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HABITAT AND RANGE OF *EUPHYDRYAS GILLETTII* (NYMPHALIDAE)

ERNEST H. WILLIAMS
Department of Biology, Hamilton College, Clinton, New York 13323

ABSTRACT. Fifteen sites occupied by *Euphydryas gillettii* are compared according to 10 characteristics. All sites are moist, open, mostly montane meadows, many with a history of disturbance, commonly fire. Population size correlates with relative availability of nectar but not with overall abundance of the usual hostplant, *Lonicera involucrata*. Habitats at higher latitudes often have a southerly exposure. Reduction in hostplant size at higher latitudes contributes to the northern range limit. Three populations likely have become extinct since 1960, but the species range does not appear to be changing.

Additional key words: nectar, *Lonicera involucrata*, biogeography, extinction.

Euphydryas gillettii (Barnes), a checkerspot butterfly, occurs in discrete, isolated populations (Williams et al. 1984) in the central and northern Rocky Mountains (Ferris & Brown 1981). It is attractive and easily caught but uncommon and not often collected. Though usually considered a montane species (Williams et al. 1984), variation in sites occupied by *E. gillettii* has not been studied, and lack of knowledge about its habitats has led to uncertainty about its range.

Here I report characteristics of sites occupied by *E. gillettii*, present range of the species, and factors influencing its distributional pattern. This study is based on direct observation of the habitats of 15 populations throughout the range, thus affording an uncommon view of habitat variability in a single insect species.

METHODS

Populations of *E. gillettii* were located through correspondence with collectors and researchers listed in Acknowledgments, examination of specimen labels in collections listed in Acknowledgments, and a survey of published reports (*News Lepid. Soc.*, Seasonal Summaries 1960–1986). When directions were sufficient to pinpoint locations on a topographic map, I visited the sites, and assessed relative population size and habitat characteristics.

Population size was determined by a one-day count of adults, egg masses, and larval webs. Egg masses of *E. gillettii* are distinctive, easily found, and readily counted, thus permitting quantitative comparisons of colony size even after the flight season; in fact, egg mass counts are better indicators of population size than adult counts because the former are independent of weather. Eggs do not begin hatching until late in the flight season (Williams et al. 1984), so developmental state of egg masses at each site indicated timing of the count relative to flight season.

Females average one to two egg masses per individual (unpubl.); thus, relative population size can be estimated from sum of egg masses and adults.

In addition to population size, I recorded nine site characteristics, and searched for evidence of disturbance. Observations were quantified as much as possible for later analysis. Each site is marked on U.S. Geological Survey and Canada Department of Energy, Mines & Resources topographic maps in my possession, and latitude and elevation were measured directly from these maps. I used a compass as well as contour lines on the maps to determine exposure. I recorded number of distinct shrubs or clumps of the usual hostplant, *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae) (Comstock 1940, Williams et al. 1984), in open areas where egg masses and adults were found. Nectar sources were identified (Hitchcock & Cronquist 1973), and relative nectar availability was determined by site comparison. Nearby trees were identified and cored with a 5 mm diam increment borer for age determination. Presence and distance to standing water and streams were recorded. I inferred source and history of disturbance from characteristics such as tree species and age, charring, stems gnawed by beavers, and location in a flood plain.

RESULTS

Populations

I visited 29 localities reported as sites for *Euphydryas gillettii* and found populations at 13. With my 2 previous study sites (Williams et al. 1984), I had a total of 15 colonies throughout the geographic distribution of the species for comparison. More than 15 egg masses and adults were found at 7 sites ("large" populations), while fewer than 15 were found at 8 sites ("small" populations) (Table 1).

Habitat Characteristics

All occupied sites are wet (Table 1). Most have a small stream passing through, though several are marshy without obvious flowing water; *E. gillettii* occurs infrequently near rivers, perhaps because of flood disturbance to hostplants, nectar sources, larvae, and adults. In habitat characteristics, *E. gillettii* is similar to its congener *E. phaeton* (Drury) (Scudder 1889). There is no observable relation between population size and type of water present.

