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Influence of Mating Frequency on Lifetime Fecundity in Wild Females of the Small White *Pieris rapae* (Lepidoptera, Pieridae)

MAMORU WATANABE and SHINYA ANDO

Department of Biology, Faculty of Education, Mie University,
Tsu-shi, Mie, 514 Japan

Abstract Females of the small white *Pieris rapae* were captured in the field and dissected to investigate whether the reproductive output of mating is affected by the number of male-donated spermatophores. Mating frequency was determined by counting spermatophores in the bursa copulatrix. During their lifespan, females had mated 3 times on average. After the adult eclosion, a female had 450 immature eggs in the ovaries. Polygamous females were estimated to lay 100 more eggs throughout the course of their lives than did monogamous ones. Thus, mating frequency is seen to be important for reproductive success in females of the species.

Key words: Egg load; immature eggs; monogamy; polygamy; *Pieris rapae*.

Introduction

Oviposition pattern and longevity of pierid butterflies in the field have been described by OHSAKI (1980). Laboratory studies showed that daily oviposition of the small white *Pieris rapae crucivora* BOISDUVAL 1836, which mates only once, reached a peak on the third day after emergence, and then declined gradually (SUZUKI, 1978). Mating frequency in relation to oviposition, however, has never been studied in the laboratory. Therefore, detailed knowledge of their lifetime reproductive success has never referred to mating frequency. Several studies have noted multiple mating in many pierid species (e.g. STERN & SMITH, 1960; SUZUKI, 1979; WIKLUND & FORSBERG, 1991).

WATANABE (1988) reported that female polyandry increases the number of eggs laid in the swallowtail butterfly. One of the benefits of repeated mating can be a substantial effect on increasing sperm supply (LEDERHOUSE, 1981). In addition for pierid butterflies, a relationship between mating frequency and lifetime fecundity has been studied on nutrient investment by males (e.g. BOGGS & WATT, 1981; RUTOWSKI *et al.*, 1983).

In this paper, we examine the possible relationship between mating frequency and the fecundity of *P. rapae* in the field. Lifetime egg production and the reproductive success are also discussed.

Materials and Methods

The data presented in this paper was obtained mainly from the summer generations of the small white *P. rapae* in Shirouma of Nagano Prefecture, which is located in a cool-temperate zone of Japan. The habitat consists of rice-fields and margins of deciduous forests where adults may feed on nectar plants, and larvae on food plants.

Females engaged in various activities, e.g., feeding, roosting, flying, copulating and ovipositing, were collected from late July through mid-August of 1989, 1990 and 1992. Sampling was made on windless, sunny days (total of 28 days). When females were captured, their abdomens were amputated and immersed in a solution of 50% ethyl alcohol, and their wing conditions and forewing length recorded. Although OHSAKI (1979) divided females into 4 age groups, we classified them into 5 age groups, on the basis of the degree of wing wear, as had been done with *P. canidia* (ANDO & WATANABE, 1992) and *P. melete* (ANDO & WATANABE, 1993), and on the rate of wing reflection of ultraviolet. UV reflection for the wild females decreases with age after emergence (ANDO & WATANABE, unpublished). The five age groups were as follows: 0: newly emerged females without visible damage, with lustrous scales showing the highest reflection rate of ultraviolet; I: fine tears and less lustrous scales; II: tears and frayed scales; III: notched tears and frayed scales; IV: broken or extensive tears and frayed scales showing the lowest rate of reflection of ultraviolet.

All females dissected were examined for the number of spermatophores in their bursa copulatrix and the number of immature eggs stored in the ovaries. Although eggs in the ovaries could be classified into three groups (mature, submature, immature), immature eggs, which included oocytes, were filled in the terminal filament, the germarium and a part of the vitellarium of the ovarioles. Eggs in the ovarioles decreased in size toward the tip of the terminal filament filled with oocytes. Since neither immature eggs nor oocytes contain yolk, they appear white. We were able to count the number of oocytes divided by the dissepiment, with the aid of a microscope.

Results and Discussion

Over a period of three years, we examined in excess of 400 females in the study area. In each year, about half the females captured were young (age 0 and I), and the sample size of the oldest females (age IV) was the smallest (13, 3 and 0 in 1989, 1990 and 1992, respectively). In age 0, 7 females were virgin in 1989. No virgin females were captured in 1990 and 1992. Although there were a few polygamous females (mated twice) of age 0, the mean mating frequency of the females of age 0 was near 1.0 (Fig. 1).

