

Effects of Landscape Structure on Movement Patterns of the Flightless Bush Cricket *Pholidoptera griseoaptera*

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ABSTRACT Because the viability of a population may depend on whether individuals can disperse, it is important for conservation planning to understand how landscape structure affects movement behavior. Some species occur in a wide range of landscapes differing greatly in structure, and the question arises of whether these species are particularly versatile in their dispersal or whether they are composed of genetically distinct populations adapted to contrasting landscapes. We performed a capture-mark-resight experiment to study movement patterns of the flightless bush cricket *Pholidoptera griseoaptera* (De Geer 1773) in two contrasting agricultural landscapes in France and Switzerland. The mean daily movement of *P. griseoaptera* was significantly higher in the landscape with patchily distributed habitat (Switzerland) than in the landscape with greater habitat connectivity (France). Net displacement rate did not differ between the two landscapes, which we attributed to the presence of more linear elements in the connected landscape, resulting in a more directed pattern of movement by *P. griseoaptera*. Significant differences in the movement patterns between landscapes with contrasting structure suggest important effects of landscape structure on movement and dispersal success. The possibility of varying dispersal ability within the same species needs to be studied in more detail because this may provide important information for sustainable landscape planning aimed at maintaining viable metapopulations, especially in formerly well-connected landscapes.

KEY WORDS dispersal strategy, habitat fragmentation, metapopulation, movement behavior, sustainable landscape planning

Dispersal is regarded as one of the key factors influencing population dynamics and the persistence of species (Hanski 1999). Movement between spatially separated patches serves many ecological purposes including increasing access to resources (Diekötter et al. 2006), genetic exchange between subpopulations (Leisham and Jamieson 2002), colonization of empty habitat patches (Kindvall and Ahlen 1992, Berggren et al. 2001), and escape from adverse environmental conditions (Hill et al. 2001). Therefore, an understanding of how animal species can respond to structural changes in the landscape is important for successful species management and sustainable landscape plan-

ning aimed at enhancing biodiversity (Vos et al. 2001, Bailey et al. 2002, Opdam et al. 2002).

A variety of habitat- and landscape-specific features are known to affect the movement behavior and dispersal of insects; these include the internal structure (With 1994, Kindvall 1999, Hein et al. 2003, Berggren 2004) and size of habitat fragments (Kindvall and Ahlen 1992, Hjermann and Ims 1996, Appelt and Poethke 1997), the characteristics of the surrounding matrix (Bieringer and Zulka 2003, Haynes and Cronin 2003), the geometrical shape of habitat fragments (Tischendorf and Wissel 1997), and the connectivity of habitat elements (Hjermann and Ims 1996, Bonte et al. 2004). In addition, theoretical and empirical studies have shown that landscape characteristics act as selective forces in the evolution of dispersal (Levin et al. 1984, Gandon and Michalakis 1999, Hill et al. 1999, Hanski et al. 2004).

However, knowledge of whether the movement behavior and dispersal of species differ among landscapes of contrasting structure is scarce, especially for less mobile animals. Many studies comparing insect movements among differently structured landscapes have focused on highly mobile species (Thomas and

