Population Structure and Dispersals of the Sulfur Butterfly *Colias erate* (Lepidoptera: Pieridae) in an Isolated Plain Located in a Cool Temperate Zone of Japan

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Abstract Mark-release-recapture techniques were used to study natural populations of *Colias erate* in the isolated plain of Shirouma, Nagano Prefecture. Adults fed on and oviposited mainly on clovers, which are abundant on the ridges of the paddy fields. Males outnumbered females in each sampling day, but the estimated number indicated a 1:1 sex ratio. The butterfly had a low frequency of yellow morph in females (less than 15%). The yellow-white morph ratio in females did not differ much from the other localities sampled in Shirouma, such as the ski slope. Males, yellow morphs and white morphs showed similar stable age structures in the summer. Females tended to remate during their life span. Dispersal varied between sexes and between morphs in females. The resident times were similar for yellow and white morphs, but males had a higher recapture rate, suggesting site fidelity. Since most of the plain is occupied by cultivated fields for rice or cabbage, the available plants for larvae and adults in the ridges may not be a limiting resource for maintaining butterfly population.

Key words: Yellow morph; white morph; sex ratio; estimated number; *Colias erate*; dispersals.

Introduction

The butterfly fauna of the cool temperate zone of central Honshu, Japan is characterized by species found in climax birch forests and of some alpine landscapes. Such habitats are targeted by developers trying to make a profit by improving the landscape for skiing in winter. In general, there are distinctive fauna of butterflies associated with vegetation (*e.g.* Hiura, 1971), some of which have disappeared locally (*e.g.* Feltwell, 1986). Several species are now considered to be endangered (*e.g.* Shibatani, 1989). New (1991) provides a broad survey of the emerging science of butterfly conservation. However, in Shirouma, Nagano Prefecture, we noticed that the proportion of some butterfly species such as the sulfur butterfly, *Colias erate*, are increasing, because many of new habitats were opened to the butterfly as a result of development. The host plants of *C. erate* consist mainly of the clovers *Trifolium repens* and *T. pratense*, both of which has been seeded on the whole surface of the ski slope. In the summer, the slope provides a perfect habitat for the butterfly. Taylor (1972)

pointed out that *Colias* populations often attain exceptionally high densities.

Originally, *C. erate* population were found in the plains of the Japanese cool temperate zone, where there are extensive cultivated fields (mainly paddy fields and cabbage fields) with villages. The butterfly was formerly restricted to open habitats, where host plants and nectar plants grow along ridges of the fields. Therefore, *C. erate* is now spreading from the plain to slopes of higher elevation, though the habitats with abundant butterflies are relatively isolated each other.

Little attention has been paid to the population ecology of *C. erate* in Japan. However, WATT *et al.* (1977) clarified the population structure (numbers, dispersal behavior, aging and residence) of three species of *Colias* butterflies in North America. TABASHNIK (1980) showed that both sexes of *C. philodice eriphyle* had a limited dispersal with less than 100 m. Although dealing mostly with other pierid butterflies (*e.g.* WATANABE, 1978; OHSAKI, 1979), the present study will provide further data on the population structure of the butterfly.

KOMAI and AE (1953) showed that *C. erate* females have yellow and white morphs. It exhibits a sex-limited color dimorphism, for adult pteridine wing pigmentation, as in many other species of the same genus (*e.g.* HOVANITZ, 1941, 1944; WATT *et al.*, 1979). Unlike American *Colias* females, except *C. scudderi* (GRAHAM *et al.*, 1980), the Japanese yellow morph never proportionally exceeds the white morph. GILCHRIST and RUTOWSKI (1986) explained the adaptive significance of the alba female morphs from the viewpoint of the reproductive success. WATT *et al.* (1989) discussed the probability that the alba female morph of *Colias* butterflies in Colorado might be a mimic of white pierine butterflies.

