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# MATE PAIRING PATTERNS OF MONARCH BUTTERFLIES (*DANAUS PLEXIPPUS* L.) AT A CALIFORNIA OVERWINTERING SITE

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**ABSTRACT.** We measured parasitism, size, fluctuating asymmetry, and wing condition of mating and nonmating monarch butterflies at a California overwintering site to document mate pairing patterns and to infer from these patterns some of the behavioral processes involved in pair formation. There was no association between parasitism levels of mating pairs, nor did these levels differ in mating and nonmating individuals. There was size-assortative mating early in the mating season i.e., relatively small males tended to couple with relatively small females and larger males coupled with larger females. Mating females were more asymmetric than nonmating females, and there was a positive assortment based on forewing asymmetry. There was also a negative correlation between size and degree of wing damage in mating females. Females that mated in the afternoon were larger than those that mated in the morning and larger size females tended to be mated less frequently than smaller ones at the end of the mating season. We argue that differences in female ability to resist matings affect pairing patterns. Large symmetrical females are probably more attractive to males, but are better able to control their pairing probability by avoiding or resisting some male mating attempts. Males might prefer large females, or large males may simply be more likely to overcome the resistance of large females.

**Additional key words:** mating, mate choice, reproductive behavior.

Low temperatures, frequent overcast weather conditions, and daylength regimes restrictive to reproductive development constrain mating activity in monarch butterflies (*Danaus plexippus* L.) at central coastal California overwintering sites to a brief but intense period during the last 4–5 weeks of the overwintering phase (Herman 1973, Hill et al. 1976, Leong et al. 1995). Unlike spring and summer generations, mating by overwintering monarchs is highly localized in both time and space.

At the majority of California overwintering sites, populations have male biased sex ratios (Tuskes & Brower 1978, Sakai 1991, Frey & Leong 1993, 1995, Nagano et al. 1993). This excess of males, plus the likelihood that the optimal number of matings is higher for males than females, can lead to a condition where the opportunity for sexual selection is stronger on males than on females (Wade & Arnold 1980, Clutton-Brock 1988, Andersson 1994). Females also disperse earlier than males from overwintering sites in California (Hill et al. 1976, Tuskes & Brower 1978, Nagano et al. 1993, Frey & Leong 1995) so that male-male competition must increase over the mating period.

The combination of large aggregations of individuals, a relatively short mating period, a male-biased sex ratio and an early female dispersal, in theory, favors courtship and pairing processes in males that minimize their time-costs and maximize their mating frequency. Under these conditions, pairing processes involving time-extensive choice, preference and/or assessment by males may have been selected against leading to a random mating pattern for a variety of phenotypic characters (Janetos 1980). In other words, males that are too selective or discriminating may miss out on many mating opportunities. On the other hand, because spermatophores represent substantial male investment (Oberhauser 1988, 1989, 1992, Svard & Wiklund 1989) and because of the large number of females at overwintering sites, some form of male choice or preference for specific female phenotypic characters might be expected which may counter tendencies toward random pairing. In addition, the variation in spermatophore mass associated with male age, size, and mating history could make it worthwhile for females to exercise choice, since spermatophore nutrients can affect fecunditity (Oberhauser 1989, 1998).

