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Female encounter rates and fighting costs of males are associated with lek size in *Drosophila mycetophaga*

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Abstract Male costs and benefits associated with male display size in field populations of an Australian lekking *Drosophila* species were examined. Results suggested that male mating success increased with display size, since matings appeared to be more common in large displays, and since the probability of males encountering a female increased as displays contained more males. Female encounter probabilities did not increase once about 20 males or more were present on a display. Male size and fighting costs tended to increase with display size. The distribution of males among displays did not follow the ideal free distribution in the sense that each male did not have equal mating opportunity per unit time. Deviation from an ideal free distribution may have been due to female preference for mating in aggregations rather than with solitary males, since in a field experiment females were more willing for mating in an aggregation of five males than with solitary males.

Key words Lek behavior · Mating ecology · Ideal free distribution · Body size · *Drosophila*

Introduction

Lek polygyny is an uncommon mating system (e.g. Davies 1991), which may be defined as an aggregated male display that females attend primarily for the purpose of fertilization (Höglund and Alatalo 1995). *Dros-*

ophila mycetophaga is one of the few *Drosophila* species in which a lek mating system has been reported (Parsons and Bock 1976, 1977; Parsons 1977, 1982; Crossley 1988; Aspi and Hoffmann 1995). Males of this species tend to form mating aggregations on the white areas underneath hard bracket fungi, and females visit these aggregations for the purpose of fertilization (Crossley 1988; Aspi and Hoffmann 1995).

Many mechanisms to explain the development and maintenance of lek systems have been suggested (see Höglund and Alatalo 1995 for a recent review). In general these mechanisms fall into classes of female- and male- initiated models (e.g. Bradbury and Gibson 1983), although some models incorporate elements from both sexes (Widemo and Owens 1995). Female-initiated models suggest that male clustering is produced by the dominant effect of female choice, whereas in male-initiated models active female choice has no effect on male settlement.

The male- and female-initiated models have different predictions about the distribution of males and females among leks (Alatalo et al. 1992; Höglund et al. 1993; Bradbury et al. 1986, 1989; Höglund and Alatalo 1995). If male settlement is independent of female preference, the distribution of males should be proportional to the number of opposite sex present, i.e. it should be ideal-free. On the other hand, if females for some reason prefer to mate in leks instead of mating with solitary males, it would be predicted that per capita number of females and average male mating success should increase with aggregation size.

Although male mating success does not always increase with lek size (Deutsch 1994), it has been shown in several field studies that males benefit by displaying in large mating aggregations in some lekking species (e.g. Alatalo et al. 1992; Höglund et al. 1993; Nishida 1993; Shelly 1987). However, despite this, there are small aggregations in these species. If average male mating success increases with lek size, why don't solitary males join to larger aggregations? An obvious answer is that male costs in the form of agonistic behavior may also increase

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with lek size (Höglund et al. 1993; Höglund and Alatalo 1995), and subordinate males may not be capable of attending large display sites.

The aim of this paper is to examine male benefits and costs associated with lek size in *D. mycetophaga*. These have been examined in a few vertebrate species (Alatalo et al. 1992; Deutch 1994; Höglund et al. 1993), but to our knowledge the association between lek size and male costs has not been studied in any invertebrate species under field conditions.

In this study we examined variation in male benefits, costs and male size across a range of male displays in *D. mycetophaga*. We considered specifically the following questions:

1. Are male-female encounter probabilities and male mating success associated with the numbers of males present in a display?
2. Are females more willing to mate with aggregated rather than solitary males?
3. Do male fighting costs increase with aggregation size?
4. Is there an association between male size and number of males present in a display?

Materials and methods

The species

D. mycetophaga is a fairly large (body length *c.* 2.9 mm) species belonging to the subgenus *Hirtodrosophila*, and is conspicuous since wings in both sexes are patterned (Bock 1976). Males of this species aggregate on communal mating areas underneath hard bracket fungi (Parsons 1977, 1982; Parsons and Bock 1976, 1977), and females seem to visit these aggregations for the purpose of fertilization (Crossley 1988; Aspi and Hoffmann 1995).

