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The ecology and social behaviour of the Neotropical butterfly *Heliconius xanthocles* Bates in Colombia

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The mimicry, population ecology, adult behaviour and life cycle of *Heliconius xanthocles* were studied at two sites in Colombian tropical forest. The results were compared with the known biology of other *Heliconius* species. *H. xanthocles* is probably unpalatable and is a Müllerian comimic of some other species. In the Amazon basin *H. xanthocles* belongs to the 'dennis ray' mimicry ring of the Heliconiini, which includes *Eueides tales, H. burneyi, H. elevatus, H. melpomene* and *H. erato.* In the Rio Negro valley, where the latter species either do not exist or have different mimetic allegiances, the 'dennis-ray' pattern of *H. xanthocles* breaks down. The adults are pollen-feeders, like other *Heliconius*, but they also visit other food sources such as bird droppings. During a mark-recapture programme in the Río Negro, adults were found to be almost entirely restricted to small areas near their foodplant *Passiflora praeacuta.* Females were rarer than males, but this was probably due to a behavioural difference between the sexes. The males had a Fisher-Ford survival rate of 0.95 per day and a life expectancy of 19 days. Population size estimates of males were between 11 and 17 individuals. These estimates are lower than, but comparable to those for other *Heliconius.* Males as well as females visit the larval foodplant, and an adult male was observed hovering over a small group of larvae. The females lay batches of 12–41 eggs. The largest batch (41 eggs) was laid co-operatively by two females. The larvae are gregarious feeders on shoot-tips of *Passiflora praeacuta,* and all life stages are described for the first time. Predation on the larvae by a bug is described. The pupa has a distinctive morphology unlike that of other *Heliconius.* The adult population ecology, mimicry and larval behaviour are discussed.

KEY WORDS: – *Heliconius* – Lepidoptera – mimicry – population ecology – mark release – life-cycle – social behaviour – oviposition.

CONTENTS

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INTRODUCTION

As Clutton-Brock & Harvey (1978) point out, to explain species differences among vertebrates has required a great deal of comparative data: earlier explanations for species traits verged on the ridiculous because they ignored the presence or absence of the same traits in other species. In theory, the comparative examination of species traits in insects should prove relatively easy. Insects usually have more species within a group, more individuals within a given area, and shorter generation times than do the vertebrates. In order to test hypotheses about the sociobiology of the heliconiine butterflies (Benson, 1971; Turner, 1971b; Gilbert, 1975) much better comparative information is needed on this group than is at present available.

The butterflies of the tribe Heliconiini (Lepidoptera: Nymphalinae) have recently become important in the study of animal behaviour, mimicry and aposematism, insect-plant coevolution, demography and biogeography. Results of some of these studies reveal that butterflies of the genus *Heliconius* exhibit unusually complex social behaviour and very specialized relationships with plants. *H. charitonia* (Linn.), *H. erato* (Linn.), *H. ethilla* Godart and *H. sara* (Fab.) show well-defined home-range behaviour and high longevity, and these species also have a tendency to return to particular sites, night after night, where they roost communally (Turner, 1971a; Ehrlich & Gilbert, 1973; Cook, Thomason & Young, 1976; authors' unpublished observations). The larvae of these and other *Heliconius* feed on creepers of the genus *Passiflora* and are usually restricted to the growing shoots of these plants (Brown, 1973; Benson, Brown & Gilbert, 1976). The adults of *Heliconius* are able to incorporate amino acids from the pollen of *Anguria* and *Gurania* flowers (Cucurbitaceae) and *Heliconius* is the only genus of butterflies known to have a toothed proboscis capable of masticating pollen (Gilbert, 1972). This extra nitrogen source enables *Heliconius* species to maintain a long reproductive life in comparison to close relatives such as *Dryas* (Dunlap-Pianka, Boggs & Gilbert, 1977). Gilbert (1975) suggests that the mutualism that exists between pollen-donor *Anguria* plants and pollinator *Heliconius* has allowed the development in the butterfly of complex behaviour, leading to efficient exploitation of *Passiflora* growing shoots which are rare, both temporally and spatially.

This paper presents observations on the mimicry, the larval and adult ecology and the social behaviour of *H. xanthocles,* a moderately rare species which is confined to the Amazon Basin and its periphery. The biology of the species is compared with what is known of other heliconiines.

LOCALITIES

H. xanthocles was observed in two locations in submontane forest on the eastern slopes of the eastern Andes in Colombia.

The first locality was in the upper Río Negro Gorge* at Pipiralito, Meta (km 91 on the main Bogotá-Villavicencio highway). The nearest town was Guayabetal, Cundinamarca. The study site was in secondary vegetation, bordered by primary forest that had been selectively felled. The elevation was approximately 1000 m above sea-level. Access to the site, across the Río Negro Gorge from the road, was by means of manually-drawn cable-car. Observations were made between 7 May and 5 June, and again on 20 July 1977.

