

VARIATION IN *PLEBEJUS ICARIOIDES* (LYCÆNIDÆ)
I. FOODPLANT SPECIFICITY

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The importance of ecology in the evolution of species has been accepted and stressed by biologists. Abundance and distribution of organisms is usually considered in studies of speciation. The evolution of foodplant specificity and the influence of the foodplant in phytophagous insects, however, has received comparatively little attention. DETHIER (1953, 1954), REMINGTON (1952), REMINGTON and PEASE (1955), and others, have called attention to the importance of this subject. REMINGTON and PEASE (1955:4) have suggested that lepidopterists can add much to our knowledge of insect-food plant relations with "the guidance of the experimental method and comparative observation." Knowledge of "biological" or "foodplant races" of insects is but one aspect which provides us with much data on which to base taxonomic and evolutionary conclusions. As more data are accumulated, the greater is our assurance that the conclusions are founded on criteria consistent with the conceptual model of major evolutionary factors. A concerted effort by lepidopterists would elevate foodplant associations from a mere catalog of observations to a useful tool.

The purpose of this paper is to record the known foodplants of the butterfly *Plebejus (Icaricia) icarioides* (Bdv.) along with some pertinent observations on specificity, distribution, and other factors which may have effects on variation within the insect. The study is based both on an extended collecting trip throughout western North America made by both authors in 1959, and earlier studies by DOWNEY. We are grateful to Dr. DAVID B. DUNN, University of Missouri, for his kindness in determining the foodplants herein reported.

P. icarioides comprises a polytypic array of numerous discontinuous populations occupying most of the continent of North America west of the Central Great Plains region. Within this area the majority of populations are in the Canadian and Transition life zones of MERRIAM. Because of this restriction, the elevation at which they live generally is higher in the south and lower in the north. Populations can be found from sea level (Vancouver Island, B. C.; San Francisco and Morro Bay, Calif.) to over 10,000' in elevation (White Mountains, Calif.; Wasatch Mountains, Utah; Weston Pass, Colo.). The species is further restricted to the distribution of the plant genus *Lupinus* on which the larvæ feed.

NEWCOMER (1911) has accurately described the complete life cycle of *P. icarioides* under the name *Lycæna fulla* Edw. COMSTOCK and DAMMERS (1935) also described the life cycle of southern California representatives of this species (= *Plebejus icarioides evius* Bdv.). The reader is referred to these works for detailed descriptions and drawings of the egg, the larval stages, and the pupa.

Since its original description in 1852, no less than twenty-four names have been applied to this single species or portions of it; twelve subspecies are still commonly mentioned in the literature. In a later paper, the senior author will discuss the taxonomy of the species, and attempt to show the artificiality of the subspecies concept in this species. The many names used however, give indication of the variability of the different populations. HOVANITZ (1937) described the species as a *Rassenkreis* (a circle of races) and called attention to its complexity. He further suggested some environmental (habitat restriction) and physiological (foodplant differences) causes of the subspeciation. Although the main emphasis of his work was on synonymy and the fixation of the type localities for the three subspecies included, his hypothesis on the cause of the subspeciation offers a distinct challenge for further work.

During field observations in nine western states and two Canadian provinces, the butterfly was never collected where lupine plants were not discovered within fifty yards of the site of capture. The majority of specimens were collected in direct association with the plant. In most localities, the presence of more than one species of lupine prevented the use of adult association as a criterion of host specificity. Consequently, no lupine was classified as a host plant unless either females were observed ovipositing on the tissues, or eggs or larvæ were found on the plant. Often when the eggs alone were discovered, thorough inspection of the plant revealed characteristic larval damage which verified the utilization of the plant as a food source by the butterfly. Other lupines in the locality of a host lupine also were searched and collected to determine if they were also being utilized, and as insurance that the eggs on the first lupine were not deposited just as an oviposition response. Table 1 gives the species of the genus *Lupinus* which serve as host plants of listed populations of the butterfly. These include published sources and new records established in this study.

The distribution of many of these species of lupine is sympatric (see Jepson, 1951, and Dunn, 1955). However, never more than one species of *Lupinus* was found to be a host plant in any one locality during one season. The nearest approach to two hosts in one area at one time

occurred at Austin Summit, Nevada, and involved a hybrid as mentioned below. Two instances were noted which may indicate a change in food plant in one locality over several years time. The usefulness of this observation is somewhat mitigated by difficulties in the taxonomy of the lupine. HOVANITZ (1937) reported that the population from Twin Peaks, San Francisco, California was feeding on *L. variicolor* Steud. DOWNEY found this population in 1954 and 1955 feeding on *L. albifrons* Bth. var. *collinus* Hel. WILLIAMS (1908) states that *P. icarioides* larvæ from "about the [environs] of San Francisco" fed on *L. micranthus* Dougl., and "could not be induced to eat other legumes." There is some question as to the population affinities of the larvæ studied by WILLIAMS, but they were probably not from the beach populations, since he referred to *Lycæna pheres* in the same paper. This name was used at that time for what we now believe to be a unique (and perhaps extinct) beach population of *P. icarioides*. Possibly the San Francisco populations from higher elevations utilize all three lupines: *L. variicolor* Steud., *L. albifrons* Bth., and *L. micranthus* Dougl. However, it is our opinion that the few small populations left in this vicinity feed only on *L. albifrons* Bth.