D. mycetophaga provides many benefits for this kind of study. The size of mating displays varies from solitary males to aggregations consisting of over one hundred flies, and considerable variation in display size can be found in a small area (Aspi and Hoffmann 1995). Agonistic behavior between males has not been found in all gregarious insect species (Nishida 1993), but in *D. mycetophaga* it seems to be frequent (Crossley 1988; Aspi and Hoffmann 1995). Due to position effect it is often difficult to get information about male competitive ability, which could be used in interlek or even in intralek comparisons (see e.g. Robacker et al. 1991). However, it seems that in *Drosophila* male size could be used as an indirect measure of male dominance, because male dominance and territorial success are closely connected with size (e.g. Shelly 1987; Boake 1989; Hoffmann 1987, 1990).

Hoffmann and Blows (1992) have shown that the use of bracket fungi as mating arenas can provide feeding and breeding resources for females when there are exudates on the fungi produced by burrowing tineid moth larvae. However, males in *D. mycetophaga* do not settle directly on these resources (Hoffmann and Blows 1992), and do not defend them (Aspi and Hoffmann 1995). The presence or absence of exudates also does not influence where leks are formed, since fly aggregations are just as likely to occur on fungi without exudates as those with them (Aspi and Hoffmann 1995). Accordingly, *D. mycetophaga* seems to meet the definitions of Bradbury (1985) and Höglund and Alatalo (1995) of a lekking species.

Study sites

Data were collected in two populations (Kalorama and Madalya). Both populations occur in middle-altitude cool rainforests of

south-eastern Australia. The Madalya site is situated in the valley of Jack River in Strzelecki Ranges, about 200 km south-west from Melbourne. The Kalorama site is on the slopes of Mount Dandenong, about 50 km west of Melbourne. Other details may be found in Aspi and Hoffmann (1995).

Copulations, mate encounter rates and display size

All accessible bracket fungi in their white phase of development along a 300-m transect were chosen for observations in the Madalya study area. The site was inspected before the observation period and each bracket fungus was individually marked. Fungi along the transect line were inspected 25 times over a 3 month period between 29 December and 21 March. During each inspection the number of flies in male displays and copulating pairs were counted.

Transect data provided some information about number of copulations in relation to number of flies in male displays. However, because males and females could not be distinguished when on mating arenas (see Crossley 1988), they do not indicate the relative proportions of males and females in male displays. To determine this, four collections of flies were made from multiple male displays. One collection was made in Kalorama (20 December) and three at the Madalya site (19 January, 10 February, and 21 March). All flies in occupied male displays were collected with the aid of an aspirator between 1200 and 1400 hours, when the number of flies on male displays is largest (J. Aspi, unpublished work). After the first Madalya collection, flies that had been sexed and counted were released on the same fungi from which they had been collected. Flies from other collections were not released.

Copulations with solitary and aggregated males

Since copulations were rare and since sexes could not be distinguished in the field, we had limited data on whether females were relatively more willing to mate in aggregations than with solitary males. We therefore directly tested female willingness to mate in the presence of one male or several males in a field experiment using virgin females reared in the laboratory. Unfortunately there were insufficient females to test if there was an association between mating success and lek size (as opposed to solitary versus aggregated males).

The laboratory females were the F₁ offspring of field females collected at Sherbrooke forest near the Kalorama site. Culture vials containing agar-sugar media and commercial mushroom (see Crossley 1988) were kept at 20°C and in a 12:12 light-dark cycle. Females were sexed within a few hours of emergence, marked with a small dot of acrylic paint, and maintained in individual food vials to ensure that they were virgins. Males were caught from a large lek at Sherbrooke forest and were also maintained in food vials.

