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The Influence of Female Post-Emergence Behavior on the Time Schedule of Male Mate-Locating in *Pieris rapae crucivora*

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ABSTRACT—Previous theoretical studies and some empirical studies suggested that the factors which affect female availability should influence male reproductive behavior. We noticed the female post-emergence behavior as one such factor, and investigated how it might influence male reproductive strategy in the butterfly, *Pieris rapae crucivora*. In the field and the laboratory newly-emerged females stayed on the underside of leaves 2.5 hr after emergence before they flew voluntarily into the open where they are more visible to males. Time spent before initial flight correlated negatively with ambient temperature, and initial flights increased significantly the possibility that the female would be detected by males. To evaluate whether these results could explain the time schedule of males' search for females in the field, female availability was estimated by shifting the observed schedule of female emergence according to the relationship between initial flight and effective cumulative temperature. The resultant female availability correlated well with temporal changes observed in the number of mate-seeking males. Thermal conditions may influence male reproductive behavior via female post-emergence behavior, as well as via male body temperature.

INTRODUCTION

Most male reproductive effort is devoted to securing mates. Especially in those species lacking parental care, a male's reproductive success is largely determined by the number of females he secures. This causes competition among males for access to females. Such intense competition is believed to produce different strategies to secure mates, including territorial behavior, attraction of females by signaling, active search and so on. Thornhill and Alcock (1983) argued that scramble competition occurs when male territoriality is less advantageous, since many males compete for females so intensely that they can afford little effort for female guarding, or when it is difficult to predict the availability of females. In such cases the most important factor affecting mate securing may be the ability to locate mates as quickly and often as possible (Odendaal *et al*., 1985).

Scramble competition occurs in some lepidopterans (Rutowski, 1991). Especially in the species in which females mate only once and virgin females are the most valuable resource to males, male butterflies may compete for the virgin females by active searching flight (Rutowski, 1991). When many males compete for the same resources, each male's reproductive success depends on the behavior of other competing males. This is predicted to cause the ideal free distribution, in which the number of female-searching males is proportional to the availability of females at any time (Wiklund and Fagerström, 1977; Bulmer, 1983; Iwasa *et al*., 1983; Parker and Courtney, 1983; Iwasa and Odendaal, 1984; Iwasa and Haccou, 1994). An original ideal free model holds good when males can know the distribution of females exactly, when they can search for female at any time and when the capability to secure females is homogeneous (Fretwell, 1972). Those assumptions are not always valid in the field, and then the distribution of competitors often deviates from an ideal free distribution over resources (Parker and Sutherland, 1986).

This is the case in the cabbage butterfly, *Pieris rapae crucivora* (Pieridae), because there exists a discrepancy between when receptive females are abundant and when males search for females (Iwasa and Obara, 1989). Female butterflies eclose in the early morning with the eclosion peak around 0600 hr, and they become receptive to males half an hour after emergence (Obara, 1987). Males, however, start searching for females around 1 hr later than female emergence with the activity peak a few hours later than the peak of female emergence (Iwasa and Obara, 1989; Hirota and Obara, 2000a, b). It follows that males do not realize an ideal free distribution over the abundance of receptive females. Iwasa and Obara (1989) suggested that such a discrepancy could be explained by an ideal free model, given that some factors restricted the male's efficiency in locating females in the early morning.

What factors influence the male's efficiency in mate-location? An alternative is thermoregulatory constraints on flight ability, which were reported in many insects (Heinrich, 1996).

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If thermal conditions restrict males' activity at specific time, their distribution deviates from an ideal free distribution. Mate-locating flight of male *P. rapae crucivora* is also influenced by thermal conditions, since the number of female-searching males was explained significantly by quadratic and cubic regressions of air temperature on most of observation days (Hirota and Obara, 2000b). Males performed the female-searching flight more frequently at intermediate air temperatures. This is consistent with the report that the performance of thoracic flight muscle declines as the thoracic temperature deviates from the optimum (May, 1983; Marden, 1995). However, the air temperatures at which male female-search reached the peak ranged so widely from 24 to 29°C that it was difficult for a common regression model to predict the diurnal schedules of male female-search throughout different days (Hirota and Obara, 2000b). It follows that male mate-locating flight does not solely depend on the performance of flight muscle (Bitzer and Shaw, 1995; Rutowski *et al*., 1996). Rutowski *et al*. (1996) reported that male *Asterocampa leilia* (Nymphalidae) often did not perform the mate-locating flight even when thermal conditions were optimal, and suggested that the male adjusted his female-locating behavior to follow the time of female eclosion.

