Gregarious caterpillars and evolution of mimicry in H. doris

SUMMARY

The known biology of H.doris is reviewed. Adult H. doris mimic a variety of other Heliconius. The species is often polymorphic for mimetic, and sometimes non-mimetic, patterns in any one area. Tests have shown that adult H. doris, like other Heliconius, are rather unpalatable to two species of birds, so the mimicry is presumably Mullerian. The polymorphisms of the different mimetic morphs in this species are apparently caused by a balance between directional selection for one morph and immigration from areas where other morphs are selected. The eggs are laid in large masses of between 80 and 800 on new growth of Passiflora spp. Eggs are sometimes laid cooperatively by a number of females. The larvae are gregarious, and when they are mature, they descend to pupate in a tight cluster near the base of their hostplant vine. Groups of between 40 and 1200 pupae have been reported.

We report the time course of mortality in three case-histories of H. doris young stages, in Corcovado National Park, Costa Rica. Mortality agents were Trichogrammatid egg parasites, Vespid wasps, ants, Chalcidid pupal parasites and disease. None of the smaller two groups of immature stages survived. A third, very large group of 1204 larvae pupated continuously over a period of at least three weeks. Initially survival was 80%, but it later dropped to 30% or less, because of an increase in the number of chalcidids, ants and disease. Marked newly-eclosed adults from this group of pupae were recaptured less frequently than adults captured and released in a standard mark-recapture programme. Higher dispersal rates of teneral adults probably caused this discrepancy. Many field-captured adults also disappeared, but a proportion showed home-range behaviour with residency times of up to 37 days in small subareas of the study site. A male-biased sex ratio from the pupae is reported, and the sexes differ in their larval development times. We suspect that a higher mortality of female larvae, which are exposed to predation for longer, results in the sex bias.

Our data on mortality shows that large groups of eggs, larvae and pupae in H. doris produce many survivors because they swamp

the small numbers of predators and parasites. We suggest that clustered egg-laying evolved in order to take advantage of this effecton mortality of the young stages. Other advantages of gregarious caterpillars do not seem likely for H. doris. In order to satiate predators with her own offspring, a newly-eclosed female might be expected to fly to a distant hostplant where parasites are not common, and away from her own birthsite where parasites will have increased in number. Similarly, males should search for virgin females in a distant area. This explains why H. doris shows a high dispersal rate and little home-range behaviour. H. doris and other cluster-laying Heliconius have less racial differentiation and poorer mimetic adaptation than Heliconius which lay single eggs. Lowered racial differentiation is an expected result of greater dispersal which is itself a result of selection for predator satiation by gregarious caterpillars. We conclude that the gregariousness of H. doris and other Heliconius evolved in order to satiate local predators and parasites. This evolutionary choice has caused the adults to be more dispersive, which has in turn wrecked the abilities of these species to adapt to local mimetic conditions.

GREGARIOUS CATERPILLARS AND EVOLUTION IN HELICONIUS DORIS

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Introduction

Gregarious behaviour of caterpillars occurs throughout the Lepidoptera. Gregariousness may allow larvae to breach various hostplant defenses or to benefit from group-enhanced predator discouragement. All life cycle stages can benefit from predator satiation. The genus *Heliconius*, a well-studied group of Neotropical butterflies, has species with caterpillars which are completely solitary and cannibalistic to species with extremely gregarious caterpillars. In this paper we describe the biology of *Heliconius doris*, the species with the most extreme larval grouping behaviour in the genus. Our data on the survival of gregarious pupae favour a predator satiation hypothesis of gregarious behaviour. *H.doris* has a dispersal rate greater than that of *Heliconius* that lay solitary eggs, and we here present reasons why gregariousness and dispersal should be associated. This association between life history traits has linked such disparate phenomena as the evolution of gregariousness and the evolution of mimicry in *Heliconius*.

Taxonomy, Biogeography and Mimicry

Heliconius doris is an aberrant member of its genus in larval, pupal and adult morphology (Beebe *et al*. 1960, Emsley 1965), and has been placed in its own subgenus, *Laparus*, by Turner (1968). Behaviourally, *H. doris* is similar to other *Heliconius* in its pollen-feeding (Mallet & Jackson 1980, Brown 1981), but is reported not to show the home-range behaviour found in other species (Benson 1971). We found the latter not to be entirely true (see below). *H. doris* occurs throughout the neotropics from Mexico to Brazil. Unlike some *Heliconius* such as *H. erato* and *H. melpomene*, adult *H. doris* are often polymorphic for colour-pattern in any one area and are poorly-differentiated racially (Emsley 1965, Brown *et al*. 1974). In those cases where population samples have been taken the most common morphs are mimetic, but rarer morphs are frequently non-mimetic (see appendix 1 for details). Little is known of the genetics of the polymorphisms because previous studies have assumed that a clutch of eggs or larvae was the offspring of a single mated pair (Sheppard 1963, Cook & Brower 1969), and it is now known that a single clutch of H. doris eggs can be laid by several females (Mallet & Jackson 1980). Sheppard's data and the data of Cook and Brower were at odds with respect to dominance relationships of colour pattern elements, perhaps for this reason.

