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THE INFLUENCE OF ENVIRONMENTAL FACTORS ON ROOSTING IN THE BLACK SWALLOWTAIL, *PAPILIO POLYXENES ASTERIUS* STOLL (PAPILIONIDAE)

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ABSTRACT. Black swallowtails, *Papilio polyxenes asterius* Stoll, roost singly in west sloping old-fields in central New York. A frenetic search flight, triggered by decreasing radiation regardless of temperature, precedes roosting. Search flights allow swallowtails to check the suitability of various roosts. Roosts selected favor dorsal basking for as long as possible under decreasing solar radiation. Dorsal basking on the roost ceases, and a roosting posture is assumed when a body temperature high enough for flight can no longer be maintained. Selection for efficient roosting is strong since most adult deaths apparently occur when individuals are roosting. Selection for mimetic or cryptic wing patterns is expected to influence the exposed undersurface of the hindwing more strongly than other wing surfaces hidden during roosting.

Butterflies are active during daylight hours when ambient conditions of radiation and temperature are high enough to allow behavioral maintenance of body temperatures suitable for flight (Vielmetter, 1958; Watt, 1968; Heinrich, 1972). As radiation and ambient temperature fall during the evening, butterflies seek night roosts where they remain until the next morning. Some species roost in aggregations (Crane, 1957; Urquhart, 1960; Benson and Emmel, 1973; Larsen, 1973; Muysshondt and Muysshondt, 1974; Turner, 1975; Young and Thomason, 1975), but most roost singly.

Little is known of roosting behavior in most butterflies in spite of the widely read query concerning roosts in the introduction to Klots' (1951:7) popular field guide. The popular literature is full of comments about butterflies disappearing into trees and fields during evening hours but no detailed study has ever been reported for a species which roosts singly.

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Many butterflies bask in the sun as long as possible in the evening, often on the actual perch that will be used as the night roost. Such behavior has been termed "vesper warming" by Clench (1966). Basking on the roost has been recorded in the hesperiids *Thymelicus lineola* Ochsenheimer and *Ancyloxypha numitor* Fabricius, the lycaenids *Everes comyntas* Godart and *Lycaena phlaeas* L., and the nymphaline *Phyciodes tharos* Drury (Clench, 1966). Powell (1968) records similar behavior for *Incisalia iroides* (Boisduval) (Lycaenidae).

Several authors have suggested that some species choose roosts which are shaded in the setting sun and therefore illuminated by the rising sun earlier the following morning (MacNeill, 1964; Clench, 1966). Such behavior would favor earlier warming by basking the following morning and could conceivably lengthen the period of diurnal activity. Roosting in shadows cast by the setting sun has been observed in *Hesperia* spp. (MacNeill, 1964) and in the satyrines *Euptychia rubricata* Edwards and *Cercyonis meadii* Edwards (Clench, 1966). MacNeill described roosting *Hesperia* as flying directly away from the sun and roosting on the eastern side of bushes. Clench noted the movements of a *Speyeria aphrodite* F. (Nymphalidae). By lining a tree up with the setting sun and then flying directly toward the sun, the butterfly arrived at the shaded side of the intervening tree. After repeating this behavior three or four times, it flew off and roosted in a field. It remains unclear if such shade seeking during roosting is widespread among butterflies, let alone the mechanism by which this is accomplished.

The environmental cues which release roosting behavior have been inadequately studied. When ambient radiation and temperature are low enough to prevent maintenance of a body temperature suitable for flight in the nymphalid *Argynnis paphia* (L.), roosting results (Vielmetter, 1958). This does not explain the onset of roosting on warm evenings when ambient temperatures allow sustained and active flight in the absence of direct insolation. Larsen (1973) has suggested that the timing of roosting events may depend more on decreasing radiation from the setting sun than on decreasing ambient temperature.

From the preceding it seems that selection of the roost site in a given species may involve one of three different roosting patterns: 1) Roosting in shadows cast by the setting sun, therefore hastening exposure to the rising sun the following morning, 2) roosting and basking in areas having maximal exposure to the setting sun, thereby prolonging the period when body temperatures suitable for flight may be maintained, or 3) roosting in areas not related to the position of the sun.

