Dispersal of Grasshoppers (Orthoptera: Saltatoria) by Wandering Flocks of Sheep on Calcareous Grassland in Southwest Germany

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Synopsis

Available data indicate that grazing lifestock may play an important role in the dispersal of numerous animal and plant species by providing a means of transport from one location to another. But detailed information is still lacking. In many parts of Europe transhumant shepherding was common in historic times. Flocks often travelled hundreds of kilometers between summer and winter pastures. We investigated a wandering flock of sheep in southwest Germany (Swabian Alb) in 1995 with respect to its significance for transporting grasshoppers (Saltatoria). Most grasshopper species inhabiting dry, meager grassland (Mesobromion) more or less regularly ride on sheep. Jumping-up is obviously not induced by any specific qualities of the sheep itself, but by mechanical or visual disturbances caused by the flock. 66% of 701 experimentally applied grasshoppers left the sheep within 10 minutes, but 5% were carried for more than 30 minutes. Distances of up to 700 meters were recorded, which may be far beyond the individual active dispersal capability of several grasshopper species. Frequency and distance of grasshoppers' transport depend on species, sex and weather.

grasshoppers, Saltatoria, dispersal, shepherding, calcareous grassland, pastures, nature conservation, phoresy, Germany

1 Introduction

Most Central European landscapes have been exposed to various types of extensive pastoralism for centuries and have been strongly influenced by this type of landuse (ELLENBERG 1986). Among others, poor calcareous grassland areas originate from the wandering grazing of domesticated animals, predominantly sheep (transhumant shepherding). In Germany, shepherding reached its climax in the second half of the 19th century (1864: approx. 29,7 million sheep). Since then, it declined rapidly (1989: approx. 4 million sheep) due to decreasing profits, social changes, and the development of modern agricultural practices (cf. WILKE 1992, BEINLICH & PLACHTER 1995). However, flocks of sheep persist to be an important element in the management of calcareous grasslands, although pastoral practices have changed from long-distance transhumance to local migration or paddock keeping (BEINLICH & PLACHTER 1995).

Wandering flocks of sheep may contribute to the dispersal of plant and even animal species and to the connectivity of populations by their passive transport of diaspores, eggs, or individuals (zoochory, phoresy). But presently, only very little data is available. FISCHER & al. (1996) demonstrated that a flock of sheep in Southwest Germany carried diaspores of many plant species, grasshoppers, and snails for long periods of time and over considerable distances.

This study focuses on the dispersal of grasshoppers by wandering flocks of sheep. In experiments with some tamed sheep and a sheep dummy, the behaviour of several grasshopper species and the transport capability of the vectors were analyzed.

2 Study area and methods

Observations and experiments were carried out on the pastures of a wandering flock of about 450 merino sheep (»Merino-Landschaf«) in the Swabian Alb near Münsingen, State of Baden-Württemberg, from May to September 1995. The Swabian Alb is presently one of the most important pastoral areas for transhumant shepherding in Germany (JACOBEIT 1961). This kind of pastoralism has a long tradition in this region and has resulted in vast, dry, meager grasslands (Mesobromion).

One basic question is, whether grasshoppers actively jump onto sheep or whether they land on sheep accidentally. This can hardly be analyzed within a flock of living animals. Therefore, a sheep dummy with an original pelt was used to imitate a resting sheep. The dummy was placed on grassland nearby, but in the path of the flock to facilitate observations. For seven days in the months of June, July, and September the reactions of grasshoppers to the dummy were registered over periods of one to five hours. All observations of grasshoppers on the dummy were recorded, as well as their reactions to the behaviour of the flock.

The frequency of grasshoppers landing on sheep was analysed following FISCHER & al. (1996) by

Table 1
Grasshopper species experimentally applied to tamed sheep. Ecological classification according to HARZ (1957), JAKOVLEV & KRÜGER (1954), and INGRISCH (1988). Morph: m = macropterous, b = brachypterous;

	Species	Morph	Ecological classification
Caelifera	*Chorthippus biguttulus*	m	mesophilic to xerophilic
	Chorthippus parallelus	b	mesophilic
	Euthystira brachyptera	b	no definite ecological preference
	Stenobothrus lineatus	m	xerophilic
Ensifera	*Metrioptera bicolor*	b	xerophilic
	Metrioptera roeselii	b	mesophilic to hygrophilic

standardized observation walks through the flock. Each walk was continued until 100 sheep had been visually observed. This required between five and nineteen minutes. The collection of transported grasshoppers was not possible due to the timidity of the sheep, but nevertheless, the determination of the grasshopper species was usually possible, sometimes by using binoculars.

