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(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. Diehl 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.

Diehl 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 the 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
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 on limestone or sand. Detailed descriptions of the study

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Study site (coordinates)</th>
<th>Period when adults were observed</th>
<th>Total hours of observations</th>
<th>Hours of nocturnal surveys</th>
<th>Number of matings observed</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. lineatus</em></td>
<td>Leutratal nr Jena, Germany (lat 50° 52'N, long 11° 34'E)</td>
<td>7 July – 15 Nov 1994, 20 July – 3 Sep 1995</td>
<td>400</td>
<td>320</td>
<td>34</td>
</tr>
<tr>
<td><em>C. parallelus</em></td>
<td>Heath nr Veluwe, Netherlands (lat 51° 08'N, long 5° 04'E)</td>
<td>11 July – 4 Sep 1996</td>
<td>100</td>
<td>70</td>
<td>3</td>
</tr>
<tr>
<td><em>E. brachyptera</em></td>
<td>Kernberge in Jena (lat 50° 92'N, long 11° 62'E)</td>
<td>18 July – 12 Aug 1996</td>
<td>55</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td><em>O. germanica</em></td>
<td>gravel pit Steudnitz (lat 51° 01'N, long 11° 70'E)</td>
<td>6 July – 27 Oct 1994</td>
<td>350</td>
<td>0</td>
<td>6</td>
</tr>
</tbody>
</table>
tered per hour of day, as calculated from the 10-min counts. Across all species, we conducted \( \text{ca} \) 1100 hours of investigation, \( \text{ca} \) 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./m\(^2\).

Diel change in MA.—In both \( G. \) \( \text{rufus} \) and \( S. \) \( \text{lineatus} \), only nocturnal matings were observed and the majority of surveys took place at night (Table 1). In \( C. \) \( \text{parallellus} \) 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 \( E. \) \( \text{brachyptera} \) matings were evenly distributed over the daytime (Fig. 1).

Surveys of \( O. \) \( \text{germanica} \) 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 \( O. \) \( \text{germanica} \).

Seasonal change of MA and age of mating individuals.—During nocturnal surveys, \( S. \) \( \text{lineatus} \) 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 \( \pm \) 12.7 d in 1994 and 19.3 \( \pm \) 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 \( G. \) \( \text{rufus} \) decreased over the season. In 1994,
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 darkness, 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), *Bryodema tuberculata* (Fabricius) (Bornhalm 1991), *Chorthippus biguttulus* (Linnaeus) (Kriegbaum 1988), *Bimüller 1991), *Miramella formosanta* (Fruhstorfer) (Köhler et al. 1999) and *Hieroglyphus nigrorepletes* 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 mate 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...
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 have identified (Hartmann & Loher 1996, 1999) 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 Locusta migratoria (Linnaeus) (Boldyrev 1929) 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

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

<table>
<thead>
<tr>
<th>MA peaks</th>
<th>Species</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>day and night</td>
<td>Schistocerca gregaria (Forskål)</td>
<td>Ellis &amp; Ashall 1957</td>
</tr>
<tr>
<td></td>
<td>5 spp. of Leptysmina Lobosceliana femoralis</td>
<td>Rowell unpub. in Riede 1987</td>
</tr>
<tr>
<td>at night</td>
<td>Melanoplus differentialis (Thomas)</td>
<td>Kyl 1938</td>
</tr>
<tr>
<td></td>
<td>Nomadacris septemfasciata (Serville)</td>
<td>Burnett 1951</td>
</tr>
<tr>
<td></td>
<td>Ligurotettix spp.</td>
<td>Greenfield 1997</td>
</tr>
<tr>
<td></td>
<td>Chorthippus viridifasciata (De Geer)</td>
<td>Niedzlek-Feaver 1995</td>
</tr>
<tr>
<td></td>
<td>Oedipoda germanica (Latreille)</td>
<td>present study</td>
</tr>
<tr>
<td></td>
<td>Phymateus leposus (Fabricius)</td>
<td>Köhler et al., unpub. data</td>
</tr>
<tr>
<td>midday</td>
<td>Zonocerus elegans (Thunberg)</td>
<td>Wickler &amp; Seibt 1985</td>
</tr>
<tr>
<td></td>
<td>Calidacris spec.</td>
<td>Riede 1987</td>
</tr>
<tr>
<td></td>
<td>Hieroglyphus nigrorepletus Bolivar</td>
<td>Srivastava 1956</td>
</tr>
<tr>
<td></td>
<td>Atractomorpha crenulata (Fabricius)</td>
<td>Srivastava 1957</td>
</tr>
<tr>
<td></td>
<td>Anacridium aegyptium (Linnaeus)</td>
<td>Fedorov 1927</td>
</tr>
<tr>
<td></td>
<td>Melanoplus sanguinipes (Fabricius)</td>
<td>Pickford &amp; Gillott 1972</td>
</tr>
<tr>
<td></td>
<td>Calliptamus plebejus (Walker)</td>
<td>Köhler, unpub. Data</td>
</tr>
</tbody>
</table>
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