

Mate-Locating Behavior of Western North American Butterflies. II. New Observations and Morphological Adaptations

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Abstract. New observations on mate-locating behavior of various western United States butterflies and skippers are given. Some species show a certain amount of flexibility in behavior, especially at high density when several normally hilltopping species search for mates around dense stands of the larval foodplant. Several data sets were examined that indicate the rarity of hilltopping species compared to other species, that seem to reaffirm the usefulness of hilltopping at low density. Perching species, when compared with closely related patrolling species, have more pointed forewings and more powerful thoraxes compared to the size of the wings; perching species commonly have faster wingbeat frequency, and often have the forewing veins more crowded toward the costa. These adaptations presumably give perching species a powerful takeoff from rest for the approach and maneuver to a passing female. Females do not need this takeoff and tend to have more patroller-type wings.

Introduction

Scott (1975) reported the methods that males use to find females in many western North American butterflies and skippers. This paper gives additional information, including species not previously studied, and much more extensive observations on some species previously studied.

A few definitions are worth repeating. In *perching behavior*, males rest at characteristic sites and investigate passing objects by flying out at them to search for females; females fly to these sites to mate, then depart. In *patrolling behavior*, males fly almost continuously in search of females. In the third paragraph of page 2 of Scott (1975), the sentence "In patrolling species, interactions occurred predominantly when resting males investigated moving objects," was created by the printer by combining parts of the two adjacent sentences. It is wrong and should be crossed out. Perching males investigate females by flying from a resting position, whereas patrolling males investigate females by spotting and pursuing them while flying.

Methods are those of Scott (1975). Twenty-four-hour Standard Time (not Daylight Saving Time) is used. All observations were done in the foothills of the Front Range in Jefferson County, Colorado, unless

otherwise stated.

New Observations on Mate-Locating Behavior

Papilio eurymedon (Lucas). In 1980 adults of *eurymedon* and *P. glaucus rutulus* were unusually common in the Front Range foothills. Male *eurymedon* were found to choose open lanes among trees on hilltops and ridgetops, where they patrol back and forth in the little forest glades. Males seldom rest; they patrol most of the time. Males are usually found on hilltops, but they sometimes feed on mud or flowers in valley bottoms. One male was observed chasing a *rutulus* in a gulch at a patch of *Apocynum* flowers.

Papilio glaucus rutulus (Lucas). Male *rutulus* were also encountered frequently patrolling in little forest glades on hilltops and ridgetops. However, whereas *eurymedon* males stayed a long time and returned repeatedly to a given spot, *rutulus* males stayed only briefly before departing, presumably to other wooded slopes and valley bottoms. *P. multicaudata* (Kirby) patrols in gulch or valley bottoms only (Scott, 1975), so *rutulus* seems to have a generalist strategy, while the other two species are specialized.

Papilio zelicaon form *nitra* Edw. Considerable effort was made to study *nitra* in 1980, when adults were the most common I have ever found them in the foothills of the Front Range Colorado. Males patrol and perch on hilltops as reported by Scott (1975). Fisher (1977) showed that *nitra* is a form of *zelicaon* Lucas. A 1981 cross of a typical male *nitra* X female *zelicaon* from Jefferson County Colorado supports this conclusion, as typical *nitra* and *zelicaon* offspring resulted. Male behavior of *nitra* and the sympatric form *zelicaon* and *P. polyxenes* Fab. were observed for differences. One phenomenon became apparent: *nitra* males seem to occur nearly always on the topmost point of a series of hills. In 42 observations in 1979-1981, *nitra* males were found on the topmost hill at a locality, and in only 13 cases was *nitra* found on a lower adjacent hill. In contrast, form *zelicaon* when common is distributed rather continuously from the top points of the ends of the ridges, along the ridges sloping up to the high points, and on top of the hills as well. *P. polyxenes* males often occur on the highest point also, but they are also often found perching on a shelf-like slope just below the hilltop itself. These behaviors of *zelicaon* and *polyxenes* are understandable because they distribute the males along the ridge system where females come to mate. But *nitra* is rare—seldom more than one male found at a locality and usually none—and it does seem to be found on the topmost points more often than would be expected if it interacted with other individuals like an ordinary male *zelicaon*. At one locality 48 different male *zelicaon* were found, all over the ridge system, but the three male *nitra* found were only on the topmost two adjacent points of the mountain. Perhaps form *nitra* gains an advantage in mating if

