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MATE-LOCATING BEHAVIOR OF WESTERN NORTH AMERICAN BUTTERFLIES

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Abstract. Mate-locating behavior, including the methods used to locate mates, the location of mating in relation to the larval foodplants and to topography, and the time of day of mating, was studied in 284 species of western north american butterflies and skippers. 18 pairs of congeneric species of butterflies and skippers were found to mate at contrasting topographic sites; the use of separate mating sites by these congeneric species certainly prevents, and may result from, interference competition during mate-locating behavior. Some trends in mate-locating behavior were observed: 1) perching species more often tend to mate in restricted sites in the habitat, and more often mate during a restricted part of the day, than do patrolling species; 2) perching rather than patrolling behavior is more frequent in species that have only 1-2 rather than 3-4 broods; 3) species emerging at the end rather than at the start of the season, and species with large movements, more often have patrolling rather than perching behavior and more often mate throughout the habitat rather than in restricted sites; 4) species feeding on shrubs or trees rather than on herbs more often tend to be perching rather than patrolling species and more often tend to mate during a restricted part of the day; 5) high mountain species usually patrol and mate at any time of day. Mate-locating behavior provides many useful taxonomic characters; closely related species usually have similar mate-locating behavior. Despite the trends noted above, different mate-locating strategies are often used by species feeding on the same larval foodplants. The strategy used often seems to be that used by a taxonomic relative feeding on other plants, but convergence of mate-locating behavior of taxonomically distant species feeding on the same plants has sometimes occurred.

MATE-LOCATING BEHAVIOR IS DEFINED as behavior which brings the sexes together for mating. It includes the methods used to find mates, the location of mating, and time of day of initiation of mating (Scott, 1974a).

Elsewhere I presented a general discussion of mate-locating behavior of butterflies (Scott, 1974a). There are three methods used to locate mates: *perching behavior* (males rest at characteristic sites and investigate passing objects by flying out at them to search for females; females generally fly to these sites to mate, then they depart), *patrolling behavior* (males fly almost continuously in search of females), and use of pheromones from more than a few meters away (this method seems quite rare).

Movement, size, wing color, wing pattern, and odor are stimuli which can be transmitted during sexual communication in the approach of a male to a female (Scott, 1973a). Perching males are highly attracted to moving objects, whereas patrolling males often are attracted to motionless objects resembling in some way females. A patrolling male may rarely find a female which gives off a pheromone when he wanders near her position. Perching species usually mate in limited areas of the habitat, often during only part of the day, whereas patrolling species usually mate throughout the habitat at any time of day.

This paper is a detailed survey of mate-locating behavior of several hundred western North American butterflies (Papilionoidea and Hesperioidea). In it I summarize mate-locating behavior for each species, and attempt in the discussion to determine major trends of behavior among all the species.

METHODS

To determine mate-locating behavior, adult behavior was observed, especially interactions between males and between sexes (including courtship and mating). In perching species, such interactions occurred predominantly when resting males investigated moving objects. In patrolling species, interactions occurred predominantly when resting males investigated moving objects. In patrolling species, interactions occurred predominantly when flying males investigated either flying or resting individuals. Perching and patrolling differ from resting and flying respectively, by the addition of investigative behavior. In a few species, noted in the results, both behavior patterns occur.

Location and time of day of mating were determined from field observations of such interactions. Varied topographic and vegetational sites were studied when possible to make sure that a restricted location of mating was characteristic of the population rather than due to limited opportunity.

Time of day of mating in this paper refers to initiation of mating. Therefore, field observations of copulating pairs were used with caution when initiation of mating was not seen. This is because copulation occasionally lasts several hours (very rarely several days) (Scott, 1973a), so that time of observation of the pair lags behind time of initiation. It is therefore possible to observe a copulating pair in the afternoon, if in that species courtship only occurs in the morning. Therefore time of day of mate-locating behavior, courtship and initiation of mating, were

given priority over time of observation of copulating pairs whose initiation was not seen. Species which are stated herein to court and mate during only part of the day were carefully studied to make sure that the restricted mating period was characteristic of the population and not a result of inclement or unusual weather.

The ideal method of studying the mate-locating behavior is to observe and record all details of male-male and male-female interactions, including dozens of completed courtships. For some species in this paper such as *Precis coenia* the data are based on more than 40 completed courtships in addition to other courtships and male behavior. However, it is not necessary to observe many completed courtships to determine mate-locating behavior. In all the species so far studied in detail (see literature cited), the following statements are true. In butterflies, the mating process always involves an investigation by the male of other individuals. Mating therefore occurs only at the locations where males investigate other individuals, and only during the time of day when males investigate other individuals. The method of mate-location is determined by observing whether males fly or sit before interacting with other individuals. These statements suggest that a complete description of mate-locating behavior can therefore be based only on male behavior, but observations of completed courtship are desirable supplements for confirmation. I include some species in this paper for which no completed courtships were seen.

Study of mate-locating behavior of butterflies can easily be carried out by those readers willing to spend field time observing behavior. The basic method is to observe interactions (male-male and male-female) and to record when and where these occur, and whether the male was resting or flying just prior to the interaction. Observations of resting or flying alone are of very little value without observations of interactions. Again I emphasize that perching and patrolling as I define them differ from resting and flying respectively in that perching and patrolling males investigate other individuals, whereas resting and flying males may not. I emphasize this because some people are treating the words perching and patrolling as the same as resting and flying respectively; to avoid such confusion it may eventually be necessary to propose special latin names for perching and patrolling behavior.

Some authors would use territoriality prominently in a discussion of mate-locating behavior. Territoriality may be defined

as males remaining in a small area to search for females, where males intentionally drive away other males. It may therefore be the fourth criterion for classification of mate-locating behavior (the first three being where mating occurs, when it occurs during the day, and the method used to locate females (perching or patrolling usually)). I do not use "territoriality" because no butterfly has conclusively been shown to be territorial with my interpretation of the vertebrate definition of territoriality (Scott, 1974a), and because demonstration of territoriality requires detailed study of movement of marked individuals which are beyond the scope of this paper. Some previous authors have used "territoriality" for what I call perching behavior, other authors have used it for what I call patrolling behavior where males sometimes return to the same spot, and still other authors apparently do not use it in any consistent manner. The methods and terms used in this paper were operationally constructed for use with butterflies, whereas "territoriality" was originally used for vertebrates and has since been applied so loosely that its meaning has become diffuse and the benefits from its use (especially with invertebrates) have become few.

RESULTS

These studies were conducted mainly in Colorado, especially the eastern slope of the continental divide and adjacent plains, and to a lesser extent in other western North American states and provinces, especially California. Eleven species were studied in detail in Colorado and California from 1969 to 1973 (see literature cited). During 1972 to 1974 over 200 field days were spent, mainly in Colorado, gathering data for this paper.

Supporting data including localities and times of observations of interactions, courtship and mating are not included in this paper due to space limitations; these data can be obtained from the author should they prove important to the reader. As a compromise I have indicated the quality of the observations as follows (a—about 100 or more observations of interactions, conclusions unlikely to change with further study; b—about 50-100 observations of interactions, conclusions may change slightly with detailed study; c—less than 50 observations of interactions, conclusions may change somewhat with further study and are presented mainly to increase the taxonomic variety studied). Localities studied are the eastern slope of the continental divide and adjacent plains of Colorado (Jefferson, Boulder, Douglas, El Paso, Clear Creek, Park, Chaffee, Custer, Pueblo, Fremont,

and Saguache Counties) unless otherwise stated. An asterisk is used for species occurring in the Pueblo area (Pueblo, Fremont, Custer, Chaffee, Huerfano, and Saguache Counties, Colorado) because these are analyzed in the discussion. Shields & Emmel (1973) have also compiled a list of mating times, and Shields (1967) provides information on several species not mentioned here. Several errors in Table 2 of Scott (1974a) are corrected herein. All times are reported as 24-hour standard time. The words "all day" in any context mean that interactions occurred at least from before 0900 to after 1500.

PAPILIONIDAE

Parnassius clodius. Males patrol all day about meadows and hillsides near the larval host. They patrol most often in swales, and often dip down between shrubs to search there; males have a somewhat bobbing flight (Nevada, El Dorado, and Siskiyou Cos. Calif.—b).

**Parnassius phoebus*. Males patrol all day in open areas where the larval host is abundant, slightly more frequently in sheltered sites (Scott, 1973b). Patrolling is most frequent on the leeward side of ridges both in Colorado and in California (Alpine & Siskiyou Cos.). Males patrol about ½m above ground, with a faster and steadier flight than *P. clodius* (a).

**Papilio polyxenes*, **P. bairdii*, **P. zelicaon* (and form *nitra*). Males patrol and sometimes perch, throughout the day (about 0900-1530 for Colorado *zelicaon*). At the usual fairly low density, males patrol but often perch, mainly on large hilltops. At high density and in the absence of hilltops males patrol and mate near the larval hosts (Guppy, 1969). In riparian forest, males perch in clearings among the trees (Sacramento, California, Arthur Shapiro, pers. comm.). Some hilltopping males in some localities may patrol only in a restricted area of a hilltop; this behavior might possibly be territorial (a).

Papilio indra. Males perch and patrol all day at about equal frequency, on somewhat sheltered rocky outcrops just below a hilltop (Jefferson Co. Colo. & Napa Co. Calif.) (b).

**Papilio rutulus*. Males patrol all day up and down streams with much riparian vegetation (they rarely patrol on hilltops for a few minutes in Colorado and Napa Co. Calif., then depart). In Davis, California, a suburb, males patrol about sunlit openings in wooded parts of the city (b).

**Papilio multicaudata*. Males patrol all day up and down canyon bottoms, which are usually drier than those frequented

by *P. rutulus* (a).

Papilio eurymedon. Males patrol (and sometimes perch) all day on large hilltops; males often patrol a small area there (Colorado, Napa Co. Calif.) (b).

Battus philenor. Males patrol all day on hillsides and flats near the larval host in Contra Costa and Yolo Co. California (they occasionally patrol on hilltops near Austin Texas and in Napa Co. California) (c).

PIERIDAE

**Anthocaris sara*. Males patrol all day up and down valley bottoms, or more haphazardly on flat land, but always near trees in forested areas (b).

Anthocaris lanceolata. Males patrol all day mainly in valley bottoms or steep hillside draws (El Dorado & Nevada Cos. Calif.) (c).