There is little consensus on monarch mating patterns at overwintering sites, or on what determines female mating frequencies. Males actively pursue females and either capture them in rapid flight or "pounce" on them as they roost in the canopy vegetation. In either case, the pair often falls to the ground where the mating attempt continues (Pliske 1975, Hill et al. 1976, pers. obs. by Frey, Leong & Oberhauser). Tuskes and Brower (1978) suggested that pairing among overwintering Californian monarchs was random, while Van Hook (1993), studying overwintering Mexican monarchs, reported that small males and large females were more likely to be in the mating population. On the other hand, Frey (unpubl. data) found that relatively small males tended to couple with relatively small females and larger males coupled with larger females among 100 pairs of mating monarchs during the early stages of the 1992 mating season at a central coastal California overwintering site. Both sexes mate repeatedly, with females and males mating up to 12 and 19 times, respectively, during their lives in captivity (Oberhauser, unpubl. data). Wild captured monarch females contained up to 10 spermatophores (Pliske 1973, Brower 1985, Leong et al. 1995). A prevailing view for their high mating frequency is that it results from the females' inability to resist male mating attempts (Rothchild 1978, Forsberg & Wiklund 1989, Boppre 1993) and from a male takedown strategy that "apparently precludes precopulatory female choice" (Van Hook 1993). This view holds that female monarch options in mating are limited and dominated by male activity and male decision processes.

We studied pairing of monarch butterflies at a central California overwintering site during their late winter/early spring phase of intense reproductive activity, looking for the effects of four characters on pairing probability and assortative mating. In addition to determining mating patterns, we hoped to be able to infer from these patterns some of the behavioral processes involved.

## MATERIALS AND METHODS

**Study populations.** Our 1.43 ha study site is at the North Beach campground, Pismo Beach, California (35°07′46″N, 120°37′53″W), midway along the California coastline. Dominant vegetation includes blue gum, *Eucalyptus globulus*, with scattered Monterey cypress, *Cupressus macrocarpa*, and Monterey pine, *Pinus radiata*. Another overwintering site occurs 2.0 km to the south. Peak population abundance estimates made during late December by mark-release-recapture studies were 225,000 (1990–1991), 160,000 (1991–1992), and 25,000 (1992–1993) individuals. In 1993, the year mating pairs were collected, the population declined from 22,000 individuals in late January to about 3000 butterflies on March 1 (Frey, unpubl. data). The male sex ratio increased from 56% to 73% during this period.

**Data collection and analysis.** We measured parasite state (i.e., the neogregarine protozoan *Ophryocystis elektroscirrha*), degree of bilateral wing asymmetry (i.e., fluctuating asymmetry), wing size, and degree of wing damage. The first three characters have figured prominently in recent models on the evolution of mating patterns (e.g., parasitism: Hamilton & Zuk 1982, Zuk 1987, Simmons 1990, Houde & Torio 1992; fluctuating asymmetry: Moller 1990, Thornhill 1992, Liggett et al. 1993, Watson & Thornhill 1994; size: McCauley 1982, Crespi 1989). Since much of monarch courtship activity involves rapid flight (Pliske 1975) and since overwintering females often disperse widely from overwintering mating sites to deposit eggs (Cockrell et al. 1993, Nagano et al. 1993, Riley 1993), wing condition may also be an important factor subject to sexual selection. A total of 141 mating pairs was collected between 0930 and 1600 PST over 30 days from 29 January to 28 February 1993. Fifty-five of these were taken to the laboratory and measured for parasite state, wing damage, wing fluctuating asymmetry, and size. The remaining 86 pairs were measured for all characters except parasitism in the field and subsequently released. Butterflies were collected from clusters throughout the 1990–1991, 1991–1992, and 1992–1993 overwintering seasons in order to establish trends in size and wing damage. These were measured for wing length and wing damage in the lab. Females were also collected from clusters on 3 February and 3 March 1992 to determine the relationship between female size and prior mating history. Their forewing lengths were measured to the nearest mm and the contents of their bursa copulatrix examined by dissection under 12× magnification.

*Ophryocystis elektroscirrha* is a tissue-specific neogregarine protozoan parasite of monarchs and the Florida queen butterfly, *D. gilippus berenice* Cramer (McLaughlin & Meyers 1970). Spores of the parasite are located on the scales and other adult integument. We used Leong et al.'s (1992) technique to determine the incidence and level of infection.

Damage to the wings of butterflies occurs as scale loss, membrane tears and torn or missing pieces. Scale loss is difficult to quantify, so wing damage in this study was operationally defined as the number of wings per individual either torn and/or with a portion missing and was scaled from 0 (no wings damaged) to 4 (all four wings damaged).