The number of matings increased with the age in each year. The pattern of

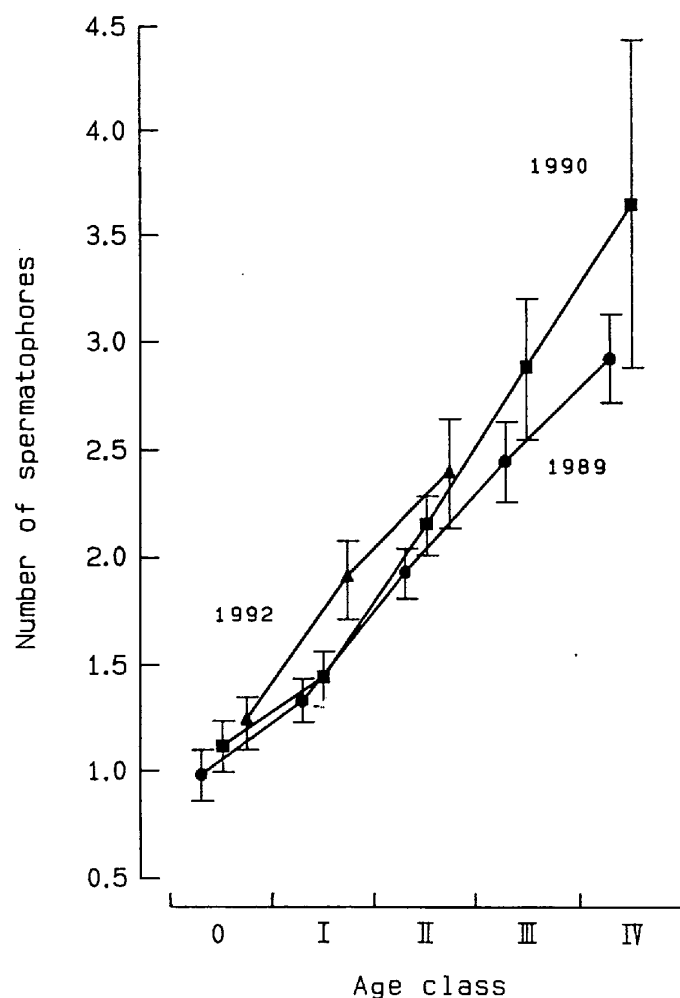


Fig. 1. Change in the mean number of spermatophores in wild females of *Pieris rapae* for 5 age classes (0, I, II, III and IV). Circles, squares and triangles indicate the data for 1989, 1990 and 1992, respectively. Each bar represents SE.

change was similar in all three of the years, though we have no females of the age III and IV in 1992. In the oldest age group (IV), females mated three times on average in each year.

Positive correlations between mating frequency and population density have been noted in many butterfly species (e.g. PLISKE, 1973). ODENDAAL *et al.* (1985) showed that females exhibit little or no choice of mate. Such studies suggest that at high density the competition among males for females becomes more intense and the number of matings increases. The rate of increase in the number of matings with age was similar for *P. rapae* taken in three years. Since the estimated male density changed year to year in this study area (WATANABE *et al.*, unpublished), the number of active males searching for mates may differ in the three years. Therefore, the male density did not affect the number of matings performed by females.