the topmost point receives more females. Form *nitra* appears only in hilly areas in its range, which is consistent with the hypothesis. There are perhaps survival differences between *zelicaon* and *nitra* also that prevent *nitra* from occurring at higher altitude than the Transition Zone foothills (form *zelicaon* extends to the Canadian Zone and sometimes higher). Hybridization with *polyxenes* seems to occur frequently also (intermediates between *nitra* and *polyxenes* of every possible combination fly along with *nitra*, *zelicaon* and *polyxenes*), and hybridization probably first introduced the black genes into the *zelicaon* gene pool. Because *polyxenes* is a lower altitude insect than *zelicaon* in general, the influx of *polyxenes* genes into *zelicaon* that probably created *nitra* may have included linked genes giving *nitra* a survival advantage at low altitude.

Pieris callidice occidentalis (Reakirt). Males patrol almost constantly, and patrol and chase others on hillsides as well as hilltops, although at low density hilltops are the most reliable places to find them. Localities studied were the foothills of the Jefferson County Front Range; Loveland Pass, Summit County Colorado; various alpine sites in the San Juan Mountains of Hinsdale and Ouray Counties, Colorado; Mt. Sherman, Park County, Colorado.

Colias pelidne Bd. & LeC. Males patrol about $\frac{1}{2}$ m above ground all day in valley bottoms or slopes near shrubby willows and *Vaccinium* (Round Lake, Wind River Mountains, Sublette County, Wyoming).

Colias scudderii scudderii Reak. Males patrol swiftly all day about shrub willow areas in valley bottoms (So. Rio Grande Reservoir, Hinsdale County, Colorado; Loveland Pass, Summit County, Colorado; Toll Ranch, Gilpin County, Colorado; north of Greenhorn Peak, Pueblo County, Colorado).

Colias scudderii harroweri Klots. Males patrol, in morning at least, in bogs with small shrub willows (Canyon Creek, Wind River Mountains, Fremont County, Wyoming).

Erebia magdalena Streck. Males patrol all day over rockslides as Scott (1975) states, but extensive observations indicate that males patrol much more often in hollows in the rockslide than on evenly sloping or convex parts of the rockslide, which they cross fairly rapidly (Loveland Pass, Clear Creek County, Colorado, various sites in alpine San Juan Mountains, Colorado).

Oeneis jutta (Hubn.). Males perch, and occasionally patrol, in partly shaded small forest clearings (about 3-6 m wide) on fallen lodgepole pine logs and sometimes tree trunks or other objects, mainly in gently sloping swales in grassy forest. They do this at midday at least, in Middle Park, Grand County, Colorado.

Oeneis chryxus (Dbl. dy.). At timberline at several localities in the San Juan Mountains in Hinsdale County, Colorado, male *chryxus* perch in gulch bottoms and investigate passing objects, rather than on hilltops as

they do in most areas. The only hilltops there are far above timberline where *chryxus* was not found, so the *chryxus* of this area have evidently adjusted for the lack of nearby hilltops.

