PATTERNED PERCHING BEHAVIOR IN TWO *CALLOPHRYS* (*MITOURA*) (LYCAENIDAE)

KURT JOHNSON[1]
Department of Biology, City University of New York, Convent Avenue and
West 138th Street, New York, New York 10031

AND

PETER M. BORGO[2]
Department of Marine Studies, University of Delaware, Newark, Delaware 19711

Several species of Nearctic butterflies are well-known for the habitual attachment of their adults to the larval food plant, which serves as a substrate for a behavior popularly called "perching." Notable among these are tree-feeding species such as the nymphalids *Asterocampa celtis* (Boisduval & LeConte) and *A. clyton* (Boisduval & LeConte) on hackberry (*Celtis* spp., Urticaceae) and lycaenids of the taxon *Callophrys* (*Mitoura*), which feed on various Cupressaceae. Except for visits to food sources, adults of these species confine their flight activities to the immediate vicinity of trees, where they are often seen flying out from the branches and returning. Although these habits are often noted in popular studies and regional works, no published research has dealt with their details or nature. The term "perching" has been used as a general category in mate finding in butterflies (Scott, 1973), but such "perching" probably merits distinction from the particular behavior displayed by the aforementioned tree feeders.

The perching species *Callophrys* (*Mitoura*) *siva* (Edwards) and *C.* (*M.*) *gryneus* (Hübner) are exclusive *Juniperus* feeders, utilizing a broad spectrum of morphologically and chemically divergent *Juniperus* species that replace each other geographically over a wide area of the Nearctic region (Johnson, 1976). The present paper treats the tree-perching behavior of *C.* (*M.*) *siva* and *C.* (*M.*) *gryneus* as studied on two of their larval food plants, *J. scopulorum* Sarg. and *J. virginiana* L., respectively. The purpose is to outline the outstanding characteristics of the behavior, consider what environmental stimulus-response relationships are present, and comment on their significance.

Perching Behavior and Environmental Stimuli

Many aspects of insect behavior have been described in the literature and defined into types and categories. Most of these are not applicable

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[1] Museum Research Associate, Museum of Natural History, University of Wisconsin, Stevens Point, Wisconsin 54481 and Research Associate, Allyn Museum of Entomology, Sarasota, Florida 33580.

[2] Present address: 535 Park Avenue, Burlington, Wisconsin 53105.

to specific observations until thorough physiological data is available on a species. Thus, it is best to introduce perching behavior by reviewing literature that concern characteristics of behavior which are observable in the field.

Specific activities of insects result from the continuous "release" of fixed behavior patterns and pattern combinations, which are the insects' response to evolutionarily defined stimuli within its niche. Stimuli may include extrinsic factors (e.g., gravity, light, temperature, humidity, air movements, sound, chemicals, food, mates and other biota) or intrinsic ones (e.g., hormones, feeding rhythms, and mating rhythms). Stimuli are processed into particular released behavior through specific adaptations and interactions of sense receptors. A process may involve a single stimulus and a single receptor, screening of stimuli by a single receptor or balancing of stimuli by several receptors. Generally, many factors, each of which could release such fixed patterns of behavior, are working on many receptors (Jander, 1957).

For the field investigator, one subject for study is the role of light. Two factors may be active, depending on the physiological adaptations of the insects: a relationship to the sun's polarized light (sky light) and/or the position or intensity of the sun itself.

Sky-patterns of polarized light are caused by the varying directions of oscillation of light as it is distributed from the sun. Insects may respond to polarized light directly (von Frisch, 1960), to its different patterns of reflection from the substrate (Kalmus, 1958; Smith & Baylor, 1960) or to both (Jander & Waterman, 1960). Especially important to insects is the relationship in the sky of points of equal degrees of polarization. When connected by hypothetical lines, these points form mathematical planes, and it is to these planes that many insects have become sensorily adapted. In other words, orientation to sky points of certain degrees of polarization causes an insect to react along a certain plane in relation to the source of light and the environment. The most important of these planes for many insects is the planc formed by connecting the points of maximum polarization—70%. This plane runs perpendicular to the straight line from sun to earth, a line which is generally referred to as the electric or "e" vector of light. Reactions and orientations along this perpendicular plane have received much study, and four basic posturing positions have been shown to occur in insects: the parallel position (0° from "e" vector), the vertical position (90° from the "e" vector) and the angular positions (±45° from the "e" vector) (Jander & Waterman, 1960). In polarization-adapted insects, the ratio of occurrence of these positions varies with species and factors such as temperature (Willington *et al.*, 1951; Henson, 1954) and excitement (Jander & Waterman, 1960).