The following study examines in detail the roosting behavior of the

black swallowtail, *Papilio polyxenes asterius* Stoll, and determines what environmental cues direct such behavior. It constitutes the first study of roosting in papilionids [see observations of Gibson and Panchen (1975) on the African *Papilio demodocus* Esper] and the first detailed study of non-gregarious roosting for any butterfly.

MATERIALS AND METHODS

The black or parsnip swallowtail, *Papilio p. asterius* is frequently seen in open clearings and fields throughout eastern North America. The territorial males may be observed for lengthy periods in relatively small areas (Lederhouse, 1978). The darker females are more transient, usually observed flying quickly across these open areas.

Roosting was studied in an old field near Brooktondale, southeast of Ithaca, Tompkins County, New York during the summer of 1975 (Fig. 3). This field was bounded on the north and east by corn fields and on the south and west by dense woody growth. The field was divided into a grid consisting of 276 squares each 10 meters on a side. The relative elevation of each corner of every grid square was established by surveying. Slopes and aspects (compass headings) for every grid square were determined by treating each square as a planar surface with corner elevations most nearly matching those measured. Plant densities for each square were measured by direct count for large, conspicuous species or by counting within a randomly placed 0.5 m² circle for smaller and more numerous species. Only the most abundant plant species are treated in this study. Plant nomenclature follows Fernald (1950).

During each study period, gross solar radiation and ambient temperature were recorded using a centrally-located radiometer and hygrothermograph. Sunset times were established by reference to published readings of the U.S. Naval Observatory for Binghamton, New York (U.S. Printing Office, 1959).

Observations of individual behavior were made by persistently following one swallowtail during the evening hours until it selected a roost. This was difficult due to the rapid and erratic flight of individuals seeking roosts; more often than not the butterfly was lost from sight. Additional data were obtained by systematically walking over the entire grid during dusk noting the location and microhabitat of individuals already on roosts. Observations of behavior during the middle of the day were taken from concurrent research by one of us (J. E. R.) and used for comparative purposes.

Clock times (EDT) were recorded at the onset of flights preceding roosting. Times were also recorded when butterflies were seen to assume

TABLE 1. Behavioral responses and ambient environmental factors associated with roosting in *Papilio polyxenes* compared with values for those variables associated with other diurnal activity.

| | Roosting | Non-roosting |
|---|-------------------------------|-------------------------------|
| | $\bar{x} \pm \text{S.D. (N)}$ | $\bar{x} \pm \text{S.D. (N)}$ |
| Flight duration** (seconds) | 96 \pm 111 (19) | 33 \pm 52 (651) |
| Perch duration (seconds) | (Overnight) | 132 \pm 208 (807) |
| Perch height* (cm) | 53 \pm 18 (36) | 64 \pm 27 (794) |
| Air temperature 150 cm above the ground when roost posture assumed** (Centigrade) | 23.9 \pm 3.6 (50) | 27.3 \pm 2.7 (801) |
| Relative humidity when roost posture assumed** (%) | 76 \pm 16 (37) | 58 \pm 11 (640) |
| Solar radiation when roost posture assumed** (cal/cm ² /min) | .16 \pm .20 (15) | .85 \pm .15 (254) |

Asterisks indicate significance level of two-tailed Student's t-test for differences between roosting and non-roosting mean values: * (.05 > P > .01); ** (P < .01).

a roosting posture with folded wings or when they were discovered already in this posture. Identification of individuals at a distance was made possible by marking the marginal and submarginal row of wing spots with felt-tip pens (Lederhouse, 1978).

RESULTS

Roosting Search Flight

Roosting was always preceded by an extremely rapid and erratic flight of longer average duration than flights at other times of the day (Table 1). The shift from non-roosting activity into this search flight was not gradual but occurred abruptly, the individuals accelerating and often disappearing from sight in seconds. In the 8 cases where a single butterfly was observed throughout a search flight, movement was seen to be circular, the butterfly flying in circles often more than 5 m above the ground. During these flights, which avoided shaded areas, individuals often returned to certain spots in the field, flying low and dipping down into the vegetation.

Search flights were repeatedly interrupted by short periods of perching, lasting one or two seconds. These were on potential roosts which either were not stable in the wind, were deflected greatly by the butterfly's weight, did not provide a good gripping surface (smooth grass culms), were very far from the ground, or were in the deep shade. Butterflies did not select the roost directly but only remained on those perches which were suitable after abandoning many perches which were not.

