Dispersal: an alternative mating tactic conditional on sex ratio and body size

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Summary. Small male milkweed beetles are less successful at obtaining mates than are larger males. Larger males usually win fights and prevent smaller males from obtaining mates and from choosing larger more fecund females as mates. When sex ratios are male-biased, smaller males are particularly likely to experience these mating disadvantages. It follows that smaller males should be especially responsive to their local competitive environment and behave so as to minimize the mating disadvantages of their smaller size. This paper tests the hypothesis that smaller males disperse from host plant patches with male-biased sex ratios and remain in patches with female-biased sex ratios more readily than larger males.

Results show both larger and smaller males disperse from patches with male-biased sex ratios more frequently than from patches with female-biased sex ratios. As predicted, however, small males are more likely to disperse from patches with male-biased sex ratios and remain in patches with female-biased sex ratios than are larger males.

The data also show that smaller males dispersing from patches with male-biased sex ratios obtain more matings than non-dispersing males.

For milkweed beetles, moving between patches can be viewed as an alternative mating tactic conditional on male body size and local sex ratio.

Introduction

In heterogeneous environments, conditions experienced by individuals at their present location may not be indicative of conditions elsewhere. This observation has given rise to the idea that dispersal

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is an adaptive response to poor environmental conditions (Southwood 1977; Solbreck 1978). For organisms actively seeking mates, sexual behavior and mate abundance may play a role in initiating dispersal between habitat patches (Shapiro 1970). In this paper I argue that where the number and type of competitors and mates varies spatially, dispersal may be a viable alternative mating tactic (sensu Dominey 1984; but see Caro and Bateson 1986) for certain members of the population.

Dominey defined an alternative mating tactic "As one of several stated behavioral options" that are "functionally equivalent" (Dominey 1984, pp. 385, 386). Milkweed beetle *Tetraopes tetraophthalmus* (Forster) (Coleoptera: Cerambycidae) movement meets these criteria. For milkweed beetles, between-patch movements are behaviorally distinct from within-patch movements. When flying beetles encounter host plant patch edges they utilize flight paths that are either likely or unlikely to result in their emigration from the patch (Lawrence 1986b). All indications are that at least males move primarily to locate receptive mates (Lawrence 1987a).

The sex ratio in the small, isolated milkweed patches milkweed beetles frequently inhabit varies considerably in time and space. In these patches, members of one sex are often twice as abundant as members of the other sex (Lawrence 1986a, 1987b). Because of the variation in the abundance of receptive females associated with sex ratio differences, the mating conditions encountered by males vary from patch to patch. The sex ratio in a patch influences male mating behavior by affecting male choice of potential mates and the frequency of male – male fights (Lawrence 1986a; McCauley 1982).

In many insect species body size also influences the choice of mating tactic (Alcock et al. 1977;

Johnson 1982; Johnson and Hubbell 1984). Most often larger males compete for females or territories and smaller males will adopt – or be forced into – "satellite" or "sneak" tactics (Cade 1980; Dominey 1984; O'Neill and Evans 1983). In milkweed beetles body size exhibits continuous variation (Mason 1964; McCauley 1979; Lawrence 1986a) and affects male mating behavior. Where sex ratios are female-biased, competition between males for mates is low and males of all sizes mate with equal frequency. Under these conditions, male beetles, especially larger individuals, preferentially mate with larger females which are known to be more fecund (Price and Willson 1976; Lawrence 1986b). When sex ratios are male-biased, male beetles do not choose between potential mates on the basis of size, but do compete with each other for access to females. Larger males win more fights than smaller males (McCauley 1982; Lawrence 1986a) and mate more frequently than smaller males (Lawrence 1986a).

As a result of these mating patterns smaller males have potentially lower fitness than larger males for two reasons. First, they obtain fewer copulations than larger males and second, they often mate with smaller, less fecund females (Lawrence 1986a). Potentially lower fitness of smaller males is, however, sex ratio dependent. Where sex ratios are male-biased, smaller males will be especially disadvantaged and as a result smaller males might minimize disadvantages of their size by emigrating more frequently than larger males from patches with male-biased sex ratios. Although both larger and smaller males should remain in patches with female-biased sex ratios, smaller males should be particularly likely to do so because female-biased conditions are the only ones where they are likely to mate. In this paper I test the hypotheses that: 1) smaller males should leave patches with male-biased sex ratios more readily than larger males, and 2) smaller males should remain in patches with female-biased sex ratios more readily than larger males. I also report the mating success of individuals employing different movement tactics.