Because body mass varies greatly with hydration level (Crespi 1989, Leong et al. 1992), lipids (Brower 1985) and recent reproductive history (Oberhauser 1988, 1989, 1992, Jones et al. 1986, Svard & Wiklund 1989), we used forewing length as a measure of size. Forewings were measured to the nearest mm from the base of the discal cell to the furthermost point in cell $R_4$ on the wing apex. Body size was defined as the average of the length of both forewings. In cases where the apex of either wing was damaged, size was measured as the length of the intact wing.

Following Leary and Allendorf (1989), Parsons (1992), Thornhill (1992), and Liggett et al. (1993), fluctuating asymmetry was defined as random deviations from perfect bilateral symmetry between right and left-side structures. A measure of fluctuating asymmetry (FA) was derived from wing length measurements. Forewing length FA was computed as the absolute value of the differences between forewing lengths.

## RESULTS

***Ophryocystis* parasitism.** Both infection rate (68%) and level (mean ± SE = 39.6 ± 10.4 spores) for the mating sample and general population butterflies combined were similar to those reported by Leong et al. (1992) for the general population at this site during the 1991 season. To test the null hypothesis of random assortment for pairing based on parasitism, Spearman's test of association was conducted on male parasite infection level versus that of his partner. There was no significant association between the parasite infection level of partners ($r_s$ = 0.222, n = 55, p = 0.095). Neither the incidence ($\chi^2$ = 1.05, df = 1, p =

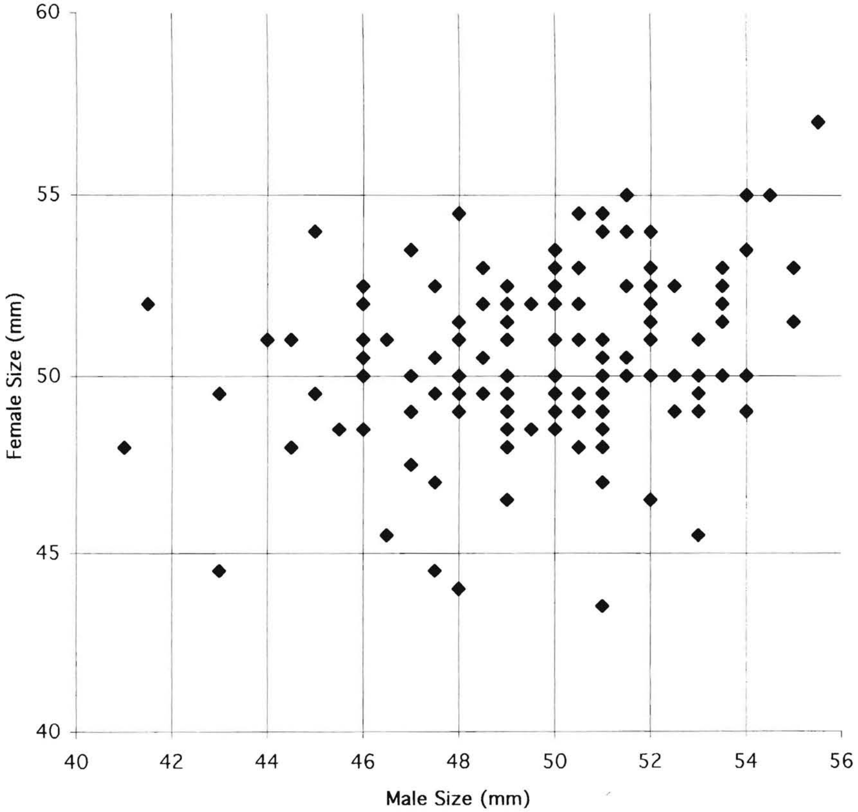

FIG. 1. Wing length association between pairs of mating butterflies. ($r = 0.27$, $F = 10.5$, $df = 1, 136$, $p < 0.01$).