A. cethura. Males patrol on windless sides of ridgetops at least from 1130-1430 (Churchill Co. Nevada) (c).

**Euchloe ausonides*. Males patrol all day in open areas, slightly more frequently in valley bottoms than elsewhere, in Colorado and Contra Costa Co. Calif. (a; Scott, 1975a).

**E. olympia*. Males patrol all day on hilltops (b).

E. hyantis. Males patrol all day usually on hilltops, but sometimes throughout the habitat or restricted to areas of larval foodplant (Napa & Nevada Cos. Calif., Churchill & Lander Cos. Nevada, Pima Co. Arizona) (b).

**Colias meadi*, **alexandra*, **eurytheme*, **philodice*. Males patrol all day in open areas regardless of topography. (b).

C. occidentalis. Males patrol all day in valley bottoms, open woods, or on hillsides near the larval host (Colusa & Lake Cos. Calif.) (c).

C. cesonia. Males patrol all day, especially in valley bottoms and on flats (Pima & Santa Cruz Cos. Arizona) (c).

Eurema nicippe, *mexicana*, *proterpia*, *boisduvaliana*. Males patrol all day, mainly in gullies and flats (Pima & Santa Cruz Cos. Arizona) (c).

**Nathalis iole*. Males patrol all day several cm. above ground, mostly in gullies, roadsides, or flat land (c).

**Pieris chlorodice beckeri*. Males patrol all day up and down usually dry arroyo bottoms (Colorado, and Churchill Co. Nevada; b).

**P. sisymbri*. Males patrol all day, usually on hilltops, haphazardly when on flat land (Colorado, and Napa, Colusa, &

Alpine Cos. Calif.) (a).

**P. callidice occidentalis*. Males patrol all day, mainly on hilltops when they are available (b).

**P. protodice*. Males patrol all day, often on hilltops, but often on flat land when hilltops are unavailable (b).

**P. napi*. Males patrol all day along partly shaded streams in forests. Except for *A. sara*, the other Pieridae prefer open areas (b).

**P. rapae*. Males patrol all day near larval hosts near riparian vegetation in native habitats and on flat land in cultivated areas. They share the slow patrolling flight of *P. napi* (b).

**Neophasia menapia*. Males patrol all day, circling slowly about the larval foodplant trees (b).

Phoebis sennae. Males patrol all day, often on flat land (Mexico and Texas).

NYMPHALIDAE

**Euptychia dorothea*. Males patrol all day up and down narrow dry shaded gullies (b).

E. rubricata. Males patrol all day, usually in semi-shaded sites such as gullies (Texas) (c).

Euptychia cymela. Males patrol all day, mainly in woods under shading trees (Ohio, and Yuma Co. Colo.) (c).

**Coenonympha tullia*. Males patrol all day in grassy areas regardless of topography (a).

**Neominois ridingsii*. Males perch (and seldom patrol briefly) from about 0750 to about 1100, strongly from 0830 to 1000, and rarely later in the day, on small (3m) grassy hilltops, mesas, or saddles (Fremont Co. Colo., Scott, 1973c). Behavior in Mono Co. Calif. is similar (a).

**Cercyonis pegala*. Males patrol all day in grassy areas, mainly around riparian trees (b).

**C. oetus*. Males patrol all day in open grassy areas regardless of topography (b).

C. sthenele. Males patrol all day in grassy areas, often in gullies and valley bottoms (California, Colorado) (c).

**C. meadi*. Males patrol all day everywhere in the habitat but most often in valley bottoms and in woods (b).

Oeneis nevadensis. Males perch all day on fallen trees and other objects in lanes of valley bottom forest (Siskiyou Co. Calif., c). Males also perch on hilltops, but I have not seen this.

**O. chryxus*. Males perch (and occasionally patrol briefly) all day, usually on hilltops or on sloping ridgetops (Colo.) (b).

O. c. wallda males perch and when disturbed patrol before settling, all day on ridgetops (Inyo Co. Calif.).

**O. alberta*. Males perch, and often patrol 10 m or less, all day among bunch grasses, usually in somewhat sheltered hollows of hillsides and valley bottoms (c).

**O. uhleri*. Males perch, and occasionally patrol short distances, all day on slopes at the base of bunch-grass community, or on a trail below the bunch grass community, usually on south-facing slopes (b).

O. polixenes. Males mainly patrol but sometimes perch (patrolling flights are often 10 m or more) all day in swales on grassy north-facing slopes (b).

**O. melissa*. Males perch, and often patrol, all day in rocky areas of hilltops and ridgetops (b).

O. taygete. Males perch and patrol all day on grassy hillsides and sometimes on hilltops (b).

**Erebia magdalena*. Males patrol all day over rockslides (b).

**E. epipsodea*. Males patrol all day over wet grassy meadows or swales (b).

E. theano. Males patrol all day about grassy areas on slopes or in bogs; males appear to be very local and spend most of their time sitting among vegetation (Hinsdale Co. Colo., c).

E. callias. Males patrol all day usually over alpine cushion plant community, often over rounded ridges, but sometimes on slopes (b).

Gyrocheilus patrobas. Males patrol all day, usually in shady grassy areas in oak woodland (southern Arizona, c).

**Euptoieta claudia*. Males patrol all day in every topographic situation in open areas, especially on flats (b).

Speyeria nokomis. Males patrol all day in spring-fed meadows, especially in valley bottoms if the spring is on a slope. Males fly about $\frac{1}{2}$ m above ground and dip into hollows to search (Mono Co. Calif., Kane Co. Utah, Uinta Co. Utah, Mesa Co. Colo., b).

**S. aphrodite*. Males patrol all day, mainly in open areas, regardless of topography (a).

**S. edwardsii*. Males patrol all day in open areas regardless of topography, but several males patrolled in a small space just below the summit of a large hilltop, remaining there for several hours (b).

**S. coronis*. Males patrol all day in open areas regardless of topography (*S. aphrodite*, *edwardsii*, and *coronis* often patrol

the bottoms of valleys) (b).

S. zerene. Males patrol all day in open areas regardless of topography (Routt Co. Colo.; Idaho) (b).

S. callippe. Mate-locating behavior occurs all day. In the Front Range of Colorado, males patrol and occasionally perch on shrubs etc., mainly on hilltops until about 1300, when they patrol (very rarely perch) more generally on hillsides. Courtship and mating occur all day despite this behavioral switch. Males patrol in fairly open areas close to the ground, in contrast to the preceding four species of *Speyeria* which patrol about 1 m above ground (b). In Glenn and El Dorado Counties, California, males patrol all day about ½ m above ground in the flat forest (c). At Mt. Diablo, Contra Costa Co. Calif., males sometimes perch on shrubs, grass, etc., and also patrol. Perching was noticed sometimes until about 1200, after when males would only patrol. Perching and patrolling occurred only on the upper 100 feet of the hilltop, mostly in clearings on the ridge (c).

S. atlantis. Males patrol all day in wet meadows and along streams in Colorado (b) and Coconino Co. Arizona, and patrol about open forest all day in Glenn Co. Calif. (c).

S. egleis. Males patrol all day, mostly along shaded forest lanes such as abandoned roads, about 1/3 m above ground (Routt Co. Colo., b). In Mendocino and Alpine Cos. California, males patrol all day near the ground mostly on hilltops (c).

**S. mormonia*. Males patrol all day just above the ground in open vegetated areas regardless of topography, usually in meadows at lower elevations (b).

**Boloria selene*. Males patrol all day in wet meadows and springs, usually on fairly level land but sometimes on hillsides (b).

B. eunomia. Males patrol all day among the willows of willow bogs, often near the edge of a bog. (b).

B. frigga. Males patrol all day, in willow bogs, usually in low spots between a slope and a flat, in mixed willow-grass parts of the willow bog (but some males can be found throughout the bog) (b).

**B. freija*. Males patrol all day in open areas near the larval hosts, usually at the edge of a bog or stream, often on hillsides (b).

**B. titania*. Males patrol all day in open areas, usually swales and valley bottoms, in meadows or bogs. At willow bog localities, males patrol the borders of the bog but rarely enter the bog

center (b).

B. toddi. Males patrol all day in moist meadows (Alberta, Summit Co. Colo.) (c).

B. epithore. Males patrol all day in moist shrubby meadows and moist open woods, primarily in valley bottoms (Siskiyou & Glenn Cos. Calif., b).

B. alberta. Males patrol all day over open nearly barren or vegetated flats and hillside scree slopes, especially where *Dryas octopetala* is abundant (Alberta, c).

B. astarte. Males patrol all day on ridgetops and hilltops, usually just below the leeward edge of the ridgetop or plateau (Alberta, c).

B. kriemhild. Males patrol, at least during morning and mid-day, over moist meadows, usually where aspen is common (Montana, c).

**Euphydryas chalcedona*. Males perch and occasionally patrol all day. Perching often occurs on shrubs in hollows below a slope (Napa Co. Calif., b). Near Rosita, Custer Co., Colo. (*E. c.* near *eurytion*), males patrol all day in meadows, especially in grassy swales (b). At Aspen, Pitkin Co. Colo., males patrol all day all over a hill (c). In the foothills of the Colorado Front Range (*E. c. capella*), males usually perch but sometimes patrol, all day on low and large hilltops (c). At Diamond Peak, Moffat Co. Colo. (*E. c.* near *bernadetta*), behavior is very similar to *capella* (c). In Sevier Co. Utah, males patrol as in *eurytion* (c). In El Dorado and Alpine Cos. Calif. (b), *E. c. sierra* males patrol and sometimes perch all day on hilltops at low density, but mainly patrol throughout the habitat especially over flowers at high density.

Euphydryas editha. In western Colorado (Moffat Co. and Pitkin Co., b) males patrol and often perch all day on ridgetops and hilltops. At Connors Pass, White Pine Co. Nevada (c), males mainly perch on hilltops. At Jasper Ridge, San Mateo Co. Calif., males only patrol all day (Labine, 1966). At Butts Canyon, Napa Co. Calif. (c) males perch and patrol about equally on ridgetops all day. At Blue Ravine, Sierra Co. Calif. (c), males patrol and sometimes perch on shrubs on a serpentine slope. At Goat Mtn., Colusa Co., Calif. (c) behavior is similar but is on a ridgetop. At Mono Pass, Inyo Co. Calif. (c), males patrol and sometimes perch all day on a ridgetop.

**Poladryas minuta*. Males perch and rarely patrol on ridgetops and hilltops from about 0700 to 1230; from about 1230 to

about 1500 males patrol, usually on hillsides and flats etc. near flowers. Courtship occurs throughout the day (a; Scott, 1974).