The relevance of ideas such as population structure in relation to female morphs may depend on how the dispersal of individuals or the distribution of populations are affected by vegetation or landscape configuration, respectively. The aim of the present study was thus to obtain quantitative information on the adult population structure of *C. erate* in one of their original habitats, a plain. As major tools, we used mark-recapture techniques to estimate population size, longevity and dispersal. The proportion of the yellow morphs in the females was also estimated by random samplings in neighboring habitats. Since the mating frequency of each female sampled was examined by dissection, this comparison will help in understanding the *C. erate* population structure.

Materials and Methods

Populations of *C. erate* were studied in an isolated plain of the Kamishiro area, Shirouma, at 750 m elevation in 1990–1991 (Fig. 1). The plain is surrounded by hills or mountains with deciduous and coniferous forests. Only toward the north of the plain do the narrow paddy fields continue to next plain located along Hime-kawa river. Female population samples were obtained from
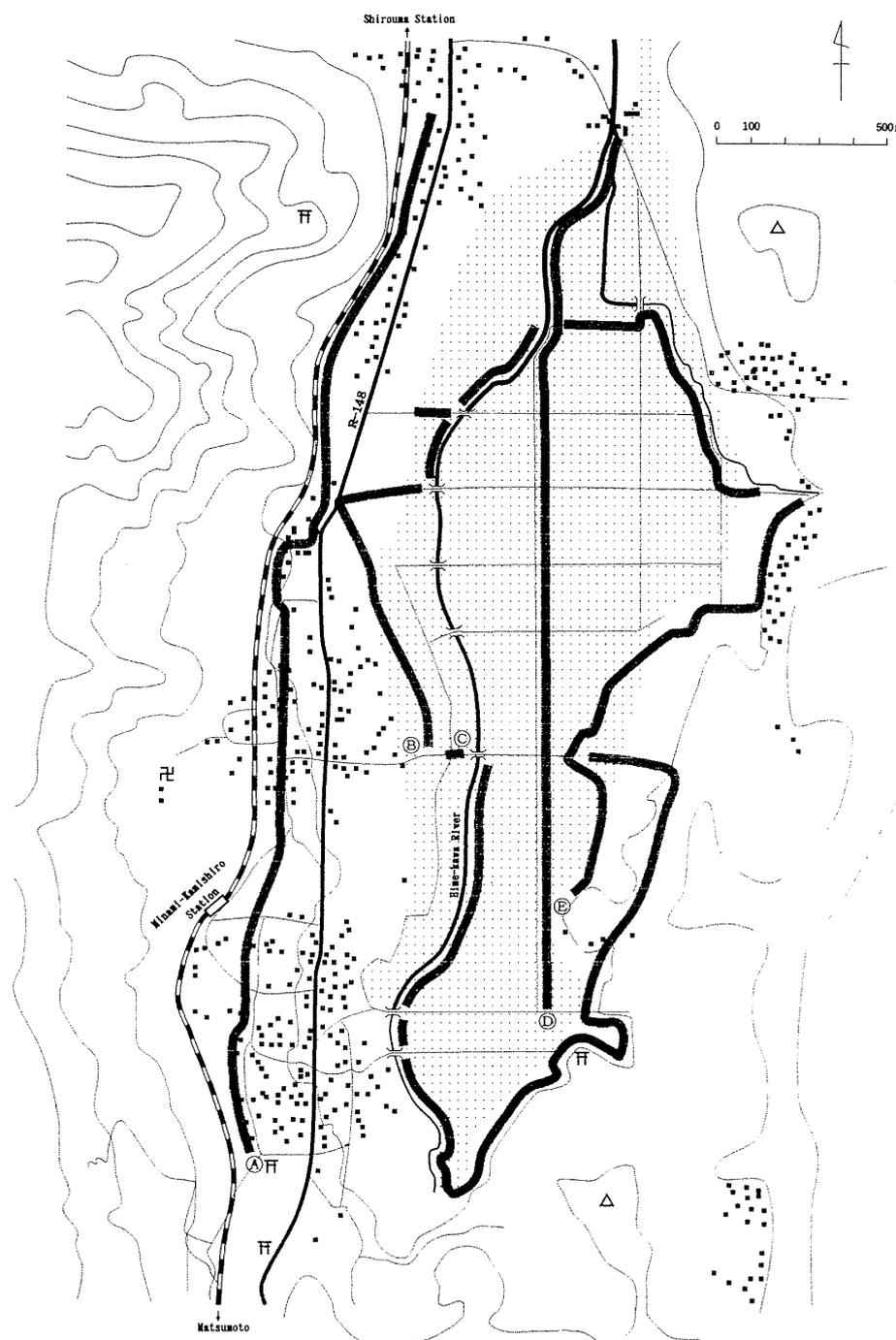
Fig. 1. Map of the study plain for *Colias erate*, Kamishiro, Shirouma, Nagano Prefecture. Heavy lines (A–E) represent survey lines of natural insect populations for the mark-recapture method. Shaded areas show paddy fields, and villages are indicated by the aggregation of small black squares that mean houses and buildings. One of the ski slopes used in the study is approximately 4 km south and the other study sites are max 18 km north of the edge of the map.