Behavior on the Roost

Eventually a suitable roost was located and the butterfly positioned itself so that the frontal plane of its body was perpendicular to the incident radiation from the setting sun, spread its wings, raised its abdomen between the spread anal margins of the hindwings, and then remained motionless (Fig. 1). This basking continued for several minutes, being longer on warm evenings than on cool or hazy ones.

Basking ceased if the butterfly came under the advancing shadows of the surrounding vegetation. At the end of basking the abdomen was suddenly lowered, the wings dorsally appressed and swept back such that the hindwings almost totally covered the front wings, and the body brought parallel with the stem or head of the roost plant (Fig. 2). The posture was maintained throughout the night.

The following morning, basking occurred as soon as direct sun fell on the roost. Morning basking appeared identical to that occurring in the evening. Butterflies were seen to rotate about the roost so as to be perpendicular to the rising sun. Morning basking was never seen earlier than two hours after sunrise and usually occurred between 0800 and 0900 (EDT) in July and early August.

Effects of Ambient Temperature and Radiation on Roosting

Mean values of ambient temperature, relative humidity, and solar radiation all differed between roosting and non-roosting situations (Table 1). It was not surprising that the evening hours associated with roosting had significantly lower radiation, lower temperature, and higher relative humidity than earlier in the day.

Papilio polyxenes males are incapable of sustained flight with thoracic temperatures below 24 C (Rawlins, unpublished). This value matches that of the average air temperature when the roost posture with folded wings was observed in the evening (23.9 C). Since radiation was very low at these times, body temperatures would rapidly approach ambient levels in quiescent individuals. Several times individuals which had been roosting less than one minute following vigorous flight were observed to be incapable of sustained flight if disturbed. For example, one female disturbed under .09 cal/cm²/min radiation and 23.3 C ambient temperature was unable to remain airborne and crashed into the grass after a gliding flight of about 5 m. This suggests that the roost posture is assumed under decreasing radiation when ambient temperatures drop below the range of body temperatures allowing activity.

The onset of roost search flight during July and August paralleled the time of meteorological sunset (Fig. 7). This suggests that the onset of



TABLE 2. Plant species used as roosts by *Papilio polyxenes*.

| Roost species | Number on heads or apices | Number on stems or culms | Total |
|---------------------------------|------------------------------|-----------------------------|-------|
| <i>Tragopogon pratensis</i> L.* | 4 | 1 | 5 |
| <i>Lonicera morrowi</i> Gray | 0 | 1 | 1 |
| <i>Potentilla recta</i> L.* | 1 | 0 | 1 |
| <i>Solidago altissima</i> L. | 0 | 2 | 2 |
| <i>Linaria vulgaris</i> Hill | 0 | 1 | 1 |
| Total dicotyledons | 5 | 5 | 10 |
| <i>Dactylis glomerata</i> L. | 2 | 0 | 2 |
| <i>Phleum pratense</i> L. | 12 | 4 | 16 |
| Other grasses | 2 | 7 | 9 |
| Total grasses | 16 | 11 | 27 |
| Total roosts | 21 | 16 | 37 |
| Percent of total | 57% | 43% | 100% |

* All roosts were on dead, leafless scapes of the previous season.

the search flight is cued by decreasing radiation even though flying or basking on the roost continues until ambient temperatures fall to levels preventing further activity.

The occurrence of abbreviated search flights during sudden radiation drops preceding thunderstorms provided additional evidence that decreasing radiation triggers such search flights. One male patrolling an area high in the field abruptly switched into erratic search flight behavior with the sudden darkening before a thunderstorm even though air temperature 1.5 m above the ground was 26.7 C. After being forced down minutes later by heavy rain, this male assumed the roosting posture in an air temperature of 20.6 C. With the return of direct sun, basking commenced.

Description of the Roost

Seventy-three percent of the plants selected for roosts were grasses, the remainder being dicotyledonous species (Table 2). Sixty percent of the roosts on dicots were on leafless scapes of dead plants from the previous season. Such plants constituted less than five percent of the total stems within any grid square in the field.