There appears to be a correlation between colony size and nectar abundance ($\chi^2 = 3.2$, df = 1, P = 0.07). Only two sites have large populations with low nectar availability, but these populations are marginally "large" (sites 7 & 9, Table 1). Total amount of nectar is also important in *Euphydryas editha* (Boisduval), influencing its population

TABLE 1. Characteristics of 15 sites occupied by *Euphydryas gillettii*.

Site no.	Colony size[1]	*Lonicera invol.* abundance[2]	Nectar availability	Nearby trees (age of largest to nearest 5 yr)	Water (stream width)	Disturbance
1	>30	>30	High	Lodgepole pine (75) Engelmann spruce (65)	Stream (<1 m)	Fire[3]
2	>30	>30	High	Quaking aspen (60) Subalpine fir (75)	Streams (<1 m)	None; meadow edge
3	7	10	Low	Engelmann spruce (150)	Stream (1–3 m)	None; meadow edge
4	2	10	Low	Lodgepole pine (55)	Marshy	Fire; wet soil
5	4	20	Low	Lodgepole pine (90) Quaking aspen (65)	Stream (<1 m)	Fire; logging
6	>30	20	High	Subalpine fir (155) Lodgepole pine (15)	Streams (<1 m)	Fire[3]; logging
7	18	10	Low	Cottonwood (40) Lodgepole pine	Stream (1–3 m)	Beaver activity
8	21	10	High	Lodgepole pine (65)	Stream (>5 m)	Flooding
9	22	20	Low	Lodgepole pine (95) Engelmann spruce (70)	Marshy, stream (<1 m)	Wet soil
10	8	>30	High	Lodgepole pine (55) Engelmann spruce (50) Subalpine fir (40)	Stream (<1 m)	Fire?; meadow edge
11	7	5	Low	Subalpine fir (95) Engelmann spruce	Marshy	Fire[3]
12	3	>30	Low	Lodgepole pine	Stream (1–3 m)	Flooding; fire?
13	1	20	Low	Engelmann spruce (195) Lodgepole pine (40)	Stream (1–3 m)	Fire[3]
14	2	20	Low	Willow (no trees)	Marshy, stream (<1 m)	Wet soil; grazing
15	>30	5	High	Lodgepole pine (75)	Marshy	None; meadow edge

[1] Total number eggs and adults.
[2] Approximate number *Lonicera* clumps in 30 × 30 m quadrat.
[3] Charred tree trunks.

dynamics (Murphy et al. 1983). Nectar is supplied by a number of genera (Table 2), mostly commonly *Aster, Senecio,* and *Agoseris,* but each occurs conspicuously at no more than 9 of the 15 sites. Williams et al. (1984) found the butterflies to switch nectar sources readily when an early source senesces. Total amount of nectar thus appears more important than particular sources.

Hostplants were considered highly abundant when there were more than 15 distinct shrubs or clumps. In contrast to nectar availability, hostplant abundance does not correlate directly with population size ($\chi^2 = 0.1$, df = 1, $P > 0.5$). Reasons are considered later.

Most sites have been disturbed (Table 1), with fire being the commonest natural source. Lodgepole pine, *Pinus contorta* Dougl., is com-

TABLE 2. Common nectar sources for *Euphydryas gillettii* at 15 study sites.

Genus	Number of sites where present	Genus	Number of sites where present
Aster	9	*Polygonum*	2
Senecio	8	*Antennaria*	1
Agoseris	7	*Chrysanthemum*	1
Geranium	6	*Cirsium*	1
Achillea	5	*Geum*	1
Heracleum	5	*Helianthella*	1
Potentilla	4	*Saxifraga*	1
Valeriana	3	*Solidago*	1

mon near colonies (Table 1), indicating common disturbance history in these areas (Pfister et al. 1977). Whatever the cause, disturbance opens a site for growth by more hostplants and nectar sources. The few sites not clearly showing disturbance are on edges of permanent wet meadows of grasses and sedges.

At higher latitudes, occupied sites occur at lower elevations (Fig. 1, $r^2 = 0.49$, $P < 0.005$). This result likely reflects colder climates and reduced height of mountains at higher latitudes. Furthermore, importance of a minimum growing season length is shown in frequent southerly exposure of sites at higher latitudes, in contrast to the variable exposure of sites at lower latitudes (Fig. 1). All large northern populations occupy sites with southern exposure, while southern sites show no observable relation between population size and exposure. Williams (1981) demonstrated the importance of within-habitat exposure effects; current results suggest larger-scale influences as well.

