Oecologia (1989) 78:283–288

Oecologia

Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae)

F.J. Odendaal[1], **P. Turchin**[2,*], **and F.R. Stermitz**[3]

[1] Department of Zoology, Duke University, Durham, NC 27706, USA
[2] Department of Zoology, NJ-15, University of Washington, Seattle, WA 98195, USA
[3] Department of Chemistry, Colorado State University, Fort Collins, CO 80523, USA

Summary. We studied behavioral mechanisms underlying the spatial distribution of *Euphydryas anicia* (Lepidoptera: Nymphalidae) females searching for larval host plants on a flat plain in Colorado. The rate of female movement, as represented by an empirically estimated diffusion coefficient, is affected by two factors. First, when searching in areas of high host-plant density, females tend to make sharper turns and fly for shorter distances between landings, compared to areas of low plant density. As a result, the rate of female displacement is lowered when they search in areas of high host-plant density, and thus females tend to aggregate in such areas. The second factor affecting female movement is the presence of males. Harassment by males induces females to increase the rate of their movement, and females are often chased out of host patches by males. Our results explain the observed spatial and temporal patterns of female distribution in relation to the distribution of host plants and males. In years when host plants are plentiful, harrassement by males in one host patch induces females to move to another. This pattern of female movement tends to disrupt the relationship between the spatial distributions of host plants and females, as well as females and males. In the year when hosts were concentrated in a single large patch, females could not easily avoid male harassment, and consequently we observed strong correlations of female – host distributions and male – female distributions.

Key words: Butterfly movement – Correlated random walk – Diffusion coefficient – *Euphydryas anicia* – Insect-plant interaction – Male harassment

An important aim of population ecology is to explain the spatial patterns of animal distribution. One of the most important factors affecting the distribution of female butterflies is the distribution of the larval hosts and of nectar sources. Yet, the success at locating resource items is largely determined by the manner in which individual insects search (Jones 1977). Factors other than the need for food and oviposition may thus modify the spatial relationship between resources and female insects by influencing female movements. In this paper we examine how this relationship is affected by the harassment of females by males.

The genus *Euphydryas* has been studied extensively, especially its geographical distribution, microdistribution and interactions with nectar and larval host plants (e.g. Ehrlich et al. 1975; Ehrlich and Murphy 1981). Drawing on this background, we aimed to elucidate the behavioral mechanisms underlying spatial patterns of female *Euphydryas anicia* in a relatively simple habitat in Colorado. The site is situated on a flat plain so that the topographical and microclimatic factors (e.g. Shields 1967; Singer 1972) are expected to play a minor role, simplifying the task of understanding the patterns of population distribution within the site (Odendaal et al. 1988).

Several factors may affect the distribution of *Euphydryas* females. For example, in a related species, *Euphydryas chalcedona*, both nectar and larval host plants influence the distribution of females (Murphy et al. 1984). Another factor affecting female distribution may be intersexual interactions. *Euphydryas* males harass already-mated females (Brussard et al. 1974; Odendaal et al. 1985) but the effect of this on female distribution has not been documented beyond observations that mated females often avoid males by flying away from them (Odendaal et al. 1989).

Our hypothesis is that two forces act simultaneously on females. On one hand, females search for host plants in such way that they aggregate in areas where their resources are concentrated. On the other hand, males are attracted to areas of high female density, and their harassment will induce females to leave such areas. The balance between the two forces will ultimately determine where the average female spends most of her time. To test this hypothesis, we studied the movement behavior and spatial patterns of male and female *E. anicia* over a four-year period in a Colorado population. Dramatic year to year differences in plant distributions serendipitously provided us with a grand scale natural experiment to test our hypothesis.