Oeneis melissa (Fab.). Males usually perch, and sometimes patrol, on rocky hilltops and ridgetops. In 1980, on a very windy day, males were observed perching and chasing in steep rocky chutes on hillsides also. On calmer days males were observed chasing on rockslides on slopes as well as hilltops. *O. melissa* seems restricted to rocky areas, whereas *O. polixenes* (Fab.) and *bore edwardsi* dos Passos males perch and patrol in heavily vegetated swales from the middle to the base of slopes, or swales in flatter hummocky areas, based on extensive 1979-1981 observations (for *melissa*, McClelland Mountain, Clear Creek County, Colorado; Loveland Pass, Clear Creek County, Colorado; Hermit Pass, Custer County, Colorado; Mt. Sherman, Park County, Colorado. For *polixenes*, Loveland Pass, Mt. Lincoln, Park County, Colorado, McClelland Mountain, Mt. Sherman. For *bore*, Cottonwood Pass, Chaffee County, Colorado, and many alpine sites in San Juan Mountains, Colorado).

Speyeria edwardsii (Reak.). Males frequently patrol all day in shrubby areas just below hilltops, although they sometimes patrol elsewhere also. Many males were seen to patrol there, often in areas where *Papilio indra* Reak. perches just off the summit, and a copulating pair was found off of a hilltop at one site.

Boloria improba acrocnema G. & S. Males patrol slowly all day about 10 cm above ground in moist slopes and swales. Males were observed chasing and courting females, and pursuing *Speyeria mormonia* etc., from 0905 to 1540 (San Juan Mountains, Colorado). Another paper gives the complete life history, and its ecology, and assigns it to *B. improba*.

Boloria napaea halli (Hoffm.). Males patrol swiftly all day about $\frac{1}{3}$ m above ground, in moist meadows where *Polygonum bistortoides* (Pursh.) Small is common (Wind River Mountains, Sublette County, Wyoming).

Boloria kriemhild (Streck.). Males patrol all day about $\frac{1}{3}$ m above ground in moist meadows or boggy areas (Wind River Mountains, Sublette County, Wyoming).

Chlosyne palla (Bdv.). At a low density population in 1980, males perched on small dirt plateaus in the gulch bottom, as described by Scott (1975) (near Idledale, Jefferson County, Colorado). However, at another site, the same hillside burn where *Erynnis martialis* was common on Ralston Butte, adults and the larval foodplant *Erigeron speciosus* var. *macranthus* (Nutt.) Cronquist were both very common. Males patrolled about a north and northeast facing hillside near the plants, in an area which was partly grassy, partly covered with shrubs, and partly open woodland. Numerous courtships were observed, and egg clusters were found on the foodplant.

Chlosyne gabbii damoetas (Skinner). Males both perch and patrol

frequently in rocky hollows and chutes, and roads cut across rockslides, all day in the San Juan Mountains, Colorado.

Poladryas minuta minuta (Edw.). Observations in 1972 in Baylor County, Texas, and in 1978, 1979, and 1980 in Colfax County, New Mexico, show that the mate-locating system is the same as that of *P. minuta arachne* (Edw.). Males perch on hilltops and ridgetops in the morning (at least from 0730-1130), then depart and are found on flowers elsewhere in the afternoon.

Nymphalis milberti Godart. Extensive observations in 1980 show that the main sites of mate location are the slopes and especially rocky places just below a hilltop, usually on the west (sunny) side of the hill. These places are the same perching sites as for *Papilio indra*, and the two species are usually found together. Other sites such as gully banks are chosen rarely (one observation by Scott, 1975, on the Colorado plains in Boulder County), at least where hills are available (the gully bank observations was on the Colorado plains). Males perch from late morning until late afternoon; observations were made at 1050, 1100, 1115, 1130, 1200, 1213, 1215, 1230, 1330, 1340, 1413, 1445, and many others in the afternoon. These observations were all in the spring, as the fall overwintering individuals do not seem to show mate-locating behavior. In *Nymphalis antiopa* (L.) only the spring overwintering adults have been observed chasing and mating also (one mating observed 28 April 1965 in Gregory Canyon, Boulder County, Colorado).