Benson (1971) gave two pieces of evidence that indicate H. doris is what he called "ecologically palatable". First, some of the Silverbeak Tanagers in the experiments of Brower et al. (1963) repeatedly accepted H. doris. Second, the observed polymorphism in H. doris is expected if the species is palatable and a Batesian mimic. Batesian mimicry would tend to maintain a number of morphs by frequency-dependent selection, whereas if H. doris were a distasteful Mullerian mimic, directional selection in favour of the morph which mimics the most common comimic is expected. Although in the experiments of Brower et al. (1963) the birds attacked 29% of the H. doris offered, they rejected 62% of those they attacked. These same birds attacked and ate all of the palatable Euptychia butterflies offered as controls. It seems very unlikely that a bird, having attacked a palatable butterfly would then reject it on the basis of memory of unpalatable models as Benson (1971) seems to suggest. On the Osa peninsula, Costa Rica Chai-Peng (pers. comm.) recently tested the palatability of various butterflies to a female Jacamar (Galbula melanogenia). Chai found that after some hours without feeding, the Jacamar began to attack and eat Heliconius, although she always ignored Heliconius when there were palatable butterflies in the cage. When the bird began to attack Heliconius she sometimes swallowed them whole, and sometimes rejected them. Chai observed both behaviours with respect to H. doris. In one experiment an individual H. doris was attacked and rejected three times, while during the same run the bird had eaten other Heliconius, including H. erato, H. ismenius and H. hewitsoni, supposedly highly unpalatable species (Brower et al. 1963, Benson 1971). In our opinion, both Chai's experiments and those of Brower et al. (1963) show H. doris to be unpalatable. It follows that the various forms of H. doris are Mullerian mimics, though their mimicry may have a Batesian component if the comimics teach the birds to avoid a particular colour-pattern more often than does *H. doris* itself. Anyway, the geographic distribution of morphs suggests mimicry, whether it is viewed as Batesian or Mullerian (Appendix 1). But there are usually non-mimetic morphs, which could not be maintained by either type of mimicry, in any one area. We suggest in Appendix 1 that polymorphism in *H. doris* is chiefly maintained by a balance between directional selection for Mullerian mimicry and immigration.

Hostplants and Oviposition

The reported hostplants of *H. doris* are *Passiflora acuminata*, *P. riparia* and *P. praeacuta* in South America, *P. laurifolia* and *P. serrato-digitata* in Trinidad and *P. ambigua* in Central America (Benson *et al*.1976, Mallet & Jackson 1980). All of these are in the *Passiflora* subgenus *Granadilla*. In addition, we have strong circumstantial evidence that *H. doris* uses a species of subgenus *Astrophea*. In the forest islands of the southern Rupununi savannas, Guyana, we found a cluster of eclosing *H. doris* pupae under a loop in the trunk of a large vine of *P. (Astrophea) leptopoda*. The only other *Passiflora* nearby was *P. vespertilio* in the subgenus *Plectostemma*. Pupae are typically found close to or on the base of their larval hostplant (Cook & Brower 1969, and see below).

Females lay flat rafts of small, evenly-spaced eggs. They choose newly-expanding leaves several nodes back from an active shoot-tip, and several females may contribute eggs to the same egg mass. We have seen rafts of 200, 140, and 79 eggs on *P. praeacuta* in Colombia, *P. acuminata* in Guyana and *P. ambigua* in Costa Rica respectively. In the Colombian observation two females cooperatively oviposited in a single raft on a shoot of a very large plant (Mallet & Jackson 1980). The two subsequent observations were egg mass discoveries on smaller plants, both plants with less than 100 leaves. A mass of 800 eggs has been reported (Benson *et al*. 1976) and below we report a mass of 1204 pupae. These very large numbers of offspring certainly could not all have come from single females.

Behaviour of Immatures

The larvae are gregarious, feeding on both young and older leaves. The larvae are yellow with black heads and spines. Literature descriptions of larvae include black bands on the body (Beebe *et al.* 1960), but this trait appears to be variable. Bands did not appear until fifth instar in larvae reared from Guyana, and among batches of larvae descending from Costa Rican *P. ambigua* vines to pupate both banded and unbanded larvae occurred.

H. doris pupate gregariously. Groups of larvae descend on major stems of the plant on which they are feeding. Near ground level or at the bottom of a loop where the stem ascends in both directions, the larvae form a compact linear group on the underside of the vine. Also, groups of larvae sometimes move to the undersurfaces of nearby leaves or sticks. Each individual spins a silk pad; together they produce a solid mat of silk from which they hang and pupate. The pupae are tightly crowded together and touching, with no space between them. If there are sequential groups of larvae descending, larvae may intersperse themselves in among groups that have already pupated. We have seen the following group sizes and structures. In Guyana, a linear group of eclosing pupae were on the trunk of the hostplant at ground level. In Corcovado National Park, Osa Peninsula, Costa Rica, we have seen groups of pupae on or near three *P. ambigua* vines. 40 pupae and hanging larvae covered the undersurfaces of two adjacent leaves near the base of a small defoliated hostplant vine (basal dia. 1 cm). On the order of 50 empty pupal skins were in a linear mass at the nadir of a thick hostplant stem that was draped between two trees; the pupae were 5m above the ground. Finally a series of larval groups from a very large hostplant vine descended continually during a period of at least 20 days. They pupated on and around the base of the vine. A total of 1204 pupae and pupal skins were later collected, so this represents a minimum number of pupae originally present.

Generally, *H. doris* pupae lack spines, in marked contrast to all other known *Heliconius* pupae. The pupal description of Beebe _et al_. (1960) mentions collections of _H. doris_ pupae with spines, and Turner (1968), observing museum specimens, figures and discusses the curious presence or absence of spines in _H. doris_ pupae. Among the group of 1204 pupae at Corcovado, an individual was foundwith six pairs of spines on abdominal segments 2 to 8, the longest (on segments 3 and 4) being 3 mm long. This pupa was found by itself, well separated from the main group. All the other pupae were spineless. Possibly the close proximity of other individuals at pupation inhibits an ancestral spined condition.

Mortality

We observed three groups of _H. doris_ for which we obtained survivorship data. Since these events are rarely observed, we will describe each in detail and allude to them in the discussion. All data is from Sirena, Corcovado National Park, Osa Peninsula, Costa Rica. This is an area of mixed second-growth and primary lowland rainforest.

