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A LABORATORY STUDY OF
GREGARIOUS ROOSTING IN
THE BUTTERFLY
HELICONIUS MELPOMENE

by

James L. B. MALLETT (1)

(Department of Agricultural Biology,
University of Newcastle-upon-Tyne,
Newcastle-upon-Tyne,
England.) (2)

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all correspondence: % O.T.S., Ciudad Universitaria, COSTA RICA.
(2) Present address: Department of Zoology, University of Texas, Austin,
Texas 78712, U.S.A.

1) INTRODUCTION

A certain amount of recent research has been focussed on butterflies of the genus Heliconius which exhibit some almost vertebrate-like behaviour. The adults form tight population groups or demes, and, during the daytime, individuals from a deme move within a particular home range (TURNER, 1971; EHRLICH & GILBERT, 1973; COOK et al., 1976; MALLET & JACKSON, 1980). At sunset the adults of some species cluster together to roost on specific twigs, and individuals are faithful to the roost, returning to the same site night after night (JONES, 1930; YOUNG & THOMASON, 1975; YOUNG & CAROLAN, 1976; YOUNG, 1978).

A number of explanations have been proposed to explain this nocturnal roosting behaviour. JONES (1930) suggested that the individuals of the presumably distasteful and aposematic species H. charitonia (L.) clump together so as to warn away predators more effectively than would solitary butterflies. More recently BENSON (1971) suggested that the tight deme structure and presumed low genetic interchange between demes in Heliconius allowed the initial evolution of aposematism to arise by kin selection. GILBERT (1975) proposed that other altruisms may also be maintained by kin selection in Heliconius, for example the possibility that experienced individuals lead inexperienced close relatives to scarce food plants. The essence of these kin selection theories ^{is} ~~are~~ that altruism, such as the initial evolution of bright warning colour, ^{is} ~~are~~ likely to be selected against. An insect which is 'selfish' is likely to survive longer and produce more offspring. But if the altruistic act (such as self-sacrifice necessary to teach avian predators that butterflies with similar colour patterns are distasteful), benefits the close kin of an individual, this may in some circumstances increase the 'inclusive fitness' of that individual. By protecting its own kin, an individual may increase the likelihood that its own genes, which it shares with close relatives, will be passed on to future generations (HAMILTON, 1964).

In spite of these rather involved theories, very little groundwork has been done on the actual roosting behaviour of Heliconius, although BENSON (1971) saw the roost as the central focus of the home range, and to GILBERT (1975) the roost was the site of 'information transfer' between close kin. JONES (1930) observed day to day fidelity of marked individuals to the roost in H. charitonia. TURNER (1971) and BENSON (1972) showed that individuals of H. erato (L.) from a particular home range normally roosted within that home range. YOUNG & THOMASON (1975) studied roost fidelity over several months in H. charitonia. YOUNG & CAROLAN (1976) further studied day to day roost fidelity in the same species and noticed 'intra-specific encounters' on the roost, which they assumed to be aggressive bids by flying individuals to displace roosting individuals. They also found that butterflies tended to arrive on the roost earlier in the afternoon and leave the roost later in the morning on cold, wet, cloudy days than on warm, sunny days.

In the present study experimental techniques were used to determine the factors that influence roosting of H. melpomene thelxiope, a native of the Belém region, Brazil. The study was performed under seminatural conditions in a greenhouse laboratory.

2) MATERIALS AND METHODS

(i) The greenhouse insectary

A greenhouse on the roof of the Department of Agriculture, University of Newcastle-upon-Tyne, was used as an insectary. It is of irregular polyhedral shape, about 9m³ in volume. Thermostatically controlled air-conditioning and pipe and blower heating were fitted. In addition the outside windows were double-glazed, which helped to avoid cold traps near the windows where butterflies could have collected.

(ii) Rearing H. melpomene

The H. melpomene stock was obtained from the Department of Genetics insectary, at the University of Liverpool. By maintaining about five plants of Passiflora caerulea (Passion Flower, a convenient larval host plant) in the insectary and five plants in a separate recovery greenhouse, and changing plants when they appeared to be suffering damaging levels of attack, it was possible to maintain a stock of over 10 and sometimes over 30 H. melpomene adults alive at any one time.

Adult food sources are important for Heliconius butterflies (GILBERT, 1972), and under some conditions they can live for up to six months in the field (EHRlich & GILBERT, 1973) if they are given access to specific pollen donor plants. Honey solution was provided in artificial flowers made from small specimen tubes filled with a 30:70 (approx.) solution of honey:water. The solution was usually changed daily, and not less than once every two days as it was liable to ferment. Cut and potted flowers were also provided when available. Senecio squalida (Ragwort) is very common on weed patches in Newcastle, and this flower provides

both nectar and pollen. Pollen can also be gathered by H. melpomene from Impatiens (Busy lizzy) and Pelargonium (Geraniums). Potted Asclepias curassavica and cut Buddleia are also good sources of nectar. With these food sources available, adult life span could be as much as three months.

(iii) Marking individual H. melpomene

Each individual was marked, using an Indian ink pen, with an unique number, and its date of eclosion from the pupa (if known), age and sex recorded.

(iv) Video recordings of roosting behaviour

Sony cassette system video apparatus was used to obtain the results in section 3 (i). The camera was fitted with a powerful zoom/macro lens. The editing monitor had a facility for 1/10 speed running, timing of sequences to the nearest 0.1 sec., and a lockable pause control. Using these facilities, the ethograms of figures 5-8 were obtained. The pause control permitted key incidents to be frozen on the monitor screen and traced, but details of the butterfly leg position &c were often difficult to make out. Individuals could be identified after they had roosted, so that it was often possible to determine the sex of individuals interacting on the roost.

(v) Recordings of roosting time

If the times of roosting were to be determined on any evening, the recording was started at least one hour before sunset. The number of individuals on the roost was counted once every five minutes (at the clock marks, e.g. 1810, 1815, 1820 &c), until all the butterflies ceased flying. The 'time of 100% roosting'

was thus the clock mark that came after the time that the last butterfly roosted. In this way the results in section 3 (iii) were obtained.

The results in section 3 (ii) were obtained by noting the marked number of each butterfly during counting after every five minute period. This was a laborious process which required great patience in order not to disturb the roosted butterflies while approaching close enough to see the marks on their undersides. It was only performed when very young individuals were in the populations.

(vi) Weather and sunset

The only light used in the greenhouse was from outside the windowpanes. Thus the butterflies could only see natural light, and a small amount of street-light eight storeys below. The time of sunset was calculated by means of a computer programme from the Hewlett-Packard 2000E BASIC library at NUMAC, Newcastle University. The programme calculates astronomical solar phenomena for any date or station. The calculated figures obtained in this way appeared to be accurate according to the Newcastle Meteorological Office data, which was itself interpolated from the 'Nautical Almanac'. The sunset was rounded to the nearest five minute clock mark, and 'minutes before sunset' thus refers to the number of clock marks before this approximate sunset time that a particular roosting event occurred.

The light meter used in this study was a 'Corning-Eel portable photoelectric photometer', used for public health measurements in England. The meter readings are converted into Lux light units by multiplying by 10 and a correction factor for daylight of 0.89.

Temperature was measured using a maximum/minimum thermometer, both before and after the observation period on any evening. The mean of the two readings

was used in all discussions of the effect of temperature.

Measurements of atmospheric pressure and cloud cover were obtained from the Meteorological Office, Newcastle-upon-Tyne. The met. office takes readings hourly at about a quarter to the hour, and the reading nearest sunset was chosen for the analysis of the effect of climatic factors in section 3 (iii).

(vii) The choice experiments

The apparatus finally used in the choice experiments of section 3 (iv) is shown in figure 1. The wire cross-member is 40 cm from the tip of one butterfly or model to the other. The vertical member was 20 cm long and attached to the window frame by a drawing pin at the top. The cross member was 174cm from the ground. A background of white or black card was taped to the glass about 2 cm behind the choice apparatus. Various different models (shown life-size in figure 13, section 3 (iv)), could be placed on the side arms to test which were the most attractive to flying butterflies.

Each run took up a whole sunset flying period, and the numbers of close approaches of all individuals in the insectary to each model or dead individual ~~was~~ ^{were} recorded. The individual butterfly identities could not be made out, so the responses recorded should be regarded as properties of the whole population. Experiments with single individuals were not attempted.

(viii) UV photography

The photography was kindly undertaken by Miss A. Rutherford of the Department of Photography, University of Newcastle. Unfortunately no UV-pass filter was available that could be lens-mounted. Bowans Multilec electronic flashes were

used and these were covered by Chance OX9A UV-pass filters. The camera used was a Leica with a Leitz Wetzlar Focotar 50 mm lens (not designed for UV photography). The problems with using this system are (a) that the glass of the lens probably itself acts as a UV filter and (b) the light entering the camera from the butterflies could have been partially generated by fluorescence. (b) can be corrected for by placing a UV filter (Wratten 2E) over the lens in order to obtain a comparison between UV + fluorescence photographs (without 2E filter) and fluorescence only photographs (with 2E filter). In all cases fluorescence was very low when pairs of photographs were taken under identical conditions of aperture, filmspeed and development.

The butterflies photographed were mainly specimens collected in Colombia during 1977.

3) RESULTS

(i) General description of roosting behaviour and intraspecific encounters

The sequence of behaviour that leads up to final roosting can be summarized as follows:-

About an hour or two before sunset, butterflies in the field collect near the roosting area (H. erato, H. charitonia, H. sara and H. melpomene - CRANE, 1955; TURNER, 1971; BENSON, 1971, 1972; YOUNG & THOMASON, 1975; YOUNG & CAROLAN, 1976, and personal observations). This could not be shown in the small greenhouse cubicle used in the present study.

Most of the H. melpomene in the greenhouse 'perch' (that is, tarsi on a leaf, stalk or other surface, wings folded in the upright position). A few individuals fly about intermittently, hovering momentarily near the roost or indulging in 'social chasing behaviour' (CRANE, 1955) with other flying individuals.

As the sun lowers in the sky, some of the butterflies leave their perching positions and fly up to the roost. After hovering near the different twigs on the roost, they eventually settle in the 'roosting' position (that is, hanging by their tarsal claws from a twig on the roost, with their wings folded downwards -- figure 2). Roosts in the field and in the lab always seem to have certain physical characteristics: (a) the individual twigs from which Heliconius hang are very slender (ca. 1 mm in diameter) and must usually be situated over about 1 m height of clear airspace. (b) there must be a number of such twigs within the roost such that a number of individuals can collect there. (c) the usual substrate for roosting in Heliconius is a tangle of dead creepers suspended from living vegetation. These are apparently ideal because they have plenty

of laterally-directed tendrils of sufficient diameter to comply with conditions (a) and (b). Very fine wire or dead twigs can substitute for dead tendrils.

Roosting individuals of H. melpomene show a sexual difference in wing-folding. In figure 2 it can be seen that the male has most of the forewing visible, whereas the female holds the hindwing over the forewing, partially covering the forewing markings. In figure 3 the female hindwing covers the forewing markings even more completely. The position of the female in figure 3 is the same as that adopted by solitarily sleeping H. numata[♀] in the laboratory, and by communally roosting female H. sara, H. erato (personal observations) and H. charitonia (see photos in YOUNG & THOMASON, 1975) in the field. The female sleeping position is only taken up at sunset: after dark, the female position relaxes to that of the male in figure 2, but can be reinduced with a flashlight. Female H. melpomene in the greenhouse do not always have the forewings fully covered as in figure 3, even at sunset; this could be due to suboptimal laboratory conditions, to behavioural degeneracy in the ten-year-old stock or to genuine species-specific differences.

Other previously perched individuals now take to the wing, either alone or in small groups. They patrol the roosting area, chasing other flying butterflies or hovering near perched individuals. Also at this time, flying individuals may perform brief hovering bouts at roosted individuals: this behaviour will subsequently be referred to as 'intraspecific encounters' or 'roosting interactions'. Roosting interactions may be (flying protagonists first, roosted recipients second), male-male, male-female, female-male, or female-female. However the most prominent of these are the male-female interactions (figure 4), which may last up to several minutes as opposed to of the order of a second for all other types of interactions. A number of different interactions were recorded as ethograms, taken from videotape recordings, in figures 5 - 8.