Reaction to the position and/or intensity of the light source itself involves phototaxis. Insects may be positively or negatively phototactic, and the degree of their response may vary with increase in brightness of the source and/or higher contrast between the source and environment (Robinson & Robinson, 1950; Robinson, 1952), temperature or excitation (Mell, 1954; Marten, 1956), or the physiological tolerances of the sense organs (Verheijen, 1958). These reactions to polarized light or the sun itself can go on simultaneously in the environment.

Gravity is another factor that often cooperates with functions performed by the visual organs (Schwartzkopff, 1965) and is usually sensed through proprioreception. It is best to consider the influence of gravity in separate data since it may involve co-actions of various receptors, elicit patterns of response independent of other observations, or even be observed as alternative positive and negative influences in other observed patterns (Markl & Lindauer, 1965). Statistical data that indicate the roles of all of these factors in *Callophrys* (*Mitoura*) behavior were discovered in the present study and are presented below.

METHODS AND MATERIALS

Field-condition studies are neither the only nor most ideal method for studying complex behaviors. The number of inferences that can be drawn concerning possible physiological relationships is limited (Goldsmith, 1965), espccially since such inferences depend largely on distinct knowledge of the physiology of the insect's sense organs (Hodgson, 1965). However, appropriately designed experiments are useful for discovering good subject species, basic behavior patterns, and possible parameters for laboratory experiments (Mazokhin-Porshnyakov, 1969, pp. 121 f., 134 f., and 213 f.). In the present study, data samples totaling 471 randomly selected perch positions were gathered in 1973 and 1974. Initially, to compare the behavior of *C.* (*M.*) *gryneus* and *C.* (*M.*) *siva*, two juniper habitats were selected where sample trees could fulfill the following requirements: nearly equal mean tree height; presence of extremes of height, but similar range; all trees adjacent; and a workable population of *Mitoura*. These sites were: off County Rd. 547, near Lakehurst Naval Air Station, Ocean Co., New Jersey, and Catholic Cemetery, Chadron, Dawes Co., Nebraska. Because of the desire to investigate the possible role of perching behavior in geographic distributions and food plant selection, an extremely northern (apparently transplanted) *C.* (*M.*) *gryneus* colony was studied at New London, Merrimack Co., New Hampshire. Similarly, an effort was made to study the behavior in an arid area, where small juniper morphs occur, but this attempt (by a third co-worker) failed as a result of inclement weather.

The trees numbered at these sites comprised a "base sample" from which trees to be used for treatments could be drawn by random numbers. Because of daily movements by the butterflies in the habitat, treatment trees were actually drawn from a "sub-sample" made up of the number of trees being utilized for perching before each treatment. When the "treatment tree" was selected, the "treatment insect" was designated arbitrarily, and randomness was assured by measuring and recording data on five consecutive choices of perch following the initial flight from the tree. Motivation for flying was either natural movement or from nudging of the appropriate twig by the investigator. Early samples confirmed that such "aided" and "unaided" movements showed no significant mathematical differences in analysis. If the treatment insect changed trees, the change was noted and the sample continued. The time between tree changing allowed study of the types of trees chosen for perching. Accordingly, a "selected mean tree height" was calculated for each study area based on the number of times certain trees were chosen for perching. If an insect flew out of the area and the five-choice treatment could not be completed, the remaining perches were considered to be zero for all measurements and observations. Perch locations were designated by lifting a colored loop of string or wire to the perch site; tree and perch heights were measured with a graduated measuring rod. The measurement method was tested against known heights by the "t" test and showed no significant differences when used to the nearest centimeter up to 4 m. Above this height, measurements were rounded to the nearest decimeter. The latter method had to be used only in the supplementary samples mentioned below.

For comparison, supplementary areas (medium-size trees at Tuckerton, New Jersey and tall trees at Blackbird State Park, Delaware) were sampled, some by the above method; other data were culled from earlier observations at Long Pine Recreation Area, Brown Co., Nebraska. These data were not used in the random sample analysis of measurements, but were enumerated.

In this paper, any statistical value listed without an accompanying probability was not significant above $p = 0.20$, except in the few cases where extraordinarily high χ^2 values were significant beyond question.

