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HANDLING EFFECTS IN *HELICONIUS*: WHERE DO ALL THE BUTTERFLIES GO?

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SUMMARY

(1) 'Handling effects' (abnormally high disappearance rates of net-captured individuals) exist in several species of butterfly, but it is not known whether this increased disappearance is due to dispersal, mortality, or avoidance of capture. In this paper we report work with *Heliconius* butterflies to differentiate between these alternatives.

(2) We experimentally investigated handling effects of marked *Heliconius* individuals at flowers of the vine *Psiguria warscewiczii*. Individuals were less likely to return to flowers after being captured and handled than after being identified by sight alone. This handling effect lasted up to 2 days after capture.

(3) On the other hand, fidelity to particular nocturnal roost sites was not affected by initial capture and marking or recapture during the day, apart from a short-term effect on the night of the day that captures were made. *Heliconius* avoid specific sites where they have been handled, but do not completely desert their home ranges: handling effects are not due to increased dispersal or mortality. This is the first time that such an effect has been shown in insects.

(4) Because of these handling effects, mark–recapture estimates of population size are likely to be inaccurate. For butterflies like *Heliconius*, it may be necessary to catch almost all the individuals in an area to obtain a good estimate of population size, whereupon the Lincoln Index becomes unnecessary. Judging by the high rates of recapture, many studies may achieve this.

(5) The natural equivalent of handling effects could enable *Heliconius* to avoid areas with poor resources, or sites where predators are likely to attack.

INTRODUCTION

Ecological studies of animals frequently use estimates of population sizes of the species under study. For insects, the techniques used include sweep sampling, light trapping, mark–recapture, or visual sampling along a transect. These methods are all liable to bias because insects behave idiosyncratically; species, and even individuals within species, behave differently from one another.

Mark–recapture studies are especially prone to bias because a key assumption is that marked and unmarked animals in a population mix randomly, and are equally

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recapturable. Several recent experiments have now shown that capture and handling reduces the probability that butterflies are recaptured or resighted (Singer & Wedlake 1981; Lederhouse 1982; Morton 1982, 1984). These 'handling effects' can be caused both by initial marking and capture, and by recapture of already marked individuals.

In these studies there is only circumstantial evidence on the fates of individuals affected by handling (Singer & Wedlake 1981; Morton 1982, 1984): compared with unhandled individuals, handled butterflies may disperse more, die more, or simply avoid sites where they have been captured. Lederhouse (1982) concluded that handling effects in *Papilio polyxenes* were due to dispersal rather than avoidance of capture or mortality. However, the evidence used by Lederhouse to discount avoidance of capture—a high estimated 'sampling intensity' measured during a mark–recapture programme—is exactly the sort of evidence that is inadmissible if a handling effect exists; it is still not entirely clear whether the handled butterflies left the area completely or became more wary (either of the sites of capture, or of Lederhouse himself). Lederhouse's released (unhandled) *P. polyxenes* controls were laboratory-reared; thus, strictly they do not exclude a higher probability of capture-induced mortality of handled individuals, though they do exclude marking-induced mortality.