A wooden frame was built over a fungus with dimensions of 20 × 15 cm, about 80 cm above the ground. Muslin cloth was placed over the frame and extended to the ground to prevent movement of the flies away from the fungus. Observations were made of the underside of the fungus whilst lying on the ground.

Prior to a trial, a single male or five males was aspirated into the cage and allowed to settle on the fungus for 15 min. A female was then aspirated into the cage and the behavior of the flies on the mating area was observed for 60 minutes.

Male fighting costs and display size

The behavior of the flies on leks of different sizes (number of males varying between 2 and 18) was videotaped. Male behavior was analysed from 12 20-min recordings made from different leks. After a recording was completed, all flies from a fungus were collected and sexed.

Because *D. mycetophaga* males use the mating arena uniformly and can thus encounter almost any other male on the same male display (Aspi and Hoffmann 1995), the behavior of more than one male on the same lek could not be used as independent samples.

Only the behavior of one male was therefore analyzed regardless of the size of a lek. The number of encounters in which the male participated and the total amount of time used in aggressive behavior were measured.

When male agonistic behavior in *Drosophila* is analyzed, the encounter is often considered to start when males orientate towards each other (e.g. Hoffmann 1987). However, in leks with many possible opponents it was often difficult to determine when the interacting males orientated towards each other. An encounter between males was therefore considered to have started when a male touched another male by using his front legs or threatened him by slashing his wings. Encounters were considered complete when both males turned away from an opponent, or when the winning male stopped chasing his opponent. The size of a lek in these recordings was taken as the mean number of males present during the recording.

Male size in solitary and aggregated male displays

Two samples of flies were measured from the collection made on 10 February and 21 March at the Madalya study site. The wings of each male were mounted on a glass microscope slide covered with two-sided tape. Size was estimated from the length of the left wing taken from the anterior cross vein to the intersection of longitudinal vein 3 with the distal wing margin. Measurements were made with the Trace image analysis program (Leading Edge Technologies).

Results

Copulations, mate encounter rates and display size

During transect inspections, only eight copulations were observed on fungi (Table 1). When fungi carrying solitary males were excluded from the analysis (because solitary males do not constitute a mating aggregation), the number of flies on a fungus where copulation occurred was larger than the median on the other fungi. Differences were significant with two-tailed tests except in two collections (Table 1), and significant in all collections with one-tailed tests except in one collection. Overall, the fact that copulations occurred in larger leks in eight out of eight collections is significant by a sign test ($P = 0.004$). These data suggest that copulations

tended to occur relatively more frequently in large male displays. However, because males and females were not separated, we do not know if females are more likely to mate in large aggregations, or if these results simply reflect the fact that large aggregations contain more females.

Data on collections sorted for sex (Table 2) indicate that the number of females and males in each sample is positively correlated. In addition, the likelihood of females encountering males was positively correlated with the number of males present in three of the four collections. The only exception was the second Madalya sample when few females were collected.

Hoffmann and Blows (1992) provide data on female and male numbers per fungus in two populations of *D. mycetophaga*. In one of their samples collected in Kalorama in February 1991, there was a significant correlation between male and female numbers ($r_s = 0.97$, $n = 9$, $P < 0.001$), whereas in another sample from Jumbuk (near Madalya site in Strzelecki Ranges) the correlation was not significant ($r_s = 0.42$, $n = 10$, $P = 0.230$). From their published data (Table 1 in Hoffmann and Blows 1992), correlations between the number of males present and per capita number of females can be computed. In the Kalorama collection there was a significant positive correlation ($r_s = 0.73$, $n = 9$, $P = 0.025$), but in the Jumbuk collection the correlation was not significant ($r_s = 0.50$, $n = 10$, $P = 0.142$). When their data are combined with the present results, correlations between number of males and both absolute and relative number of females are positive in each of the six samples (sign test $P = 0.016$). Thus large aggregations generally have more females per male than small ones.