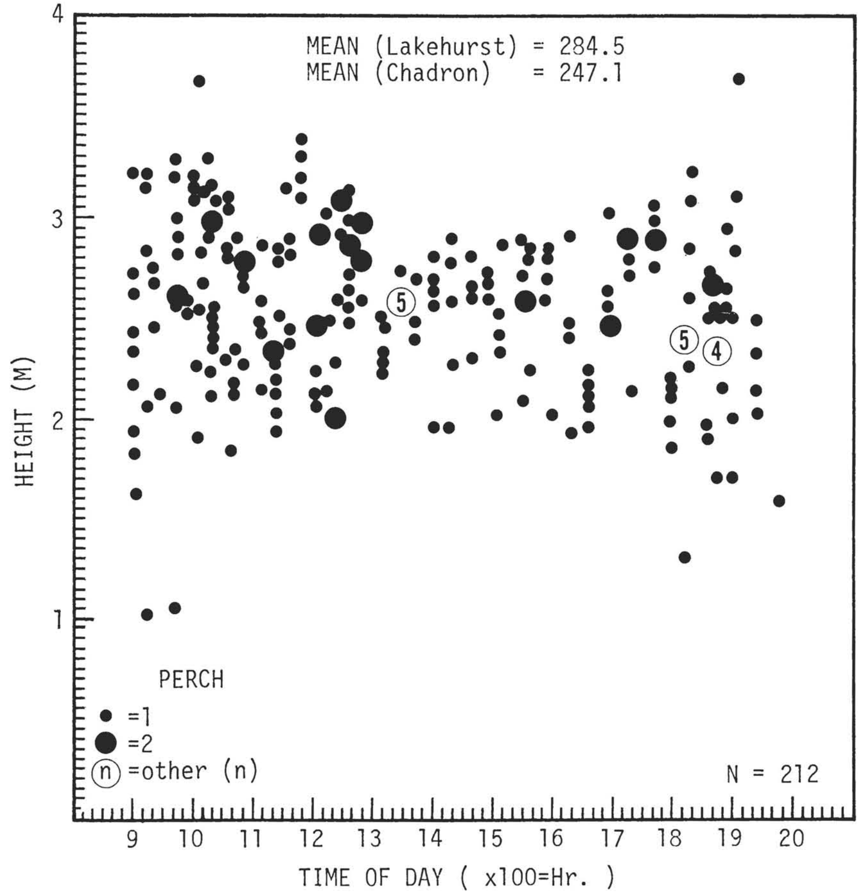

Fig. 1. Heights of perch plotted against time of day at Lakehurst and Chadron.

RESULTS

Perch Location

Perch location and sunlight. The role of sunlight showed general and specific consequences in the behavior. At Chadron and Lakehurst, of 239 perches recorded, only 3 were not in direct sunlight ($\chi^2 = 226.8$), and at New London this ratio was 232/1 ($\chi^2 = 229.0$). These samples were always made in sunny or partly sunny weather, and although some activity by the insects occurs during overcast warm weather, it may involve stimulus-response mechanisms that are not comparable to those subject to this investigation.

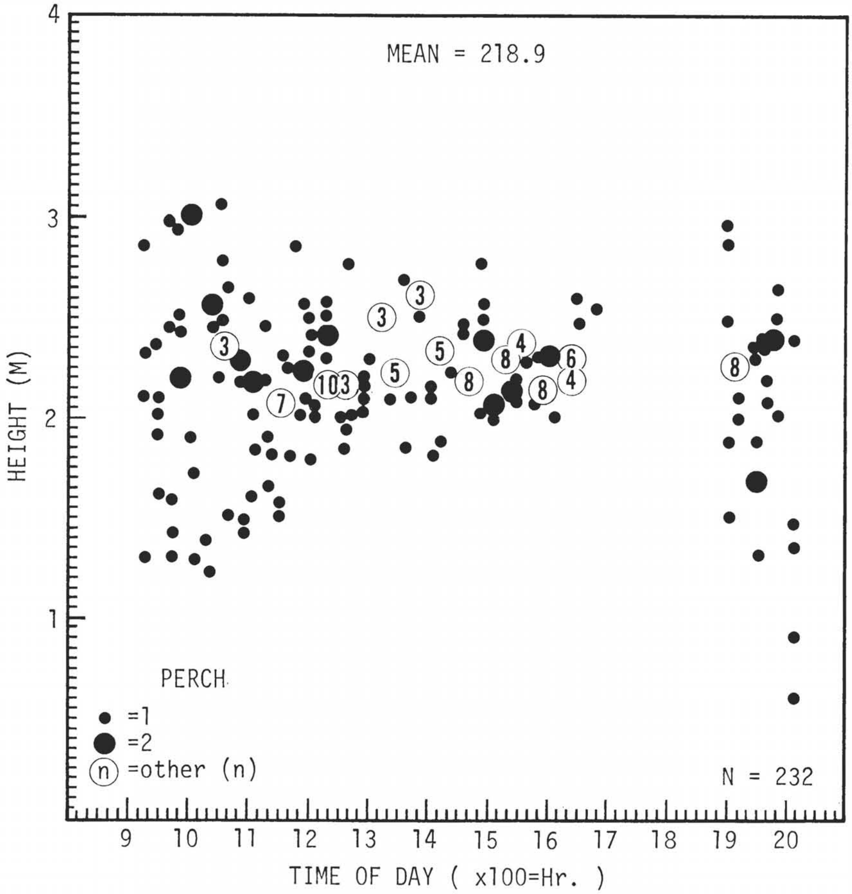

Fig. 2. Heights of perch plotted against time of day at New London.

