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Source: Journal of Orthoptera Research, 10(2) : 263-269

Published By: Orthopterists' Society

URL: [https://doi.org/10.1665/1082-6467\(2001\)010\[0263:DASMPI\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2001)010[0263:DASMPI]2.0.CO;2)

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Diel and seasonal mating peaks in grasshopper populations (Caelifera: Acrididae)

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Abstract

In most central European grasshopper populations, matings are very rarely observed. For five species we here quantify how frequently matings are observed. In total, only 78 matings were recorded over a period of 1100 observation hours in five acridid grasshopper species. We formally define the term mating activity (MA) as the proportion of individuals mating at a given time. MA in *Oedipoda germanica*, but not *Euthystira brachyptera*, took place preferentially around noon. In *Stenobothrus lineatus*, *Gomphocerippus rufus* and *Chorthippus parallelus*, matings possibly extended into the night. We also found evidence for a seasonal decrease in MA in *S. lineatus* and *G. rufus* but not in *C. parallelus* and *O. germanica*. Mating females were younger than the population average in *S. lineatus*, *G. rufus* and *O. germanica*. A review of the literature revealed a seasonal decline in MA in other species as well. Diel mating peaks are not very distinct, though some species seem to mate exclusively at night, some have peaks during the hottest parts of the day, and a third group seems to avoid the hot midday periods.

Key words

Caelifera, copulation, female age, mating behavior, mating frequency

Introduction

In grasshopper field populations the occurrence of mating may change dramatically in space and time. This can sometimes lead to dense mating aggregations (e.g., Wickler & Seibt 1985) and population mating peaks (e.g., Ellis & Ashall 1957). In order to quantify this, we here define the proportion of individuals mating at a given time as mating activity (MA). MA may vary over both the course of the day and seasonally.

Diel changes in MA may be associated with the thermoregulation of individuals (Chappell & Whitman 1990). Peaks during the warmest parts of the day can be expected under cold conditions when individuals need to heat up for activity. Under hot climates, however, individuals need to avoid the highest temperatures and, therefore, may mate mainly in the morning, the late afternoon, or at night. MA peaks may also be related to sensory modalities of mate

finding. For instance, when males visually search for females, mating may be restricted to daylight. Another example would be the decrease in song activity during the hottest parts of day in the katydid *Decticus verrucivorus* (Linnaeus). The lack of singing activity was related to a low sound transmission rate (Keuper *et al.* 1986) and may well lead to a distinct bimodal MA pattern over the course of the day. Biotic factors like predation pressure may also play a role in shaping diel mating patterns. For instance, in katydids of the genus *Poecilimon*, predation is assumed to be the main cause of occurrence of either nocturnal or diurnal singing and hence mate attraction (Heller & von Helversen 1993). Finally, length of copulation may influence diel MA. Species that mate for a long period or late in the afternoon may not finish mating and separate before nightfall, but continue throughout the night (Fedorov 1927, Whitman 1985).

Seasonal MA peaks can occur when environmental conditions delay mating or restrict it to a limited period of time (e.g., reproductive diapause Orshan & Pener 1979, Pener & Orshan 1980). The synchronized eclosion of adults in connection with an age-dependent decline of mating frequency may also lead to seasonal MA peaks, most obvious in monogamous species that mate only early in the season.

Periods of increased MA are important in population ecology for two reasons. First, MA peaks may restrict the mating success of immigrant individuals because immigrants are often old (Köhler 1999) and may miss opportunities to mate early in the season. A decrease in gene flow may, therefore, be expected (Reinhardt & Köhler, forthcoming). Second, both sexes adjust their mating strategies to mate availability (Andersson 1994). The time between matings is the most important component of the difference between the sex ratio and the operational sex ratio of a population. The operational sex ratio is one of the most important predictors for the direction of sexual selection (Kvarnemo & Ahnesjö 1996).

In the field, very high MA have been reported (Wickler & Seibt 1985, Whitman 1985). This strongly contrasts with

Table 1. Summary of the populations studied and the number of matings recorded in relation to the sampling effort.