Further observations on this species were made in the eastern (Amazonian) foothills of the Andes at Villa Garzón†, Putumayo (km 10 on the road Mocoa-Puerto Asis. Villa Garzón is labelled Villa Amazónica on most maps, as the town was renamed in 1976 in honour of its founder, Don Julio Garzón). Slightly disturbed forest is present about 1 km from the town, on the northern banks of the Río Mocoa where hilly terrain has prevented extensive agricultural development. The altitude was approximately 300 m, and observations were made between 2 July and 7 September 1977.

H. xanthocles was very locally distributed in its habitat, compared to butterflies such as *H. erato* and *H. melpomene* (Linn.). We found it at moderately high densities only near stands of its foodplant, *Passiflora praeacuta* Mast., which was itself locally distributed compared with plants such as *P. auriculata* H.B.K. on which *H. erato* larvae were commonly found.

DESCRIPTION OF ADULT *H. XANTHOCLES*

In this section, and the next section on mimicry of *H. xanthocles,* standard *Heliconius* terminology has been used to describe colour patterns. There are two major types discussed. (1) A pattern like the *Heliconius* on the righthand side of Fig. 1 is called 'dennis-ray'. 'Dennis' refers to an orange-red basal patch on the forewing, and 'ray' refers to the radiate orange-red hindwing pattern. There is also a yellow bar on the anteromedial part of the forewing. Dennis-ray heliconiines are usually confined to the Amazon basin. (2) The 'postman' pattern refers to the presence of a broad red medial bar on the forewing of an otherwise black *Heliconius,* like *H. erato* at the bottom left of Fig. 1. Postman *Heliconius* may also have a yellow hindwing band as in *H. erato* and *H. melpomene* of the upper Putumayo (not figured); *H. erato* (Fig. 1) and *H. melpomene* in the Río Negro do not have the hindwing band. Postman *Heliconius* are usually extra-amazonian.

The upper Río Negro *H. xanthocles flavosia* Kaye is polymorphic: both males and females occur with crimson forewing 'dennis' and reduced crimson hindwing 'ray' patterns (Fig. 1, left, top three butterflies) with a broad or narrow yellow forewing band. These represent forms 'flavosia' and 'fassli' Neustetter respectively. In the Río Negro, six out of 23 butterflies whose patterns were noted during the capture-recapture experiments had narrow yellow bands, while the remaining 17 had broad forewing bands. The dennis and ray pattern is almost entirely absent from the underside of the Río Negro *H. xanthocles.*