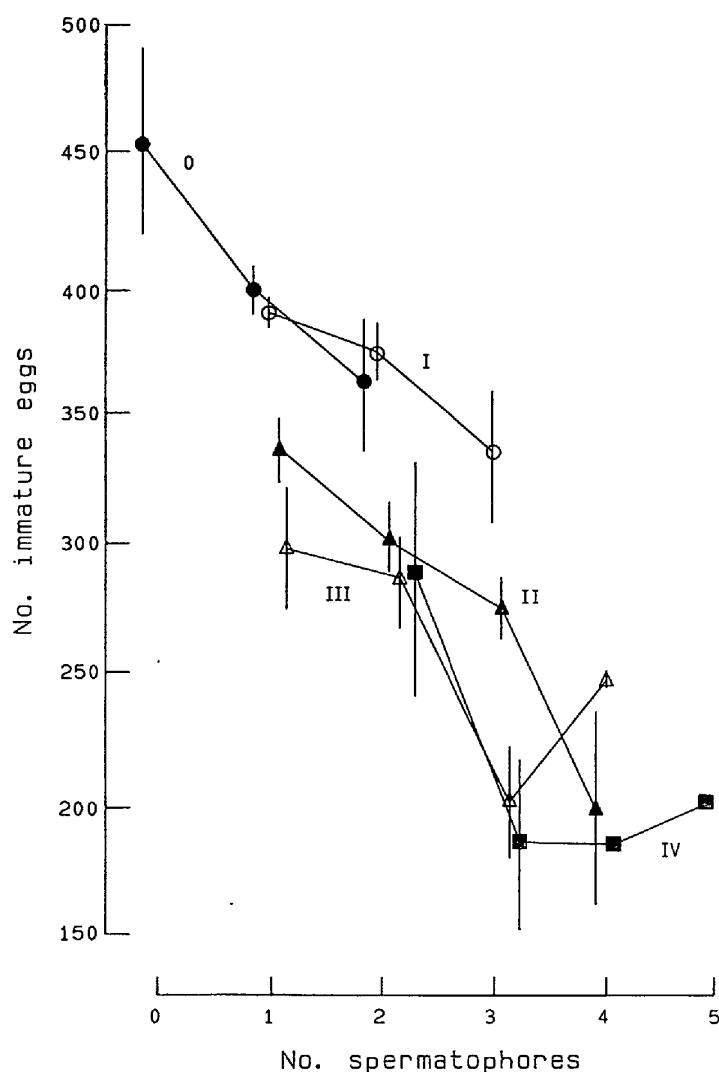


Fig. 2. Change in the number of immature eggs of respective ages (0, I, II, III and IV) in relation to mating frequency in wild females of *Pieris rapae*. Each bar represents SE.

Virgin females loaded about 450 immature eggs. Since there was a relatively small number of mature and submature eggs in the ovaries of young virgin females (WATANABE & ANDO, unpublished), the fecundity of *P. rapae* was estimated at 550.

Figure 2 shows the lifetime changes in the number of immature eggs in relation to mating frequency. When a female mated once, the number of immature eggs decreased to 400. The remainder (50 immature eggs) were likely to develop into mature eggs to be laid.

The number of immature eggs decreased with the increase in mating frequency in each age class. Since there were less than 100 mature and submature eggs loaded in most females (WATANABE & ANDO, unpublished), the decrease in the immature eggs resulted from absorption or oviposition. However, no fused eggs were ob-

served in the ovaries, suggesting that few eggs were consumed for somatic maintenance. Thus, in cases where no addition of immature eggs were added during the adult stage, the decreasing number of immature eggs in the ovaries was thought to be due to oviposition. Because a virgin female had 450 immature eggs, a monogamous female of age III may have laid 150 eggs. On the other hand, the oldest female (age IV) that mated more than 3 times, loaded 200 immature eggs, suggesting that she had laid 250 eggs. Although we were unable to capture monogamous females of age IV in the sampling period of three years, monogamous females might be apt to load more eggs than polygamous ones.

One of the benefits from polyandry in butterflies may be to achieve an adequate sperm supply. LABINE (1966) pointed out that sperm may deteriorate with age and must be replaced with a fresh supply, because there may be too few spermatozoa in one insemination to fertilize all of the eggs that a female will lay. On the other hand, SUZUKI (1978) has argued that as a rule one mating provides a female with enough sperm to fertilize all eggs in *P. rapae*.

NORRIS (1936) found a relationship between fecundity and the quality of the nectar eaten by female adults of some lepidopteran species. RIDLEY (1988) summarized the influence of mating frequency on the fecundity in butterflies. Females of the swallowtail butterfly allocated their available energy (fat body+nectar) for egg production and somatic maintenance (WATANABE, 1992). In *Heliconius charitonius* both ovarian capacity and daily egg production were determined ultimately by the quality of larval nutrition (DUNLAP-PIANKA, 1979). It has proven difficult to demonstrate any positive effect of male-derived nutrients on female fecundity (JONES *et al.*, 1986). However, the number of eggs actually laid was dependent upon mating frequency in *P. rapae*. Spermatophores have been shown to increase female reproductive output in some butterfly species (BOGGS & GILBERT, 1979; WATANABE, 1988). In addition, female polyandry may also increase genetic diversity of their offspring.

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