Methods

The animals and the study site

Euphydryas anicia Doubleday and Hewitson occurs in scattered populations over the western half of the United States (White 1979; Cullenward et al. 1979; Ferris and Brown

---

[*] *Present address and address for offprint requests:* Southern Forest Experimental Station, 2500 Shreveport Hwy, Pineville, LA 71360, USA

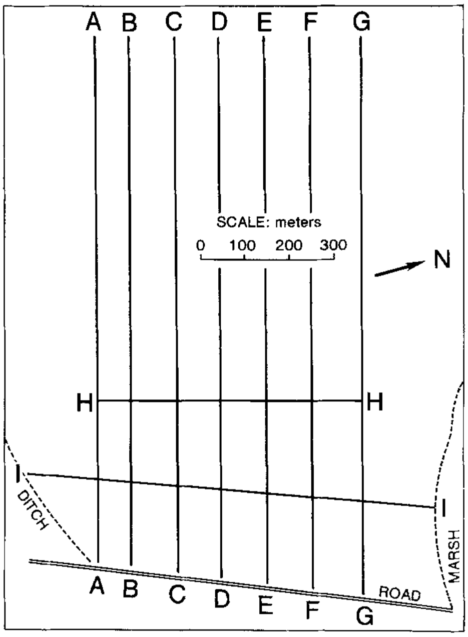

Fig. 1. A Map of the study site with transects

1981). Near Red Hill Pass, 11 km east of Fairplay, Park Co., Colorado, a population occurs in an approximately square kilometer area of a flat, high altitude (2900 m) intermontane plain. In 1983 we measured out transects within the part of the plain occupied by the population (Fig. 1). In 1985 transects A to E were expanded to have similar lengths to F and G.

The flight season is short. After snow has melted (early to mid-May) postdiapause larvae feed on *Castilleja integra* and *Besseya plantaginea* (Scrophulariaceae), pupate, and emerge as adult butterflies in mid-June. About four to five weeks pass from the first emergence to the disappearance of the last butterfly. The first several days only males emerge as in other protandrous *Euphydryas* (e.g. Iwasa et al. 1983). Plants grow low and sparsely on the site, providing excellent visibility for observing and following adult butterflies.

Male and female butterfly distribution

Male and female distributions along the transects were determined by two observers walking slowly at an even pace along the transect line and recording the positions of male and female butterflies in two five meter wide strips on either side of the line. In 1983, 1985 and 1986, this was done at the height of the flight season but in 1984 during the last quarter of the season. To quantify the degree of clumping in the distribution of female butterflies we calculated the ratio of variance to mean (or the coefficient of dispersion) for butterfly counts in 25 meter segments of a transect. The standard deviations of the estimated coefficients of dispersion were calculated by the jacknife method (Reed 1983). Using regression analysis we determined whether the distribution of males was affected by the distribution of females, as well as whether females were affected by the distribution of host plants.

Plant distributions

Adults secure nectar mainly from *Draba streptocarpa, Hymenoxys richardsonii,* and late in the flight season from *Potentilla hippiana.* Host and nectar plants are distributed throughout the site, though often patchily. In 1983 we measured 5 x 5 m quadrats at points 25 m apart along transects A through G. At the end of June, or beginning of July each year, except 1984, we counted all larval host plants and adult nectar sources in each quadrat.

Movement of female butterflies

During the flight season of 1986 individual females were marked and followed by a team of two researchers, one recording behavioral events with a hand-held Radioshack TRS-80 computer, and the other marking landing points with numbered flags. Female behavior was classified into five categories: flying, being chased by a male, nectaring, ovipositing and resting. We recorded the duration of each behavioral event and followed a female until it was lost, or until the weather conditions became unfavorable for flight. After the observations were discontinued for each female, we measured the distances and directions between the consecutive landing points. The paths of animals can be approximated by a connected series of straight lines characterized by the two parameters: move length and turning angle (Kareiva and Shigesada 1983).

In 1986, the year we followed females, larval host plants were extremely patchy, with almost all plants located in one patch (Fig. 2). To quantify the effect of host plants on female movements we followed females released in two areas: within the host patch, and outside the patch in the area where there were no host plants. Three butterflies were followed from a hostless area to a host patch; the turning angle that included the crossing was omitted because it is not clear whether it should be grouped with those inside or outside a host patch. The rest of the butterflies did not cross between low-host and high-host areas. While following females, we recorded their encounters with males. This allowed us to measure the effect of encounters with males on female movement.

A qualitative model relating individual movement to population distribution

Since random walk models and the associated diffusion equations have proved to be a valuable tool in representing animal movement (Levin 1981; Okubo 1980; Kareiva 1983), we used this theoretical framework to relate the movement patterns of female butterflies to their spatial distribution. The diffusion equation specifies how the spatial distributions of animals changes with time as a result of movement. The parameter of the diffusion equation, called the diffusion coefficient or D, measures the rate of random dispersal. High diffusion coefficient implies a high movement rate within, and high emigration rate out of a unit of area. Thus, we expect to find few butterflies in the areas where D is high, and conversely, many butterflies in the areas where their movement is characterized by a low diffusion coefficient (Skellam 1973).