In this paper we make use of the unique features of *Heliconius* to investigate the fates of handled individuals. *Heliconius* are long-lived, unpalatable, warningly coloured tropical butterflies with surprisingly sophisticated behaviour. They are known to develop home ranges, and repeatedly return to the same individual inflorescences of plants, especially of *Psiguria* and *Gurania* vines (Cucurbitaceae), for meals of nectar and pollen (Gilbert 1975; Brown 1981; Turner 1981; Murawski 1986; Murawski & Gilbert 1986). The home range of an individual *Heliconius* also includes one or more repeatedly used sites of nocturnal gregarious roosting (Jones 1930; Turner 1971; Young & Thomason 1975; Young & Carolan 1976; Young 1978; Waller & Gilbert 1982; Mallet 1984, 1986a). The locations of the roosts of *H. charitonia* and *H. erato* are usually 50–500 m from feeding sites, and are probably learned because these butterflies orient to their roost sites using landmarks rather than characteristics of the perches themselves (Jones 1930; Mallet 1986a). *H. erato* that roost together at night often differ consistently in their diurnal movements, suggesting that daytime home range movements are also learned rather than imposed by the environment (Mallet 1986a). In past studies, mark–recapture techniques were used to investigate these behaviours, so it is of interest to know whether capture, handling and marking affect the probability of return to sites within the home range. Some studies have used Lincoln Index-based mark–recapture methods to estimate population size and daily survival rates of *Heliconius* (Turner 1971; Ehrlich & Gilbert 1973; Cook, Thomason & Young 1976; Mallet & Jackson 1980); these estimates will be inaccurate if handling affects the probability of recapture. Mallet & Jackson (1980) noticed that individuals of *Heliconius xanthocles* seemed to avoid sites where they had previously been captured. In this paper, we present results that permit a fine-scale analysis of handling effects in five species of *Heliconius* from Costa Rica. As well as discussing the importance of our results for ecological studies, we show how the natural equivalent of a handling effect might help an insect to survive in a complex biotic environment.

MATERIALS AND METHODS

During a long-term study at Sirena, Parque Nacional Corcovado, Peninsula de Osa, Costa Rica, we captured, marked and released individuals of ten species of *Heliconius*:

this work is reviewed by Gilbert 1984. In the experiments and observations described here, we saw only the most common of these species: *H. erato petiverana* Doubleday, *H. melpomene rosina* Boisduval, *H. hecale zuleika* Hewitson, *H. ismenius clarescens* Butler, and *H. pachinus* Salvin. For colour illustrations of the species see Gilbert (1984) and De Vries (1986).

We used a standard method for marking *Heliconius* (Ehrlich & Gilbert 1973): we caught each adult individual with a net, wrote a unique number on the undersides of its wings with a waterproof pen, recorded data on its sex, wing wear, and behaviour, and then immediately released the butterfly at the site of capture. We also recaptured *Heliconius* with nets, but recapture involved less handling than capture because it was not necessary to renumber marked butterflies.

One of us (J.M.) also used non-standard marking methods which avoid the potential traumata of capture and handling. In a pupal release experiment of 1981, caterpillars of *H. erato* were reared under optimal conditions and then replaced, as pupae before eclosion, on the individual host-plant where they had been laid as eggs by wild females. Individually coded spot marks (system of Ehrlich & Davidson 1960) were placed, using a waterproof pen, on the undersides of the wings of 108 *H. erato* just after eclosion. Forty-nine of these butterflies were later recaptured or found on roosts. These releases were performed to examine the dispersal of newly-eclosed *H. erato*; for details, see Mallet (1986b). A further six individuals were spot-marked at night on the gregarious roosts, without causing flight. Another two individuals were not spot-marked, but had characteristic wing damage. All of these individuals were thus identifiable on nocturnal roosts before capture, and at capture we numbered them using the standard method.

We investigated the behaviour of numbered butterflies by observing and capturing individuals feeding at flowers of *Psiguria warscewiczii* vines. Butterflies were handled and observed (experimental days) or observed only (control days) on 4 days over a 7-day period, with each experimental or control day separated by a day on which no captures or observations were made. Each worker watched at a single station where *Psiguria* flowers were present on all 4 days. Two of the five stations used were only 30 m apart, but the remainder were separated by at least 100 m from their nearest neighbours. There were many other *Psiguria* and other suitable flowers blooming in the vicinity, so our coverage of local floral resources was not at all complete. On the control days 3 and 5, the butterflies were allowed to visit the flowers without handling, and each individual was visually identified and recorded every time it visited. On the experimental days 1 and 7, all *Heliconius* visitors were captured, handled and marked, or recaptured and handled, using the standard method. To make sure that we recorded flower visitors with equal probability on all days, we visually identified the marked butterflies on days 1 and 7 before netting them. In cases where a single individual was seen or captured at two or more sites, we analysed that individual's behaviour only at the site where it was first captured or seen (10% of all *Heliconius* were in this category). We have used these experiments to compare the return frequencies of handled and unhandled *Heliconius*, on the same (Results, section 1) and on subsequent days (Results, section 2).