Another alternative is the discrepancy between female abundance and female availability. If males can not locate a female or mate with her although females are abundant, they should not search for females. *P. rapae crucivora* females were observed to emerge inconspicuously under the dense leaves of host plants and stay there for a while, and then take flight and move into open space (Suzuki, unpublished). If females which stay under leaves are invisible, males can not easily find females until they are available to males in open space (Iwasa and Obara, 1989). It follows that we should expect males to realize an ideal free distribution not over time when females eclose, but over time when newly-emerged females become conspicuous for males. However, no study has quantitatively revealed how long newly-emerged females stay under leaves and how inconspicuous the females which stay there are for males. It is necessary to investigate how the mate-locating behavior of males is influenced by female post-emergence behavior as well as by thermoregulatory constraints on male's flight ability.

In the present study we carried out field observation and experiments to reveal how females behave after emergence and how their post-emergence behavior influences their availability to mate-locating males. We then analyzed statistically whether female availability in open space or thermal condition explains better the diurnal schedule of male female-search.

METHODS

Butterfly

Butterflies used for this study were obtained from eggs laid on the leaves of potted cabbages, *Brassica oleracea* L. by females collected in Fuchu-city, Tokyo, Japan. The eggs on the potted cabbages were kept in a mesh-walled tent in the field, and were allowed to hatch and grow to pupae.

Experiment I: Female behaviors after emergence

To investigate how newly-emerged female stay under the leaves, their behavior was observed in a field and laboratory. Some female pupae were put into a refrigerator just before adult emergence, and kept there until needed. Thirteen females were observed for post-emergence behavior in an outdoor net cage (9.5×10.5×3 m) in a field on the campus of Tokyo University of Agriculture and Technology in July and August 1997, when sunrise was at 4:36 to 4:59. For this purpose pupae were attached to the underside of leaves of potted cabbages, *Brassica oleracea* L. We observed the females from emergence until they moved onto the upside of leaves.

To avoid disturbing stimuli that might occur outdoors, we observed 34 females for the post-emergence behavior in the laboratory in July to September 1997. Each female pupa was placed in a 15 cm diameter plastic cup with a 20 cm wood stick, which rested against the cup wall. When newly-emerged, a female hung from the stick while she expanded and hardened her wings. The female was stimulated for ten seconds with the male specimen which was rotated by an electric motor (6 revolutions per sec) to imitate a flying male (Itoh and Obara, 1994). This stimulus was presented to a female every ten min after she emerged.

To investigate the influence of ambient temperature on female post-emergence behavior, 126 females were observed without artificial stimuli at the room temperature of 18 to 30°C in May and June 1999. The fluctuating room temperature was recorded every 30 sec (TASCO, Data logger TMS-50E). Based on the measured data, the mean temperature was calculated for each female. The effective cumulative temperature after eclosion was also calculated to analyze the influence of ambient temperature on the developmental process after emergence. We estimated the probability distribution of female initial flight over the effective cumulative temperature (Kaplan and Meier, 1958).

Experiment II: Female position and male searching efficiency

We observed male responses to different female specimens in June and August 1997. Male were caught in the field, anaesthetized with CO_2 gas and marked with oil-soluble markers of different colors on the dorsal surface of their wings. Marked males were released into an outdoor cage (9.5×10.5×3 m) in which *Brassica campetris*, a host plant, and buckwheat flowers (*Fagopyrum esculentum*), a nectar source, were available. Female specimens in resting position with the wings closed were made 2 to 3 days before the experiments. They were presented to males in three different manners (Fig. 1); motionless on the underside of the leaf, rotated at 7 revolutions per sec with an electric motor above the leaf, and motionless on the upside of the leaf. These imitated, respectively, a female motionless just after adult emergence, a female flying over the cabbage field following the take-off from the underside of the leaf, and a female alighting after the flight. We presented two of the three female specimens simultaneously a meter apart, to 40 marked males flying in the cage. The location of the specimens was changed arbitrarily every ten min. The experiments were carried out around ten o'clock on sunny days, when the male butterflies search for females most actively (Iwasa and Obara, 1989; Hirota and Obara, 2000a, b).