Case 1: We found a raft of 79 eggs on June 19, 1980. The raft was on a hostplant vine with less than 50 leaves in a forest treefall. There were no other hostplants in the treefall. Two days later there were 73 eggs and 6 first instar larvae. One of the eggs was blackened and later produced 5 female and 1 male _Trichogramma_ parasitoids (Chalcidoidea: Trichogrammatidae). On the following day there were 26 first instar larvae and a Vespid wasp was busily chewing one of these. The next day there were no larvae remaining.

Case 2: On February 9, 1981, 60 fourth instar larvae were feeding on a small trailside vine of less than 100 leaves (basal dia. 1 cm). Other hostplant vines were common in the vicinity. When checked again on February 14, the plant was stripped and we found hanging larvae and pupae beneath two leaves near the hostplant base. There were 22 larvae, 16 pupae, and the remaining cremasters from two pupae that had been eaten (the cremaster is the terminal part of the pupal skin which attaches the pupa to the silk pad).

One of the larvae had had its head bitten off, one of the pupae had been partially eaten near the base and a Vespid wasp was chewing one of the cremasters. There were 3 to five Chalcidid wasps flying in the area and one of these was seen ovipositing in a pupa. On February 17 there were 21 entire pupae and one carcase with a gaping hole in its side. Ants in the genus Crematogaster were chewing the carcase. On February 20, 11 entire pupae were left, and one pupa had a gaping hole in its side with many Crematogaster around the cremaster. By February 23 there was no trace of the pupae.

Case 3: The most extraordinary discovery was on February 8, 1981, hereafter referred to as day 1. The base of an immense hostplant vine and the surrounding leaves and sticks were coated with hundreds of H. doris pupae, and larvae continued to descend for a further 16 days. The vine had a basal diameter of 2.9 cm and the branches covered the crown of a large Inga tree. The vine appeared to be substantially defoliated.

On day 1 a single Chalcidid wasp was seen near the pupae. On day 3 there were more than 10 Chalcidids flying in the area and one was seen ovipositing in a pupa. A few individuals of Dolichoderus (Monacis) bispinosus, a large Dolichoderine ant, were chewing 6 or 7 pupae. By day 11 a yellow cloud of Chalcidids had accumulated. There were many D. bispinosus feasting among the pupae, and it was obvious that many pupae were dead and rotting. The mass stank and was attracting Drosophilids, Sarcophagids, and other flies. By day 16 there were no more larvae descending.

The pupae could be separated into 3 spatially and temporally distinguishable groups: those that had eclosed before day 1, those that were pupae on day 1, and those that pupated after day 1. Pupal skins and remains were collected after the main eclosion periods of the respective groups. The latter two groups contained 78 intact pupae of stragglers that had not eclosed before collection. These were isolated and their fates later recorded. The rest of the pupal remains were sorted into the following categories:

Eclosed: Pupae that successfully eclosed left thin papery shells, and the shed linings of the trachaeae stretched anteriorly from the spiracles.

Parasitoids: Chalcidid wasps left perfectly circular holes in an otherwise entire pupa.

Did not eclose: These pupae had ragged holes or, if the head and thorax region had fallen off, the remaining abdominal segments showed no trace of tracheal linings. A parasitized pupa which subsequently lost its top would be classified here.

Cremaster: When only the cremaster was left stuck in the silk mat nothing could be discerned other than that a pupa used to hang there.

The results are presented in Table 1. Overall survival to eclosion for the analysed pupal skins was 50.7% (n=1116). For most pupae the sex could be determined by characteristic folds in the terminal abdominal segments. The sexes did not significantly differ in either group classification or fate, and we have combined the sexes for the mortality data of Table 1.

In cases 1 and 2 the groups were too small and did not satiate the local predators. In case 3, a much larger group, the Chalcidids and other predators were satiated, but a predator numerical response caused higher and higher mortality for latecomers. The nature of the functional and numerical responses is complex and involves interactions between the different predators. In case 3 there were several puzzling features of the change in numbers of Chalcidids and ants. Dolichoderine ants are noted for their ability to lay pheromone trails and recruit rapidly to resources. Yet, in this case, their numbers built up rather slowly over many days: if they had been recruiting to the pupae directly they could presumably have finished off the entire brood in a couple of days. The number of adult Chalcidids also grew slowly during the observation period. The Chalcidids certainly had the potential for a rapid increase. 19 pupae from which Chalcidids emerged averaged 13.4 females and 3.2 males per pupa. In spite of this the incidence of parasitoid exit holes in the analysed pupal skins was low, 7.3%, and did not significantly increase through time. Our observations on other Heliconius pupae confirm Alexander's (1961) statement that live healthy pupae are not readily attacked by ants, but that once

Table 1: Mortality data for *H. doris* pupae

A. Pupal remains classified in situ after eclosion

Group	Sample Size	Eclosed %	Did not Eclose %	Chalcidids %	Cremaster %
eclosed before discovery	♂ 177 ♀ 123 ? 2	80.8	8.6	7.6	3.0
pupae during discovery	♂ 298 ♀ 231 ? 34	44.6	26.1	8.2	21.1
eclosed after discovery	♂ 105 ♀ 106 ? 40	28.3	61.0	4.8	6.0
totals	1116	50.7	29.2	7.3	12.8

B. Isolated entire pupae from the latter two groups of A

Sample Size	Eclosed %	Chalcidids %	Rotten %
♂ 36 ♀ 29 ? 13	25.6	51.3	23.1

C. Grand total observed: 1204 (includes 10 voucher specimens collected).

a pupa has a wound or is dead it becomes much more susceptible. Ants could inhibit the growth of the Chalcidid population by preferentially eating parasitized pupae and possibly by disturbing ovipositing females. Of the 78 pupae that were isolated from ant attack, a much higher proportion produced Chalcidids (51.3%) than in the last group in the field population (4.8%), though the proportion of butterflies eclosing from the pupae was similar in isolated and field pupae (25.6% v.s. 28.3%: see table 1 for details). These results indicate that parasitized pupae are more susceptible to ant attack which would cause them to enter the "did not eclose" and "cremaster" classes. Pathogens are another source of mortality that probably exhibits a numerical response: of the 78 isolated pupae 23.1% rotted, whereas the mortality of earlier eclosing pupae had been lower - a maximum of 11.6%.