Samples of host lupine from Pequop Summit, Elko County, Nevada, were identified in 1956 by D. DUNN as *L. arbustus calcaratus* (Kell.) Dunn. The 1959 population from exactly the same locality was feeding on *L. holosericeus* Nutt. ex Torr. & Gray. DUNN informs the authors, however, that the latter is a poorly defined taxon. The latter species was not present in the small plant sample taken in 1955 from the area.

Occasionally two or more lupine species which are known to be host lupines in other areas occur together. In all such cases the butterfly selected only one host. Since this has a bearing on the specificity of the populations involved, the following examples are given.

As can be noted on Table 1, *Lupinus latifolius* Agardh. is the only known host plant of *P. icarioides* at Boggs Lake, Lake County, California. Also common in this locality, but not used as a host plant by the butterfly is *L. albifrons* Benth. The latter species is a host plant for populations in Berkeley (Berkeley Hills) and San Francisco (Twin Peaks), California. *L. latifolius* is also a host plant at Fawn Lodge near Weaverville, Trinity County, California, and at Shawnigan Lake, Vancouver Island, British Columbia. BARNES and McDUNNOUGH (1919) state that BLACKMORE noted that the *icarioides* population at Goldstream, Brit. Col., utilizes *columbianus* (Heller), which is now considered a variety of *latifolius*. Just across the Strait of Juan de Fuca in Washington, the population on Hurricane Ridge in the Olympic Mountains feeds on *Lupinus glacialis*

Table 1. *LUPINUS* HOST PLANTS OF VARIOUS POPULATIONS OF *PLEBEJUS ICARIOIDES*

Species of <i>Lupinus</i>	Host localities	Reference and year noted
<i>albifrons</i> Benth.	Berkeley, CALIF.	1955
<i>albifrons</i> var. <i>collinus</i> Greene	Twin Peaks, San Francisco, CALIF.	1954, 1955
<i>andersonii</i> S. Wats.	Mt. Conness, CALIF.;	Montgomery*, 1959
	Diamond Lake, Crescent Lake, and Mammoth Lakes, ORE.	1959
<i>arbustus silvicola</i> (Heller) Dunn	Silver Lake & Twin Lake, CALIF.	1955, 1959
<i>arbustus calcaratus</i> (Kell.) Dunn	Pequop Summit, NEV.	1955
<i>argenteus</i> var. <i>tenellus</i> (Dougl. ex G. Don) Dunn	Eureka, NEV.; McGee Creek, CALIF.	1959
<i>caudatus</i> Kell.	Big Cottonwood Canyon, UTAH; Austin Summit & Eastgate, NEV.; LeeVining, CALIF.	1955, 1959
<i>caudatus</i> Kell. × <i>Lupinus</i> sp.?	Austin Summit, NEV.	1955
<i>chamissonis</i> Eschs.	San Francisco, CALIF. (beach)	Williams, 1910; Hovanitz, 1937
<i>densiflorus</i> var. <i>gloriosus</i> (C. P. Sm.)	Frazier Park, CALIF.	Montgomery*, 1959
<i>fulcratus</i> Greene	Meyers & Fallen Leaf Lake, CALIF.	1955, 1959
<i>glacialis</i> C. P. Sm.	Hurricane Ridge, WASH.	1959
<i>holosericeus</i> Nutt. ex Torr. & Gray	Lamoille & Pequop Summit, NEV.	1959
<i>latifolius</i> J. G. Agardh.	Weaverville and Boggs Lake, CALIF.;	1955
	Shawnigan Lake, BRIT. COL.	1959
<i>latifolius</i> var. <i>columbianus</i> (Heller) C. P. Sm.	Goldstream, BRIT. COL.	Barnes & McD., 1919
<i>leptostachyus</i> Greene	Bondurant, WYO.	1959
<i>meionanthus</i> Gray	Lake Tahoe, CALIF.	Newcomer, 1911
	Sonora Pass, CALIF.	1959
<i>micranthus</i> Dougl.	San Francisco, CALIF.	Williams, 1908
<i>sericeus</i> Pursh	Avon, COLO.; Parley's Cany., UTAH;	
	Butte, MONT.; Gallatin Cany. & South Gate, Y.N.P., WYO.	1959
<i>sericeus egglestonianus</i> C. P. Sm.	Gallatin Cany., MONT.	1959
<i>sericeus</i> Pursh × <i>leucophyllus</i> Dougl.	Half Moon Lake, WYO.	1959
<i>sericeus</i> Pursh × <i>caudatus</i> Kell.	Jenny Lake, WYO.	1959
<i>variicolor</i> Steud.	Twin Peaks, San Francisco, CALIF.	Hovanitz, 1937