In another experiment designed to determine how readily males locate females in different conditions, two female specimens were placed more than three meters apart in an outdoor cage (12×24×2 m), where 52 marked males were released. One of two specimens was located on the upside of leaves, and the other was on the underside. The specimens were moved to the different plants every five min, and the side to which the specimens were attached to was changed alternately. We observed and recorded which male contacted specimens at what time from 10:30 to 12:10 on June 11 1999, from which we could determined how long it took males to discover the specimens.

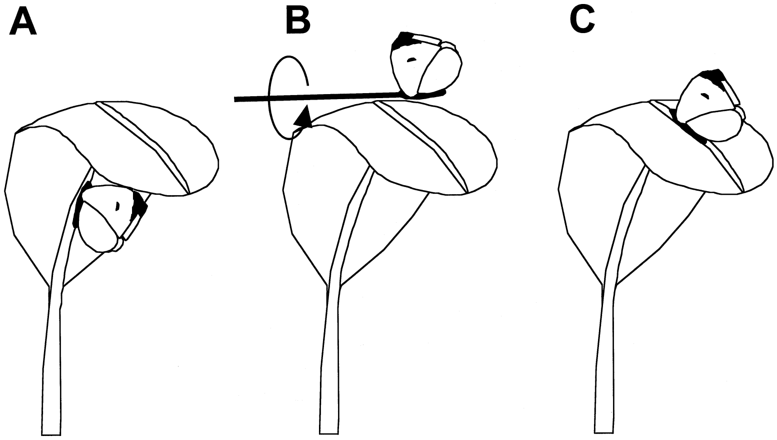

Fig. 1. Three different presentations of female specimen to males. A; motionless on the underside of the leaf. B; rotated with an electric motor above the leaf. C; motionless on the upside of the leaf.

Experiment III: Female emergence and male searching schedule

To determine whether the female post-emergence behavior influences the time schedule of male female-search by making them available to males a few hr after their emergence, we observed the diurnal schedule of female emergence and male female-search, to which the effect of the post-emergence behavior was applied. Thirty pupae were reared in the laboratory and left under the natural condition from the day before observation. Time when females emerged was observed from dawn August 11, 1984, when sunrise was at 4:56. On the same day, temporal change of male female-search activity was observed in the cabbage field every 30 min. from 4:30 to 16:00. The female-search behavior was characterized by slow zigzag flight less than 15 cm above the leaves of *B. oleracea* (Ohtani, 1985; Hirota and Obara, 2000a). Males were also frequently observed flying under the leaves of *B. olerace* searching for females. Immediately after counting the number of active males, air temperature were recorded with TNA-120, TASCO Japan co. ltd.

The timing of the initial flights of newly-emerged females was estimated according to the relationship between time to initial flight and ambient temperature. For each female, the probability distribution of initial flight over time was calculated by assigning the effective cumulative temperature to which she was exposed after eclosion to the Kaplan-Meier's estimate which was calculated in Experiment I. The probability distributions for all females were then summed to produce the time schedule of initial flight.

To evaluate which of air temperature and female availability has a crucial influence on the diurnal schedule of male female-search, we carried out the multiple regression analysis. Regression analysis was performed with four independent valuables; female availability, air temperature, and the square and cube of air temperature, since the number of female-searching males was explained significantly by quadratic and cubic regressions of air temperature (Hirota and Obara, 2000b). The R^2-values corrected with the degree of freedom were calculated and compared.

RESULTS

Experiment I: Post-emergence behavior of the newly-emerged females

The field observation showed that newly-emerged females remain near their cast-off skin for 2.46±0.68 (mean±s.d.; range=1.3–3.6) hours after emergence. At that time, they flew a short distance from their emergence site on the underside of leaves (initial flight; Fig. 2). After the initial flight they alit on the upside of leaves. Thereafter, female butterflies spent large parts of the emergence day on the upside of leaves, although they sometimes visited flowers.

