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Dispersal and gene flow in a butterfly with home range behavior: *Heliconius erato* (Lepidoptera: Nymphalidae)

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Summary. *Heliconius* butterflies have been found to have low rates of dispersal in previous mark-recapture studies, and this lack of movement is due home-range behavior. An experiment on *Heliconius erato* was designed to investigate movement from the site of pupal eclosion. It was found that most of the movement occurs before the first capture of an individual in a mark-recapture study. After incorporating this early movement, the dispersal parameter, σ, is estimated to be at least 296 m ($\pm$30 m jackknifed standard error), and the "neighborhood population size", N, is about 50–150 individuals. These estimates of σ and N are more than 2 and 5 times larger, respectively, than estimates based on standard mark-recapture data, though they are small compared with estimates from other butterfly species. Severe limitations of using dispersal experiments to estimate gene flow and neighborhood size are discussed. Genetic data from color pattern loci in hybrid zones and from electrophoresis suggest that, if anything, the estimates of σ and N that I have obtained are still too low. Genetic and dispersal data together show that kin selection is an unlikely mechanism for the evolution of warning color and other supposed altruisms in *Heliconius*, unless occasional genetic drift is also involved.

Ever since Fisher (1930) put forward his "fundamental theorem of natural selection" and Wright published what he later called the "shifting balance" theory (Wright 1931, 1978), there has been a split between two camps of evolutionary biologists. If gene flow rates are high, evolution will be dominated by natural selection as in Fisher's model; if gene flow is low, continuous populations become split into smaller "neighborhoods" or "demes" (Wright 1969) in which genetic drift is more likely. Disagreements about natural levels of gene flow are involved in many of the major arguments in evolutionary biology: allopatric vs. semigeographic speciation (Ehlrich and Raven 1969; Endler 1977; Carson and Templeton 1984; Barton and Charlesworth 1984); neutrality vs. selection in protein evolution (Lewontin 1974); and recently in theories of the selective maintenance of sex (Shields 1982). Estimates of gene flow should be particularly useful for understanding clines: Endler (1977) and Barton and Hewitt (1981) used measures of dispersal to analyse processes in clines and hybrid zones but came to differing conclusions as to whether divergence of the hybridizing taxa occurred during a past period of isolation. Many of these controversies can be traced to inadequate knowledge of natural gene flow.

Although dispersal and gene flow have never previously been measured in *Heliconius*, mark-recapture studies have shown low rates of movement. Individuals return daily to sites for adult and larval hostplants (Turner 1971a; Ehrlich and Gilbert 1973; Cook et al. 1976; Mallet and Jackson 1980), and nightly to sites of gregarious roosting (Turner 1971a; Brown 1981; Waller and Gilbert 1982). These home ranges are almost certainly learned rather than imposed by the environment because individuals that consistently roost together at night often have consistently different diurnal home ranges (Mallet 1984). This site fidelity suggested that adult *Heliconius* might live in family groups, and has led to a spate of theories that invoke kin selection in the evolution of apparent altruisms in *Heliconius* such as unpalatability (Benson 1971; Turner 1971b), warning color patterns (Turner 1971b) and food-sharing behavior (Gilbert 1977). These speculations have been widely cited in reviews (e.g. Edmunds 1974; Wilson 1975; Harvey and Greenwood 1978; Brown 1981; Hiam 1982; Harvey et al. 1982), sometimes without the reservations of their original authors.

The hidden assumption in these ideas is that the lack of movement measured during mark-recapture surveys reflects an absence of gene flow. However, newly eclosed *Heliconius* adults might disperse before they find and learn the resources used by their parents, and this movement could have been missed in previous studies. Juvenile dispersal is well known in vertebrates with learned home ranges, such as reptiles (Kerster 1964), mammals and birds (Greenwood 1980). Prereproductive dispersal is also well known in adult insects, especially in females, and is called the "oogenesis-flight syndrome" (Johnson 1969). If *Heliconius* behave similarly, gene flow could have been underestimated.

With these possibilities in mind, I designed an experiment on *H. erato* (i) to investigate whether dispersal of newly eclosed butterflies could be an important component of the total dispersal, (ii) to measure the overall dispersal rate, (iii) to estimate the accuracy of this measure, (iv) to estimate the "neighborhood population size", and (v) to use these results to find out whether population-level kin selection could be important in the evolution of *Heliconius*.

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Materials and methods

The butterfly *Heliconius erato petiverana* Doubleday is a brightly colored, long-lived, low-density denizen of the Central American rainforest (Benson 1971; Smiley 1978). *Heliconius* are unpalatable to the jacamar *Galbula ruficauda*, an insectivorous bird that attacks butterflies in Costa Rica (P. Chai, pers. comm.), as well as to other neotropical vertebrates (Turner 1984). In February-December 1981, 10 species of *Heliconius*, including 522 individuals of *H. e. petiverana*, were studied by means of mark-recapture. The study site was a 1×2 km area of mixed primary lowland rainforest and second growth at Sirena, Parque Nacional Corcovado, Peninsula de Osa, Costa Rica (Gilbert 1984). When an individual was captured, its sex and forewing length, and the site and date were recorded. If the butterfly was unmarked, it was uniquely numbered with a black "Sharpie" pen on the underside of the forewing and released. If marked, the number was recorded before release.