Individual *H. erato*, *H. melpomene*, and occasional *H. hecale* can be found and identified on their nocturnal roosts because they usually roost low, less than 2 m above ground (Mallet 1984, 1986a). During July 1980, more than twenty gregarious roost sites were found and visited nightly by J.M., and the identification number of each individual was recorded. We use these data combined with records of diurnal capture (mostly not from the experiments described above) to determine the effect of handling on the roosting habits of fifty-six individual *Heliconius* (Results, section 3). In 1981, when the *H. erato* pupal release experiment was in progress (Mallet 1986b), many *H. erato* roosts were found and visited at least once a week. Numbered, spot-marked or otherwise identifiable individuals were recorded from each roost. We later captured and numbered, using the standard method, seventeen previously unhandled individuals which had already been observed roosting. We use these individuals to investigate the effect of initial capture and marking on return to the roost (Results, section 4).

We found no behavioural differences between sites or sexes, so the data were combined within each species for the analysis.

RESULTS

(1) *Effect of handling on returns to flowers on the same day*

A smaller percentage of *Heliconius* returned to a given *Psiguria* on days 1 (15%) and 7 (15%) after being handled on those same days than returned after observation alone on days 3 (59%) and 5 (63%; Table 1). Significantly fewer *H. hecale* ($\chi_1^2 = 8{\cdot}81$, $P < 0{\cdot}005$), *H. ismenius* (Fisher exact $P = 0{\cdot}017$), and combined *Heliconius* ($\chi_1^2 = 20{\cdot}32$, $P < 0{\cdot}0001$) revisited the experimental flowers on day 1 than on day 3 (used as a control for day 1); and significantly fewer *H. hecale* ($\chi_1^2 = 16{\cdot}61$, $P < 0{\cdot}001$), *H. pachinus* (Fisher exact $P = 0{\cdot}006$), and combined *Heliconius* ($\chi_1^2 = 28{\cdot}48$, $P < 0{\cdot}0001$) revisited on day 7 than on day 5 (used as a control for day 7). The median numbers of visits per individual were significantly higher on days when butterflies were unmolested for these same species/day combinations (Mann-Whitney *U*-tests on original data).

(2) *Effect of handling on returns to flowers on subsequent days*

A lower percentage of handled than unhandled individuals returned to *Psiguria* plants on subsequent days (Table 1). On day 3 only 17% returned of those which visited (and were handled) on day 1, compared with 51% returned on day 5 of those that visited (unmolested) on day 3. This difference is significant overall ($\chi_1^2 = 12{\cdot}77$, $P < 0{\cdot}001$) and individually significant for one of the abundant species, *H. ismenius* (Fisher exact $P = 0{\cdot}013$). The effect of handling may last up to 4 days: only 25% of those which visited *Psiguria* and were handled on day 1 returned on day 5, while 43% of those which visited on day 3 (unmolested) returned on day 7; however this difference was not significant ($\chi_1^2 = 3{\cdot}30$, for combined *Heliconius*).

(3) *Effect of handling during recapture on roost site fidelity*

The above results show that capture and handling reduce the tendency of *Heliconius* to return to flowers. Three explanations for this seem possible: (i) butterflies which have been captured might abandon their home ranges and disperse from the site; (ii) their survival might be reduced; (iii) they might remain within the area, but avoid the specific *Psiguria* patch where they had been captured and handled. Observations of gregarious roosts were used to test these possibilities.