To test the riding times on living sheep, 701 grasshoppers, including at least 50 individuals of each species and sex, were applied to the coat of tamed sheep within the flock (cf. FISCHER & al. 1996). Six grasshopper species were selected for this experiment, which have abundant populations in the observation area and represent a variety of different ecological requirements (Table 1). The grasshoppers were collected nearby the plot where the flock had just been grazing. The individuals were marked using paint markers (edding 780) and kept in large containers until application on a sheep was possible. Wherever possible, three males and three females of one grasshopper species were used for each application. The transporting sheep was tracked until the last grasshopper abandoned it. Disruptive impacts, which might have caused grasshoppers to jump off, were systematically recorded.

In addition, sheep were visually examined for transported grasshoppers, in particular while the flock was driven from one pasture to another. Since the exact time at which these »random riders« jumped up is unknown, the recorded riding times have to be taken as a minimum.

Weather conditions probably influence the »jumping-up probability« of the grasshoppers as well as their riding time on sheep. Therefore, temperature and relative humidity were measured at the beginning of each observation walk and each experimental application of grasshoppers. A digital electronic instrument (sensitivity: +/− 0.1 °C, 1% relative humidity) was placed one meter above ground level and shaded by the body of the person taking the measurements. Surface temperature of the sheep's fleece was determined in the same way.

Since it is not possible to record directly all the jumping-up events of grasshoppers in a moving flock of sheep, the number of grasshoppers recorded within standardized observation walks was taken as an indicator for the occurrance of such an event. But of course, this indicator depends on densities of the populations and on habitat structure and thus on the local situation. To eliminate this variance, observation walks from only one specific pasture plot were analysed to examine the effects of weather. Within this plot, 24 observation walks were carried out on three days (8^{th} to 10^{th} September 1995).

3 Results

3.1 Jump-up on sheep

Up to 25 grasshoppers at a time, juveniles included, were observed on the dummy sheep. High numbers were only present, if sheep grazed near the dummy (Table 2). Without the presence of the flock, a total of four grasshoppers climbed onto the dummy in one period of investigation. Obviously, disturbances by sheep within the flock positively effect the jumping-up of grasshoppers onto sheep since they try to escape from being trampled. There is no indication that grasshoppers actively approach and jump onto sheep, although temperatures on the surface of the wool, as measured on live sheep in the flock as well as on a dummy sheep, are often considerably higher than the surrounding air-temperature (Fig. 1).

3.2 Grasshopper species and frequency on sheep

During standardized walks through the flock and random observations, almost all the species present in the observation area were recorded on sheep (Table 3).

Individuals of *Gryllus campetris* are not likely to be observed riding on sheep because this species tries to escape from being trampled by hiding below ground. *Psophus stridulus* and *Tetrix subulata* appeared only within a small pasture plot and therefore might have been overlooked while riding on sheep.

The number of grasshoppers during 85 standardized observation walks (each walk with 100 sheep visually searched) varied between none and 66 individuals (Fig. 2). During 88% of all walks, no more than 20 grasshoppers were counted.

3.3 Riding times and covered distances

Within the grazing or wandering flock, 462 of a total of 701 observed grasshoppers (66%) left the transporting sheep within 10 minutes, another 127 (18%)

Table 2

Grasshoppers observed on a dummy sheep before and after the flock of sheep passed by. The species of juvenile individuals (j) could not be determined. *C. biguttulus* and *C. brunneus* could not be discriminated; (f) = female, (m) = male. Before the arrival of the flock, a total of only four individuals was recorded, whereas 35 were recorded after the flock had passed.