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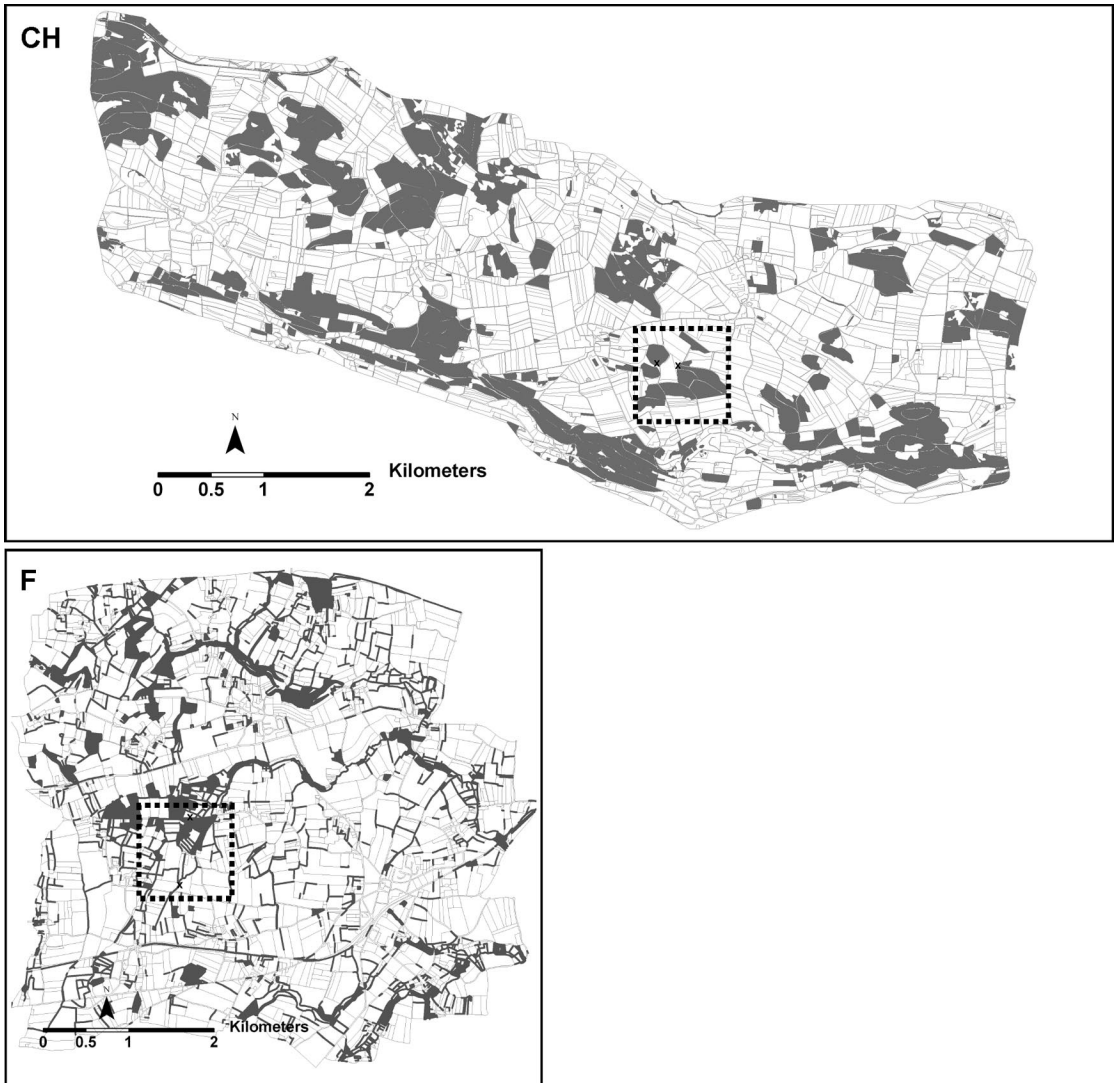


Fig. 1. Spatial distribution of the two main habitats of *P. griseoptera*, woodlots and hedgerows, in the two agricultural landscapes in Switzerland (CH) and France (F). Release points were located within the marked areas.

Harrison 1992, Hanski 1999, Hill et al. 1999, Hanski et al. 2004); much less is known about flightless insects, which are more likely to be affected by differences in landscape structure.

In Europe, many different types of agriculture landscape have developed over past centuries (Meeus 1993), and despite intensification, there remains a great diversity of landscape structure. The fact that some species occur across a wide range of landscapes raises the question of whether these species are particularly flexible in their dispersal ability or whether they consist of populations adapted to varying local conditions. If the latter is the case, different populations are likely to respond differently to continuing changes in the agricultural landscape, depending on the kind of conditions to which they are historically adapted.