The diffusion coefficient D can be estimated empirically. The most commonly used method consists of point-releasing a number of insects and then measuring their positions at later censuses (Dobzhansky and Wright 1943; Kareiva 1982). In this case the diffusion coefficient is related to the squared displacements by the following formula (Okubo 1980):

$$D = R^2(t)/4t \qquad (1)$$

where $R^2(t)$ is the average squared displacement of individuals from the release point at time t. The same formula can be used if individual insects are followed from some starting point, and their successive displacements from that point are measured, as we have done. However, we are primarily interested not in measuring D *per se*, but in understanding how host plants and males affect D. The link between movement parameters of individuals and the diffusion coefficient is provided by the correlated random walk model of Kareiva and Shigesada (1983). They show that the expected net squared displacement after n moves is given by the following formula:

$$E(R^2{}_n) = n\,E(\ell^2) + 2\,n\,E(\ell)^2\,c/(1-c). \tag{2}$$

where $E(\ell)$ is the expected value of move length, $E(\ell^2)$ the expected value of move length squared, and c is the expected value of the cosine of turning angle. This formula assumes that the distribution of turning angles is symmetric around 0, and that n is large. If animals are moving at fixed time intervals T, then the total time elapsed after n moves would be $t = nT$, and we could substitue (2) into (1):

$$D = \frac{E(\ell^2) + 2\,E(\ell)^2\,c/(1-c)}{4\,T} \tag{3}$$

Real butterflies do not fly at regular time intervals. However, since our aim here is not precise quantitative prediction, but rather a qualitative model relating the patterns of individual movement to the resulting spatial patterns at the population level, we can use the average move duration in place of T in (3) (Lovely and Dahlquist 1975). Note that all the quantities on the right side can be estimated from the empirically derived distributions of move lenghts, move durations, and turning angles. Thus from the female movement data we can estimate the diffusion coefficients and, more importantly, how D should vary with host plant and male density. Knowing how D is influenced by host plants and males will, in turn, elucidate the effect of these factors on female spatial distribution.

Statistical analysis

The diffusion coefficient provides a very useful summary statistic with which to measure the effect of ecological variables affecting dispersal, such as host plant and male distributions. To estimate the precision of the estimate of D (i.e. its variance), we utilized a nonparametric resampling technique known as the bootstrap (Efron 1979). Since both the variation in move distances and turning angles within each female, and the variation in movement parameters among females contribute to the variance of D, we bootstrapped our data in the following way. First, we sampled with replacement our data set of 27 female paths. This means that some paths may have been drawn more than once, while others were not drawn. When we had 27 sample paths, we again sampled move distances and turning angles with replacement within each path. Finally, we calculated D from these "pseudodata". The entire process was repeated 1000 times (each time selecting a different set of sample paths with different sets of sample moves), yielding 1000 bootstrap values of the diffusion coefficient. The estimate of the variance of D is the sample variance of the D values generated by the bootstrap (for the explanation of the bootstrap method see Diaconis and Efron 1983).

Is female movement outside host patches directional?

The qualitative model described above assumes that female movement is not oriented, i.e. that the direction of any displacement between two consecutive landing points does not depend on the absolute compass direction, but only on the direction of the previous move. In particular, we assume that females travelling through a hostless area do not bias their movement towards the host patch, and that females do not have a preferred direction. If this assumption is violated, then our model of correlated random walk is inappropriate, and one should rather use a model of random walk with external bias.

Recently, Marsh and Jones (1988) have developed a test procedure for using track data to distinguish between the models of biased random walk and of correlated random walk. They showed that if movement is biased, then a certain quantity that depends on the average cosines and sines of move directions and turning angles (called Δ by Marsh and Jones) is positive. Conversely, if movement is unbiased, then the statistic Δ is negative. We calculated the value of this statistic for females moving outside the host patch and used the test described in Marsh and Jones (1988) to distinguish between the hypotheses of biased vs unbiased movement. In this analysis we used only those moves during which females were not harassed by males.