another five localities around Shirouma in 1989–1994 including slopes for ski (elevation 800–1000 m). Frequencies of yellow and white morphs were assessed by random hand-net sampling.

Adults *C. erate* fly in the plain from late May through September. The host plants (*T. repens* and *T. pratense*) are locally abundant legume available for oviposition and larval feeding. Adults feed nectar on variety of composites and on the host plants when they are in bloom. The former can be found in the villages and the latter is abundant over the plain throughout their flight season. Both sexes usually fly along village paths and the ridges of paddy fields. The circumstance of the area including the villages and the paddy fields is secondary deciduous forests or planted coniferous forests where no adults have been found.

Adult censuses were carried out along the survey lines in the study area on mostly clear days from 22th July to 4th August in 1991, during which the *C. erate* population was considered to be stable. It took about 2 hours to patrol one survey line. As shown in Fig. 1, survey line A was located in the villages and the others (B-E) were in the paddy fields. Plants in the survey lines were occasionally trimmed by residents and farmers. Consequently, vegetation along the lines was less than 30 cm tall and the common altitude of the flight of *C. erate* was usually less than 1 m.

Adults were captured with a butterfly net and mapped. Each was given on individual number that was marked with a black color felt-tipped pen on the undersurface of the left hind wing. Every butterfly captured was released immediately at the same capturing site after recording the date, site name, sex and the age. The marking was considered to have minor effects on their flight activities (and the probability of predation) because most butterflies began to fly normally soon after marking. Butterflies wounded during marking were treated as dead individuals in the calculations.

The age of the butterfly was estimated mainly by wing condition, as in the case of the other pierid butterflies (WATT *et al.*, 1977; ANDO & WATANABE, 1992, 1993; WATANABE & ANDO, 1993). It was rated as follows: 1, freshly emerged without visible damage; 2, fine tears and less lustrous scales; 3, noticeable wear of scales; 4, wings showing fraying or tearing in their cuticle; 5, wings with extensive scale wear and cuticle damage.

In most butterfly populations, the recapture probabilities of the two sexes were different (*e.g.* WATT *et al.*, 1977; WATANABE, 1978; KIRITANI *et al.*, 1984). The sexes of *C. erate* were processed separately through JOLLY's analysis (JOLLY, 1965). The mark-recapture data for yellow morph females were also separated from the data for white morphs.

Since a male butterfly ejaculates a spermatophore in the bursa copulatrix of female at each mating, spermatophore counts in individual females provide an index of mating frequency (*e.g.* BURNS, 1968; WATANABE & ANDO, 1993).

Females of both morphs were thoroughly collected for a few days in the study period in each study field and dissected to examine the spermatophore numbers.

Results

Population structures in relation to the yellow-white morph ratio in females

C. erate is thought to have overlapping generations and the population is thought to increase each summer. Individuals were of mixed ages in sampling time. Table 1 shows the results of extensively studied populations, examining sex ratio and yellow-white morph ratio in females.