Chlosyne palla. In Gilpin and Routt Cos. Colorado (b), males perch, and sometimes patrol, all day, on slight prominences such as mine dumps in a valley bottom or on the outer edge of a dirt road rounding a hillside. In El Dorado County Calif. (c) males patrol and perch about equally, usually in valley bottoms, roadside ditches, or swales, all day. Males patrolled near flowers on a ridgetop once in Napa Co. Calif. (c).

Chlosyne defnita. Males patrol just above the ground all day, all over the ridgetops, hillsides, and gulches where a population occurs (western Texas, b).

Chlosyne chinatiensis. Males patrol all day just above the ground, mainly on ridgetops where *Agave lecheguilla* is abundant; colonies may be somewhat local, being scarce on a ridge and common on an adjacent ridge (western Texas, c).

Chlosyne theona. Males patrol all day on flats mostly (Mexico, c). In southwest Texas and central Arizona males often occur on hilltops, however (c).

Chlosyne neumoegei. Males perch, and sometimes patrol, in gulch bottoms (like *Phyciodes mylitta*) at least from 1130 to 1440 when observations were made (Pima Co. Ariz., c). In San Bernardino Co. Calif. males perch in gulch bottoms all day (c).

Chlosyne hoffmanni. Males patrol all day about $\frac{1}{2}$ m above ground about valley bottom meadows, swales, and adjacent shrubland near the larval host (Siskiyou Co. Calif., c), and in roadside ditches (El Dorado Co. Calif., c).

**Chlosyne acastus*. Males perch, and sometimes patrol, in dry washes and gullies all day (Fremont Co. Colorado, southern Utah, b).

**Chlosyne damoetus*. Males patrol all day over rockslides where the larval host is abundant (Custer Co. Colo., c). In Alberta and California (Tuolumne, Mono, and Alpine Counties) behavior is similar but males often patrol up and down chutes in the rockslide (c).

**Chlosyne leanira fulvia*. Males court and mate all day. At fairly low density, males perch and occasionally patrol on low hilltops near the larval host. Several times high density was encountered, and males patrolled and mated in a relatively small area where the population was concentrated (b). *C. l. alma* males perch, and sometimes patrol some after an encounter, on hilltops (Kern Co. Calif., c). *C. l. leanira* males mainly perch

and sometimes patrol on hilltops all day (Napa Co. Calif., c).

Chlosyne elada. Males patrol all day about ½ m above the ground throughout the habitat, often on flats (Arizona, Texas, Mexico, c).

**Chlosyne gorgone*. Courtship and mating occur all day. On hilltops, males mainly perch and seldom patrol. On hillsides and valleys, males almost always patrol (b).

**Chlosyne nycteis*. Males patrol all day along streamsides near *Rudbeckia laciniata* (b).

Chlosyne lacinia. Courtship and mating occur all day. Like *C. gorgone*, males patrol and sometimes perch on hilltops in Texas, but elsewhere they mostly patrol (Mexico) (c).

**Phyciodes tharos*. Males patrol all day in wet meadows and streamsides (b).

**Phyciodes campestris*. Males patrol all day just above the ground, mostly in meadows, grassy swales and valley bottoms (Nevada & Yolo Co. California, and Colorado, a).

**Phyciodes picta*. Males patrol all day just above the ground in colonies mainly on flat land such as near streams, vacant fields, beside railroad tracks, etc. (b).

Phyciodes pallida. Courtship and mating occur all day. Males usually perch in gullies on 1 m tall twigs or other objects. At Red Rocks, Jefferson County, Colorado, most males perched in gullies but some males patrolled on slopes near a hilltop and rarely males are found on hilltops (b). At Connors Pass, White Pine County, Nevada, all three males observed patrolled on ridgetops.

Phyciodes mylitta. Mating occurs all day. In California and Arizona males usually perch in gullies or between riparian shrubs and a hillside (and occasionally patrol about 1/3 m above ground, b). However, in agricultural areas of Idaho, Washington, and central California, males patrolled near *Cirsium arvense*, a larval host growing in waste places (b).

Phyciodes orseis. Males perch all day, and occasionally patrol, in gullies and between riparian shrubs and hillsides (Siskiyou Co. California, Douglas Co. Nevada; b).

Phyciodes phaon. Males patrol all day, mostly on flats near the larval hosts (western Texas, c).

Phyciodes vesta. Males patrol all day, often on flats, often near waterholes in arid areas (Texas, c).

Phyciodes texana. Males usually perch (and occasionally patrol about 1 m above ground), all day, mainly in gulches and

dry stream beds (southern Arizona, c).

Microtia dymas. Males patrol slowly all day, most often in gullies and flats in hilly areas (southern Arizona, western Texas; c).

Microtia elva. Males patrol slowly all day all over the habitat, although colonies are somewhat local (Mexico, c).

**Polygonia satyrus*. Males perch on vegetation in gullies or along tree-shaded banks, from about 1230 to late afternoon (b).

**Polygonia faunus* ("hylas"). Males perch on shrubs or rocks etc. in gullies, from roughly about 1300 to late afternoon (b). My observations on *Polygonia* and *Nymphalis*, especially *P. faunus*, indicate that hibernating individuals usually mate in spring.

**Polygonia zephyrus*. Males perch on bushes or stones, logs, etc. in valley bottoms, from roughly about 1230 to late afternoon (perching most actively after about 1300) (southern Colorado, and Douglas Co. Nevada) (a).

P. oreas. In California, males perch on shrubs and small trees in small clearings in valley bottoms (sometimes 3m above ground), at least in the afternoon when observations were made (c).

**Nymphalis antiopa*. Males perch, and occasionally patrol, in gullies or swales, and in valley bottoms, from about 1130 to at least 1700 (start of perching behavior is gradual) (b).

**N. californica*. Males perch, and occasionally patrol, starting about 1400 and perching until 1700 at least, especially on ridgetops, or on banks of valley bottoms, and on flat land on the side of trees, etc. (California, Colorado) (b).

**N. milberti*. Males perch usually behind shrubs on hilltops, sometimes on logs etc. next to gully banks. Males arrive between 1050 (rarely) and about 1400, averaging perhaps 1230, and then perch until late afternoon (b).

**Vanessa atalanta*. Males perch, usually on the leeward side of shrubs on hilltops, or on porch roofs of farm houses, and in similar situations (b).

**V. virginiensis*. Males perch, often on shrubs on hilltops, or on the leeward side of shrubs on flats (c).

**V. caryae*. Males perch, on shrubs on hilltops, or on flat land on the ground behind cars or people or other large objects (c) (Colorado and Yolo Co. Calif., c).

**V. cardui*. Males perch and sometimes patrol, usually on shrubs on hilltops at low density. All four *Vanessa* species first

arrive on hilltops at about 1330 plus or minus an hour or more depending on meteorological conditions (Shields, 1967), and most mating and courtship and perching occurs after this time until as late as 1930 in June. The situation is not this simple, however. In 1973 *V. cardui* was extremely abundant in Colorado. Numerous interactions between individuals were seen from 0800 onward, although intensity and frequency of interactions was greatest in afternoon especially late afternoon. Mrs. Betsy Webb of the Denver Museum of Natural History observed a complete courtship and mating at about 1200. Interactions occurred wherever individuals were, including hillsides (a).

Precis coenia. Males perch all day on flat bare spots in fields, trails, etc. (Scott, 1975b; a).

Adelpha bredowii. Males perch on 1-2 m shrubs usually in gulches, and sometimes patrol, all day (Napa Co. Calif.; c). Courtship occasionally occurred on Buckeye flowers.

**Limenitis weidemeyeri*. Males perch, and rarely patrol, all day in gullies and valley bottoms on bushes and treelimits about 2-3 m above ground (a).

L. lorquini. Males perch all day on shrubs about 2-3 m above ground (Siskiyou Co. Calif.) in valley bottoms (c).

**L. archippus*. Males patrol all day along willow groves along streams and irrigation ditches (b).

L. arthemis arizonensis. Males patrol all day along willow groves; rarely in Texas males patrol a small area of a hilltop (southern Arizona, western Texas; c).

**Asterocampa celtis*. Males perch on small trees along gullies, on the rocks and logs and other objects at the side of a gully, and often on my hat or net in a gully, or on the larval host trees on flat land. Males perch most actively from early afternoon to dusk, but interactions occur all day, as in *V. cardui*.

Asterocampa leilia. Males perch all day on rocks etc. in gully bottoms, although there may be a gradual change in activity as in *A. celtis* (s. Arizona, w. Texas; c).

**Anaea andria*. Males perch all day in clearings among cottonwood groves, on stones, logs, and branch tips up to 3 m above ground in the clearings (c).

**Danaus plexippus*. Males patrol in flat areas near the larval host, and interactions occur all day as early as 0800 (b, Colorado). Dr. Lincoln P. Brower (pers. comm.) has observed many matings all day in California, where mating occurs in early spring at the roosting sites. The preference of *D. gilippus* for mating in afternoon more than in morning may have been due to the warmer afternoon weather (Brower et al. 1965).

LYCAENIDAE

Calephelis arizonensis. Males perch all day in narrow gully bottoms, on plants about $\frac{1}{2}$ m above the gully bottom such as grass inflorescences (Santa Cruz Co. Ariz., c).

C. rawsoni freemani. Males perch all day on vegetation in narrow gullies, or at the side of broader gulches (Chisos Mts. Texas, c). Two other *Calephelis* spp., *C. nemesis* and *C. wrighti*, behave differently. They remain on or near the larval hosts (*Clematis* in southern Texas and *Bebbia juncea* near Blythe, California respectively), and occasionally perch and may also patrol there (c).

**Apodemia nais*. A population was studied in Custer Co. Colo. (b) in which individuals occurred on and near *Ceanothus* bushes. Males perched usually on $\frac{1}{5}$ m tall dead stalks in open areas partly surrounded by shrubs between the mouth of the gulch and a roadside ditch, occasionally on the tip of a *Cercocarpus* shrub in a clearing at the mouth of the gulch. Perching behavior started almost precisely at 1130 in three days observations and lasted until about 1430. Before and after this perching period, and seldom during, males feed on *Ceanothus* flowers where females oviposit on *Ceanothus*.

**Apodemia mormo*. Males perch near the larval foodplant (*Eriogonum jamesi* in Chaffee County, Colo., where most observations were), mostly in depressions such as gullies cutting into hillsides, and depressions at bases of slopes. Perching starts about 1100 and continues til 1430 or later. In the morning males mainly feed on the larval host and fly away when disturbed.