To further examine the relationship between the distribution of males on a fungus and female access, data from flies sampled in all four collections and the two earlier collections were pooled, ignoring a fungus with one female and no males. Although fungi with only a single displaying male were the most common in this pooled sample, comprising 39.2% of all occupied fungi,

Table 1 Number of flies on fungi where copulation occurred and on other fungi inspected at the same time

Total no. of fungi examined	No. of flies in a fungus with copulation	Number of flies in other fungi		
		Median number of flies in aggregations	95% confidence limits for the median	No. of solitary flies
17	16 ^{NS}	3.0	2–19	8
18	5 ^{NS}	3.5	2–23	9
22	54**	10.0	2–26	5
15	30*	2.0	2–4	3
15	30*	2.0	2–4	3
13	27*	2.5	2–8	6
15	26*	3.5	2–9	6
17	15**	7.0	3–10	5

** $P < 0.01$, * $P < 0.05$, ^{NS} $P > 0.05$. Binomial test, testing whether number of flies in aggregations with copulation is different from the median number of flies in other fungi inspected at same time (see Zar 1984, p. 114)

Table 2 Association between number of males present, female presence and encounter probability. Data are given for four samples of *Drosophila mycetophaga* collected on bracket fungi. The number of fungi sampled, total number of flies collected, and sex

Sample	No. of fungi	No. of flies	Sex ratio	r_s for number of males with:	
				Females per fungus	Females per male
Madalya 1	18	77	87.0	0.67*	0.59*
2	17	56	87.5	0.98***	0.35
3	22	439	70.4	0.98***	0.64**
Kalorama	11	61	70.5	0.85**	0.73*

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

only 6.0% of males displayed on their own. On the other hand, very large leks are uncommon. Only 6.0% of male displays were equal or larger than twenty males. Nevertheless, 44.3% of the males displayed at these large sites. The correlation between number of males and females in the pooled sample was highly significant ($r_s = 0.85$, $P < 0.001$, $n = 84$), even when the solitary displaying males are excluded ($r_s = 0.83$, $P < 0.001$, $n = 51$). A linear relationship between male and female numbers was evident (Fig. 1a). A Poisson regression model with the logarithmic number of males as an explanatory variable provided an adequate prediction of female numbers ($G_{(82)} = 95.20$, $P = 0.15$).

Even though fungi with a single displaying male were quite common, the female encounter probability for solitary male displays was low. Only one female was collected from fungi occupied by a single male ($n = 33$) giving an encounter probability of 0.03 (SD = 0.17). For aggregations equal to or larger than two the mean encounter probability (0.36, SD = 0.33), was significantly greater (Mann-Whitney with normal approximation $Z = 11.5$, $P < 0.001$) than that of the single male displays.

The association between number of males and per capita number of females across the entire range of male display sizes including solitary males is presented in Fig. 1b. There is a positive correlation between display size and per capita number of females ($r_s = 0.69$, $P < 0.001$, $n = 84$). This correlation was partly due to the low female encounter probability for single male displays. However, if single male displays were excluded, the correlation between these variables remained significant ($r_s = 0.32$, $P < 0.05$, $n = 51$).

The per capita number of females may level off after male display size exceeds a moderate number of males, and may even decrease in very large aggregations (Fig. 1b). The correlation between male display size and number of females per male was negative when display size was equal to or larger than 20 ($r_s = -0.70$, $P > 0.05$, $n = 5$), whereas there was a positive correlation with displays smaller than 20 ($r_s = 0.68$, $P < 0.001$, $n = 79$). For a statistical test of nonlinearity, a linear Poisson regression model was first fitted to explain the association between number of males and per capita number of females. Female number was used as the

ratio (percentage males) are given. Spearman rank correlations (r_s) were computed between the number of males and number of females on a fungus, as well as between the number of males and the number of females per male on a fungus

dependent variable in the model. The number of males was first set as an offset (i.e. explanatory variable with a coefficient of 1), and the remaining variation explained again with the number of males. If the relationship between male number and per capita number of females is linear, adding a quadratic term in this regression model should not increase the fit over the simpler model. However, the quadratic term improved the fit signifi-