The ethogram in figure 5A shows a male-female courtship interaction, taken from a video recording made during the day. Figures 5B, 5C and 6 show similar approaches by single males to single roosting females. The male behaviour during courtship is similar to male behaviour during male-female roosting interactions in the following respects: (a) the male hovers forward over the female and performs a number of wingflicks during which androconial friction patches on the anterior part of the hindwing are exposed (illustration figure 4; recorded as vertical bars on ethograms, figures 5A and 6, first 20 secs.). The wingflicks cause a rapid backwards motion, whereupon the slow forward hovering begins again. The whole process takes about 1 sec., and may be repeated many times for several minutes, both in unsuccessful courtship and in roosting interactions. (b) sometimes, during a roosting interaction, the male lands beside the female on the roost, and, exposing its friction patches and recurving its abdomen, attempts to mate with the female (illustrated in figure 9 b; ethogram figure 6, t=68 sec.).

Female behaviour during daytime courtship and male-female roosting interactions is also similar, as follows (the chief difference being that the female is upside-down when being approached on the roost): (a) the female opens its wings and usually maintains them spread while the male is hovering nearby (figure 4). Here it should be mentioned that the closure of wings by a female on the approach of a male H. melpomene usually indicates readiness to mate; whereas, if the wings are open, even the most persistent male finds it impossible to reach the female genital opening with the tip of its own abdomen. If the male departs, the wings are eventually closed (figure 6, t=117 sec. onwards). (b) the female intermittently flutters its wings for short periods when approached by a male. The wing-fluttering is accompanied by anal gland eversion (illustration figure 9A). The behaviour sequences are similar, but not identical to those recorded by CRANE (1955, 1957) for courting males and unreceptive females of H. erato. The scent of a mated female Heliconius probably acts as an 'antiaphrodisiac' pheromone (GILBERT, 1976).

Male-male roosting interactions are less extended than male-female interactions (ethogram figure 7). When an individual (either male or female) approaches a roosting male, the latter may respond by fluttering its wings for a short period (figure 9C), exposing its friction patches and opening its claspers. Female-male and female-female interactions are also of short duration (ethogram figure 8). In addition to differences in duration, male-male, female-male and female-female roosting interactions do not necessarily include wing-flapping reactions of the recipient, whereas intermittent wing-flapping reactions of a female during long duration ^{approaches} of a male are characteristic. Durations of roosting interactions recorded on video are shown in table 1.

The durations of female-male interactions were not significantly different from the durations of female-female interactions ($t=0.775$, d.f.=10, $P>0.4$, two-tailed), and can therefore be combined. The durations of male-male interactions were not significantly different from the durations of female-female and female-male interactions combined ($t=0.886$, d.f.=20, $P>0.3$, two-tailed). On the other hand male-female interactions last significantly longer than male-male interactions ($t=3.27$, d.f.=11.1, $P<0.01$, two-tailed, variances assumed unequal) and female-male and female-female interactions combined ($t=3.34$, d.f.=11.0, $P<0.01$, two-tailed, variances assumed unequal). In addition, the duration variance ratio, of male-female to all other types of interaction combined, is significant ($F=21.0^2/1.05^2=440$, d.f.₁=11, d.f.₂=21, $P<0.01$). In conclusion, roosting interactions are homogeneous with mean durations of about one second, apart from male-female interactions which have significantly higher means and variances.

The outcomes of these interactions can be almost any of those imaginable.

- (a) The normal outcome is that the flying protagonist departs to continue to fly about the roosting area, or to hover at other roosted or perched individuals.
- (b) The protagonist may depart to roost either near or some distance away from the recipient of its previous attentions.
- (c) The protagonist may disturb the

recipient so that both fly away. Or (d), the protagonist may usurp the recipient and itself roost on the vacated twig. These possibilities are all shown in the ethograms, figures 5-8. The likelihoods of the different outcomes appear to decrease from (a) to (d). But the overall outcome of the behaviour is always the same: after sunset, almost all of the butterflies are found to be roosting on the same group of twigs provided, night after night.

(ii) The effect of age and sex on time of roosting in *H. melpomene*

Data for the variation in time of roosting with age are plotted in figures 10 and 11. In figure 10, the ambient temperature in the insectary was around 23°C and data were recorded on 28 March, 5,9,10,16 and 17 April 1978. Weather conditions were sunny, cloudy to clear, sunny to overcast, sunny to overcast, overcast but bright, and overcast, respectively. Figure 11 shows similar data recorded at an ambient temperature of 28°C for the dates 19, 20, 22, June and 10 and 23 July 1978. Weather conditions were sunny, cloudy but some sun, cloudy with sunny spells, sunny and sunny respectively. The presence of young individuals in the populations was used to select the dates on which the data were collected rather than weather conditions, and it is here assumed that the presence of young, and the ages of the individuals are effectively random with respect to the weather of the dates on which data were collected. This is important as section 3 (iii) shows that weather has a rather strong influence on time of roosting in *H. melpomene*.

It can be seen from figures 10 and 11 that individuals less than about five days old roost earlier than older individuals. This corresponds to a period of relative inactivity after hatching in the butterflies, when flight is weak and the wings are not fully hardened. During this time the individuals do not appear to feed, and the males do not mate. Although there is no clear cut-

off age when individuals start to roost nearer to sunset, it can be seen that at both temperatures the butterflies come out of this 'callow' phase at about five days. The difference in roosting time between callow and mature adults can now be tested. At 23°C: young individuals (≤ 4 days) roosted at a mean of 97.5 minutes before sunset, $s=5.84$, $n=12$; old individuals (> 4 days) roosted at a mean of 55.6 mins. before sunset, $s=33.4$, $n=48$; $t=8.19$, $d.f.=56.4$ (variances assumed unequal); or $t=4.30$, $d.f.=58$ (variances assumed equal); in both cases $P < 0.001$ (two-tailed). At 28°C: young individuals (≤ 4 days) roosted at a mean of 66.9 mins before sunset, $s=21.6$, $n=18$; old individuals (> 4 days) roosted at a mean of 32.1 mins before sunset, $s=30.0$, $n=96$; $t=5.87$, $d.f.=32.4$ (variances assumed unequal); or $t=4.69$, $d.f.=112$ (variances assumed equal); in both cases $P < 0.001$ (two-tailed). It is concluded that callow individuals roost significantly earlier than older individuals.

Sexual differences might possibly affect roosting time, and the following test was performed on older individuals alone (> 4 days). At 23°C: old males roosted at a mean of 63.1 mins before sunset, $s=27.6$, $n=18$; old females at $m=51.2$ mins before sunset, $s=36.2$, $n=30$; $t=1.20$, $d.f.=46$, $P > 0.2$ (equal variances, two-tailed). At 28°C: old males roosted at a mean of 33.4 mins before sunset, $s=30.9$, $n=55$; old females at $m=30.5$, $s=29.0$, $n=41$; $t=0.463$, $d.f.=94$, $P > 0.6$ (equal variances, two-tailed). Thus the roosting times of males and females do not differ significantly from each other under either temperature regime.

It should be noted that the roosting times and ages of some individual H. melpomene were recorded on more than one day; so that although there are 60 points in fig. 10 and 114 points in fig. 11, these come from only 18 and 55 individuals respectively, and all of the points cannot be said to be strictly independent of one another. However the dates of the recording were chosen because of the presence of young individuals in the population of known

ages, and without any bias towards the roosting times of the individuals present. Male, female and young individual's roosting times, which were recorded more than once on different dates, are therefore affected by similar amounts of non-independence. In spite of these doubts, I believe that the high significance of the young v.s. old comparison demonstrates that the difference is real.

(iii) The effect of weather and light on time of roosting in H. melpomene

Roosting and the time of sunset

Roosting is strongly linked to the time of sunset (figure 12) at different times of year; clearly no statistical test is needed to show this. This suggests that light intensity may be having a direct effect on the time of roosting in individuals, because it would be difficult to imagine other environmental variables, such as temperature (controlled in the greenhouse), humidity or atmospheric pressure, varying as exactly in phase with the time of sunset.

The effect of weather on roosting time

This section examines the variation of roosting time due to light intensity and other factors. In the ensuing analysis the time of 100% roost occupancy has been chosen as this avoids the variation in occupancy time due to the changing proportions of callow and older individuals in the population (see section 3 (ii)). Another sort of error is not so easy to exclude: as clouds moved over the greenhouse, light meter readings become erratic, causing sudden increases or decreases in light intensity. The data for the freak conditions of 25 March 1978 and 11 April 1978 were excluded in order to avoid extreme errors of this kind: (a) On 25 March heavy rain and dark conditions caused an early high roost occupancy (87% and 100% at 45 and 30 mins before sunset respectively), but by

1845 GMT (45 mins before sunset) the weather had cleared to give high light readings. (b) Similarly on 11 April a heavy snowstorm before the start of the experiment caused 100% roost occupancy by 75 and 60 min before sunset in spite of the high light intensity due to sunny conditions from 1835 BST (90 minutes before sunset) onwards.

Table 2 shows 100% roost occupancy times for a number of dates at both 23°C and 28°C, together with data on a number of climatic factors. The results of correlation analysis of the data in table 2 are shown in table 3. It can be seen from table 3 that the time of roosting of the last butterfly correlates best (negatively) with light intensity at 30 mins before sunset. However the (positive) correlation with cloud cover is also significant, although less so. This is probably because the 0-8 scale of cloud cover acts as an inverse guide to light intensity, but does not take into account the thickness of cover, which also has a strong effect on light intensity at ground level. Atmospheric pressure, on the other hand shows no correlation, in spite of the possibility that the weather is linked to pressure. In addition the time of roosting showed no correlation with the mean temperature recorded during each observation period (in spite of thermostatic control, the mean temperature at this time of the evening varied between 23 and 25.25 °C at '23°C' and 25 and 30 °C at '28°C'. Even the use of both sets of temperature data together showed no correlation with roosting time ($r=-0.292$; d.f.=21, $P>0.1$ NS). Unfortunately no accurate data were obtained on humidity: the humidity was kept high by the use of trays full of water and was normally about 80% RH at around sunset, measured with a coil hygrometer.

In conclusion, time of roosting (of the last individual to roost) is best explained by the light intensity on any particular day. The light intensity

itself varies in proportion to the amount of cloud blocking out the light of the sun, but no satisfactory measure of cloud density + cover has been found.

(iv) Experiments to determine the attractiveness of various models to flying individuals of H. melpomene during the roosting period

As shown in section 3 (i), flying H. melpomene approach roosted individuals at about sunset in what were called 'roosting interactions'. It was found that dead individuals or strips of card suspended from wire, and even blobs of black paint on the glasshouse walls were also approached in a similar way by flying individuals. However, prolonged male-female type interactions were absent when models or dead individuals were used. This section describes a number of choice experiments that were used to decide what characteristics of these objects attract flying individuals.

Early experiments showed that dead H. melpomene, with pale markings blacked out and suspended on wires in the roosting position, attract more attention than control dead H. melpomene (equivalent amount of black on black part of wings, pale marks untouched). The result was surprising and exactly the reverse to that found in Colombian rainforest for H. erato (Mallet and Jackson, in prep.). The sex of the dead H. melpomene was apparently unimportant for attraction. Unfortunately, live butterflies frequently used the test apparatus as a roosting twig, which made interpretation of the results subsequent to the roosting of the first individual difficult. The reason for this roosting appears to be that the wire of the apparatus (and often the dead butterflies themselves) provided an ideal roosting substrate. The generally white-painted surfaces and lack of vegetation that was characteristic of the greenhouse environment

provided a very different backdrop to the trunks and vegetation of the Colombian site referred to above, and this suggested that the background could have been important in causing the divergent results of choice experiments on H. erato and H. melpomene.

The revised choice tests allowed backgrounds to be changed (black or white card). The problem of roosting on the apparatus was also avoided because the lack of free space nearby and/or the increased distance from the roost prevented settling by the butterflies. The apparatus is shown in figure 1, and the cardboard models used are shown in figure 13. The results of the experiments are shown in table 4. The position (left or right) of the models could have been important in influencing the choices of individuals, so all experiments (except expts. 5-7) were repeated at least once, by reversing the position of the models and retesting on a second night. The results have been analysed by means of contingency tables using either Fisher's exact test or χ^2 tests (all tests are two-tailed; χ^2 values employ Yates' correction unless otherwise stated); this method tests for the effects of any change of position or pattern of models, or of background in paired experiments, and makes no assumptions (nor deductions) about the expected choice frequencies in any test. Finally it should be mentioned that each individual in any experiment, or in a number of experiments may have approached the models a variable number of times; no attempt was made to determine the identity or sex of the individuals approaching the models. The experiment may be said to have been performed on the whole population in the greenhouse at that time, and the choices made should be regarded as the properties of the population of H. melpomene under seminatural conditions.

