MOVEMENTS OF *EUCHLOE AUSONIDES* (PIERIDAE)

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Until recently, most butterflies have been thought to be quite sedentary, except for a few migratory species. This paper and that of Brussard & Ehrlich (1970) report quite large flights of non-migratory species, showing that, perhaps like most taxa, butterfly species form a continuum from those having sedentary habits to those which are migratory. This paper is part of a broader study on movements of diurnal Lepidoptera (Hesperioidea and Papilionoidea) emphasizing the relationship between adult behavior, especially mate-locating behavior, and movements. Previous papers showed that mate-locating behavior, mating, movements, feeding, oviposition, and basking affected each other and were adapted to local topographic and climatic conditions (Scott, 1973a, b). Local adaptation was found to promote convergence of magnitude of movements and behavior between two sympatric species (Scott, 1973c). The present paper deals with adult movements of *Euchloe ausonides* Lucas and the effect of density, mating behavior, feeding, and oviposition on movements. *E. ausonides* was studied in April, 1969, and during the springs of 1970 through 1972, at near sea level on Point Richmond, Contra Costa County, California (Fig. 1).

METHODS

The methods used are mainly those of Scott (1974). Butterflies were marked individually using the method of Ehrlich & Davidson (1960), and immediately released at the site of capture. Marking was done throughout the area; numbers (Fig. 1) were used to aid in pinpointing the exact site of each capture. On a map of the movements of each recaptured individual, various distances were measured (Table 1). Midpoint age between captures is determined by finding the age midway between two captures after designating the first capture day 0. Correlations between distances or velocities and midpoint age determine whether movements change with age.

RESULTS

Description of movements. A mark-recapture study was conducted in April, 1969. Individuals were marked and released over the portion of the hill south of area 38 (Fig. 1), and recapturing was carried out over

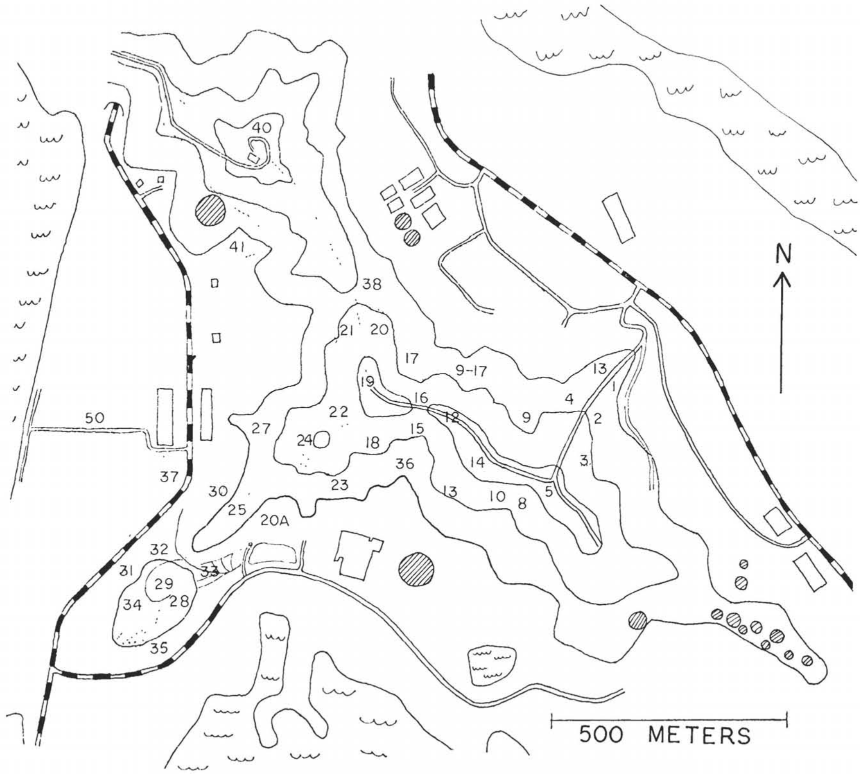

Fig. 1. Study area at Point Richmond, Contra Costa County, California. Numbers are markers used as aids in locating capture sites. Double lines are dirt roads. Round circles are tanks. Polygons are buildings. Contour interval 30 meters (maximum elevation 112 m).

the entire hill. Movements varied from none (over periods of several days) to large [one male traversed the entire hill four times in three days, and moved 1460 meters (air distance) in one day]. Movement parameters were greater for females than for males (Table 1). Total distance (D) was greater for males but range and velocities were greater for females; apparently females move more unidirectionally, while males tend to stay in one area more than females. Females are very good colonizers; I found eggs on introduced *Brassica nigra* plants at the Berkeley, California marina (created by dumping dirt into the bay), which is about three miles from the nearest colony. Movements do not change significantly with age; correlations between midpoint age and movement parameters (Table 1) were very small.

