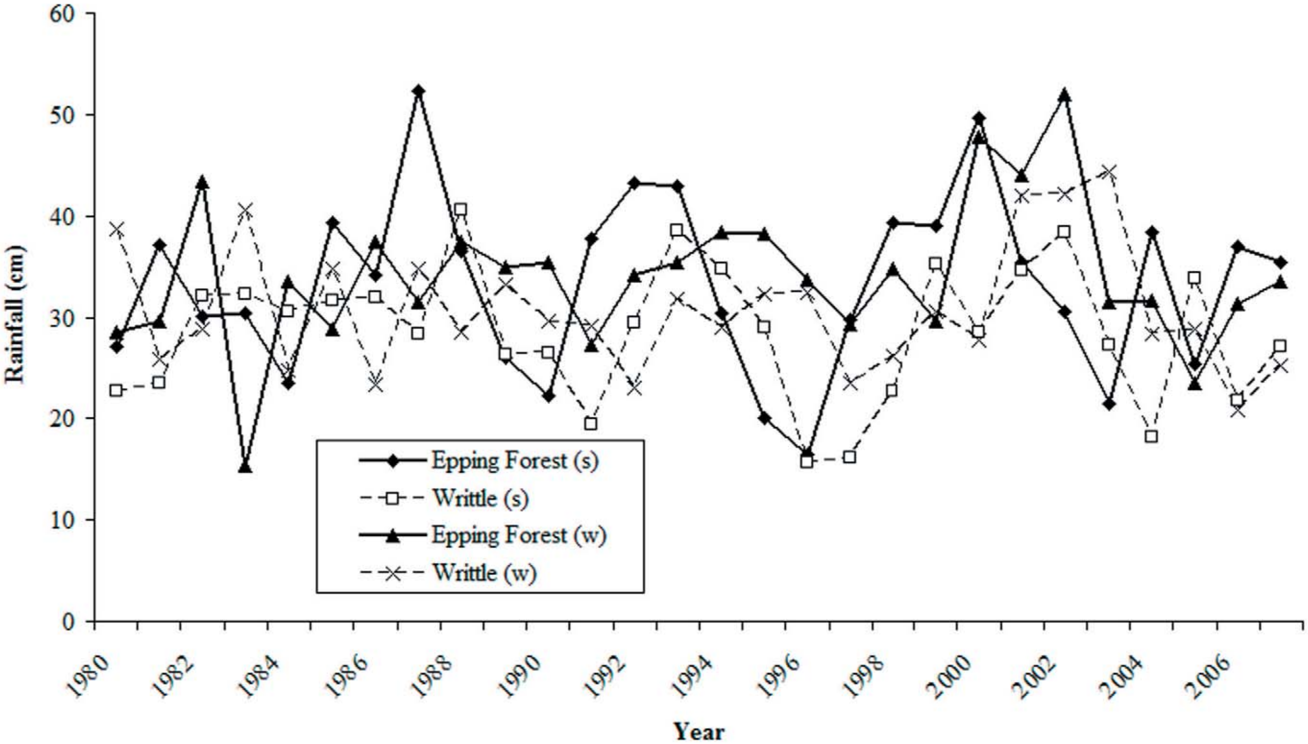

Fig. 4. Total summer (s) (April-September) and winter (w) precipitation (October-March) for Epping Forest and Writtle (1980-2007), southeast England.

Discussion

This study confirmed the importance of Epping Forest (40% of occupied monads in the survey were in the Forest), a large (*ca* 2400 ha) and continuous area with a great diversity of habitats, for the conservation of *O. viridulus* in Essex Co. The Forest has numerous populations of this grasshopper, and these are often connected by wide woodland rides and green lanes (Table 1). The existence of large tracts of dense beech, *Fagus sylvatica,* and hornbeam, *Carpinus betulus,* woodland in the heart of the Forest may make it difficult for individuals to move between different populations and exchange genetic material. This grasshopper is completely absent from the shadiest areas of the Forest around Loughton Camp (Gardiner 2007a) and may find it difficult to traverse these cool and shady woods.

The Forest is markedly different from 1878 when the Epping Forest Act was introduced, the cessation of pollarding in the late 1800s/early 1900s led to the canopy closing in and the decline of cattle grazing during that period allowed natural succession of the open plains to birch *Betula* spp. woodland (Hoy 2001). This cessation of traditional management led to the decline (and probable extirpation) of many insects including *E. lapponicus*, *M. maculatus*, and *T. viridissima* in the Forest. However, the Forest is now being managed in a more traditional way with pollarding and cattle grazing being reinstated (Dagley & Samuels 1999).