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Figs. 1-2. Postures of *Papilio polyxenes* on the roost. 1. Adult female in dorsal basking posture on culms of grass. 2. Male in folded-wing posture on short head of *Phleum pratense*.

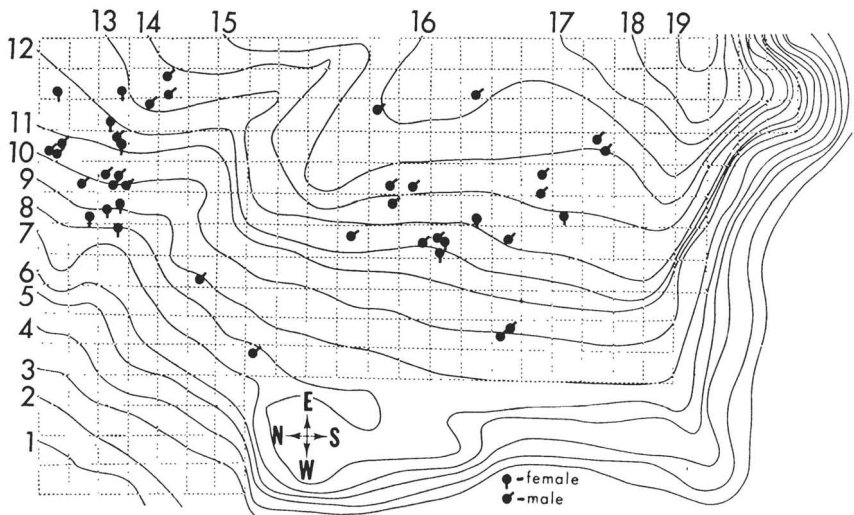


Fig. 3. Topography of study area showing location of roosts. Each small grid square is 10 m square. Numbers in margins give elevation of isoclines in meters above lowest point in field (northwest corner).

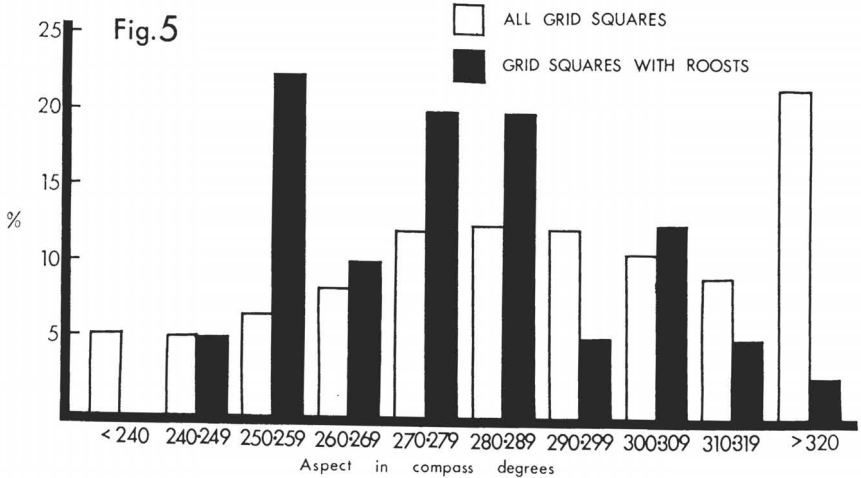
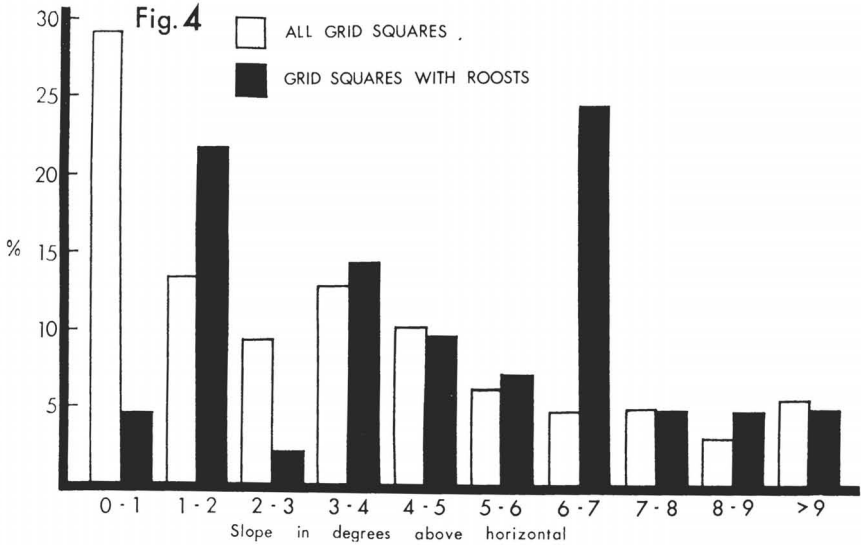
Roosts on plant inflorescences or apices were more frequent than roosts on culms or stems. Such heads may provide roosts which are easier to cling to or are less deflected by the butterfly's weight.