Table 4 shows that flying individuals will approach dead H. melpomene of either sex, or pieces of black (figure 13, A & D) or mainly black (B) card on white backgrounds. Less effective are white (C) or partially white (B) models,

or unblackened dead H. melpomene on black backgrounds. Little or no attraction was evinced by black models (A) or blacked dead individuals on black backgrounds, or by all-white models (C) on white backgrounds. The glue used to stick the models to the wire did not cause any attraction on its own (experiments 8 & 9, $P=4 \times 10^{-23}$, in comparison with a dead male on white background).

A dead female with pale markings blacked out was more attractive than a control on a white background (expts 2 & 4, $\chi^2=16.326$, $P<0.001$), and less attractive on a dark background (expts 1 & 3, $P=0.00077$). Comparison of blacked and control dead butterflies in the same position but with different backgrounds (expts 1 & 2, $P=0.00677$; expts 3 & 4, $P=0.00041$), show that these preferences were not due to odour or other preferences for individual dead butterflies. Blacking the pale markings of the control female altered the response of live butterflies (expts 4 & 6, $\chi^2=3.386$ NS; without Yates' correction, $\chi^2=4.050$, $P<0.05$), showing that these differences in response on a white background were probably due to blackening.

A black model (A) is approached as readily as an unblackened dead male; there was no significant choice between them (expts 10 & 11, $P=0.74005$; expts 12 & 13, $\chi^2=1.082$ NS) which suggests that the odour of the dead butterfly is unimportant for the close approach by live individuals.

Experiments 1-4 were repeated with models instead of dead insects by comparing an all-black model (A) with a model with a simple stripe (B). A was more attractive than B on a white background (expts 14 & 15, $P=0.00003$) and less attractive on a black background (expts 16 & 17, $\chi^2=3.494$, $P>0.05$; without Yates' correction, $\chi^2=4.647$, $P<0.05$). Changing the background from black to white caused a reversal of choice between models A and B (expts 14 & 17, $\chi^2=20.345$, $P<0.001$; expts 15 & 16, $P=0.023$) showing that the identity or odour of the

model by itself has no effect on choice between these models. These results are accentuated in the comparison between all-black (A) and all-white (C) models on black or white backgrounds. On a white background A is preferred (expts 20 & (21+22), $P=3 \times 10^{-8}$) whilst on a black background, C is preferred (expts 18 & 19, $P=0.00226$). That this is not due to preferences for individual models is shown by comparing the models A and C in the same positions and varying the background (expts 19 & 20, $P=4 \times 10^{-7}$; expts 18 & (21+22), $P=0.00057$).

The shape of models was apparently unimportant: a black model (A) compared with a crude oblong piece of card (D) evinced little preference from the butterflies (expts 23 & 24, $P=0.19171$) on a white background. The butterflies frequently made approaches to the black background (25cm x 44cm), apparently undirected to one or other of the choices. Perhaps the reason for the small number of close approaches to choices presented on the black background was that the background itself acted as a supernormal stimulus ^{in the} /generally white-painted environment, so making the model stimuli undistinguishable.

UV photography of dead specimens showed that the upperside colours of most Heliconius and other Heliconiini absorb ultraviolet on all wing-pattern colours including yellow on the upperside, whereas yellows and even markings that are red on the upperside may reflect UV on the underside (in the case of H. erato hyدارا and H. clysonimus, pale scales cover the red area on the underside). It has not been thought ^{worthwhile} to figure the UV photographs as problems with the method cast doubt on the results. However the results are in broad agreement with those of CRANE (1954). The species used are shown in table 5.

4) DISCUSSION

i) The response of H. melpomene to light intensity near sunset

Section 3 (iii) shows that roosting behaviour is strongly linked (a) to the time of sunset and (b) to the weather-dependent light intensity at this time. This is best explained as a simple response to decreasing light intensity. The response to light intensity may be adaptive in that on very cloudy afternoons or evenings (i.e. when there is a high probability of rain in their natural habitat) roosting may be accomplished before the onset of rain. CRANE (1955) and YOUNG & CAROLAN (1976) have also shown that roosting is earlier on overcast days or on days with heavy rainfall in H. erato and H. charitonia, which is what is expected from these findings in H. melpomene.

(ii) The mechanism of aggregation in H. melpomene

An experiment by JONES (1930) showed that memory plays a large part in guiding experienced individuals of H. charitonia to the roosting site, rather than odour markers. MALLET & JACKSON (in prep.) found that H. erato in Colombia showed similar memory ability: when the dead vines on which mature adults roosted were destroyed by heavy rain, butterflies roosted on the tendrils on new dead vines hung artificially near the old roosting site. It is probable that experienced H. melpomene have a similar ability to remember the positions of roosting sites, but this was not testable in the 9m³ greenhouse cubicle used in the present study.

Little data is available to suggest how inexperienced wild Heliconius find their way to the roosting site. Possibly the behaviour known as 'social

chasing' (CRANE, 1955, 1957) is important in the field, if younger individuals follow more experienced individuals to the roosting site. Another possibility is that inexperienced individuals find species-specific roosting sites by choosing the correct habitat type for the species. Roosts of Heliconius are frequently found in dead vegetation overhanging streams or paths (personal observations). In the field, very fresh (of unknown age, but presumably callow) individuals /are sometimes found sleeping well away from any roosts, but as they become older, they either join the main roosts or disappear entirely. In section 3 (ii) it was found that individuals of up to 4 days of age roost rather earlier than more mature individuals. If the behaviour of H. melpomene and H. erato is similar in this respect, this result suggests that the callow individuals would be unable to chase maturer individuals to the roost, and are therefore forced to sleep elsewhere.

Given the appropriate light conditions, the flying individuals become attracted to dead H. melpomene or even crude models of roosted individuals (section 3 (iv)). They approach such objects closely, and the fact that such models or dead individuals vary in their attractiveness according to the background against which they are placed shows that this attractiveness is primarily visual, rather than olfactory. In the absence of such models, it is normally other individuals that are roosted which attract this attention. The roosted individuals often respond to these approaches by fluttering their wings and exposing the various pheromone-disseminating structures that are diurnally used in mating (CRANE, 1955, 1957) or unsuccessful courtship (GILBERT, 1976). It seems probable that the flying individuals of H. melpomene may respond to these pheromones by choosing a roosting site very close to such visual stimuli that 'smell right', rather than roosting close to visual stimuli that do not provide the correct odour. There is no clear evidence of this in H. melpomene because of the small size of the greenhouse. However, the field results of MALLET &

JACKSON (in prep.) show that although H. erato will approach roosting individuals of H. sara (as well as dead H. sara hung in imitation of the roosting position), roosts of H. sara and H. erato are usually species-specific and set apart from each other.

If the above assumptions are correct, it seems that young flying H. melpomene in the roosting area use visual stimuli as primary components for attraction and pheromones as secondary (close-range) components that induce landing near other roosted individuals (see table 6). Although not proved, this hypothesis seems testable.

The visual stimuli that attract H. melpomene to conspecifics on the roost, dead individuals or models of roosted individuals, are likely to involve parts of the electromagnetic spectrum invisible to the vertebrate eye. CRANE (1955) showed that H. erato can differentiate between UV-absorbing and UV-reflecting whites. Since the wings of roosted individuals are folded, the UV-reflectant undersides of many Heliconiini that are known to roost gregariously (CRANE, 1954; present study, table 5) may be important for the attraction of flying individuals to the roost in the evening. In contrast, CRANE (1955) found that only UV-absorbing colours attracted male H. erato to females during the day. But this interpretation runs counter to the results of section 3 (iv); in the greenhouse a dead individual with intact pale marks or a black model with a pale stripe attracts less attention than a dead individual with blacked-out pale markings or an all-black model. In section 3 (iv) it was found that background was important. If we hypothesise that the natural forest 'backdrop' is poor in UV, or is mottled UV-grey, then it seems probable that a black butterfly with bright UV-reflecting spots will show up maximally. This is exactly the colour pattern of most of the higher Heliconiini, and this hypothesis could easily be tested in the field.

If the above hypothesis is correct, then female roosting position in H. erato and H. melpomene - the wings are folded so as to obscure more of the UV-reflecting underside markings than in the male (figures 2 and 3) - may be an evolved strategy to reduce male attentions which can escalate, in H. melpomene at least, into unnecessarily long attempts at courtship. However there are a number of other hypotheses possible!

Perhaps the most difficult problem about roosting in Heliconius is to determine the selective advantage of nocturnal aggregations for the individuals of the species that possess them. The present work does little to clarify this question.

5) SUMMARY

- 1) The gregarious roosting behaviour of a neotropical butterfly, H. melpomene, was studied under semi-natural conditions in a greenhouse insectary.
- 2) Some butterflies fly to the roost near sunset and rest, wings downwards, hanging on the tips of fine tendrils or twigs. The female position is slightly different to the male position, but some time after sunset the female position relaxes back to a male-like position.
- 3) Using videotape, it was determined that flying males and females hover at already roosted individuals of both sexes. Most of these pairwise interactions were of short duration, but males hovered at females for longer periods than found in any other pairwise interactions. In these male-female interactions, the behaviour of both individuals was similar to that in unsuccessful courtship during the day. In many interactions the insects exposed presumed pheromone-disseminating structures. No matings were observed on the roost, and the outcomes of these interactions were not determinate.
- 4) Males and females roosted at similar times, but very young (callow) individuals roosted significantly earlier and interacted less than older individuals.
- 5) The time of 100% roost occupancy accurately tracked the time of sunset during the year.
- 6) The variation of the time of 100% roost occupancy around sunset was best explained by differences in light intensity due to changes in cloud cover on different evenings.

- 7) Near sunset, flying individuals approach dead butterflies or even crude models as well as live, roosted butterflies. It was found that a model that contrasts with its background is approached more readily than a non-contrasting model.
- 8) Photography showed that the undersides of many Heliconiini reflect ultraviolet light, whereas the uppersides absorb ultraviolet.
- 9) The adaptive value of the response to light intensity is discussed.
- 10) A possible mechanism of aggregation in Heliconius is discussed.

ZUSAMMENFASSUNG

- 1) Das Verhalten eines neotropischen Schmetterlings, H. melpomene wurde am gemeinschaftlichen Ruheplatz in einem Gewächshausinsektarium unter halbnatürlichen Bedingungen untersucht.
- 2) Gegen Sonnenuntergang flogen einige Schmetterlinge zum Ruheplatz und ruhten, Flügel nach unten, an der Spitze von feinen Ranken oder Zweigen. Die Position der Weibchen unterschied sich leicht von der der Männchen, entspannte sich aber einige Zeit nach Sonnenuntergang zu einer Männchen-ähnlichen Stellung.
- 3) Videotape-Aufnahmen zeigten, dass fliegende Männchen und Weibchen schon ruhende Tiere von beiderlei Geschlecht umschwebten. Diese paarweisen Interaktionen waren meist von kurzer Dauer, jedoch schwebten Männchen für längere Zeit um Weibchen, als für jede andere paarweise Interaktion gefunden wurde. Das Verhalten beider Tiere in diesen Männchen-Weibchen-Interaktionen glich dem bei erfolgloser Balz während des Tages. Bei vielen dieser Interaktionen exponierten die Insekten vermutlich Pheromon-ausscheidende Strukturen. Paarungen am Ruheplatz wurden nicht beobachtet, und die Resultate der Interaktionen waren variabel.
- 4) Männchen und Weibchen ruhten zur gleichen Zeit. Sehr junge Tiere ruhten deutlich früher und zeigten weniger Interaktionen als ältere Tiere.
- 5) Der Zeitpunkt 100%-iger Ruheplatzbelegung folgte dem Zeitpunkt des Sonnenuntergangs während des Jahres genau.

