

Habitat use and dispersal characteristic by *Stethophyma grossum*: the role of habitat isolation and stable habitat conditions towards low dispersal

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Received: 22 November 2009 / Accepted: 22 July 2010 / Published online: 8 August 2010
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Abstract Species in a highly fragmented environment, such as the intensively used agricultural landscapes of Europe, are expected to be in danger of extinction. We hypothesize according to Kisdi's theory (Am Nat 159:579–596, 2002) that species in fragmented landscapes with isolated habitats in general tend to possess low dispersal. In order to verify this hypothesis we studied the movement patterns of *Stethophyma grossum*, a hygrophilous species of wetlands, by mark–release–recapture techniques in a landscape with scattered suitable habitats over 3 years. The study focused on the major population in this landscape (site #1) as dispersal behaviour was assumed to be greatest. Actually, marked individuals of *S. grossum* were never found in any further suitable habitats in close vicinity to site #1. Despite that the peatland meadow of study site #1 was all over covered with homogenous vegetation only 6% (1.8 ha) of the whole area (30 ha) were occupied by *S. grossum*. The mean recapture rate over 3 years amounted to 39% with no significant differences between males and females. Both covered little distances within their mean range size of 1.8 ha; the median distances were 36.91 m for males and 26.65 m for females. We confirm the hypothesis that sub-populations of species in longstanding naturally isolated habitats, which habitat conditions have been stable; evolved low dispersal with

little movements which are routine movements to find mating partners or food.

Keywords Acrididae · Fragmented suitable habitats · Mark–release–recapture experiment · Movement pattern · Peatland meadow · *Stethophyma grossum*

Introduction

Dispersal capacity can affect the survival of species in fragmented landscapes in which habitat quality exhibits spatiotemporal variation (Hanski 2004). As with any other trait, dispersal behavior of an individual is affected by its genetic constitution, by its environment, and by the interaction between the two (Nathan et al. 2008). Theoretical work has shown that habitat fragmentation can select either for increased or decreased dispersal propensity (Jansen and Vitalis 2007). Increasing fragmentation makes it less likely that a dispersing individual will reach another habitat patch, hence selecting for decreased dispersal rate (Ovas-kainen et al. 2008). Increasing fragmentation can also influence other factors, such as the level of inbreeding and relatedness of individuals in local populations, which are likely to influence the evolution of dispersal (Thomas 2000). Further, the evolutionary response to landscape structure can be masked by phenotypic plasticity (Merckx and van Dyck 2006). Merckx and van Dyck (2006) showed that in populations of the speckled wood butterfly (*Pararge aegeria*) both the landscape of the genetic origin and the landscape of the individual development contributed substantially to variation in flight morphology. Furthermore, other authors have suggested that species of relative stable habitat structures, which have been naturally and gradually isolated, could evolved low dispersal (Mathias et al. 2001;

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Kisdi 2002). Compared with many other life-history traits, dispersal capacity is a complex trait whose relevance for evolution is difficult to define and measure. Therefore, studying animal movement and understanding the factors affecting movement have become important subjects in conservation biology and landscape management.

Grasshoppers are excellent subjects for detailed dispersal studies. Most of them are flightless and if they are capable of flight, they cover only short distances. Therefore, they are easy to catch and to mark (Buchweitz and Walter 1992). *Stethophyma grossum*, the large marsh grasshopper, is distributed throughout Europe and Siberia. In Germany, *S. grossum* is ranked as an endangered species (Maas et al. 2002) and is likely susceptible to extinction since ongoing large-scale drainage of wetlands as well as the fragmentation of their habitats endanger their occurrences (Detzel 1998; Lang and Schlapp 2003). A similar situation has been described for other European countries (Cotton 1980; Holst 1986; Storozhenko and Gorochov 1992; Griffioen 1996; Defaut et al. 2004; Baur et al. 2006). Current reports have assumed that the populations of *S. grossum* slightly increase in central Baden-Württemberg—SW Germany (Trautner and Hermann 2008). Trautner and Hermann (2008) have postulated that the colonisation of new sites could be caused by higher air humidity and temperatures in spring due to climatic changes. Whether *S. grossum* failed to be noticed before or whether the species actually colonised new sites, could not be verified unequivocally. For example, in Mecklenburg—Western Pomerania (NE Germany) the locations of *S. grossum* increased because of the intensified progress of mapping in recent years (Wranik et al. 2008) but are not correlated with actual dispersal. However, base investigations on the dispersal of *S. grossum* are relatively rare. The few investigations of movement of *S. grossum* have suggested a low dispersal behaviour (Marzelli 1994; Sörensen 1996; Malkus 1997) with covered distances of 250 m on average and of 1,500 m at most (Griffioen 1996). It has been pointed out, for example by Detzel (1998) that studies on movement patterns lack over different years in relation to habitat and landscape history.