Heights of perch were plotted against time of day as in Figs. 1 and 2. The dots form an "hourglass-on-its-side" configuration characterized by greater dispersal of height of perch in morning and late afternoon-evening than at midday. This gradual shift in degree of dispersal was confirmed by correlation coefficients (cf. Fig. 3). These were also used to designate three "periods" apparent in the behavior: morning "expansion" (0700–1245 hr), midday "compression" (1245–1445 hr) and late afternoon–evening "expansion" (1445–1900 hr) [all ST]. These three periods are significant because they demonstrate changes in the behavior in relation to the angle of the sun, which will be discussed further.

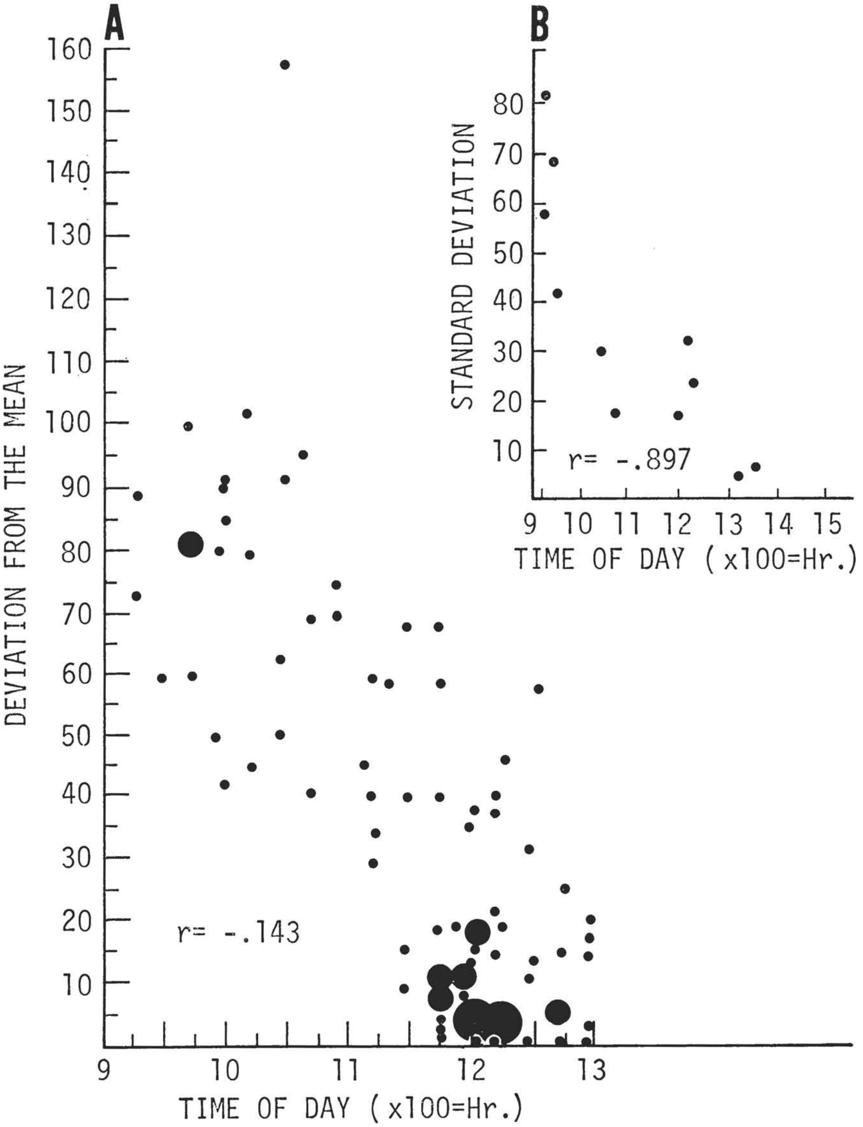

Fig. 3. Correlation coefficients. (A) Deviation from the sample mean of each perch at New London (morning expansion period) correlated with time: r = –.143; p = .10–.05; n = 145. Small dot = 1; medium dot = 2; large dot = 3. (B) Standard deviation of each treatment from the sample mean at Chadron (morning expansion period) correlated with time: r = –.897; p = .001; n = 11. Not shown: deviation from the sample mean of the mean perch height of each treatment at Chadron (evening expansion period) correlated with time (scaled opposite direction): r = .478; p = .05; n = 20.