There is some evidence from this study that *O. viridulus* abundance is higher on cattle-grazed sites in the Forest, than those without livestock present (Table 5). Certainly, scrub encroachment in the absence of grassland management by grazing is a serious threat to sites such as Lippitts Hill, where it appears that the loss of open grassland has already caused the extirpation of this insect (Table 5). Even sites managed for cattle production need the correct intensity of grazing to maintain their open status and prevent the encroachment of scrub (Fig. 5); currently, there are approximately 1-2 cows/10 ha in the cattle-grazed transect sites (Dagley 2008). Given the encroachment of bracken *Pteridium aquilinum* at Long Running (the most important population in the Forest) and Deershelter Plain in particular, grazing intensities may need to be reviewed on a regular basis to ensure that livestock numbers are high enough to prevent the loss of open wet heathland valuable to *O. viridulus*.

However, intensive management may also threaten *O. viridulus* in Epping Forest. For example, in the grazed pasture at the base of Lippitts Hill, it is intensive horse grazing which creates a very short sward (< 10 cm in height) in midsummer. Heavy poaching from horse hooves creates extensive bare, unvegetated ground containing uncommon plants such as marsh cudweed *Gnaphalium uliginosum*; however, this habitat is not favorable for *O. viridulus* or Orthoptera generally (Gardiner & Haines 2008). Ironically, scrub encroachment from an absence of grassland management has probably removed *O. viridulus* from the upper slopes of Lippitts Hill.

Trampling from walkers at sites such as Pillows Mounds leads to extremely short grassland swards, particularly in combination with uncontrolled intensive rabbit grazing (Table 5). It seems the prognosis is not good for *O. viridulus* in Epping Forest, despite cattle grazing maintaining favorable wet heathland; the probable decline in the Forest for this grasshopper being approximately 40% since 1997.

Outside of Epping Forest, populations of this grasshopper at Mill Green Common in Writtle Forest have suffered from cessation of grazing in the 1950s and subsequent encroachment of *Betula* scrub and oak *Quercus* spp. onto over 80% of the formerly open heathland (Smith 2003). This encroachment has not relented in the last decade, despite efforts to clear scrub on the last remaining portion of heathland, as a consequence *O. viridulus* appears to have become extinct in Writtle Forest (Gardiner & Gardiner 2009). It must be hoped that livestock grazing can be reintroduced to commons to benefit insect populations. The establishment of Commons Councils under Part 2 of the Commons Act 2006 will provide a useful incentive to clear scrub and reinstate grazing on the remaining commons

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Fig. 5. English Longhorn cattle grazing Sunshine Plain in Epping Forest, note the tall wet heathland favored by *O. viridulus*. Cattle are grazing young birch *Betula* spp. trees, which if left unmanaged would lead to natural succession of the open habitat to woodland and the extirpation of the grasshopper. For color version, see Plate VIII.

such as Mill Green (DEFRA 2008).

The problem for the conservation of *O. viridulus* outside of Epping Forest is the high degree of isolation for the remaining populations; the median nearest-neighbor distance is 4 km, and some populations are isolated by > 20 km. These are insurmountable distances for a species that disperses, on average, only 4 to 7 m/week (Southwood & Waloff 1967). Low-population colonies that exist in small areas of favorable, unprotected (no conservation designations) habitat, which are highly isolated from other populations, are most at risk of extinction due to natural events such as drought or human intervention [ploughing, inappropriate site management; Gardiner *et al*. (2003)]. Therefore, populations of *O. viridulus* which are highly isolated, such as in the fen in Good Easter (isolation: 10.7 km), and exist in a small area of habitat (fen and adjoining woodland complex is just 3 ha in size), are highly vulnerable to extinction. The Good Easter population was first discovered in June 2007, but the site was unfortunately subjected to soil excavations for a new agricultural reservoir later in the summer (Gardiner 2008). The grasshopper was not refound in a survey of the fen and woodland in 2008, or on the 2010 transect walk, and it may have become extinct in the area; recolonization is unlikely as no populations exist in the surrounding intensively farmed countryside.

The vulnerability of the unimproved grassland sites near to Stansted Airport in the west of the County (Start Hill and Takeley Meadow) is high, as there is a proposed second runway (Generation 2 plans). Fortunately, the proposed runway has been dropped from government plans for the immediate future. The unimproved Takeley Meadows are very herb-rich, containing uncommon Essex plants such as pyramidal orchid *Anacamptis pyramidalis*, spiny restharrow *Ononis spinosa* and yellow-rattle *Rhinanthus minor*. The continued cutting of these meadows for hay in late summer should maintain the small populations of *O. viridulus*.