After handling, marked *Heliconius* almost always returned to the roost they had previously used. In 1980, there were roosting records for fifty-six marked *Heliconius* which had at least one capture on a day that immediately followed a recorded night on the roost. For each of these butterflies, we chose the first such capture day in the individual's record of captures. Of the fifty-six, all but one returned to the roost (Table 2a). It is likely

TABLE 1. Recaptures at *Psiguria* on the same and subsequent days

Species	Day sighted or captured	Total individs. captured or sighted each day	Percentage of individuals resighted or recaptured on particular days				Mean number of visits per individual
			Day 1	Day 3	Day 5	Day 7	
H. hecale, $n = 54$ individuals							
	1	22	14	27	23	23	1·2
	3	17		59	47	35	3·1
	5	17			82	71	4·9
	7	26				19	1·3
H. ismenius, $n = 41$ individuals							
	1	19	26	16	32	26	1·3
	3	9		78	67	67	3·7
	5	17			41	65	5·4
	7	24				17	1·2
H. melpomene, $n = 5$ individuals							
	1	2	0	0	50	0	1
	3	1		0	0	0	1
	5	1			0	0	1
	7	2				0	1
H. erato, $n = 15$ individuals							
	1	7	0	0	0	29	1
	3	4		50	50	0	1·5
	5	3			67	0	2·0
	7	5				0	1
H. pachinus, $n = 21$ individuals							
	1	9	11	11	33	22	1·1
	3	6		50	50	67	3·0
	5	8			75	63	4·9
	7	11				9	1·1
All *Heliconius*, $n = 136$ individuals							
	1	59	15	17	25	24	1·2
	3	37		59	51	43	3·2
	5	46			63	61	4·8
	7	68				15	1·3

TABLE 2. The effect of capture on roosting fidelity

Species	Number observed roosting the night before	Number not returning to roost the night of handling or non-handling	Number not returning on next night	Number never returning to roost
(a) After handling				
H. erato	45	16	12	1
H. melpomene	8	1	2	0
H. hecale	3	0	1	0
(b) After non-handling				
H. erato	44	6	10	1
H. melpomene	8	0	0	0
H. hecale	3	1	1	1

that the tendency of an individual *Heliconius* to disappear from the roost does not change over a short period of constant conditions. This leads to a null hypothesis that the tendency to return to the roost after a day without handling (but close to the time of handling) will be the same as the tendency to return to the roost after a day in which handling took place. To select the control day of non-handling, we selected a day in the record of each individual which was immediately preceded by a night on the roost, and during which the individual was not captured. The control day was chosen as the first available for each individual after the handling episode used above, and returns to the roost on that night and on subsequent nights are recorded in Table 2b. The same individuals appear in Table 2b as in Table 2a, except for the single *H. erato* that was never seen again after the handling episode. Comparing the numbers of individuals that never returned after handling (1 of 56) with the numbers that never returned after non-handling (2 of 55), the null hypothesis of equal tendency to roost cannot be rejected (by inspection). However, handling does appear to cause the temporary absence of some individuals from the roost the night after handling: 17 of 56 did not return to the roost the night after handling compared with 7 of 55 which did not return the night after non-handling (Table 2; $\chi_1^2 = 5{\cdot}09$, $P < 0{\cdot}025$). There is also a significant difference within *H. erato* alone ($\chi_1^2 = 5{\cdot}74$, $P < 0{\cdot}025$). The comparison on the next night after the chosen days is not significant (Table 2a, b: $\chi_1^2 = 0{\cdot}75$, for combined *Heliconius*), suggesting that the handling effect on roosting lasts no longer than one day.

(4) *Effect of handling during capture and marking on roost site fidelity*

So far, all of the observations made without handling *Heliconius* (at flowers and on the roost) have relied on at least one initial handling event during which each individual was marked. Therefore, our observations and experiments in sections 1–3 do not show whether the initial handling and marking episode itself has any effect. By spot-marking newly eclosed or roosting *H. erato*, it was possible to mark individuals without handling them. Some of these butterflies were observed and identified on roosts before they were captured, and so can be used to gauge the effect of initial capture, handling, and marking on wild butterflies.