We hypothesize according to Kisdi's theory (2002) that species in fragmented landscapes with isolated habitats in general tend to possess low dispersal. In contrast, Trautner and Hermann (2008) have postulated that isolated populations in a fragmented landscape could possess a high dispersal under favourable climatic conditions. In order to confirm one of these hypotheses we studied the movement patterns of *Stethophyma grossum* using a mark–release–recapture techniques in a landscape with scattered suitable habitats over 3 years. The aims of the study were to determine the distances moved by *S. grossum* in a highly fragmented landscape along with variation in movements between years, sexes and with time of day.

Methods

The species

S. grossum is a hygrophilous species (Teichmann 1958; Lorz and Clausnitzer 1988) and common in marshy landscapes or wetlands with sedge reeds and rushes (Tümpel 1901; Schiemenz 1975; Buchweitz and Weier 1990; Detzel 1998; Handke and Adena 2001). The decisive habitat characteristics are a continuously high atmospheric humidity near the ground, with high soil humidity graduated over one growing season and heterogeneous vertical structure of the vegetation (Sonneck et al. 2008). The eggs are laid during summer and autumn near the ground and require high soil humidity (Ingrisch 1983). They hatch from June until September in the following year. The nymphs occupy the same habitat like the adults and proceed through five instars before becoming adults at the end of June at the earliest (Ingrisch and Köhler 1998). This species has one generation per year. Individuals generally move by jumping. Adult males produce snapping or clicking sounds from July to September as long as the temperature is high or the weather is sunny. The characteristic song, the species' size and its conspicuous colour makes the species easy to find.

Study area

The study was carried out in Mecklenburg—Western Pomerania (NE Germany) in a region of about 100 km² where five populations of *Stethophyma grossum* are known. A large study area was chosen because recent work has shown that the classification of a species as *sedentary* may be related more to the size of the study area than to the species' actual dispersal ability. Some so-called *sedentary* species have been shown subsequently to be able to disperse several kilometres (Reich 2006). A landscape with an average percentage of good quality habitats was chosen in order to prevent underestimation of movement due to isolation effects. The climate data of the study area are given in Table 1. Figure 1 shows the five populations (in the following referred to as study site #1 to #5) lying in the study area dominated by cultivated land, forest, peatland and grassland. In ancient times the study sites built a swampland net or were part of a swampland net and were certainly quickly colonised by *Stethophyma grossum* radiant from adjacent occurrences (Sonneck et al. 2008). Current population units are isolated by agriculture, forestry or settlement structures (Fig. 1) and the process of fragmentation and isolation in the region continuous (Crosby 1986; Blackbourn 2006).