Males heavily outnumbered females in the plain (1991). As is frequently the case in many butterfly species, there may be clear behavioral difference between the males and females. Long-term observations in Shirouma (unpublished) show that males incessantly wander back and forth within a particular habitat, while

Table 1. Sample-based sex ratios, yellow-white morph ratios, the age ratings, mating frequencies and adult sizes of *Colias erate* in relation to habitats and years ($\pm$SD). Except for Koruchina, samples were restricted to late July and early August. See text for details of the age rating system.

	Location	Year	Sex and morph	Number sampled	Yellow in ♀ (%)	Age rating	Number of sper-matophores	Forewing length (mm)
Plain	Misora	1989	Yellow ♀	4	15	2.5±0.50	1.8±0.50	—
			White ♀	22		2.5±1.01	1.6±0.61	—
	Kamishiro	1990	Yellow ♀	32	15	2.2±1.33	1.5±0.51	29.5±1.46
			White ♀	182		2.2±1.11	1.5±0.70	29.8±1.35
	Kamishiro	1991*	Yellow ♀	26	14	2.5±0.95	—	29.2±1.68
			White ♀	164		2.2±0.92	—	30.0±1.76
			♂	345		2.1±1.00	—	28.7±1.63
Slope	Kashima-yari	1991	Yellow ♀	6	14	3.2±2.04	1.7±0.58	29.2±1.14
			White ♀	36		2.4±1.31	1.4±0.65	29.6±1.44
	Tsugaike	1993	Yellow ♀	13	11	2.0±1.16	1.4±0.65	30.2±1.70
			White ♀	101		1.6±0.82	1.3±0.49	30.4±1.53
	Hakuba 47	1993	Yellow ♀	2	15	2.0±1.41	1.5±0.71	30.8±0.78
			White ♀	11		2.1±0.70	1.3±0.47	29.4±0.51
	Kashima-yari	1994	Yellow ♀	9	10	3.5±1.24	2.4±0.74	30.1±0.84
			White ♀	80		3.3±1.16	2.0±0.65	29.0±1.84
	Koruchina	1994**	Yellow ♀	5	11	1.9±0.59	1.5±0.45	29.1±1.33
			White ♀	41		2.1±0.88	1.5±0.67	29.4±0.91

  * Samples were based on marked butterflies.
** Late June.

the females fly one way with intermittent feeding and ovipositing. Not only did this cause a relatively small proportion of the females to be marked in the study plain, but the probability of recapturing a marked female was considerably lower than that of recapturing a marked male.

During the study period, there was a predominance of white morph females in each study field. The white morphs comprised about 85% in the plains and the slopes of Shirouma. Although we did not estimate the number of morphs in each study field, the density of females must differ in the fields and year by year. Therefore, little change in the relative frequency of white and yellow morphs among females appear in the population structure.

Table 1 also suggests that females often mated more than once by the spermatophore counts in the bursa copulatrix. There was no significant difference in the number of spermatophores carried in the bursa copulatrix between the two morphs sampled. In general, the mean number of spermatophores is apt to increase with the mean age rating. Since the age rating was stable in the summer, female activity for mating was also similar in each field and each year.

Population parameters estimated in 1991

Adult *C. erates* were found in every open grassy area in the study plain, but concentrated in the ridges of the paddy fields and village paths. These areas supplied adult and larval food sources. Since no puddle aggregations were formed in the study plain, the mark-recapture work was done mainly along the ridges and the paths, where most adults showed not only feeding or resting behaviors, but also mating and ovipositing behaviors.

Table 2 shows estimated population densities for the whole plain. Estimated standard deviations (SD) could not be calculated for yellow morphs because of the small number of recaptures. There was a relatively constant numbers of males, about 229 individuals a day roughly averaged. On the other hand, the estimated population size of the yellow morphs was quite small. Each standard deviation of the white morphs was always larger than each estimated number. The daily number, roughly averaged for each morph, was 24 and 204 for yellow and white morphs, respectively. Therefore, the yellow morphs occupied about 11% of the female population in the plain, and the daily estimated number of total females was the same as that of the males.