- 6) Schwankungen des Zeitpunkts 100%-iger Ruheplatzbelegung in Bezug auf den Sonnenuntergang liessen sich durch Unterschiede in der Lichtintensität aufgrund unterschiedlicher Bewölkung an verschiedenen Abenden erklären.
- 7) Fliegende Tiere näherten sich gegen Sonnenuntergang toten Schmetterlingen und selbst groben Attrappen ebenso wie lebenden ruhenden Schmetterlingen. Es wurde gezeigt, dass eine vom Untergrund kontrastierende Attrappe eher angefliegen wurde als eine nichtkontrastierende.
- 8) Fotografien zeigten, dass die Unterseite vieler Heliconiini ultraviolettes Licht reflektiert, wohingegen die Oberseite ultraviolettes Licht absorbiert.
- 9) Der adaptive Wert der Reaktion auf Lichtintensität wird diskutiert.
- 10) Ein möglicher Mechanismus der Versammlung bei Heliconius wird diskutiert.

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TABLE 1. Durations of roosting interactions

TYPE OF INTERACTION	SAMPLE SIZE	MEAN DURATION/SEC	SD/SEC
male-female	12	21.1	21.0
male-male	10	1.20	1.38
female-female	3	1.07	0.961
female-male	9	0.711	0.601
<u>combinations</u>			
female-female) +) female-male)	12	0.800	0.676
male-male) female-female) female-male)	22	0.982	1.05

TABLE 2. - Climatic effects on roosting behaviour in H. melpomene

Date (1978)	Light intensity, 30 min before sunset (lux/8.9)	Corrected atmospheric pressure, reading nearest sunset (m Bar)	Cloud cover, reading nearest sunset (Scale 0-8)	Time at which 100% of butterflies roosted (mins before sunset)
<u>(A) at 28° Centigrade</u>				
13/vi	36	1021.9	7	5
15	4.2	1008.9	8	10
19	42	1017.9	2	-15
13/vii	22.5	1026.7	8	5
21	15	1016.2	3	10
23	39	1007.9	4	0
27	15	1010.0	7.5	20
30	8	1014.6	8	40
4/viii	33	1013.4	7	5
8	25	1011.6	8	15
9	43	1020.3	7	10
<u>(B) at 23° Centigrade</u>				
23/iii	50	992.4	4	10
24	42	1005.3	8	10
28	60	989.5	5	5
30	53	996.9	1	15
31	28	1000.0	8	30
2/iv	15	1017.4	8	30
3	15	1024.1	8	15
4	36	1029.7	8	25
5	52	1033.0	6	0
6	28	1032.9	8	25
8	51	1019.1	4	10
9	58	1006.9	2	0

TABLE 3. Climatic effects on roosting behaviour in *H. melpomene*

time when 100% roosting occup- ancy is reached correlated with:	Temperature /°C					
	23			28		
	r	d.f.	P	r	d.f.	P
light intensity	-0.781	10	0.005	-0.671	9	0.05
cloud cover	0.585	10	0.05	0.623	9	0.05
atmospheric pressure	0.198	10	0.1NS	-0.206	9	0.1NS
temperature	-0.130	10	0.1NS	-0.311	9	0.1NS

TABLE 4. Results of H. melpomene choice experiments

experiment number	date 1978	background black or white	models used		numbers of close approaches	
			left	right	left	right
1	6/iii	b	♀1	♀2*	7	1
2	7/iii	w	♀1	♀2*	80	133
3	8/iii	b	♀2*	♀1	1	11
4	9/iii	w	♀2*	♀1	67	41
5 #	13/iii	w	♀2*	♀1*	1	1
6	14/iii	w	♀2*	♀1*	23	28
7	24/iii	b	♀2*	♀1*	1	0
8	19/vi	w	-	♂1	0	38
9	20/vi	w	♂1	-	40	0
10	22/vi	w	A1	♂1	10	4
11	23/vi	w	♂1	A1	17	9
12	26/vi	w	A1	♂1	20	17
13	27/vi	w	♂1	A1	26	12
14	29/vi	w	A1	B1	42	7
15	5/vii	w	B2	A2	2	9
16	9/vii	b	B2	A2	13	7
17	13/vii	b	A1	B1	11	21
18	21/vii	b	C1	A2	6	0
19	23/vii	b	A1	C2	2	9
20	27/vii	w	A1	C2	26	0
21 #	30/vii	w	C1	A2	0	1
22	4/viii	w	C1	A2	1	9
23	8/viii	w	D1	A2	50	21
24	9/viii	w	A2	D1	6	6

♀2, ♂1 = dead individuals, sex shown, identity number.

♀2* = dead individual, blacked-out pale markings

- = glue only

A,B,C,D = models, see figure 2.15

experiments 5 and 21 were repeated in experiments 6 and 12

TABLE 5. Species of Heliconiini showing UV absorbance on upperside and UV reflection on underside

whether roosts	species	remarks
(+)	<u>Agraulis vanillae lucina</u> C. & R. Felder <u>Dryas julia julia</u> Fabr.	poor UV refl un
+	<u>Eueides aliphera aliphera</u> Godart <u>E. tales calathus</u> Stichel	UV refl white hw marginal spots up & un
-	<u>Heliconius xanthocles melittus</u> Stau. <u>H. cydno temerinda</u> Hewitson	UV refl on hw white spots up & un
-	<u>H. numata "laura"</u> Neustetter	UV refl on white up & un fw marks
-	<u>H. n. messene</u> Felder & Felder	poor UV refl un
+	<u>H. melponene thelxiope</u> Hubner	the race used in this study
+	<u>H. m. aglaope</u> Felder & Felder	
+	<u>H. wallacei flavescens</u> Weymer	
+	<u>H. erato hydara</u> Hewitson	
+	<u>H. e. lativitta</u> Butler	
+	<u>H. sara thamar</u> Hubner	
+	<u>H. charitonia vasquezae</u> Comstock & Brown	

+ indicates species known to roost

(+) indicates species known to form loose aggregations under leaves

- indicates species known not to roost

hw = hindwing

fw = forewing

up = upperside

un = underside

TABLE 6. Mechanisms whereby individuals of *H. melpomene* find roosts of conspecifics.

type of mechanism	mechanisms of localization by individuals:	
	experienced	inexperienced
	DAYTIME HABITAT, HOME-RANGE	
primary localization	memory	(social chasing of experienced individuals)
	↓	
	REGION OF ROOST	
primary attraction	memory <u>or</u> (UV) visual attraction to roosted individuals	(UV) visual attraction to roosted individuals
	↓	
	ROOSTING SITE	
secondary components of attraction (species identification)	memory or (pheromonal)	(pheromonal)
	↓	
	ROOSTING NEXT TO INDIVIDUALS OF CORRECT SPECIES	

PARENTHESES INDICATE THAT THE CONNECTION HAS NOT BEEN PROVED, BUT SEEMS PROBABLE

FIG (1)

