

MATING BEHAVIOR OF *MALACOSOMA DISSTRIA* AT TWO LEVELS OF MATE COMPETITION

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ABSTRACT

During a 3-year field study 2 levels of mate competition were observed in *Malacosoma disstria* Hübner, the forest tent caterpillar. Levels were indicated by the mean number per year of male attempts to mate females which were already in copula (interference rate). Sex ratio at emergence and population density probably determined interference rates. In the low level of mate competition, matings started late in the day and were short in duration, with some males terminating matings. In contrast, at the high level, matings began earlier and ended later with some females rejecting males and some males prolonging matings. The greater mate competition reflected a higher operational sex ratio, which probably increased the likelihood of some males finding females earlier and enhanced opportunities for females to be selective. Furthermore, the chance of sperm competition would be greater and prolonged matings were likely responses to this. Male terminated matings probably were responses to low chance of sperm competition.

RESUMEN

Durante un estudio de campo de 3 años se observaron 2 niveles de competencia de aparear en *Malacosoma disstria* Hübner. Los niveles fueron indicados por el promedio por año de tentativas por los machos de aparear con hembras ya en cópula (rango de interferencia). El rango de interferencia probablemente fue determinado por la razón de sexo y por la densidad de la población. Al nivel bajo de competencia de aparear, los apareamientos empezaron tarde en el día y duraron corto tiempo, con unos machos terminando los apareamientos. Al contraste, al nivel alto, los apareamientos empezaron más temprano y terminaron más tarde, con unas hembras rechazando los machos, y unos machos prolongando los apareamientos. La competencia mas intensa reflejo una razón operacional de sexo mas alta, la cual probablemente aumentó la probabilidad de que unos machos encontraron las hembras más temprano, y aumentó las oportunidades para las hembras ser selectivas. Además, la probabilidad de competencia de esperma sería mayor, y apareamientos prolongados fueron respuestas probables a esta condición. Los apareamientos terminados por los machos probablemente fueron respuestas a una probabilidad baja de competencia de espermas.

We examined the mating behavior of *Malacosoma disstria* Hübner, the forest tent caterpillar (Lepidoptera: Lasiocampidae), in the field at 2 levels of mate competition. Mate competition was defined as the contest among males for access to females. The relationship between mating behavior and intensity of mate competition has been explored in several insect orders: Diptera (Borgia 1980), Hemiptera (McLain 1981, Sillén-Tullberg 1981), and Odonata (Pajunen 1966, Uéda 1979). Parker (1974) and Wade and Arnold (1980) have provided theoretical discussions on the subject. This

was the first study to link the intensity of mate competition with mating behavior in Lepidoptera.

Bieman (1980) described mate search in *M. disstria*. Males began to fly from cocoon to cocoon of conspecifics in late afternoon; this behavior continued into twilight and ceased after dark. Males found females on or near their cocoons which were wrapped in live leaves of herbs and woody plants. Although females can emit pheromone (Struble 1970, Percy and Weatherston 1971, Chisholm et al. 1980), Bieman (1980) observed that males engaged in close range search did not seem to rely on pheromone for orientation. Males hovered near any cocoon even though most contained parasitic flies. Once a female was located, the male hovered at her side. He then moved back bending his abdomen towards her and pushed its tip in the direction of her bursa copulatrix. Copulation frequently followed.

Females did not move more than a few cm until twilight when they flew. The first preparations for female flight occurred when they began fanning their wings. Wing fanning took place during twilight whether or not females were mating or had mated. Wing fanning which occurred during mating was usually the first sign of its end. Females flew away soon after parting from their mates. Oviposition was concluded within 2 hours of wing fanning (Bieman 1980). The moths are nonfeeding (Stehr and Cook 1968). Hodson (1941) discovered that the male and female moths lived about 5 days. The females usually laid their single egg mass within 3 or 4 hours of emergence but males appeared to be reproductively active throughout their lives.