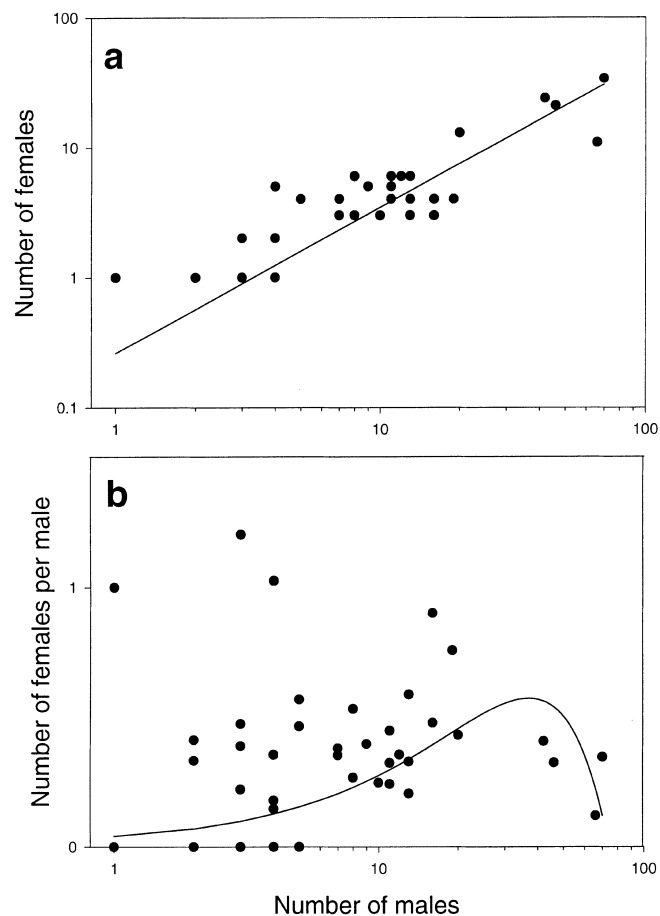


Fig. 1 Relationship between **a** the number of males and females, and **b** the number of males and per capita number of females in each display. The solid line represents fitted values of logarithmic and quadratic regression models

cantly ($G_{(1)} = 5.84$, $P = 0.015$), suggesting a significant drop in encounter rate in very large aggregations.

Copulations with solitary and aggregated males

A total of 16 trials were conducted, 8 with solitary male and 8 with five males in the mating arena. Only one of the eight females (12.5%) exposed to solitary males copulated, whereas six of the eight females (75.0%) copulated in trials conducted with five males. The difference in copulating frequency was significant (Fisher's exact two-tailed test, $P = 0.046$). This difference does not reflect a lack of courtship in the solitary treatment because all solitary males persistently courted the females.

Male fighting costs and display size

Aggressive encounters between males were common. There were on average 0.59 (SD = 0.64) encounters per male per minute. Because the encounters were generally short (mean = 7.24, SD = 5.43 s), males spent on average 5.7% (SD = 4.8) of their time in aggressive behavior. The number of aggressive encounters per male (Fig. 2a) increased significantly with mean male lek size ($r_s = 0.84$, $P < 0.01$, $n = 12$). The proportion of total time used in aggressive behavior (Fig. 2b) was also correlated with male lek size ($r_s = 0.65$, $P < 0.05$, $n = 12$). Both correlations remained significant after sequential Bonferroni correction (e.g. Rice 1989).

Male size in solitary and aggregated male displays

The wing length of 256 males from 33 displays was measured. There was a significant correlation between male wing length and the size of the display ($r_s = 0.31$, $P < 0.001$, $n = 256$) suggesting that the largest males were concentrated on the largest displays. The mean wing length of males alone on fungi was 1.95 mm (SD = 0.10), which was not significantly ($t = 0.43$, $P > 0.05$, $df = 254$) shorter than the mean length (1.96, SD = 0.11 mm) of males in aggregated male displays. The correlation between male wing length and display size was significant even when fungi with one male were excluded ($r_s = 0.27$, $P < 0.01$, $n = 245$).