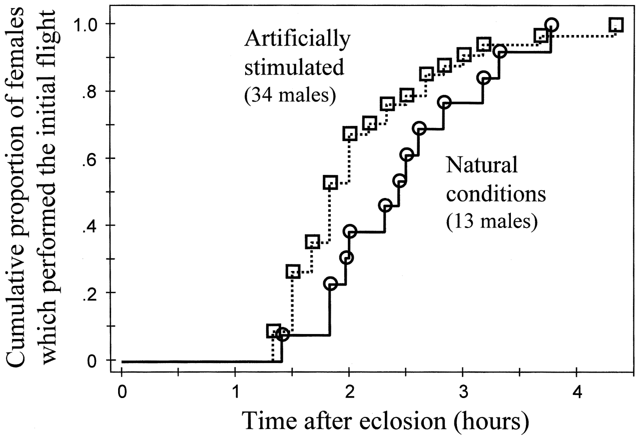

Fig. 2. The time spent by a newly-emerged female butterflies before they started initial flight in the field (circle and solid line), and when stimulated every 10 sec following emergence (square and broken line).

The laboratory experiment also showed that females stayed motionless on the emergence site long after emergence (Fig. 2). During this they did not fly in response to rotating male specimens, although they did tilt their body axis toward it. Female butterflies flew voluntarily at 2.13±0.69 (range=1.2–4.2) hours after emergence. Although the females appeared to fly slightly earlier under the stimulated experiment than under the natural condition, there was not a significant difference (Savage test, $n_1=13$, $n_2=34$, $S=17.4$, $p=0.15$, referred to Savage 1956).

The laboratory observations revealed a significant influence of temperature on the time of initial flight (Fig. 3A). We normalized the distribution of times to voluntary initial flight with a reciprocal transformation (D'Agostino-Pearson test (Zar, 1999); before transformation, $K^2=57.8$, $p<0.001$; after transformation, $K^2=1.63$, $p=0.44$), and found that the time from eclosion to initial flight correlated negatively with mean ambi-

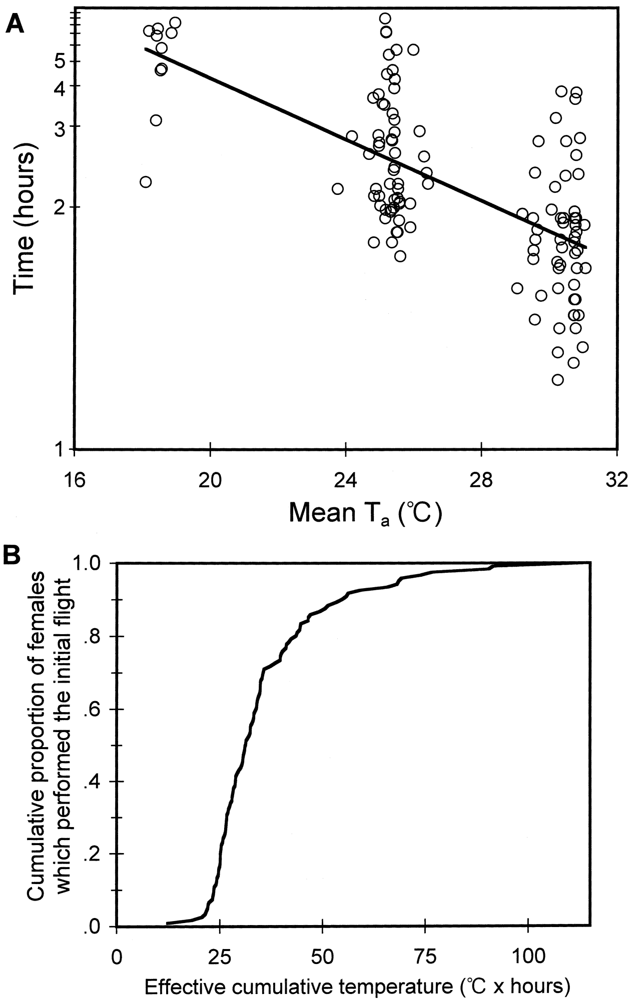

Fig. 3. Influence of ambient temperature (T_a) on time spent before initial flight (A). Y-axis is graduated as reciprocal scale. B; Kaplan-Meier's estimate of the proportion of females over effective cumulative temperature who flew out.