The mark–release–recapture experiment was primarily carried out at study site #1, the Große Bruchwiese (54°09'00.1"N, 12°25'02.2"E; Fig. 1) where the largest population of *S. grossum* could be found and dispersal

Table 1 Survey of climate data

	Jan	Feb	Mar	Apr	Mai	Juni	Juli	Aug	Sep	Okt	Nov	Dez	Sum
2005													
Precipitations (mm)	49	64	42	15	102	43	117	57	38	49	50	77	703
Sunshine hours (h)	53	65	149	223	180	234	207	194	188	178	86	32	1,788
Mean temperature (°C)	3	0	1	8	12	15	18	16	15	10	4	1	9
2006													
Precipitations (mm)	21	66	48	42	64	36	16	138	41	42	78	45	636
Sunshine hours (h)	65	47	94	117	237	246	374	165	209	98	52	37	1,740
Mean temperature (°C)	−3	0	0	7	12	16	21	17	17	12	7	6	9
2007													
Precipitations (mm)	95	60	60	6	61	150	125	92	68	26	60	68	871
Sunshine hours (h)	41	45	168	272	224	193	178	188	126	105	59	12	1,611
Mean temperature (°C)	5	2	6	9	13	17	17	17	13	8	4	3	10
2008													
Precipitations (mm)	62	40	76	72	20	31	26	85	24	68	59	60	621
Sunshine hours (h)	31	83	123	136	358	280	273	154	119	84	34	26	1,701
Mean temperature (°C)	3	4	4	7	12	16	18	17	13	9	6	2	9

behaviour was assumed to be greatest. The Große Bruchwiese (30 ha) was a typical peatland meadow which was crossed by parallel ditches and surrounded by oak and beech forest (Fig. 1b). The vegetation was homogenous and mainly composed of *Agrostis stolonifera*, *Caltha palustris*, *Cardamine pratensis*, *Carex acutiformis*, *C. nigra*, *Glyceria fluitans*, *Holcus lanatus*, *Juncus effusus*, *Lychnis flos-cuculi*, *Phalaris arundinacea*, *Poa palustris*, *P. trivialis*, *Potentilla anserina* and *Ranunculus acris* (Sonneck et al. 2008). Some alders of 3–4 m height were growing mainly in the ditches south and north of the mean range size (1.8 ha) of *S. grossum* individuals (cp. Fig. 1b). Monitoring at sites #2 to #5 was conducted at regular intervals to check whether individuals marked at the study site #1 could be found in order to test Trautner’s and Hermann’s hypothesis.

Grasshopper sampling method

Mark–release–recapture experiments were carried out during the adult stage of *S. grossum* at study site #1 (Große Bruchwiese) in 2006 (30th July to 17th September), 2007 (25th July to 23rd August) and 2008 (11th August to 9th September). The study started when the first adult individuals could be found (end of July) and ran until no adult individual could be found any more (usually mid-end September). In 2007 the study had to be finished at the end of August because mowing had taken place. Usually the peatland meadow is mowed in Mai or June before *S. grossum* became adult but wet conditions at study site #1 due to high precipitations in March and April 2007 retarded the mowing and therefore, affected the adult phase of *S. grossum*.