**Hypaurotis crysalus*. Males patrol over and around tops of the larval host trees, starting (gradually) about 1400 and ending about 1730 (Scott, 1974d; a).

Atlides halesus. Males perch on treetops on hilltops, at least in the afternoon when observations were made (Arizona, New Mexico) (c).

**Strymon melinus*. Males perch on small trees on hilltops when available (on tall shrubs elsewhere) from about 1300 (roughly) to nearly dusk (b).

**Harkenclenus titus*. Males perch on small shrubs on hilltops (on taller shrubs if a colony occurs on flat land), from about 1000 (not earlier) to late afternoon. Mating sometimes occurs on the larval host (*Prunus virginiana*) (b).

**Satyrrium acadica*. Males perch (and seldom patrol) on

small willow or other plants about 1 m tall, especially on low plants growing out from a willow grove (up to 3-4 m away from the grove), from about 1350 to dusk (b).

Satyrium californica. Males perch (and occasionally patrol) on top of 2-6 m trees and shrubs on ridges and hilltops usually, from about 1400 to dusk (Jefferson Co. Colorado, and Napa Co. Calif., b). One courtship occurred on a Buckeye flower in California.

**Satyrium sylvinus*. Males perch (and seldom patrol) on small willow or other plants, especially those growing a few m out from a willow grove, from about 950 (not earlier) to late afternoon (about 1500) (Colorado, b). The same behavior was observed in Mono Co. California and Lander Co. Nevada in afternoon (c).

**Satyrium liparops*. Males perch on bushes or tree limbs about 1-2 m tall or less (sometimes on the side of a small tree) in gullies in the Front Range of Colorado (b). Perching and courting occur all day. In Routt Co. Colo. males perched on such shrubs on hilltops at least in morning (c).

**Satyrium calanus*. Males perch all day on small shrubs or other objects in gullies or depressions in oak groves in southern Colorado (b). In Routt County, Colo., however, males perched on small shrubs on hilltops at least in morning (c).

S. auretorum. Males perch and sometimes patrol on top of about 5 m tall oak trees on ridgetops and hilltops, mainly from about 1445 to dusk. Courtship sometimes occurs on Buckeye flowers. I noticed that *S. auretorum* and *S. californica* usually perched on separate trees (Napa Co. Calif., b).

S. tetra. Males perch on the *side* of shrubs and trees (commonly 1-2 m above ground on the shrub). They do this on hilltops (from about 1345 to dusk in Napa County, from about 900-1000 to dusk but mainly from 1230 onward in Contra Costa Co. Calif. (Mt. Diablo)), and they perch also on the side of tall shrubs on or near the larval host (*Cercocarpus betuloides*) in a valley bottom (late afternoon to dusk, Napa Co.), More work is needed on the time of day of mating; there seems to be a clear preference for late afternoon to dusk (b).

S. saepium. Males perch all day about 1 m above ground on small shrubs or halfway up larger ones on ridgetops and hilltops (Jefferson Co., Colorado, c; Contra Costa Co., Calif., c). In Colusa Co. Calif. males perched all day on the side of shrubs on the side facing the hillside, in addition to hilltops (c).

**S. behrii*. Males perch all day on top of shrubs or small trees on hilltops (b).

S. fuliginosum. Males usually sit on shrubs including the larval hostplant lupines, and every few minutes patrol erratically about the canopy of the lupines. They do this usually about shrubs in the lee of a ridgetop from at least 1130 to 1600 (Tuolumne and Alpine Cos. Calif., c).

**Callophrys spinetorum*. Males perch all day on top of prominent trees, especially on hilltops (Gilpin Co. Colo., Arizona; c).

**Callophrys nelsoni siva*. Males perch all day on top and sides of junipers, especially those on a ridge (often sloping) rather than those in a valley (Colorado, b). Behavior of *C. n. nelsoni* in El Dorado Co. Calif. is very similar; courtship sometimes occurs on flowers.

**Callophrys augustinus*. Males perch all day near the larval host in small open spots on ridges on the ground or larval host on the sunny side of the clearing, or on the uphill side of bushes where the ridgetop slopes downward from the crest (Douglas Co. Colo., b). In Nevada and Siskiyou and Alpine Cos. Calif. behavior is similar, males perch on top of shrubs on slopes or at the top of a slope, starting at 845 or earlier and continuing through the day (b). Powell's (1968) observations are similar although he did not observe perching in early morning probably due to unsuitable weather.

**C. polios*. Males perch all day in swales and narrow valley bottoms, in small clearings and on trails near the ground there, on or near the larval host (b).

**C. mossii*. Males in Jefferson & Boulder Cos. Colorado perch all day in gullies, in fairly open level sunny spots next to a sunlit bank of the gully (b). In San Mateo Co. Calif., males perch in a similar situation, on shrubs where a grassy hillside meets on a shrub belt extending to the valley bottom (c). In Nevada and Siskiyou Cos. California, males perch all day on top of shrubs sometimes at the upper part of a shrubless sloping swale or on prominent shrubs on a slope below an open space, but more often perch on shrubs at the top edge of a precipice (b).

**C. eryphon*. Males perch all day on the side of small trees (usually *Pinus ponderosa* in Colorado), about 2 m above the ground, almost exclusively in narrow valley bottoms and gulch bottoms (Jefferson County Colorado, b; El Dorado, and Siski-

you Cos. Calif., c).

**Callophrys apama*. Males perch all day in gullies on grass stems and other objects there (a).

C. dumetorum (Napa and Marin Cos. Calif., b) and *C. dumetorum viridis* (San Mateo Co. Calif., b). Males perch (and occasionally patrol) all day on small shrubs or other objects near the larval host, frequently on small or large hilltops.

C. affinis. Males perch all day on small shrubs (mainly *Artemisia tridentata*) on ridgetops and hilltops (Pitkin Co. Colorado; Lander Co. Nevada; Sweet Grass Co. Montana; c).

C. sheridani. Males perch all day near the larval host, in depressions on grassy hillsides, or occasionally in shallow roadside depressions, in Colorado (b) and southern New Mexico (c). In El Dorado and Alpine Cos. California (*C. s. lemberti*), males perch all day near the larval host in sheltered hollows, on shrubs or rocks or the ground (b). In Churchill Co. Nevada, *C. s. lemberti-comstocki* perched on shrubs or the ground in a gulch bottom next to a SW-facing slope (c).

Erora laeta quaderna. Males perch on top of trees on hilltops, at least in afternoon when observations were made (New Mexico, Arizona; c).

Phaeostrymon alcestis. Males patrol about the canopy of *Sapindus drummondi* trees, the larval host, and often patrol during cloudy, windy, or rainy weather (as does *Hypaurotis crysalus* which has an almost identical mate-locating system.) Patrolling occurs from about 1400 to about 1800. In the morning males are mostly at flowers and mostly only females are found on the larval host trees; during the mating period both sexes occur on larval host trees (Baca Co. Colorado, b).

Habrodais grunus. Behavior is very similar to *H. crysalus*. Males start to patrol about *Quercus chrysolepsis* about 1400 and then patrol near the leaves until dusk. They patrol most frequently on the shady side of a group of trees. (Mt. Diablo, Contra Costa Co. Calif., c).

**Lycaena arota*. Males perch on branches of shrubs and trees 1-2 m above ground in small clearings in many different topographic situations, usually valley bottoms. A clearing likely to have a perching male is about 3-5 m in diameter, reasonably level, and surrounded by tall trees or steep hillsides. When abundant, males may perch at the side of large gulches where a few trees approximate a clearing. Males perch from about 0700 to as late as 1230. In El Paso County, Colorado, males

mostly stopped perching by about 1130, but in Chaffee County males stopped by about 1230 (part of this difference may be due to the sun rising earlier in El Paso than in Chaffee County) (a; Scott, 1974b).

**L. cupreus*. Males perch and often patrol all day in hollows of rockslides near the larval host (Clear Creek & Custer Cos. Colorado, c). In El Dorado Co. Calif., males patrol and sometimes perch all day mostly in rocky depressions (c).

**L. heteronea*. Males patrol all day, like the Plebejini they resemble, near the larval host (*Eriogonum umbellatum* in the Colorado Front Range) on hillsides etc. regardless of topography (b).

**L. xanthoides*. Males perch and occasionally patrol, all day on 1 m or less vegetation beside trails through fields or beside streams, and often court on flowers in afternoon (b, Jefferson Co. Colorado and Contra Costa Co. Calif.; Scott & Opler, 1975).

L. editha. Males perch all day in shallow narrow gullies and in shallow depressions in meadows, usually on low vegetation (Moffat Co. Colorado, and California, c).

**L. rubidus*. Males perch all day on vegetation in dry gullies and along streams, or along dirt trails through fields when high density fills more suitable sites (Colorado, b). The same behavior occurs in afternoon in Mono Co. California (c).

**L. thoe*. Males perch all day on vegetation 1 m or less above ground along streams and on prominent vegetation in or bordering a meadow where the larval host is abundant (b).

**L. helloides*. Males perch and sometimes patrol all day in depressions of wet meadows and especially along streams, usually on $\frac{1}{2}$ m tall vegetation. Males sometimes patrol especially in the montane meadows of Colorado, and mate-locating behavior occurs in wetter habitats than in *L. rubidus* (b). In Lander Co. Nevada males patrol and perch around *Polygonum* plants at least in afternoon (c).

L. nivalis. Males perch all day in shallow usually bare depressions, such as a shallow ($\frac{1}{2}$ m deep, 2 m broad) gully, and shallow depressions in an abandoned slightly inclined dirt road usually next to the valley bottom; the perching sites are hard to describe verbally, but males remain there often for most of a day (Gilpin Co. Colorado; Mono, El Dorado, and Siskiyou Cos. California; b).

L. gorgon. Males patrol and perch, all day on low vegetation near the larval hosts (California) (c).

L. mariposa. Males perch in hollows and valley bottoms in clearings often in dense forest, at least during midday (Yakima Co. Washington, c) and afternoon (Siskiyou Co. California, c).

**Hemiargus isola*. Males patrol erratically all day regardless of topography, often on flat land and in meadows where a larval host (*Trifolium repens*) occurs (c).

Hemiargus ceraunus. Males patrol erratically all day throughout the habitat, usually in valleys and on flats (Arizona, Mexico, c).

Leptotes marina. Males patrol very erratically (with a non-linear flight) all day throughout the habitat, usually in valley bottoms where most of the larval foodplants occur (c).