Of 108 *H. erato* released as pupae (Mallet 1986b), eleven individuals were captured and marked after at least one night's roosting observation. All of these returned to the roost at least once (on average 9·1 observed nights) after capture. This 100% return of captured and marked individuals to their roosts suggests that capture and marking have little effect on the roosting sites of these butterflies. A further eight unmarked *H. erato* were also identifiable on roosts by means of wing damage or because they had been spot-marked on the roosts. Of these, six were eventually captured, handled, and marked with standard numbers. Of the six, five returned to their roosts on subsequent nights. So, overall, only one out of seventeen roosting butterflies (6%) disappeared after its first capture, and even this disappearance could have been due to natural death or dispersal. We do not know whether handling reduces the probability that spot-marked *H. erato* return to the roost in the short term (as with the previously handled butterflies in section 3) because roosting observations were not made nightly in 1981. Although it is difficult to find an appropriate null hypothesis for these data, we can conclude that initial capture and handling does not affect the long-term roosting behaviour of a high proportion of individuals.

DISCUSSION

This work shows that *Heliconius* which have been handled at *Psiguria* plants are less likely to return to the same or subsequent days than unhandled individuals. We have also demonstrated that handling does not cause a complete change of home range or reduced survival of individuals, since capture, marking, and handling rarely, if ever, prevent individuals from returning to their nocturnal roost sites. The only effect of capture on roosting is short-term; individuals less frequently returned to roosts on the first evening after handling than on subsequent evenings immediately after a day of non-handling. As far as we are aware, this is the first time that handling has been shown to cause insects to avoid capture sites in one part of their living area while maintaining their presence in another part of that area.

This conclusion could be criticized on the basis that the more abundant species (*H. hecale*, *H. ismenius*, and *H. pachinus*) were the main contributors to the handling experiments performed at *Psiguria* flowers, whereas the *H. erato* roosts contributed most to the examination of handling effects on roosting behaviour. However, there is no reason to suspect that *Heliconius* species behave very differently from each other in this respect, and our data show consistent handling effects on visits to *Psiguria*, and a consistent absence of handling effects on roost fidelity, for all *Heliconius* on which we have data.

The handling effects we have demonstrated last at least 2 days. Judging from the regularity with which *Heliconius* are recaptured at their sites of capture, handling may not affect behaviour much longer, but this remains to be proved. Because handling may have at least a short-term effect, behavioural observations of marked *Heliconius* should, if possible, be made without handling. Our group now uses a variety of methods to identify marked butterflies at flowers or at roosts; binoculars, telescopes and movie cameras are employed, as well as the naked eye.

Mark–recapture estimates of population size are bound to be affected by the handling effects we have encountered. A Lincoln Index estimate of the population of *Heliconius* individuals from which flower visitors are drawn, based on the numbers of visitors on days 1 and 3 of the handling experiment (Table 1), gives $59 \times 37/10 = 218$. The estimate between days 3 and 5 gives $37 \times 46/19 = 90$; that between 5 and 7 gives $46 \times 68/28 = 112$. The large numbers of butterflies that were not recaptured after being handled on day 1 cause the population size to be overestimated when the estimate is based on resightings on day 3, but the next two estimates are consistent at about half of the first estimate. However, ecologists usually want to estimate the total population size, not just the population size of individuals that have learned the whereabouts of a particular group of flowers. It is difficult to estimate total population sizes of insects like *Heliconius* because home range behaviour restricts the number of individuals the ecologist encounters; this effect causes the numbers to be underestimated even if the habitat is sampled randomly. The handling effects we have discovered might even increase the accuracy of the estimates of *Heliconius* numbers by causing some mixing of the population. However, the tendency to overestimate because of net-shyness, and the tendency to underestimate because of non-random movement are both unpredictable. We agree with Morton (1984) that population estimates based on the Lincoln Index should be taken as an approximate guide only, and that no amount of mathematical refinement will make them any better because of their reliance on random (or at least a predictable model of) mixing of marked and unmarked individuals. The non-random behaviour of animals like *Heliconius* makes estimating population size difficult.