Date	Time	Temp.	before	after	Comment
6/20/95	14:00 – 15:00	30 °C	–	–	Flock did not closely pass by the dummy
7/1/95	10:00 – 11:00	32 °C	–	–	Flock did not closely pass by the dummy
7/3/95	15:00 – 19:00	24 °C	3 Caelifera (j)	20 Caelifera (j) 5 Ensifera (j)	Flock grazed close to the dummy
7/5/95	12:00 – 17:00	22 °C	–	–	Flock passed by >10 m from the dummy
9/16/95	14:00 – 16:00	18 °C	1 *C. parallelus* (f)	2 *C. parallelus* (f) 1 *C. parallelus* (m) 1 *C. biguttulus/brunneus* (m)	Flock grazed close to the dummy
9/17/95	12:00 – 14:00	20 °C	–	1 *C. biguttulus/brunneus* (m) 3 *C. biguttulus/brunneus* (f)	Flock passed by approx. 5 m from the dummy
9/26/95	16:00 – 17:00	14 °C	–	1 *C. parallelus* (f) 1 *S. lineatus* (m)	Flock passed by close to the dummy

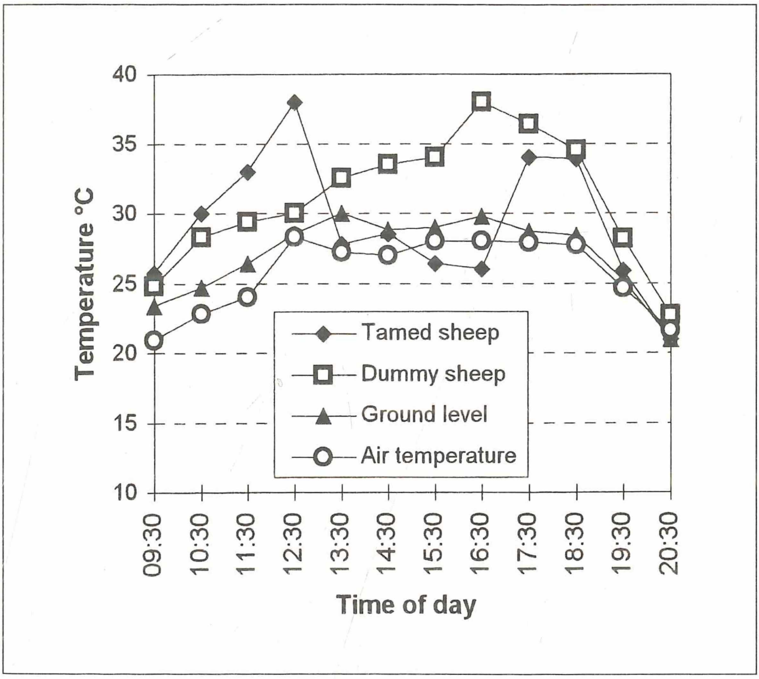

Fig. 1

Course of temperature during a sunny day in July 1995. Temperature was taken every hour on the surface of the wool of a tamed sheep and a dummy sheep as well as at ground level (in the vegetation) and about one meter above ground (air temperature). From 13:00 till 17:00 the flock rested in the shade of trees to escape the heat. This explains the decrease in temperature on the living sheep during this time period.

Table 3
Species set of grasshoppers (nomenclature according to DETZEL 1995) within the observation area, and species observed on sheep:
x = definite observation;
(x) = most likely observed, but identification not clear,
– = no observation.

Grasshopper species		
in the observation area		observed on sheep
Chorthippus biguttulus	(LINNAEUS, 1758)	x
Chorthippus brunneus	(THUNBERG, 1815)	(x)
Chorthippus parallelus	(ZETTERSTEDT, 1821)	x
Decticus verrucivorus	(LINNAEUS, 1758)	x
Euthystira brachyptera	(OCSKAY, 1826)	x
Isophya kraussii	BRUNNER VON WATTENWYL, 1878	(x)
Gomphocerippus rufus	(LINNAEUS, 1758)	x
Gryllus campestris	LINNAEUS, 1758	–
Metrioptera bicolor	(PHILIPPI, 1830)	x
Metrioptera brachyptera	(LINNAEUS, 1761)	x
Metrioptera roeselii	(HAGENBACH, 1822)	x
Omocestus viridulus	(LINNAEUS, 1758)	x
Pholidoptera griseoaptera	(DE GEER, 1773)	x
Platycleis albopunctata	(GOEZE, 1778)	x
Psophus stridulus	(LINNAEUS, 1758)	–
Stenobothrus lineatus	(PANZER, 1796)	x
Tettigonia cantans	(FUESSLY, 1775)	x
Tettigonia viridissima	LINNAEUS, 1758	x
Tetrix bipunctata	(LINNAEUS, 1758)	(x)
Tetrix tenuicornis	(SAHLBERG, 1893)	(x)
Tetrix subulata	(LINNAEUS, 1758)	–