In case 2, one or more Vespid wasps and Chalcidid wasps were the predators. The pupae were all killed, but, in addition, the Chalcidids were unsuccessful. Predator satiation may also benefit gregarious eggs. In case 1, a single egg out of 79 was parasitized by _Trichogramma_. Why this occurred raises intriguing questions about the biology of _Trichogramma_; the wasp was "satiated" after one _Heliconius_ egg. _H. hewitsoni_ also lays clutches of eggs, and JL (unpublished) has found a number of clutches of this species which contain single _Trichogramma_-parasitized eggs.

Dispersal

As part of a joint project with Lawrence E. Gilbert, Darlyne and Alex Murawski and Annie Simpson de Gamboa, we marked and released individuals of all species of _Heliconius_ in a 2 x 1.5 km study area in order to obtain data on population size, survival and mobility of these species. Marking _H. doris_ involved hand-netting the butterfly, hereafter referred to as "numbered" because we wrote an unique number on the undersurface of both forewings using a "Sharpie" indelible marker pen. We also marked newly-eclosed _H. doris_ from case 3, hereafter referred to as "dotted" because, in order to avoid damage to their still-fragile wings, we used a single dot as a mark. Subsequent captures were checked for the presence of these dots during "numbering". The site of each capture or recapture was also recorded.

Summary of Mortality Section

Suggestion for final paragraph of Mortality section

In conclusion, mortality trends in cases 1 - 3 show that the young stages of *H. doris* in some cases survived because they satiated predators, parasites and pathogens; while in other cases these agents completely destroyed batches of caterpillars and pupae. The slow build-up of pupal mortality over time in case 3 (table 1) shows satiation becoming less effective as mortality agents exhibited a numerical response to the pupae. At first satiation was very effective: over 80% of butterflies eclosed. But in spite of mortality increases, more than 25% of butterflies were still eclosing from the last batches to pupate, so predator satiation was still occurring in the face of a complicated numerical response of predators, parasitoids and pathogens.

Our data show that at least some "numbered" individuals are recaptured near their first site of capture up to two months later (Figure 1). We have often seen the same individual *H. doris* repeatedly visiting the same *Anguria* inflorescences for nectar and pollen over a period of several weeks, and some male *H. doris* repeatedly visited the pupae eclosing in case 3. On the other hand, Figure 1 also shows that many short-term recaptures (up to 15 days) have moved considerable distances and probably move thereafter out of our study area. Although *H. doris* appears to be capable of home-range behaviour a proportion of individuals disperse.

Newly-eclosed "dotted" adults seemed even more likely to disperse than mature "numbered" individuals. During February and March 1980, 15 "numbered" females were captured and 3 of these were later recaptured. A much lower proportion, only 4 of 70 females "dotted" at eclosion were recaptured, but the difference is not significant (χ^2_1=1.71). 34 out of 89 "numbered" males were recaptured whereas only 4 of 146 males "dotted" at eclosion were recaptured (χ^2_1=48.72, $P<0.0001$). The large number of "numbered" males that were subsequently recaptured is partly due to a swarm of males that repeatedly returned to the pupae of case 3 until all the pupae had eclosed. The difference in recapture rates between newly-eclosed "dotted" adults and those "numbered" in the mark-release programme is almost certainly due to higher dispersal rather than higher mortality of newly-eclosed adults: similar studies of other newly-eclosed *Heliconius* have given recapture (and therefore, minimal survival) rates of about 30% in both *H. hewitsoni* and *H. erato* (JL and JM unpublished). Of the 8 recaptures of *H. doris* "dotted" at eclosion, 6 almost certainly represent captures of individuals that were "dotted" within a few days before, as these were all recaptured within 100m of the eclosion site at the time other eclosions were still occurring. Of the other two recaptures, one was a male that had moved 630m and was twice recaptured at least 8 days after the last "dot" was put on an eclosing butterfly. The other was a female that was twice recaptured after only a short distance move of 140m, at least 33 days after the last mark could have been placed on it. So it seems that very few "dotted" individuals remained in the eclosion area after hardening their wings.