Species	Study site (coordinates)	Period when adults were observed	Total hours of observations	Hours of nocturnal surveys	Number of matings observed
<i>S. lineatus</i>	Leutratal nr Jena, Germany (lat 50° 52'N, long 11° 34'E)	7 July – 15 Nov 1994 20 July – 3 Sep 1995	400	320	34
<i>C. parallelus</i>	Heath nr Veluwe, Netherlands (lat 51° 08'N, long 5° 04'E)	11 July – 4 Sep 1996	100	70	3
<i>G. rufus</i>	Leutratal nr Jena (lat 50° 52'N, long 11° 34'E)	22 Aug – 25 Nov 1994 19 Aug – 12 Dec 1995	200	150	15
<i>E. brachyptera</i>	Kernberge in Jena (lat 50° 92'N, long 11° 62'E)	18 July – 12 Aug 1996	55	0	20
<i>O. germanica</i>	gravel pit Steudnitz (lat 51° 01'N, long 11° 70'E)	6 July – 27 Oct 1994	350	0	6

our observations in central Europe, where matings are hardly seen in any grasshopper species and hence MAs are low. We use large observational data sets in order to quantify this rarity and draw some conclusions about diel and seasonal changes in the MA of five central European grasshopper species. We review the literature for data about temporal mating patterns in the Caelifera in order to provide a base for future research.

Methods

Between 1994 and 1996, we conducted intense population ecological studies of five caeliferan species at four different sites (Table 1). All sites are nutrient-poor meadows on limestone or sand. Detailed descriptions of the study sites are given by Heinrich *et al.* (1998) for the nature reserve Leutratal (Germany), by Wagner (2000) for the gravel pit Steudnitz (Germany), by Opitz *et al.* (1998) for the Veluwe area (The Netherlands), and by Reinhardt (1998) for the site in the Kernberge region (Germany). Life-history data of central European grasshopper species are reviewed by Ingrisch & Köhler (1998) and Köhler (1999). Details for the studied populations and methods can be found in Samietz (1998) for *Stenobothrus lineatus* (Panzer), in Opitz *et al.* (1998) for *Chorthippus parallelus* (Zetterstedt), in Opitz (1996) and Opitz & Köhler (1997) for *Gomphocerippus rufus* (Linnaeus), and in Wagner (2000) for *Oedipoda germanica* (Latreille). In the environs of Jena, the years 1994 and 1995 were warmer, but wetter than average during July, whereas 1996 was cooler when compared to the period of 1961 to 1990; all years had a higher than average rainfall during the summer (Heinrich *et al.* 1998, Wagner 2000). No such data are available for the Veluwe area. The phenology of the

species is highly synchronized with most individuals eclosing over a 2-w period. Marking of young grasshopper adults was started early in the season when 30 to 60% of the individuals were still nymphs and marking was continued for a further period, varying with respect to species. The day of marking was regarded as day one of their adult life. This type of age estimation has an advantage over others (see Köhler *et al.* 2000), in that individuals do not need to be killed, an essential for population ecological studies.

Individuals were resighted over the whole season by means of both nocturnal surveys of individuals marked with reflecting tape (Heller & von Helversen 1990), and diurnal surveys, except for *Euthystira brachyptera* (Ocskay) (see below). For instance, in *S. lineatus*, the average resight rates during nocturnal surveys were 70.5% (s 13.8%) in males, and 75.4% (s 14.1%) in females. During diurnal observation surveys in this species, resight rates ranged between 10 and 20% (Samietz 1998). In *O. germanica*, the average resight rate of marked individuals during the night was about 65% and thus about 10% higher during the nocturnal surveys (Wagner 2000). For logistic reasons, night surveys (if any) were not carried out in succession to day surveys. Surveys were made by walking in the study sites and intensively searching for marked individuals, to maximize resight numbers of marked individuals.