In order to test for movement of newly-eclosed *H. erato*, I collected eggs (which in *H. erato* are laid singly) or larvae from hostplants (4 species of *Passiflora*, subgenus *Plectostemma*: see Mallet 1984). These individuals were reared singly under natural shade temperatures at the park headquarters to the pupal stage, using an excess of fresh hostplant of the *Passiflora* sp. on which they were originally found. In their last larval instars, caterpillars were placed singly on foodplant sprigs standing in water and covered with netting. The pupae were returned to and placed on their natal hostplant before eclosion. After wing expansion, but before complete wing hardening and flight, each adult was marked with a unique numerically coded set of dots using "Rotring" or "Sharpie" pens. The length of the forewing was measured to the nearest mm. These manipulations were possible without handling the butterfly, which was then periodically checked until its first flight, usually an hour or more after eclosion and marking. I followed this procedure to provide a reasonably large sample of pupae, which could not have been found in the wild because of predation, parasitism, larval wandering before pupation, and the cryptic coloring of pupae. By rearing eggs laid by wild females, I avoided the possibility of artificially selecting captive butterflies for reduced dispersal. Since the pupae were released exactly where they had been found as eggs, I avoided disturbing any group structure that may have existed before the manipulation. In this way 106 butterflies were released over the 10.5 month period, together with two individuals that were marked after eclosion from wild pupae, making a total of 108 individuals (50 males, 56 females and 2 of unrecorded sex) released. If, in the mark-recapture study, a released individual was recaptured, the dot-pattern was carefully noted and the individual was numbered and again released. A total of $n=49$ individuals (27 males and 22 females) of the released individuals were eventually recaptured, and are subsequently referred to as "pupal releases".

To determine the importance of movement by individuals released from the pupa, I systematically sampled control individuals that were captured as part of the standard mark-recapture program. For each pupal release that was recaptured I selected from the data the next wild-caught individual (hereafter "field capture") of the same sex that had been recaptured at least once. These field captures acted as pairwise controls for sex, date, weather conditions, and intensity of sampling, and were used to estimate home range movements.

For each individual, the distances, x, between release site and site of first capture, and between each sequential pair of captures were measured using a map of the study area prepared by L.E. Gilbert and coworkers. There was no evidence for a directional bias of movement, other than that caused by irregularities in the shape of the sample area (see Mallet 1984), so the mean axial movement can be assumed to have zero magnitude. The axial dispersal parameter σ can be estimated as $\sqrt{\sum x^2/2n}$ (Kerster 1964; Crumpacker and Williams 1973), being the standard deviation along any one axis of a two-dimensional dispersal distribution. To reduce bias and to obtain some idea of measurement accuracy I used the "jackknife" method to estimate σ and its standard error (Mosteller and Tukey 1977). The jackknife uses the internal consistency of the data to estimate standard errors. Since these could be inaccurate if used in t-tests because they come from markedly asymmetrical distributions of data (Mosteller and Tukey 1977), I instead used non-parametric procedures to compare movements between groups (Wilcoxon matched-paris signed-ranks tests, and Mann-Whitney U tests). The important use of the jackknife in this case is to gain an idea of the reliability of the estimate of σ with a small sample size. (A computer program for jackknifing dispersal is available from the author).

In *Heliconius* there is a post-eclosion refractory period lasting about 4 days, followed by a constant reproductive period that lasts for up to 6 months until death (Dunlap-Pianka et al. 1977; pers. obs.). I assume that an individual makes a dispersal movement from its natal hostplant with parameter σ_d during the refractory period, and that it subsequently settles into a home range and distributes eggs or sperm with parameter σ_h about the centre of the home range for the rest of its life. If σ_d and σ_h are independent in direction and magnitude, the total per-generation dispersal can be estimated as $\sigma_t^2 = \sigma_d^2 + \sigma_h^2$. Later in this paper I argue that dispersal from eclosion to first recapture is an (under) estimate of σ_d, and that standard mark-recapture procedures can give a good estimate of σ_h. The neighborhood size, or number of individuals within a circle of radius 2σ, is estimated as $N = 4\pi\sigma_t^2 d$ (Wright 1969), where d is the effective population density. The actual density in our study site varied between about 1.33 individuals per hectare in the central study area (Gilbert 1984; Gilbert et al. in prep.), and a minimum of about 0.5 individuals per hectare in the peripheral regions of the study area (Mallet unpublished).