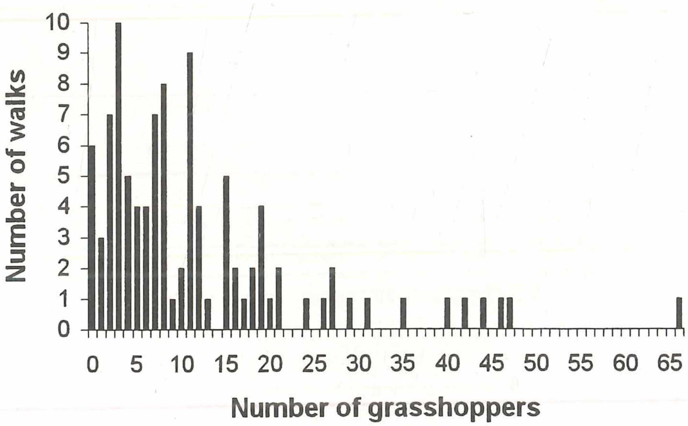

Fig. 2
Distribution of frequencies of grasshoppers during 85 standardized walks, each walk with 100 sheep visually searched.

rested 10 to 20 minutes on the sheep whilst another 38 individuals (5%) rode on the sheep for more than 30 minutes (Fig. 3). Distances covered were not only dependent on the riding times, but also on the behaviour of the flock. Accordingly, the distances covered by a sheep while transporting a specific grasshopper specimen varied greatly from 0 to 700 meters (Fig. 3). Yet, this does not necessarily correspond to the real dispersal distances for the grasshoppers, since the sheep rarely walked in a straight line but zig-zaged or walked in circles. However, in one case the flock was quickly driven in a straight line from one pasture to another and there, too, the observed maximum distance for a riding grasshopper specimen (a juvenile Caelifera) was about 700 meters. Additional grasshoppers were recorded as having covered more than 100 meters in similar situations, including experimentally applied ones as well as »random riders« (Table 4).

3.4 Riding times in relation to species and sex

Roughly half (363 out of 701 individuals) of the experimentally applied grasshoppers abandoned the sheep due to a distinct impact, mainly caused by the behaviour of the transporting sheep, i.e. contact with another sheep or with plants such as high grass, shrubs and trees. These cases were eliminated before analysing the riding times for species and sexes (Fig. 4). The highest median riding times were recorded for *S. lineatus* and *M. bicolor.* For some species, male and female riding times differed significantly: Males of *M. bicolor* and *M. roeselii* rode significantly longer ($p < 0,05$) whereas in *C. parallelus* the females stayed significantly longer on the sheep ($p < 0,01$; SPEARMAN's rank correlation). This might be true for *S. lineatus* too, but data is insufficient to prove it statistically ($p = 0,122$). For *C. biguttulus* and *E. brachyptera* sex-dependent differences in riding times are not probable ($p = 0,951$ and $p = 0,676$).

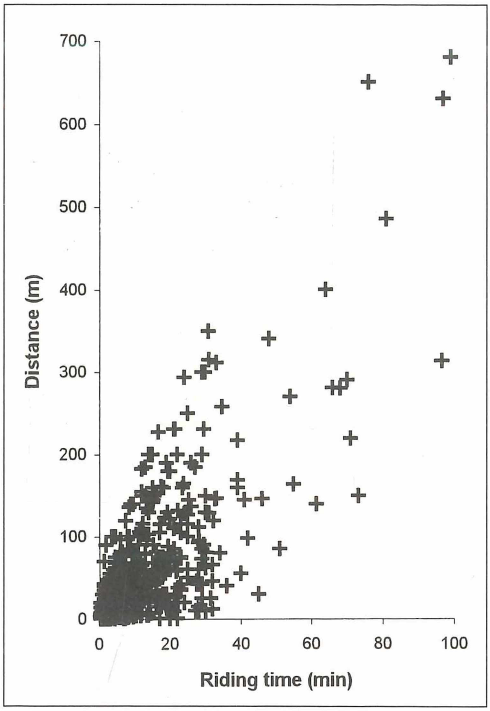

Fig. 3
Correlation of riding times and covered distances of 701 grasshoppers which had been experimentally applied on tamed sheep.