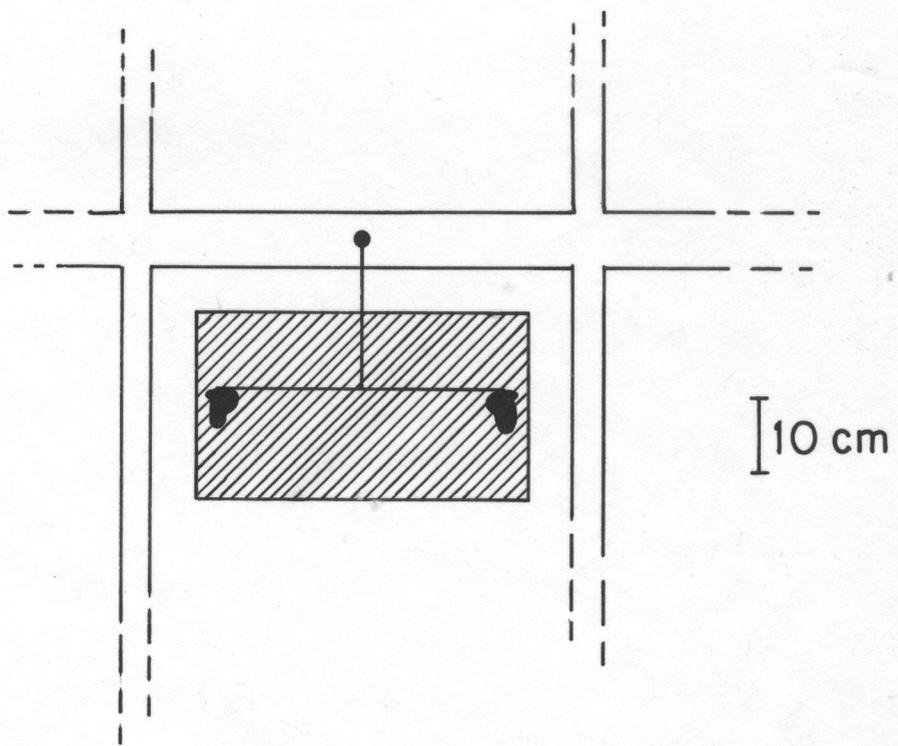


FIG 2

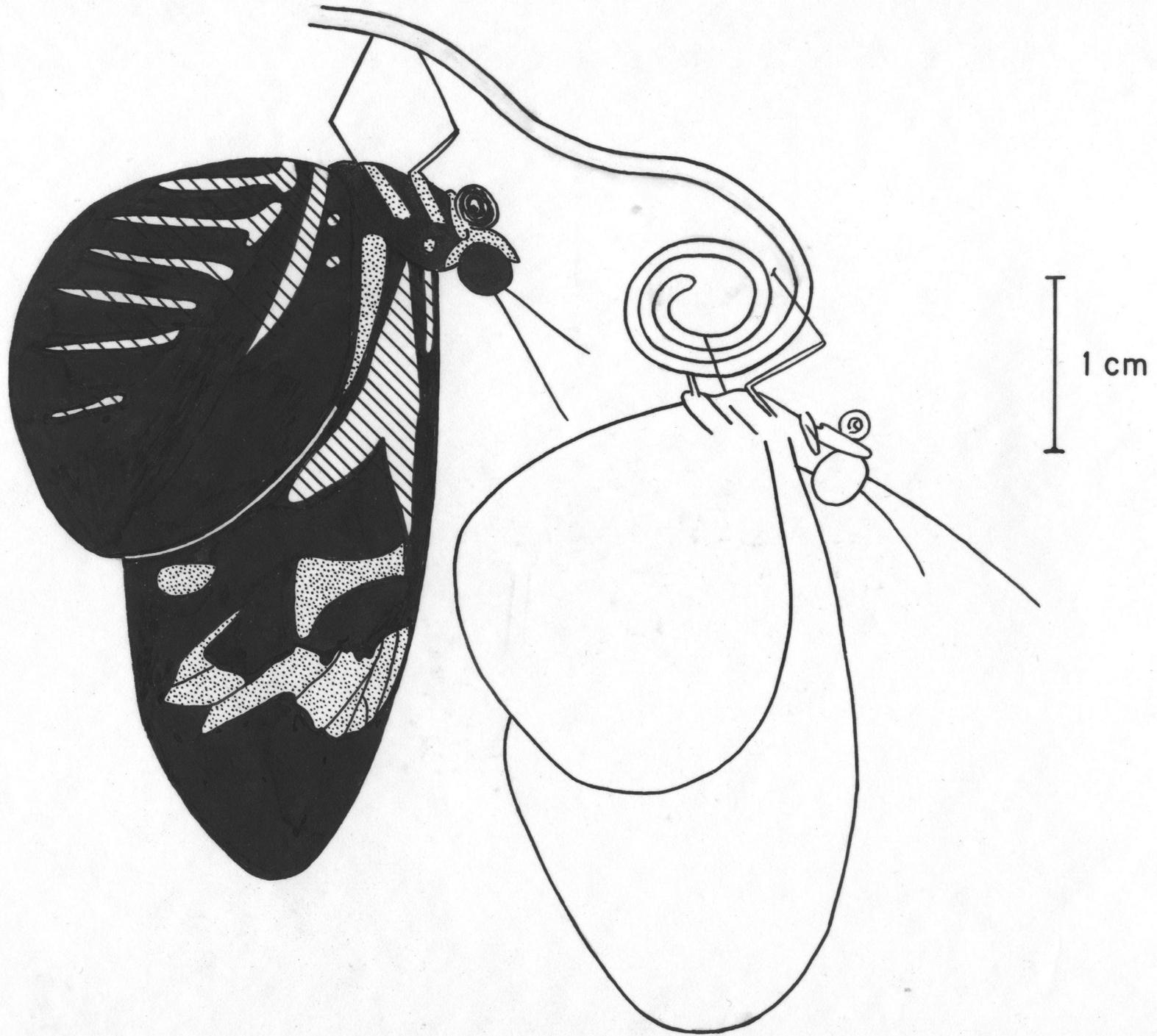
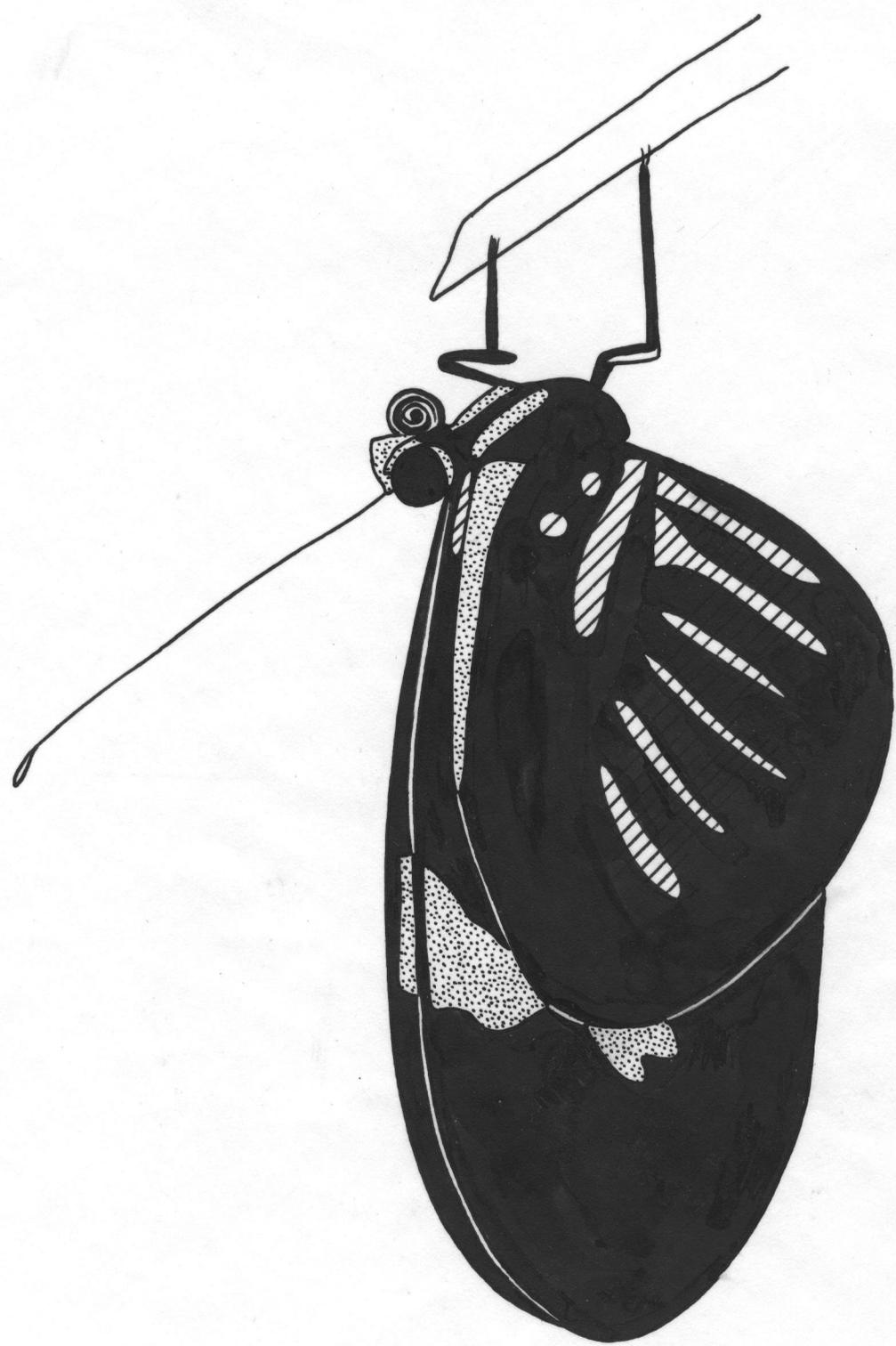


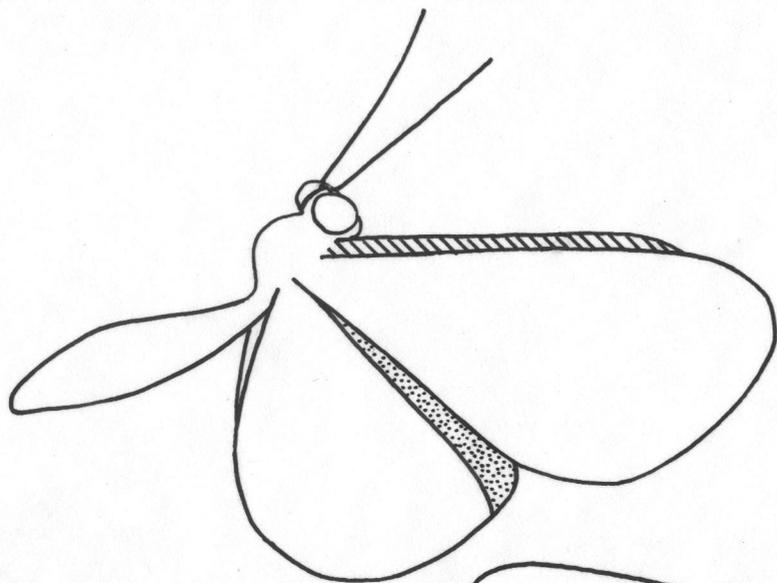
FIG (3)



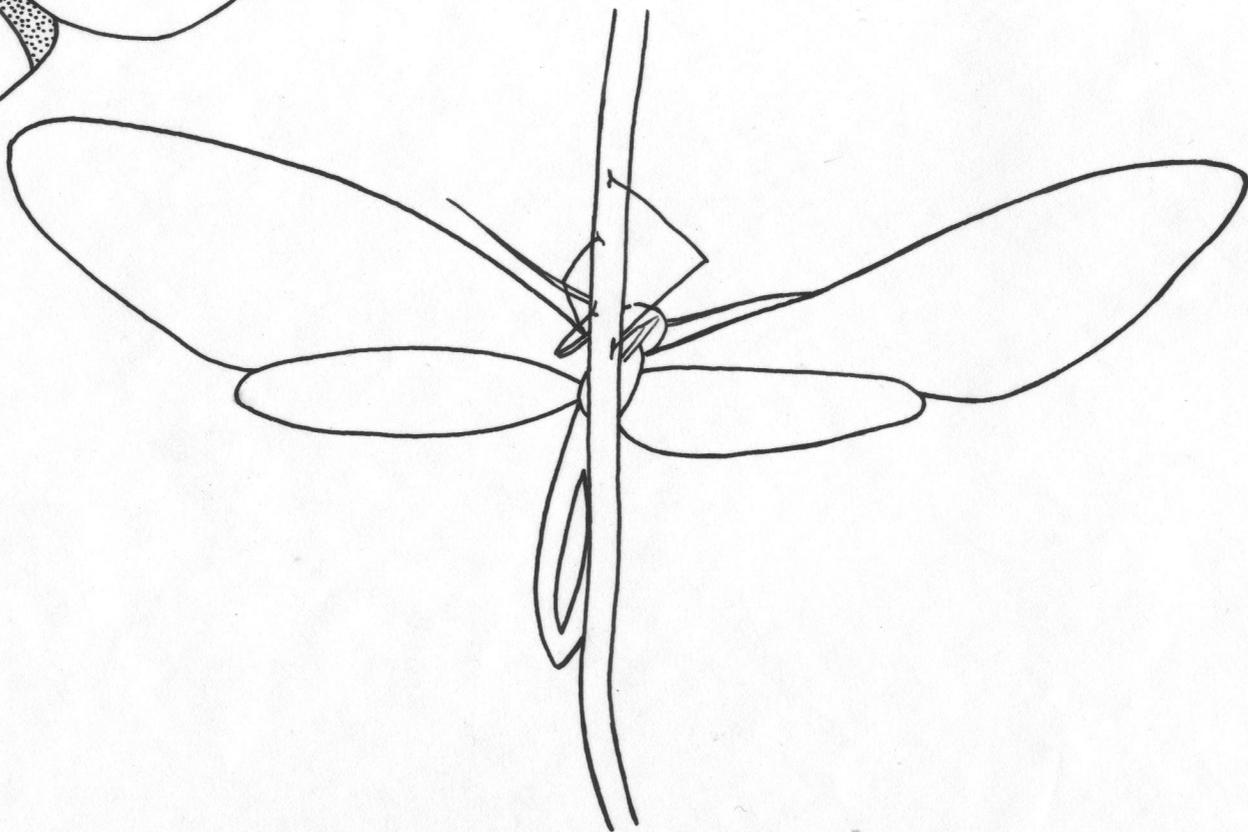
1 cm

FIG (4)

217



1 cm



FIGURES 5-8. Ethograms made from video recordings of *H. melpomene*

Key

- = individual flying
- = individual hovering close to a roosted individual
-

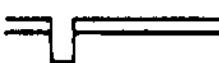
 = individual flying, then hovering at roosted individual, then flying free again.
- 
 ----- = male hovering at roosted female; each vertical bar on left represents a wingflick of the male when it is directly over the female. During these flicks the friction patches are exposed
- 
 ----- = individual roosted with wings open and fluttering on left; on right, wings closed.

Fig. (5)