SCOTT (1973) and WATT *et al.* (1977) pointed out that JOLLY's "survival" estimates should be closely correlated with residence for wild butterfly populations. Table 2 also shows the residence rate of males in the whole plain. The rough average of the residence rate of males (0.746) yielded an expected residence time of 3.4 days $[=(\ln(0.746)^{-1})^{-1}]$. In general, both morphs displayed shorter residence than males. Accordingly, the expected residence time was ca. 2.0 and ca. 2.7 days for yellow and white morphs, respectively. These

Table 2. Estimated daily numbers ($\hat{N}$) and residences ($\hat{\phi}$) for Kamishiro population
of *Colias erate* in 1991, calculated as described in the text
for mark-recapture data ($\pm$SD).

	Date	♂	Yellow ♀	White ♀
$\hat{N}$	24/Jul	360±216	—	186± 223
	25/Jul	149± 99	—	43± 45
	26/Jul	191± 78	—	60± 66
	27/Jul	190± 72	42	560± 712
	29/Jul	98± 22	—	264± 362
	30/Jul	138± 27	12	—
	31/Jul	450±112	8	111± 960
	1/Aug	383±150	5	314±1143
	2/Aug	102± 20	—	96± 774
	Average	229	24	204
$\hat{\phi}$	23/Jul	0.635	—	0.467
	24/Jul	0.593±0.201	—	0.319±0.242
	25/Jul	1.155±0.390	—	1.600±1.640
	26/Jul	0.711±0.185	3.500±3.260	1.230±1.409
	27/Jul	0.808±0.151	0.500	0.695±0.794
	29/Jul	0.840±0.123	0.500	0.075
	30/Jul	1.999±0.406	0.500±0.250	3.583
	31/Jul	0.769±0.283	0.438±0.220	1.226±0.853
	1/Aug	0.354±0.122	0.667±0.272	0.659±0.575
	Average*	0.746	0.601	0.691

* The daily residence was regarded as 1 for the calculation of average when the value was more than 1.

values may be due to greater dispersal.

Each survey line was split into sections which were identified by some land marks or by topographic features. The section lengths were 100–500 m. Every site where an adult *C. erate* captured was pooled into a respective section. Figure 2 presents the mean recapture decay in a section for males, yellow morphs and white morphs. Each recapture rate was transformed by angular transmission for the statistical test. Males tended to stay in the same section after releasing, while white morphs dispersed. Yellow morphs showed lesser dispersal than the white morphs for 3 days after releasing, though there was no significant difference in the recapture rate between the morphs, and the recapture rate was zero at 4 days after release.