Males sometimes attempt to mate with females which are already in copula (Bieman and Witter 1982). This occurs up until females begin wing fanning. Late arriving males are called interferers, and the mean number of times pairs encounter late mating attempts (interference rate) gives an indication of the intensity of mate competition in a given year. We compared mating behavior in one year with a high interference rate with that of 2 years with low interference rates.

METHODS

Mating behavior was observed in 1976, 1977, and 1978. We chose plots in open areas with small trees and high moth population densities (monitored by pupal population densities). The 1976 and 1977 plots, approximately 0.25 ha each, were located in an outbreak in Ontonagon County, Michigan. The 1976 plot was not reused in 1977 because a plot was found with a higher population density 4 km to the north. The 1978 plot was also about 0.25 ha and was located in an outbreak area in St. Louis County, Minnesota. Trembling aspen, *Populus tremuloides* Michaux, less than 10 m tall was the predominant tree species and bracken fern, *Pteridium aquilinum* (L.), covered the ground in all plots. Moths were observed during the period of adult emergence on 6 and 8 July 1976, 22 to 28 June 1977, and 8 to 14 July 1978.

Observation began before male flight, which was the onset of mating activity, and was concluded at midnight. We scanned plots for solitary females and mating pairs; one complete scan took about 15 minutes. Once a pair or solitary female was found it was watched continuously until the female flew away or midnight, whichever came first. Because of the way we scanned, some matings went unobserved for up to 15 minutes. The start was

observed in 6 of 16 matings in 1976, 6 of 10 in 1977 and 3 of 5 in 1978. In the other cases, the times when the matings were found were used as starts.

We recorded the time of each mating start (start), female wing fanning (fanning), and mating end (end). The time elapsed between fanning and end was referred to as prolongation. Its value could be negative; this would occur if a mating ended before fanning. In 1976, 4 of 16 pairs had not completed mating at midnight. However, all females had fanned by then. Therefore in 1976, the means for end and prolongation were underestimated.

We noted: (1) whether or not males held on to the substrate (leaves, cocoon surfaces, or twigs) during copulation, (2) movement of mating moths, (3) mating attempts by interferers (also called encounters with interferers or instances of interference), (4) mate rejections, and (5) the sex of moth which terminated a mating. We defined one mating attempt by an interferer as all of the abdominal probes made by the individual until he departed. A mate rejection referred to any time a male flew away without mating with a solitary female after she walked away or shielded her bursa copulatrix from his probing abdomen. The moth which pulled away from or shook loose from its mate at the end of a mating was considered the mating terminator.

Time was recorded in CDT and then standardized as min after sunset for each sample member. Standard deviations are given along with means.

RESULTS

INTERFERENCE RATES

The 1977 and 1978 interference rates, which were not statistically different, were 3.5 and 10.5%, respectively, of the 1976 value (Table 1). This indicates 2 different levels of mate competition: high in 1976 and low in 1977 and 1978. Since no differences in any of the mating variables between 1977 and 1978 were found, we combined results for these years (Table 1).

MATING BEHAVIOR IN THE LOW INTERFERENCE YEARS

Matings started late in the day (Table 1) and no females rejected mating attempts ($n = 9$). Males held on to the substrate throughout copulations. Matings ended early; prolongations never exceeded 8 min (Table 1). In fact in 1977, 2 males terminated matings and flew away. They had mated 34 and 85 min before separating. Their mates remained in the position they maintained during mating, respectively, for 117 and 57 min before wing fanning. This accounts for the negative means for prolongation in 1977 and the combined totals of 1977 and 1978. The means without the 2 negative values were 4.1 ± 3.4 min in 1977 and 4.3 ± 3.0 min for the combined total of 1977 and 1978. No other males terminated matings. Interestingly, the male which ended his mating 57 min prior to fanning had endured interference twice. He was the only male to encounter interferers in 1977.