Effect of density on movements. To determine whether the large

TABLE 1. *Euchloe ausonides* movement data. Sample size of capitalized statistics is number of individuals recaptured; sample size of subscripted statistics and correlations is total number of recaptures. n = not significantly different from 0 (test of zero correlation).

Movement parameter	Definition prior to averaging	Males	Females
Number marked		97	48
Number recaptured		54	19
Total number of recaptures		110	25
Ave. T (days)	Days between first and last capture	4.43	4.00
Ave. t_i (days)	Days between i'th and (i + 1)th capture	2.17	3.04
Ave. R (meters)	Meters between the two farthest capture points	329.	366.
Ave. D (meters)	Sum of all d_i's of an individual	463.	387.
Ave. d_i (meters)	Meters between i'th and (i + 1)'th capture	227.	294.
Ave. V (meters per day)	D/T	139.	179.
Ave. v_i (m/day)	d_i/t_i	161.	183.
Correlation d_i and t_i		$+.036^{n}$	
Partial correlation d_i and t_i, age constant		$+.041^{n}$	
Correlation v_i and age		$+.126^{n}$	
Correlation d_i and age		$+.132^{n}$	
Partial correlation d_i and age, t constant		$+.133^{n}$	
Correlation t_i and age		$-.029^{n}$	

TABLE 2. Population size estimates for *Euchloe ausonides* using five different methods.

Method	Population Size: Males	Population Size: Both Sexes
Jolly (1966)	100	200
Craig's method 1 (Southwood, 1966)	—	227
Craig's method 2 (Southwood, 1966)	—	218
Edwards & Eberhardt (1967) method 1	—	368
Edwards & Eberhardt (1967) method 2	—	376

flights observed were due to overcrowding, population size was determined from 19 to 27 April using five different methods (Table 2). Jolly's (1966) method is probably the best (Southwood, 1966) as daily survival rates are probabilities rather than exact values. Estimates using the methods of Edwards & Eberhardt (1967) seem too large (Table 2). Because the density is the lowest of all eleven species of diurnal Lepidoptera that I have studied, I believe that density alone did not increase dispersal.

Effect of mating behavior on movements. The method of locating mates may play a part in movements of males. Males fly (patrol) all day about a meter above the ground searching for females. Males approach white paper models and other light butterflies (*Coenonympha tullia californica* Westwood and *Pieris rapae* L.) and other *Euchloe* individuals to within about 20 cm, then either turn away and continue flight, or hover in courtship. Females fly almost continuously also. Both sexes fly at a rapid rate of about 5 meters per second, and often travel 100 meters or more without stopping.

Weather affects this flight activity considerably: cloud cover, cold, and high winds curtail activity. Basking, either with the wings spread nearly to the sides or with the wings closed, and with the wing surfaces oriented nearly perpendicular to the sun's rays, may permit activity during less favorable weather.

Mating occurs at all times of the day whenever weather is suitable. Six copulating pairs were found from 0934 to 1552 (24-hr. ST), and 22 courtships were observed from 0850 to 1630. If a flying male encounters a flying female, they first hover near each other, with the male behind. Next the female lands and the male lands behind her and bends his abdomen to clasp hers. Once I observed a female remaining quiescent on a flower while the male landed and initiated copulation. Females often mate more than once (of 39 wild females dissected, one had no spermatophores, 27 had one, 10 had two, and one had three).