Figure 3 presents *C. erate* dispersal in the plain. Males gradually dispersed after release ($P < 0.01$), while there was no significant difference for both morphs between the distance of the dispersal and the days elapsed. There was a little movement between survey lines for males. The average dispersal for males is approximately 161 m in the day after release, a distance contained in a single
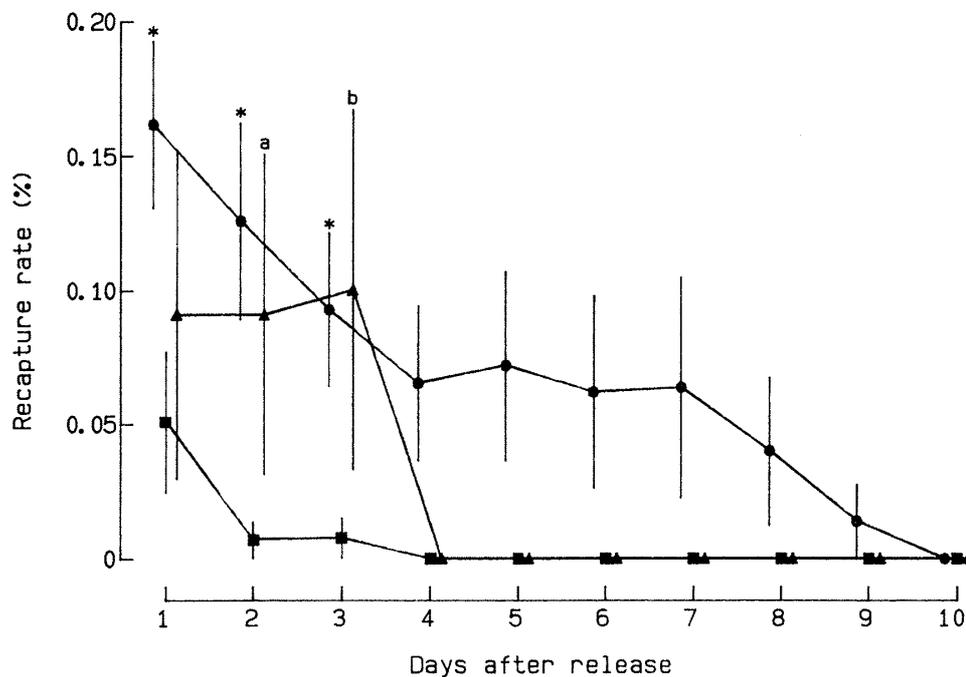
Fig. 2. Recapture duration decay plot for male (circle), yellow morph (triangle) and white morph (square) of *Colias erate* ($\pm$SE). The abscissa is the recapture duration, which is the time between first and last captures of a given individual in days. The ordinate is the recapture rate in the same section released. a, b and * mean 0.117, 0.115 and less than 0.01 of P-value for U-test compared with the data of white morphs, respectively.

section. Several days after release, recaptured males had a greater ranges. The longest dispersal seen was 1936 m at 11 days after release. However, the mean distance from the release site was very low compared to the area of the plain. On the other hand, movements between the survey lines for both morphs were witnessed within a few days after release. The average dispersal was approximately 344 m and 415 m for yellow and white morphs, respectively. No significant difference between the morphs was observed in the dispersal, though white morphs had a larger distance. The longest dispersals seen were 1760 m in 2 days and 913 m in 3 days after release for yellow and white morphs, respectively.