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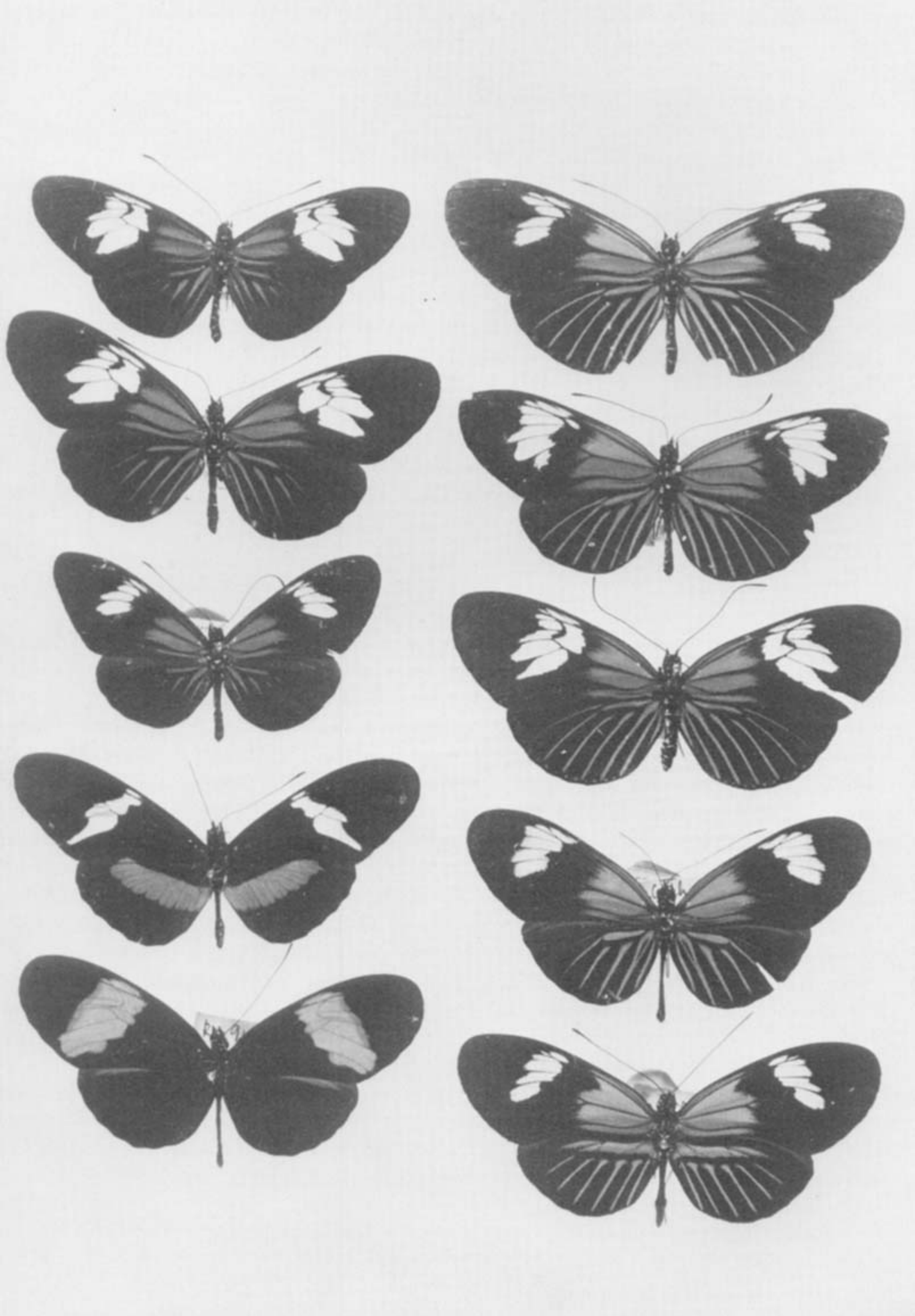
* The Río Negro site was approximately at 4°15'N, 73°45'W. Throughout this paper, 'Río Negro' refers only to that river situated between Bogotá and Villavicencio, in Meta, Colombia. We do not refer to the large and well-known tributary of the Amazon of the same name, nor to any of the other myriad Rios Negros either in Colombia or in the rest of South America.

† The coordinates of Villa Garzón are approx. 1°N, 76°30'W. Villa Garzón, Putumayo, should not be confused with Garzón, Huila, which is situated in the Magdalena valley of Colombia.



Polymorphism is also present in Villa Garzón: seven out of eight specimens collected had narrow forewing bands, only one having a broad band. The Villa Garzón individuals have orange dennis and well-developed ray patterns (unlike *flavosia* of the Río Negro valley) approximating to *melittus* Staud. (yellow band narrow or very narrow) with some individuals (yellow band broad) resulting from introgression of *flavosia* or *melete* Felder & Felder from the north, or *explicata* Stichel from the upper Putumayo. The forms observed are portrayed in Fig. 1, right, top three butterflies. Dennis and ray patterns are well-developed on the undersides of the wings of Villa Garzón individuals.

The subspecific taxonomy of *H. xanthocles* will shortly be reviewed (Holzinger & Brown, in prep.). Dr Keith S. Brown Jr has kindly suggested the above nomenclature, although he emphasizes that he is not yet sure which names Dr Holzinger and he will finally apply.

MIMICRY

Heliconius species are aposematic and distasteful (Brower, Brower & Collins, 1963), and show Müllerian mimicry that frequently crosses taxonomic borders within as well as outside *Heliconius,* while species within subgroups of the genus may look completely different and belong to different mimicry rings (Turner, 1976). *H. xanthocles* and *H. hecuba* together form an aberrant species group which is apparently distantly related to other species groups within *Heliconius* (Emsley, 1965).

In Villa Garzón, *H. xanthocles* flies with *H. erato,* which is here present as hybrid forms between the Amazon basin dennis-ray subspecies *lativitta* Butler (Fig. 1, right, fourth from top), and the upper Putumayo postman-patterned subspecies *dignus* Stichel of the Andean slopes. Subspecies *dignus* has a red forewing bar and yellow hindwing stripe, without dennis or ray. *H. melpomene,* a close mimic of *H. erato* throughout their co-occurring ranges, similarly occurs as hybrids between the dennis-ray *aglaope* Felder & Felder (Fig. 1, bottom right), and the postman subspecies *bellula* Stichel. Also present in Villa Garzón at lower density are the following dennis-ray species: *Eueides tales calathus* Stichel, *H. (Neruda) aoede bartletti* Druce, *H. burneyi* (Hübner) transitional *lindigii* Felder & Felder/*hübneri* Staudinger and *H. elevatus elevatus* Nöldner. The narrow yellow forewing band in all of these species, with the exception of the very rare *H. burneyi,* is also normally present in *H. xanthocles* in this region (seven out of eight individuals captured), as is fully-developed ray.