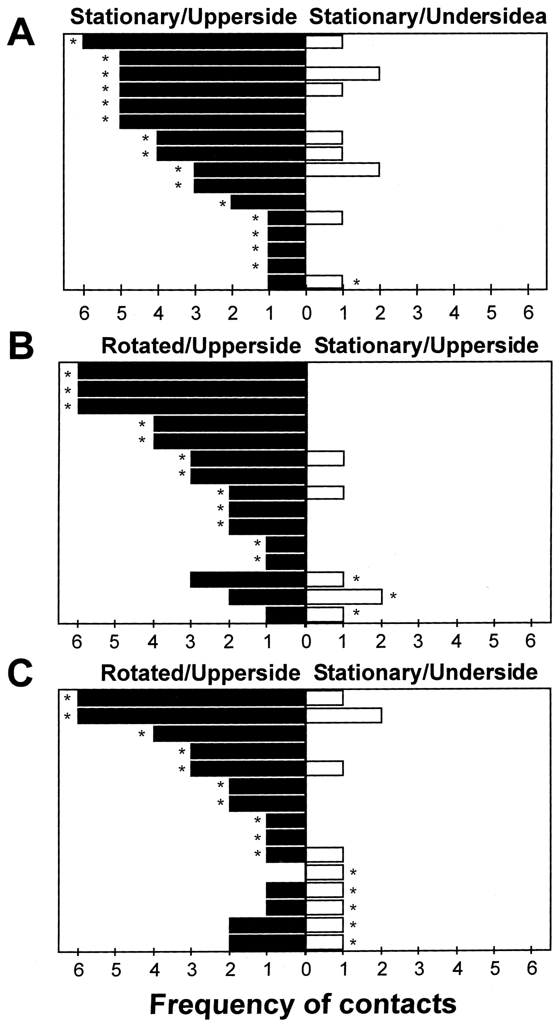

Fig. 4. The effect of female position and motion on the female-location by males. The female-locations were significantly more in the female on the upside than the underside (A), more in the rotated females than stationary ones (B) and more in the females rotated on the upside than on the females staying stationary on the upside of a leaf (C). Asterisks; the specimen to which males approached first.

ent temperature ($y=0.032x-0.40$, $R^2=0.42$, $n=121$, $p<0.01$; Fig. 3A, solid line). Effective cumulative temperature was calculated by the formula, effective cumulative temperature= (hr)× [(observed temperature)–12.6], because the base temperature was expected to be 12.6°C from the regression line of Fig. 3A. Fig. 3B shows how the proportion of females moving to the upside changed over effective cumulative temperature (Kaplan-Meier estimation). The most of females moved to the upside after they experienced 25 to 50 (°C · hours) of effective cumulative temperature.

Experiment II: Female position and males' searching efficiency

16 of 40 males were observed to find, approach and contact the female specimens either on the under- or upside of the leaves. Fifteen of them visited first the specimen on the upside of the leaf and 14 of these visited these specimens more frequently than those on the underside of the leaf (Fig. 4A; Wilcoxon signed-rank test, $n=16$, $T^-=0$, $p=0.0009$).

When the stationary and rotating specimens on the upside of the leaves were presented, 15 of 40 males approached and courted them. Twelve of these males visited first the rotating specimen, and these males and one of three males which visited first the stationary specimen visited the rotating specimen more frequently (Fig. 4B; Wilcoxon signed-rank test, $n=15$, $T^-=0$, $p=0.001$).

When the rotating specimen above the leaf and the stationary one on the underside of the leaf were presented, 15 of 40 males courted them. Ten males courted first the rotating specimen, and nine of them and two of five males which approached first the stationary specimen approached the rotating specimen more frequently (Fig. 4C; Wilcoxon signed-rank test, $n=15$, $T^-=0$, $p=0.001$).

Fig. 5 shows the cumulative proportion of males over time that successfully located a female specimen (Kaplan-Meier estimate). In 1.6 hr of observation it reached 90% for the specimen on the upside, whereas 23% for the specimen on the