Apodemia nais (Edw.). In 1980 the mate-locating repertoire of *nais* was expanded somewhat. Males were observed chasing and investigating others at 0850, 0900, 0915 to 1030, 0930, 1230, 1300-1330, 1412, 1420, and 1430, extending the time span of male mate-locating behavior considerably (Scott, 1975 reported 1130-1430 in a gulch bottom). Males were observed perching in sloping gulches in 1978 and 1979. In 1980 adults were abundant on slopes near their larval foodplant, *Ceanothus fendleri*. Males perch often in hillside swales there, and males often patrol in an erratic flight over the canopy of the blooming *Ceanothus* and between the plants. Perching males fly out at other insects from their perches. Courtship was observed as early as 0900 as a male repeatedly followed a female ovipositing on the *Ceanothus*. Perching males rest on twigs etc. about $\frac{1}{4}$ m above ground, the height of the prostrate *C. fendleri* plants. Density was high in 1980, which may have increased the areas (and times?) used for mate location.

Strymon melinus Hubn. Males normally perch on small trees or shrubs on hilltops in afternoon only (Scott, 1975), but in 1979 three males were observed perching there at 1115, unusually early for the species.

Callophrys sheridanii ssp. Near Paradox in Montrose County, Colorado, males of this ssp. (an undescribed spp. basically intermediate between *s. sheridanii* Edw. and *s. sheridanii comstocki* but with fewer ventral hindwing

spots than either) perch on shrubs and other objects about $\frac{1}{2}$ m above ground in the bottom of gulches, at least from 1200-1400, when a few chases were observed; behavior is very similar to a Churchill County, Nevada, *sheridani* population described by Scott (1975).

Vaga blackbruni (Tuely). On Oahu, Hawaii, males patrolled and chased others on the canopy (3-7 m high) of prominent trees on a hilltop. They patrolled the sunlit part of the canopy during sunny periods (from 1300-1400 at least) and rested on leaves when clouds obscured the sun.

Plebejus melissa Edw. Males patrol like other blues to find females. One male however, was observed perching on a 15 cm tall plant and darting out at passing blues, at 1235 in the foothills of Jefferson County, Colorado, 28 June 1978. Perching behavior is very rare in this species however; the only species of blue (Polyommataini) which I have studied that frequently has perching behavior is *Everes amyntula* (Bdv.) (Scott, 1975).

Thorybes mexicana (H.-S.). Males almost always perch on hilltops, based on extensive observations at numerous localities. However, in 1977 at the Moffat Tunnel in Gilpin County, where there are no hilltops for miles (only valley and wooded hillsides), males were observed perching in swales and a courtship was seen at 1235 in a swale. Near Hopewell Lake, Rio Arriba County, New Mexico, where no hilltops were available, a male was observed perching and chasing in a swale, and others perched on a slight prominence on a hillside.

Thorybes pylades (Scud.). This species is normally rare in Colorado, and the observations cited for Texas and Colorado by Scott (1975) were nearly all done in west Texas, where males perched in a gulch. In 1980 many males were watched in Jefferson County, Colorado; all perched and investigated over butterflies on or near hilltops, not in gulches, at about 0859, 0911, 0937, 0944, 1141, 1400, 1415, 1500, and 1540. *T. pylades* therefore seems to be a hilltopper in general (they also perch on hilltops in Arizona, Utah and El Dorado and Colusa Counties, California), except in West Texas where hilltops were not studied. The Colorado males observed all perched between shrubs or small trees, either on the very top of the hill or within 12 m of the hilltop on the sunny side of the hill, except for one male which perched in a small ($\frac{2}{3}$ m deep) depression in a hillside. Males rested on twigs, etc. roughly $\frac{1}{2}$ m above ground, between flights investigating other butterflies, flies, etc. Ray Stanford (pers. comm.) observed that males at Aspen, Pitkin County, Colorado, perch among shrubs on hills a short distance from the exact top of the hill where *Thorybes mexicana* and *Erynnis brizo* (Bdv. & LeC.) perch. *T. mexicana* males perch on stones, etc. on the top of a hill, usually in open areas, in contrast to *pylades* which perches among shrubs, often on the top but frequently a short distance from the top. Comparison no. 12 on page 31 of Scott (1975) between *pylades* and *mexicana* is therefore more like the comparison between *Papilio zelicaon* and *P. indra* (which mate on the top

of the hill versus just off the top) than like the other comparisons.