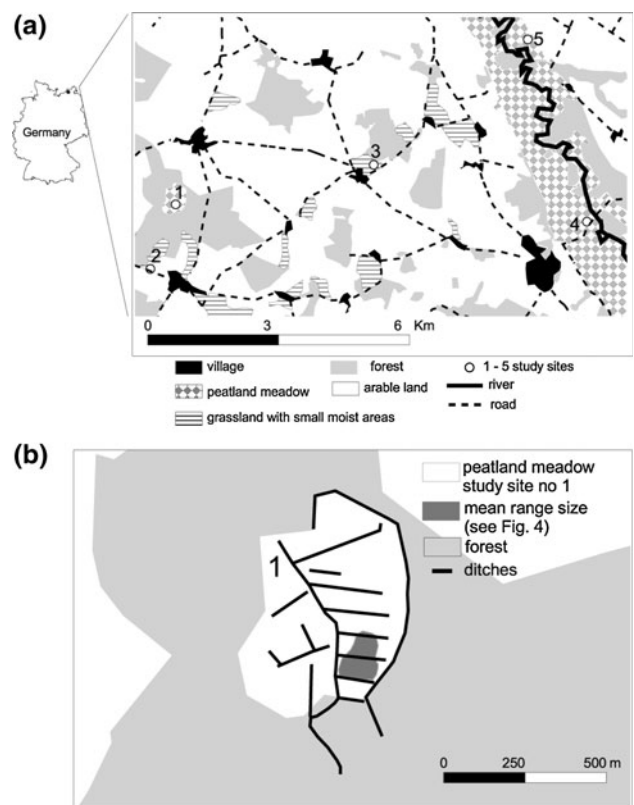


Fig. 1 a Section from the study area in Mecklenburg—Western Pomerania (NE Germany) with the 5 study sites and b detailed view at study site #1 (Große Bruchwiese, 30 ha) showing the mean range size (1.8 ha) of *S. grossum* individuals compiled between 2006 and 2008

The study sites were monitored every second or third day except for rainy, cloudy or cold days. Then the monitoring was conducted at the following day. The mark–

release–recapture experiments were performed by systematic interlocking movements from south to north. For this purpose, a (permanent) grid of 20×20 m cells was staked out at the study sites using marked pegs thus facilitating mapping of catches on the notebook. The captured grasshoppers were individually marked on one hind wing with a three-digit numbers (Arabic numerals) using permanent black overhead projector pen (Faber-Castell Multimark 1513 permanent, Germany), and immediately released at the place of capture. Additionally, a self-adhesive reflecting foil (7610 HIGH GAIN SCOTCHLITE) of a size of 3×9 mm was attached at the distal end of the saltatorial leg of some individuals to provide a more effective monitoring at night (see Opitz and Köhler 1997; Opitz et al. 1998). Giving a reflective marking to all caught individuals was not practicable because sometimes up to four individuals were caught at one position. Nightly observations were carried out in 2007 and 2008 using a head torch (Led Lenser: Optoelectronics) which made the marked individuals detectable within distances up to 50 m. Date of capture, location, and sex were recorded for every marked and recaptured grasshopper. The mark–release–recapture experiments took 5h at each monitoring. Nightly observations took 1–2 h.

Data processing

The information of the daily notes was transferred to a geographical information system (GIS, Arc View).

The number of marked male and female individuals and their number of recapture are shown in Table 2. The recapture rate was calculated as percentage of all once recaptured individuals out of all marked individuals. The population size was calculated with following equation:

$$N = (n \times M)/x$$

where N is the population size, n is the size of the sample, M are the marked individuals and x is the number of recaptures (see Begon et al. 2009). Such a calculation can be carried out after every monitoring, beginning with the second. Therefore, the mean population size was computed. The distances covered by males and females were calculated as a straight line from one capture point to the other (Fig. 4). The grasshoppers real movement in space could not be recorded without applying telemetry (Amstrup et al. 2005). Based on the predominant grasshopper's movement at the study site #1, the mean range size was computed as a geometric shape around this movement patterns. Usually, individuals could not be caught beyond that mean range size. The distances were divided into modal classes (see Fig. 3). The total covered distance is the sum of all single distances covered by one individual. The influence of sex and year of the study on relative frequency of movement was determined by t test and monofactorial variance analysis (ANOVA), respectively. Further, an analysis of correlation between climate data and population size (see Tables 1, 2) was done after Pearson.

Table 2 Comparison of recapture and dispersal statistics between males and females of *Stethophyma grossum* in 2006, 2007 and 2008

	2006		2007		2008	
	Males	Females	Males	Females	Males	Females
No. of marked individuals	75	52	170	173	157	64
One recapture	47	18	51	50	63	24
Two recapture	22	4	11	11	24	8
Three recapture	9	3	3	3	5	1
Four recapture				1	1	
Five recapture				1		
Six recapture				1		
Sum of total recaptures	78	25	65	67	93	33
Recapture rate (%)	63	35	30	29	40	38
Sum of diurnal recaptures	47 (63%)	18 (35%)	24 (14%)	41 (24%)	44 (28%)	21 (33%)
Sum of nocturnal recaptures			41 (24%)	26 (15%)	49 (31%)	12 (19%)
Population size	207 Individuals		539 Individuals		392 Individuals	
Min. distance covered (m)	1.4	0.8	0.7	1.1	0.7	1.4
Max. distance covered (m)	219.9	128.5	165.9	155.0	191.8	177.6
Median distance covered (m)	42.6	20.6	25.4	23.0	42.8	36.4
Longest live span found (d)	50	45				