MATING BEHAVIOR IN THE HIGH INTERFERENCE YEAR

Matings began early in the day (Table 1) and 4 of 6 females, which were observed before they mated, rejected mating attempts. These females moved a few cm away from approaching males or pushed their abdomens to

TABLE 1. INTERFERENCE RATES AND TIMING OF MATINGS.

N per year Variables ¹	Year			
	1976	1977	1978	1977 + 1978
Interference rate ²	16	10	5	15
Start ³	5.7 ± 5.4a	0.2 ± 0.6b	0.6 ± 0.5b	0.3 ± 0.6b
Fanning ⁴	—108.0 ± 25.0a min	—61.4 ± 54.3b min	—39.2 ± 41.8b min	—54.0 ± 50.1b min
End	49.5 ± 82.7a min	38.6 ± 30.2a min	38.2 ± 20.4a min	38.5 ± 26.7a min
Prolongation ⁵	89.4 ± 66.9a min	24.3 ± 65.3b min	42.8 ± 22.0b min	30.5 ± 54.5b min
	39.9 ± 54.1a min	—14.3 ± 41.6b min	4.6 ± 2.9ab min	—8.0 ± 34.6b min

¹Standard deviation is given with means. Means for a variable followed by the same letter were not significantly different ($P < 0.05$, Mann Whitney U-Test).

²Interference rate is the mean number per mating of male attempts to copulate females which are already in copula.

³Time for start, fanning and end is given as min after sunset. A minus sign preceding these times indicates min before sunset.

⁴Fanning is the time when females first fan wings.

⁵Prolongation = end — fanning.

the substrate making their bursa copulatrix inaccessible. Seven mating males did not hold on to the substrate for the entire time prior to fanning. We referred to them as hangers and the 9 males which held on to the substrate the entire time before fanning were called holders. The hangers held on by their claspers an average of 74.0 ± 60.5 min. One female, which previously rejected a mating attempt, flipped off her mate, which had hung for the whole 90 min mating, and remated 5 min later. The new mate held on to a leaf for its entire 93 min mating. Only 1 difference in the mating variables was found between hangers and holders: the interference rate for hangers (10.4 ± 4.5) was greater than that for holders (2.0 ± 1.9) (Mann Whitney U-Test, $P < 0.05$). Eighty-one percent of the interferences (8.4 encounters per mating) occurred while the hangers were suspended. This was 4.2 times as much interference as holders encountered during entire matings. Thus, it appeared that hanging males were more likely to attract interferers.

Males frequently resisted female efforts to end matings. Seven of 16 prolongations were longer than the maximum of 8 min observed during the low interference years; these ranged from 20 to 140 min. There was no relationship between the number of interferences per mating and length of prolongation for 1976 (Spearman's rank correlation coefficient = -0.034 , $P > 0.1$). Three males involved in the long prolongations hung during them. One of these flew in tandem with the female until landing in another tree where the mating continued. Four other males also involved in long prolongations walked during them in the direction that their mates pulled; distances walked ranged from 5 cm to more than 50 cm. Walking was observed only once in the low interference years. Considering all years, hanging and walking occurred during prolongation in all 7 matings prolonged more than 8 min and in only 2 of 24 prolonged 8 min or less. These behaviors appeared to reduce the ability of the female to escape the male.

DISCUSSION

Sex ratio and population density probably influence the intensity of mate competition (Parker 1974, Wade and Arnold 1980). If the sex ratio of moths increases, the interference rate should also increase. Increases in population may result in shifts in behavior which would add to the number of interferers, or would decrease the distance between individuals making it more likely for searching males to encounter mating pairs. Demographic conditions were consistent with the levels of mate competition observed in this study. In 1976, a sex ratio at emergence of 1.65 was determined for an area within 1 km of our plot (Lorimer, unpublished). In contrast, a sex ratio of 1.01 was found for the 1978 plot (Bieman 1980). The sex ratio was unknown for the 1977 plot. The moth population density was at least 10 times greater in 1976 than 1977 and 1978 (Bieman 1980).