Discussion

In many studies on pierid populations, male captures outnumbered female captures (*e.g.* WATT *et al.*, 1977; WATANABE, 1978; OHSAKI, 1979). The present study shows that in *C. erate*, as well, more males were captured. Field observations suggest that females tend to fly short distances between stops for oviposition and nectaring, while males fly much farther between stops. This difference in flight activity could make females less re-catchable. Similar sexual dimorphism in
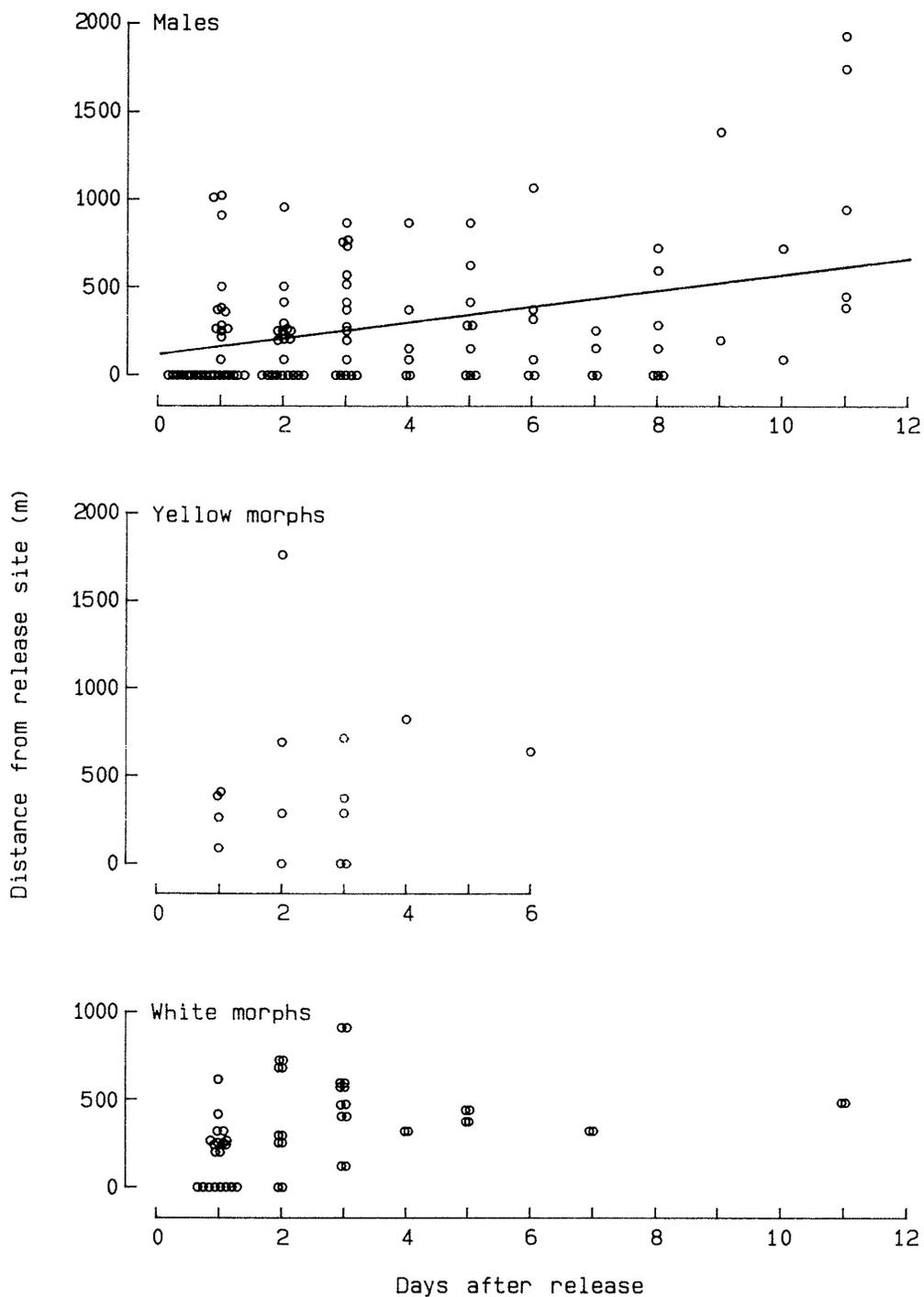
Fig. 3. Dispersal by *Colias erate* in the plain from a release site. The slope of each line is a regression of the distance on days elapsed between release and recapture. The line is significantly different from zero (slope=47.5, F=16.25, P<0.01).

flight activity has been observed in other butterfly species (*e.g.* BRUSSARD & EHRLICH, 1970; TABASHNIK, 1980). An analysis of the movements of recaptured females also showed that they may have different dispersal behaviors from males. For *C. philodice* a sex ratio bias towards males with short life expectancies of 2–5 days has been reported (WATT *et al.*, 1979; TABASHNIK, 1980). KINGSOLVER (1983) discussed these differences in terms of the different reproductive strategies of males and females. However, the daily numbers for males and females were estimated to be equal, though SDs for females were higher than those for males.

SHAPIRO (1970) pointed out that adult samples approach a 1 : 1 sex ratio at low densities, and that the normal sex ratio is distorted by female emigration. EHRLICH *et al.* (1984) discussed that the skewed sex ratio appears to be caused by a higher rate of female emigration and possibly higher female adult mortality. In the present study, however, the equal number of males and females suggested that males do not outnumber females in *C. erate* populations. Both sexes may have similar nutritional requirements. Because larval host plants also supply nectar for adult feeding, they spend much time in the plain. The extent of the plain may also provide a diverse minor habitat (ELTON, 1949) for the butterfly, such as open ridges, the edges of forest and semi-shaded areas in villages. Therefore, *C. erate* can maintain its population within the plain.