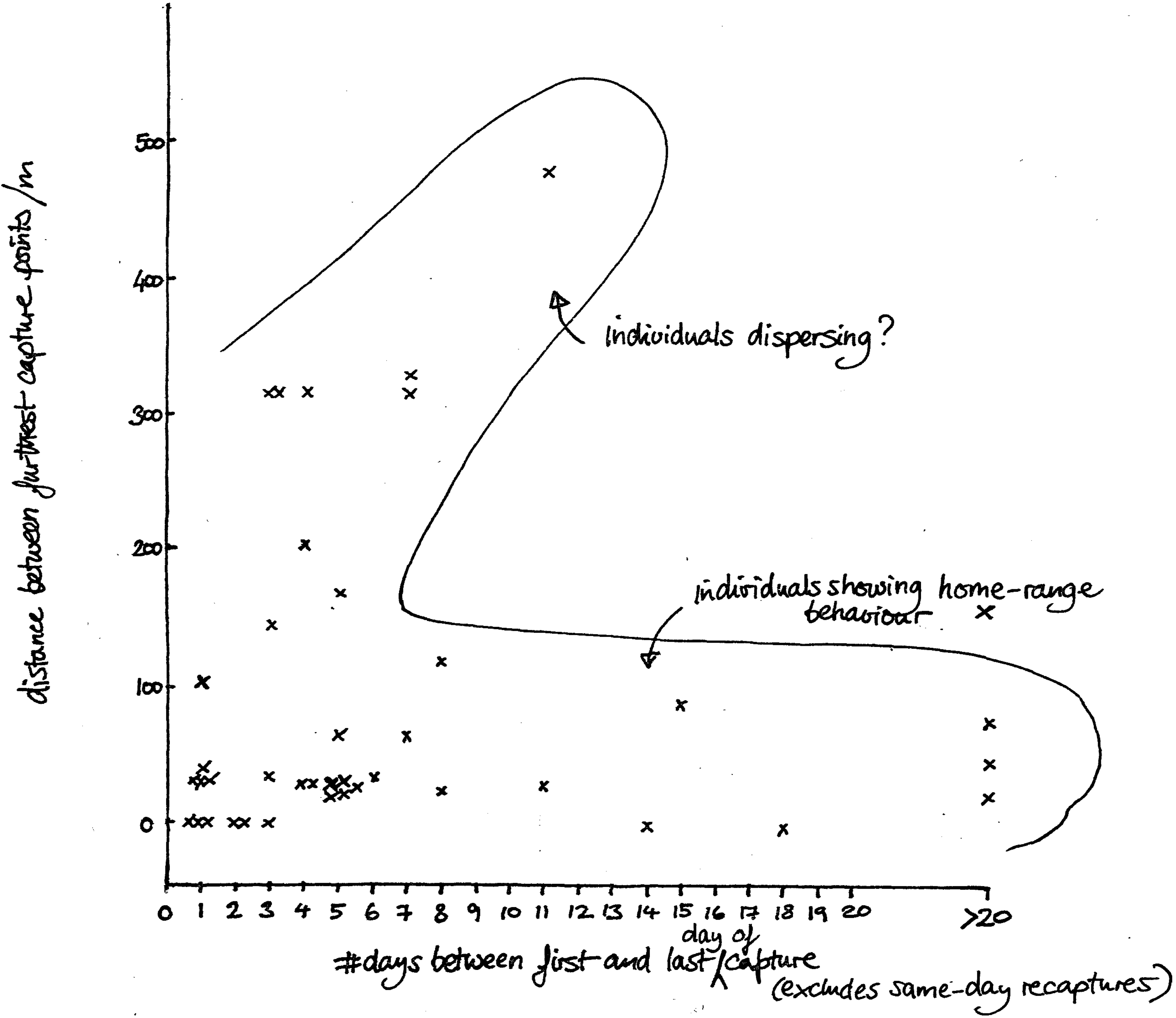

FIGURE 1: Home-range and dispersal behaviour in H. doris.

Sex Ratio

The ratio of males to females calculated from the pupal skins (Table 1) was 0.56±0.01 (binomial standard deviation). If male and female eggs are equally costly to produce, a 50:50 sex ratio is expected when the eggs are laid (Fisher 1930). If a 50:50 sex ratio and a binomial sample distribution are assumed, the probability of obtaining a sample as or more extreme than ours (male or female bias) is 0.00013. If all the pupae for which the sex could not be determined had been female, the probability increases to 0.0529. Male and female pupae did not significantly differ in group classification or mortality rate. Sheppard (1963) and Cook and Brower (1969) also had male biases of similar magnitude in their reared material. An interesting finding was that the number of males that we "dotted" was similar to the number of male pupal skins classified as eclosing, while the number of "dotted" females was only 54% of the corresponding pupal skins. On days that we did not watch the pupae large blocks of females must have eclosed to produce this discrepancy. These results could be explained if females required slightly different developmental times, perhaps longer to supply developing eggs. A male-biased pupal sex ratio would result from the longer time females were exposed to predation as larvae. Males and females from the same egg mass would diverge in time of eclosion. Although a chi-square test of independence between group classification and sex ratio was not significant, the earliest group had more males than expected, and the last group to eclose had more females than expected (see Table 1). Obviously there was some temporal separation of male and female eclosion times, which suggests different developmental rates.

Discussion

Why would a female *H. doris* lay eggs in clusters? Benson *et al*. (1976) suggested resource limitation: suitable shoots of very large *Passiflora* (*Granadilla*)vines are limiting in space and time. We do not agree with this hypothesis for two reasons: Firstly, *H. doris* does not necessarily require very large vines, and secondly, in none of the sites where we have found H. doris was its local hostplant particularly rare.

If a group of larvae can more easily penetrate and feed on tough leaves, then every individual would benefit. This is a very difficult phenomenon to demonstrate (Long 1953, 1955, Jordan 1981). When solitary larvae or small groups are shown to develop more slowly than large groups, it is difficult to determine whether this detriment is due to increased mechanical difficulty or disruption of endogenous feeding rhythms or other behaviours normally coordinated within a large group. Janzen (pers. comm.) has suggested that gregarious larvae can rapidly eat an entire leaf before localized defensive responses by the plant occur. If gregariousness in caterpillars has evolved as a way of dealing with leaf toughness and secondary compounds, then we might expect lepidopteran species with gregarious larvae to be present on plant species from which closely-related lepidopterans with solitary larvae are excluded. This does not seem to be true for Heliconius: many species of Passiflora particularly in South America, are fed on both by solitary and gregarious Heliconius species (Benson et al. 1976, Mallet and Jackson 1980). Analysis of the data of Benson et al.(1976) shows that 35 species of Passiflora are used by gregarious species of Heliconius, and of these only 8 species are not used by one or more Heliconius with solitary larvae. 7 of the latter Passiflora are rare species of the subgenus Astrophea; more detailed work would almost certainly show one or more Heliconius with solitary larvae feed on them. The eighth species, P. (Granadilla) riparia is almost certainly fed on by some melpomoneiform solitary Heliconius species, as are its close relatives. In Corcovado, new growth of the hostplant of H. doris, P. ambigua, is also fed on by H. pachinus, and possibly by H. ismenius, two species with solitary larvae. Other species of Passiflora at Corcovado are hostplants either for both gregarious and solitary species of Heliconius, or for solitary species of Heliconius only, or for no species of Heliconius. There are no species of Passiflora at Corcovado which are hosts only to gregarious species of Heliconius. It is possible that gregarious species eat up available new growth, and therefore need to move to older, tougher, less suitable leaves which only gregarious larvae can exploit well.