The high interference rate in 1976 probably reflected a larger ratio of searching males to receptive females (operational sex ratio, Emlen and Oring 1977) than the low rates in 1977 and 1978. A higher operational sex ratio would increase the likelihood of some males finding females earlier and the greater number of early starts in the high interference year supports this.

A higher operational sex ratio would also increase the opportunities for females to be selective. Mate rejections, which were observed only in the

interference year, support this contention. It was unlikely that rejections resulted only because females were unreceptive due to previous matings since females mated within minutes of rejecting males. The basis for the rejections is unknown (see Rutkowski 1982 for a discussion on mate choice in Lepidoptera). Hangers provide further evidence for greater female choice in the high interference year. We believe these males hung to counteract their mates' efforts to reject them. This reaction, like the similar responses made by males during prolongation, would reduce the ability of the female to escape the male. It is probably harder for a female to pull apart from a male that is not connected to an unmovable object than one that is. This hanging response did not always succeed. One female did fling off her hanging mate, but 90 min elapsed before the male fell off.

However, if hanging reduces the chance of rejection, why do most males hold on to the substrate? We speculate there are costs to hanging. Hanging may be more energetically costly than holding, and pairs with hangers attract more interference (probably resulting because of the enhanced conspicuousness of these mating pairs), which increases the chances of interferers inflicting wounds. These wounds can impede or stop reproductive activity (Bieman and Witter 1982). Therefore, males may hold on to the substrate unless they are attempting to prolong the period of copulation.

In the lesser wax moth, *Achroia grisella* (Fabricius) (Lepidoptera: Pyralidae), males sometimes prolong second matings in order to pass through a refractory period (Greenfield and Coffelt 1983). This is an unlikely explanation for the long prolongations observed in 1976 since the highly competitive situation found in 1976 would not have promoted opportunities for remating.

Sperm competition, the competition of sperm from 2 or more males for the fertilization of eggs within a female (Parker 1970), was a likely component of *M. disstria* mating behavior. We propose that long prolongations occurring during the high level of mate competition were responses to high probabilities of sperm competition as Sillén-Tullberg (1981) suggested for *Lygaeus equestris* L. (Hemiptera: Lygaeidae). We offer 2 hypotheses of how prolonged matings would lower the chances of sperm competition: (1) the longer a male extends a copulation the fewer males his mate encounters after the mating, (2) the percentage of eggs fertilized increases the longer a male delays his mate from remating; thus, we expect sperm precedence to be like that of the eastern spruce budworm, *Choristoneura fumiferana* (Clemens). In *C. fumiferana*, there appears to be a positive relationship between a first male's success at fertilizing eggs and time passed before a second male copulates (Retnakaran 1974).

Male terminated matings observed in the low levels of mate competition may be responses to low probabilities of sperm competition. Males can fertilize more than 1 female in a day (Stehr and Cook 1968). Therefore, if the chance of a female encountering a second male is low, males which terminate their matings may have the opportunity to search for additional mates in the same evening.

Instead of prolonging matings longer than 8 min or terminating them, most males responded in an intermediate manner. These males may also be counteracting the possibility of sperm competition albeit to a lesser degree than males which prolonged matings past 8 min. Matings prior to fanning averaged longer than 75 min in all years and over 150 min in 1976. It was

unlikely that all this time, particularly the additional 75 min in 1976, was used for passing sperm. Some mating time was probably spent guarding females from remating.

How males determine whether to end matings before fanning, allow females to break loose soon after, or resist female efforts to terminate matings is largely unanswered. Males apparently did not decide to prolong matings on the basis of contact with interferers. There was no relationship between the number of encounters with interferers and length of prolongations within the high interference year. Furthermore, the only male to experience interference in 1977 was one of 2 males which terminated matings. The role that age, physical condition, and mating experience played in deciding termination strategy remains unknown.

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