Methods

Data are from a mark-recapture study conducted during the summer of 1982 in Webster, New Hampshire, USA. Details of the methods can be found in Lawrence (1987b) and only a brief summary will be presented here. On all but two days between June 24 and August 3, six discrete patches of milkweeds in an abandoned field were censused for milkweed beetles. Upon initial capture a unique number was painted onto an elytron of each beetle, and the length of the elytron was
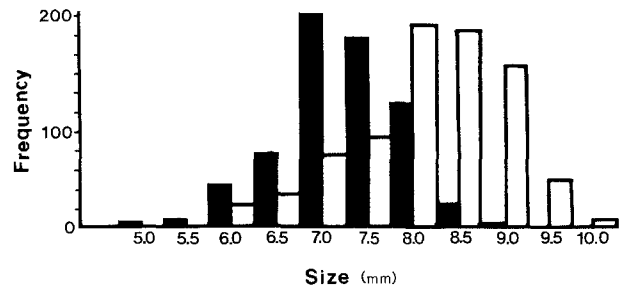

Fig. 1. Body size distribution for males (*solid bars*) and females (*open bars*)

determined using hand held calipers. At initial capture, and on all recaptures, the location, mating status, and mating partner of each beetle was recorded.

The six milkweed patches ranged in size from 364 m^2 to 23 m^2 and were separated by between 8 and 35 m of old field vegetation devoid of milkweed plants. Average beetle densities ranged from 1.6 to 0.38 beetles/m^2. Average daily population sizes were as high as 202 and as low as 13 beetles/patch. Sex ratios ranged from more than 2:1 to more than 1:2 males:females (Lawrence 1987b).

For the purpose of analysis, each patch was classified as having a male-biased, female-biased, or even sex ratio on each day of the study. Even sex ratios were considered to be from 1:1.1 to 1.1:1 males:females. To assure that sex ratio classes are discrete, data from patches with even sex ratios are not considered here, and throughout the paper sex ratios will be considered as either male- or female-biased. It should be noted, however, that the behavior of beetles in patches with even sex ratios is intermediate to behavior in patches with more biased sex ratios (Lawrence 1986a, b). Dividing sex ratio into smaller classes is undesirable for the present analysis because it produces cells with prohibitively small counts. Since, however, sex ratio is correlated with behavior (Lawrence 1987a), combining the data into two sex ratio classes will tend to obscure differences and hence provide a conservative test of the proposed hypothesis. This approach is used throughout the paper.

Since the aim of this paper is to see if the sex ratio experienced by beetles of different sizes influences the probability that they will move to a different patch, it is important to constrain the time between recaptures so that a beetle's experience at its last recapture accurately reflects the conditions leading up to its most recent move. To accomplish this, all recaptures not occurring on successive days were discarded for the purposes of analysis. Thus each of the 1162 data represent the observation of a beetle on two successive days during which its mating status and local sex ratio were known.

The distribution of male and female elytron sizes are shown (Fig. 1). Both male and female beetles were classified as either larger or smaller. Males ≤ 7.0 mm and females ≤ 8.0 mm in elytron length were classified as smaller while all other individuals were classified as larger. Movements between recaptures were classified as either within-patch or between-patch, and mating status was classified as either mating or not mating.

The data were analyzed using log linear models and χ^2 tests of independence as described by Sokal and Rohlf (1981). In several cases it was necessary to make several comparisons using the same data. While repeated use of the same data is undesirable, the significance levels obtained were unambiguous, minimizing difficulties in interpretation.

The same data were used to examine the effects of body size, sex ratio, and movement behavior on subsequent mating

success. Data from intermediate sized males (7.0 mm) exhibited intermediate mating success (see also Lawrence 1986a) and were excluded from the analysis.

Results

Table 1 A presents data on the number of males recaptured in the same or different milkweed patch from that which they occupied the previous day as a function of (1) the sex ratio in the patch they occupied the prior day, and (2) their body size.

Log linear models were used to examine the data for three way interactions between body size, sex ratio, and movement behavior. Results indicate that body size and sex ratio interact to influence movement behavior ($\chi_1^2 = 4.17$, $P = 0.041$) necessitating the use of separate 2×2 contingency tables for each level of the third variable (Sokal and Rohlf 1981).