Figure 1. *Left, top to bottom: H. xanthocles flavosia* ♂, broad forewing band, Rio Negro; *H. x. flavosia* ♀, broad forewing band, Rio Negro; *H. x. flavosia* ♂, narrow banded form, Rio Negro; *H. clysonimus* ♀, Fusagasuga (similar to Rio Negro forms); *H. erato hydara* ♂, 'postman'-form, Rio Negro (*H. melpomene* also has the 'postman' pattern in this area).

Right, top to bottom: H. xanthocles melittus ♀, very narrow forewing band, Villa Garzón; *H. x. melittus* ♂, narrow forewing band, Villa Garzón; *H. x. melittus* ♀, broad forewing band, Villa Garzón; *H. erato lativitta* ♂, 'dennis-ray' form, Rio Caquetá, Putumayo; *H. melpomene aglaope* ♀, 'dennis-ray' form, Rio Caquetá, Putumayo.

All butterflies are black with yellow (pale) and red (grey) markings. 'Forewing band' refers to the median band across the forewing. 'Dennis' refers to the basal patch of red colour in the forewing of *H. xanthocles flavosia* on the left, and all the Amazonian *Heliconius* on the right of the figure. 'Ray' refers to the red hindwing pattern for these same butterflies.

Presumably therefore, *H. xanthocles* belongs to the dennis-ray mimicry ring characteristic of upper Amazonian heliconiines in the Villa Garzón region.

In the Río Negro valley, *H. xanthocles flavosia* is sympatric with *H. erato hydara* Hewitson, *H. numata messene* Felder & Felder, *H. melpomene melpomene* and *H. heurippa* Hewitson, all common species in the region, and none of which displays dennis or ray markings. The species which most closely resembles *H. xanthocles* in this area is *H. clysonimus clysonimus* Latreille, a species restricted to between 500 and 2000 m above sea-level (Brown, personal communication). We mistook *H. clysonimus* in flight for *H. xanthocles* on several occasions during the capture-recapture programme, and it is possible that the reduction in ray of *H. x. flavosia,* compared with that of the Amazonian subspecies, is associated with mimetic convergence to *H. clysonimus.* It is interesting that the dennis and ray of *H. x. flavosia* is a bloody crimson colour, close to the red of the hindwing bar of *H. clysonimus,* rather than to the more orange colour of *H. xanthocles* and its heliconian comimics at Villa Garzón (except *H. burneyi*). The crimson colour may just be discerned as a darker shade in Fig. 1.

At high altitudes above Mocoa, Putumayo, a third form, *H. x. explicata* Stichel, flies with the pure postman-patterned races *H. erato dignus* and *H. melpomene bellula* (Brown, 1975). *H. x. explicata* has dennis and ray nearly absent, resulting in a black butterfly with broad yellow forewing bands.

From these three areas it appears that, in Colombia, where Amazonian dennis and ray patterns predominate among heliconiines, *H. xanthocles* tends to show strong mimicry with these butterflies. Where this pattern is absent among local heliconiines, the yellow forewing band of *H. xanthocles* becomes more variable, and the dennis-ray pattern tends to become reduced. In the Río Negro at 1000 m altitude there is a suggestion of convergence of *H. xanthocles* with *H. clysonimus.* This observation conforms to the pattern expected of a Müllerian mimic, although there are other areas where *H. xanthocles* does not lose its radiate pattern in the presence of postman *H. erato* and *H. melpomene* (Brown & Mielke, 1972).

ADULT BEHAVIOUR AND POPULATION ECOLOGY

Heliconius xanthocles in both study areas showed "large-scale promenading behaviour" (Brown & Mielke, 1972). In the Río Negro site, males flew up and down a path in secondary vegetation bordered by forest, during sunny spells in the predominantly rainy weather we experienced. The butterflies used only part of the path, especially around a plant of *P. praeacuta.* In the Villa Garzón forest we discovered a natural tree-fall opening where a plant of *P. praeacuta* and other creepers had grown over the old tree-trunk in a swath of vegetation. We had only to wait a few minutes before individuals of *H. xanthocles* flew down from the canopy, dashing at characteristically high speeds along the edges of the overhanging vegetation and around the clearing.