But this chicken-and-egg argument fails to explain the initial evolution of gregariousness, and anyway, Heliconiines that are habitual feeders on old leaves are rather poor in gregarious species (Benson et al. 1976, Brown 1981).

Other mechanisms favouring gregarious behaviour involve protection from natural enemies. Hamilton (1971) suggested that individuals benefit from grouping because of the cover that other group members provide. The behaviour of the predator was extremely simple: the predator appeared at random and took the nearest prey. With such a predator, grouping was favoured by individual selection even though average mortality might be higher for grouped prey. If such were the case, an adult female H. doris would not be expected to lay her eggs in clusters in the first place. Holling (1965) concentrated more on predator behaviour in his models of functional response. In the Holling model, various factors can contribute to changing the "attack threshold" of a predator for a particular prey. The change in the attack threshold can be increased by decreasing predator gut capacity; predators become satiated. The attack threshold can also be elevated by learning after encounters with noxious or distasteful prey. Both of these effects cause a deaccelerating functional response to increasing prey density. Predator satiation has been invoked to explain mast years in trees (Janzen 1971), and enhanced predator learning has been suggested to explain the clumping of aposematic eggs (Stamp 1980, Snyder and Snyder 1971) and the extreme gregariousness of adult Monarch butterflies. Brower et al. (1977) estimated that there were more than 14 million Monarchs at one of the over-wintering sites in Mexico, and the resultant enhancement of predator learning was proposed to favour gregariousness and the evolution of "automimicry", the mimicry of distasteful members of a population by palatable members of the same population (Tuskes and Brower 1978). Predator satiation is also an important factor, since some birds at the Mexico site have learned to eat non-toxic portions of Monarchs. These birds show no signs of being deterred (Calvert et al. 1979), but there are not enough birds to eat all the butterflies. A third way in which predator functional response can deaccelerate with increasing prey density is through enhanced prey defense at high prey density. Prey in a group may have improved sensory capabilities or enhanced fighting abilities (Tostawaryk 1972). The above mechanisms all favour gregariousness in terms of average mortality of solitary individuals, even though the probability of mortality is not the same for all members but depends heavily on position within the group.

Consider this simple model. The probability of being killed is the product of the probability of being discovered and the probability of being eaten once discovered. Since a group is larger and more conspicuous, its probability of discovery is higher than that of a solitary individual. The average probability of being eaten once discovered is lower for a group than for a solitary individual because of predator satiation, predator learning or enhanced group defense. However, if a member of a group is on the periphery, its probability of being eaten once discovered is higher on the average. If the periphery probability of death became higher than the probability of death for solitary individuals, and if the peripheral members could assess their positions, the group should fall apart. Many gregarious caterpillars can twitch violently and/or spit noxious fluids in response to a single larva being attacked (e.g. Tostawaryk 1972, Farris and Appleby 1980, pers. obs. of H. hewitsoni) and even fairly small groups of larvae may be favoured. Pupae on the other hand, have a rather restricted behavioural repertoire. For grouping to be favoured among pupae the group would either have to be very large or very distasteful. This may explain why relatively palatable butterflies such as Asterocampa clyton begin life as gregarious larvae but disperse widely during later instars. Probably the large group sizes and distastefulness of H. doris result in even peripheral positions being favoured over pupating alone.

If H. doris is saturating local predators and parasites by clumping its eggs, larvae and pupae, we might expect that the adults would disperse from their eclosion area. For a female the advantage would be that the hostplants in the area from which she emerged are likely to be either defoliated and/or infested with parasites and predators that have numerically responded to the larval group from which she emerged. For a male, there is a low probability of future successful broods in the area, so he too should disperse to other areas in search of virgin females. This high dispersal is exactly what happens in H. doris. Figure 1 shows that some individuals may have home range behaviour, but that most individuals are recaptured less than ten days after their initial capture, and many are recaptured father far from their capture site, which suggests that individuals disperse. In addition, newly-eclosed adults disperse even more than older adults.

These results on dispersal agree with Benson's (1971) argument that H. doris is highly dispersive, although we do find that some individuals show home range behaviour. As explained above we do not agree with Benson that H. doris is "ecologically palatable"; this species actually seems rather, though not very, unpalatable to the two bird species tested. This might suggest a disagreement with Benson's thesis that kin selection appears to have helped in the evolution of unpalatability in Heliconiines. But predation by vertebrates seems especially likely just after eclosion and during the first feeble flights of H. doris individuals. If selection acted just prior to dispersal, kin selection could be very important in the evolution of unpalatability: newly-eclosed H. doris seem often to be surrounded by scores of brothers and sisters, as well as by unrelated individuals.

In contrast, an adult of a single-egg-laying species that ecloses would expect to find good food and mating possibilities near its birth site, and should not need to disperse so far. Studies with solitary-egg-laying species of Heliconius have shown that most individuals show home-range behaviour which is restricted to a few hectares (Turner 1971, Ehrlich and Gilbert 1973, Cook et al. 1976), and preliminary studies show that newly-eclosed individuals of the solitary-egg-laying H. erato do not move far from their birthplace (JM, unpublished data).

If gregariousness of early stages in Heliconius species other than H. doris is a means of satiation of predators and parasites, then such species may also be expected to have a less viscous population structure than species with solitary larvae. Only one electrophoretic study on Heliconius has been published (Turner et al. 1979). Evidence of greater differentiation between populations of

H. erato (solitary larvae) and *H. sara* (gregarious larvae) is given in their Figure 2. For *H. sara* only about 7% of between-population comparisons at particular loci had genetic identities, I (normalized probability of genetic identity), less than 0.8, whereas for *H. erato* about 15% of between-population comparisons had I less than 0.8.