Results

Movement of pupal releases compared with that of field captures

The data for first movement distances (between sites of release and of first capture for pupal releases, and between sites of first and second capture for field captures) are shown in Table 1. *H. erato* moved further from their pupal release site to their first site of capture ($\sigma = 266$ m; see Table 2) than did field-captured individuals between their first and second capture sites ($\sigma = 132$ m). Figure 1 shows the moves plotted on a map of the study site: clearly field captures would underestimate the genetic connectedness of different parts of the study site. These pupal release and field

Table 1. Winglengths and movement distances of *H. erato*

For each sex, matched pairs of pupal releases and field captures are shown in order of capture. For each individual, the winglength, *w*, is shown next to distance moved, *x*, between eclosion and site of first capture (for pupal releases) and between sites of capture and first recapture (for field captures). Dashes indicate missing winglength data

Males				Females			
Pupal releases		Field captures		Pupal releases		Field captures	
w (mm)	*x* (Dm)	*w* (mm)	*x* (Dm)	*w* (mm)	*x* (Dm)	*w* (mm)	*x* (Dm)
–	6	33	14	31	0	32	6
35	48	30	4	33	8	32	0
38	62	38	26	–	72	35	0
36	32	35	4	–	46	32	0
34	40	32	4	37	16	18	0
35	82	36	6	36	6	35	16
37	100	35	30	33	6	33	0
38	58	31	0	32	2	27	10
35	16	33	0	31	56	34	4
34	10	30	2	34	16	35	24
38	72	30	6	34	0	30	6
32	24	35	6	36	26	30	8
35	68	35	8	33	2	34	4
36	44	35	84	37	42	35	0
38	2	38	22	33	6	31	2
34	40	35	0	34	16	33	20
35	6	32	0	34	14	33	0
37	54	31	14	34	0	36	8
34	8	34	22	33	14	–	24
36	66	36	0	33	8	36	0
35	14	32	28	35	10	34	0
34	20	33	28	35	6	34	8
39	2	31	0				
36	50	–	40				
37	14	34	0				
34	2	35	18				
36	4	36	4				

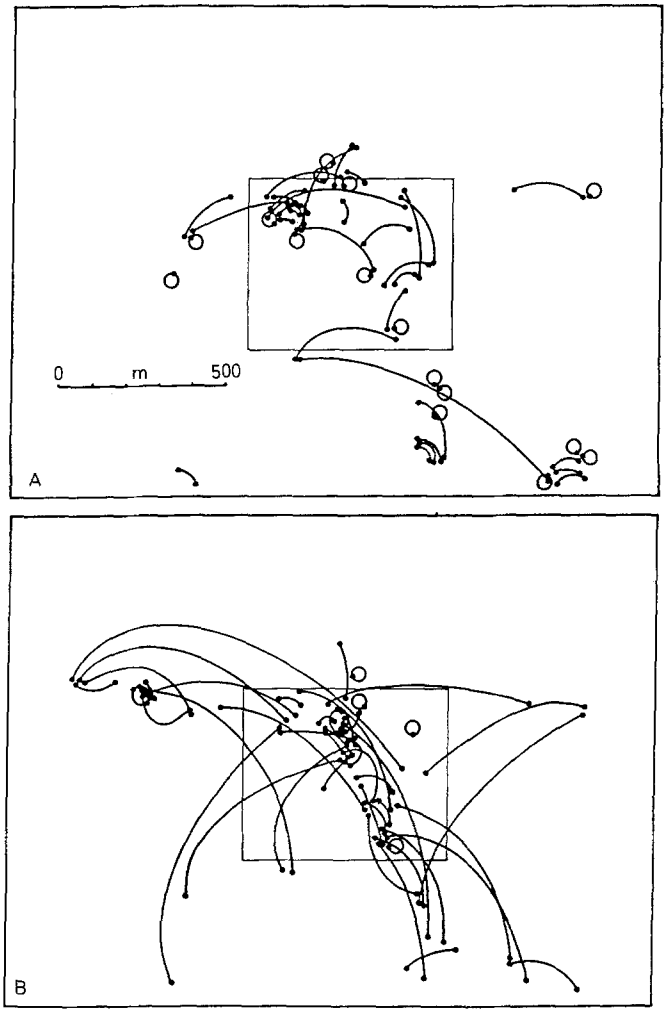

Fig. 1A, B. Movements of field-captured and pupal-released *H. erato*. **A** Movements of 49 field-captured *H. erato* between first and second capture within the Sirena study site. Movements are represented by lines connecting dots at the sites of capture. A circle connecting a dot to itself represents a recapture at the site of first capture. The central rectangle is the area within which Gilbert's (1984) mark-recapture study was performed. The scale is in m. **B** Movements of 49 pupal-released *H. erato* between eclosion and first capture. Symbols as above

capture movements are significantly different (Wilcoxon matched-pairs test, $P<0.001$). Jackknifed dispersal parameters, broken down by sex, of pupal released and field captured butterflies are shown in Table 2. Within pupal releases, males moved further than females (Mann-Whitney U test, $P=0.02$); within field captures, males again moved further, but this was not significant ($P=0.15$).