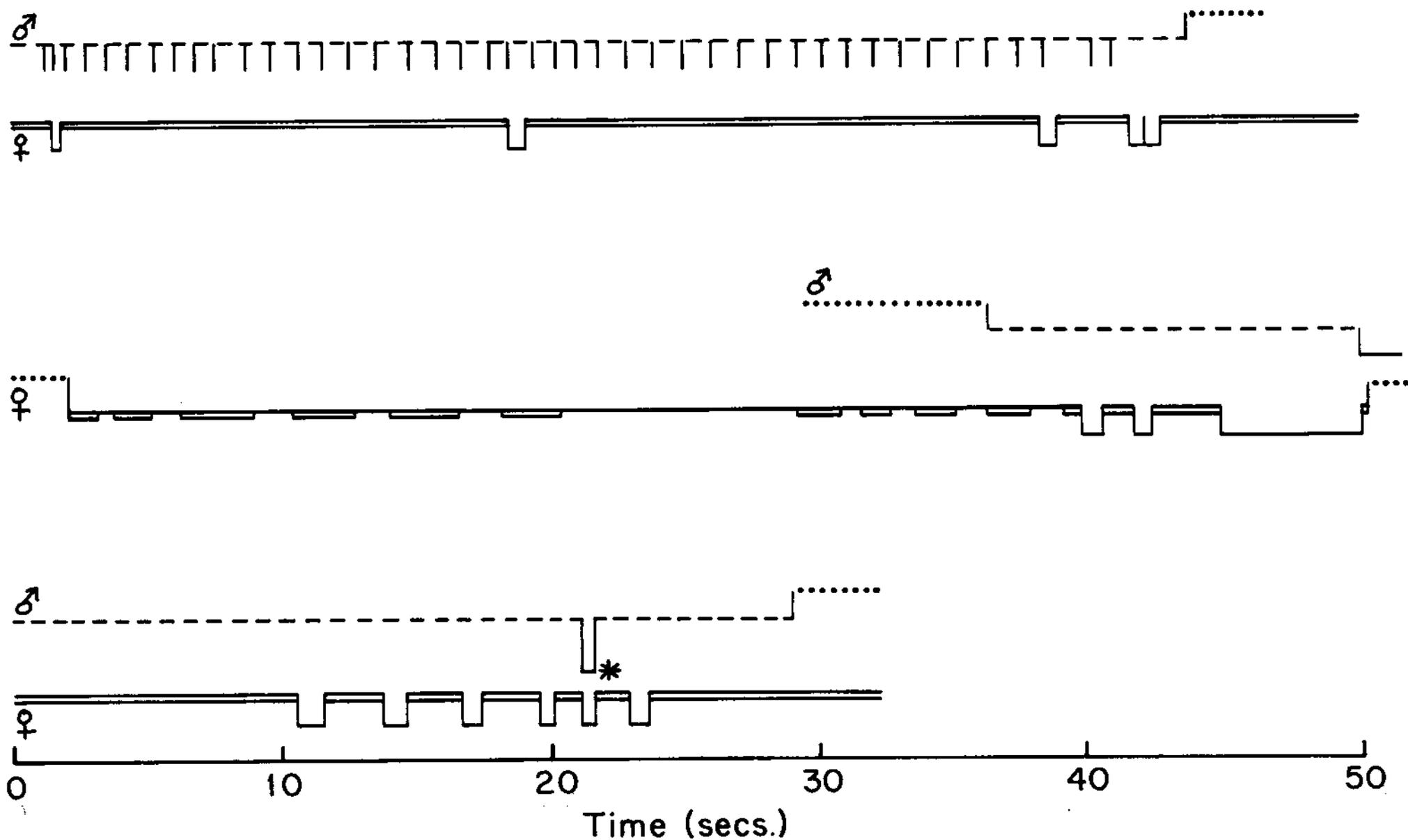
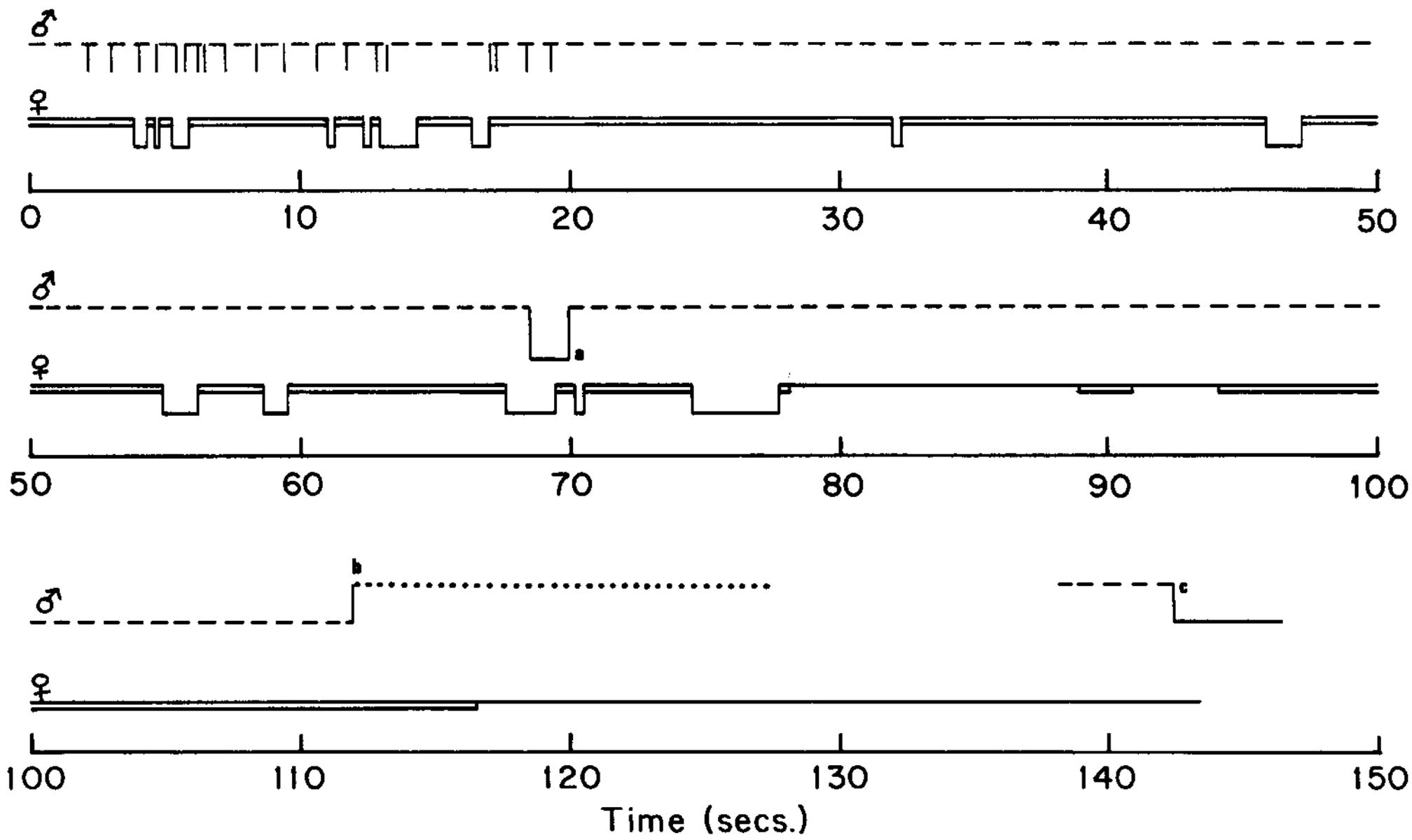
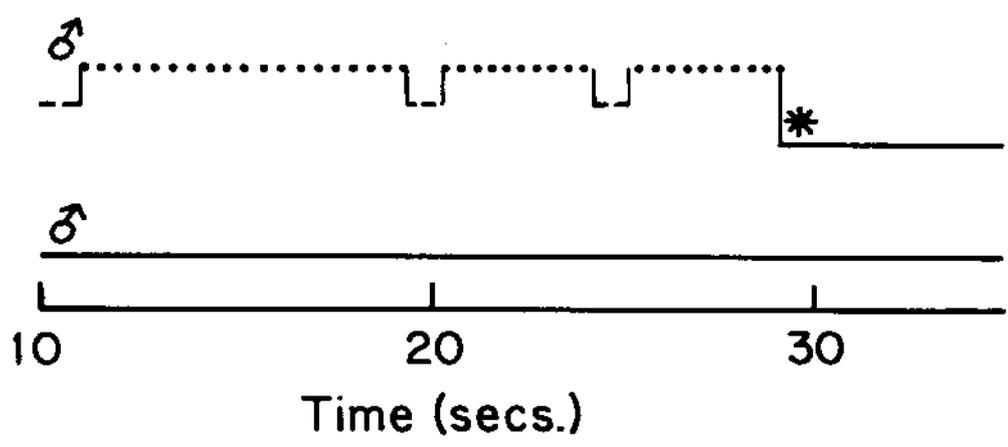
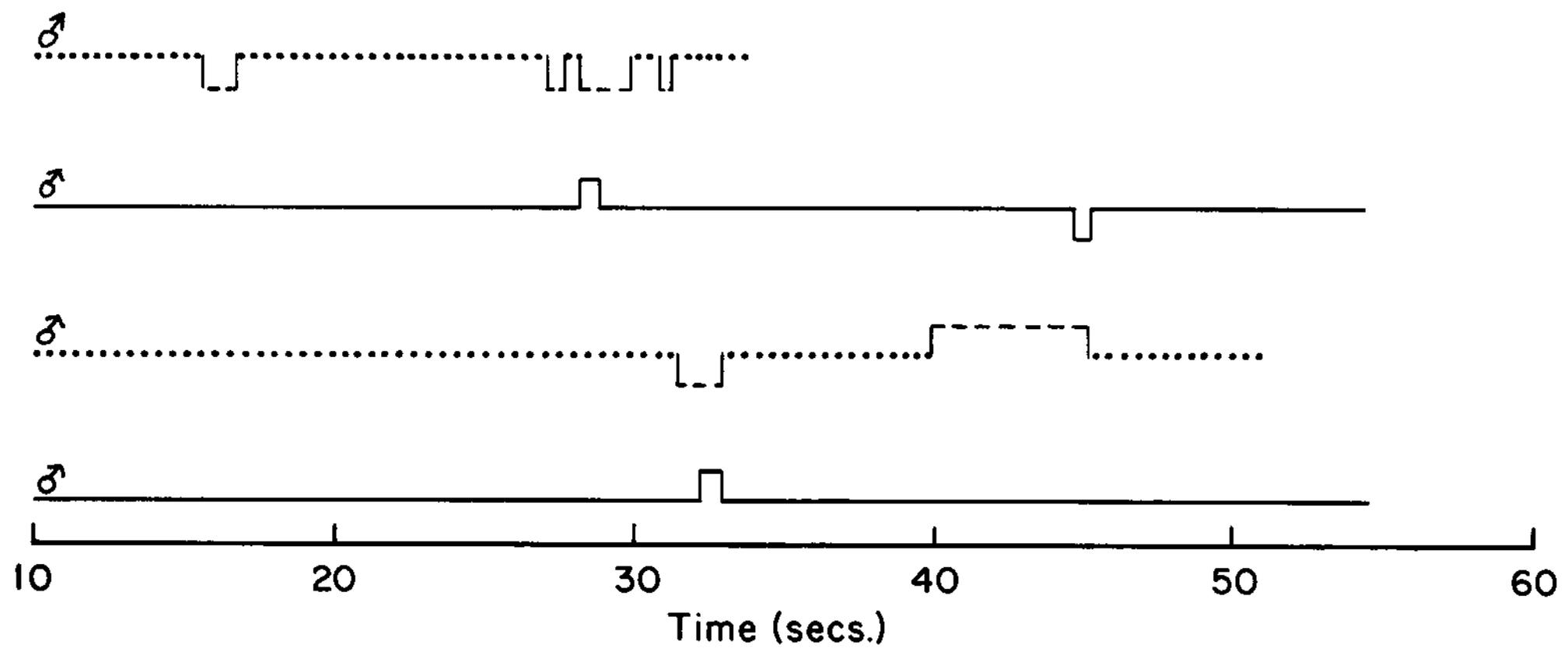


Fig (6)