0.305) nor level of infection (Wilcoxon $z = 0.408$, $p = 0.683$) by *O. elektroscirrha* differed between male and female mating partners. Likewise, the distribution of the mating sample infected ($\chi^2 = 1.06$, $df = 1$, $p = 0.303$) and their spore count (Mann-Whitney $z = -1.17$, $p = 0.233$) did not differ from those of the general population.

**Size.** Fig. 1 shows the relationship between the size of the 1993 mating partners. A significant positive association between forewing length of partners is indicated for the overall season. Size related pairing patterns were also examined for seasonal trends (Table 1). During the early phase (the first two weeks of mating) significant size related assortative pairing occurred, but that trend, while positive, was non-significant during the final two weeks of the study (Table 1a). Neither males nor females of the mating population differed in wing length from their same-sex general population counterparts during early or late 1993 season

TABLE 1. Size relationships for butterflies captured during the 1993 mating season from clusters or from ground pairs: (a) associations between mating partner's wing length using Spearman rank correlation; (b) male forewing length compared using two sample $t$-tests; (c) female forewing length compared using two sample $t$-tests.

| Season | Sex | Comparision | Mean (s.e.) | Statistic | p | N |
|---|---|---|---|---|---|---|
| (a) | | | | | | |
| early season | males & females | mating partners | | $r = 0.34$ | 0.002 | 78 |
| late season | males & females | mating partners | | $r = 0.21$ | 0.111 | 60 |
| (b) | | | | | | |
| early season | males | mating vs. | 49.4 (0.3) | $t = 1.84$ | 0.07 | 78 |
| | | clusters | 50.7 (0.5) | | | 20 |
| late season | males | mating vs. | 50.5 (0.3) | $t = 0.34$ | 0.74 | 60 |
| | | clusters | 50.7 (0.4) | | | 22 |
| (c) | | | | | | |
| early season | females | mating vs. | 50.6 (0.2) | $t = 1.01$ | 0.31 | 81 |
| | | clusters | 50.0 (0.5) | | | 18 |
| late season | females | mating vs. | 50.4 (0.3) | $t = 1.78$ | 0.08 | 60 |
| | | clusters | 49.2 (0.6) | | | 20 |

comparisons (Table 1b, c). Butterflies collected from clusters throughout the 1991–1993 overwintering seasons were not sexually dimorphic by size (1991: unpaired $t = 1.53$, df = 267, 269, p = 0.13; 1992: $t = 0.34$, df = 83, 67, p = 0.74; 1993: $t = 1.02$, df = 37, 39, p = 0.31). During the 1993 season, forty two pairs of mating butterflies were collected prior to 1130 PST and 48 pairs collected after 1230 PST: the size of males mating in the morning was not significantly different from males mating in the afternoon (unpaired $t = -1.604$, p = 0.11). However, females mating in the afternoon, were significantly larger than females mating in the morning (unpaired $t = -3.126$, p = 0.0024) and this pattern was consistent during both the early part of the season as well as during the last two weeks of mating.

**Fluctuating Asymmetry (FA).** Contingency analysis for incidence of male FA (i.e., presence or absence of asymmetric wings) with that of his partner are given in Table 2a. Positive assortment between partners was indicated for forewing length FA during the first two weeks, but not during late season mating. Cases where both partners were asymmetric or in which neither were asymmetric occurred more frequently than predicted due to chance. The majority of individuals of both the 1993 general population and those captured during mating had symmetrical length forewings (72% and 86% for general population males and females respectively; 56% and 52% for mating males and females respectively). When asymmetry occurred within a group it was balanced i.e., the number with right side bias did not differ significantly ($p > 0.05$) from the number with left side bias. The forewing length asymmetry of