Female white morphs were much more abundant than yellow morphs. No striking yearly change in the relative frequency of yellow and white morphs captured was found. Differences in catchability between the two morphs are unlikely as in the case of GILCHRIST and RUTOWSKI (1986). Not only is evidence of a difference in activity levels lacking (*e.g.* LEIGH & SMITH, 1959), but our collection procedure tended to flush females from their perches, minimizing the importance of any residual differences.

The yellow morphs in *C. erate* females comprised about 11–15%. In the estimated numbers of both morphs calculated by the JOLLY's method, it was about 11%. KOMAI and AE (1953) pointed out that the disparity in numbers for yellow-white morphs is more pronounced in samples from northeastern localities (ca. 23%) than those from southwestern localities (ca. 47%) in Japan. By contrast, WATT (1973) stated that a *C. meadii* population in Wyoming has a yellow phenotype frequency of roughly 90%. For *C. alexandra*, the yellow morph frequency was 87.4%, while for *C. scudderi* 10–15% (GRAHAM *et al.*, 1980). HOVANITZ (1944) concluded that a north to south gradient is produced in white gene frequency, there being nearly 100% white in the far north. The results of this study support that the cool weather may have biased the disparity further.

The average age rating of *C. erate* was 2–2.5 relatively similar in each field and year (Table 1). In contrast, in 1994 there was a shortened emergence period

due to little precipitation in the rainy season. This year was marked by a severe midsummer drought with extraordinary high temperatures. Since the nectar production by plants and their own growth are highly dependent on an adequate water supply, the drought may have reduced the adult numbers both by interfering with larval growth and by accelerating the aging of adults. Consequently, the age rating would have increased. In the other years, as the older individuals died and were replaced by newly emerged individuals, the average age ratings may have maintained low levels until the emergence rate dropped in the autumn.

In general, the age rating was related to several measures of reproduction condition. In *Colias*, each spermatophore in the bursa copulatrix remains recognizable through the female's life span (*e.g.* GRAHAM *et al.*, 1980). Thus, it was clear that older females tended to have more spermatophores, as has been recorded in other butterfly species (*e.g.* RUTOWSKI *et al.*, 1981).

The movement of females out of their natal field is reflected in the observed changes in population structure. Similar patterns have been observed in *C. eurytheme* (GILCHRIST & RUTOWSKI, 1986). Yellow and white morphs differ physiologically in several important ways (*e.g.* WATT, 1973), and it is possible that the two morphs have different thresholds of pheromone detection that vary depending on environmental conditions (SAPPINGTON & TAYLOR, 1990). The prolonged residence by females in the study plain may increase the number of spermatophores through their life span. However, there was no clear difference in residence between the two morphs.

Male *C. erate* showed site fidelity in spite of many available habitats in the plain. WATANABE *et al.* (1985) reported that male swallowtail butterflies repeatedly visited a habitat within a day if they preferred it. Only a few movements more than 1000 m in a day were found. However, we have seen that the dispersal of females can vary widely between survey lines or between the morphs. No female was found at the same section 4 days after release, suggesting that it took a few days to fly across a section. In fact, average movement was more than 300 m for both morphs.

Only minor differences in the residence in the plain and in the site fidelity could be found between two morphs of female *C. erate*. Yellow and white morphs fly as adults at the same time in the summer resulting in the same age structure and feed from many of the same nectar sources. It would be necessary to examine the co-occurrence patterns of the two morphs.

BERNSTEIN (1980) stated that the harvest of alfalfa causes a destruction of *C. lesbia* populations, thus affecting the sex ratio. However, adult resources might not be a limiting factor, which would explain the relatively consistant large numbers of adults in the study plain. As long as the plain is continued to be cultivated, little habitat destruction may support the populations of *C. erate*. However, since suitable larval host plants are available in the whole surface

of a wide areas such as ski slopes, other factors must be restricting the size of population.

Acknowledgments

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