**Plebejus melissa*. Males patrol all day throughout the habitat, mainly near the larval hosts (b).

P. argyrognomon. Males patrol all day near the larval hosts on hillsides, flats, mainly in bunch-grassland near forest in Hinsdale Co. Colorado (c) or in moist meadows (Siskiyou Co. Calif., c).

**P. saepiolus*. Males patrol all day near *Trifolium*, the larval hosts, mainly in meadows, moist swales, and streamsides where these plants grow (b).

**P. icarioides*. Males patrol all day near *Lupinus* species, the larval hosts (b).

**P. acmon*. Males patrol all day near the larval hosts, wherever they grow on hillsides and flats, etc. (Colorado, California; b).

P. lupini. Males patrol all day about the larval foodplant *Eriogonum* plants (El Dorado Co., Nevada Co., Tulare Co. California; b).

**P. shasta*. Males patrol all day about 10 cm or less above the ground near the larval host in alpine cushion plant communities which have about 50% bare ground. These communities often occur on ridges and saddles and steep slopes (Colorado, b; Mono & Tuolumne Cos. Calif., c).

**Agriades glandon*. Males patrol all day near the larval hosts (*Androsace* species) often in valley bottoms.

**Brephidium exilis*. Males patrol all day around the larval hosts, which mainly grow on flats. Males fly weakly among and a few cm from branches of the larval hosts (Stockton, California; c).

**Glaucopsyche lygdamus*. Males patrol all day near the larval hosts in valley bottoms, hillsides, etc. (b).

**G. pius*. Males patrol all day near the larval host (*Lupinus argenteus*) in valley bottoms or hillsides (b).

Philotes enoptes, **P. battoides*, **P. rita*. Males patrol all day on and between the larval host plants regardless of topography. Males and females often alight and feed on these plants (b for each species).

P. spaldingi. Males patrol all day near but not on *Eriogonum racemosum* (the larval host), patrolling more swiftly and erratically and slightly higher off the ground than the preceding three *Philotes* species. Males patrol in open pinyon-juniper woodland on flats and hillsides (b).

P. sonorensis. Males patrol weakly all day along the base of cliffs or sometimes on steep rocky slopes, always near the larval foodplants (California) (c).

P. speciosa. Males patrol all day about 6" above ground in swales or gully bottoms near the larval foodplant (Kern Co. Calif., c).

**Everes comyntas*. Males patrol all day near the ground near the larval host (*Trifolium repens* in Colorado), mainly in meadows and streamsides where this plant grows (b).

**E. amyntula*. Of all the Plebejini, this species most nearly approaches a perching species. Males often patrol, but often perch in depressions such as between a hillside and riparian shrubs or at the mouth of a tiny gully. Perching males investigate passing individuals, then patrol back and forth before returning to the vicinity of the previous perch. Mate-locating behavior occurs all day (Jefferson Co. Colorado; Siskiyou Co. Calif.; b).

**Celastrina argiolus*. In Napa Co. California males patrol all day over *Aesculus* trees throughout the habitat (c). Males patrol all day about shrubs and low trees, especially in valley bottoms and seldom on ridges etc. in Colorado (b). In southern Arizona and western Texas males often patrol about shrubs on hilltops (c).

HESPERIIDAE

**Epargyreus clarus*. Males perch in gullies on vegetation 1-2 m above ground. Perching starts about 0730 depending on temperature, and ends about 1315; after this period males mainly hang upside down from vegetation (b).

Zestusa dorus. Males perch on tips of branches of oak trees at the edge of a hilltop, at least in afternoon. Males also sit on

tree limbs overhanging streams where they feed on mud, but I have not yet seen perching behavior there; further observations are needed (southern Arizona, c).

**Thorybes pylades*. Males perch all day (few observations were made in afternoon) in gullies in west Texas and Colorado (c). In Utah and Arizona (Coconino Co.) and California (Colusa Co.) males perched all day on hilltops (c).

T. diversus. Males perch in tiny (often 3 m in diameter) forest openings where the presumed legume larval host is common on flat land and gentle slopes, at least 1330 to 1600 when observations were made (Tuolumne Co. Calif., b).

**T. mexicana*. Males perch all day on stones etc. on hilltops (Colorado, b; Tuolumne Co. California, c). *T. confusis* in central Texas perches on hilltops at least in afternoon (c) so may have similar behavior.

**Erynnis icelus*. Males perch and occasionally patrol, all day in slight depressions and shallow gullies near aspen trees (Gilpin Co. Colorado, b; Siskiyou Co. California, c).

**E. brizo*. Males perch all day on hilltops, often perching on the ground, sometimes on small shrubs. Males may fly back and forth before returning to a perch, which is a peculiarity occasionally seen in other *Erynnis* species also (b).

**E. persius*. Males perch all day on hilltops, on the ground and on low twigs often beside larger shrubs on the hilltop (a).

**E. afranius*. Males perch all day in gullies and swales, such as sunlit indentations in gully banks in morning and late afternoon, small gullies and narrow valley bottoms at midday (b).

**E. martialis*. Males perch all day on hilltops, mainly on the ground or on low twigs (b).

**E. telemachus*. Males perch all day in gullies, mainly on vegetation about 1 m above ground there (Colorado, a). In Colorado one copulating pair was found near a hilltop, and in Utah one male was observed perching on a hilltop.

**E. horatius*. Males perch all day on hilltops, usually on 1/3 m twigs, seldom on the ground (Colorado, b). In Texas males flew about small areas of hilltops before resting again, whereas Colorado males usually settled more rapidly.

**E. pacuvius*. Males perch all day on hilltops on low shrubs and other objects (in Jefferson and Douglas Co. Colorado, b; Colusa Co., California, c).

E. tristis. Males perch on hilltops all day, on barb-wire fence or a twig about 1 m above ground there. Males some-

times patrol about a few times before resting again (Napa Co. California, c).

E. proprius. Males perch all day, mainly in clearings on the sunlit side of ridgetops a few m from the ridgetop, but sometimes also on banks (such as roadcuts) in valley bottoms (California, b). *E. p. meridianus* males perch on hilltops all day (Coconino Co. Arizona and western Texas; c).

Autochton cellus. Males perch in gullies on about 2 m tall vegetation, at least in afternoon when observations were made (Cochise Co. Arizona and western Texas; c).

**Pyrgus communis*. Males perch, and often patrol, all day, in swales and valley bottoms and similar situations. Perching males often patrol about a small area before returning to a perch. Males perch more when suitable depressions are available (b).

P. philetas. Males patrol and occasionally perch, in gulches and valley bottoms, waterholes, etc., all day (southern Arizona; c).

P. scriptura. Males patrol, and occasionally perch, all day in low areas of prairie, shallow gullies, and other depressions. Flight is only about 10-20 cm above ground (b).

**P. xanthus*. Males patrol, and often perch especially in gullies, all day near the larval host at high density, but at the usual low density males occur in small mostly dry gullies several meters deep and broad, where they often sit on the bottom or the sunlit side of the gulch (Colorado, New Mexico; b).

P. ruralis. Males patrol (and occasionally perch) about 10 cm above the ground all day, mainly in valley bottoms or grassy swales (Siskiyou and El Dorado Cos. California, c).

**P. centaurae*. Males patrol and occasionally perch, all day, in swales, valley bottoms, low spots next to bogs. Males perch more often at low temperatures, and patrol more often at high temperatures (c).

Staphylus ceos. Males patrol all day in gulches and valley bottoms, flying faster than *P. catullus* (southern Arizona, western Texas; c).

**Pholisora catullus*. Males patrol all day just above the ground in roadside ditches, gulches, dry reservoir bottoms, and other depressions (b).

**P. mejicanus*. Males patrol all day in the same manner and locations as *P. catullus*; the two species cannot be distinguished during flight (c).

**P. alpheus*. Males patrol in gullies and around the larval host shrubs, apparently all day (few observations were made in afternoon; c).

P. graciellae. Males patrol in gulches but mainly patrol through and around the larval host shrubs on flats, at least in morning and early afternoon (California, c).

P. libya. Males patrol in gullies and in and about the larval host shrubs at least in morning and early afternoon (Indio, California; c).

Systasea evansi. Males perch (they usually fly back and forth before resting again) in gulches apparently all day (few observations were made in afternoon) (southern Arizona, western Texas; c). *S. pulverulenta* had very similar behavior when observed at midday (western Texas; c).

Celotes nessus. Males patrol all day just above the ground (flight is rather weak) in gulches and along roadsides and other depressions. Males rest often so they may perch occasionally (southern Arizona, western Texas; c). *C. limpia* in western Texas with a longer distal prong on the male valva has nearly identical behavior (few observations; c).

Carterocephalus palaemon. Males perch on grass stalks and other objects about 1/3 m above ground, and often patrol as well, all day, in sedge swales in wet valley bottoms (Siskiyou Co. Calif.; c).

Copaesodes aurantiaca. Males perch all day in gullies on vegetation about 1 m tall and have a very fast flight (Coconino Co. Arizona, southern Arizona and western Texas; b).

**Piruna pirus*. Males patrol all day usually in valley bottoms and gulches; males patrol several cm from the canopy of low plants averaging 1 m or less above ground, and patrol following the contours of the vegetation (b).

Ancyloxypha arene. Males patrol weakly all day over grass at the edges of springs and reservoirs (western Texas, southern Arizona; b).

A. numitor. Males patrol weakly all day over and among grasses at the edges of streams and reservoirs and at springs (Ohio, c; Yuma Co. Colorado, c).

Adopaeoides prittwittzi. Males patrol fairly weakly over watercress flowers and occasionally over grasses at a spring, at least in morning when observations were made (southern Arizona, c).

**Oarisma garita*. Males patrol weakly to rapidly all day in

tall grass of meadows, valley bottoms, and to a lesser extent on hillsides (b).

**O. edwardsii*. Males patrol often rapidly all day in grassy openings between shrubs, throughout the habitat but more often in valley bottoms than on hillsides (c).

**Yvretta rhesus*. Males perch all day on small (2 m tall) prairie mesa tops when these are present, on flat land occasionally (c).

Y. carus. Males perched at least from 1200 to 1400 when observations were made, on flat bare ground next to the probable larval host, a short grass growing next to a waterhole, and on sand bars. Females were mostly on the short grass, and some individuals fed on mud (Pima Co. Arizona; c).

**Stinga morrisoni*. Males perch all day on hilltops and ridges, often just below a shrub or between trees on the hilltop whereas *Hesperia pahaska* males usually perch in more open sites (b).

**Hesperia uncas*. Males perch all day on small (2 m tall) prairie mesa tops or small hilltops, but perch on smaller hilltops than most other *Hesperia*. *H. uncas* is very similar to *Y. rhesus* in behavior and appearance (b).