Range

Available records of *E. gillettii* are mapped in Fig. 2. Sightings are concentrated in the mountainous regions of W Wyoming, central Idaho, NW Montana, and SW Alberta. Some regions for which there are only older records, such as Yellowstone National Park and SW Montana, undoubtedly support populations, but their inaccessibility makes collecting sporadic. Continued existence of *E. gillettii* in extreme SW Wyoming is questionable because extensive search has failed to uncover specimens (C. F. Gillette pers. comm.). A reported record from central Montana may be erroneous. There is also a single museum specimen from Ontario, but improbable date as well as location suggest mislabeling.

Sites in Alberta have smaller populations of butterflies than do those farther south, and all northern sites have one characteristic in common: *Lonicera involucrata* does not reach the large size and luxuriant growth characteristic of Wyoming and Montana sites. In moist areas at higher

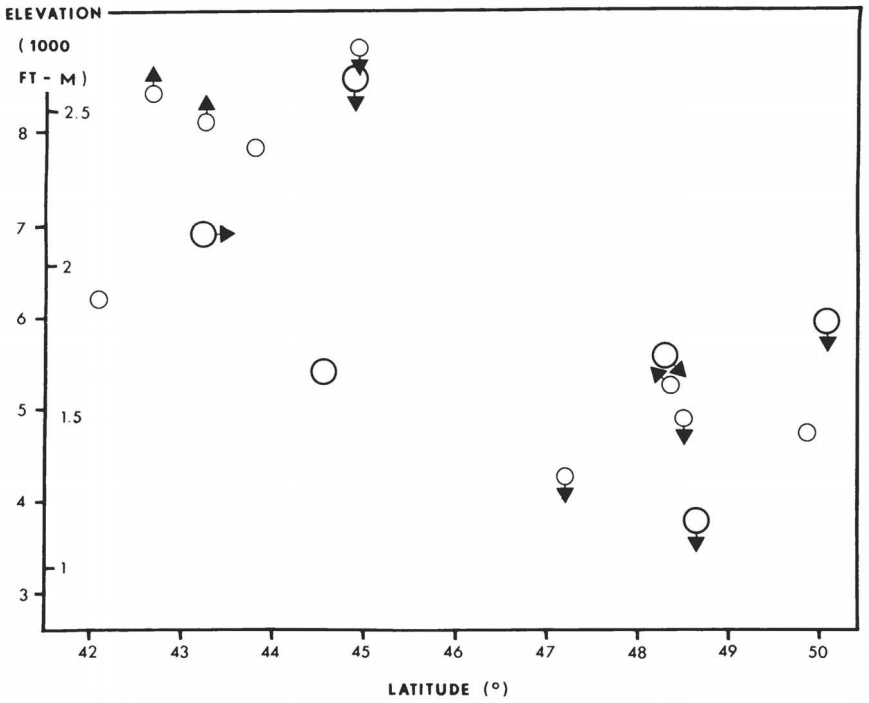

FIG. 1. Elevation and latitude of fifteen *Euphydryas gillettii* sites. Large circles represent "large" populations. Arrows pointing down indicate sites with southerly exposure; those pointing right, easterly exposure; etc. Absence of arrow indicates site has no obvious slope.

latitudes, willows (*Salix* spp.) are often taller than *L. involucrata*, shading them and making them less accessible to searching females; this rarely occurs at lower latitudes. Oviposition sites are therefore scarcer than at lower latitudes, because oviposition occurs on the highest leaves of hostplants that are fully exposed to sunlight (Williams 1981, Williams et al. 1984).