*In letter from J. C. Montgomery, 1960

C. P. Sm. even though *latifolius* occurs there commonly. In this locality, the local form of *Glaucoopsyche lygdamus* feeds on *latifolius* and some competition between the two species for the same host may exist. Lacking sufficient data on the factor of competition between species, we hesitate to suggest that a physiological "character displacement" has forced the competitors to their respective lupine hosts.

Populations from the same locality in Eureka, Nevada, utilized *L. argentus* var. *tenellus* (Dougl. ex G. Don) Dunn when sampled in 1955 and 1959. The McGee Creek, Mono County, California, and Mt. Charleston, Nevada, populations also utilized this species. Though present in the environment of a population from Lamoille, Nevada, *tenellus* was rejected in favor of *holosericeus* Nutt. *Lupinus leptostachyus* Greene occurs both at Bondurant and Half Moon Lake, Wyoming, but it is the host plant only in the former locality. The Half Moon Lake population feeds on a hybrid, *L. sericeus* \times *L. leucophyllus*.

Foodplant associations could not always be established, particularly in areas where the butterfly was rare or absent on the day collections were made. Many species of *Lupinus* listed in Table 1 were very common in other regions, and undoubtedly serve as hosts in localities other than those indicated. Other species of lupine were collected, both from areas of known-host populations and elsewhere, but were never found to be utilized by the butterfly. These include the following: *albicaulis* Dougl. ex Hook; *alpestris* A. Nels.; *confertus* Kell.; *excubitus* Jones; *lobbii* Gray ex Greene; *lyalii* Gray; *polyphyllus superbus* (Heller) Munz; *pratensis* Heller; *spathulatus* Rydb.; and *succulentus* Dougl. ex Kock.

The only eggs found that were not on lupine were collected at Fawn Lodge, Trinity County, California, where seven eggs were located on a single leaf of Mullein (*Verbascum thapsus* L.) and one egg on an adjacent stem of grass (*Poa* sp?). A large lupine which also contained eggs surrounded the latter two plants, and very possibly a single female laid all the eggs. There seems to be a marked preference on the part of the female for hirsute plants. When gravid females are caged with two or more types of non-host lupine, more eggs are invariably found on the hairiest species. At Austin Summit, Nevada, several broad-leaved, more densely hirsute plants were located in the midst of an extensive stand of *Lupinus caudatus* Kell., which was the host plant for the local population of butterfly. There was such a marked difference between the two types of plant that two species of plants were thought to be involved, even though we were cognizant of the effects of hybridization. Dunn identified the hirsute plant as a hybrid of *L. caudatus* \times *Lupinus* sp.? The average number of eggs on the normal lupine in the vicinity

was one egg per plant. Over twelve eggs per plant occurred on the hirsute hybrid. Knowledge of this oviposition response helped us on numerous occasions. For example, eggs were discovered at Rutherford, California, after collecting a few adults in the vicinity of five different species of annual and perennial lupines, by the simple expediency of initial search on the most hirsute variety. Subsequent examination of all other species of lupine in the area failed to reveal a single egg.

An attempt was made to use the number of eggs per lupine stalk as an indication of population size. So many variables were encountered however, that a satisfactory correlation could not be made. Egg density varies with the number of lupine host plants available in an area, as well as other ecological factors. By far the greatest number of eggs per plant per unit area was found in central and marginal Great Basin populations. This is probably due to the more stringent physical factors of the environment (particularly moisture) which necessitate an adaptive response on the part of the populations in the area to a shorter active life and a longer diapause. More adults and eggs were found at one lupine patch in Eureka, Nevada, for instance, than were located in a comparable expanse of lupine in the central Sierra Nevada Mountains. In areas outside of the Great Basin, rarely were over seventy-five eggs discovered in one day. However, at Pequop Summit, Nevada, over 350 eggs were collected in a little over three hours. In sixteen localities (picked at random) from which eggs were collected on annual lupine species, 2519 stalks were examined and 272 had one or more eggs, (11%). We seldom had to examine many stalks before eggs were discovered, and with this indication, if 100 stalks had no eggs we felt fairly safe in assuming the plant involved was not a host.