At the Río Negro site individuals frequently had blobs of moistened pollen adhering to their coiled probosces in the same way as *H. erato,* which is known to extract amino acids from *Anguria* and *Gurania* pollen (Gilbert, 1972). In Villa Garzón, individuals of *H. xanthocles* were observed to visit inflorescences of *Anguria* at forest edges, but in the Río Negro no *Anguria* or *Gurania* plants were found near the study site. However, in the last locality *H. xanthocles* visited a white-flowered species of *Elaterium* (Cucurbitaceae) as well as an orange-flowered

Hamelia bush. We have also observed *H. xanthocles* feeding at bird droppings and even at human spittle; perhaps these also acted as sources of organic nitrogen.

A capture-recapture programme was undertaken at the Río Negro over a period of four weeks (7 May – 5 June 1977), in order to estimate population size and survival rate of *H. xanthocles*. Butterflies were caught at known stations along the path already mentioned, and were found to be restricted to a portion of the path about 50 m on either side of the larval foodplant *P. praeacuta*. The butterflies were marked at first capture with individual numbers on the underside forewing yellow band, using a fine-tipped spirit marker pen. Condition (fresh, intermediate or worn), sex and forewing band types were noted, and the butterflies were then released. Only the first-time recaptures on each sampling date were used in the analysis.

Out of 37 butterflies caught in the Río Negro site, only nine were females, and no female was ever recaptured, so that males only could be used in the analysis. A similar, but less extreme sexual difference has been observed by Ehrlich & Gilbert (1973) in *H. ethilla*: for the latter species the differences were attributed to differences between the behaviour of the sexes, as a one-to-one sex ratio was present in laboratory populations.

Total captures (including recaptures) of males were 62, the total number of males taking part in the analysis being 24. These small sample sizes reflect partly the poor weather and partly the small size of the population. We suspect that some of the individuals came to recognize the threat of the fieldworkers' nets: near one station the normal flight path of the butterflies changed after we had had a particularly fruitful day's catch, apparently so as to avoid a position at which we had been accustomed to wait. Thus capture may not have been random, but the analysis gives some idea of the demography of these butterflies.

The data were analysed by the Fisher-Ford method (Fisher & Ford, 1947), for which a computer programme was written. We made two analyses. Firstly the population was analysed daily, giving population size estimates of between eight and 48 and a Fisher-Ford survival rate of $s = 0.94$ per day (Table 1). Secondly, the data were lumped into weekly intervals, giving more stable population size estimates of between 11 and 17, and $s = 0.69$ per week, or $s = 0.95$ per day (Table 2).

Disappearance rate (dispersal + mortality) is thus approximately 0.05 per day. On 20 July 1977 J. M. was able, in a sunny spell during appalling weather, to observe a marked male *H. xanthocles* (no. 12). This individual had been caught for the first time and marked on 15 May, and thus had been alive in the Río Negro site for 66 days, showing that *H. xanthocles* could survive for periods comparable to those so far recorded for *H. erato, H. ethilla* and *H. charitonia* (Turner, 1971a; Ehrlich & Gilbert, 1973; Cook *et al.*, 1976). The life expectancy of the butterflies using the crude approximation of the exponential failure law is given by the expression $e = -1/\ln s$. For $s = 0.05$ this gives $e = 19$ days, considerably higher than those so far recorded in temperate species of Lepidoptera. In *Panaxia dominula* for example, $s = 0.84$, giving a life expectancy, e, of only 6 days. It is not known whether life expectancy is significantly less in *H. xanthocles* than in *H. ethilla* ($e = 50$ days), *H. erato* ($e = 100$ days), *H. charitonia* ($e = 30$–80 days) (Turner, 1971a; Ehrlich & Gilbert, 1973; Cook *et al.*, 1976); but clearly some *H. xanthocles* may live for a very long period of time.

We unfortunately were unable to determine whether *H. xanthocles* roosts communally in the manner of other heliconiines. However, at approximately 12

Table 1. Results of Fisher-Ford analysis of *Heliconius xanthocles* capture-recapture data: males only, analysed at intervals of one day. The days on which no captures were made have been excluded

Sampling date 1977	No. of individuals captured (and released)	Population estimate
7 May	2	–
8 May	5	∞
14 May	5	7.85265
15 May	13	19.7561
20 May	3	48.4318
22 May	9	13.8033
27 May	1	18.8759
28 May	2	12.4410
29 May	2	38.7981
4 June	2	9.77285
5 June	6	9.38485

Fisher-Ford survival rate (s_d) = 0.9389 per day. Death (+ dispersal) rate = 1-s_d = 0.0611 per day. Life expectancy = 15.8614 days.