Butterflies on roosts are significantly closer to the ground than those perched during daily activity (Table 1). The maximum height of vegetation within a one meter radius of each roost averaged greater than twice the roost height (110 ± 17 cm, $N = 33$). Roosts were invariably in open areas of the vegetation where contact of the roosting butterfly with surrounding plants was impossible in all but the heaviest winds.

Description of the Roost Sites

Roosting occurred primarily on sites which sloped toward the west and were at the higher elevations in the field (Fig. 3). There were no differences between the roosting sites of males and those of females.

The distribution of slopes for the ten meter grid squares in which roosting occurred differed significantly from that of slopes for all grid squares in the field (Kolmogorov-Smirnov Test; $.05 > P > .01$) (Siegel, 1954) (Fig. 4). The average slope of 53 roost sites was 4.2 ± 2.5 (S.D.) degrees above the horizontal. Similarly, the distribution of aspect values toward which roost sites sloped differed significantly from that for all grid



Figs. 4-5. Frequency distributions of slope (4) and aspect (5) values for all grid squares in study area compared with distributions for only those grid squares containing roosts.

sites in the field ($P < .01$) (Fig. 5) even though the field predominantly sloped toward the west.

The density distribution of yellow goat's-beard (*Tragopogon pratensis* L.) and rough-fruited cinquefoil (*Potentilla recta* L.) for roosting sites