H. lindseyi. Males usually patrol slowly (about ½ m per sec.) by fluttering about 15 cm above the grass, and males perch between these flights, all day, in grassland usually near the top of a ridge (Napa Co. Calif.; b).

**H. comma*. Males perch all day in southern Colorado and central Colorado (b) on hilltops. At high density at some localities (Chaffee and Jefferson Cos. Colorado, c) males investigate passing individuals while at mud. In Utah and Nevada and Mono Co. California, males of *H. c. harpalus* perch on hilltops or on flat areas when hilltops are not present, and males court at flowers (b). In El Dorado Co. California (c) males perched all day on the outer edge of a road on a steep slope. In Marin Co. California (c), *H. c. dodgei* males perched in bunch grass where the local population occurs and not on adjacent hilltops where *H. columbia* perches.

H. juba. Males perch all day in gullies, rocky depressions, and valley bottoms, both in Jefferson Co. Colorado (c) and in El Dorado Co. California (c).

**H. nevada*. Males perch all day on small to large hilltops and ridges (Custer and Park Counties Colorado, b; Tuolumne Co. California, c).

**H. viridis*. Males perch all day on rocks or bare ground of gullies and valley bottoms (Colorado, b; Texas, c).

H. columbia. Males perch all day on ridgetops and hilltops on low shrubs and rocks (Marin and Napa Counties, California, b).

**H. pahaska*. Males perch all day on hilltops and ridgetops on rocks or short plants (a; Scott, 1973d).

**H. leonardus pawnee* and *H. l. montana*. Males perch all day on small to large hilltops, or on flats near *Liatris punctata* flowers (b).

H. ottoe. Males perch all day on flowers, especially thistle. Males almost never occur away from these flowers, and by releasing other individuals near males on flowers it was found that males investigate other individuals all day. These flowers occurred in a valley bottom (Boulder Co. Colorado, c).

H. miriamae. Males perch all day on rocks or sometimes on the ground (especially those rocks that are sunlit and out of the wind) on alpine hilltops and ridgetops. Males have an extremely fast flight (Inyo and Mono Co. California, c).

H. woodgatei. Males perch all day on hilltops where they sit on rocks etc. on or near the ground (southern Arizona, c).

Hylephila phyleus. Males perch all day on prominent plants or hedges on lawns, grassy swales, and similar sites (Clark Co. Nevada, c; Yolo Co., California, c).

**Atalopedes campestris*. Males perch all day in grassy meadows and swales Fremont Co. Colorado, c; central Texas, c).

Nastra julia. Males perch all day in grassy swales such as along roads and irrigation ditches (SW of Parker, Arizona, c).

Lerodea eufala. Males perch all day in grassy swales and flats, along irrigation ditches (SW of Parker, Arizona, c; Yolo Co. California, c).

L. arabus. Males perch all day in gulches and along streams near large clumps of the presumed larval host grass. Males perch on vegetation as much as a meter above ground (Pima Co. Arizona, c).

Paratrytone melane. Males perch all day in grassy swales, gullies, lawns (California, c).

**Polites origenes*. Males perch all day in grassy swales and openings in valley bottoms (b).

**P. themistocles*. Males perch all day in grassy swales, depressions in meadows and lawns (b).

P. mystic. Males perch all day in low spots of meadows and

grassy streamsides (b).

**P. sonora*. Males perch all day in low spots of moist grassy meadows (Park, Chaffee, and Saguache Counties Colorado, c). In El Dorado and Tulare Counties California, behavior was similar but at high density courtships were frequent at flowers (c).

**P. sabuleti*. Males perch all day in low spots of alkaline flats where larval host is abundant, in low spots of meadows, and on flowers on flat land (Colorado, Clark & Nye Cos. Nevada, Mono & Inyo Cos. California, Emery & Millard Cos. Utah; a).

**P. draco*. Males perch all day in low spots of meadows and in gullies (b).

P. coras. Males perch all day in grassy swales and low spots of meadows (c).

Ochlodes sylvanoides. Males perch all day in gullies and valley bottoms on vegetation about 1 m above ground (Colorado, b). In Yolo Co. California, males perch in nooks among shrubs, often on ridgetops (c).

O. agricola. Males perch mainly in the shade of shrubs about 1/3 m above ground at the edges of clearings throughout the habitat, and males often court at flowers all day.

O. yuma. Males perch all day in low spots near the larval host, especially in depressions between this host (*Phragmites*) growing at a river edge and the bank. Males perch on large rocks or 1 m tall vegetation (California, c; Mesa Co. California, b).

**O. snowi*. Males perch all day in gullies on rocks or 1 m vegetation, and some courtships occur at flowers (a; Scott, 1973d).

**Poanes taxiles*. Males perch all day in gullies and valley bottoms, especially in shaded areas, on vegetation about a meter or more high. Males perch in more shaded locations and in cloudier weather than does *Poanes hobomok* (a).

**P. hobomok*. Males perch all day on vegetation about 2 m above the bottom of gullies and valley bottoms (b).

**Atrytone delaware*. Males perch all day in grassy swales, mainly in valley bottoms (b).

A. arogos. The main activity of both sexes is feeding on flowers. However, feeding males do not investigate individuals released nearby (contrasting with *H. ottoe*). After many failures in observing interactions at flowers I finally observed males perching on low (about 10 cm) vegetation on a gently sloping base of a hillside covered with *Andropogon*, the larval host.

A few males perched in a grassy swale below a similar slope. In three days observations perching started about 1320 and continued until late afternoon until rain or clouds stopped activity. This mating period is strange because it occurred during cloudy and sometimes rainy weather; perching males were often seen to rapidly vibrate their wings during cloudy periods, apparently as a heat gain device (shown to raise body temperature by Krogh & Zeuthen, 1941; Kammer, 1970). Additional observations are desirable to confirm this mating period (c).

**Euphyes vestris*. Males perch in gullies all day on about 1 m vegetation (Colorado, a; in California males perch in swales in coastal meadows, c).

E. bimacula. Males perch all day in low spots of moist sedge marshes, on about 1 m stalks of clumps slightly taller than surrounding vegetation (Yuma Co. Colorado, c).

**Atrytonopsis hianna*. Males perch all day on or near the ground on 2-4 m wide relatively flat clearings of valley bottoms, and occasionally in similar situations on slopes near the larval host (c).

**A. vierecki*. Males perch all day in gulches, usually on 1 m tall vegetation (Colorado, c; Cimarron Co. Oklahoma, c).

A. cestus and *A. ovinia*. In two days observations in Pima Co. Arizona, males perched on rocks on south-facing sides of gullies, especially gullies 3-7 m high next to hillsides and flowers. Males perched from early morning to about 1200, and in afternoon fed on flowers and rested (without interacting) on gully walls (c for each).

A. pittacus. Males perch all day, almost always in gullies in southern Arizona and western Texas (c), although near Alpine, Texas males also perched in a depression on the sloping leeward side of a hilltop about 3 m from the top (c).

**Amblyscirtes simius*. Males perch on top of small prairie plateaus, ridgetops and hilltops, from about 0740 to about 1050, with maximum perching from 0830 to 0930 (a; Scott, 1973c).

**A. aenus*. Males perch all day in gully bottoms, especially on rocks in rocky areas of the gully (b).

**A. vialis*. Males perch all day in narrow valley bottoms with much vegetation, usually perching on 1 m vegetation (b).

**A. oslari*. Males perch all day in gully bottoms and roadside ditches, especially in sandy spots on the gully bottom (b).

**A. eos*. Males perch all day in gullies and valley bottoms, on flat usually grassy spots on or just beside the gully bottom (c).

**A. phylace*. Males perch all day in mostly bare depressions, such as a depression at the mouth of a small gully opening onto a flat, a roadside cut below a small gully, etc. The perching locations change throughout the day as males choose sunlit locations (b).

A. nysa. Males perch all day near or on the bottom of narrow gullies (Texas, c).

A. texanae. Males perch all day in gullies on rocks or other objects (western Texas, c).

Agathymus mariae. Males perch in morning near the larval host (western Texas, c).

A. remingtoni estelleae. Males perch in morning near the larval host, especially at the base of a slope (western Texas, c).

**Megathymus streckeri*. Males perch on hillsides and flats near the larval host. My observations were only in morning, but Scott Ellis (written communication) has observed mating at 1300 in *M. s. leussleri* and much chasing between males in late afternoon in *M. s. streckeri* in southern Colorado (c). Mr. Kilian Roever, however, states (pers. comm.) that male activity in *M. s. streckeri* and *M. yuccae* ceases after midday.

**M. yuccae*. Males perch near the larval host at least in morning (c). Scott Ellis (pers. comm.) has observed strong perching behavior from about 0900-1100, "but the males seem to disappear in the afternoon."

DISCUSSION

Before making generalizations, I will mention some of the most unusual species. Some species both perch and patrol frequently (most perching species patrol infrequently, and many patrolling species sometimes perch). The best examples are most *Oeneis* and *Pyrgus* species; others are the *Papilio machaon* group (*P. zelicaon*, *bairdii*, *polyxenes*), *P. eurymedon*, *Limenitis wiedemeyeri*, *Nymphalis antiopa*, *N. californica*, *Phyciodes mylitta*, *P. pallida*, *P. texana*, *Euphydryas* spp., *Poladryas minuta*, *Chlosyne palla*, *C. acastus*, *C. gorgone*, *C. lacinia*, *C. leanira*, *C. theona*, *Calephelis nemesis*, *Lycaena cupreus*, and *Everes amyntula*. *P. minuta* differs from the others in that males mainly perch in the morning, but mainly patrol in the afternoon. *Speyeria callippe* is unusual in that the location of patrolling changes somewhat during the day. In several patrolling species, males seem to patrol about the tops of shrubs late in the day, apparently seeking roosting females (*Boloria titania*, *Plebejus melissa*).

The study of mate-locating behavior provides numerous useful taxonomic characters. For instance, in *Amblyscirtes* the three species groups previously recognized on morphological grounds also differ in mate-locating behavior. *A. simius* differs from other *Amblyscirtes* by mating only part of the day and on ridgetops but not in gullies; *A. phylace* differs by mating at the mouth of small gulches and in roadside ditches (the other *Amblyscirtes* mate in deep gullies). Perching or patrolling behavior and the time of day of mating seem to be rather conservative characters that are useful in comparing genera or higher taxa; the location of mating often differs between congeneric species and is very useful for intrageneric classification.