Both larger ($\chi_1^2 = 13.3$, $P = 0.0003$) and smaller ($\chi_1^2 = 34.3$, $P = 0.0001$) males emigrated from patches with male-biased sex ratio significantly more frequently than they emigrated from patches with female-biased sex ratios. Both size classes of males left patches with male-biased sex ratios. Both size classes of males left patches with male-biased sex ratios with equal frequency (32.1%, 25/78 vs. 34.7%, 17/49; $\chi_1^2 = 0.10$, $P = 0.76$). Larger males left patches with female-biased sex ratios significantly more frequently (13.1%, 29/198 vs. 5.4%, 11/203) than smaller males ($\chi_1^2 = 7.12$, $P = 0.008$).

These results confirm those of the initial log linear model and indicate that body size and sex ratio interact to influence male milkweed beetle dispersal.

Effects of single factors on male emigration

Body size. Irrespective of sex ratio, larger males ($\chi_1^2 = 5.62$, $P = 0.018$) moved between patches significantly more frequently than smaller individuals. The mean distance moved between patches by larger and smaller males did not differ (Table 2). In contrast, larger males remaining in a patch between recaptures moved significantly farther than smaller males (Table 2).

Sex ratio. Irrespective of body size, males emigrated more frequently from patches with male-biased sex ratios than they did from patches with female-biased sex ratios (Table 3). These differences are significant ($\chi_1^2 = 5.48$, $P = 0.02$) and are consistent with experimental results presented elsewhere (Lawrence, 1987a).

Table 1. The number of males and females of each size class observed to have moved from, or remained in patches with male- or female-biased sex ratios

A) Males

Movement behavior	Body size blass: larger		Total
	Male-biased sex ratio	Female-biased sex ratio	
No between-patch movement	53	172	225
Between-patch movement	25	26	51
Sub-total	78	198	276

Movement behavior	Body size class: smaller		Total
	Male-biased sex ratio	Female-biased sex ratio	
No between-patch movement	32	192	224
Between-patch movement	17	11	28
Sub-total	49	203	252
Total	127	401	528

B) Females

Movement behavior	Body size class: larger		Total
	Male-biased sex ratio	Female-biased sex ratio	
No between-patch movement	82	261	343
Between-patch movement	6	20	26
Sub-total	88	281	369

Movement behavior	Body size class: smaller		Total
	Male-biased sex ratio	Female-biased sex ratio	
No between-patch movement	27	230	257
Between-patch movement	2	6	8
Sub-total	29	236	265
Total	117	517	634

Table 2. Distances moved within and between host plant patches by males and females of larger and smaller size classes and standard errors

Sex	Body size	Flight type	Mean distance moved	N	t	df	P<
Male	smaller	within	2.64±0.27	224	-3.46	420	0.006
Male	larger	within	4.17±0.35	225			
Male	smaller	between	39.24±4.74	28	-1.52	77	0.13
Male	larger	between	49.78±4.43	51			
Female	smaller	within	2.13±0.24	257	-0.62	598	9,54
Female	larger	within	2.33±0.20	343			
Female	smaller	between	31.46±3.96	8	-3.06	32	0.004
Female	larger	between	51.16±3.69	26			

Table 3. The proportion of males and females remaining in patches or dispersing between patches as a function of sex ratio class in their initial patch are compared using 2 × 2 contingency tables. Males emigrate from patches with male-biased sex ratios more than from patches with female-biased sex ratios. Females leave patches at the same rate irrespective of sex ratio

A) Males

Movement behavior	Sex ratio in patch at day 1		Total
	Male-biased	Female-biased	
No between-patch movement	85 (67.0%)	364 (90.8%)	449 (88.9%)
Between-patch movement	42 (33.0%)	37 (9.2%)	79 (15.0)
Total	127	401	528

$\chi_1^2 = 5.48$, $P = 0.02$

B) Females

Movement behavior	Sex ratio in patch at day 1		Total
	Male-biased	Female-biased	
No between-patch movement	109 (93.2%)	491 (95.0%)	600 (94.6%)
Between-patch movement	8 (6.8%)	26 (5.0%)	34 (5.4%)
Total	117	517	634

$\chi_1^2 = 0.06$, $P = 0.80$

Mating. Previous mating status does not effect emigration frequency. Males left patches in which they had just mated at the same rate as they left patches in which they had not mated ($\chi_1^2 = 0.05$, $P = 0.83$).