Females reject males by means of two sterotyped behavior patterns. (1) Resting females spread the wings flat and raise the abdomen almost vertically; this posture is used by unreceptive females of most Pieridae (Scott, 1973b). The male may hover over the posturing female for up to 20 minutes in the case of young newly mated females. If the female was mated and apparently older, the male usually flew away after less than 30 seconds. Females in this posture alternately open and close the terminal abdominal flaps, exposing an elaborate apparatus consisting of six membranous lobes. (2) In a few instances, the female (with male behind) rose in the air as high as seven meters before the male flew away. In many other instances of discontinued courtship, both sexes began hovering, but then the male (or occasionally the female) merely flew away. Because females can rapidly discourage males, harassment by males probably has little effect on female movements.

Mating and courtship occurred everywhere on the hill. However more patrolling males and courtships were seen in hollows and valley bottoms than on ridges. This tendency to follow valley bottoms may contribute to longer movements because it promotes more unidirectional flight.

Effect of feeding on movements. Both sexes often feed on flowers, especially during warm weather. They prefer flowers of the main larval host, *Brassica nigra*, and often visit another crucifer, *Raphanus sativus*. Occasional visits were made to flowering plants of other families, including *Cirsium* sp., *Achillea* sp., *Plantago lanceolata, Brodiaea pulchella, Erodium* sp., *Eschscholtzia californica, Wyetha helenoides, Sisyrinchium bellum, Althaea rosea, Rubus* sp., and *Ranunculus* sp. The favored cruciferous flowers were widespread. This may have increased movements somewhat, but individuals do not need to move the observed distances merely to locate flowers.

Effect of oviposition and larval foodplants on movements. Oviposition occurred throughout the day from 0917 to 1507. Eggs are laid singly in the middle of the unopened flower buds of crucifers. If a plant has more than one such inflorescence, more eggs are found on the terminal inflorescences than on lower ones. Females almost always lay only one egg per plant, and then usually fly more than three meters before laying another. At the study site, plants usually had from one to several eggs, but one plant had ten eggs on it. Hundreds of eggs were found there on *Brassica nigra*, but three eggs were found on *Raphanus sativus*, a less common species. Adults were raised from larvae found on *B. nigra*. Larvae feed on the reproductive parts of the plant, and may destroy a considerable part of the potential seed-producing structures. The following additional crucifers have been recorded either as larval hostplants or as oviposition sites of *E. ausonides* in other areas: *Descurainia californica, Arabis drummondi, A. fendleri, A. glabra, Erysimum capitatum, Sisymbrium altissimum,* and *Brassica kaber* (Remington, 1952; Shields et al., 1969; P. Opler, pers. comm.; Riotte, 1968). Oviposition behavior of females certainly is correlated with long-range flights of females, and many of the larval foodplants are plants of disturbed habitats, having a weedy distribution, which must favor large movements as well.

DISCUSSION AND CONCLUSIONS

There can be two main reasons for long-range flights in a population: (1) movements may be largely due to past long-term selective pressure, or due to the (2) short-term necessity for locating vital "resources" such as flowers, oviposition sites, and mates. I think that large flights of *E. ausonides* are mainly a hereditary response to past selection for locating these resources, first, because so many other species of Pieridae have apparently large movements (e.g., *Colias eurytheme* Boisduval, Stern & Smith, 1960; *Pieris protodice* Boisduval & Le Conte, Shapiro, 1970; *Ascia monuste* L., Nielsen, 1961), and, secondly, because movements of the sexes are very similar despite differing short-term necessities (mates and flowers for males, flowers and oviposition sites for females, although the distribution of virgin females must be roughly similar to the distribution of oviposition sites; males carrying the main burden of locating mates). In *E. ausonides* there is selection for long-range flights of females because of single oviposition on the widespread, weedy larval foodplants, which at the study site are introduced, early successional plants. These plants may attain high densities and then die out as plant succession proceeds; *E. ausonides* must disperse from regions having declining plant populations to areas where the foodplants are colonizing. Flight patterns of males must be roughly similar to flight patterns among females in order to locate mates. The greater movements of females than males seem to be due to the oviposition behavior of females, and the necessity for females to colonize new habitats. Adults need not remain near the larval hostplants for nectar, because they do not feed only on the flowers of the larval hosts, and they must emerge before the larval hosts complete blooming, in order to oviposit on flower buds.

The population density at the study site apparently did not cause long-range flights.