Table 2. Data and results of Fisher-Ford analysis; males only, analysed at intervals of one week. Recapture data shown in the form of a "pyramid diagram" (Fisher & Ford, 1947). Numbers in the row to the left of each asterisk represent numbers caught during the asterisked week that were recaptures from previous weeks. Numbers in the column below each asterisk represent numbers of individuals caught during the asterisked week that were also caught on subsequent weeks

Date 1977	Week no.	No. individuals captured (and released)	Recaptures from previous weeks	Population estimate
7–8 May	1	7	*	–
14–15 May	2	16	5 *	15.4381
20–22 May	3	11	3 7 *	15.7874
27–29 May	4	5	0 2 3 *	17.4728
4–5 June	5	7	1 4 3 2 *	10.8418

s_w=0.6892 per week; Fisher-Ford survival rate (s_d)=$\sqrt[7]{s_w}$=0.9482 per day. Death (+dispersal) rate=0.0518 per day. Life expectancy (e)= 18.8006 days.

noon on 27 May 1977 (a very wet morning on the Río Negro), a marked individual male (no. 21) was observed hanging, wings downward and folded, from a dead twig under the canopy of overgrowing trees near a logging clearing. About a yard away a single *H. clysonimus,* its possible comimic, was resting in a similar manner. These positions are similar to those adopted by communally-roosting species of *Heliconius,* but further evidence is needed to show whether or not *H. xanthocles* can be counted among them.

We have watched both females and males of *H. sara* and *H. xanthocles* visiting their larval foodplants and hovering near larvae. It was in fact this behaviour that first attracted our attention to the larval stages of *H. xanthocles* and *H. sara* in the

Río Negro site, as well as their foodplants *P. praeacuta* and *P. auriculata* respectively. Brown & Benson (1977) have noticed male as well as female *H. hermathena* visiting their larval foodplants. While the females are probably locating oviposition sites, the male behaviour is rather less obviously explicable. Brown & Benson (1977) suggest that males cue in on the larval foodplant as a means of locating areas where there is a high probability of virgin females emerging.