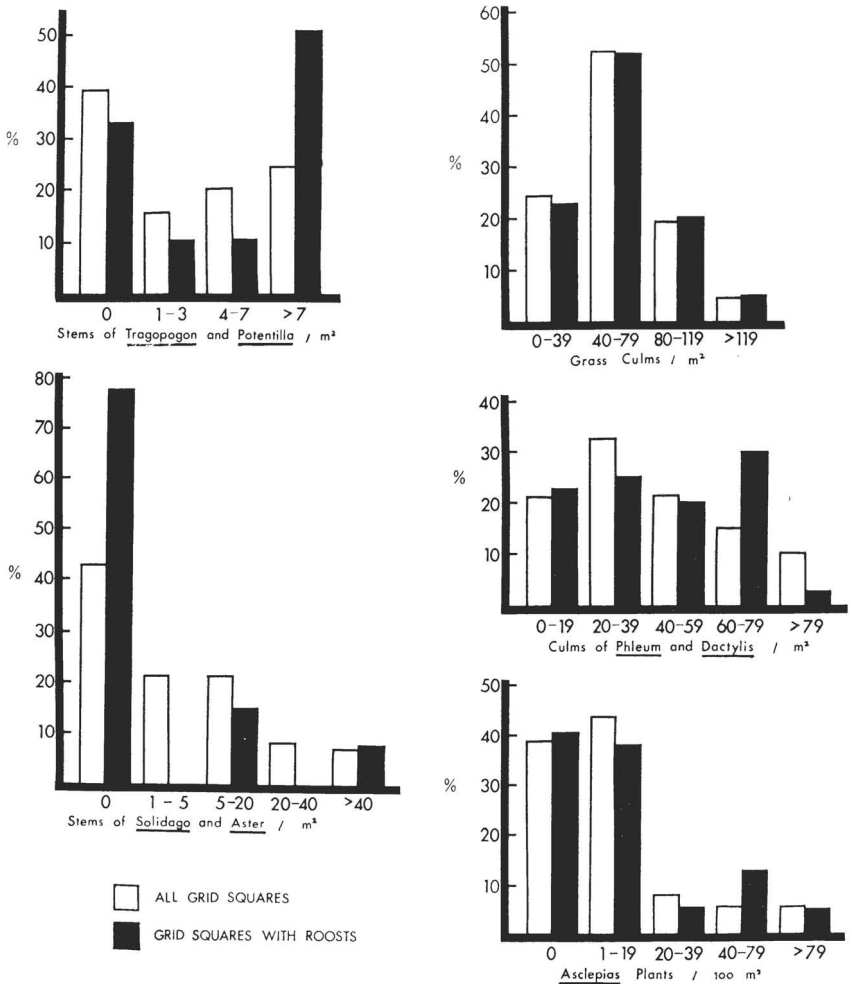


Fig. 6. Frequency distributions of various plant densities for all grid squares in study area compared with distributions for only those grid squares containing roosts.

differed significantly from that for all sites in the field, the density being higher for roosting sites (Kolmogorov-Smirnov Test; $.05 > P > .01$) (Fig. 6).

The density distribution of goldenrod (*Solidago* spp.) and New England aster (*Aster novae-angliae* L.) also differed significantly ($P < .01$). Roosts did not occur where *Solidago* and *Aster* were at highest density; these species usually form dense stands of plants which contact each other greatly in the wind.

On the other hand, density distributions of all grass species, of just orchard grass (*Dactylis glomerata* L.) and timothy (*Phleum pratense* L.) taken together, and of common milkweed (*Asclepias syriaca* L.) did not differ significantly ($P > .05$) between roosting sites and all field sites.

Survivorship on the Roost

Roosting individuals were quiescent and could easily be approached and caught by hand. Such inability to escape suggested that predation during roosting might be a major, if not the chief, cause of mortality in black swallowtail adults.

Twenty-six roosts were visited the following morning before basking occurred. Two male butterflies were missing from their roosts and were never seen again in the study area. Probability of death per night on the roost was estimated as being $2/26 = 0.077$ for all butterflies regardless of sex. Thus, an adult could be expected to live through an average of 8.7 nights assuming no other sources of adult mortality were considered [$(1 - .077)^{8.7} = 0.5$]. If only males were considered the probability of death on the roost per night was estimated by $2/21 = 0.095$. The average life expectancy of males was through 6.9 nights ignoring other sources of mortality.

DISCUSSION

Black swallowtails favor roosting sites which will allow them to continue basking for as long as possible under decreasing radiation. Selection of relatively open roost sites which slope toward the west favors the maintenance of body temperatures suitable for continued activity for as long as possible. There is no indication of any behavior which would favor warming the following morning. The presence of such behavior in other butterfly species needs more study.

The only unique behavior associated with roosting is the roost search flight. It is this flight which provides the mechanism by which a suitable roost is selected. Repetitive brief perches during this flight allow the butterfly to test and reject perches which are unstable, in the shade, or are disturbed by other vegetation. Frenetic activity during the search flight may provide enough body heat metabolically to allow flight to continue under conditions which would prevent further activity if the butterfly were motionless for a short period.

Since the search flight occurs in the sun, roosts which are finally selected tend to be on sites having the longest and most direct exposure to the setting sun. Roosting individuals on level sites are more susceptible