The greater dispersal of pupal releases could have resulted if reared individuals were more healthy than field individuals. In *Heliconius*, winglength is correlated with adult weight, and, in females, with egg production (Dunlap-Pianka 1979), and so is an indicator of health. The winglengths of pupal releases *H. erato* ($\bar{w}=35$ mm) were significantly greater than those of field captures ($\bar{w}=33$ mm; Mann-Whitney U test, $P<0.005$), almost certainly because of larval food limitation in the field (pers. obs.). Winglength was correlated with the movement distances of pupal releases (Spearman rank correlation, $r_s=0.379$, $P<0.01$), though not with movements of field captures ($r_s=0.205$, NS). Very little variation is explained by the least squares regression of movement distance on winglength (11%), taking the 44 pairs of field captured an pupal released butterflies for which complete data on winglength exists as 88 separate data points; the regression is also strongly influenced by a few points and the residuals have a skewed distribution. When the logarithm of the distance

Table 2. Jackknifed dispersal parameters, σ, with standard errors. (Using data from Table 1)

Pupal releases		Field captures	
Males (m)	Females (m)	Males (m)	Females (m)
318±39	186±41	166±47	72±14
Both sexes		Both sexes	
266±29[a]		131±33[b]	

[a] $\sigma=264$ m using standard estimator
[b] $\sigma=128$ m using standard estimator

moved (setting 0 m to 10 m, the smallest detectable distance) was regressed on winglength, the fit was only improved slightly, to 12% of the variation explained. A Wilcoxon matched-pairs test shows that the residuals of the distances from this regression are larger in pupal released than in field captured butterflies ($P<0.01$), showing that winglength cannot explain the dispersal differences between the groups. Winglength is such a feeble predictor of dispersal distance that it will be ignored in the rest of this analysis.

Dispersal can be increased by releasing a large number of butterflies in a small area (Dethier and Macarthur 1964); it was for this reason that I trickled eclosing butterflies into areas scattered throughout the study site during the 10.5 month period. Since 49 pupal releases were recaptured, compared with a total of 522 *H. erato* captured during the study period, the population augmentation was of the order of $49/522 \simeq 9\%$. It is probable that the butterflies' behavior would have been little altered by a population increase of this amount, which is of smaller order than natural population fluctuations (Gilbert 1984).

Measurement of overall dispersal and its accuracy

The sex ratio of captured wild butterflies was about 2♂:1♀ (Gilbert et al. in prep.), but the reared released butterflies (50:56) did not deviate significantly from 1:1. If behavior differences were causing the observed sex ratio in the field, this should be observed in a male-biased sex ratio of recaptured pupal-released *H. erato*. However the sex ratio of recaptured pupal releases was 27:22, not significantly different from the release ratio ($X_1^2=1.25$). The causes of the field sex ratio are therefore uncertain: reduced survival in females and/or adult behavior differences not detected with the small sample sizes in this study could have been important (see also Ehrlich et al. 1984). For the purposes of estimating dispersal, I have here assumed that the males and females disperse and contribute genes in proportion to their recapture frequency in the study, so that σ is calculated simply by using all individuals.

The dispersal rates of *H. erato*, broken down by the number of times individuals were recaptured, are shown in Table 3. The major advantage of the pupal release method is that σ_{0-1} (movement before capture) can be estimated: other movements (σ_{1-2}, σ_{2-3}, ..., i.e. movements between 1st and 2nd captures, 2nd and 3rd, &c) could be estimated either from field captures or from pupal release data; and it is gratifying that σ's that overlap between data sets in Table 3A and B are similar.

The jackknifed standard errors in Table 3 give an idea of the intrinsic accuracy of σ. These estimates and their standard errors of course assume that no individuals moved out of the study area, but the assumption is probably incorrect. Table 3A shows that the movements between sites of pupal release and first recapture (σ_{0-1}) are lower in individuals that are captured many times. It is therefore likely that σ_d for *all* individuals (including those never captured) is even greater than σ_{0-1} for individuals recaptured at least once. Individuals probably moved out of the study site even if they were captured: one pupal released individual moved 1,000 m between sites of release and first capture, and 820 m between sites of first and second capture, completely traversing the study site and showing that such long distance moves are possible. Thus the dispersal from the pupa, σ_d, is probably more than 266 m.

Table 3. Jackknifed σ between captures

A Pupal releases

Number of times captured	n	σ_{0-1} (m)	σ_{1-2} (m)	σ_{2-3} (m)
≧1	49	266±29[a]		
≧2	22	256±56	171±55	
≧3	11	194±69	100±15	103±18

[a] $\sigma_{0-1}=248\pm26$ m with single largest move (1,000 m) excluded

B Field captures

Number of times captured	n	σ_{0-1} (m)	σ_{1-2} (m)	σ_{2-3} (m)	σ_{3-4} (m)
≧1	–	?			
≧2	49	?	132±33[a]		
≧3	37	?	104±14	91±13	
≧4	18	?	84±15	87±13	86±19

[a] $\sigma_{1-2}=97\pm13$ m with single single largest move (840 m) excluded

Note: σ_{0-1}, σ_{1-2}, etc., represent dispersal parameters of movements of site of pupal eclosion to site of first capture, from site of first to site of second capture, etc

In order to estimate gene flow, I assume that individuals moving long distances mate and leave as many offspring as individuals making shorter moves. This is likely, because both dispersers and "remainders" are naive: they must learn unfamiliar environments in order to develop a home range. Wild caught *H. erato* that were transferred several km developed home range behavior in the new area (unpublished experiment in Colombia, 1977), and this was also true for dispersing pupal releases in the present study. Pupal released females were all mated (detected by the smell of the abdominal stink clubs, see Gilbert 1976) by the time they were recaptured; some of them were mated by males patrolling the hostplants just after eclosion, while I was watching them. In insectary populations of *H. erato* males perch on female pupae the day before eclosion and mate with them as they eclose (Gilbert 1976), and this "pupal-mating" behavior occurs in field populations of *H. hewitsoni* (Longino 1984). However, I did not see pupal-mating in my studies of *H. erato*, though I at first put pupae out immediately after pupation. The single wild female pupa of *H. erato* that I found before eclosion was not pupal-mated either. In conclusion there is no evidence that conditions in my experiment were different from the field situation or that dispersing individuals were unable to survive and reproduce.