TABLE 2. Fluctuating asymmetry relationships for butterflies captured during the 1993 mating season from clusters or from ground pairs: (a) tests of independence of presence or absence of FA in one mating partner with the other partner using contingency analysis; (b) male forewing length asymmetry compared using Mann-Whitney tests; (c) female forewing length asymmetry compared using Mann-Whitney tests.

| Season | Sex | Comparision | Mean (SE) | Statistic | p | N |
|---|---|---|---|---|---|---|
| (a) | | | | | | |
| early | males & females | mating partners | | $\chi^2 = 6.14$, df = 1 | 0.013 | 59 |
| late | males & females | mating partners | | $\chi^2 = 0.01$, df = 1 | 0.938 | 60 |
| (b) | | | | | | |
| early | males | mating vs. | 0.68 (0.10) | $z = 1.75$ | 0.08 | 66 |
| | | clusters | 0.40 (0.16) | | | 22 |
| late | males | matings vs. | 0.45 (0.11) | $z = 1.16$ | 0.25 | 60 |
| | | clusters | 0.21 (0.14) | | | 17 |
| (c) | | | | | | |
| early | females | mating vs. | 0.76 (0.11) | $z = 3.31$ | 0.0009 | 75 |
| | | clusters | 0.56 (0.06) | | | 17 |
| late | females | mating vs. | 0.46 (0.07) | $z = 1.94$ | 0.053 | 56 |
| | | clusters | 0.21 (0.09) | | | 19 |

mating females was greater than that of general population females during the early phase of mating, and differences approached significance during the last two weeks (Table 2c). On the other hand, male FA did not differ significantly between mating and cluster-captured males during either phase of the mating season (Table 2b).

**Wing damage.** Mating males had greater wing damage scores (males = 1.57) than their partners (females = 0.95). Early season mating males were significantly more damaged than cluster-captured males, but late season differences were not significant (Table 3a). Mating females did not differ from general population females during either mating phase. For mating pairs, the number of damaged wings of one butterfly was independent of the damage status of its partner during both phases of mating (Table 3c).

**Interaction between wing damage and size.** Table 4 shows associations between size and number of damaged wings of mating individuals and general population butterflies for the overall 1993 season. Mating males showed a positive (but non significant) relationship between size and wing damage, with larger males tending to be more damaged. In contrast, mating female size was inversely related to the amount of wing damage. Among general population butterflies, neither male nor female size was associated with wing damage. Association between wing damage and mating butterfly size was examined for both the first two weeks of the season and the following two weeks. Neither male ($r_s = 0.634$, $p = 0.5$) nor female ($r_s = -0.829$, $p = 0.407$) mating individu-

TABLE 3. Wing damage relationships for butterflies captured during the 1993 mating season from clusters or from ground pairs: (a) number of male wings damaged compared using Mann-Whitney tests; (b) number of female wings damaged compared using Mann-Whitney tests; (c) associations between mating partner's wing damage using Spearman rank correlation.

| Season | Sex | Comparision | Mean (SE) | Statistic | p | N |
|---|---|---|---|---|---|---|
| (a) | | | | | | |
| early | males | mating vs. | 1.8 (0.1) | z = 2.17 | 0.03 | 81 |
| | | clusters | 1.1 (0.3) | | | 20 |
| late | males | mating vs. | 1.3 (0.2) | z = 0.59 | 0.71 | 60 |
| | | clusters | 1.1 (0.2) | | | 18 |
| (b) | | | | | | |
| early | females | mating vs. | 0.9 (0.1) | z = 1.21 | 0.23 | 81 |
| | | clusters | 0.6 (0.2) | | | 18 |
| late | females | mating vs. | 1.0 (0.1) | z = 0.54 | 0.59 | 60 |
| | | clusters | 0.9 (0.2) | | | 21 |
| (c) | | | | | | |
| early | males & females | mating partners | r = 0.08 | z = 0.72 | 0.47 | 81 |
| late | males & females | mating partners | r = 0.09 | z = −0.005 | 0.99 | 60 |

als had a significant relationship between size and wing damage early in the study. However, late season patterns were significant and in opposing directions: larger males had increasing wing damage ($r_s = 2.622$, $p = 0.009$), while female size was inversely related to damage ($r_s = -2.096$, $p = 0.036$).