Results

Recapture rates, sex ratio and population size

Individuals marked at study site #1 were never caught at study sites #2 to #5. At study site #1 (Große Bruchwiese) both sexes were abundant but both the number of marked individuals and the sex ratio varied during the three-years running study (Table 2). The population size and the recapture rates differed between the years (Table 2) and a greater portion of males than females were recaptured in 2006 and 2008, but not in 2007.

In 2006 ten monitoring (only diurnal) were carried out. 75 males and 52 females were caught and marked (Table 2); the total population size averaged 207 individuals according to the equation given in the methods. In 2006, the longest life span found, which was of course as long as the period of study (refer to methods), amounted to 50 days for males and to 45 days for females. A longer longevity has not been reached during the 3 years running study. In 2007 the period of study comprised nine monitoring including four nocturnal monitoring. Much more individuals were caught and marked (see Table 2) and also the population (on average 539 individuals) was greater than in 2006. In 2008 four daily and three nightly monitoring were carried out. The population comprised on average 392 individuals.

To sum up, more than the half of the total population was integrated in the mark–release–recapture experiments in all 3 years. The additional nocturnal monitoring was very effective especially to recapture males (Table 2; Fig. 2). In 2007, the nocturnal recapture rate of males amounted to 24% while the diurnal recapture rate amounted to 14%. In 2008, only a slight difference between nocturnal and diurnal recapture rate of males could be achieved. At night

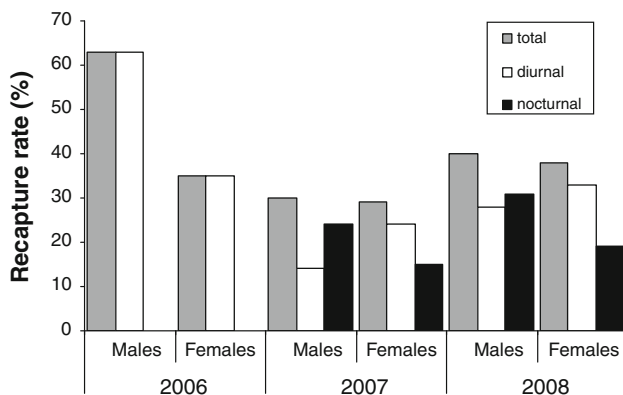


Fig. 2 Comparison of total recapture rate, diurnal and nocturnal recapture rate between males and females of *Stethophyma grossum* in 2006, 2007 and 2008. The recapture rate is the percentage of all once recaptured individuals out of all marked individuals. Diurnal and nocturnal recapture rates include also multiple recaptures

the smaller males of *S. grossum* were easier to detect, in parts within distances up to 75 m, because they sat at the top of the vegetation. The bigger females sat both night and day at the bottom of the vegetation and were always easier to find during daylight hours (Table 2; Fig. 2). At night the females were partially covered by the vegetation and could be detected if the beam of the head torch was directed to the ground. Within distances more than 10 m no females were detectable at night.

The population sizes were not influenced by precipitation ($r = -0.23$), sunshine hours ($r = -0.61$) or temperatures ($r = -0.14$) during dormancy phase (Oct to Mar in Table 1 compared with population size in Table 2). The population size was also not influenced by precipitation (atmospheric humidity) in spring and summer of the same year ($r = -0.24$, $r = -0.08$, $r = -0.33$), but by spring sunshine hours at least in 2007 ($r = 0.97$). High atmospheric humidity and simultaneously high temperatures in August and September—the period of oviposition—seem to influence positively the population size (see Table 2) of the following year ($r = 0.97$, $r = 0.99$, $r = 0.79$).