Location of mating can be placed into two general categories: 1) mating primarily occurs near the larval foodplants; 2) alternatively, mating occurs in specific topographic sites regardless of the distribution of the larval foodplants. If the larval foodplants are generally distributed within the flight area of the population regardless of topography (such as throughout a bog in a bog species, or throughout the habitat) patrolling behavior seems to be the usual mate-locating method, but often mating occurs in specific topographic sites such as gullies or hilltops (such as some *Hesperia* species that feed as larvae on widespread grasses). If larval foodplants are spotty in distribution within the normal flight area of a population (such as *Apodemia nais* which feeds on *Ceanothus fendleri*) perching behavior seems to be the usual strategy. If the foodplants are linearly distributed (such as streamside willows), in many species males patrol along the stream (*Limenitis achippus*), and in some species males perch there (*Satyrrium sylvinus*).

The strategy of mating in topographically distinct sites is often used for bringing the sexes together in species in which the larval foodplants occur throughout the habitat. Often several types of sites appear adequate to this function: closely related species may mate in different types of sites.

I found that eighteen congeneric pairs of butterflies rendezvous for mating in contrasting topographic sites. These eighteen pairs are listed below. The first species of the pair mates on hilltops, the second species in gulches, valley bottoms, or, for *P. indra*, rocky outcrops just below a hilltop. The foodplants of the species as larvae are listed. Localities studied are listed. 1) *Papilio eurymedon* (*Ceanothus fendleri*; Red Rocks, Jefferson Co. Colorado) and *P. multicaudata* (*Prunus virginiana*;

Red Rocks, and Jarre Canyon, Douglas Co. Colorado, Hardscrabble Canyon, Custer Co. Colorado). 2) *P. zelicaon* (*Harbouria trachypleura*; Red Rocks) and *P. indra* (*H. trachypleura*; Red Rocks). 3) *Euchloe olympia* (various Cruciferae undetermined for Colorado; Red Rocks, Jarre Canyon, and the Arkansas River Canyon, Fremont Co. Colorado and NW of Pueblo, Colorado) and *E. ausonides* (various Cruciferae; Red Rocks, Jarre Canyon, Hardscrabble Canyon). 4) *Pieris sisymbri* (various Cruciferae undetermined for Colorado; Jarre Canyon, Arkansas River Canyon, and NW of Pueblo) and *P. chlorodice* (= *beckeri*) (Arkansas River Canyon, NW Pueblo; various Cruciferae such as *Stanleya pinnata*). 5) *Oeneis melissa* (unknown monocotyledons; Loveland Pass and Mt. Evans, Clear Creek Co. Colorado) and *O. polixenes* (same foodplants and localities). 6) *O. chryxus* (unknown grasses; Jarre Canyon, and Gregory Canyon, Boulder Co. Colorado, and Greenhorn Peak, Huerfano Co. Colorado, and Rosita, Custer Co. Colorado) and *O. uhleri* (unknown grasses; same localities except for Rosita). 7) *Speyeria callippe* (*Viola*; Red Rocks) and *S. atlantis* (same foodplants and locality, Arkansas River Canyon). 8) *Chlosyne gorgone* (*Helianthus pumilus*; Red Rocks, Hardscrabble Canyon, and Green Mountain, Jefferson Co. Colorado) and *C. nycteis* (*Rudbeckia laciniata*; same localities except for Green Mountain). 9) *Nymphalis californica* (*Ceanothus fendleri*; Jarre Canyon) and *N. antiopa* (*Salix*, *Populus*, *Ulmus*, *Celtis*; Red Rocks, Jarre Canyon, Gregory Canyon, Hardscrabble Canyon). 10) *Callophrys augustinus* (*Arctostaphylos uva-ursi*; Russel Ridge, Douglas Co. Colorado) and *C. polios* (*A. uva-ursi*; Gregory Canyon, Russel Ridge). 11) *Satyrium californica* (*Ceanothus fendleri*; Red Rocks) and *S. acadica* (*Salix exigua*; Canon City, Fremont Co. Colorado). 12) *Thorybes mexicana* (various Leguminosae undetermined for Colorado; Red Rocks, Greenhorn Peak) and *T. pylades* (same foodplants; Red Rocks). 13) *Erynnis brizo* (*Quercus gambellii*; Red Rocks, Jarre Canyon) and *E. icelus* (*Populus tremuloides*; Central City, Gilpin Co. Colorado). 14) *Erynnis persius* (*Astragalus*, *Thermopsis*, and other legumes; Red Rocks, Jarre Canyon, Rosita, Arkansas River Canyon) and *E. afranius* (*Astragalus*, *Lupinus*, *Lotus*, and other legumes; Red Rocks, Green Mountain, and Wetmore, Custer Co. Colorado). 15) *Erynnis horatius* (*Quercus gambellii*; Red Rocks, Jarre Canyon, Oak Creek Canyon S. of Canon City, Colorado) and *E. telemachus* (same foodplant; same localities

and Hardscrabble Canyon). 16) *Hesperia pahaska* (*Bouteloua gracilis*; Red Rocks, Green Mountain, Arkansas River Canyon, Platte River Canyon, Douglas Co. Colorado) and *H. viridis* (*B. gracilis*; same localities except Platte River Canyon, and Pueblo, Colorado, and Black Mesa, Kenton Co. Oklahoma). 17) *Hesperia comma* (various grasses; Red Rocks, Arkansas River Canyon, Rosita, Platte River Canyon) and *H. juba* (various grasses undetermined in Colorado; Red Rocks, Green Mountain). 18) *Amblyscirtes simius* (*B. gracilis*; Arkansas River Canyon, and near Saguache, Saguache Co. Colorado) and *A. oslari* (grasses undetermined in Colorado; Red Rocks, Arkansas River Canyon, Gregory Canyon, Hardscrabble Canyon).

The use of separate mating sites by these congeneric species certainly prevents, and may result from, interference competition during mate-locating behavior. Interference between butterflies during mate-locating behavior arises from the generalized nature of the stimuli involved in visual communication between the sexes (Scott, 1973a, 1974a). Mate-locating behavior is a process of screening flying or resting objects for receptive females. Perception of the insect compound eye is poor for shapes, but good for movement. The size and color pattern of the two species of a pair is very similar in most cases. Males probably cannot distinguish color pattern differences as small as those between most of the congeners. Male butterflies sometimes investigate resting individuals, and often investigate aerial objects of a great variety of shapes and colors including other insects, birds, etc. Pheromones which might enable interspecific males to avoid interaction are currently unknown. Both perching and patrolling species appear to delineate a space around them in which moving and occasionally resting objects are investigated ("moveable individual space"). Two congeneric males do not occur in the same space for long because investigative interactions occur after which at most one male remains. Intense con- and interspecific interactions occur where males are concentrated. These interactions result in interference competition for time, space, and energy; time is lost (in which a passing female might be missed), the probability of being in a favorable mating arena is less, energy is wasted, and courtships with receptive females are often disrupted (another male often investigates a courting pair and the two males then often interact, ending courtship).

In some of these congeneric pairs interference competition

itself may have resulted in the evolution of separate mating sites. If two species have the same mating sites and if interference competition between them is great, when a mutation for mating at another site arises in one species (especially the rarer species) mating may be more successful at the second site and the proportion of individuals of that species mating there will gradually increase, ultimately resulting in genetic fixation. As selection proceeds, as the proportion of the selected species mating at the first site drops the selection against those mating at the first site will intensify because an increasing proportion of individuals encountered there will be nonconspecific. Rapid fixation of mating at the second site for the one species will then occur due to the continual increase of selection intensity against mating at the first site. This mechanism would be most rapid in two species which are postzygotically, but not prezygotically, reproductively isolated, which could occur if postzygotic but not prezygotic reproductive isolation developed in two allopatric populations which then became sympatric.

Most butterfly species mate at any time of day. Restricted time of day of mating occurs often in some taxa (Nymphalini, Riodininae, Theclini, Megathyminae), rarely in other taxa (Satyrinae, Apaturini, Lycaenini, Pyrginae, Hesperinae), and with my current knowledge not at all in many taxa (Papilionidae, Pieridae, Argynnini, Melitaeini, Limenitini, Charaxinae, Danainae, Plebejini).

There is an altitudinal trend in the time of day of mating. Of 284 species for which mate-locating behavior is reported herein, only 35 mate during a restricted part of the day (included are five species, *Vanessa* spp. and *Asterocampa celtis*, which seem to mate more frequently late in the day). All of these 35 species are primarily desert, foothills, or plains species rather than high mountain species. The primarily high mountain species all mate at any time of day.

Inclement weather is frequent in spring and fall. It is significant that only two species that mate during only part of the day are univoltine and mate in the spring (*Megathymus yucca*, *Polygonia faunus*). In *P. faunus* long life of the hibernating adults allows them to wait for good weather. The other species are univoltine and emerge in summer, or are multivoltine.

Mate-locating is an energy-demanding process, and greatly exposes males to predation. Perhaps more dependable weather in the foothills and plains compared with the alpine zone, and

in summer compared with spring, allows some species to reduce the hours devoted to mating (and sometimes reduced adult feeding) without seriously decreasing the proportion of females mating. At high altitude and in early spring, however, inclement weather requires that animals make use of all available periods of suitable weather, no matter what time of day these occur. Time of day of mating seems to have evolved as a compromise between energy (and predation?) losses and inseminating the maximum number of females.

Those species which mate only in early morning or in afternoon and early evening mate on sunlit areas such as treetops and hilltops; species mating at other times can mate in gullies and other locations that do not receive early and late sunlight.

Scott and Scott (1976) present an ecological analysis of the butterflies of an area of southern Colorado. I determined mate-locating behavior of the species in that area, and the following analysis attempts to determine how the behavioral and ecological characteristics of a species influence or are influenced by its mate-locating behavior.

To quantify mate-locating behavior, the following three qualitative indices were constructed: a) perching-patrolling index (1-males almost always perch prior to encounters; 4-males almost always patrol prior to encounters; 2 and 3 intermediate); b) location of mating index (1-mate in quite restricted sites of the habitat such as hilltops; 4-mate almost anywhere in the habitat; 2 and 3 intermediate); c) time of day of mating index (duration of the daily mating period of a species in hours, divided by 2; a mating period of "all day" is assumed to be 8 hours in duration).

Perching species in southern Colorado have a strong tendency to mate in restricted sites in the habitat, as predicted by Scott (1974a). The evidence is that the correlation (product-moment) between the perching-patrolling index and the location of mating index for the 159 species is .54 ($p < .01$), which means that perching species tend to mate in restricted sites and patrolling species tend to mate more generally in the habitat.