The only hope may be to sample almost all individuals in a habitat, although this may be difficult for species which are short-lived, or which fly too high to be readily captured. At very high sampling intensities the Lincoln Index becomes useless because the total number known alive converges to the Lincoln estimate. At Sirena, usually more than 75% of *H. erato* seen on roosts were marked, so the errors in population estimates of at least this species (Gilbert 1984) should be low. High recapture rates in all species of *Heliconius* that have been studied (Turner 1971; Ehrlich & Gilbert 1973; Cook, Thomason & Young

1976; Mallet & Jackson 1980) suggest that the errors are not big, although as pointed out by Lederhouse (1982) and Morton (1982, 1984), high rates of recapture do not necessarily show that marked and unmarked individuals are captured at random.

These experiments also give some insight into the natural ecology of *Heliconius*. Butterflies exploit the environment in two distinct ways. Some appear to wander widely in search of nectar and oviposition plants: these nomads include Danainae (Eanes & Koehn 1979; Paul Davis, pers. comm.), Ithomiinae (Brown & Vasconcelos Neto 1976), and American troidine Papilionidae (Brown, Damman & Feeny 1981). Other butterflies such as *Euphydryas* (Gilbert & Singer 1973) and *Heliconius* (Ehrlich & Gilbert 1973) have very restricted home range movements; individuals repeatedly visit sites where adult and larval food-plants grow. In *Heliconius* the home range includes repeatedly visited perches used for gregarious roosting (Mallet 1986a). Between these nomadic and home range extremes fall many other (perhaps most) butterflies, which disperse widely but can set up temporary home ranges (e.g. the heliconiine *Agraulis vanillae*; J. Mallet & J. Longino, unpublished). Gilbert (1975) points out that the home ranges of *Heliconius* are an adaptation to permit full exploitation of rare, but temporarily constant adult and larval food-plants. It follows that nomadic butterflies should have commoner and/or less stable resources, though we are not aware that this has been tested.

Butterflies like *Heliconius* that have learned home ranges must be positively reinforced by pollen, nectar, oviposition, mating and safe roosting sites. Similarly, if a butterfly has the navigational abilities and memory necessary for exploiting a home range, it must also be able to avoid unprofitable sites. One explanation of the handling effects we have observed is that *Heliconius* avoid *Psiguria* plants where they have not found nectar or pollen; in our experiment they were captured before they fed.

A second explanation is that the butterflies avoid places where they have been attacked by predators, a trauma perhaps similar to net capture. Butterfly-eating birds such as *Galbula* spp., the jacamars (Sherry 1983; Chai 1986) hunt from the same perch for hours, and often return on subsequent days. Since *Heliconius* are unpalatable and warningly coloured, an individual that has escaped alive from a predator's jaws might be less liable to future attack by the same animal. However, jacamars do attack and even eat *Heliconius* if very hungry (Chai 1986), though they usually avoid them if other prey are available. *Heliconius* might simply avoid the traumatic site, or they may be able to see and avoid the predator (or human) itself. In any case, all of these explanations involve the avoidance of unprofitable areas of a home range.

These results are relevant for studies of a wide variety of animals, many of which may have the 'intelligence' to avoid capture or capture sites in the way we have demonstrated. Most insects have some site-specific behaviour (e.g. temporary home range behaviour, or male perching territories) which might be prone to a handling effect of this sort. Although circumstantial evidence implicates dispersal as a cause of handling effect in one study of *Papilio* (Lederhouse 1982), most butterflies and many other insects seem capable of learning profitable sites for feeding, mating or roosting within an area, and of avoiding those parts of an area which are unprofitable as was found here. Insect behaviour could be vastly more complex and subtle than is catered for in most ecological studies.

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