DISCUSSION

There appear to be four reasons for lack of correlation between population size and abundance of *L. involucrata*. First, and most importantly, this plant grows in moist areas regardless of amount of sunlight, while the butterfly requires sunlit hostplants (Williams 1981). In fact, the most luxuriant hostplants often grow in shade of conifers, but are not used as oviposition sites. Second, an extension of the first, much *L. involucrata* is over-shaded by willows at high latitudes, thus providing fewer potential oviposition sites in such areas. Third, some *Euphy-*

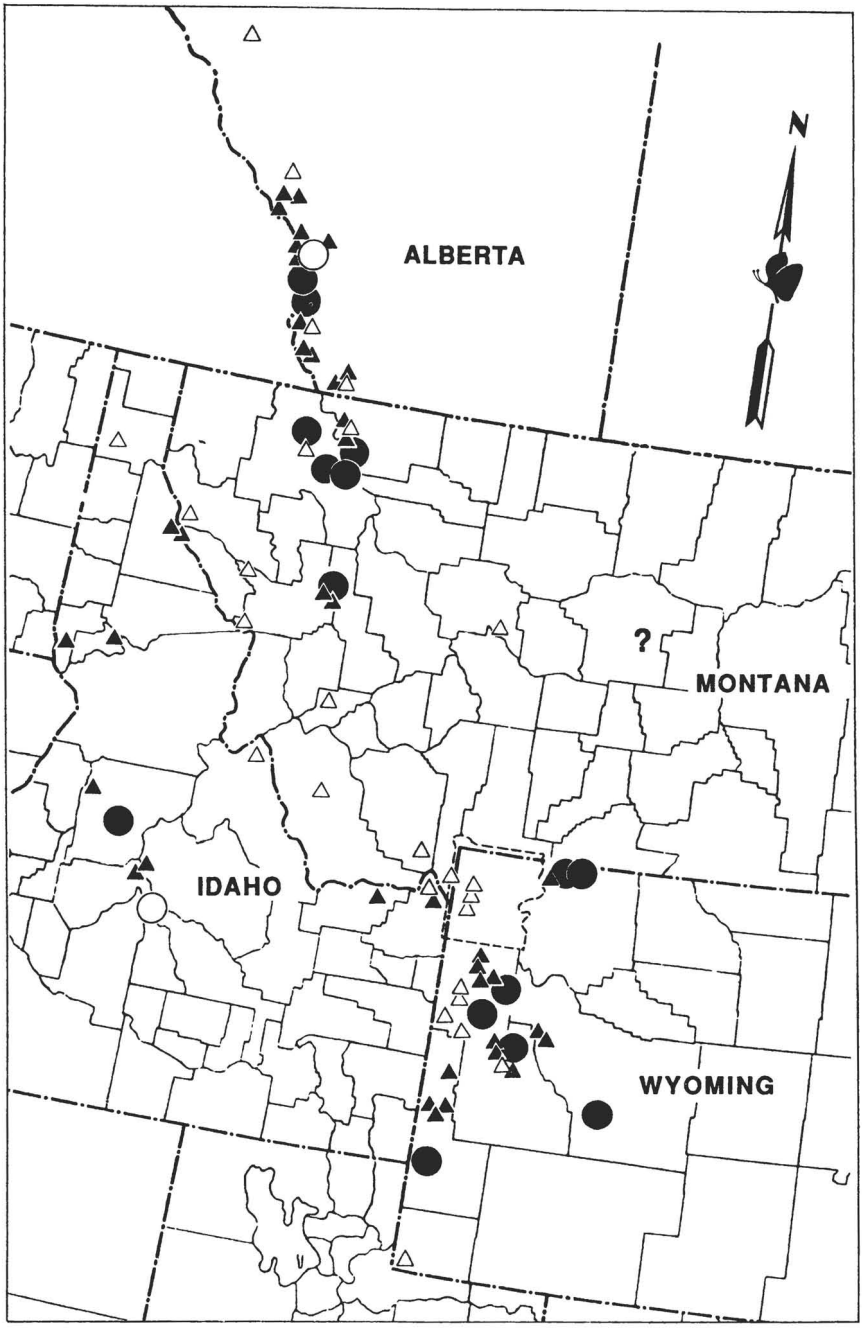

FIG. 2. Range of *Euphydryas gillettii*. Closed circles are sites described in this study; open circles are locations of populations believed extinct; closed triangles are locations

dryas gillettii populations are mostly biennial (Williams et al. 1984), and so may fluctuate greatly in abundance from year to year. While most *E. gillettii* sites are characterized by abundant *Lonicera involucrata*, these three factors limit the size of an observed butterfly population to less than might be expected given the total amount of *Lonicera*. The fourth reason is butterfly use of alternative hostplants.