The estimates of movement of field captured *H. erato* are rather stable around $\sigma=90$–100 m (especially if the single largest 840 m move is excluded: Table 3B). This estimate agrees approximately with previous work on home-range in *H. erato* (Turner 1971a; Smiley 1978), and is probably a good estimate of σ_h, the scattering of eggs and sperm in the home range.

It is complicated to estimate the overall dispersal, σ_t, because dispersal movements may continue after individuals have been captured for the first time (the single 840 m move by field-captured male is a probable example). It is

even possible that a fraction of all individuals never develop home-range behavior, and continue to disperse throughout their lives. A compromise will be to take σ_{0-1} (pupal releases) to estimate σ_d, the dispersal parameter, and σ_{1-2} (field captures) to estimate σ_h, the home-range scattering of eggs and sperm; so that the overall dispersal parameter is:

$\sigma_t \simeq \sqrt{266^2+132^2} \simeq 296$ m (± 30 m SE).

(Note: using the standard estimator instead of the jackknife, $\sigma_t = 293$ m, as reported in Mallet 1984, 1985.) σ_t will underestimate dispersal if individuals that move tend to leave the study site or if some dispersal movements are still found in σ_{1-2} (their home range σ_h^2 should be added).

Neighborhood size

The neighborhood deme size of *H. erato* can now be estimated as:

$N = 4\pi\sigma_t^2 d \sim 55$ if population density, $d = 0.00005$ m^{-2}
~ 147 if $d = 0.000133$ m^{-2}.

The effective densities of neighborhoods are often lower than the actual densities because of non-random contributions by individuals to future generations (Kerster 1964; Wright 1969; Crow and Kimura 1970), but here dispersal has probably been underestimated, so it is unknown whether these neighborhood estimates are too low or too high. However, the neighborhood size is more sensitive to underestimating σ than to overestimating d, because the former is incorporated as the square of the linear value.

Inbreeding statistics (F_{st}, the genetic correlation between two alleles taken at random from within a neighborhood relative to alleles taken at random from any neighborhood) can be interpolated for various numbers of neighborhoods using graphs supplied by Wright (1951). For *H. erato*, F_{st} of single neighborhoods relative to 100 million neighborhoods varies between 0.1 and 0.2. Relative to 100 local neighborhoods, F_{st} is between 0.04 and 0.02.

Discussion

In order to measure gene flow directly, the movements of individuals need to be studied, but dispersal may give an inflated impression of gene flow for three possible reasons. First, individuals that move long distances may not reproduce, both because the environment of distant sites is not as suitable for survival as nearby sites and because dispersal itself is more risky than staying put (Richardson 1970; Endler 1977; Shields 1982). Second, the life history of the dispersing individuals may be important: if individuals mostly reproduce early in dispersal, the gene flow will be less than that indicated by the distance of movement (Endler 1977, 1979). Third, large numbers of individuals are often released in dispersal experiments, perhaps leading to unnatural dispersal caused by crowding (Endler 1977). As a result, many workers feel that gene flow has been overestimated by dispersal studies (Ehrlich and Raven 1969; Levin and Kerster 1974; Endler 1977; Shields 1982).

On the other hand, dispersal experiments might easily underestimate gene flow, for a number of reasons. First, individuals often disappear in dispersal experiments, either because they die, or because they have moved beyond the edge of the study site. Those who measure dispersal assume that all disappearances from the study site die without reproducing, otherwise an "unbiased" measure would be impossible (Crumpacker and Williams 1973)! Secondly dispersal studies may severely underestimate gene flow if dispersal is episodic. This is the case in many species that colonize ephemeral habitats but remain within these habitats for a number of generations (Richardson 1970). Third, dispersal often declines with age; estimates of dispersal might easily be too low if a dispersal stage goes unnoticed, as shown by this study. Fourth, foreign individuals could be favored either in mate choice (Ehrman and Probber 1978), or because their descendants have reduced inbreeding depression (Richardson 1970; but see above for the reverse of this argument).

Calculations of effective neighborhoods size are even more problematic. First, they depend on all the ambiguities of dispersal measures outlined above. Second, they require estimating the frequency distribution of individuals' reproductive contributions to the next generation (Kerster 1964; Greenwood 1974; Begon 1977): This estimation is nearly impossible in the field and is only tenuously relevant if performed in the laboratory. Third, the available measures of neighborhood size (Wright 1969) assume a uniform spatial distribution of individuals, which is hardly ever likely (Felsenstein 1976). Fourth, even if all these problems were resolved, the estimate would only be valid in the measured population.