The flightless bush cricket *Pholidoptera griseoptera* (De Geer 1773) (Orthoptera: Tettigoniidae) is a habitat generalist that occurs in forest edges and hedgerows—habitats that are represented in most European agricultural landscapes. Because of its restricted mobility and its distribution across landscapes of varying composition, *P. griseoptera* is a particularly interesting species for studying the effects of landscape structure on movement and dispersal. In this paper, we describe a capture-mark-resight (CMR) experiment in which animals were released into two differently structured agricultural landscapes: one in Switzerland and one in France. We tested for differences in basic mobility, net displacement, and straightness of movement of *P. griseoptera* by comparing means of movement parameters among countries with two replicate sites nested within country.

Table 1. Characterization of the release sites

	Switzerland	France
Location	47°35'58" N, 8°50'17" E	48°32'02" N, 1°33'49" W
Altitude	≈500 m a.s.l.	≈35 m a.s.l.
Mean annual precipitation	700–1,100 mm	700–900 mm
Mean annual temperature	10°C	11°C
Date of release	25 July	14 August
Area percentage of <i>P. griseoptera</i> habitat	25%	10%
Number of patches of <i>P. griseoptera</i> habitat	630	476
Edge length of <i>P. griseoptera</i> habitat	255 km	267 km
LSI of <i>P. griseoptera</i> habitat	27.62	53.02

The main habitat of *P. griseoptera* within the two studied agricultural landscapes in Switzerland and France is represented by woodlots and hedgerows.

Materials and Methods

Study Species. The dark bush cricket *Pholidoptera griseoptera* occurs throughout much of Europe (Maas et al. 2002). It is typically found along woodland edges and hedgerows (Samietz 1995), and these landscape elements are the main sites for both feeding and reproduction. Other vegetation types such as meso- and xerothermic grasslands and reed beds (Samietz 1995) may serve as additional feeding habitats.

Pholidoptera griseoptera is polyphagous, feeding on both plants (e.g., *Rubus fruticosus* L. agg., *Taraxacum officinale* Wiggers, *Urtica dioica* L.) and arthropods (e.g., caterpillars, flies, and spiders) (Ingrisch 1976). Because of its biennial life cycle, the species requires uncultivated habitats (Hartley and Warne 1973). Eggs are laid during the summer and autumn months in the axils of leaves, in pithy stems, or in decaying wood, and hatch in spring of the year after next. The nymphs go through seven instars before they reach the adult stage. The imagos, 13–18 mm long (Bellmann 1993), are flightless, and macropterous individuals have never been observed. They can be found from mid-July until November and are active during both day and night.

Study Areas. The study was conducted in two European agricultural landscapes that differed in the relative proportions and the spatial configuration of woodlands and hedgerows (Fig. 1; Table 1). While the landscape in Switzerland has a high proportion of patchily distributed woodlands within a matrix of agricultural land, the area in France has a dense network of hedgerows. Within each landscape type, mark-recapture studies were conducted at two different sites with a typical mix of woody, seminatural elements representing the main habitat of *P. griseoptera* (Fig. 1).

The Swiss study area was in the Canton of Thurgau, close to the Nussbaumer Seen and the town of Buch (Table 1). Two forest patches where *P. griseoptera* was known to occur were chosen for the capture-mark-resight experiment (CMR). One site (CH₁) was situated on the margin of a rather open, deciduous forest with a well-developed shrub layer bordering grassland (Fig. 2). The second site (CH₂), on a forest margin bordered by a gravel path, had a dense, hedge-like structure. The forest showed a sparse ground cover of bramble and dry grasses (Fig. 2).

The French study area was in the northeastern part of Brittany, close to the Bay of Mont-Saint-Michel and near the town of Pleine-Fougères (Table 1). In this area, *P. griseoptera* occurred commonly in shrub habitats, hedgerows, and woodlands (Dusoulier 1999). Two hedgerows were chosen for the release of marked animals. One hedgerow (F₁) was bordered on one side by a ditch that was overgrown by bramble and bracken and a paved road, and on the other by bracken (*Pteridium aquilinum* L. Kuhn) (Fig. 2). The second hedgerow (F₂) was bordered on both sides by grassland (Fig. 2).