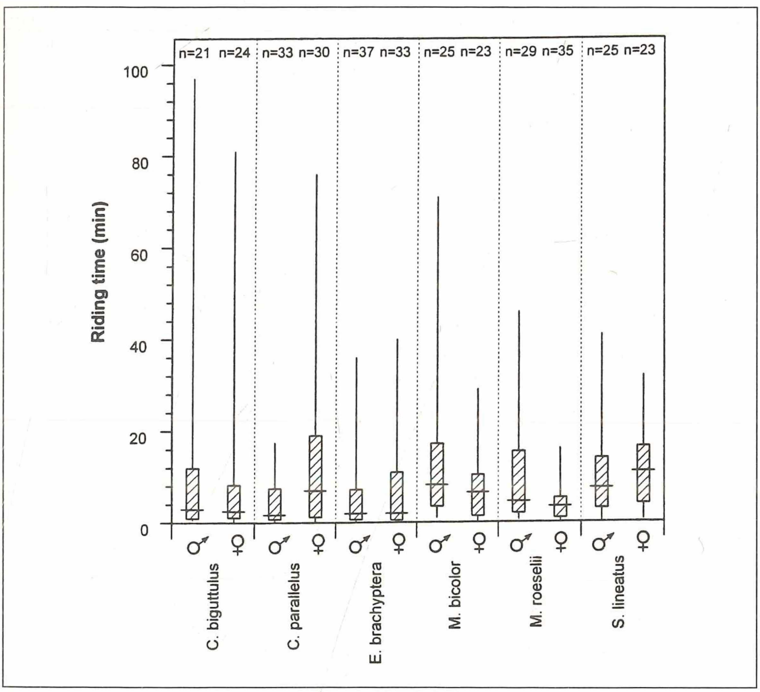

Fig. 4
Riding time by species and sex. Individuals jumping off sheep due to obvious impacts are omitted. Box-and-whisker plots:
top of vertical line = maximum, top of the box = 3rd quartile, middle dash = median, bottom of the box = 1st quartile, bottom of vertical line = minimum; n = number of individuals.

3.5 Influence of temperature and humidity

Comparing the number of riding grasshoppers to temperature and humidity, jumping-up of grasshoppers occured to be more frequently if the temperature was high, and less frequently during humid weather. Both results are significant on the 1% level (SPEARMAN's rank correlation).

The tendencies are reversed for the time span of the ride: Grasshoppers rode for longer periods of time if temperature was low and humidity was high. These results are significant on the 1% level, too.

Two application experiments were carried out just before it started to rain. Remarkably, all three individuals stuck on the sheep for riding distances of more than 100 meters (Table 4). Thus, high activity during good weather conditions, followed by sudden climatic deterioration and consequently lowered activity, might be optimal preconditions for long-distance phoresy of the grasshoppers.

4 Discussion

Large-scale seasonal migrations are only typical for a few locust-species (e.g. JOERN & GAINES 1990). In contrast, most grasshoppers and bush crickets undertake only small-scale movements (KÖHLER 1996). Even lifetime mobility seems not to exceed 20 to 50 meters for most individuals in the temperate climatic zones (AIKMAN & HEWITT 1972; KÖHLER 1996). However, it is probable for several species, that some individuals in each population have a stronger tendency for dispersal than others (e.g. KINDVALL & AHLÉN 1992; KÖHLER 1996). Consequently, the potential for large-scale dispersal is limited to only a few individuals within a population, and living or technical vectors might substantially help individuals to reach habitats far away.

It was shown in this study that the majority of grasshoppers jumping on sheep remained there for just a few minutes. Nevertheless, within five minutes, grasshoppers were observed to cover distances of up to 100 meters riding on sheep. In *M. bicolor* for instance, this distance might be the upper limit of active (re-)colonization over a shorter period of time (KINDVALL & ALHÉN 1992).

The proportion of grasshoppers riding on a sheep for more than 100 meters might appear very low. During five months of observation and in a flock of 450 sheep, only 16 individuals could be recorded as having covered more than 100 meters. But to assess the effect of passive transportation, we must consider that according to FISCHER & MATTERN (1987) there are over 100.000 sheep in the Swabian Alb region alone and that transhumant pasturing was much more common in historic times. Thus, even very rare events of large-scale transportation, which are most probable according to the data presented here, should – in total and over longer periods of time – strongly widen the individual dispersal ability of many grasshopper species.