Results

Nectar and larval host plant distribution

The distribution of females did not significantly correlate with the distribution of nectar plants (1983, $r = 0.03$; 1985, $r = 0.06$; 1986, $r = -0.02$).

The distribution of larval host plants changed dramatically from 1983 to 1986. In 1983 the plants were distributed relatively evenly throughout the study area, as evidenced by the comparatively low coefficient of dispersion, or the variance to mean ratio (Table 1). In 1985 the distribution was more clumped, but part of this increase in CD is due to a higher mean density. In 1986 plants were extremely patchy: although the mean density was the same as in 1983, the CD was almost eight times higher. The coefficient of dispersion is sensitive to changes in density (Reed 1983) so that a better indicator of patchiness may be the percentage of our sampling quadrats that did not have any host plants. In 1983 and 1985 host plants were absent from only 8% and 4% of quadrats, respectively, while in 1986 fully 64% of quadrats were empty of host plants (Fig. 2).

In 1983 and 1985 the distribution of females was not affected by the distribution of host plants (Table 2). In 1986, however, there was a highly significant relationship between the densities of females and plants (Table 2). There were two or three times as many females on the average within the host patch as outside it.

Distribution of males in relation to females

In 1983, 1984 and 1985, as opposed to 1986, the association between males and females was very weak. In 1983 and 1984 the density of males did not regress significantly on that of females (Table 3). In 1985 the regression was significant only on one date, but even for that date the proportion of variance explained by regression, R^2, was very low (Table 3). In 1986, on the other hand, the proportion of vari-

Table 1. Coefficient of dispersion of the distribution of larval plants

Year	Mean	Variance	Jacknife estimates V/m	SE of V/m
1983	7.78	61.42	8.0	1.1
1985	23.61	507.53	21.6	2.4
1986	7.33	379.52	54.0	13.7

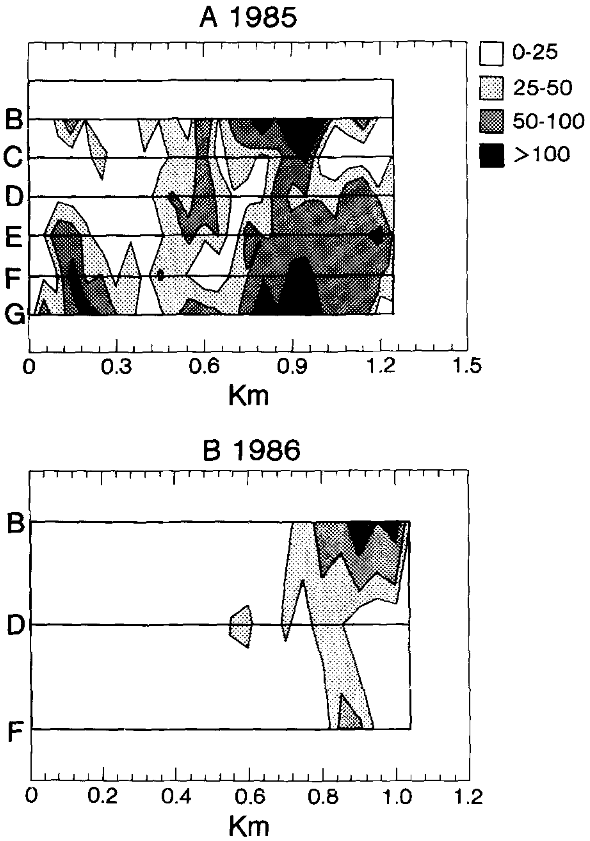

Fig. 2A, B. The distribution of host plants in 1985 and in 1986

Table 2. Regression of female density on host-plant density (numbers per 25 m of transect)

Date	df	F-value	Prob	Corr coeff
1983				
12 July	1,175	1.12	NS	−0.075
1985				
20 June	1,292	0.00	NS	0.001
1986				
19 June	1,115	11.86	<0.001	0.306

ance in male density explained by the presence of females was much higher (Table 3).

Analysis of female movement

Move distances. The distance traveled during a move increased several fold if the female was chased by at least one male (Fig. 3 and Table 4). There was also a strong effect of plant density on moves uninterrupted by chases: within high density areas moves were much shorter than outside (Table 4).