**Mating frequency, female size and fluctuating asymmetry.** Table 5 presents population size, sex ratio and spermatophore data for general population females captured from clusters in 1992. As in the 1993 mating season, the overwintering reproductive phase in 1992 was characterized by a declining population, an increasingly male biased sex ratio, and an increasing proportion of the general population females that were multiply mated. The coefficient of variation for spermatophores per female decreased from 88% to 36% during the 1992 reproductive season, indicating that the mating histories of females became increasingly uniform. Early in the mating phase no relationship existed between female size and number of prior matings (i.e., number of spermatophores present in her bursa copulatrix); toward the end of the mat-

TABLE 4. Association between wing damage and size among mating individuals and members of the general population, 1993, using Spearman rank (see text for seasonal trend).

| Group | N | r | p |
|---|---|---|---|
| mating males | 138 | 0.152 | 0.076 |
| mating females | 141 | −0.176 | 0.037 |
| general population males | 40 | −0.161 | 0.316 |
| general population females | 38 | 0.059 | 0.722 |

TABLE 5. General population demographics, female mating history and Spearman rank correlation between wing length and number of spermatophores for clustering females captured early or late during 1992.

| Date | Abundance | Sex ratio (% male) | Spermatophores % female | N | r | p |
|---|---|---|---|---|---|---|
| 3 Feb | 100,000 | 65 | 1.2 ± 0.2 | 25 | 0.084 | 0.68 |
| 3 Mar | 25,000 | 85 | 5.9 ± 0.5 | 23 | −0.496 | 0.02 |

ing phase there was a significant inverse relationship between size and mating (cf. Feb 3 and Mar 3, Table 5) and a positive relationship between spermatophore number and female forewing FA ($r_s = 0.325$, $p = 0.028$).

## DISCUSSION

Two of the characters we measured, forewing size and fluctuating asymmetry, showed positive assortment between individuals of mating pairs early in the mating season. Larger females also were more likely to mate in the afternoon than in the morning. In addition, by the end of the season a negative relationship existed between female size and spermatophore count, with small females containing more spermatophores. FA was associated with female mating patterns as well: mating females had a greater incidence and degree of FA than cluster-captured females, and females with asymmetric wing lengths had higher spermatophore counts at the end of the season. There was also an interaction between size and wing damage in both sexes among mating butterflies late in the overwintering season, with a positive association between size and wing damage among males and a negative association between female size and wing damage. The level of parasitism was independent among members of mating pairs, and had no effect on mating likelihood.

Adaptive explanations for female multiple mating are varied, and hypotheses that apply to mating patterns in monarch butterflies include: assurance of adequate sperm supply (Gromko et al. 1984), increased genetic quality from later matings (Halliday 1983, Birkhead et. al. 1993), increased genetic diversity (Halliday & Arnold 1987), and obtaining male derived nutrients (Oberhauser 1989, Wells et al. 1990, Wells et al. 1993). However, female fitness is negatively impacted in other insects by excessive sexual harassment by males (Odendaal et al. 1989, Cook et al. 1994, Rowe et al. 1994, Stone 1995), and there could be non-trivial costs of mating too frequently in female monarchs. Females mating several times in rapid succession have increased mortality from ruptured bursae copulatrix (Oberhauser 1989). Other potential costs include: (1) wasted time and energy; (2) increased risk of wing damage thus limiting dispersal range; (3) substantial increase in flight load; and (4) delayed dispersal and later initiation of egg laying.