A slightly different approach was used in *E. brachyptera*. At various times of the day one observer (KR) walked through the meadow and counted the number of males, females and copulations encountered per 10-min intervals ($n = 40$). All copulating pairs were collected, so there was no opportunity for counting the same matings twice. The MA per hour is thus the average number of mating females found at a given hour of the day, divided by the number of females encoun-

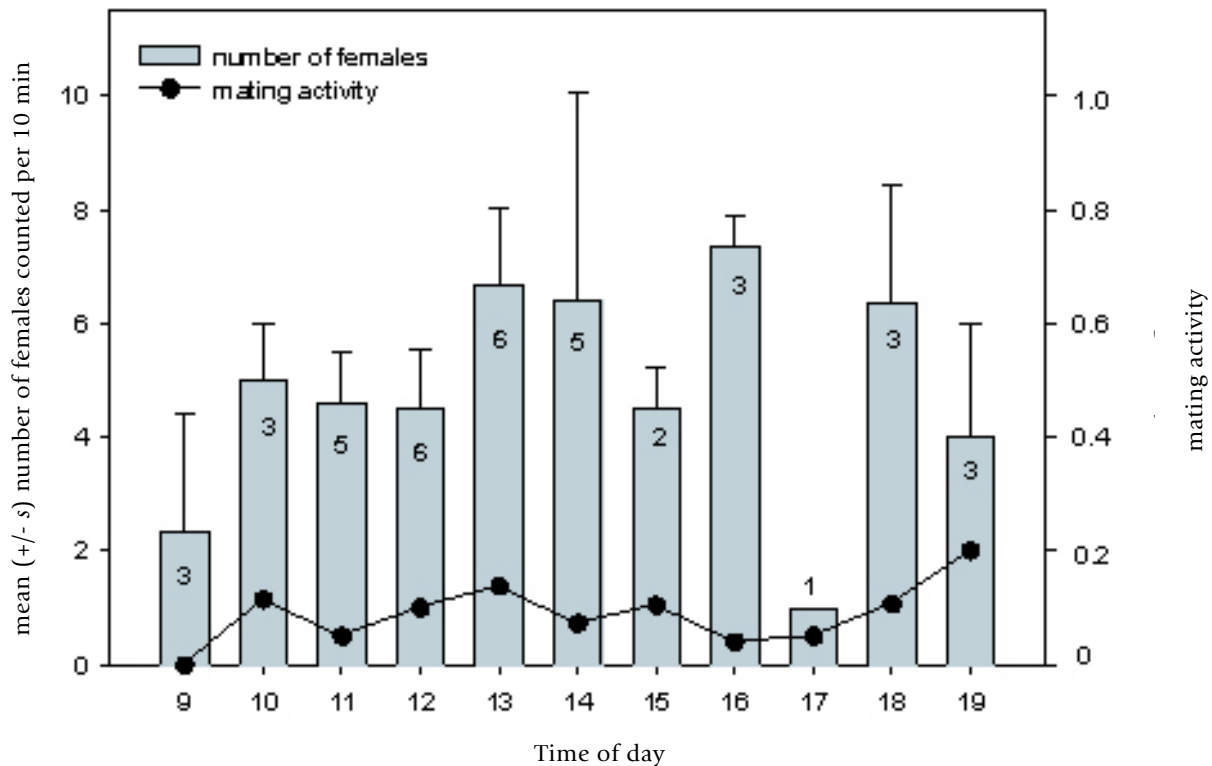


Fig. 1. Diel variation in MA (the proportion of females engaged in copulation) in the grasshopper *Euthystira brachyptera* in relation to time of day (black line) and the average number of females seen in a 10-min interval (bars). The numbers in the bars denote the number of 10-min intervals sampled.

tered per hour of day, as calculated from the 10-min counts.

Across all species, we conducted *ca* 1100 hours of investigation, *ca* 60% of which were at night (Table 1).

Results

Overall, we observed 78 matings (Table 1). Thus, we needed on average more than 14 h of observation before spotting a mating grasshopper pair, despite moderate grasshopper densities of 0.2 to 1.4 ind./m².