Table 3. Regression of male on female density (numbers per 25 m of transect)

Date	df	F-value	Prob	R^2
1983				
12 July	1,199	3.34	NS	0.02
1984				
15 July	1,175	1.82	NS	0.01
1985				
19 June	1,298	1.46	NS	0.01
20 June	1,298	21.71	<0.001	0.07
21 June	1,298	2.25	NS	0.01
1986				
19 June	1,115	52.33	<0.001	0.31

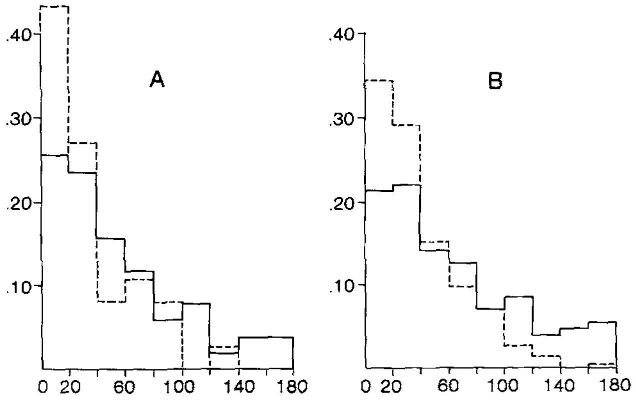

Fig. 3A, B. The distribution of move distances in **A**. Areas of high plant density and **B**. Areas of low plant density. Dotted lines represent moves that contained chases and solid lines represent moves without chases

Turning angles. The distribution of turning angles was symmetrical around 0, i.e. females did not preferentially turn to the left or to the right. Therefore we consider only the absolute value of the turning angle.

While the incidence of male chases had a weak and statistically insignificant effect on the mean turning angle (Table 4), plant density strongly affected the distribution of turning angles (Table 4, Fig. 4). In areas of low plant density females tended to follow highly directional paths. They reversed their direction very rarely, since almost all turning angles are less than 90 degrees. In areas of high plant density females followed much more "erratic" paths, and reversed their direction half as often as they preserved it.

Comparison between the hypotheses of biased and unbiased movement. The value of Δ-statistic based on the movement data of females flying outside the host patch without male interference was −0.43. This value lies outside the 99% confidence interval calculated under the assumption that

Table 4.

	Low density	High density
	Move Length: means ± SE (sample size)	
CHASES	16.50 ± 2.53 (37)	12.60 ± 1.78 (51)
NONCHASES	6.67 ± 0.75 (224)	2.66 ± 0.25 (258)
	Turn Angle: means ± SE (sample size)	
CHASES	31.62 ± 5.15 (37)	51.47 ± 6.43 (51)
NONCHASES	35.47 ± 2.06 (224)	58.37 ± 3.01 (254)

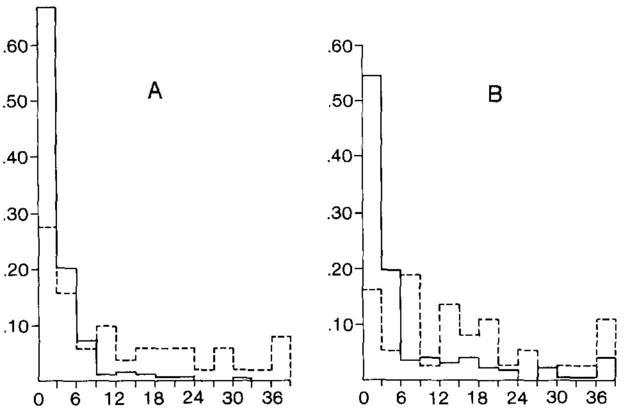

Fig. 4 A, B. The distribution of flight angles in **A**. Flights that contained chases and in **B**. Flights that did not contain chases. Solid lines represent flight angles in areas of high plant density and dotted lines represent flight angles in areas of low plant density

Table 5. Scaled estimates of the diffusion coefficients. The estimates are expressed in the units of the diffusion coefficient for females moving within a host patch undisturbed by males. Confidence intervals are in square brackets

	No Chases	Chases
Outside Host Patch	13.2 [3.2, 40.1]	74.7 [18.4, 193.4]
Within the Host Patch	1 [0.3, 2.1]	19.1 [8.4, 35.7]

movement is oriented, [0.00, 0.16]. The confidence interval calculated by assuming unoriented movement, on the other hand, was [−0.46, −0.08], which includes the estimated Δ. We conclude that the observed pattern of female movement does not contradict our assumption that movement is unbiased.