Unimproved grassland was very vulnerable to ploughing and chemical fertilizer input after World War II in the 1950s, its generally 'flat' topography making it particularly easy to destroy (Rackham 1986). Therefore, very little old grassland remains in Essex Co. and this is reflected in the highly fragmented populations of *O. viridulus* outside of Epping Forest. The importance of the remaining widespread populations at Danbury Common and Hatfield Forest is high (21-30 km from center of Epping Forest, Fig. 1). The Hatfield Forest populations survived improvement (weedkilling, fertilizer inputs and ploughing) of the plains by the National Trust in the 1950s, probably because some of the terrain was physically inaccessible (particularly the fens) and escaped destruction (Rackham 1989). The fens would have provided a refuge for *O. viridulus* from the detrimental effects of ploughing which destroys grasshopper eggs (Lockwood 2004, Gardiner *et al*. 2005b, Gardiner 2007b). The remaining Hatfield Forest populations exist in a large area of cattle-grazed grassland (the Forest is 420 ha in size) protected by a SSSI designation, although it is likely that the stocking intensity (*ca* 1 cow/ha) is too high, creating short swards (< 10 cm in height) over much of the plains in summer.

Medieval hunting grounds such as Epping and Hatfield Forest are extremely important in the future conservation of this grasshopper in Essex Co. The main future threat to *O. viridulus* in the Essex Forests is likely to be summer droughts caused by climate change,

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which may lead to drying out of its damp grassland habitats such as the fens in Hatfield Forest. Worryingly, there has been a probable 60% decline in the *O. viridulus* population outside of Epping Forest since 1997; if this trend continues it could be almost entirely extirpated from the wider Essex countryside.

However, despite the probable decline of *O. viridulus* in the County, Epping Forest may still be suitable for this grasshopper due to a higher precipitation (Fig. 4) than in other areas of Essex Co. such as Writtle. The wetter climate promotes growth of tall wet heathland vegetation dominated by the grass *M. caerulea*, which creates a 'cooler' microclimate and higher humidity than shorter grasslands. It is likely that this large grasshopper may be unable to tolerate the hot microclimates of short grass (Gardiner & Hassall 2009), and may seek refuge in the shade of taller vegetation and grass tussocks in *M. caerulea* vegetation. *O. viridulus* lays its eggs at the base of grass blades just above the soil surface (Marshall & Haes 1988). Nearly all grasshopper species deposit their eggs below ground; above-ground egg deposition is generally only found among wetland acridids (Stauffer & Whitman 1997). This suggests that *O. viridulus* is adapted to moist (mesic) or wet (hydric) habitats, and perhaps not to dry environments. The damp, humid heathland inhabited by this grasshopper in Epping Forest may provide enough humidity to prevent nymphal or adult dehydration in summer (Unwin & Corbet 1991).

If summer droughts become more frequent (summer precipitation may decrease by 35% under a low emissions scenario; ECC 2002), then *O. viridulus*, which is a grasshopper of mid-to-late summer (Fig. 2), may suffer population loss via increased desiccation. For example, in Culm grasslands in north Devon (study reported in Gardiner *et al*. 2005b), there was a marked decrease (*ca* 49%) in the abundance of *O. viridulus* between 2002 (35 adults/ha) and 2004 (18 adults/ha) measured using standardized transect walks (Gardiner unpub. data). This may be related to the drought in 2003, when rainfall was extremely low with very high air temperatures (*ca* 38°C). In the Culm pastures, *O. viridulus* density was very low in summer 2003 (10 adults/ha, *ca* 71% decrease from 2002), which may indicate severe desiccation-mortality of this grasshopper in southwest England. Desiccation-mortality is common in insects, particularly Lepidoptera (Pollard & Yates 1993). For example, in 1976, extremely hot and dry summer weather reduced moth populations in Essex Co. (Gardiner & Field 2004).

O. viridulus is an extremely adaptable grasshopper, being found from sea level to 1000 m in the UK (Marshall & Haes 1988) and >2400 m in Europe (Berner 2005). The grasshopper is widespread throughout the UK, but has always been more restricted in its distribution in the southeast and east of England, in areas of low precipitation with free-draining soils (Haes & Harding 1997).