CMR Experiment. CMR experiments were conducted over a period of 10 d in both landscapes in July and August 2002 (Table 1). Individuals captured in the study areas were kept individually in portable cool boxes (≈10°C) before and after marking. During captivity, animals were provided with leaves of *T. officinale*. The maximum period in captivity was 36 h. Adults were marked using a single tag of reflective tape (4 by 9 mm; 3M Scotchlite 7610 high gain fixed with Tesa second glue gel) covering both the lateral and distal side of the pronotum (see also Heller and von Helversen 1990, Kindvall 1999). An identification number was written on the distal part of the reflective tag using a permanent marker. This marking technique seemed to cause less distress to the animals than tags fixed around the femur.

Release procedures were the same at each site, with approximately equal numbers of males and females being released within an area of 2 m² around each release point. In Switzerland, 100 (50/m²) marked individuals were released at the edge of each of the two forest patches. In France, however, where the habitat elements were narrow hedgerows, the number of animals released per site was 50 (25/m²).

An area of 300 m radius around each point of release (including both habitat elements and cultivated land) was carefully searched for marked animals on 10 consecutive nights after release. Observers wore headlamps and could readily locate marked individuals by their reflective tags without handling them or disturbing their immediate vicinity. The positions of individuals were recorded using measuring tapes and suitable landmarks.

Analysis. Landscape characteristics were quantified by calculating the area percentage, the number of