In spite of the possibility of enormous variability in neighborhood size, electrophoresis shows that there are large genetic differences between populations of plant and animal species that have low dispersal, and small genetic differences between populations of species that range more widely (Neveo 1978; Gottlieb 1981); taxa clearly do have characteristic neighborhood structures. The problem is just one of estimation: it may be nearly impossible to deduce the genetic structure of species by studying dispersal. Instead, it will probably be better to look at gene frequency data for measures of population structure, especially if methods become available that are relatively independent of selection (e.g. Slatkin 1981, 1985; Barton in prep.). Although the outlook is gloomy for absolute measurements of population structure, dispersal experiments can still be useful in making comparisons if the conditions of the experiments are carefully controlled. As a negative example of this kind of approach, it has recently been found that σ for *Drosophila* dispersal is heavily influenced by the geometry of the experimental arena: *post hoc* removal of trap-spacing differences from the data results in all the experiments producing similar results (Endler 1979, Taylor et al. 1984). Neighborhood size estimates can be used for similar comparative purposes, even though their absolute values are dubious.

In this experiment, I have attempted to minimize the factors that lead to overestimating gene flow. First, *H. erato* that disperse are likely to survive in their new home ranges over the distance scales I have measured. Second, *Heliconius* do not decline in fecundity over time (Dunlap-Pianka et al. 1977), and third, I have avoided crowding the butterflies into a release site by trickling them into the population over 10.5 months. I have probably underestimated dispersal because of the possibility that some butterflies dispersed out of the site. I have shown that movements from the pupa to the site of first capture need to be taken into ac-

count, and I have done so in this paper. The mating structure and fitnesses of dispersers vs. "remainders" are not known, which may reduce or increase gene flow as discussed above. My measures of neighborhood size will be underestimates if dispersal has itself been underestimated as I suspect, or overestimates if non-random contributions of offspring are more important. These problems can be sidestepped by making comparisons. My results show that ignoring dispersal from the pupa leads to a more than 2-fold underestimate of σ, which results in a more than 5-fold underestimate of neighborhood size. Nonetheless, my estimates of neighborhood size are lower than those measured for North American *Colias* species, a number of which have $N > 2{,}000$ (Watt et al. 1977, 1979).

The genetic correlation (F_{st}) between two alleles chosen at random within an *H. erato* deme relative to 100 local demes is 0.05 or less, according to the calculations made above. Although this estimate is unreliable, genetic evidence also backs a conclusion of low subdivision. First, electrophoretic allele frequencies vary little over the whole range of *H. erato*, and there is a high average heterozygosity within any one area (Turner et al. 1976). Second, color pattern allele frequencies change smoothly across hybrid zones between races of *H. erato*. Polymorphic populations within the zones are similar in allele frequencies to populations up to 5 km away, even though selection for warning color should fix the most common morph in any given neighborhood (Mallet 1985). Gene flow apparently obliterates the local differences in gene frequency that would build up if the species had highly structured, genetically independent populations. Nonetheless, *H. erato* is expected to have considerably more population structure than the monarch butterfly *Danaus plexippus*. An F_{st} of 0.004 was measured during the southward migration of this species in the United States (Eanes and Koehn 1979).

An important reason why σ may be underestimated in studies such as my own is that long range dispersal may be episodic. Many *Passiflora* species, the larval foodplants of *H. erato* and other *Heliconius*, germinate and grow only in disturbed areas such as treefalls, landslides, and streambanks (Mallet 1984). *Heliconius* depend on dispersal for their survival: if there were no dispersal to new lightgaps, these species could quickly go extinct as the habitats they occupied grew up into mature forest. During these colonization/extinction cycles, there must be many occasions when single, or a few mated females found new demes. These colonizations are likely to produce most of the long-term gene flow, and will not be noticed in short-term experiments such as mine. Paradoxically, the long-term neighborhood sizes of populations will be considerably lowered by this kind of dispersal, since the effective population size is the harmonic mean of the per-generation population sizes (Crow and Kimura 1970). The long-term effects of colonization and extinction are to increase σ, and, at the same time, to reduce N. This effect is likely to be important for many species (e.g. *Drosophila*, Richardson 1970) which depend on resources that are temporarily available in any given area.

It is difficult to imagine warning color evolving in a cryptic, but unpalatable prey, because a mutant warningly colored individual is by definition more obvious to predators than its conspecifics. Once a warning color somehow reaches a critical frequency in a population, predators learn the new pattern, which may then become fixed by individual selection. It is usually supposed that warning colors and unpalatability evolved deterministically in kin-structured populations (Fisher 1930; Harvey and Greenwood 1978). Unfortunately for this hypothesis, many aposematic butterflies such as *Danaus* (Urquhart 1960; Eanes and Koehn 1979; Calvert et al. 1979), ithomiines (Gilbert 1969; Brown and Benson 1974; Brown and Vasconcellos Neto 1976), and troidine swallowtails (Brown et al. 1981) are known to disperse widely. In contrast, *Heliconius* species seemed to have the low rates of dispersal required for kin selection (Benson 1971; Turner 1971b; Harvey and Greenwood 1978; Harvey et al. 1982). A recent model of the evolution of warning color has shown that a new color morph can increase deterministically (by "family" selection) provided that the number of prey families within each predator territory is low (Harvey et al. 1982). The values of all the parameters used in the model are not known for *H. erato*, but the low genetic correlation within neighborhoods suggests that the offspring of many different parents will be found within the same predator territory. Adjacent subsamples from sites within color pattern hybrid zones of *H. erato* and *H. melpomene* confirm this empirically (Mallet 1984, 1985). Novel warning colors of adult butterflies seem more likely to evolve during drastic reductions of N that accompany colonization of newly created habitat. Instead of reffering to this occasional, stochastic process as kin or group selection, following Wright (1978 and earlier), I call this process a "shifting balance" (Mallet 1984, 1985; see also Benson 1971 for a kin selection model which involves genetic drift).