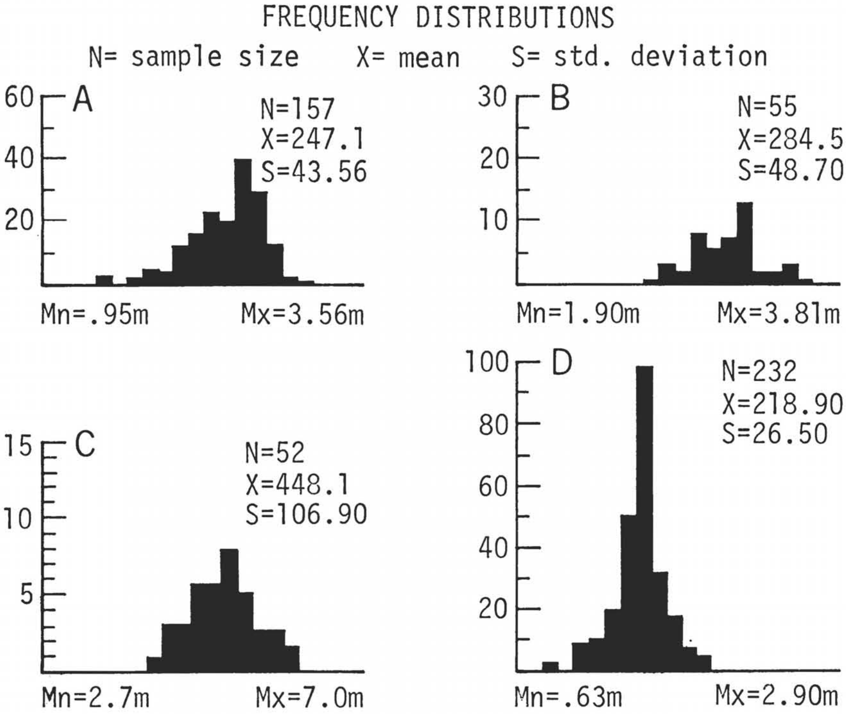

Fig. 4. Frequency distributions of heights of perch: A, Chadron; B, Lakehurst; C, Long Pine; D, New London. Lakehurst, Chadron, and New London: 20 categories, each 20 cm. Long Pine: 20 categories, each 35 cm. Maximum and minimum perch height are indicated.

Perch location and height. Frequency distributions of heights of perches (Fig. 4) skewed right, which indicated preference for height. This indication was further confirmed by calculation of "selected mean tree height" for each sample area, in which the height of each tree was multiplied by the number of times it was selected for perching and the mean was computed. These were always higher than the mean tree height of the sample. Furthermore, frequencies of heights of individual trees selected for perching, plotted against availability of these heights in the sample (Fig. 5), showed similar preference. Together, these data indicate that choice of perch as a whole forms a gradually shifting and somewhat symmetrical pattern in relation to time of day and is distinctly preferenced for heights.

Perch location and tree surface. Percent of height of tree used per time of day was evaluated as in Figure 6. The entire figure (dots and hatches) shows the frequency of use of heights (in percent) for