The current research from Essex Co. suggests there may be a threshold precipitation level, below which the grasshopper is more isolated in its occurrence. I propose that in Essex, *O. viridulus* is frequent in Epping Forest, where annual precipitation exceeds 65 cm, but is more patchily distributed throughout the rest of the County where precipitation is generally < 60 cm/year (data from Writtle College Weather Station), and completely absent from the eastern coastal regions such as the Dengie Peninsular (data from Burnham Weather Station), where precipitation is approximately 45 cm/year (Figs 1, 4). Outside of the higher precipitation areas in Essex Co. such as Epping Forest, *O. viridulus* is more commonly recorded in damp, unimproved grasslands on clay soils with *H. lanatus* swards, which traditionally have high water retention in winter and early summer (Jermyn 1974). Therefore, it is suggested that this grasshopper needs soils with a high water-holding capacity in low precipitation areas of the County to persist.

In higher precipitation areas, *O. viridulus* may display adaptability and may be able to tolerate more freely draining soils, such as the sands and gravels in Epping Forest which support wet heathland/acid grassland dominated by *M. caerulea* (Tables 3 and 4). In Norfolk Co., where precipitation is generally higher than in Essex (mid Essex annual precipitation 58 cm, mid Norfolk 62 cm), *O. viridulus* is a much more widespread insect, occurring in 77% of 10 x 10-km grid squares, compared to only 40% of surveyed grid squares in Essex Co. since 1980. Richmond (2001) suggests that in Norfolk it tolerates a wide range of habitats and has good dispersal ability, which is certainly not the case in Essex Co., except in its stronghold in Epping Forest.

It is clear that scrub encroachment threatens the future persistence of many Essex populations of *O. viridulus* (indeed, it is a threat to 12 transect sites; Table 5), in combination with mowing (threat to six sites), trampling from large numbers of walkers (threat to five sites) and intensive rabbit grazing (threat to four sites) that creates very short swards in midsummer that are unsuitable for this grasshopper. Given the large range of land management issues currently affecting this grasshopper and leading to a probable decline of 50% since 1997 (across all transect sites), its future does not appear promising in Essex Co.

Drying out of wet heathland and damp grassland may also render sites more vulnerable to scrub encroachment, which may have caused the extirpation of *O. viridulus* from Writtle Forest (Gardiner & Gardiner 2009). This grasshopper may become increasingly restricted to Epping Forest in the future due to that locale's higher precipitation, as many populations outside of the Forest could be lost due to drought conditions. Air temperatures are increasing in Essex Co. (Gardiner 2009a); therefore, higher evaporation in hot summers could exacerbate the problems for this grasshopper outside of Epping Forest. However, precipitation levels have remained relatively constant in the County since 1980, so any decrease in rainfall due to droughts is not yet evident (Fig. 4). Essex County Council (2002) predict a decline in relative humidity in the southeast of England, with humidity reduced by 10% by the 2080s, if a high-emissions scenario is assumed. This decline in humidity could have disastrous impacts on mesic and wetland insects, particularly *O. viridulus*; this effect is likely to be increased in severity in areas of low precipitation such as Essex Co.

English orthopterists are already concerned that this insect is disappearing from its favored wet grassland haunts (P. Sutton pers. comm.). Jeremy Dagley and Magda Charalambous have noticed a decline in *O. viridulus* numbers over the last 4 y on experimental plots at Silwood Park (Imperial College) in Berkshire; their study appears to substantiate the anecdotal reports of a decline for this grasshopper.

Given concerns about this species it may be important to prevent further drainage of ecologically valuable wetlands and promote appropriate conservation management of remaining sites (*e.g.*, such as cattle grazing in Epping Forest). The Wetland Vision Project outlines a 50-year plan for wetland preservation in the UK, and aims to conserve, rehabilitate, and create new wetland ecosystems as part of a strategy for adapting to climate change (The Wetland Vision Project 2009). The project outlines potential areas for wetland restoration which include Epping Forest, the Lee Valley and the south Essex marshes, landscapes where *O. viridulus* is currently found. Such large-scale wetland creation would allow populations of this declining grasshopper to exist in a changing climate and build resilience to future threats. It is probably only these large-scale wetland creation projects which can now secure the future of *O.*

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viridulus in Essex Co. by establishing landscape-scale areas managed by livestock grazing, which have a greater resilience to threats such as scrub encroachment and drought.

This study could be viewed with some caution, as *O. viridulus* has undoubtedly been overlooked in some areas of Essex Co. due to a lack of recorders. Inevitably, distribution maps reflect the presence of active field recorders rather than the insects themselves (Wake 1997). However, this comprehensive survey of the entire County over a 28-y period, in which every 5 × 5 km square was visited at least once, ensures recording coverage was relatively even. *O. viridulus* is also not easily overlooked, as it has a loud stridulation (Richmond 2001). There were more recorders in the northeast of the County near Colchester (Wake 1997) where this grasshopper has rarely been noted, so it is probably not the case that the distribution of *O. viridulus* reflects the presence of recorders.

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