Erynnis pacuvius (Lintner) and *E. martialis* (Scud.). *Pacuvius* is normally rare in Colorado, seldom more than one seen per day, but at Ralston Butte in Jefferson County, Colorado in 1980, an old east-facing burn was found with a large population of *Ceanothus fendleri* plants, the larval food of both species. Males of both *Erynnis* were common and patrolled rapidly between and over *fendleri* bushes looking for females (often chasing other males). Under normal density conditions (Scott, 1975), males of both species perch on hilltops and are rarely seen elsewhere. *E. pacuvius* males also patrolled near hillside *Ceanothus* at Golden Gate Canyon, Jefferson County, where this plant and adults were very common.

Erynnis brizo. Males normally perch on hilltops, but when they are abundant I have also observed many males patrolling among the larval foodplant (*Quercus gambellii*) on hillsides at Jarre Canyon, Douglas County, Colorado. The only copulating pair found there was on the hilltop.

Polites sonora (Scudder). Courtship is frequent at flowers (of *Cirsium drummondii* var. *acaulescens* in Colorado) in Colorado as well as in California, in addition to the usual male perching in low spots of meadows (east of Gunnison, Gunnison County, Colorado; Toll Ranch, Gilpin County, Colorado).

Hesperia leonardus montana (Skin.). Courtships occur mainly at flowers, all day, and little or no mate-location seems to occur elsewhere. A hilltop 50 m from where *montana* was common attracted *H. pahaska* Leuss. earlier in the summer, but no *montana* when *montana* was common on *Liatris punctata* flowers nearby (near Deckers to town of South Platte, Douglas and Jefferson Counties, Colorado).

Hesperia uncas Edw. This species normally perches on small ridges or hills to find females, but in 1980 at a patch of *Cirsium vulgare* thistles I observed a male which had been resting on a thistle flower pursuing a female in a valley bottom. *Hesperia ottoe* Edw. males that were resting on flowers were pursuing passing objects there also, but this is the only mate-locating behavior known for *ottoe*, which seldom occurs away from flowers (Scott, 1975).

Hilltopping and Rarity Revisited

Scott (1970) found that species that mate on hilltops were only one fourth as common on the average as species mating elsewhere. However, several of the species listed as hilltoppers in Table 3 of that paper were later (Scott, 1975 and this paper) found not to be hilltoppers (*Hesperia juba* (Scudd.), *Erynnis icelus* (Scudd. & Burg.), *E. afranius* (Lintner), *E. telemachus* Burns, *Euchloe ausonia ausonides* Lucas, and *Speyeria coronis* (Behr)) because, although they rarely occur on hilltops, they do not show mate-locating behavior on hilltops. Recalculating the data when these species are transferred to the non-hilltopping category, the mean abun-

dance of hilltoppers is 0.24 specimens per hour, the mean for non-hilltoppers is 0.97 specimens per hour. The difference actually is increased; now the hilltoppers are less than one fourth as common as the non-hilltoppers.

This study (Scott, 1970) only considered spring species (March-May), so it may be worthwhile to consider another data set for the whole season using different methods. Marc Epstein and I have accumulated records for the butterflies and skippers of Red Rocks Park, Jefferson County, Colorado, from 1963 to 1980. Thousands of records were obtained, by 13 collectors; we will publish a paper on their phenology elsewhere. The records for each species were plotted, each brood delineated, and for each brood for which the number of records N is greater than or equal to 5, the standard deviation of flight date was calculated, which is an estimate of the "spread" of the flight period. The abundance of one brood of a species can be calculated as the number of records divided by twice the standard deviation. Dividing by twice the standard deviation compensates for differences in lengths of flight periods, and the resulting records per day abundance is roughly comparable to the specimens per hour of Scott (1970). The average abundance of non-hilltoppers is 0.60 records per day (for 49 broods), the average for hilltoppers is 0.47 (for 24 broods). There is still considerable difference between them (p less than 0.05), despite the fact that the protocol is not favorable for showing such differences (only presence or absence on a given day is recorded rather than the actual number of individuals seen or collected, so slight differences are apt to be obscured). The average number of records per species is also greater for non-hilltoppers (19.6) than for hilltoppers (14.5), although the average standard deviations of flight time are very similar (17.4 versus 16.6 days).