Discussion

For leks to evolve, the per capita mating success of males in aggregated male displays must be higher than for males in solitary displays. In *D. mycetophaga* the probability of encountering a female was lower in solitary than in aggregated male displays, and increased with male display size, since female flies were relatively more abundant in large aggregations. The association

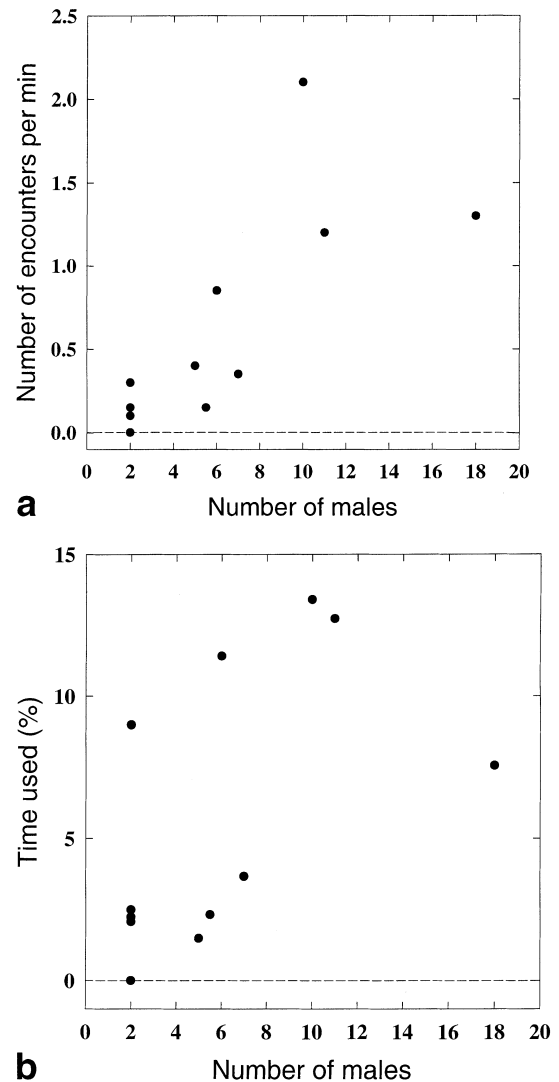


Fig. 2 Relationships between mean number of males present in a display and **a** number of agonistic encounters per male per minute, and **b** percentage of total time used in agonistic behavior

between display size and per capita number of females was not linear, leveling off after the number of males exceeded around 20. This type of relationship is not unusual (Alatalo et al. 1992; Bradbury et al. 1989). The female encounter data therefore helps to explain how lekking evolved in *D. mycetophaga*.

Unfortunately, it is not clear if increased female encounter probability in large aggregations translates into increased mating success. Matings in *D. mycetophaga* displays appear rare, consistent with data from other lekking or hilltopping insect species (Alcock 1987; Burla 1990; Parsons 1977; Shelly 1987; Spieth 1984). Observations of copulations suggested that they were more likely to occur in large displays, but we were unable to correct for the number of females on the displays. The only direct evidence we have is from caged experiments; these suggest that the mating success of aggregated males may be higher than that of solitary males.

There is some evidence that male mating success increases with aggregation size in the stink bug, *Megacopta punctissitatum* (Hibino 1986) and in the coreid bug, *Colpula lativentris* (Nishida 1993). However, among lekking Hawaiian *Drosophila* species, the few results obtained so far are inconsistent. In *D. conformis* females visited the largest of three field aggregations most often (Shelly 1990), whereas in a laboratory study of another Hawaiian species, *D. grimshawi*, there was no association between number of female visits and lek size (Droney 1994).