Diel change in MA.—In both *G. rufus* and *S. lineatus*, only nocturnal matings were observed and the majority of surveys took place at night (Table 1). In *C. parallelus* twelve systematic search days carried out between 1115 and 1700 (total 70 h) revealed two matings of unmarked individuals at 1400. During 16 nocturnal surveys, carried out between 2200 and 0130 (total 30 h), only a single mating was observed, this on 16 August at 2245.

In *E. brachyptera* matings were evenly distributed over the daytime (Fig. 1).

Surveys of *O. germanica* were evenly distributed between 0900 and 1800 local time (total 350 h). Only six matings were observed. Five of them took place between

1045 and 1430. The sixth female copulated for 50 min in the late afternoon when ambient temperatures (34°C) were exceptionally high. In a further 4 y of less intense investigations, only one nocturnal mating has ever been recorded. Because the resight probability of individuals is about 10% higher during the night than the day (Wagner 2000), the one occurrence of a nocturnal mating is indeed an exception in *O. germanica*.

Seasonal change of MA and age of mating individuals.—During nocturnal surveys, *S. lineatus* females showed a decrease in MA over the season, especially in 1995 (Fig. 2). The second peak in 1994 results from a single mating female out of 10 still alive and indicates that this female has mated a second time. Note that males eclose before females (Samietz 1998). All matings but one were observed between day 5 and day 20 of the adult life span. In 1994 the one exception was a female mating at an age of 51 d (second peak in 1994, Fig. 2). In both years MA in females peaked around an age of 10 d and declined afterwards. As the mean (\pm s) lifespans of females were 22.8 ± 12.7 d in 1994 and 19.3 ± 17.1 d in 1995 (Samietz 1998), this indicates that mating females were younger than the population average. In males the mating peak occurred about 5 d later, around an age of 15 d.

The MA of *G. rufus* decreased over the season. In 1994,

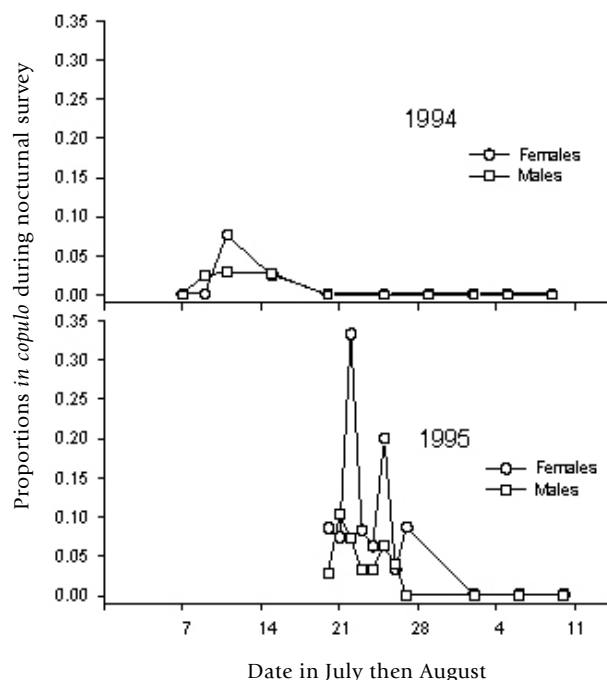


Fig. 2. Seasonal variation in MA (the proportion of individuals engaged in copulation) of marked male and female grasshoppers *S. lineatus* in the field. Recordings were stopped when the number of marked individuals was less than 15.

three of the four matings were observed during the first third of the surveys, the fourth in the second half. In 1995, 7 of 11 matings (64%) were observed in the first third of the monitorings, 9 (82%) in the first 50% of the survey nights. These data are partly supported by the age distribution of mating *G. rufus* females and males that were between 2–68 and 2–55 d of age, respectively. Whereas the age of mating females (mean 25 d) was indeed below the population average of 32 d (indicating early mating), males and females found mating in 1995 (means 26 and 25 d, respectively) were only slightly below the population mean of 28 and 27 d, respectively. Marked males found mating in 1994 (mean age 23 d) were as old as the mean of the population (24 d).