Perching species in southern Colorado also tend to mate only during restricted times of day rather than at any time of the day. The correlation between the perching-patrolling index and the time of day of mating index is .34 ($p < .01$).

Perching behavior in southern Colorado is much more common in species that have only 1 or 2 broods during the season

than in species with 3-4 broods (Table 1).

No consistent changes of mate-locating behavior with altitude were observed for the southern Colorado butterflies, except that above timberline all the species mate all day, and almost all species patrol there.

Southern Colorado butterflies that emerge at the end of the season tend to have patrolling behavior and tend to mate throughout the habitat much more frequently than species that emerge at the start of the season (Table 2).

The 159 species were placed into five categories depending on the meagre (usually) to extensive data I have concerning their movements (Scott, 1976). The only trends found (Table 3) are that species with very large movements more often tend to be patrolling species and to mate throughout the habitat.

No consistent relationship between the frequency with which a southern Colorado species feeds on flowers of the larval host and mate-locating behavior was observed.

Larval foodplants of the southern Colorado butterflies were given by Scott and Scott (1976). Tables 4 and 5 relate mate-locating behavior to the larval foodplants. Species feeding on shrubs or trees rather than on herbs more often tend to be perching species and more often tend to mate during a restricted period during the day.

I now attempt to determine the effect of the distribution of larval foodplants on mate-locating behavior in a different way, by examining the mate-locating behavior of various western U. S. butterflies that have the same larval foodplants, to discover whether convergent evolution occurs. The following comparisons were made.

1) *Ceanothus fendleri* (plants spottily but sometimes generally distributed on south-facing hillsides and dry valley bottoms). Mating generally occurs in hilltops or gulches: *Erynnis pacuvius*, *E. martialis*, *Papilio eurymedon*, *Satyrium saepium*, *S. californica*, and often *Nymphalis californica* mate on hilltops (*N. californica* sometimes mates in gulches etc.), and *Apodemia nais* mates in low spots in gulches near *Ceanothus*.

2) *Eriogonum umbellatum* (generally distributed on steep hillsides, mesas, and other locations). Two strategies occur. *Plebejus acmon*, *Philotes enoptes*, and *Lycaena heteronea* patrol regardless of topography (*L. heteronea* is the only *Lycaena* with mainly patrolling behavior, and has apparently convergently evolved patrolling behavior). *Callophrys sheridani*, *C. affinis*,

and *C. apama* (this species probably feeds on *E. umbellatum*, but no proof exists) mate in hilltops, gullies, or hillside depressions depending on the species.

3) *Salix exigua* (linearly clumped distribution along streams and irrigation ditches). Two strategies occur. *Satyrrium sylvinus* and *S. acadica* perch on the plant, while *Nymphalis antiopa* and *Limenitis weidemeyeri* perch in valley bottoms near willows. *Papilio rutulus* and *L. archippus* patrol near the willows. The difference in strategy of the two *Limenitis* may be due to their different habitats: *L. archippus* occurs on the plains where *S. exigua* is more continuously distributed, whereas *L. weidemeyeri* occurs mainly in the foothills (and larvae feed on other Salicaceae as well) where the foodplants are more spotty and there are more varied topographic sites.

4) *Quercus gambellii* (generally distributed, sometimes in groves). In *Hypaurotis crysalus*, in which all activities are carried out on the plant (Scott, 1974), males patrol. *Satyrrium calanus*, *S. liparops* (which may not feed on this oak species in Colorado), *Erynnis telemachus*, *E. brizo*, and *E. horatius* mate in gulches or hilltops.

5) *Prunus virginiana* (usually in small groves, mainly in valley bottoms). *Papilio multicaudata* patrols up and down valley bottoms, but *Harkenclenus titus* perches on hilltops.

6) *Sedum lanceolatum* (generally distributed on hillsides, etc.). *Parnassius phoebus* patrols on hillsides and meadows near the plants, but *Callophrys mossii* perches in gullies and is a foothills species whereas *P. phoebus* usually occurs in grasslands at higher altitude.

7) *Pinus* species (generally distributed). *Neophasia menapia* patrols throughout the habitat, but *Callophrys eryphon* perches in gulch bottoms.

8) *Ribes* species (throughout the habitat, but more often in valley bottoms). *Polygonia zephyrus* and *Lycaena arota* both perch mainly in valley bottoms.

9) *Celtis reticulata* (in groves on flats and in valley bottoms). *Asterocampa celtis*, *Nymphalis antiopa*, and *Polygonia interrogationis* all perch in valley bottoms on or near the *Celtis* plants.

10) *Cirsium* spp. (clumped weeds often on disturbed areas). *Vanessa cardui* perches often on hilltops (and feeds on many

other plants as larvae), whereas *Phyciodes pallida*, *P. mylitta*, and *P. orseis* mainly perch in gullies.

11) *Sphaeralcea coccinea* (widely distributed, mainly on flats). *Vanessa caryae* perches often on hilltops, but *Pyrgus scriptura* and *P. communis* patrol and perch in swales.

12) *Atriplex* spp. (clumped in alkaline areas usually on flats). *Brephidium exilis*, and *Pholisora alpheus* and its congeners, patrol near *Atriplex*, or patrol in gullies (*Pholisora*).

13) *Astragalus* spp. (mostly generally distributed in open areas). Most species patrol (*Colias eurytheme*, *C. philodice*, *C. alexandra*, *Hemiargus isola*, *Leptotes marina*, *Everes amyntula*, *Plebejus acmon*), but *Erynnis persius* perches on ridgetops.

14) *Lupinus argenteus* (clumped, often in valley bottoms on deep soil). *Plebejus icarioides*, *Glaucopsyche lygdamus*, and *G. piasus* patrol, but *Erynnis afranius* perches in gullies.

15) *Trifolium* (usually clumped in moist meadows except near timberline). *Colias cesonia*, *C. meadii*, *Plebejus saepiolus*, and *Everes comyntas* patrol, but *Thorybes pylades*, which has other hosts, perches in gulches.

16) *Bouteloua gracilis* (very widely distributed). *Neominois ridingsii*, *Amblyscirtes simius*, *Yvretta rhesus*, *Hesperia pahaska*, *H. viridis*, *H. uncas*, and *H. comma* all mate on hilltops or gulches.

It is clear from the above mate-locating behavior of species with the same larval foodplants that for a given situation there is usually more than one strategy of locating females. Behavior is likely to be similar in taxonomically closely related species. Distantly related species often have different behavior, but sometimes they have convergently evolved the same behavior. Perhaps the most spectacular examples of convergence are *Philotes* and *Lycaena heteronea*, and *Neominois ridingsii* and *Amblyscirtes simius*.

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Table 1. Change of behavioral characteristics with number of broods. *Brephidium exilis*, with 5 broods, is placed with the 4-brood group. Figures are averages. Means and standard deviations for all the variables for all 159 species are also given.

No. of broods	Number of Broods				Mean	Standard Deviation
	1	2	3	4		
No. of species	108	22	17	12	1.59	.98
Perching-patrolling Index	2.32	1.93	2.82	3.58	2.41	1.41
Location of Mating Index	2.28	1.87	2.29	2.83	2.27	.88
Time of Day of Mating Index	3.76	3.42	3.85	3.83	3.73	.67

Table 2. Change of behavioral characteristics throughout the season for single brood species only. Figures are averages.

	May	Time of Emergence						August-early Sept
		early June	mid June	late June	early July	mid July	late July	
No. of species	12	12	13	10	19	14	16	11
Perching-patrolling Index	1.83	1.92	1.85	1.60	2.74	2.14	2.87	3.18
Location of Mating Index	1.92	1.92	2.23	1.80	2.42	2.14	2.75	2.86
Time of Day of Mating Index	3.55	4.00	4.00	3.63	3.83	3.66	3.46	4.00

Table 3. Means of behavioral characteristics for species with different magnitude of movements.

	Magnitude of Movements				
	Very Localized Species	Neither Migratory or very Local	Apparently Can Move Several Kilometers	Can Move Several Kilometers	Migrate Thousands of Kilometers
No. of species	24	102	16	15	2
Perching-patrolling Index	2.29	2.20	2.62	3.80	2.50
Location of Mating Index	2.04	2.18	2.12	3.40	2.00
Time of Day of Mating Index	3.35	3.84	3.35	4.00	3.50

Table 4. Means of behavioral characteristics for species with different larval foodplants.

Larval Foodplants	No. of Species	Perching-Patrolling Index	Location of Mating Index	Time of Day of Mating Index
Salicaceae	10	2.40	2.10	3.30
<i>Prunus</i>	3	2.00	1.67	3.60
<i>Rumex</i>	5	1.40	1.80	4.00
<i>Asclepias-Croton-Celtis</i>	3	2.00	1.67	3.73
<i>Urtica</i>	4	1.00	2.00	2.35
Malvaceae	3	2.00	2.33	3.50
Chenopodiaceae-Amaranthaceae	4	4.00	2.00	4.00
<i>Ribes</i>	2	1.00	2.00	2.10
<i>Sedum</i>	2	2.50	3.00	4.00
<i>Androsace</i>	1	4.00	4.00	4.00
<i>Viola</i>	7	4.00	3.43	4.00
Ericaceae	3	2.00	2.00	4.00
<i>Potentilla</i>	2	2.50	2.00	4.00
Scrophulariaceae	3	2.50	2.67	4.00
Compositae	11	3.00	1.91	3.77
<i>Cercocarpus</i>	1	1.00	1.00	4.00
<i>Quercus</i>	5	1.60	1.80	3.56
<i>Pinus-Juniperus-Arceuthobium</i>	4	1.75	2.75	4.00
<i>Ceanothus</i>	4	1.25	1.25	2.87
<i>Eriogonum</i>	7	3.14	3.43	3.67
Leguminosae	18	3.11	2.83	3.94
Umbelliferae	2	3.00	2.00	4.00
Cruciferae	9	4.00	2.11	4.00
Polyphagous (<i>S. melinus</i> , <i>C. argiulus</i>)	2	2.50	2.00	3.00
Grasses or sedges	42	1.81	2.06	3.88
<i>Yucca</i>	2	1.00	3.00	2.65

Table 5. Means of behavioral characteristics for species feeding on herbs and on shrubs.

	Herbs	Shrubs-Trees
Perching-Patrolling Index	2.54	2.10
Location of Mating Index	2.29	2.20
Time of Day of Mating Index	3.84	3.46