Habitat use and dispersal

Study site #1 (Große Bruchwiese) was not colonized entirely by the large marsh grasshopper. In the years of the study, only the south-western part (~1.8 ha) was frequented (refer to mean range size in Fig. 1), although the environmental conditions were equal all over the Große Bruchwiese. An influence of the year of study on the relative frequency of movement could not be established (ANOVA, degree of freedom (df) $n - 1 = 53$, $P = 0.99$) as well as no significant differences could be detected between males and females movement in terms of the distances between captures (t -test, df $n - 1 = 26$, $P = 0.98$). The analysis of covered distances (Fig. 3) shows that most of both males and females covered distances from 0.01 to 50.00 m during the 3 years running study. Movements over

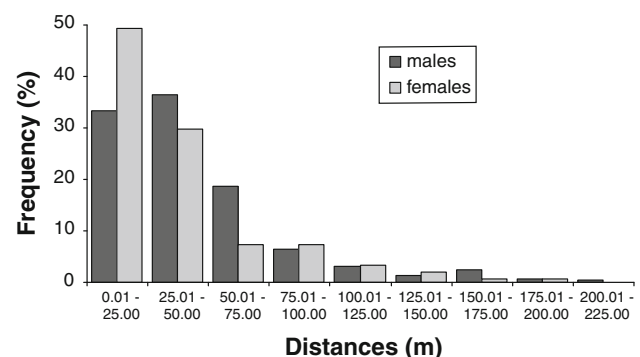


Fig. 3 Frequency of movement of *Stethophyma grossum* (sum of 2006–2008)

100 m were seldom in both sexes. Only 5% of the marked females covered distances above 100 with 177 m being the farthest distance. 8% of the marked males covered distances above 100 m. Exceptionally, one male moved nearly 220 m.

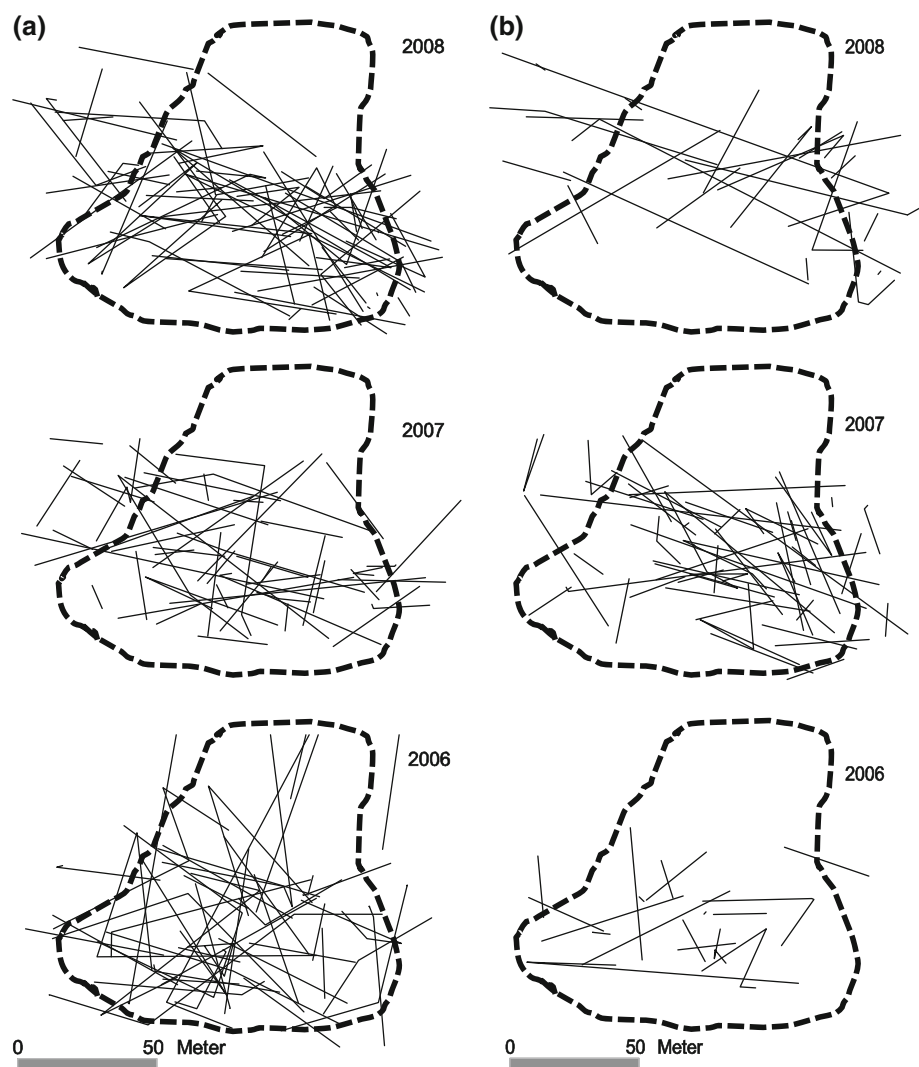
In Fig. 4 the movement patterns of male and female of *S. grossum* and their mean range size at study site #1 are depicted. Generally, the movements of both males and females were not purposeful but rather chaotic (Fig. 4). Nevertheless, the recorded movements of both males and females were focused in the southwestern part of the Große Bruchwiese (Fig. 1) and few individuals were recorded moving beyond the mean range size (Fig. 4).