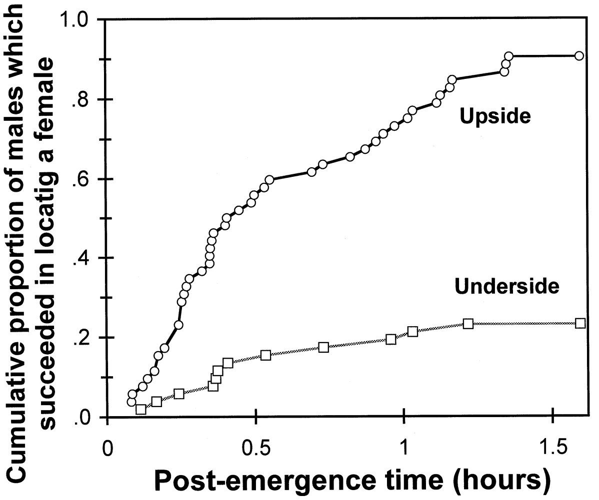

Fig. 5. Kaplan-Meier's estimate of cumulative proportion of males over time which located females.

underside. Males took longer time to discover a female specimen on the underside than that on the upside (paired Savage test, n=47 males, S=1.1, p<0.001).

Experiment III: Female emergence and male searching schedule

Fig. 6 shows the observed changes in the number of emerged females and female-searching males, and in meteorological conditions over time. Female availability was estimated by shifting the schedule of female emergence according to Kaplan-Meier's estimate of proportion of females remaining motionless over the effective cumulative temperature (Fig. 6). It starts to rise at least 1 hr later than that the temporal change of emerged females and peaked at 0800 hr another hr later. Under the thermal conditions shown in Fig. 6, females would spend 2.17 hr on average at their eclosion site before initial flight. The number of female-searching males was significantly correlated with female availability (Fig. 7, Kendall's rank correlation test, $\tau=0.81$, n=23, p<0.001).

The multiple regression analysis showed that when female availability was used as an independent valuable, the number of female-searching males was explained better and the other valuables were not significant (Table 1). In regres-

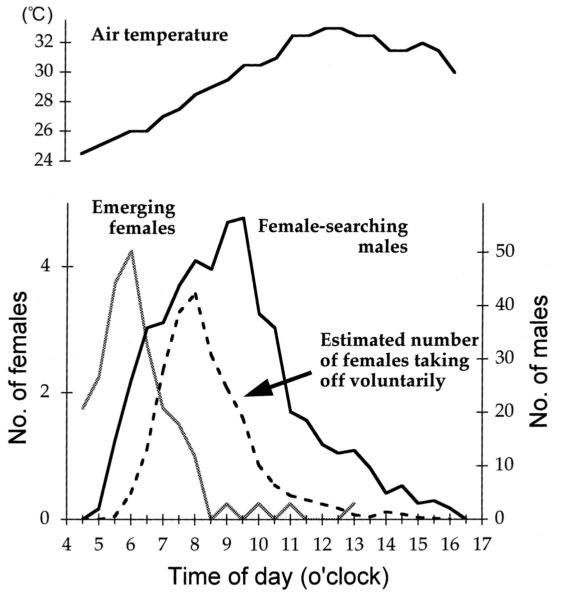

Fig. 6. Temporal change of the emerging females, female-searching males and estimated female availability.

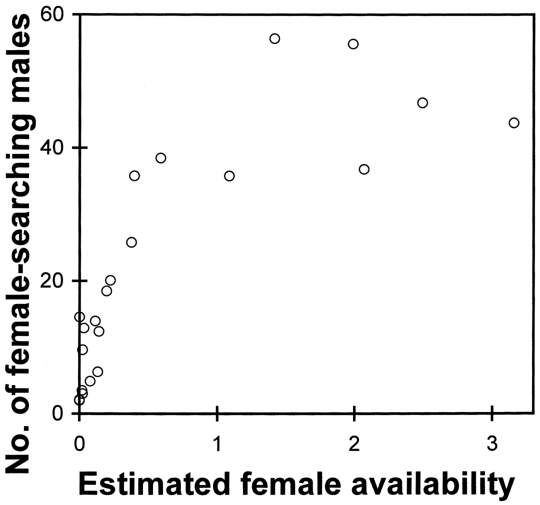

Fig. 7. Correlation between the estimated female availability as the estimated number of taking off females and the number of female-searching males.

Table 1. Multiple regression analysis of air temperature and female availability on the number of female-searching males. *, p<0.05. **, p<0.01. ***, p<0.001

Used independent valuables				R^2
			Female***	.680
Temperature			Female***	.664
Temperature	Temperature^{2}		Female***	.660
Temperature	Temperature^{2}	Temperature^{3}	Female**	.643
Temperature*	Temperature^{2*}	Temperature^{3*}		.488
Temperature**	Temperature^{2**}			.377
Temperature				.042

sion without female availability, the air-temperature also has a significant influence, but the R^2-values were smaller than that of regression with female availability.