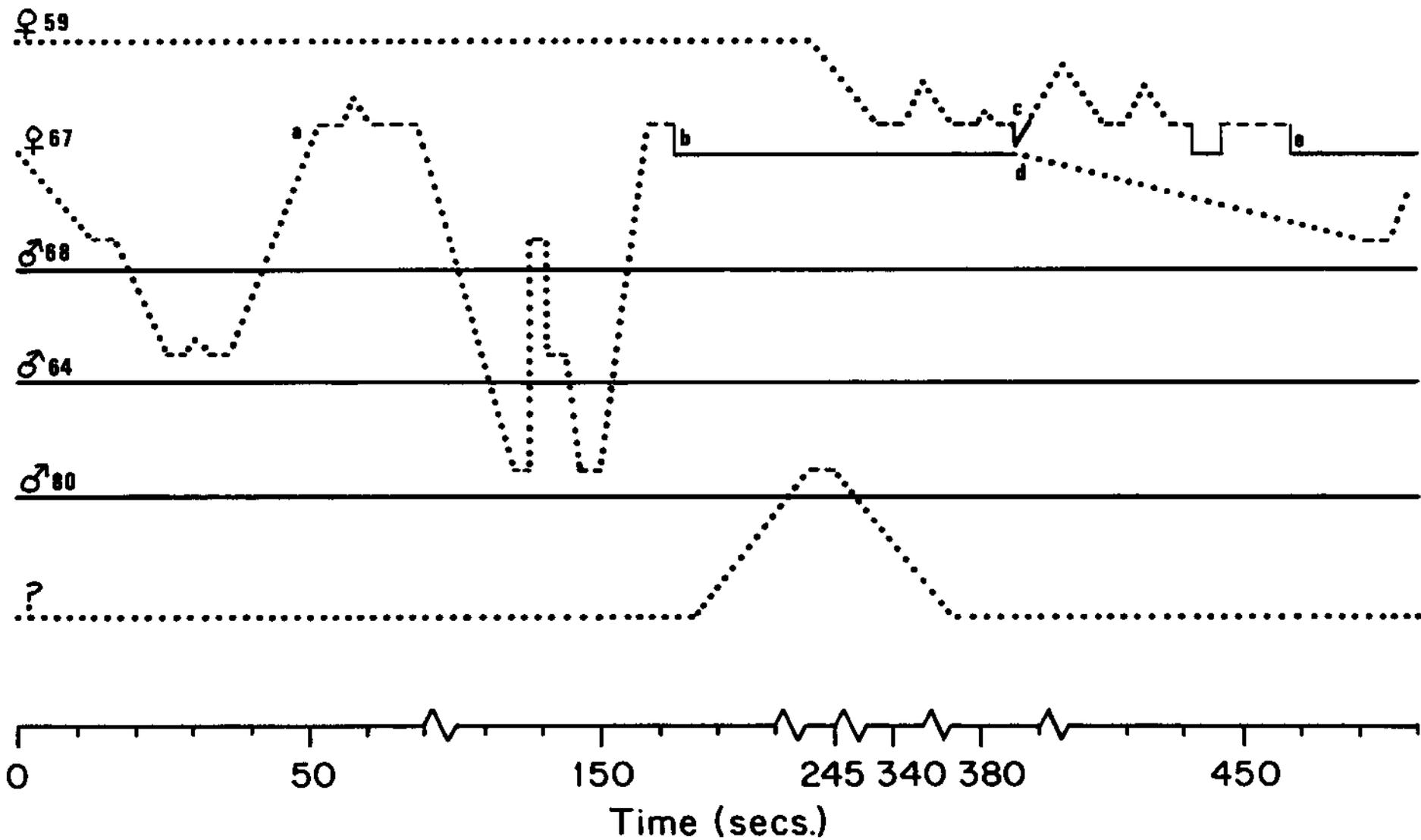
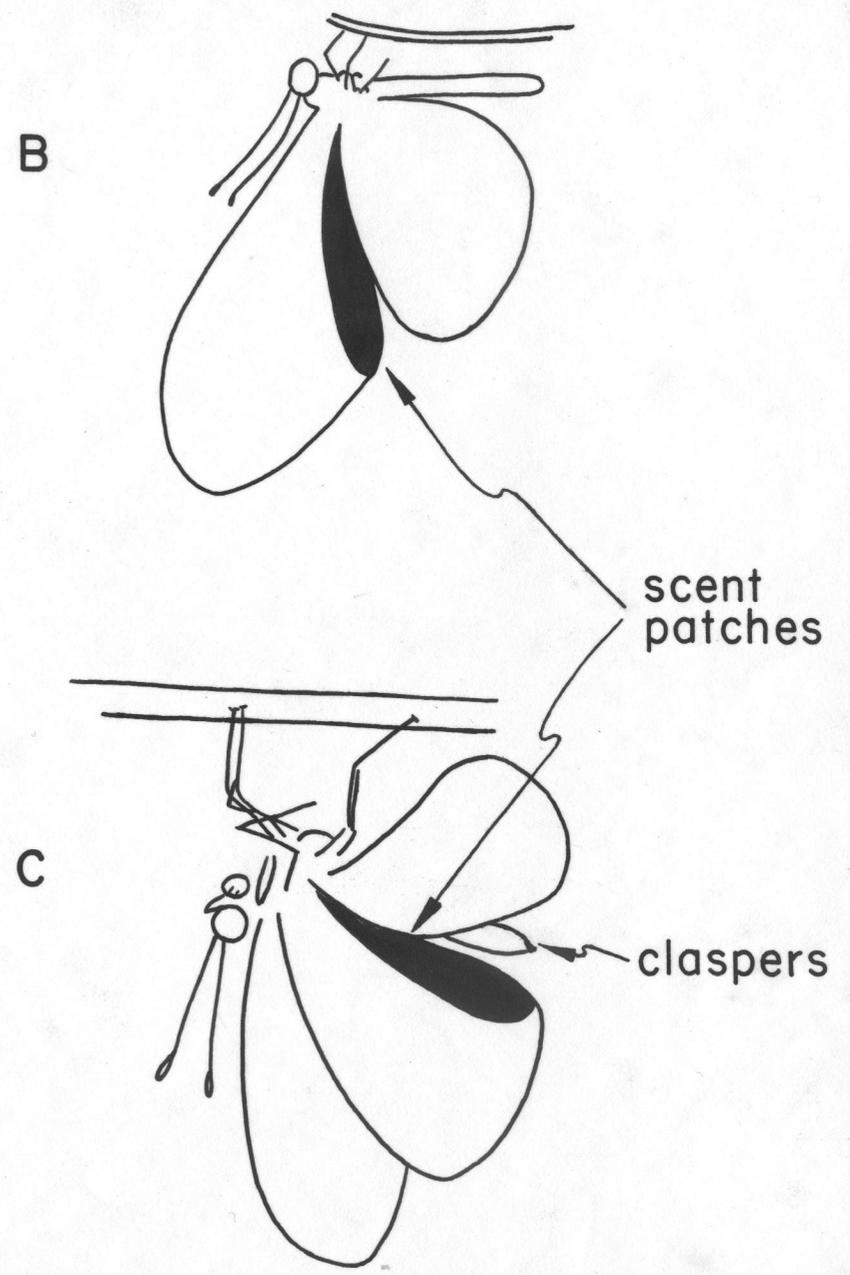
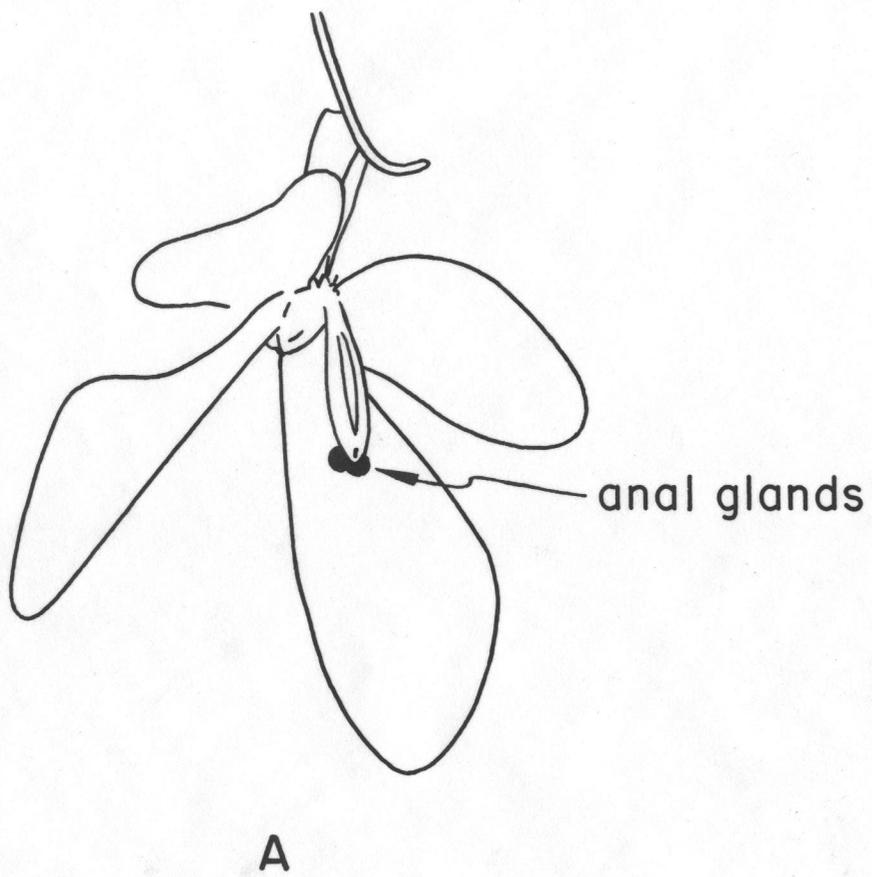


FIG 9



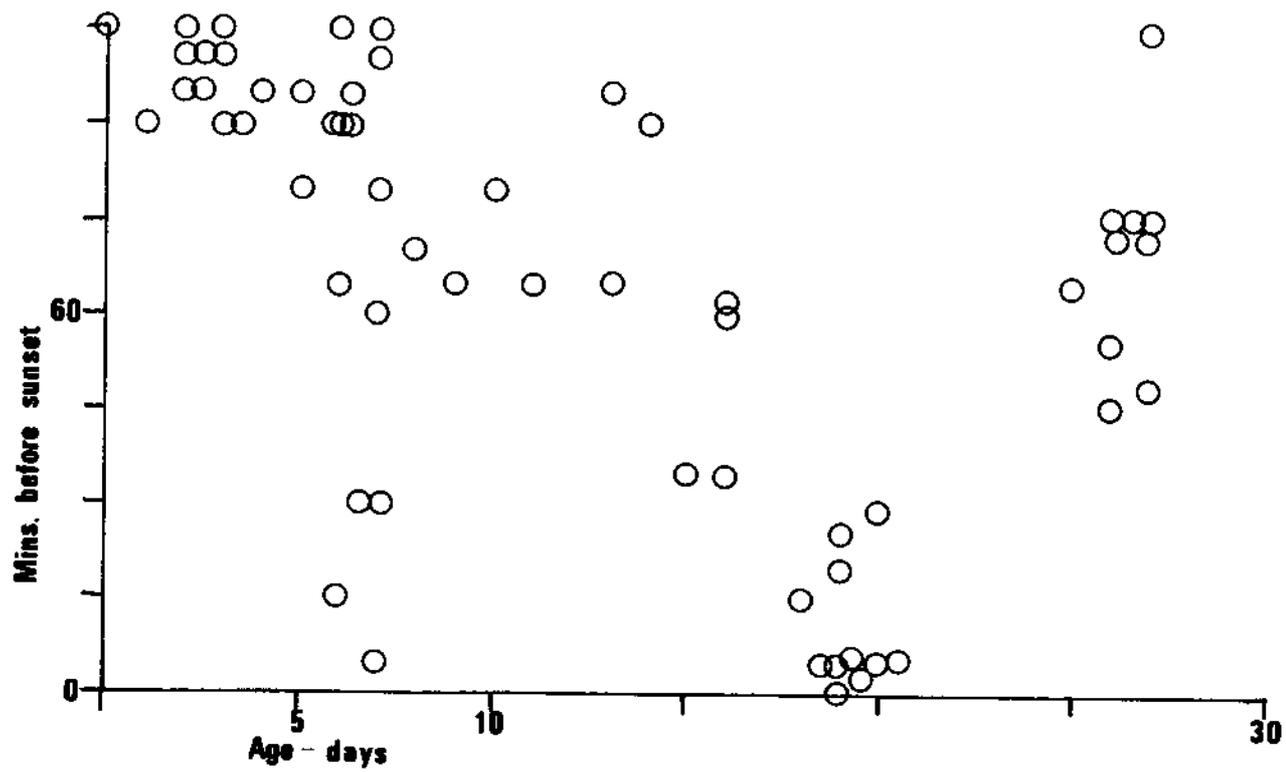


Fig 11.

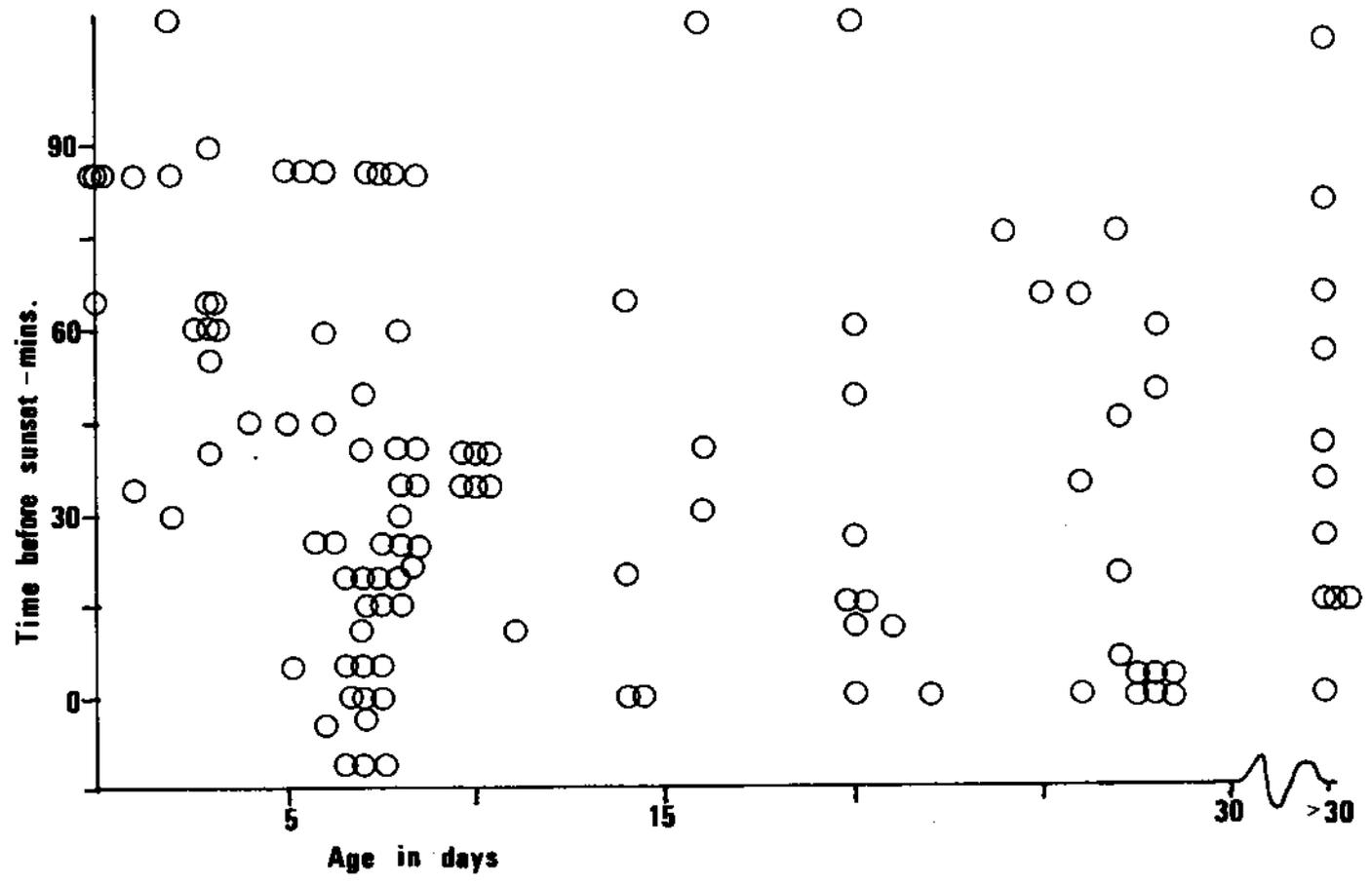


FIG (12)