Discussion

Originally, all wetland biotopes, the habitats of *S. grossum*, were connected hydrological systems whereby the com-

prehensive colonisation from Siberia all over Europe might have been possible. Natural growing high forests at least in the study region resulted in a fragmentation and isolation of *S. grossum*'s habitats. Dieckmann et al. (1999) have assumed an evolutionary ecological feedback based on reports that species in spatially heterogeneous habitats feature high dispersal whereas species in less heterogeneous habitats are characterised by low dispersal. Dispersal is an undirected movement away from the natal habitat patch (Den Boer 1990) and is a life-history trait that has profound consequences for populations, especially in heterogeneous landscapes (Dieckmann et al. 1999). Also, Kisdi (2002) has assumed that species, which live in habitats where their decisive habitat conditions do not change considerably over large-scale periods of time, feature low dispersal. The constancy of habitat conditions has been applied for habitats of *Stethophyma grossum* in our study area (Sonneck et al. 2008) and equally stable habitat conditions should be offered by most peatland meadows in the major distribution

Fig. 4 Chaotic movement of males (a) and females (b) at study site #1 (Große Bruchwiese) in 2006, 2007 and 2008. The line of movement is designated as the shortest possible connection between the points of capture. The dashed lines define the mean range size



area of the species. Actually, our study confirms Kisdi's hypothesis of low dispersal in stable, isolated habitats.

Both nymphs (see Krause 1996) and adults featured low dispersal (Table 2; Figs. 3, 4) and males and females showed chaotic movements (Fig. 4), similar to the movements of many grasshopper species which have been described as routine movement (Walls and Kenward 1998; Selas and Rafoss 1999) used to find a mating partner (Kuras et al. 2003). Routine movements are not conducive for exchange with other sub-populations or for colonization (Baguette et al. 1998, 2000; Baguette 2003; Van Duck and Baguette 2005). In conclusion, the phenomenon of low and chaotic movement has been postulated for numerous European Saltatoria (Reinhardt et al. 2005). In Germany, mark–release–recapture experiments with *S. grossum* over one season have revealed that adjacent areas were not colonised by the grasshopper if these were surrounded by trees. Newly created habitats suitable for *S. grossum* could be colonised if they lay within distances of 400 m and if they were free of any barriers like trees or roads (Marzelli 1994). It has been reported that some males of the large marsh grasshopper flew or jumped up to 41 m, but they never flew over or through trees (Sörensen 1996). This observation can be confirmed by this long-running study. The results showed that the population of *S. grossum* was concentrated in the centre of the south-western part of the Große Bruchwiese and virtual no individual moved away. The alders growing in the parallel running ditches or even the ditches themselves seemed to limit the movement of the grasshoppers (see Fig. 1; mean range size). The surrounding forest was never over flown as we never found individuals marked at study site #1 at other potential habitats (study site #2 to #5). The unique record of a male dispersal of 1,500 m (Griffioen 1996) may be an exception, which could be possible in a barrier-free landscapes. In conclusion and according to our results, the postulation of Trautner and Hermann (2008) on increased occurrences of *S. grossum* in SW Germany has to be assessed as 'failed to be noticed before'. Their hypothesis of advantageous wet and simultaneously warm spring month for *S. grossum* can not be corroborated by our results. A high population size (e.g. in 2007) was influenced by high precipitations (atmospheric humidity) and simultaneously high temperatures during the period of oviposition in the previous year. This positive correlation may be influenced by the short term of our study and has to be tested over a longer period. In fact, insects (Saltatoria) are rather affected by microclimatic factors than by macroclimatic factors. Thus, there should be no coincidence of macroclimatic factors and population size.