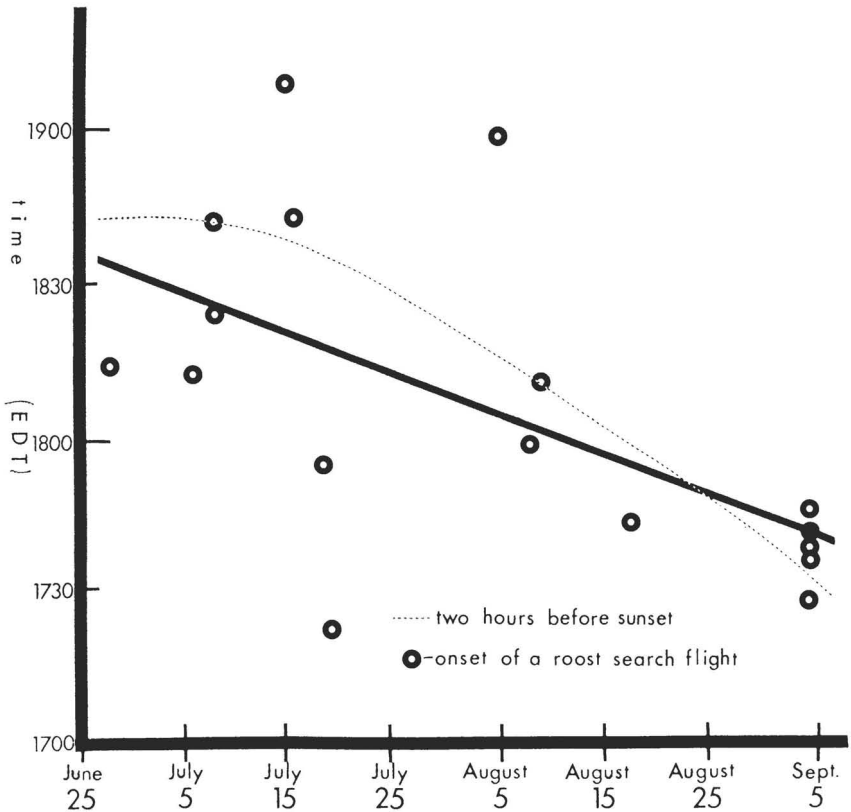


Fig. 7. Comparison of the time of onset of roost search flights with time of sunset. The solid line is a least-squares regression line of onset times with respect to date.

to being shaded by plants between them and the sun than are those on sloping sites facing the setting sun.

The onset of the erratic roost search flight is apparently triggered by decreasing radiation regardless of temperature. The shift from dorsal basking on the roost to a roosting posture with folded wings appears to occur when ambient temperature and radiation are such that body temperatures suitable for flight can no longer be maintained. There appears to be no endogenous rhythm controlling roosting. Such behavior is just as clearly associated with the onset of unfavorable conditions for flight at other times of the day.

Basking on the roost is similar to basking under more favorable conditions. There is no difference between morning and evening, making Glench's (1966) categories of "vesper" and "matutinal warming" difficult

to define for *P. polyxenes*. Basking on the roost may lengthen the period in the evening when escape from predators or selection of a different roost are still possible should a predator appear or the roost become unsuitable.

Selection for roosting behavior and roost preferences appears to be strong in view of the high mortality recorded in this study. Those individuals which fail to secure a steady, protected roost risk dislodgement and predation while cold and helpless at ground level.

In a concurrent study, Lederhouse (1978) estimated the probability of permanent disappearance per day due to dispersal and death for males after the first night of adult life to be 0.106. This value for males through the first night of imaginal life was measured as 0.532. The present estimate of male mortality on the roost (0.0953) is therefore about equal to that which Lederhouse ascribes to all causes of death plus dispersal because all marked butterflies in our study were at least two days old. It is conceivable that the large loss through the first night of adult life may be attributed to failure to find a suitable roost during that first evening or to considerable dispersal during the first day.

Death on the roost may be the chief source of mortality in this population, since not one instance of diurnal predation has been seen in over 700 hours of close observation, notwithstanding reported cases of diurnal predation by passerine birds (Erickson, 1973). Predation by ants may explain the preference shown for dead dicot scapes as roosts since ants may not frequent such plants during foraging.

If death on the roost is the major source of mortality in adult black swallowtails, then selection for mimetic or cryptic coloration patterns would probably operate most strongly on that portion of the butterfly which is exposed during roosting, the undersurface of the hindwings. We cannot help but note that the undersurface of the hindwings of members of the supposed *Battus philenor* mimetic complex are more similar in coloration than any other part of the wings. This complex includes *B. philenor* (L.), *Papilio troilus* L., *P. glaucus* L. (dark females), *P. polyxenes* F., and *Limenitis arthemis astyanax* F. (Brower, 1958). We suggest that selective advantages gained by cryptic or mimetic coloration patterns in many butterfly species may be greatest during roosting and that the exposed undersurface of the wing is more affected by such selection than is the hidden uppersurface.

In conclusion, black swallowtails select roosts which maximize exposure to the setting sun and provide stable, secure sites preventing dislodgement during the night. A roost search flight triggered by decreasing radiation is the only behavior unique to roosting and provides a

mechanism by which suitable roosts may be selected. Selection for efficient roosting is strong since death on the roost is likely to be the major source of mortality in adults.

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