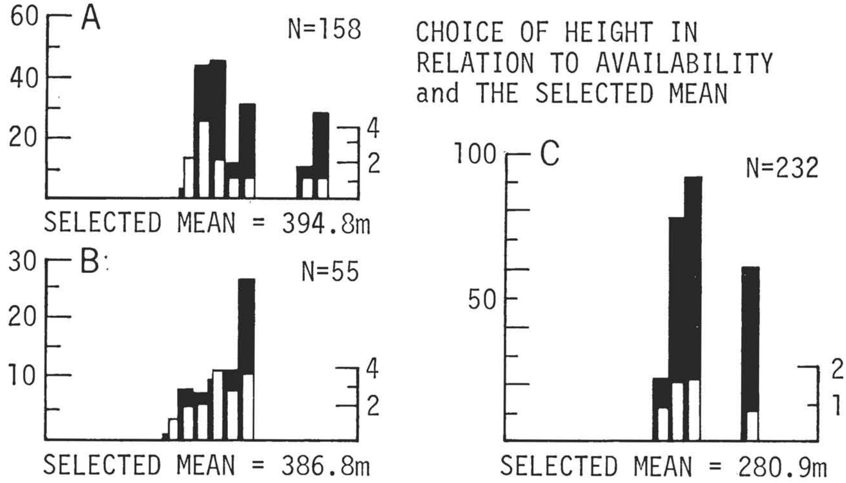

Fig. 5. Frequencies of heights of individual trees selected for perching plotted against availability of these heights. Left scale (black frequencies): height category chosen for perching. Right scale (hatched frequencies): number of trees in the sample of each category. (A) Chadron, 20 categories, each 20 cm. (B) Lakehurst, 20 categories, each 20 cm. (C) New London, 20 categories, each 17 cm. Trees in the base sample not chosen for perching are excluded. "Selected mean perch height" of each sample is indicated: the mean of—the height of each tree times the number of times chosen for perching.

the entire day; the stippled areas show morning and late afternoon–evening expansion periods, and the hatches show the midday compression period. The forming of two separate "humps" indicates that two interrelating stimulus factors are probably involved. Use of the tree in the compression period is uniformly undispersed (as also apparent on the perch height per time of day (Figs. 1, 2)) and occurs mostly high in the trees. This compression period occurs when the sun is high above the sample area and the plane of reaction to 70% polarized light is distributed horizontally along the tops and ascending angles of the trees. Height-use of the trees in the two expansion periods, however, forms two humps (there is some variation in the two samples), with the second hump being lower on the trees. The expansion periods occur when the sun is low in the sky and the plane of reaction to 70% polarized light is distributed vertically over the sides and ascending angles of the trees. Actually, this plane is continually changing, rotating from the vertical obliquely to the horizontal and back as the day continues. Apparently this rotation dictates the configuration of the perch locations through the day.

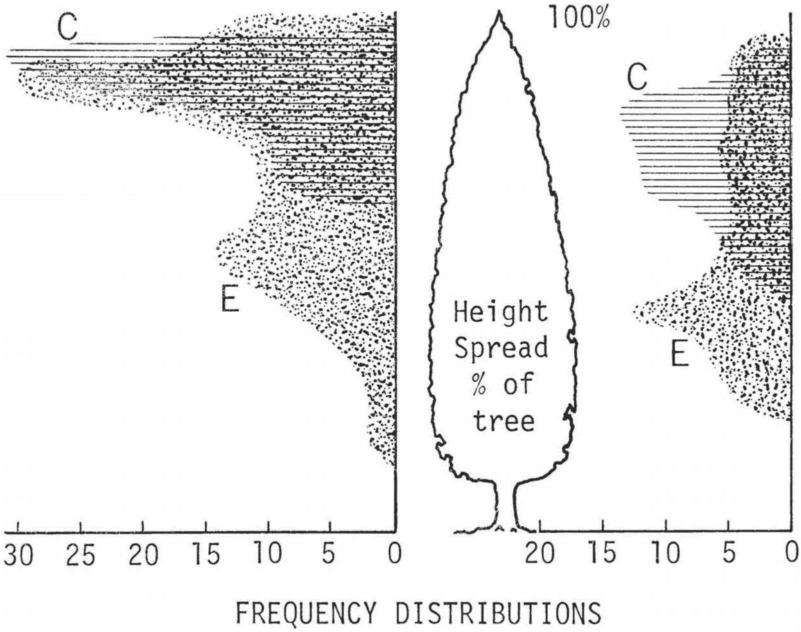

Fig. 6. Evidence of two factors influencing perch height: percent height of tree utilized per time of day. See text for discussion.

Behavioral differences between the species. It is especially interesting that the samples of *C.* (*M.*) *siva* in Nebraska and *C.* (*M.*) *gryneus* in New Jersey could be lumped together for this study. The study areas were chosen with this in mind. Early comparisons of "heights of perch"/"heights of tree" for a similar time period showed no significant difference in the behavior of the two species in the nearly duplicate habitats ($t = 1.98$; $p = 0.05$; $n = 100$).

Summary. The trees at Chadron and Lakehurst were extremely variable in height and often located meters apart. At New London all the trees were nearly the same height (except for one a bit higher), and all were immediately aside one another. This difference may be reflected in the respective patterns of selection of perch. There was little distance for flight between the trees at New London, and thus, perhaps, occurred the higher frequency of changing trees, the marked tendency to choose a perch relatively near the height of the former, and the tendency to ascend higher when the single taller tree was reached. Despite these variations, the general information of the "hour-glass-on-its-side" configuration is most compatible, in both areas, with the hypothesis that the shifting plane of reaction to polarized light, vertical to horizontal to vertical and the position of the sun itself form the basic influences on the behavior.