No clear seasonal pattern was found in *C. parallelus*. The only marked *C. parallelus* female observed mating was 23 d old.

In *O. germanica* all six matings were noticed in the second third of the monitoring period. Because females have a high age of first mating this could still mean a seasonal decline in MA. Indeed, *O. germanica* females reached a median age of 47 d; those found mating were only half as old (median 22 d).

Discussion

We found none of our species mated during the mornings. As mentioned above, there were incidences of nocturnal copulations in *G. rufus*, *S. lineatus* and *C. parallelus*. Because matings in these species are initiated by male song (Jacobs 1953) and males do not sing during hours of dark-

ness, we suggest that the nocturnal matings in these species are the result of prolonged afternoon or evening matings.

Comparison of temporal mating peaks across species.—The present field and literature data do not support the hypotheses that thermoregulation or predation are exclusively responsible for the occurrence of temporal mating peaks. A few studies suggest that MA increases during higher temperatures in moderate climates and that there are distinct lower mating activities around noon in hot climates (Table 2). There are, however, exceptions to this: namely *Nomadacris septemfasciata* and the two *Ligurotettix* species (Table 2), occur in very hot climates and it does not seem likely that the reason for a mating peak around noon is related to a physiological need for warmth. However, given that sometimes matings may increase the vulnerability to visual predators (Magnhagen 1991), it may be that grasshoppers preferentially mate at a time when their main predators are least active. Yet, there are no effective tests to distinguish between the thermoregulation or predation hypotheses.

If seasonal MA peaks were merely determined by temperature we should find peaks during midsummer in colder areas, or peaks in the beginning and end of the summer in warmer habitats. In addition, noon peaks should occur early and late in the season and noon depressions in the midseason. No such data are available in the Caelifera. Fischer *et al.* (1996) could not find distinct singing activity peaks over the course of the day for some of the gomphocerine species mentioned here. Therefore, mating peaks may not occur in these species. In the nonsinging species *O. germanica*, but not in the singing *E. brachyptera*, there was evidence for an increased MA around noon in the field.

In field or lab populations MA declined over the season in *S. lineatus* (this study), *Bryodemus tuberculata* (Fabricius) (Bornhalm 1991), *Chorthippus biguttulus* (Linnaeus) (Kriegbaum 1988, Bimüller 1991), *Miramella formosanta* (Fruhstorfe) (Köhler *et al.* 1999) and *Hieroglyphus nigrorepletus* Bolivar (Siddiqi 1989). Assuming that thermoregulation is highly optimized (Chappell & Whitman 1990, Samietz & Köhler 1998) individuals may be able to be active (and mate) during a wide range of temperatures throughout the day. While this can produce diel patterns of MA, only a negligible seasonal variation is predicted. Seasonal differences may be due rather to different predation pressures or due to age-related changes in the mating frequency.

While in one laboratory study, female age did not influence MA in *C. parallelus* over the first 8 pods laid (*ca* 30 d) (Reinhardt *et al.* 1999), it decreased in females of *M. formosanta* over the season despite constant temperatures (Köhler *et al.* 1999). Such an age-related seasonal decline in MA may be explained by an increasing reluctance or inability of females to remate with increasing age. For example, *C. biguttulus* females seem not to remate at all (Kriegbaum 1988) or rarely (Bimüller 1991). Our field results showing that mating individuals were younger than the population average in *S. lineatus*, *G. rufus* and *O. germanica*, seem to support the idea of an age-related decline. Given that in the field most females are able to mate before they lay their first egg pod (Kriegbaum & von Helversen 1992) and that oviposition is temperature dependent (see *e.g.*, Samietz

Table 2. Observations on increased mating activity (MA) in relation to the time of day.