In *Heliconius*, population structure may have an important effect on the evolution of mimicry. Species with gregarious larvae might be expected to show poorer mimetic adaptation, greater polymorphism of non-mimetic colour patterns and poorer geographic differentiation of mimicry, due to the destructive effect of gene flow on the mimetic pattern, than would species with solitary larvae. These predictions are met in *H. doris* and other *Heliconius*. *H. doris* itself is one of the least accurate mimics within *Heliconius*; the mimetic patterns are not very accurate representations of probable Mullerian comimics in many places, and there is latent polymorphism of nonmimics in many areas (Appendix 1). As Mullerian mimicry (or even Batesian mimicry) would be expected to eliminate non-mimics from the population, we suggest that the polymorphisms observed in almost all populations of *H. doris* are caused by a balance between gene flow and selection for mimicry. Most of the other species which lay eggs in clutches (more than five eggs) are poorly differentiated racially (e.g. *H. sara*, *H. wallacei*, *H. xanthocles*, *H. ricini*, *H. aoede*, *H. burneyi*) and frequently have wide zones of polymorphism between colour-pattern races (Emsley 1965, Brown *et al*. 1975, Mallet and Jackson 1980). On the other hand single-egg-layers such as *H. erato* and *H. melpomene* are usually monomorphic (excluding narrow hybrid zones) for colour pattern, and are highly differentiated into extremely diverse mimetic races. The "silvaniform" species of *Heliconius*, which are single-egg-layers, appear to contradict this principle because they are frequently polymorphic in any one area. However, each morph is usually mimetic, and these species are highly-differentiated racially (Brown 1976) which suggests viscous population structure. Their polymorphisms have been explained by temporal fluctuations of comimic Ithomiine species (Brown and Benson 1974). Table 2 shows that differentiation between adjacent areas (the refugia designated by Brown 1975) and a high total number of races

Table 2: Larval gregariousness and racial differentiation in Heliconius

Differentiation between refugia[1]

	Low				High			
	Gregarious[2] species[3]	# races[4]	Solitary[2] species	# races	Gregarious species	# races	Solitary species	# races
less than 20 races	dori	8	tele	4	godm	1	eger	4
	meth	3			aoed	11	astr	2
	wall	5			hecu	7	natt	1
	rici	1			xant	13	isme	7
	sara	7			burn	7	pard	10
	leuc	2			deme	9	atth	1
	anti	5			hewi	1	elev	8
					cong	3	luci	2
							besc	1
					eleu	3	cydn	11
					saph	4	heur	1
							tima	2
							pach	1
							herm	6
							char	9
							clys	4
							hort	1
							hecs	6
more than 20 races			numa	25			heca	28
							ethi	22
							melp	29
							erat	28

Notes

1) Low differentiation: Brown (1975) assigned at least one named race of these species to "widespread" origin rather than to origin within a particular refugium: i.e. at least one race is spread over a large area. High differentiation: Brown (1975) was able to assign all geographic races to particular refugia i.e. all races are restricted in their present distributions.

2) Gregarious: usually produces batches of more than ten eggs, larvae show synchronized behaviour. Solitary: usually lay single eggs, or if several laid together, larvae do not show synchronised behaviour. (source Brown, 1981).

3) Species: All species names are abbreviated to the first four letters of their specific names except H. hecalesia which is which is written "hecs" to distinguish it from H. hecale.

4) # Races: Numbers of races are as presented by Brown (1981).

seem to be features more of solitary than gregarious species.

Of course, many species of *Heliconius* have low numbers of races simply because they have tiny ranges. Species in Table 2 that have only one race and are of restricted distribution include 2 gregarious species and six solitary species. Many of these "species" are suspected to be little more than subspecies of polytypic species (e.g. *H. himera* sensu Brown(1975) was later included as a race of *H. erato* by Brown (1981)). A more appropriate measure of racial differentiation is the number of races divided by the total area occupied by a species. An appropriate measure of mimetic differentiation is the number of genes involved in colour pattern changes. Since neither data are readily available, Table 2 is a compromise which does, however, display that gregarious species tend to be less differentiated than solitary species. A Fisher exact probability test comparing the numbers of gregarious and solitary species in the "undifferentiated" upper left cell in Table 2 with the numbers in all the other cells ("differentiated" species) gives P=0.0052 for the contingency table with cells 7, 10, 1, 23 and all other more extreme cells. The variance of number of races is much larger among solitary than among gregarious species, $F=7.0732, \nu_1=23, \nu_2=16, P<0.001$ (two-tailed).

Gregariousness of larvae is unlikely always to be associated with high mobility for two reasons. Firstly, if gregariousness has evolved for reasons other than satiation of parasites and predators, numerical response of parasites is not likely so that emerging females can lay eggs locally without suffering great losses. Secondly, if species with solitary larvae within a taxonomic group are highly mobile for ecological reasons, gregarious species within that group may show little added mobility. For example, gregarious larvae of *Euphydryas phaeton* protect themselves by means of webbing, which discourages parasitoids, and so would be unlikely to have associated large numerical responses of parasites (Stamp 1981); indeed populations of other species of Checkerspot butterflies seem very restricted to small local areas (Gilbert and Singer 1971). The Monarch butterfly (*Danaus plexippus*), a solitary egg-layer, has one of the most open population structures known. A hypothetical gregarious *Danaus* could hardly be expected to be more mobile!

In summary, the supergregarious H. doris has virtually no racial differentiation; its morphs occur in areas where they are non-mimetic, and even when mimetic, its morphs are usually rather inaccurate mimics. The evolutionary choice by a species of butterfly to produce its larvae in batches appears to have had far-reaching effects, through the population structure of that species, on its ability to adapt to local circumstances. For H. doris and other cluster-laying Heliconius, one effect was to reduce their mimetic abilities in any one area.