Morphological Adaptations to Perching Versus Patrolling Behavior

When the wing shape, body size, and flight pattern of perching species are compared with patrolling species, differences are evident.

Perching species in many cases have the forewings more pointed, with the margin straight from about vein M_2 to the tornus, whereas patrolling species have the forewing less pointed with the margin fairly evenly convex. Among the Pyrginae, *Thorybes* and *Erynnis* perch and have the former shape, while *Staphylus*, *Pholisora* and *Celotes* patrol and have the latter shape. Among the hairstreaks, most species perch and have the former shape, but *Hypaurotis crysalus*, *Habrodais grunus*, *Satyrium fuliginosum*, and *Phaeostrymon alcestis* all patrol and have the latter shape. Among the Hesperinae, *Copaeodes aurantiaca* has the former shape and perches, but the tiny patrolling skippers *Ancyloxypha numitor*, *A. arene*, *Adopaeoides prittwitzi* and *Piruna pirus* have the latter shape. Some tiny patrolling Hesperinae (*Oarisma*) have the straight forewing margin, but the ratio of the maximum forewing length to the distance from the wing

base to the tornus is still smaller (it is about 1.50 in *Copaeodes*, about 1.26-1.38 in the other Hesperinae mentioned). This ratio is greater in the satyrs that perch (averaging 1.50 among the nine *Oeneis* and *Neominois* species) than in those that only patrol (averaging 1.34 among 13 species). The ratio is greater among the Colorado *Papilio* that frequently perch (averaging 1.68 among *bairdii*, *polyxenes*, *zelicaon*, and *indra*) than among those that nearly always patrol (averaging 1.58 among *multicaudata*, *eurymedon*, *glaucus rutulus*).

Perching species tend to have a large muscular thorax in relation to the size of the wings. When species of the same wingspan are compared, the perching species have thicker more muscular thoraxes than patrolling species. The perching species of *Polygonia* and *Vanessa*, *Asterocampa*, most hairstreaks and coppers, and most skippers (except the patrolling skippers just mentioned) have thick bodies compared to their short wings. Nearly all the butterflies with a muscular thorax are perching species. *Parnassius* seem to be exceptions (although they have rounded forewings); I think the large body of *Parnassius* may simply be very hard to crush. They are distasteful (T. Eisner, pers. comm.) and birds probably let them go after mouthing them.

Perching species also seem to have a greater wing beat frequency, a subjective field impression. Many patrolling species simply flutter past the observer.

A complete analysis of morphological adaptations would be a major study. It would include the body weight, thorax weight, forewing length and shape, and hindwing length and shape, and even the arrangement of the veins in the wings, flight speed and wing beat frequency, analyzed using the principles of aerodynamics. The forewing veins seem to be crowded toward the costa in many perching species. This complete analysis does not appear to be simple, because the optimal design of the wings appears to change with wing size. The large butterflies (*Danaus*, *Papilio*, *Speyeria*) have rather pointed forewings even if they patrol to find females. Tiny insects such as Thrips (Thysanaptera) and some tiny moths literally "swim" through the air because of their high "Reynolds Number" (Pringle, 1957), so their wings can be shaped like oars; this principle may be applicable to tiny butterflies like *Brephidium*, *Zizula* and *Philotiella*. The aerodynamic aspects of these morphological adaptations have not been adequately studied at the present time. Kammer's (1967) studies of the thorax muscle firing sequence, and Nachtigall's (1965, 1967) studies of lift and drag of dead Lepidoptera adults are a start in the study of Lepidoptera flight, but are only peripherally relevant to the problem, because studies of flying animals are needed.