Effects of body size and sex ratio on female emigration

Table 1 B presents data on the number of females recaptured in the same or different milkweed patch from that which they occupied the previous day as a function of (1) the sex ratio in the patch they occupied the prior day, and (2) their body size. Log linear models reveal no significant interaction between body size, sex ratio, and emigration ($\chi_1^2 = 1.34$, $P = 0.25$). This allows log linear models to be used to explore 2 way interactions.

The body size by sex ratio interaction is significant ($\chi_2^2 = 272$, $P < 0.001$). A greater proportion of females in patches with male-biased sex ratios are large (75.2%, 88/117) when compared to patches with female-biased sex ratios (54.3%, 281/517). Body size and dispersal also interact significantly ($\chi_2^2 = 101.0$, $P < 0.001$). A higher proportion of large females (7.1%, 26/368) moved between patches than did small females (3.0%, 8/265). This is because, although larger and smaller females emigrate from patches with male-biased sex ratios at the same rates ($\chi_1^2 = 0.0$, $P = 0.99$), larger females emigrated more frequently than smaller females from patches with female-biased sex ratios ($\chi_1^2 = 5.62$, $P = 0.018$). Larger females also moved significantly farther between patches than smaller females, but both sizes moved similar distances within patches (Table 2). Females ($\chi_1^2 = 1.08$, $P = 0.30$) left patches in which they had just mated at the same rate as patches in which they had not mated. Thus, as with males, previous mating history does not influence movement decisions.

Consequences of movement on mating success

It is desirable to determine if decisions to leave or stay in a patch affect a beetles mating success.

Table 4. The proportion of males mating and not mating in patches they remained in or moved to are compared for larger and smaller males initially occupying patches with male-biased sex ratios. Emigrating from patches with male-biased sex ratios tends to increase the mating success of smaller, but not larger males

Males in patches with male-biased sex ratios

Small sized males

Mating status	Movement behavior		Total
	Within-patch	Between-patch	
No mating	21 (84.0%)	6 (50.0%)	25 (73.0%)
Mating	4 (16.0)	6 (50.0%)	10 (27.0%)
Total	25	12	37

$\chi_1^2 = 4.75$, $P = 0.029$

Males in patches with male-biased sex ratios

Large sized males

Mating status	Movement behavior		Total
	Within-patch	Between-patch	
Not mating	25 (67.6%)	13 (72.2%)	38 (69.1%)
Mating	12 (32.4%)	5 (27.8%)	17 (30.9%)
Total	37	18	55

$\chi_1^2 = 0.12$, $P = 0.73$

To address this question it is necessary to have data on the mating success of both individuals that remain in patches and those that move. In the present study sufficient data is only available for males as males are the only sex that exhibit frequent between-patch movement.

Log linear models were used to determine if the decision to remain in or leave patches with male-biased sex ratios interacted with body size to influence subsequent mating success. The results suggest that interactions are important ($\chi_2^2 = 3.56$, $P = 0.059$). Separate 2 × 2 analysis of movement behavior and mating success for large and small males is revealing (Table 4). Staying or leaving patches with male-biased sex ratios has no effect on the subsequent mating success of large males ($\chi_1^2 = 0.123$, $P = 0.73$). Small males, however, that leave patches with male-biased sex ratios mate significantly more frequently than do small males remaining in their original patch ($\chi_1^2 = 4.75$, $P = 0.029$).

When sex ratios are female-biased, mating success, size, and movement behavior do not interact ($\chi_1^2 = 0.7$, $P = 0.42$). In this case size is the only factor determining mating success ($\chi_4^2 = 180.5$, $P < 0.001$), larger males mating more frequently than smaller males (see Lawrence, 1986a).

Discussion

The data support the hypotheses that smaller males emigrate from patches with male-biased sex ratios and remain in patches with female-biased sex ratios. As predicted, smaller males emigrate from patches with female-biased sex ratios less frequently than larger males. Several facts also suggest smaller males leave patches with male-biased sex ratios more readily than larger males. Smaller males are shown to be less likely to move between patches and to move shorter distances between recaptures than are larger males. This must be caused in part by size dependent differences in take-off tendency and flight durations (Davis 1984).