The effect of plant density and chases by males on net displacement. One thousand values were generated to bootstrap the estimates of the diffusion coefficient, D. The estimate of the diffusion coefficient is the mean of bootstrap values. The confidence interval covers 95% of bootstrapped values. Note that the confidence interval is not symmetric around the estimate, due to the skewness in the distribution of the bootstrap values (Table 5).

Discussion

The rate of female movement, as measured by the diffusion coefficient, is much higher in no hosts areas compared to areas with many hosts. This is not surprising considering female dependency on this resource (e.g. Ehrlich and Murphy 1981; Murphy et al. 1984; Singer 1982). Thus, in the absence of other factors one should see a several-fold increase in female density from areas without host plants to areas with many host plants. However, male harassment also affects female movement. By aggregating in areas of high female density males would induce females to leave, thereby eroding the correlation between females and host plants. Diffusion coefficients for females within host patches increases almost 20-fold in the presence of male harassment. In the limiting case when male density is so high that females are chased every move, the density of females within such high male density areas (see Odendaal et al. 1988), will be one-twentieth of female density in an area where there are no males (but host plant density still high). Areas as high as this theoretical limiting case may sometimes exist on the site at the height of the season when males tend to chase virtually any flying object vaguely the size of a *Euphydryas* butterfly, including other males, to the extent that males sometimes are "trapped" by their own indiscriminate and persistent chasing in male aggregations (Odendaal et al. 1988, 1989).

Our results may help explain the change in the correlation between females, males and plants from 1983/1985 to 1986. In years when plants are widely scattered over the site like in 1983 and 1985, harassment by males in one patch simply induces females to move to another. The result would be that females would not tend to aggregate in any particular area. Females may find it easy to avoid males and still have sufficient access to host plants. In 1986, on the other hand, plants were concentrated in one locality. Under such circumstances, females will find it hard to avoid males entirely because there are no hosts outside the host patch. As a consequence males may be expected to build up in the patch. By anchoring the distribution of females, host patches would indirectly anchor the distribution of males, and we have detected a strong correlation between males and females.

Male harassment presumably inflicts several costs on already-mated females. Mated females deny males access to their genitalia by assuming a rejection posture in which they energetically flutter their wings and turn their abdomens out of reach (see Odendaal et al. 1989). These often lengthy rejections on the ground may inflict a time cost on females. In *Euphydryas*, as in other species with short breeding seasons (e.g. Rutowski 1978; Hayes 1981; Courtney and Duggan 1983), females may be severely limited by the availability of time for host plant search and oviposition (Ehrlich and Murphy 1983; Kingsolver 1983a, b; Cappuccino and Kareiva 1985). Female *Euphydryas* need considerable time to locate and discriminate between host plants, and to lay their large egg batches (Singer 1982). In California, Singer and Ehrlich (1979) showed that only the offspring of the first egg batches have time to reach diapause in *E. editha* before host plants senesce. On our high altitude plain in Colorado, time for locating and choosing plants may be especially limited for *E. anicia* because of lower temperatures and the frequently bad mountain weather (Odendaal et al. 1989). Apart from possible time costs incurred through rejection behavior on the ground, the male harassment effect on flight distance and direction may presumably also influence searching behavior and female fitness (cf. Jones 1977).

Acknowledgments. Dale Roberts, Kristina Jones, Judy Anderson, Denise Stevenson and Dale Gardner assisted in the field. Mark Rausher supplied the hand-held computers. This research was supported by National Science Foundation Grant BSR-8506064. P. Turchin was supported by NSF Grant BSR-8605303.