It is likely that female monarchs attempt to minimize costs from excessive male courtship or from mating too many times. Female responses to male harassment in Lepidoptera range from rapid ascending flight as in *Colias* (Rutowski 1978) to elevated abdominal postures in *Anthocharis cardamines* (Wiklund & Fosberg 1985). Female rejection behavior has been thoroughly documented in the Queen butterfly, *Danaus gilippus berenice* (Brower et al. 1965). During ground phase mating activity, female monarchs often exhibit behaviors that make successful coupling difficult: curling the tip of their abdomen forward ventral to their abdomen and clasping it with their legs or sandwiching the tip of their abdomen between tightly closed wings. Most mating attempts are unsuccessful (Frey & Oberhauser, pers. obs).

Our results suggest that larger females more readily avoid or resist excessive mating attempts than do smaller females and that larger males were more successful at overcoming this resistance. The inverse relationship between size and mating frequency in late season general population females in 1992 (Table 5), and the fact that relatively large females in 1993 mating pairs had less wing damage than smaller mating females (Table 4), are each consistent with the hypothesis that relatively large females exercise choice as to when they mate because they are more capable of resisting mating attempts than smaller females. This is not female-choice in the traditional sense (Mason 1969, Phelan & Baker 1986) because females may not actually choose specific males. Rather, they are able to choose whether or not to mate.

Temporal mating data and patterns in FA also support the female choice hypothesis. Females that began mating in the afternoon were larger than those that began in the morning, suggesting that larger females can avoid mating attempts in the morning. Because monarchs remain in copula overnight (Svard & Wiklund 1988, Oberhauser 1989), starting to mate early in the day precludes foraging, rehydration, or other maintenance activities during this time. The fact that mating females were both more likely to be asymmetric than nonmating females and showed a greater degree of asymmetry than nonmating females suggests that symmetrical females are better able to avoid unwanted mating attempts. An alternative explanation is that males prefer small, asymmetric females, but this seems less likely, because fecundity is generally correlated with size in insects (Lederhouse 1981, Jones et al. 1982, Haukioja & Neuvonen 1985). In many taxa there is a positive correlation between the level of FA and environmental stress experienced by individuals during development (Palmer & Strobeck 1986, Hoffman & Parsons 1991). There is also a negative correlation between overall fitness or heterozygosity and FA (e.g., Leary & Allendorf 1989, Leamy 1992, Parsons 1992). These general findings suggest that it is unlikely that monarch males prefer small asymmetric females. The relatively high frequency of mating pairs in which both partners had forewing FA could indicate reduced ability at partner discrimination in both sexes or that only symmetrical males can overcome symmetrical females.

Many factors influence the evolution and maintenance of mating systems (Clutton-Brock 1988, Andersson 1994). Some of these may operate to favor mate choice by either or both sexes and result in assortative or disassortative pairing. Crespi (1989) pointed out that other factors also produce non random pairing, yet actual choice or preference may not be involved. Additional factors or conditions, e.g., declining female abundance, may favor males that pair randomly and minimize time involvement during the pairing process. For monarch males at California overwintering sites, conditions toward the end of the mating season probably favor random pairing. The general population declined from 20,000 individuals in late January 1993 to less than 2000 butterflies by the first week in March and the population became increasingly male biased. During the last two weeks of the mating period, pairing was random with respect to each of the four variables measured.

Early in the mating season, positive assortative mating based on both size and bilateral wing asymmetry occurred. There is some evidence that males were choosing larger females, and that large males were better able to obtain these preferred mates. Later in the season, two factors could be important in reversing this trend. There was more competition for mates as the sex ratio became more male-biased, and the remaining females were more likely to have mated, and thus more "reluctant" (Sugawara 1979, Oberhauser 1989, but see Rowe et al. 1994). The greater mating frequency for more asymmetric females, as measured by spermatophore counts, and the greater wing damage to smaller mating females support our modified female choice hypothesis that larger females are better able to choose when to mate.

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