Based on these data, the prediction is that all else being equal larger males will move between patches more frequently than smaller males. Smaller males, however, leave patches with male-biased sex ratios as frequently as do larger males, suggesting smaller males leave these patches at an especially high rate given their body size. This conclusion supports the hypothesis that smaller males, because of their competitive disadvantage in intersexual conflict, will benefit by dispersing from patches with male-biased sex ratios.

Just how males assess local sex ratio and body size is important. The sex ratio and female density influence the proportion of females in the population that are receptive to mating and presumably emitting pheromone (Lawrence 1987a). Thus males are probably not assessing sex ratio, but rather the correlated variable, receptive female abundance. Because of the correlation between sex ratio and mate availability, assessment of a patches suitability for obtaining mates does, however, take into account the abundance of male competitors. Direct evidence on how males assess body size is scarce. Body size assessment could be based on absolute criteria or be relative to the body size of competitors. One way to test between these possibilities would be to see if "small" males behave differently when they are the largest male in a patch with a male-biased sex ratio as opposed to when they are not the largest male present. Small males clearly leave patches with male-biased sex ratios that contain large males, but unfortunately

in the present study there were no cases of patches with male-biased sex ratios that contained only small males. Abundant data on male-male fights does show that small males tend to lose fights with larger males (McCauley 1982; Lawrence 1986a). Fights could provide a means of determining relative body size.

Perhaps surprisingly, the data indicate that previous mating experience does not influence the decision to disperse. Instead it is the probability of mating in the future as affected by body size and by sex ratio that influences dispersal behavior.

The fact that large females leave patches with female-biased sex ratios and are over represented in patches with male-biased sex ratios suggests that females may be actively seeking areas where they will be mated by large males. This possibility is not supported by previous studies showing females do not preferentially mate large males (McCauley 1982; Lawrence 1986a) and benefit only modestly from mating larger males (Lawrence 1986b). Although increased between-patch movement by large females may be explained by data indicating larger females are more capable of sustained flight than small females (Davis 1984), the question of why large females are over represented in patches with male-biased sex ratios remains unanswered.

Since few males move between patches and since only 25–40% of moving males are recaptured mating, it is difficult to determine definitively the consequences of movement behavior on individual mating success of different sized individuals. However, since only 16.0% (4/25) of smaller males remaining in male-biased patches mate, and 50.0% (6/12) of smaller males that emigrate from male-biased patches mate, the data indicate that for smaller males who successfully reach another patch, conditional movement increases the probability of mating. In addition, small males in patches with male-biased sex ratios are relegated to mating small less fecund females (Lawrence 1986b), a disadvantage that is potentially avoided by dispersing.

Since small male movement from patches where they are at a competitive disadvantage does result in increased mating success, dispersal by these beetles must be considered an alternative mating tactic. Two hypotheses have been proposed to explain the maintenance of alternative mating tactics in populations: 1) the tactics have equal average fitness and 2) alternative tactics increase the reproductive success of subordinate individuals, which nevertheless still do not equal those of dominant individuals (Dawkins 1980). It is not yet clear which of these hypotheses best fit the data presented here. Although dispersing from patches with male-biased sex ratios allows smaller males to obtain: 1) greater mating success than when remaining in patches with male-biased sex ratios, and 2) mating success equal to that of larger males, these advantages must be considered in relation to the costs associated with dispersal. Unfortunately costs of dispersal are difficult to assess. Exactly how advantageous it is for smaller males to disperse will depend on: 1) the costs (including mortality) of movement, 2) the probability of other patches having more female-biased sex ratios and/or smaller sized males than the original patch, and 3) the probability that the sex ratio in the original patch will remain male-biased with large sized males being common. These latter two considerations are partly dependent on the behavior of male beetles. Attainment of an ideal free distribution where sex ratios may or may not be uniform and larger and smaller males evenly distributed (Parker and Sutherland 1986) is complicated by the apparently stochastic variation in local sex ratio (Lawrence 1986a, 1987b).

Where the probability of mating is variable in space, dispersal may increase the likelihood of mating for segments of the populations. Results indicate moving between-patches is potentially an adaptive alternative mating tactic for smaller milkweed beetles occupying patches where the probability that they will mate is low.

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