DISCUSSION

The present study reveals that the newly-emerged females of *P. rapae crucivora* stay near their own cast-off skin until they take off to fly over at 2.46±0.68 s.d. hr after eclosion (Fig. 2). Their initial flight is voluntary, and not elicited by external stimuli. The resulting movement and change of female position significantly increases the probability that they will be detected by males (Fig. 4, 5). Males find females that are flying or perched on the upside of leaves sooner than those that are stationary under leaves. Because the operational sex ratio is male-biased in the field (Iwasa and Obara, 1989), we conclude that females will be located and copulated by males soon after their initial flight. It follows that female availability to males should parallel the daily pattern of female initial flight. Our estimate indicated that female availability increases and peaks 2.17 hr later than the emergence curve, and it was correlated significantly with the number of female-searching males (Fig. 7). The multiple regression analysis revealed that the diurnal schedule of male female-search was explained by female availability better than air temperature (Table 1). This is the first study in lepidopterans that evaluates quantitatively the influence of female post-emergence behavior on female-availability to males.

The mathematical model proposed by Iwasa and Obara (1989) predicted that the average time for a receptive female to remain unmated should be 2.7 hr under the situation shown in Fig. 6. The expected value is close to our estimate of time spent before female initial flight, 2.17 hr on the average. This suggests that female post-emergence behavior contributes greatly to the time that they to remain virgin. However, we need to repeat the experiments to evaluate statistically the consistency between the prediction of Iwasa & Obara's model and the female availability depending on their post-emergence behavior.

Thus, the present study supported our hypothesis that even when temporal distribution of competitors did not appear to parallel the abundance of resources, the ideal free model was applicable considering the factors which make resource availability differ from resource abundance. In *P. rapae crucivora*, female post-emergence behavior makes female availability peak a few hours after the peak of female abundance. However, the present study can not exclude the possibility that male distribution deviates from the ideal free distribution over female abundance because some assumptions underlying the ideal free model are not valid in this species. The ideal free model of temporal distribution holds good when competitors are allowed to locate resources at any time, when their acquisition ability is homogeneous, and when they have perfect information about resource supply.

The time when butterflies can perform active mate-locating flight is limited by the external thermal conditions, since flight ability of insects depends on the thoracic temperature (May, 1983; Marden, 1995). The activity of female-searching flight of *P. rapae crucivora* is also dependent on body temperature (Ohsaki, 1986) and air temperature (Hirota and Obara, 2000b). Especially in the early morning, low air temperature restricts the active flight of butterflies (Ohsaki, 1986; Hirota and Obara, 2000b). Hence, it is possible that the thermal conditions might constrain male female-search to peak in the later morning when air temperature is moderate. However, the multiple regression analysis revealed that female availability explained the temporal distribution of male female-search better than air temperature (Table 1). It follows that the thermal constraints on male flight behavior are not sufficient to determine the diurnal schedule of male female-search.

Ecological factors which do not influence directly male mating success limit the time when males search for females. Predation pressure was reported to prevent competitors from realizing the ideal free distribution over resources (Begon *et al*., 1996). If the predators of *P. rapae crucivora* are abundant in the early morning, males will refrain from searching for females to avoid predation. Kingsolver (1987) reported that *Pieris* butterflies were more susceptible to predation while thermal conditions did not allow them to fly actively. It follows that in the early morning when males can not fly actively, they should refrain from searching. If predation pressure is dependent on thermal conditions, however, it would not be a main cause of the diurnal schedule of male female-search, since air temperature is not a primary factor in the multiple regression analysis (Table 1).

It is possible that the foraging strategy also influences the mating strategy, and then prevents males from realizing the ideal free distribution over females. If males have to feed to maintain their body and nectars are more available in the early morning, they should visit flowers rather than searching for females in the early morning. However, male *P. rapae crucivora* visits flowers most frequently in the later morning (Hirota and Obara, 2000a). The diurnal schedule of male feeding behavior is significantly later than that of male female-search (Hirota and Obara, 2000a). Hence, in this species the foraging strategy does not prevent males from searching for females in the early morning.