References

Brussard PF, Ehrlich PR, Singer MC (1974) Adult movements and population structure in *Euphydryas editha.* Evolution 28:408–415

Cappuccino N, Kareiva P (1985) Coping with capricious environment: a population study of the rare woodland butterfly *Pieris virginiensis.* Ecology 66:152–161

Courtney SP, Duggan AE (1983) The biology of the orange tip butterfly *Anthocaris cardamines* in Britain. Ecol Entomol 8:271–281

Cullenward MJ, Ehrlich PR, White RR, Holdren CE (1979) The ecology and population genetics of an alpine checkerspot butterfly, *Euphydryas anicia,* Oecologia 38:1–12

Diaconis P, Efron B (1983) Computer-intensive methods in statistics. Sci Am 248:116–131

Dobzhansky T, Wright S (1943) Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura.* Genetics 28:304–340

Efron B (1982) The jacknife, the bootstrap and other resampling plans. SIAM Monograph No. 38

Ehrlich PR, Murphy DD (1981) The population biology of the checkerspot butterflies (*Euphydryas*). Biol Zentralbl 100:613–629

Ehrlich PR, White RR, Singer MC, McKechnie SW, Gilbert LE (1975) Checkerspot butterflies: a historical perspective. Science 176:221–298

Ferris CD, Brown FM (1981) Butterflies of the Rocky Mountain States. University of Oklahoma Press, Norman, Oklahoma, pp 331–332

Hayes JL (1981) The population ecology of a natural population of the pierid butterfly *Colias alexandria.* Oecologia 49:188–200

Iwasa Y, Odendaal FJ, Murphy DD, Ehrlich PR, Launer AL (1983) Emergence patterns in male butterflies: a hypothesis and a test. Theor Pop Biol 23:363–379

Jones R (1977) Movement patterns and egg distribution in cabbage butterflies. J Anim Ecol 46:195–212

Kareiva PM (1982) Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. Ecol Monogr 52:261–282

Kareiva PM (1983) Local movement in herbivorous insects: applying a passive diffucion model to mark-recapture field experiments. Oecologia 57:322–327

Kareiva PM, Shigesada N (1983) Analyzing insect movement as a correlated random walk. Oecologia 56:234–238

Kingsolver JG (1983a) Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. Ecology 64:534–545

Kingsolver JG (1983b) Ecological significance of flight activity in *Colias* butterflies: implications for reproductive strategy and population structure. Ecology 64:546–551

Levin SA (1981) The role of theoreticalecology in the description and understanding of populations in heterogeneous environements. Am Zool 21:865–875

Lovely PS, Dahlquist FW (1975) Statistical measures of bacterial motility and chemotaxis. J Theor Biol 50:477–496

Marsh LM, Jones RE (1988) The form and consequences of random walk movement models. (in press)

Murphy DD, Menninger MS, Ehrlich PR (1984) Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona.* Oecologia 62:269–271

Odendaal FJ, Iwasa Y, Ehrlich PR (1985) Duration of female availability and its effect on butterfly mating systems. Am Nat 125:673–678

Odendaal FJ, Turchin P, Stermitz FR (1988) An incidental-effect hypothesis explaining aggregation of males in a population of *Euphydryas anicia.* Am Nat 132:735–749

Odendaal FJ, Jones KN, Stermitz FR (1989) Mating behavior and male investment in *Euphydryas anicia* (Lepidoptera: Nymphalidae). J Res Lep (in press)

Okubo A (1980) Diffusion and Ecological Problems: Mathematical Problems. Springer, Heidelberg Berlin New York

Rausher MD (1985) Variability for host preference in insect populations: mechanistic and evolutionary models. J Insect Physiol 31(11):873–889

Reed WJ (1983) Confidence estimation of ecological aggregation indices based on counts – a robust procedure. Biometrics 39:987–998

Rutowski RL (1978) The form and function of ascending flights in *Colias* butterflies. Behav Ecol Sociobiol 3:163–172

Shields O (1967) Hilltopping. J Res Lep 6:69–178

Singer MC (1972) Complex components of habitat suitability within a butterfly colony. Science 173:75–77

Singer MC (1982) Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha.* Oecologia 52:224–229

Singer MC, Ehrlich PR (1979) Population dynamics of the checkerspot butterfly *Euphydryas editha.* Fortschr Zool 25:53–60

Skellam JG (1973) The formulation and interpretation of mathematical models of diffusionary processes in population biology. In: Bartlett MS, Hiorns RW (eds) The mathematical theory of the dynamics of biological populations. Academic Press, New York, pp 63–85

White RR (1979) Foodplant of alpine *Euphydryas anicia* (Nymphalidae). J Lep Soc 33:170–173

Received May 26, 1988