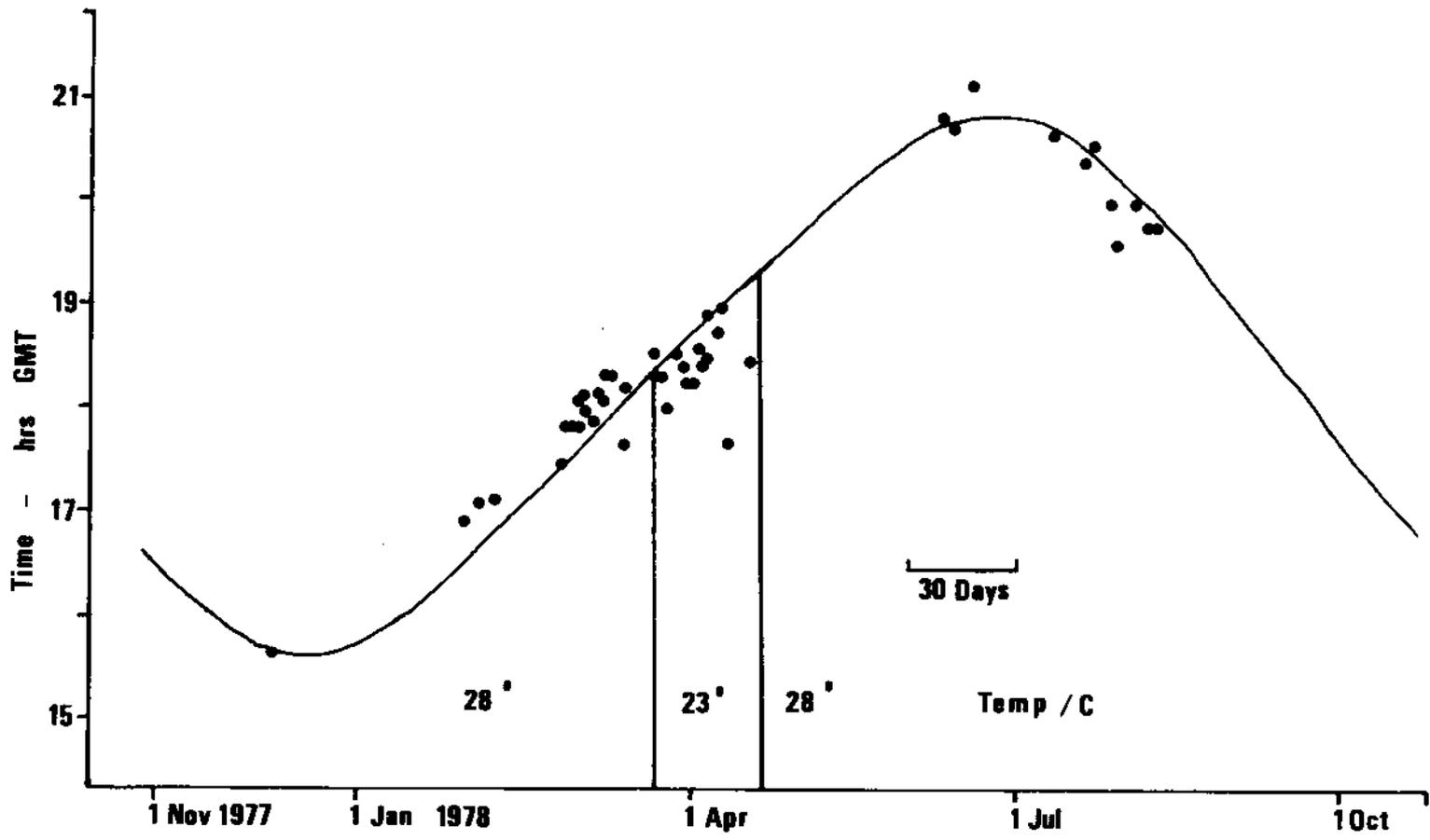
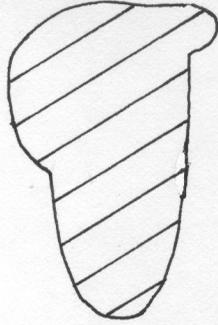
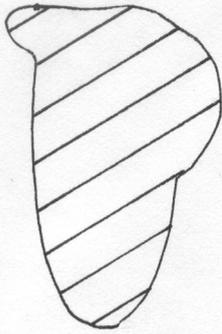
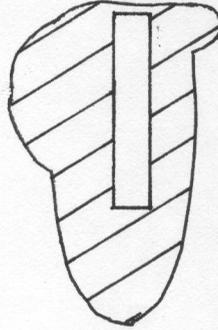
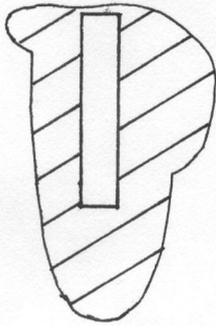


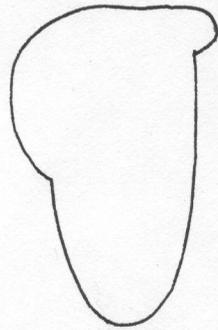
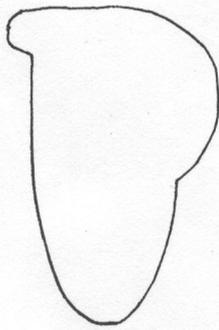
FIG (13)



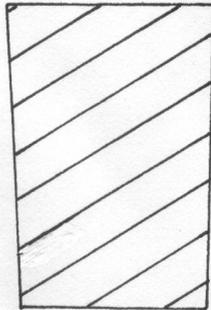
A



B



C



D

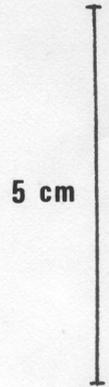


Figure legends

FIGURE 1. Choice apparatus used in section 3 (iv).

FIGURE 2. Two *H. melpomene* roosting on a tendril (traced from video frame).

H. melpomene in sleeping positions. Male (left) showing yellow (stippled) and red (hatched) underside markings on a black background. Female (right, markings not shown) has the hindwings partially covering the forewings.

FIGURE 3. Roosting position of female *H. melpomene* (traced from video frame).

Female *H. melpomene* in roosting position, showing how the hindwings cover the majority of the forewing markings. Compare the male sleeping position in figure 2. The underside markings reflect UV. Yellow markings: stippled. Red markings: hatched.

FIGURE 4. Male *H. melpomene* hovering at a roosted female (traced from video).

The male has just completed a downstroke (wingbeat frequency approximately 10 Hz.) and the androconial patch (stippled) at the anterior edge of the hindwing is being intermittently exposed. The female holds her forewings apart, also characteristic of unreceptive courted females during the day. In the daytime, such a position would be inverted so that the uppersides of her wings would face upwards.

Legends

FIGURE 5. Male-female interactions

- A. Daytime courtship interaction.
- B. Evening roosting interaction
- C. Evening roosting interaction. *= male grapples female.

FIGURE 6. A long duration male-female roosting interaction.

Note how the male presents friction scent patches (recorded in the first 20 sec. of the sequence) in a similar pattern to the daytime courtship interaction of figure 5A.

- a = alights beside female, recurves abdomen and presents androconial patches in unsuccessful mating attempt.
- b = flies away.
- c = hovers at different female and roosts.

FIGURE 7. Male-male roosting interactions

- * = roosts.

FIGURE 8. Roosting interactions

Two females and one unknown individual approaching roosting males. Hovering interactions have been lengthened for clarity.

- a = hovers near perch
- b = roosts
- c = 59 grapples with 67
- d = 67 flies away
- e = 59 roosts

Figure legends

FIGURE 9. Presumed sites of pheromone production by *H. melpomene* on the roost.

- A. Roosted female fluttering wings and everting anal glands while a male (not shown) is hovering nearby. A similar upright behaviour is shown by nonreceptive females whilst being courted by males during the daytime.
- B. Male attempting to mate with female on roost and exposing friction patches (see FIGURE 6, t=68 secs.).
- C. Roosting male fluttering wings and exposing friction patches and claspers after approach by a hovering male.

FIGURE 10. The effect of age on roosting time in *H. melpomene* at 23°C.

FIGURE 11. The effect of age on roosting time in *H. melpomene* at 28°C.

FIGURE 12. Roosting of *H. melpomene* compared with time of sunset.

The sinusoidal curve shows the variation in time of sunset throughout the year. Points represent the times when the last butterfly roosted on different nights.

FIGURE 13. Cardboard models used in choice tests.

Colours: Hatched = black card

White = white card

October 15, 1980

Dr. J.L.B. Mallet
c/o O.T.S.
Cidad Universitaria
Costa Rica

Dear Dr. Mallet:

Re: ms entitled "A laboratory study of gregarious roosting in the butterfly Heliconius melbomene".

I have received two reviews of your paper. The first recommends against publication on the grounds that he doesn't feel that there is sufficient new information and "what it does report is presented in so much detail that interesting findings are hidden eg. different wing positions in male versus females and that calls individuals roost earlier. The kin selection story has nothing to do with this paper, which is largely mechanistic and descriptive. I wonder about how much natural behaviour one can observe in a greenhouse but 9 m³! The male-female interactions are courtship attempts."

The second referee makes the following comments

1. Figs 5-8 give me no message. Info. can be easily summarized in words.
2. Figs 10 & 11 - could be summarized in short table.

AGE CATEGORIES
1-5 6-10

X TIME BEFORE
SUNSET.

3. Info. on p. 13 could go in table as
4. I don't understand the last hypothesis - If animals with white marks or intact wing were less attractive even though this might maximize UV reflections then why hypothesize that females cover these spots to protect themselves from the attention of males. Am I missing something? See also summary table 6 - what is evidence that inexperienced are attracted by UV? Summary - a detailed analysis which, as admitted by the author, tells us nothing about the importance or evolutionary significance of this behaviour.
5. Most of the figures could be cut out ie 4-12
2 & 3 combined.

Overall this second referee feels that the paper describes a solid piece of work, presented in a reasonable manner, but does not strongly recommend acceptance.

Because the journal receives far more clearly acceptable mss than can be accepted I regret that I have decided that I should not accept your paper on behalf of Behaviour.

Yours sincerely,

N. R. Liley
Editor, Behaviour

BEHAVIOUR

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6 November 1980

Dr. James Mallet
Parque Nacional Corcovado
Servicio de Parques Nacionales
Ministerio de Agricultura y Ganaderia
Apartado 10094
San Jose, Costa Rica

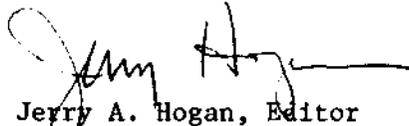
Dear Dr. Mallet:

Your letter of 13 October to Dr. McKinney has been forwarded to me. I have recently taken over as Executive Editor.

I enclose a copy of a letter from Dr. Liley that was sent to your OTS address on 15 October. As you will see, we were not able to accept your manuscript on Heliconius melpomene. I hope Dr. Liley's letter does not take 4 months to reach you, but this letter may arrive more speedily.

I am sorry we could not send you more pleasant news.

Sincerely,



Jerry A. Hogan, Editor
Department of Psychology
University of Toronto
Toronto, Canada M5S 1A1