Aside from the evolutionary implications of these data, it is clear that observations of movement during previous mark-recapture studies of *Heliconius* were inadequate for estimating gene flow because they ignored an important teneral dispersal stage. Some evidence from other butterflies support the idea that early movement is important (Scott 1973; Lederhouse 1983; Ehrlich et al. 1984; Gilbert in prep.). *Heliconius* (and probably a majority of other organisms) cannot be treated merely as diffusing gas molecules whose behavior is constant over time.

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References

Barton NH, Charlesworth B (1984) Genetic revolutions, founder effects, and speciation. Ann Rev Ecol Syst 15:133–164

Barton NH, Hewitt GM (1981) Hybrid zones and speciation. In: Atchley WR, Woodruff D (eds) Evolution and speciation. Essays in honour of MJD White. Cambridge Univ Press, Cambridge, pp 109–145

Begon M (1977) The effective size of a natural population of *Drosophila subobscura*. Heredity 38:13–18

Benson WW (1971) Evidence for the evolution of unpalatability through kin-selection in the Heliconiinae (Lepidoptera). Am Nat 105:213–226

Brown KS (1981) The biology of *Heliconius* and related genera. Ann Rev Entomol 26:427–456

Brown KS, Benson WW (1974) Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata*. Biotropica 6:205–228

Brown KS, Vasconcellos Neto J (1976) Predation of aposematic ithomiine butterflies by tanagers (*Pipraeida melanonota*). Biotropica 8:136–141

Brown KS, Damman AJ, Feeny P (1981) Troidine swallowtails in southeastern Brazil: natural history and foodplant relationships. J Res Lepid 19:199–226

Calvert WH, Hedrick LE, Brower LP (1979) Mortality of the monarch butterfly (*Danaus plexippus*) at five overwintering sites in Mexico. Science 204:847–851

Carson HL, Templeton AR (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. Ann Rev Ecol Syst 15:97–131

Cook LM, Thomason EW, Young AM (1976) Population structure, dynamics and dispersal of the tropical butterfly *Heliconius charitonius*. J Anim Ecol 45:851–863

Crow JF, Kimura M (1970) An introduction to population genetics theory. Burgess, Minneapolis

Crumpacker DW, Williams JS (1973) Density, dispersion, and population structure in *Drosophila pseudoobscura*. Ecol Monogr 43:499–538

Dethier VG, MacArthur RH (1964) A field's capacity to support a butterfly population. Nature 201:728–729

Dunlap-Pianka HL (1979) Ovarian dynamics in *Heliconius* butterflies: correlations among daily oviposition rates, egg weights, and quantitative aspects of oogenesis. J Insect Physiol 25:741–749

Dunlap-Pianka HL, Boggs CL, Gilbert LE (1977) Ovarian dynamics in heliconiine butterflies: programmed senescence versus eternal youth. Science 197:487–490

Eanes WF, Koehn RK (1979) An analysis of genetic structure in the monarch butterfly, *Danaus plexippus*. Evolution 32:784–797

Edmunds M (1974) Defence in animals. Longmans, Harlow, Essex, England

Ehrlich PR, Gilbert LE (1973) Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5:69–82

Ehrlich PR, Raven PH (1969) Differentiation of populations. Science 165:1228–1232

Ehrlich PR, Launer AE, Murphy DD (1984) Can sex ratio be defined or determined? The case of a population of checkerspot butterflies. Am Nat 124:527–539

Ehrman L, Probber J (1978) Rare *Drosophila* males: the mysterious matter of choice. Amer Sci 66:216–222

Endler JA (1977) Geographic variation, speciation, and clines. Princeton Univ Press, Princeton

Endler JA (1979) Gene flow and life history patterns. Genetics 93:263–284

Felsenstein J (1976) The theoretical population genetics of variable selection and migration. Ann Rev Genet 10:253–280

Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford

Gilbert LE (1969) Some aspects of the ecology and community structure of ithomid butterflies in Costa Rica. Research report, OTS advanced course. Ciudad Universitaria, Costa Rica, pp 68–92

Gilbert LE (1976) Postmating female odor in *Heliconius* butterflies: a male-contributed antiaphrodisiac? Science 193:419–420

Gilbert LE (1977) The role of insect plant coevolution in the organization of ecosystems. In: Labeyrie V (ed) Le comportement des insectes et les signaux issus du mileu trophique. CNRS, Paris, p 413

Gilbert LE (1984) The biology of butterfly communities. In: Vane-Wright RI, Ackery PR (eds) The biology of butterflies. Symp Roy Ent Soc Lond 11. Academic Press, London, pp 41–54