Appendix 1
Colour pattern and mimicry in H. doris

H. doris is marked on the black forewing with a broad yellow central band and a narrower distal band. In the Guiana region the forewing bands may become white instead of yellow, usually in polymorphic populations with white or yellow forewing bands. Forms with white forewing bands have also been recorded from Eastern Ecuador (Emsley, 1965). On the black hindwing there is a large rounded bar covering most of the central area of the wing. The colours of this bar vary: the "red" morph in Central America and South America West of the Andes has a broad jagged patch on the upperside; in the "blue", "yellow" and "green" morphs the bar is formed by scales of the given colours and the outline is more finely toothed; the "green" morph is apparently formed by a mixture of black and yellow pigment in scales in the bar, and is not clearly differentiable from "yellow", which has a variable area of pure yellow scales in the centre of a green band. In Amazonian South America the "red" morph has the bar deeply indented to form a rayed pattern, and is accompanied by a red so-called "dennis" mark at the base of the forewing.

The clinal distribution patterns of different forms of H. doris suggest that the most common morph is mimetic. At the northernmost end of their range all individuals are "red" (Emsley 1965; our Table 3), and appear to be rather poor mimics of female Parides spp. (Papilionidae). Further South where Heliconius with doris-like yellow and black forewings and iridescent blue hindwings occur (H. sara, H. wallacei), H. doris populations usually show an excess of "blue" morphs, although "blue" seems to decline north of Darien in Panama. Benson (1971) reports "blue" as being the commonest morph in Atlantic Costa Rica but he gave no population samples. "Blue" H. doris are rather good mimics of H. sara and H. wallacei, to our eyes at least, so the lack of many "blue" morphs in Central America may be due to the relative scarcity of H. sara and the absence of H. wallacei there: in South America these species are quite common. In South-western Colombia and Western Ecuador, "blue" morphs apparently become fixed in the population (Emsley 1965), probably because of a lack of comimics for the "red", "yellow" or "green" morphs in this region. Our samples from SE Colombia and Guyana also show

Table 3: Polymorphism of H. doris

Locality	% hindwing band			% forewing		n	collector
	red	blue	green	yel	white		
Sierra de los Tuxtlas, Mexico	100	0*	0	100	0	41	1
Osa, Pacific Costa Rica	20	1*	79	100	0	689	2
Osa, Pacific Costa Rica	24	3*	73	100	0	109	3
Chiriqui, Panama	50	0	50*	100	0	10	4
Central Panama provinces	53	21	26*	100	0	53	4
Darien, Panama	33	57	10*	100	0	39	4
Putumayo, Colombia	0	100	0	100	0	5	5
Rupununi, Guyana	0	100	0	67	33	12	5

*= non mimetic morphs in particular localities

Collectors

1 = G. Ross, L. Gilbert, D. Waller and D. Harvey (unpublished).
2 = W. Benson (1971).
3 = L. Gilbert, A. Simpson de Gamboa, J. Longino, J. Mallet, D. Murawski.
4 = G. Small (unpublished).
5 = J. Mallet (unpublished).

"blue" to be fixed, but this is probably due to small sample size as the species is known to be polymorphic nearby. In addition a reared clutch from E. Demerara, Guyana, was all "blue" (n=25, JL unpublished data), and Turner (1971) reported that "blue" H. doris predominated over "red" in Suriname and Trinidad. In the Rupununi, about 1/3 of the forewing bands of H. doris were white. In this area H. antiochus is sympatric with H. sara and is similar in appearance to H. sara except that it has white forewing bands. H. doris appears to mimic both species with its two "blue" morphs. Another area where some H. doris have white forewing bands is East Ecuador: here it may be a partial mimic of local forms of H. erato and H. melpomene, but we do not know whether these are sympatric. In the Amazonian region the "red" morph is usually rare, but its rayed pattern and the red "dennis" on the forewing show that it is a mimic of H. erato and an associated mimicry ring of species with the "dennis-ray" pattern (Emsley 1965). "Red" H. doris and H. burneyi share with each other the feature of having paired yellow forewing bands which are often inappropriate for the dennis-ray mimicry ring.

On the Pacific slopes of SW Costa Rica and in the adjacent Chiriqui province of Panama, the "yellow" morphs predominate. H. sara within this region occurs as an atypical form with a yellow hindwing margin, and is itself a comimic of the locally endemic species H. hewitsoni and H. pachinus. The "yellow" morph is an effective, but not excellent mimic of these three species, while the "red" morph is once again probably a mimic of Parides spp.

Throughout much of the range of H. doris, rare non-mimetic morphs are present. In Pacific Costa Rica and Chiriqui the "blue" morph does not have any comimics, while the "green" and "yellow" morphs appear to lack mimics throughout their whole range except within this same area. Benson (1971) suggested that these rare morphs were maintained by frequency-dependent selection favouring non-mimetic morphs in a Batesian mimicry system. One argument against this is that we would expect to see "green" and "yellow" morphs of H. doris maintained at approximately the same frequencies throughout their non-mimetic range. In fact they decline in frequency away from their apparent distribution centre, until very rare in Northern South America (Table 3, Emsley 1965). Other features of H. doris colour pattern seem to vary clinally: the "blue" morph seems to increase clinally Eastwards across Panama into Northern South America, whilst red declines over the same range (Table 3); the amount of red forewing "dennis" in the "red" morph declines from its area of mimetic usefulness in the Amazon basin into Central America, until absent in Nicaragua (Emsley 1965); the amount of red "ray" pattern on the underside of the hindwing also decreases from the Amazon basin northwards (Emsley, 1965). These patterns suggest that selection for mimetic pattern would cause morph fixation in many areas (and does in two remote areas), but does not because of immigration from adjacent areas. High dispersal rates might also explain the lack of mimetic fine tuning caused by the destructive effect of gene flow on the evolution of mimetic patterns; in H. doris even the mimetic morphs are rather inaccurate renderings of their comimics. Other species of Heliconius within a mimicry ring are so similar that they were often lumped in the same species by early taxonomists (Emsley 1964, 1965).