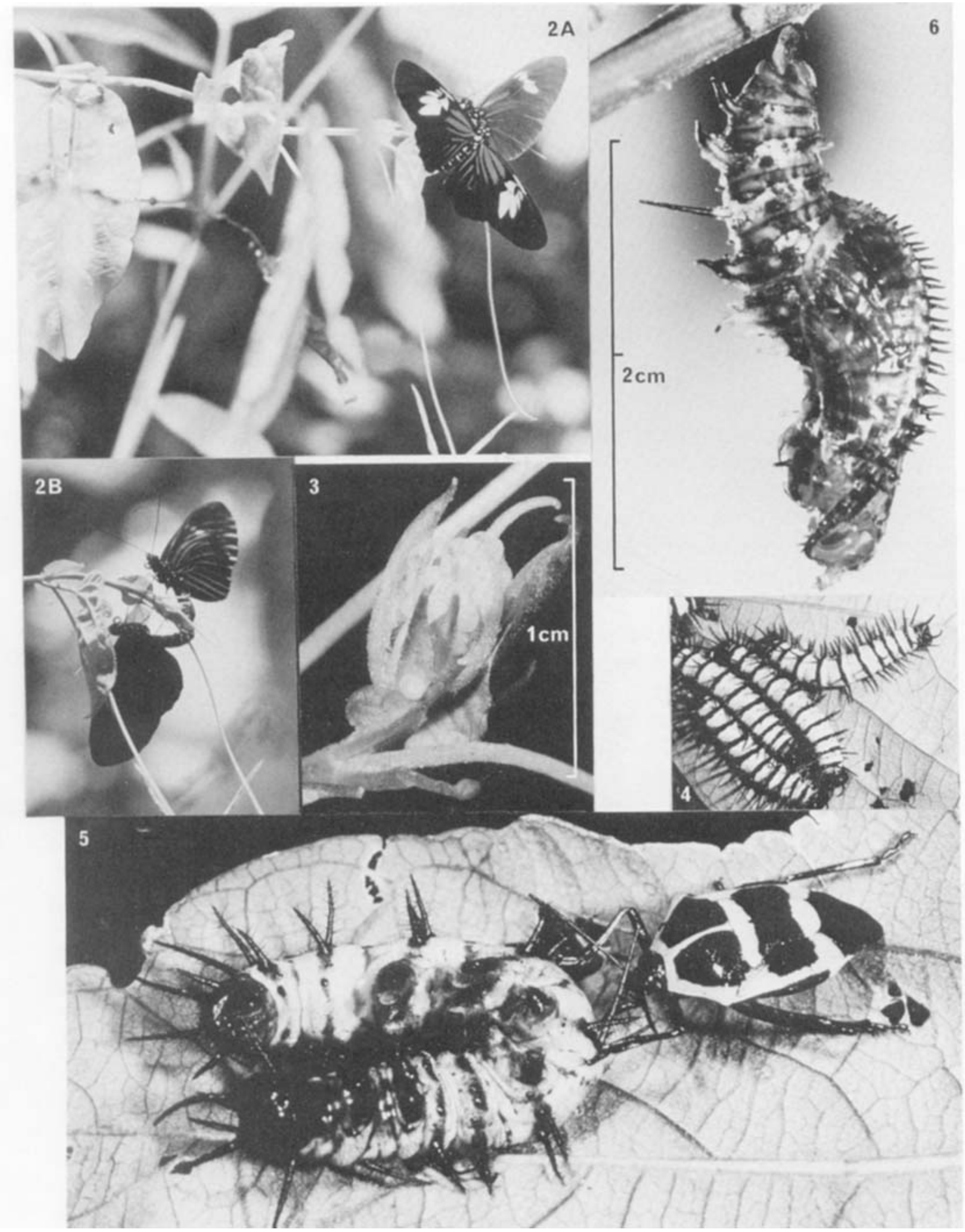
LIFE-CYCLE

Oviposition and the egg stage, cooperation of egg-laying females

On 22 May 1977 at 1210 in the Río Negro site, we observed a number of *H. xanthocles* flying round a growing shoot of *P. praeacuta.* One female (with a narrow yellow forewing band) began to lay eggs on the tip of the shoot, while a marked male (no. 2) hovered close by. Another female (broad-banded) arrived at 1215 and joined the first female in egg-laying (Fig. 2). Meanwhile another male (no. 3) hovered overhead. At 1225 the narrow-banded female left the plant, while the second female continued to oviposit until 1235. Examination of the tight clump of eggs (Fig. 3) later showed that a total of 41 had been laid by these two females. A third female, which was hovering nearby and was captured for sending to insectaries in Liverpool (the stock unfortunately did not survive), may have been about to contribute further eggs to the shoot tip.

Brown & Mielke (1972) predicted that *H. xanthocles* would show clumped oviposition behaviour, but cooperative egg-laying has been recorded only rarely in other *Heliconius*. Jocelyn Crane observed social egg-laying by two *H. sara* females in the insectary, and suspected it for *H. (Laparus) doris* (Linn.) (John R. G. Turner, personal communication), although Sheppard (1963), studying the polymorphism of *H. doris* regarded a single egg mass as certainly laid by one female only. Turner (1971b: 250) records social oviposition by two wild females of *H. sara*. Benson *et al.* (1976) report an observation of a raft of approximately 800 eggs of *H. doris,* which seems an improbably large number of eggs to be laid by one female (Brown, personal communication). The present authors were able to confirm in Villa Garzón that social egg-laying occurs in *H. doris* also: at 1530 hours on 13 Aug. 1977, two *H. doris* females were observed laying a raft of eggs on the inverted upperside of a leaf of *P. praeacuta* in the tree-fall clearing already described. The leaf was subterminal on a rapidly growing shoot, and was the oldest leaf still folded in half (as are juvenile leaves). The total of over 200 eggs were laid in the cleft formed by the upperside of the folded leaf, the eggs forming a lattice similar to that figured by Benson *et al.* (1976) for this species. At 1555 the first female *H. doris* departed; at 1620 the second female also flew away. The first female had a pollen mass attached to her proboscis in the manner of the more advanced *Heliconius*.

However, social oviposition is probably not the rule in *H. xanthocles*. On 20 July 1977 the Río Negro site was revisited, and a small side-shoot of the same *P. praeacuta* plant was found to have 12 eggs attached. About 1 km away up the side of the valley another *P. praeacuta* was located, one shoot having 18 eggs of similar type and distribution to those in Fig. 3. Both these numbers are within the range



Figures 2–6. Fig. 2. A. A pair of female *H. xanthocles* ovipositing on *P. praeacuta* at the Río Negro site. B. Same as A, a few minutes later. Fig. 3. The clutch of 41 eggs laid by the two females in Fig. 2. Fig. 4. Part of a batch of ten final instar larvae of *H. xanthocles*. Fig. 5. Predation of *H. xanthocles* larva by *Oplomus marginalis* (Pentatomidae). Fig. 6. Pupa of *H. xanthocles flavosia*.

of one female individual as each can lay at least 20 eggs (see above). In addition single *H. sara* and other cluster-laying *Heliconius* have frequently been observed ovipositing alone by numerous workers.