The sites of mate-locating behavior may affect movement. Males often fly up and down valley bottoms, and in forests fly mostly along valleys, roads, and clearings. The use of these relatively linear paths may produce greater dispersal than would occur in populations in which individuals turn randomly.

The process of mating itself seems to have little effect on movements. Courtship and mating are brief, and lack the long-distance postnuptial flight of other species such as is found in *Danaus gilippus* Cramer (Brower et al., 1965). Males apparently are not drawn to females from long distances by pheromones but seem to locate females visually. Males have androconial scales on the forewings (Opler, 1969), but in *Colias* such scales do not disseminate a pheromone (R. Silberglied, pers. comm.). The terminal abdominal lobes of females possibly emit a pheromone to repel males (Scott, 1973b), but males were not attracted by several virgin females released at the study site.

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RECORDS OF *LYCAEIDES MELISSA SAMUELIS* (LYCAENIDAE) FROM WISCONSIN

One of us (FHK) discovered a large flourishing colony of *Lycaeides melissa samuelis* Nabokov in the Seymour Township School Forest Reserve, Eau Claire County, Wisconsin on 28 May 1972. We both returned to this locality many times during 1972 to collect additional specimens, and several other colonies were discovered in an approximate 10 mile radius of the original site. Collecting dates during 1972 included May 26 and 31; June 3, 5, 6, 12, 15, 19 and 25; July 4, 5 and 7; and August 20 and 26. There appear to be at least two and possibly three broods.

The habitat where these colonies were found was fairly typical of Pine Barrens, although somewhat disturbed by plantations of *Pinus resinosa* (Red Pine). The soil is very shallow and sandy; dominant native trees are *Pinus banksiana* (Jack Pine) and *Quercus ellipsoidalis* (Hill's Oak); prevalent groundlayer plants include *Vaccinium angustifolium* (Blueberry), *Viola* sp. (violets including the rare *Viola pedata*), *Lupinus perennis* (Blue Lupine), *Arabis* sp. (Rock Cress), *Lithospermum* sp. (borage) and *Amorpha canescens* (Leadplant). Other, somewhat habitat restrictive, species of diurnal Lepidoptera which occurred here included: *Amblyscirtes samoset* (Scudder), *Wallengrenia otho* (Smith), *Hesperia sassacus* Harris, *Incisalia polios* Cook & Watson, *Incisalia niphon* (Hübner), *Glaucopsyche lygdamus* (Doubleday), *Chlosyne gorgone* (Hübner), and *Speyeria aphrodite* (Fabricius).

We both visited the colony together on June 19 and observed a female *Lycaeides melissa* ovipositing on *Lupinus perennis.* She spent a great deal of time flying over the plant, then landed and walked up and down the leaflets and stems. She would stop occasionally and make false attempts at depositing an egg. After about five minutes of observation, she paused on top of a leaflet and then, twisting her abdomen in an arc, she deposited a green egg at its edge on the lower surface.

All previous records of *Lycaeides* from Wisconsin have been attributed to *argyrognomon* (Bergstrasser), recently described as subspecies *nabokovi* Masters (1972, J. Lepid. Soc. 26: 150–154). These records of *L. argyrognomon,* a species extremely hard to distinguish superficially from *L. melissa,* include Marinette and Oconto Counties (Griewisch 1953, Lepid. News 7: 54), Brown, Waupaca, Shawano and Burnett Counties (Ebner 1970, Milwaukee Public Mus. Popular Sci. Hbk. 12) and Portage County (Johnson & Malick 1972, Rpt. 7, Mus. Nat. Hist., Univ. Wisc., Stevens Point). There is little doubt, however, that these new populations in Eau Claire County represent *L. melissa* and not *argyrognomon.* The identification is determined by maculation (the ventral hindwing margins tend to have a solid terminal line), male genitalia dissection (JHM), the foodplant (*Lupinus*), the habitat (Pine Barren instead of Canadian Zone Forest), and the existence of multiple annual broods. In addition we highly suspect that the specimens recorded from Burnett and Portage Counties should be properly attributed to *L. melissa* instead of *L. argyrognomon.* Our reasoning for this is that Pine Barrens occur in Burnett County and Oak Barrens in Portage County, but true Canadian Zone Forest occurs in neither.

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