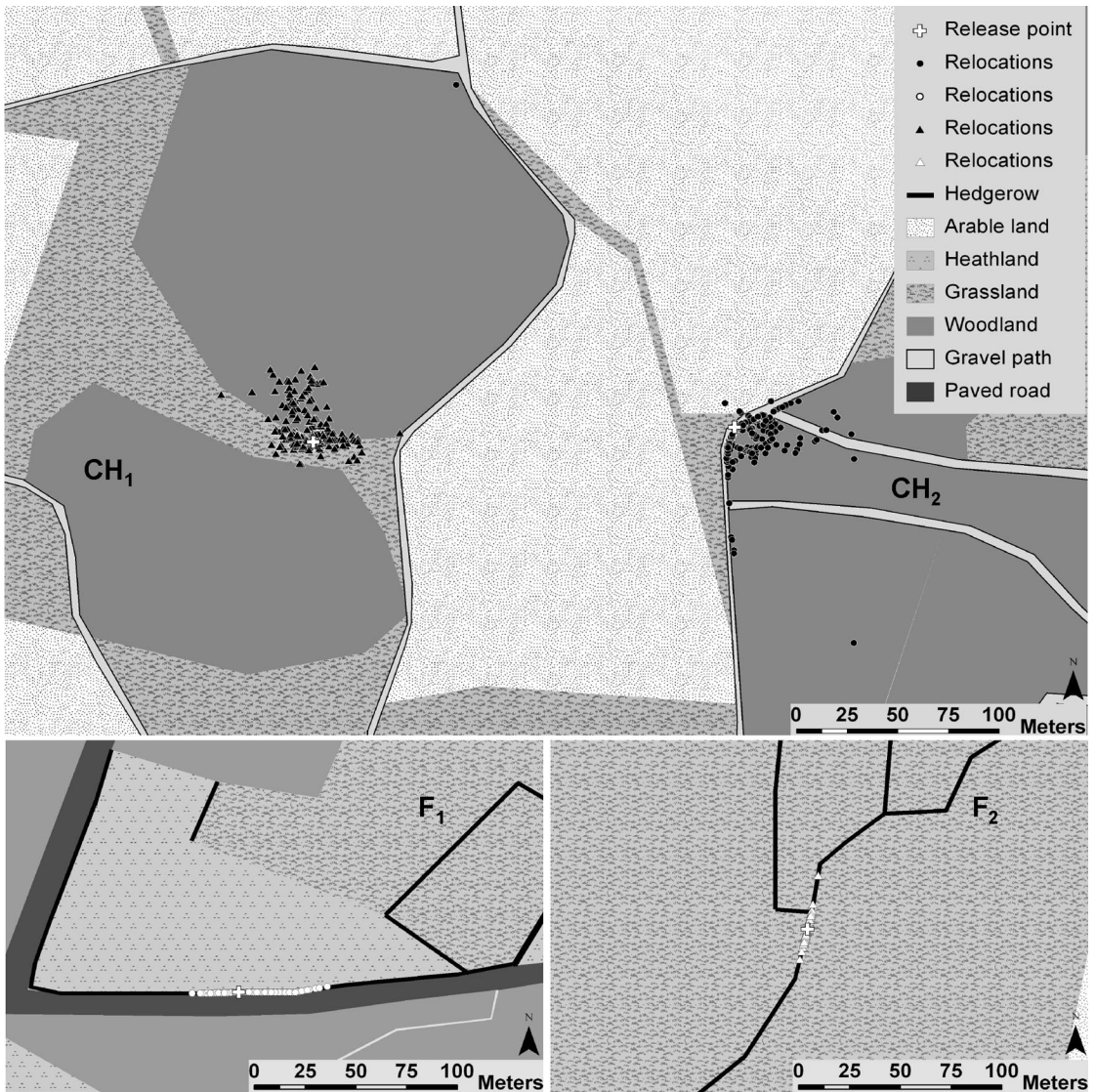


Fig. 2. Landscape characteristics and observed movement and dispersal patterns of marked individuals of *P. griseoptera* in Switzerland (CH_{1,2}) and France (F_{1,2}).

patches, the edge length, and the Landscape Shape Index (LSI) of woody seminatural elements, represented by hedgerows and woodlots in an area of 16 km² in France and 22 km² in Switzerland (Fig. 1), using FRAGSTATS (McGarigal et al. 2002). The LSI equals the total edge length of woody seminatural landscape elements e_i divided by the minimum edge length $\min e_i$, which is achieved when the habitat type of interest (woodlots and hedgerows) is maximally clumped into a single, compact patch: $LSI = e_i / \min e_i$. $LSI = 1$ when the landscape consists of a single, maximally compact patch and increases without limit as the patch type becomes more disaggregated or more linear in its spatial extent. Smaller habitat area and smaller number of patches but similar edge length of *P. griseoptera* habitat in France compared with Swit-

zerland indicate that a higher LSI in France is related to a higher linearity of habitat elements in France than in Switzerland (Table 1).

To evaluate the effects of landscape structure on movement behavior and dispersal, we calculated the mean daily movement (MDM), defined as the mean of all straight line distances between consecutive days observed for an individual, and the net displacement rate (NDR), defined as the maximum distance between the point of release and the last observed position of one individual divided by the number of days between release and the last observation. The ratio of NDR to MDM—referred to as the straightness index (SI)—was also calculated. To improve comparability between countries, we restricted the analysis to individuals that were resighted two to six times. The only

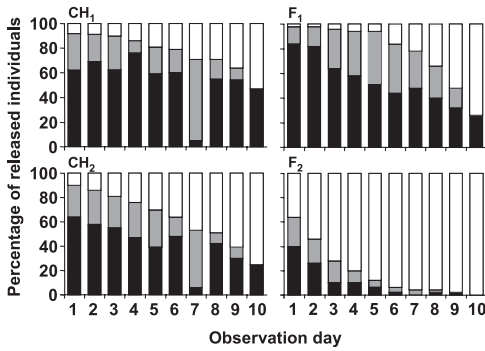


Fig. 3. Resight rates (black), missing individuals found on following days (gray), and permanently lost individuals (white) of *P. griseoptera* on each observation day for study sites in Switzerland (CH_{1,2}) and France (F_{1,2}). The number of released animals was *n* = 100 in Switzerland and *n* = 50 in France.

long distance disperser (224 m) found in the experiment was regarded as an outlier and excluded from the analysis. Point-to-point distances were calculated using ArcMap 8.2 (ESRI 2002). We did not discriminate males and females in this study because both sexes showed similar movement patterns in a previous study (Diekötter et al. 2005).

All movement parameters were ln-transformed before analysis to meet the assumptions of analysis of variance (ANOVA). A nested ANOVA model was used with sites nested within country. Because of unequal numbers of individuals recaptured at different sites (unbalanced design), the different hypotheses were tested using type III SS (Quinn and Keough 2002). Analyses were conducted using SAS 8.02 (SAS Institute 2001).