The eggs laid on 22 May were left on the plant until 30 May, when they were transported to Bogotá for observations of parasitism. However, there was a 100% hatch on 31 May, but the young larvae all died later, probably because of the conditions under which they were kept.

Benson, Brown & Gilbert (1976) report that other known foodplants of *H. xanthocles* are all included within the same subgenus (*Granadilla*) of *Passiflora* as is *P. praeacuta*. These are: *P. menispermifolia* H.B.K., *P. eichleriana* Mast., and *P. nitida* H.B.K.

The larval stages

Larvae and larval foodplant were first located on 15 May, when a male (no. 7) *H. xanthocles* was observed hovering near a batch of blackish gregarious larvae. When fully-grown, they are yellow, striped with black around the central region of each segment (except the prothorax), at the bases of the spines (Fig. 4). They have black head-capsules with black dorsal spiny head scoli which are about 1½ times the height of the head. They have typically heliconiine body spines which are black, as are the legs, prolegs and anal claspers.

The larvae are gregarious throughout life, but do not mix with other batches on the same foodplant. On 22 May, 41 ova, five second or third instar larvae and ten final instar larvae were present on the Río Negro site foodplant in separate groups according to size.

The only predator observed attacking *H. xanthocles* was *Oplomus marginalis* (Westw.), an orange and black pentatomid bug (Fig. 5). The bug pierced the cuticle of last instar larvae and sucked the contents. No parasitism of larvae was observed.

The pupa

Before pupation, the larvae showed increased locomotory activity and lost their gregariousness. The pupa (Fig. 6) was gnarled, dark brown and mahogany, with small, faint gold patches dorsally on the first abdominal segment. There are leafy dorsal protuberances with poorly-developed spines on the abdomen, and the overall appearance is similar to that figured as possibly belonging to *H. xanthocles* by Turner (1968). Dr Turner has now examined the cast pupal skin and confirms that it is nearly identical to that figured by him in 1968. The pupa was fairly mobile, loosely attached to an orange silk pad which was fastened to a *Passiflora* stem. When touched, the pupa had a tendency to wriggle from side to side, stridulating faintly.

DISCUSSION

Heliconius xanthocles (at least the males) subsists in small populations of relatively long-lived individuals near its larval foodplant, *Passiflora praeacuta*. It is not known whether the adults roost communally at night, but otherwise the adults show the high longevity, home-range behaviour, mimetic and adult foodplant associations typical of other *Heliconius* species so far studied. Gilbert (1975) suggests that mutualism, as for instance between pollen-donor plants and *Heliconius*, may allow long adult lifespans. High longevity, caused by the butterfly's ability to utilize amino acids from *Anguria* pollen, increases the possibility of finding temporarily and spatially rare oviposition sites (in this case rapidly-growing shoots of *P. praeacuta*); memory and home-range behaviour enable individuals continually to patrol areas where shoots are likely to develop (in the case of females) or areas where there is a high probability of achieving mating (in the case of males).

Müllerian mimicry with other heliconians is another mutualism which may also increase adult longevity by reducing predatory attacks by birds. This mutualism is present in the Amazonian lowlands, for example at Villa Garzón, but at higher elevations where 'dennis-ray' mimicry-rings are absent, the mimetic 'dennis-ray' patterns of *H. xanthocles* break down, which supports the hypothesis that colour pattern is moulded by mimicry. In one of these localities, the Río Negro valley, there is a possibility that *H. xanthocles* converges on *H. clysonimus*. However, there are areas in Brazil where *H. xanthocles* retains full 'dennis-ray' patterns although sympatric with postman-patterned species of *Heliconius* (Brown & Mielke, 1972).

The genus *Heliconius* has two major ways of attacking its hostplants. Firstly there are species with solitary, even cannibalistic larvae: e.g., *H. erato, H. melpomene* and *H. numata*. Secondly there are species which have gregarious larvae: e.g., *H. sara, H. wallacei, H. doris* and *H. xanthocles*. Gregariousness would seem to provide an effective display for the protection of aposematic and distasteful larvae from attack by vertebrate predators, but in fact gregariousness of larvae does not correlate very well with unpalatability among the Heliconiini (Benson, 1971), so other factors must be presumed to be involved. Under some circumstances, feeding efficiency is increased if larvae are gregarious (e.g. Ghent, 1960) and this explanation has been suggested for the gregarious larvae of *H. sapho* (Drury), which feed on a woody and tough-leaved *Passiflora, P. pittieri* Mast. (Smiley, 1978). But whatever the advantage of gregarious larvae, three widely separated groups of *Heliconius* appeared to have evolved means whereby females synchronize egg-laying to produce bigger armies of larvae than a single female could produce alone.

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