MA peaks	Species	References
day and night	<i>Schistocerca gregaria</i> (Forskål)	Ellis & Ashall 1957
at night	5 spp. of Leptysminae 3 spp. of <i>Aleuas</i> <i>Lobosceliana femoralis</i>	Rowell unpub. in Riede 1987 Carbonell 1956 Burt 1946
midday	<i>Melanoplus differentialis</i> (Thomas) <i>Nomadacris septemfasciata</i> (Serville) <i>Ligurotettix</i> spp. <i>Chortophaga viridifasciata</i> (De Geer) <i>Oedipoda germanica</i> (Latreille) <i>Phymateus leprosus</i> (Fabricius)	Kyl 1938 Burnett 1951 Greenfield 1997 Niedzlek-Feaver 1995 present study Köhler et al., unpub. data
morning and/or late afternoon	<i>Zonocerus elegans</i> (Thunberg) <i>Galidacris</i> spec. <i>Hieroglyphus nigrorapletus</i> Bolivar <i>Atractomorpha crenulata</i> (Fabricius) <i>Anacridium aegyptium</i> (Linnaeus) <i>Melanoplus sanguinipes</i> (Fabricius) <i>Calliptamus plebejus</i> (Walker)	Wickler & Seibt 1985 Riede 1987 Srivastava 1956 Srivastava 1957 Fedorov 1927 Pickford & Gillott 1972 Köhler, unpub. Data

1998 for one of the study species) it seems likely that relatively old females found mating are remating rather than mating for the first time. Age-related seasonal decline in MA may be due to changes in female receptivity through the accumulation of male seminal substances which prevent further copulation (Hartmann & Loher 1996, 1999). It is interesting to note that in *G. rufus*, where these substances have been identified (Hartmann & Loher 1996, 1999), we found a seasonal decline in MA.

Mating activity and mating frequency.—An important application of MA is in the estimation of female mating frequencies in the field. Our first method of marking individuals and counting the proportion of marked females in copulation at several times of the day or season is very labor-intensive and time consuming. With matings averaged across species, we observed only one mating per 14 observation hours. Our second method, exemplified in *E. brachyptera*, did not require marking (see also Riede 1987 for an example). Counting the proportion of mating individuals seems an easy and less onerous alternative, and it will be possible with reasonable effort to compare mating activities, i) between species in the same habitat, ii) between different populations, or iii) within populations at different times of the season. The MA thus investigated allows a calculation of field mating frequency, a key parameter in sexual selection, but rarely studied (Andersson 1994, Arnqvist & Nilsson 2000).

As stated in the introduction, MA also depends on copulation duration. Mathematically, MA in a population is the product of copulation duration and mating frequency. Therefore, when both MA and the copulation duration are known, the mating frequency can easily be calculated. This procedure requires that copulation duration does not change over

either season or time of day. Whereas no diel change in mating duration has been observed in *Chorthippus brunneus* (Thunberg) (Butlin *et al.* 1985), observation in *Locusta migratoria* (Linnaeus) (Boldyrev 1929) and *O. germanica* (Latreille) (Reinhardt & Köhler forthcoming) suggest that during cooler temperatures, copulations last longer. This includes cases where copulations are lengthened when low night temperatures arrive before mating is completed and mating pairs do not separate until the next morning, in *Anacridium aegyptium* (Linnaeus) (Fedorov 1927), in *N. septemfasciata* (Burnett 1951) and perhaps in some of our studied species. If the mating frequency of these species were to be calculated from their MA, we would observe a strong overestimation of the former because one lengthened copulation would be mistaken as many short ones.

For females, second matings were slightly longer than first ones in *C. parallelus* (Bella *et al.* 1992). Matings later in the season should then be expected to last longer, and early peaks would be more likely to remain undetected. We are therefore convinced that the seasonal peaks reported here for *S. lineatus* and *G. rufus* reflect real patterns, despite the fact that we do not know how the mating duration varies over the season.

Acknowledgements

This research was in part supported by the Deutsche Forschungsgemeinschaft (DFG grants Sa 770/1-1 and Ko 1494/1-1), by the German Ministry of Education and Research (BMBF grant 0339521A) and the state of Thuringia. We thank J. Klingelhöfer for providing unpublished data. Dr. Doug Whitman and two anonymous reviewers gave valuable comments on the manuscript.

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