Results

Resight Rates. In all study sites, the frequency of resightings tended to decrease with time since release (Fig. 3). In France, resight rates decreased rather steadily, whereas in Switzerland, they fluctuated and showed sudden drops on rainy days. Resight rates after 24 h ranged from 62% at CH₁ to 84% at F₁ and decreased after 10 d to 47% at CH₁ and 0% at F₂. The proportion of animals that was never resighted ranged

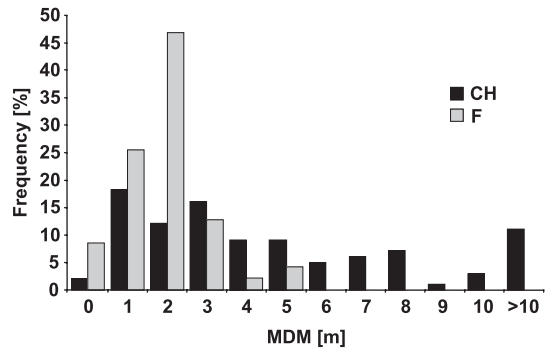


Fig. 4. Relative frequency distributions of MDM of *P. griseoptera* in Switzerland (CH) and France (F).

from 2% at F₁ to 36% at F₂. The proportion of animals that were resighted two to six times was 24% at F₂, 45% at CH₁, 63% at CH₂, and 70% at F₁.

Movement Patterns. In the Swiss landscape, several individuals were observed to cross the border between a forest edge and the adjacent matrix (Fig. 2). At CH₁, 61% of the animals resighted moved from the forest margin into the meadow on at least one occasion. Boundary crossings were observed throughout the study period, although with decreasing frequency. At CH₂, 30% of the animals resighted were observed to cross the boundary between the forest margin and the gravel road. Successful interpatch dispersal was observed at both sites with a maximum distance of 224 m covered by an individual within a period of 8 d. In the French landscapes, no marked animals were observed to leave the habitat elements in which they had been released (Fig. 2).

The untransformed mean daily movement of individual *P. griseoptera* (MDM) ranged from a minimum of 0.2 m to a maximum of 31.0 m. The MDM in Switzerland was significantly higher than in France (Table 2; Figs. 4 and 5). No significant effect of site within country was detected (Table 2). In contrast to the MDM, the NDR did not differ significantly between countries (Table 2; Fig. 5) or between sites within countries (Table 2). However, the SI did vary, being significantly higher in France than in Switzerland (Table 2; Fig. 5). Sites within countries did not differ significantly in SI (Table 2).

Table 2. Nested ANOVA of MDM, NDR, and SI observed in *P. griseoptera* released in three countries and among sites within countries

Source	df	df test	type III SS	Mean square	F	P
MDM						
Country	1	1,2	18.50	18.50	24.5	0.039
Site (country)	2	2,142	1.51	0.76	1.1	0.335
Error	142		97.42	0.69		
NDR						
Country	1	1,2	1.03	1.03	3.02	0.225
Site (country)	2	2,142	0.69	0.34	0.36	0.701
Error	142		136.93	0.96		
SI						
Country	1	1,2	21.28	21.28	27.99	0.034
Site (country)	2	2,142	1.52	0.76	1.22	0.297
Error	142		88.30	0.62		