Gottlieb LD (1981) Electrophoretic evidence and plant populations. Progr Phytochem 7:1–46

Greenwood JJD (1974) Effective population numbers in the snail *Cepea nemoralis*. Evolution 28:513–526

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Harvey PH, Greenwood PJ (1978) Anti-predator defence strategies: some evolutionary problems. In: Krebs JR, Davies NB (eds) Behavioural Ecology. Blackwell, Oxford, pp 129–151

Harvey PH, Bull JJ, Pemberton M, Paxton RJ (1982) The evolution of aposematic coloration in distasteful prey: a family model. Am Nat 119:710–719

Hiam AW (1982) Airborne models and flying mimics. Nat Hist 91(4):42–49

Johnson CG (1969) Migration and dispersal of insects by flight. Methuen, London

Kerster HW (1964) Neighborhood size in the rusty lizard, *Sceloporus olivaceus*. Evolution 18:445–457

Lederhouse RC (1983) Population structure, residency and weather related mortality in the black swallowtail butterfly, *Papilio polyxenes*. Oecologia (Berlin) 59:307–311

Levin DA, Kerster HW (1974) Gene flow in seed plants. Evolutionary Biol 7:139–220

Lewontin RC (1974) The genetic basis of evolutionary change. Columbia Univ Press, NY

Longino JT (1984) Shoots, parasitoids, and ants as forces in the population dynamics of *Heliconius hewitsoni* in Costa Rica. PhD dissertation, Univ Texas, Austin

Mallet J (1984) Population structure and evolution of *Heliconius* butterflies. PhD dissertation, Univ Texas, Austin

Mallet J (1985) Hybrid zones of *Heliconius* butterflies in Panama and the stability and movement of warning color clines. Heredity (in press)

Mallet J, Jackson DA (1980) The ecology and social behaviour of the Neotropical butterfly *Heliconius xanthocles* Bates in Columbia. Zool J Linn Soc 70:1–13

Mosteller F, Tukey JW (1977) Data analysis and regression. Addison-Wesley, Reading, Mass.

Nevo E (1978) Genetic variation in natural populations: patterns and theory. Theoret Pop Biol 13:121–177

Richardson RH (1970) Models and analyses of dispersal patterns In: Kojima K (ed) Mathematical topics in population genetics. Springer, Berlin, Heidelberg, New York, pp 79–103

Scott JA (1973) Population biology and adult behavior of the circumpolar butterfly, *Parnassius phoebus*. Ent Scand 4:161–168

Shields WM (1982) Philopatry, inbreeding, and the evolution of sex. SUNY Press, Albany

Slatkin M (1981) Estimating levels of gene flow in natural populations. Genetics 99:323–335

Slatkin M (1985) Rare alleles as indicators of gene flow. Evolution 39:53–65

Smiley JT (1978) The hostplant ecology of *Heliconius* butterflies in northeastern Costa Rica. PhD dissertation, Univ Texas, Austin

Taylor CE, Powell JR, Kekic V, Jelkovic M, Burla H (1984) Dispersal rates of the *Drosophila obscura* group: implications for population structure. Evolution 38:1397–1401

Turner JRG (1971a) Experiments on the demography of tropical butterflies. II. Longevity and home-range behaviour in *Heliconius erato*. Biotropica 3:21–31

Turner JRG (1971 b) Studies of Müllerian mimicry and its evolution in burnet moths and heliconiine butterflies. In: Creed ER (ed) Ecological genetics and evolution. Blackwell, Oxford, pp 224–260

Turner JRG (1984) Mimicry: the palatability spectrum and its consequences. In: Vane-Wright RI, Ackery PR (eds) The biology of butterflies. Symp Roy Ent Soc Lond 11. Academic Press, London, pp 141–161

Turner JRG, Johnson MS, Eanes WF (1979) Contrasted modes of evolution in the same genome: allozymes and adaptive change in *Heliconius*. Proc Natl Acad Sci USA 76:1924–1928

Urquhart FA (1960) The monarch butterfly. Toronto

Waller DA, Gilbert LE (1982) Roost recruitment and resource utilization: observations on a *Heliconius charitonia* L. roost in Mexico (Nymphalidae). J Lepid Soc 36:178–184

Watt WB, Chew FS, Snyder LRG, Watt AG, Rothschild DE (1977) Population structure of pierid butterflies. I. Numbers and movements of some montane *Colias* species. Oecologia (Berlin) 27:1–22

Watt WB, Han D, Tabashnik BE (1979) Population structure of pierid butterflies. II. A "native" population of *Colias philodice eriphyle* in Colorado. Oecologia (Berlin) 44:44–52

Wilson EO (1975) Sociobiology: the new synthesis. Belknap, Cambridge, Mass.

Wright S (1931) Evolution in Mendelian populations. Genetics 10:97–159

Wright S (1951) The genetical structure of populations. Ann Eugen 15:323–354

Wright S (1969) Evolution and genetics of populations. Volume 2. The theory of gene frequencies. Univ Chicago Press, Chicago

Wright S (1978) Evolution and the genetics of populations. Volume 4. Variability between and among natural populations. Univ Chicago Press, Chicago

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