Other dispersal studies have evidenced that within some species exchange between distinct habitats occur, that meta-population-structures exist and that this population structure is advantageous under unfavourable environmental

conditions (Kindvall 1995a, b, 1999; Berggren et al. 2001). Originally, the large marsh grasshopper must have had much more extensive dispersal-behaviour otherwise this species would not have the current spreading (see Bei-Bienko and Mishchenko 1963; Schmidt and Lilge 1996). According to Dieckmann (1999) a high dispersal may reverse in the course of the grasshopper's evolution if the environmental conditions remain constant over large time periods and if the species has a sufficiently large habitat (see also Den Boer et al. 1980; Wiens and Donoghue 2004). Reversing dispersal behaviour in *S. grossum* could be applicable at least in the investigated landscape of NE Germany. In fragmented landscapes with few suitable habitats low dispersal afford evolutionary benefit as the probability of migrants to reach new habitats is low. Individuals of stable, isolated habitats which possess low dispersal rather find mating partners and suitable habitat conditions than migrants. Thus, high selection pressure acts upon high dispersal while low dispersal is supported by a positive selection pressure.

The protection of this species in fragmented landscapes which possibly have an evolutionarily trend to low dispersal should take into account the minimum available area of the population. Lang and Schlapp (2003) have quoted an unpublished report of Faltin and Waeber (1991), whose studies have recorded 27 individuals of *S. grossum* on an average and 116 individuals at most per 100 m² on a wet meadow in Bavaria, Southeast Germany. A likewise unpublished statement of Döler and Detzel in Detzel (1998) reported 104 individuals on a quagmire area of 2,000 m², which is equate to 0.2 individuals per 100 m². Assuming 343 marked imagines in 2007 and a mean range size of 1.8 ha, then 2 individuals of *S. grossum* per 100 m² on average lived on the Große Bruchwiese. Assuming a concentration of the individuals in their mean range size (1.8 ha), the density of individuals would account for 20–30 individuals per 100 m² there. The exact density of individuals respectively the minimum available areas remain hardly to specify. In fact the general claim of the conservation is the long-run protection and continuous watching of as much remaining habitats as possible. Otherwise, the destruction of wetland biotopes can lead to a complete eradication of sub-populations of *S. grossum* (see Malkus 1997; Marzelli 1997; Detzel 1998; Höhnen et al. 2000; Maas et al. 2002; Lang and Schlapp 2003; Wallaschek et al. 2004; Grein 2005). As the population of *S. grossum* featured only low dispersal, a re-colonisation by building of meta-population structures could not be assumed.

Acknowledgments We are grateful to M. Runze for providing invaluable help in the design and implementation of the field experiments. The manuscript benefited from comments and linguistic check made by Dr. Jürgen Ott and Dr. Klaus Reinhardt. We further thank the

two anonymous reviewers whose thoughtful comments greatly improved this manuscript.

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