Although there may be a benefit of displaying in groups, there may also be costs. Aggressive male encounters occur in leks. These appeared to increase with lek size in *D. mycetophaga* because males in large leks engaged in more aggressive encounters and spent more time in these encounters. There is evidence for increased male costs in larger leks in some vertebrate species (Alatalo et al. 1992; Höglund et al. 1993) but data on invertebrates are limited. Shelly (1987) found differences in the frequency of aggressive male encounters between large and small clusters within the same lek in *D. conformis*, while Hodosh et al. (1979) showed that agonistic behavior in *D. grimshawi* increases with density under laboratory conditions. However, we are not aware of any invertebrate studies associating lek size with costs under field conditions.

Costs may help to explain why some *D. mycetophaga* males are solitary. Such males may have been forced off display sites in large leks. While solitary males were not significantly smaller than aggregated males, other factors may have influenced the ability of such males to defend areas on leks. Aggressive behavior in *Drosophila* is also influenced by age and by previous interactions with conspecifics (see Hoffmann 1990).

All male initiated models of lek evolution suggest that the distribution of males should be ideal free in sense that each male should have equal mating success per unit time. (Alatalo et al. 1992; Höglund et al. 1993; Bradbury et al. 1986, 1989; Höglund and Alatalo 1995). The most popular of the male-initiated models has been the "hotspot" model, which has also dominated theoretical perspectives (Bradbury et al. 1986; Gibson et al. 1990). This model argues that males settle in major nodes of female traffic. If only male settling in response to female density determines the number of males in a site, males should distribute themselves in proportion to the number of females present (Bradbury et al. 1986, 1989).

Bracket fungi can provide feeding and breeding resources for *D. mycetophaga* females when there are exudates on the fungi (Hoffmann and Blows 1992), suggesting that male aggregations occur where females congregate as predicted by the hotspot model. However, our previous observations have shown that the presence of exudates does not influence where male displays are formed (Aspi and Hoffmann 1995). Moreover, the present results indicate that the distribution of males in *D. mycetophaga* was not ideal free because males were more likely to encounter females on larger displays. Thus hotspot or other male-initiated models cannot to-

tally explain the maintenance of aggregations in this species. However, it is still possible that resources may have caused initial clumping in some displays (see Widemo and Owens 1995).

One reason why males in large leks may have had a greater access to females is that there is competition among the males for positions on a lek. The concept of inequality of competitors has been incorporated into the ideal free theory (Houston and McNamara 1988; Sutherland and Parker 1992). In general there are two kind of these models: continuous input and interference models (Sutherland and Parker 1992). Since we found many aggressive encounters in leks of *D. mycetophaga*, an interference model is more appropriate for this species (see Sutherland and Parker 1992; Höglund and Alatalo 1995). In interference models the number of females per male is higher in larger aggregations, because poor males are forced onto smaller leks, and highly competitive males are found in best sites (Sutherland and Parker 1992; Höglund and Alatalo 1995). Increasing male size with increasing display size suggests that there may be differences in male competitive ability in *D. mycetophaga*, as in some other lekking or landmark-defending insect species (Alcock 1993; Boake 1989; Shelly 1987).

Female preference for large aggregations is another possible factor explaining larger per capita number of females in large aggregations. Our field experiment involving manipulation of the number of males in displays suggested that females were more willing to mate in aggregations rather than with solitary males, but we do not know if this extrapolates to aggregations of different sizes. Females may favor males in aggregations for various reasons unrelated to individual male quality and attractiveness (Wittenberger 1981; Parker 1978). However, in *D. mycetophaga* aggregation size could provide some information about male quality, since larger male displays contained relatively larger males. Large males may provide genetic or non-genetic benefits like better fertilization ability or resources in the form of seminal fluids (see Markow and Ankney 1984). This possibility needs to be tested directly.

In conclusion, male access to females is greater in large aggregations but there are costs associated with displaying in such aggregations. More information is needed about possible advantages to females of mating in large aggregations, and about the association between aggregation size and male mating success.

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