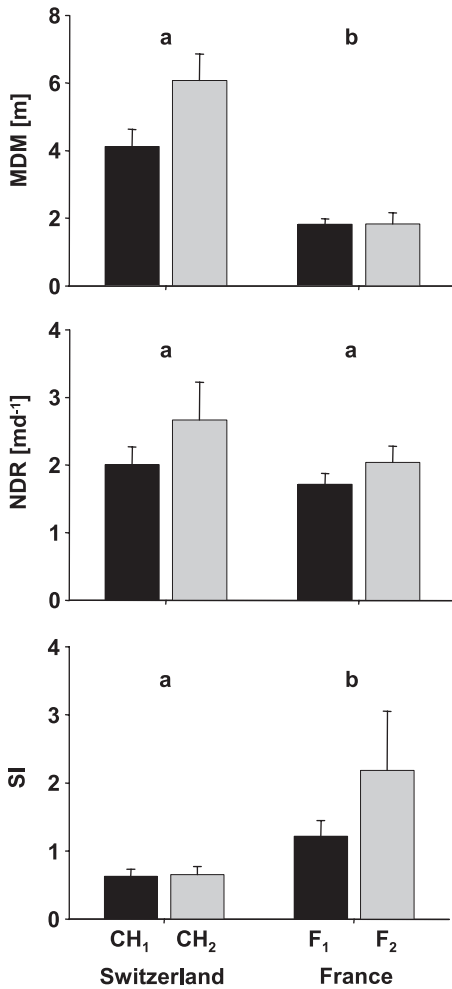


Fig. 5. Means and SEs of the untransformed parameters MDM, NDR, and SI of *P. griseoptera* for the different study sites within countries. Different letters indicate significant differences between countries.

Discussion

Resight Rates. We observed a general decrease of resight rates over time, which is characteristic for CMR studies (Narisu et al. 1999, Hein et al. 2003) and may be caused by an area-dilution effect, mortality, or the loss of markers (cf. Turchin 1998).

Although no marked individuals were found to leave the habitat elements where they were released in either of the French sites, resight rates in one of the hedgerows decreased much more rapidly than in the other. This difference cannot be explained by observer error because both sites were sampled on the same days by the same person. More likely, it was caused by a higher density of predators (e.g., birds, rodents, amphibians, reptiles, or spiders) and/or less structural protection against predators at one of the sites (Heller and von Helversen 1990, Ingrisch and Köhler 1998, Hein et al. 2003).

Movement Patterns. A comparison of the results from the two landscapes strongly suggests that landscape structure influences patterns of movement and dispersal. Thus, there were significant differences in MDM and SI between the two landscapes and also in the readiness of animals to leave suitable habitat.

For a flightless species, *P. griseoptera* in Switzerland moved surprisingly long distances and was more successful than had been expected in dispersing between patches. The mean and maximum values of the MDMs for *P. griseoptera* in Switzerland easily exceeded the means of daily movement distances observed for males (2.25 m) and females (2.16 m) of the similar-sized bush cricket *M. bicolor* (Kindvall 1999), a sedentary species that usually moves very little and is unwilling to leave its native habitat patches (Kindvall and Ahlen 1992). The observed MDM in Switzerland was well within the range of distances measured for the larger and fully winged bush cricket *Platycleis albopunctata* in suitable habitat (mesoxerophytic grassland; see Hein et al. 2003). In the well-connected landscape in France, in contrast, the mean daily movement of *P. griseoptera* was significantly lower than in Switzerland and far below the basic mobility of *M. bicolor* (Kindvall 1999).

Because we wished to study strongly contrasting landscapes, it was inevitable that the two study areas were widely separated. It is therefore possible that differences in movement behavior were also caused by factors such as climatic conditions. In fact, because the climate in both regions is rather similar and there was little different climatic conditions during the study period, we do not think that this factor was important. Another difference between the two regions was release density, which was deliberately varied to take account of the differing size of habitat patches. Intraspecific interactions have been shown to affect movement behavior in other bush cricket species (Weidemann et al. 1990, Brunzel 2002). However, because the values of MDM of *P. griseoptera* released in artificially high densities (50/m²) were similar to those recorded in an earlier study for animals released in natural densities (4/m²; Diekötter et al. 2005), we believe that release density was not an important factor either. Rather, we believe that the observed differences in the MDM between the Swiss and the French study areas reflect differences in dispersal strategy in contrasting landscapes. Such a conclusion is also consistent with previous studies (Berggren 2004).

Although there were no obvious barriers that might impede movement away from the hedgerows in either F₁ (northern side only) or F₂, no individuals were recorded outside the hedges at the French study sites. In addition to apparent physical barriers, such as roads (cf. Samways 1989), movement of *P. griseoptera* might also have been affected by edge-mediated behavior (cf. Berggren et al. 2002). For example, although highly permeable, the adjacent heathland at F₁ may have been avoided because of the abrupt change in structure, low food availability, or unsuitable microclimatic conditions. Stamps et al. (1987) and Kind-

vall (1999) interpreted such habitats as psychological rather than physical barriers to dispersal and suggested that the fraction of individuals choosing to move into less profitable habitat depends on the conditions experienced by individuals in the local patch.