Perch Posture

Posturing positions. Insects specifically adapted to polarized light and/or phototactic stimuli generally display certain fixed postures when they are stationary. Gotz (1936) and von Buddenbrock (1917) demonstrated a "turning tendency" that follows locomotion, in which the insect moves to assume its "stable" position of posture in relation to the sun. These two *Callophrys* (*Mitoura*) species displayed the four basic positions mentioned in the Discussion. Such positions have been demonstrated in a number of other insects, all of which are polarized-light adapted. Willington *et al.* (1951) and Henson (1954) showed the occurrence of these positions in particular frequencies in larvae of Lepidoptera. They were also demonstrated in *Bidessus* and *Geotrupes* (Coleoptera) by Birukow (1953) and Jander & Waterman (1960), respectively. Jacobs-Jessen (1959) showed that in *Halictus* (Hymenoptera) only two postures (0° and 90°) occurred, the two 45° postures evidently disappearing with excitation, the role of which was also confirmed by Jander & Waterman (1960). Similarly, effects of temperature or excitation have been shown in the aforementioned studies of Lepidoptera larvae.

In *Callophrys* (*Mitoura*), the 45° posture was only noted early in the periods and then disappeared. The gross ratios of 0, 45, and 90° postures were: Chadron—19/3/48; Lakehurst—23/4/17; Chadron and Lakehurst—42/7/65; Lakehurst and two supplemental sites—30/4/23; and New London—71/5/148. The 0° number is divided between the anterior and posterior toward the sun for these respective localities as follows: 6/13, 9/14, 15/27, 17/13, and 35/36.

It is clear that a discrepancy occurs if the Chadron and Lakehurst calculations are lumped together as was shown reasonable with perch location. This may not be due to species difference but because all Lakehurst (and supplemental) populations were morning expansion-period samples. Dropping the 45° posture, the combined Lakehurst and Chadron ratios of 90 to 0° posture is ca. 3:2. For New London this ratio is ca. 2:1. Thus, the difference, considering Lakehurst, may indicate that additional data would show certain postures more prevalent at certain times of day.

A number of χ^2 tests were performed on 1 × 2, 1 × 3, and 1 × 4 combinations of data from these sites as well as within and between species. It is not useful to state each calculation here except to mention that all showed a significance of at least $p = 0.05$—$p = 0.10$ to the extreme categories—0 and 90°. Similarly, the dominant frequency of 90° when compared with the sum of all others was $\chi^2 = 23.14$, $p = 0.001$ at New London and $\chi^2 = 9.78$, $p = 0.01$–0.001 at Chadron.

Special mention should be made that no locomotion was evident by these insects at the perch. Of the 471 perch choices in this study, only 6 insects showed locomotion at the perch. Thus, any "turning tendency" of movement necessary to assuming the stable posture must occur in flight before alighting.

Repetition of perch posture. There was a definite tendency for postures to repeat, at least for a brief period. This was investigated by creating an "index of repetition (IR)" and "index of nonrepetition (INR)." Each five-choice sample was evaluated as to the total combinations of repetitions or changes. Each change or repetition was given a value of $\frac{1}{5} \times$ the number of figures in the combination. (In a 90°, 90°, 90°, 0°, 0° sample the repetition value would be $\frac{2}{5} + \frac{2}{5} + \frac{3}{5} + \frac{2}{5}$ and the change value would be $\frac{2}{5}$.) These were then multiplied by 2 and added in decimals. The results were as follows: Chadron ($n = 47$)—IR = 15.4, INR = 6.6 ($\chi^2 = 3.52$, $p = 0.05$); Lakehurst ($n = 51$)—IR = 14.4, INR = 10.0 ($\chi^2 = 0.80$); and New London ($n = 226$)—IR = 76.2, INR = 34.5 ($\chi^2 = 15.62$, $p = 0.001$). There is a more graphic difference at New London, possibly because of the closeness of the trees in the sample.

There was little evidence that the insects (as commonly observed in the popular literature) often return to the exact perch from which they flew. Of the 471 perches in the sample, only 11 indicated such behavior.

Thermodynamics and perch posture. Since the physiological function of "sunning of the wings" in butterflies is well-known (Clench, 1966), the high frequency of the 90° angle position has an obvious thermodynamic value. For *Mitoura*, sunning is accomplished by closing the wings above the thorax and thus displaying one ventral primary and secondary to the sun.