Aggression among males also limits their mate-location. If some males prevent other males from searching for females, we should apply not the ideal free distribution but the ideal despotic distribution (Fretwell, 1972). Although male *P. rapae crucivora* is often observed to chase other males, we have rarely observed that the chased males refrain for searching for females. Even when the chased males left a patch, most of them returned to that patch soon after. In some lepidopterans, mate-locating males chase anything flying almost indiscriminately (*e.g*. Moore, 1987). Hence, the male-chasing behavior of this species might be an indiscriminate mate-locating behavior. It follows that the ideal despotic distribution does not occur in this species.

Homogeneity of acquisition ability (competitive weight) among competitors is also an essential assumption. If good competitors gather in good patch or the ability of competitors depends on patch types, their distribution deviates from the expectation of an original ideal free model (Parker and Sutherland, 1986). On the other hand, when all competitors are allowed to move to any patch regardless of their ability, their distribution will not deviate from the ideal free distribution (Parker and Sutherland, 1986; Houston and McNamara, 1988). It is possible that acquisition ability is different among male *P. rapae crucivora*, since there is a variance in time which males spend in searching for females (Hirota and Obara, 2000a). Therefore, further studies are necessary to reveal how the acquisition ability varies among males and whether males' distribution depends on their acquisition ability.

The last assumption of the ideal free model is competitors' perfect information about the distribution of resources. If the competitors could not know the distribution of resources, their distribution would deviate from an ideal free distribution to a random distribution (Abrahams, 1986). Since male *P. rapae crucivora* spent a long time in finding out the newly-emerged females which stayed under leaves, they could not know the abundance of receptive females immediately. In fact, even when males were observed in a cage where females were excluded, their schedule of female-search was not different from that of males which were observed in the open field (Hirota and Obara, 2000a). It follows that the diurnal schedule of female-search would not result from males' immediate response to female availability. Those facts, however, do not show that males have no information of temporal distribution of receptive females. In this species most females always eclose in the early morning, although the emergence curve is modified slightly by thermal conditions which are dependent on seasonal and meteorological factors (Obara, unpublished). If males were selected by the almost constant temporal distribution of female availability, their intrinsic schedule would have evolved to respond to the circadian rhythm involving temperature compensation to realize the ideal free distribution. In some lepidopterans, the emergence date of males is the same as that predicted by the ideal free model, although male larvae and pupae might not have perfect information to predict the emergence date of females (Iwasa *et al*., 1983; Parker and Courtney, 1983). Males of those species may have evolved life-history traits that realize the ideal free distribution over the female emergence curve. It is possible, therefore, that the temporal schedule of male female-search deviates from the ideal free distribution over the abundance of newly-emerged females, not because males do not have perfect information, but because it might be maladaptive for males to search for inconspicuous females which stay under leaves. Even if imperfect information caused the deviation from the ideal free model, it fails to explain why the temporal schedule of male female-search is correlated with the expected female availability.

Thus, it is possible that some factors which involve essential assumptions of an ideal free model prevent males from realizing an ideal free distribution the abundance of newly-emerged females. However, those factors fail to explain the correlation between the temporal schedule of male female-search and that of female initial flight. Therefore, we conclude that inconspicuousness of females which stayed under leaves is a main cause why males realize diurnal schedule of female-search which parallels the emergence curve of conspicuous females which stay above leaves.

The present study reveals a new problem as to how and why females stay under leaves for a few hours after eclosion. Since the time which females spend before initial flight is dependent on ambient temperature (Fig. 3A), it is suggested that post-emergence development involves female inactivity after eclosion. Wing-hardening time is also dependent on ambient temperature, which involves a temperature-dependent physiological process, *i.e.* sclerotization of cuticle (Obara, 1987). The sclerotization of cuticle is also essential to complete the thoracic mechanical system responsible for flight (Obara and Nakagoshi, 1974). If sclerotization of the thoracic system takes a few hours although wings are hardened after half a hour, the newly-emerged females can not fly actively. In fact, when tossed up into the air just after the wings have hardened, females glide or fly, but only weakly (Obara, 1987). If active flight is restricted, predation pressure will increase (Kingsolver, 1987). Therefore, females stay inconspicuous under leaves until their thoracic system is completed and allows them to fly actively.

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