By analogy with the wing shape of airplanes and birds, the functional utility of the morphological differences can be surmised. When a resting perching male spots a passing creature, he needs power, speed and

maneuverability from a muscular thorax and pointed wings for a quick takeoff and approach to the passerby, like a powerful stubby-winged jet plane. A patrolling male, however, needs larger wings (with extensive wing area for extra lift) and a less powerful body for a nearly constant flying search, like a glider plane. These differences are also obvious among birds (compare kestrels, hummingbirds and flycatchers to *Buteo* hawks, vultures and albatrosses, for instance).

Nachtigall (1967) found that the aerodynamic characteristics of all the species studied were similar (plots of lift and drag when the wings were held fixed to the side in wind tunnels), and the major factor increasing the lift/drag ratio was increased speed. This may mean that the ratio of thorax muscle power to wing area may be the important aspect that differs between perching and patrolling butterflies. To increase this ratio, perhaps the rear part of the forewing and the hindwing are less important in flight and so it is these parts that shrink in perching species. This shapes the wings more like a propeller which presumably gives more forward thrust for extra speed. The speed perching males need to overtake females seems to give them additional lift which compensates for the loss of these wing areas. In other insects too, it seems that the faster the wings are flapped, the narrower they become. The rapid wingbeat species like Sphingidae, flies and most wasps have narrow wings and small hindwings, whereas slow wingbeat species such as Saturniidae and grasshoppers have broad wings. Kammer (1967) found that cutting off part of the wings of *Hylephila* did not affect the wingbeat frequency much, so the wingbeat frequency seems to be an evolved aspect of the neural mechanism rather than a direct result of the wing shape.

Females of perching species do not exhibit perching behavior. As one would expect, their wings tend to be more rounded than wings of their males (compare female with male *Hesperia*, etc.).

Discussion

The explanation of the cause of hilltopping species being rarer given above (that hilltops are mating rendezvous, allowing rare species to survive; at high density mating occurs more widely in the habitat so hilltopping has little value) seems to be supported by the observational data. At high density *E. brizo*, *E. martialis* and *E. pacuvius* males (plus other species, *C. palla* and *A. nais*, that do not mate on hilltops) were all observed searching for females at dense stands of the larval foodplant, so hilltopping seemed to have little value in high density conditions. High-density species should seldom evolve hilltopping. Furthermore, Scott (1975, pp. 32-33) discussed a mechanism of evolution of separate mating sites among closely related species, in which the rarer species would be more likely to evolve mating in sites such as hilltops.

The observations seem to demonstrate a certain flexibility in mate-

locating behavior, of some species at least. Such flexibility is well known in vertebrates. The five species just cited demonstrate a flexible response to density. Shapiro (1970) found that the normal perching behavior of *Euphyes bimacula* Gr. & Rob. changed at high density. Two species (*P. eurymedon* and *P. sonora*) were observed courting at flowers, in addition to the usual places of mate location, and other cases of this are given by Scott (1975). The observations on *O. chryxus* and *T. mexicana*, plus Scott's (1975) observations on *Euphydryas*, indicate a certain amount of local adaptation to the topographic sites available in the habitat. Scott (1975) mentioned species that both perch and patrol. Theoretically, one would expect a butterfly species to evolve a mate-locating strategy or location and time of mating to improve mating success, but a species should retain the capability of mating under other circumstances if the opportunity arises. For instance, if a male of a hilltopping species flies off of a hilltop to find flowers, if a receptive female happens to be at an adjacent flower the species should retain enough flexibility for mating to occur there. After all, the ultimate purpose of special adaptations for mate-locating behavior is to increase mating efficiency. The morphological adaptations probably increase mating efficiency, because the muscular thoraxes of perching males probably enable them to catch up with more females, and the larger wing area of patrolling species probably allows them to fly farther on the same energy input and thus discover more females.

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