Perch position and gravity. The investigation of positive and negative geotaxis in these insects was hampered by the subjectivity of the observations. At first, three positions were noted in samples—head obviously upward, head obviously downward, and insect horizontal. The latter was too subjective and was abandoned, which resulted in arbitrary designation of one of the first two. The results suggest that the positioning of the head occurs at random and alternates independently of the angle of the posture: Chadron—(method abandoned); Lakehurst and two supplemental—head up = 33, head down = 22 (χ^2 = 2.20, p = 0.20–0.10), IR = 16.6, INR = 4.2 (χ^2 = 7.40, p = 0.01); and New London—head up = 102, head down = 113 (χ^2 = 0.56), IR = 73.9, INR = 16.5 (χ^2 = 33.96, p = 0.001).

Other observations. Marked lethargy was shown by the insects in early morning and late evening, with refusal to move even upon touching. Borgo, in Delaware and New Jersey, noted individuals very low in the trees (0647–0702 EST: 0.45–1.95 m) and some covered with dew. These all later activated for daytime perching. Similarly, Johnson, in Nebraska, noted refusal of the insects to fly at dusk (ca. 7 pm MST). Behavior that suggests oviposition was also observed by Johnson. The insects favored no particular part of the tree, occurring on upper branches and on twigs near the ground. Females clung to the twig, with head upward (angle posture variable), and arched the abdomen in successive movements toward the undersurface of the twig. No oviposition was ever observed. Distinct avoidance behavior was noted where a cultivated spruce tree (*Abies* sp., Pinaceae) occurred in the center of the Chadron habitat. On two occasions butterflies flew to it but veered off to perch on a nearby juniper. Other butterflies found on the junipers included *Cynthia cardui* (Nymphalidae), *Asterocampa celtis* (Nymphalidae), *Cercyonis pegala olympus* (Satyridae), and *Strymon melinus* (Lycaenidae). Each of these flew out of junipers as *Callophrys* (*Mitoura*) were being studied.

SUMMARY AND CONCLUSIONS

The data in this study strongly suggest that the perching behavior of *C.* (*M.*) *siva* and *C.* (*M.*) *gryneus* is distinctly patterned and not simply a random usage of the tree. This has strong implications with regard to all *Callophrys* (*Mitoura*) species that feed on Cupressaceae, since their behavior is generally considered similar by lepidopterists. The statistical data on changes in the behavior with time of day and on perching postures support the assumption that the insects orient to interactions of polarized light and the position of the sun. The behavior is distinctly preferenced for height, and taller trees are most often selected for perching.

These species are suggested to the physiologist for laboratory experiments to examine in greater detail the precise environmental relations of the behavior and the stimulus-response mechanisms of the insects.

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HILLTOPPING IN LEBANON

Considering the extensive literature on hilltopping (Shields (1967, J. Res. Lepid. 6: 69–178) gives nearly 200 references), it seems worthwhile to give a few notes from Lebanon on the topic. I do not recollect having seen previous references from the Levantine area.

After collecting the localized *Euchloe belemia* Esper (10 km E of Saida, 21 March 1972) for a few hours, I ascended a small rounded hillock with typical garrigue vegetation. For more than 15 min. one *Papilio machaon syriacus* Verity, two *Vanessa cardui* Linné and one *Vanessa atalanta* Linné were observed circling the top. One or more might briefly settle, but mostly all four were on the wing. There was little beating of the wings, most movement being a strong glide. No other butterflies were seen on the hilltop, and the species in question were not noted elsewhere in the vicinity. The weather was fine, with a breeze from the west.

A large and fresh male of *Iphiclides podalirius virgatus* Butler was caught on a small summit surrounded by a precipitous drop of more than 200 m on three sides, the eastern side being somewhat gentler (Cedar Mountain, 1,900 m, 17 July 1974). The specimen hardly moved its wings while gliding on the updraft produced by a breeze from the west. It must have come from Bscherré village, some 300 m lower, where the closest breeding colony is located.

In the above cases I was struck by the apparent *"joie de vivre"* of the ebullient circling and by the method of flight, which differed so much from that ordinarily seen. Two rare species, *Papilio alexanor maccabaeus* Staudinger and *Elphinstonia charlonia penia* Freyer, are nearly always found about the summits of stony outcrops. Their flight in such situations is quite normal, however, which may simply indicate the presence of their food plants—so far unknown in Lebanon.

I have little doubt that hilltopping is more common in the Middle East than the lack of recorded evidence suggests. The places where these singular aerobatic displays are performed are otherwise so unattractive that no entomologist would pay them a visit.

TORBEN B. LARSEN, *c/o IPPF, 18–20 Lower Regent St., London SW 1, England.*