In laboratory experiments, both field and laboratory hatched larvae readily accept other species of lupine. In fact, to compensate for any adult variations which may have resulted from food plant differences in his studies of this species, DOWNEY rears all larvæ on *Lupinus alba* L., a plant native to Italy and one with which none of the populations could have been associated under natural conditions. In one experiment using eggs from the population at Twin Peaks, San Francisco, California, five groups, each consisting of ten larvæ, were confined to dishes containing different species of lupine. One group was left on the natural food plant (*albifrons*) and three other groups on the following plants: *L. caudatus*, a host from Utah; *L. succulentus* Dougl. ex Knock, a non-host from Vacaville, California; and *L. alba* from Italy. A fifth group was transferred daily to one of the four types of lupine used in the other groups, so that every fifth day they received the same host species.

All larvæ emerged from the eggs within a twenty-four hour period, and were kept in a dark cabinet held at 80°F., 80 per cent relative humidity during development. All groups had an additional molt between hatching and larval diapause — two molts instead of one. They all molted at the same time, and began diapause at the same time in what could be judged to be the same health and vigor. This demonstrated that there was no apparent physiological effect of different host plants on the Twin Peaks population, at least to the diapause state. Unfortunately, few individuals from any of these groups terminated diapause five to six months later. This was due to factors other than host plant difficulties and applied to the control as well as the test groups. The ease with which larvæ from Utah, Nevada, Oregon, Washington, California, Montana, and Wyoming accept different species of lupine in the laboratory adds weight to the premise that any species of this genus of plants can serve as a host.

COMSTOCK (1927) states that the larvæ of *P. icarioides* "have been observed feeding on lupine and clover." With trust in the author's accurate determination of the larvæ, we can only state that the utilization of clover (*Trifolium*) is the exception rather than the rule with this butterfly. There is evidence of a double-brood in Southern California populations, and if such occurs, very likely there has been a food plant adjustment.

That populations were found on only one lupine in any one locality indicates a host-specificity in nature. It is also an indication of physiological divergence between populations, but seems to be based on egg-laying habits of the adults rather than nutritional requirements of the larvæ. The physiological effects may be very subtle, but the presence of an active population on a single host plant per unit area would be an *a priori* reason for assuming physiological success. The comparative success between different populations, probably measured by abundance, requires a degree of ecological and geological knowledge which is not yet attained.

The calculations of SEWALL WRIGHT indicate that the size of subpopulations and the degree of their isolation from one another have a great deal to do with population variation and subsequent taxonomic differentiation. DOWNEY (1957) has previously pointed out that the colonial nature of the subgroups of *P. icarioides* tends to reduce the rate of interbreeding between adjacent populations, and is of signal importance in accounting for the degree of polymorphism exhibited. It is our opinion that this degree of isolation is intimately associated with the local and spotty distribution of the host plant as based on edaphic

factors. We further feel that the discontinuous distribution of the host plants is of greater importance in speciation in this insect than the host specificity of individual populations.

CONCLUSIONS

1. Sixteen full species plus seven varieties or hybrids of the plant genus *Lupinus* were found to serve as host plants of different geographical populations of the butterfly *Plebejus (Icaricia) icarioides* (Bdv.). This represents a sample from thirty-four new localities scattered throughout the greater range of the species.
2. The oligophagous nature of the species was substantiated; it is restricted to members of the plant genus *Lupinus* (it is thought that the reported instance on clover is atypical). Individual populations tend to be monophagous, limiting their food plant to one species or variety.
3. Though all populations utilize only one species of lupine in a given area, some evidence indicates that a food plant change (from one lupine species to another) has occurred. This change in specificity in time is comparable with the noted differences in specificity in space.
4. Four cases were noted where populations failed to utilize a lupine species known to be a host plant in another area. It is suggested that this difference is due to an oviposition response on the part of the adult, rather than to a nutritional preference by the larva. This oviposition response appears to be directly correlated with the hirsute qualities of the lupine.
5. The fact that larvæ have been successfully reared on lupines other than their normal host provides additional evidence that any species of *Lupinus* may be utilized by *P. icarioides* as a foodplant.
6. The localized and spotty distribution of the host plant limits the distribution of the butterfly to isolated pockets, and is presumed to have a greater effect on the variability of the insect than do the assumed differences attributed to the selection of different host plants.
7. Although variation in lupine preference of the adult may indicate a subtle difference in physiology, it is assumed that the observed difference between populations is not genetically fixed. At this stage of the evolution of *Plebejus icarioides*, foodplant specificity is not an infra-specific isolating mechanism.

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