S. lineatus and *M. bicolor*, both being xerothermophilous species, are characterized by comparatively high average riding periods. One reason might be that structurally, the sheep's back resembles their natural habitat, which is bare ground. On the other hand, high average riding times might be the result of individuals being extremely tolerant to the behaviour of the transporting sheep. Even the high level of disturbance in the centre of a driven flock is not certain to cause reactions from the grasshoppers. Both

Table 4
Grasshoppers observed on sheep while the flock was driven from one pasture to another. The species of juvenile Caelifera individuals (j) could not be determined; *C. biguttulus* and *C. brunneus* could not be discriminated; m = male; f = female, * = experimentally applied individuals.

Date	Time	Temp.	Riding grasshoppers	Covered distance (in meters)
7/3/95	16:30	22 °C	2 *O. viridulus* (f) *	200 m
7/3/95	18:00	20 °C	1 Caelifera (j)	700 m
7/24/95	17:00	27 °C	2 *C. parallelus* (m)	150 m
8/25/95	13:30	20 °C	1 *G. rufus* (m)	400 m
9/2/95	13:00	17 °C	1 *S. lineatus* (f)	170 m
			1 *C. parallelus* (f)	300 m
9/2/95	15:00	15 °C	1 *S. lineatus* (m)	100 m
			1 *C. biguttulus* (m)	200 m
9/6/95	14:30	15 °C (rain)	1 *C. parallelus* (m) *	400 m
9/7/95	16:30	15 °C (rain)	2 *C. biguttulus/brunneus* (f) *	170 and 190 m
9/9/95	18:30	18 °C	1 *C. biguttulus/brunneus* (f)	250 m each
			2 *S. lineatus* (f)	

species are bound to dry, warm grasslands in Central Europe, which has been commonly grazed by lifestock for centuries. It is therefore not unlikely, that *S. lineatus* and *M. bicolor* might have adapted in behaviour and ecology to this phoretical way of dispersal (cf. FISCHER & al. 1996). In comparison with FISCHER & al. (1996), there was no evidence for short-winged grasshopper species to have longer riding times than long-winged species.

With respect to sexes, the riding behaviour of the Ensifera and Caelifera species differs significantly. Males of both Ensifera species, *M. bicolor* and *M. roeselii,* rested longer on sheep than females. In contrast, females of two out of four Caelifera species tend towards longer riding times. This corresponds with the normal activity of sexes in these species: Males of Caelifera species usually have wider mobility ranges whereas females are less active (cf. KÖHLER 1996) and consequently rest longer on sheep. According to HARZ (1957) and KINDVALL & AHLÉN (1992), in Ensifera species females are at least as active as males, and therefore – as shown in this study – having even shorter riding times on sheep than male individuals of the same species.

Population dynamics and behaviour of grasshoppers is greatly affected by weather (e.g. JOERN & GAINES 1990). Consequently, riding time and the jumping-up probability on sheep are also correlated to weather variables such as temperature and humidity. Thus, the dispersal of riding grasshoppers by sheep over long distances (100 meters and more) is more likely during cold and humid weather, as the active mobility of individuals is minimal (JOERN & GAINES 1990; RICHARDS & WALOFF 1954). On the other hand, the frequency of jumping-up individuals will be higher during good weather conditions, due to the higher activity.

5 Consequences

Fragmentation and isolation are crucial factors for the on-going local extinction of populations in current Central European landscapes. Additionally, they may cause genetic effects in isolated populations over time (cf. MERRIAM & WAGNER 1992). Within the concept of nature conservation, measures have been developed during the past decades to diminish these effects, but all of them, like habitat corridors or habitat networks, are structurally based. This study shows that at least one additional mechanism has been at work in historic landscapes: the transport of individuals by living vertebrates, especially lifestock. Even if very long-distance dispersal by sheep could not be proved in this study, it is very probable, that it might have occured as a rare, stochastic event. Considering the number of flocks in historic times and the long time periods involved, this mechanism would have strongly contributed to the connectivity of the landscape for grasshoppers, at least for species, which commonly use grassland ecosystems. For medium-distances, which are already clearly beyond the individual mobility of many species, the given data categorically demonstrated the influence of wandering sheep. Transhumant shepherding vanished not only in Southern Germany but in most parts of Europe and with it probably one of the most important functional mechanisms for the connectivity of grasshopper populations specializing in grassland habitats. It is questionable, whether structural measures to connect adjacent populations will compensate this loss.

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