In the Swiss landscape with patchily distributed habitat, *P. griseoptera* frequently left the woody elements, along which it was released. This was the case irrespective of whether forest patches were bordered by grassland (CH₁) or a gravel road (CH₂), although crossings between forest edge and grassland were more frequent than between forest edge and gravel road. The observed differences in the frequencies of animals that left wood structures into the adjacent matrix suggest the possibility of complementary resources (food or thermal) in adjacent grasslands, whereas the gravel road acted more as a potential barrier on the movement behavior of *P. griseoptera* (cf. Samways 1989). In contrast to the quantitative difference in the edge-mediated behavior of *P. griseoptera* between sites in Switzerland, the movement behaviors of *P. griseoptera* between Switzerland and France were qualitatively different and would have more pronounced effects on spatial spread than the more subtle differences in movement patterns observed within sites.

Differences in the edge-mediated behavior of *P. griseoptera* led to a significant difference in the SI of movement between the two regions studied. A significantly higher SI was observed for animals released in well-connected hedgerows in France than for animals released in patchy elements in the Swiss study area; as a result, there was a similar spatial spread (NDR) of individuals in both countries, despite the significantly lower basic mobility (MDM) of *P. griseoptera* in France. This finding leads to the general conclusion that the spatial spread of individuals depends not solely on basic mobility but also on the structure of the landscape in which the animals are moving.

The observed differences in edge transitions of *P. griseoptera* between Switzerland and France may be partly related to factors such as food availability or population densities. However, the consistent pattern of matrix avoidance in the absence of apparent physical barriers in France and the numerous transitions of *P. griseoptera* into the matrix in Switzerland could—in combination with the observed differences in MDM—also be the result of an effect of landscape structure on the evolution of dispersal strategies.

Indeed, the general heritability of mobility traits (Roff and Fairbairn 2001), the direct effects of landscape structure on movement behavior and dispersal (Keyghobadi et al. 1999, Berggren et al. 2001, Hein et al. 2003), and the recent findings on very mobile insects (Hill et al. 1999, Hanski et al. 2004) are good reasons to believe that the movement differences observed in this study are the result of selection for different patterns of dispersal behavior in landscapes of contrasting structure. In landscapes with a well-connected network of suitable habitats such as the one in France, there may be an advantage in remaining within suitable habitat and thus avoiding the risks

associated with moving through less favorable patches. In contrast, in a landscape where suitable habitats occur as scattered fragments, interpatch dispersal may be essential to counteract the effects of inbreeding and local extinctions of subpopulations (Bengtsson 1978). Results from a genetic survey on *P. griseoptera* in agricultural landscapes in Switzerland and Belgium (T.D., unpublished data) support the idea that different dispersal strategies may be favored in landscapes of contrasting structure. However, to test this idea, reciprocal CMR experiments need to be performed at several sites within landscapes that differ in the spatial arrangement of habitat patches.

In conclusion, our study showed that movement patterns and behavior of *P. griseoptera* differ between structurally distinct landscapes. Linear habitat elements such as hedgerows promote linear movement and therefore contribute to the net displacement of individuals. It seems likely that differences in the readiness of *P. griseoptera* to leave suitable habitat elements between landscapes showing a well-connected structure or patchy distribution of habitats reflect, at least in part, the different evolved strategies of dispersal in contrasting landscapes. The surprisingly long distances covered by this flightless species in patchy landscapes suggest that high dispersal ability may be both a prerequisite for, and a consequence of, species persistence in highly fragmented and disturbed agricultural landscapes.

Knowledge of how the dispersal ability of a species varies in relation to landscape structure may be essential in developing effective conservation strategies. In addition to providing adequate amounts of suitable habitat, it seems crucial that the spatial configuration of habitat elements and its projected alterations match the potentially landscape-specific dispersal strategies of target species.

Acknowledgments

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