Only at one site was the colony larger than would seem possible given the amount of nearby *L. involucrata*. That population (site 15, Table 1) lives where *L. involucrata* is uncommon, and the butterflies oviposit extensively on two other plants, *Pedicularis* and another *Lonicera* (in prep.). There are several possible reasons for dietary expansion in butterflies (Singer 1971, 1983); but whatever they may be for this population, other study populations have not followed suit, even though all known alternative hostplants grow throughout the *Euphydryas gillettii* range. Except for site 1, where an alternative hostplant was chosen at low frequency (less than 4% of egg masses, Williams & Bowers 1987), I did not find eggs on or see ovipositional behavior near other plants at the other 14 sites. Because of the known use of alternative hostplants, I expect other *E. gillettii* populations use alternative hostplants as well. The relation between population size and *Lonicera involucrata* abundance is thus weaker than has been widely accepted.

Because its hostplants and nectar sources require wet sites, and because adults and larvae require sunlit areas for warmth, *Euphydryas gillettii* most often occurs in open montane meadows. The one study population that is not montane occupies a permanently wet, grazed seepage area in the transition zone. Several populations were observed along forested edges of seemingly permanent montane meadows; such meadows may change little through time because of allelopathic interactions of meadow vegetation or soil instability. More commonly, open sites are created temporarily through disturbance. The most frequent disturbance is fire, and most study sites have clearly been affected by it. Other forms of disturbance, such as flooding, beaver activity, or human activities like grazing and logging, also serve to open forested areas.

Vegetational succession in disturbed areas leads to changes that make sites less suitable through time. In particular, encroachment by surrounding forest leads to greater evapotranspiration, producing a drier site and thereby limiting growth of hostplants and nectar sources. Furthermore, invasion by trees reduces the sunlight that reaches the shrub

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where *E. gillettii* has been seen since 1960; open triangles are records before 1960; question mark denotes uncertain record.

and herb layer, thus eliminating warmer microsites preferred for oviposition (Williams 1981).

Life in disturbed sites suggests that *E. gillettii* populations are subject to periodic extinction like *E. editha* (Singer & Ehrlich 1979), and such appears to be the case. I identified with precision one site where *E. gillettii* was collected in the 1960's, but by 1983 vegetational succession had taken place, most remaining *Lonicera involucrata* was shaded, and no sign of butterflies could be found. Furthermore, human development of recreational areas has led to loss of additional populations, one known and one suspected.

Habitat requirements of *E. gillettii*, including moisture for hostplants and nectar, and sunlight for larvae and ovipositing females, produce the limits of its geographic distribution. Thus, plains east of the Rockies and arid basins westward form effective biogeographic barriers to dispersal in either direction because of lack of water. Holdren and Ehrlich (1981) have shown that another arid region, the Red Desert of S Wyoming, is the southern barrier since they successfully transplanted individuals across the barrier to central Colorado where one colony has survived since 1977. Their transplant locales are similar to natural habitats farther north in being wet and having an abundance of nectar and *Lonicera involucrata*.

The northern range limit has been assumed to result from lower temperatures and shorter growing season. However, all the Alberta sites have much smaller *L. involucrata*, and willows dominate northern wet sites by growing taller than other shrubs. All populations of the butterfly at higher latitudes are smaller as well. Although no northern populations have been found to use hostplants other than *L. involucrata*, alternative hostplants used elsewhere also decline in abundance at higher latitudes. It seems likely that competition by willows reduces size and perhaps density of potential hostplants. Thus, fewer oviposition sites and poorer (more shaded) ones would be found during normal hostplant searching by females (Williams et al. 1984). I suggest that loss of oviposition sites contributes, along with shorter growing season, to the northern limit.

Euphydryas gillettii is uncommon, but there is no evidence that its range has been changing in recent decades. The greatest conservation advantage this species has compared to other uncommon species is that its habitat lies largely in mountainous areas that are not readily accessible and in which there is little immediate potential for human modification. Its greatest conservation disadvantage is its occurrence through a limited range in discrete, localized populations, which are individually susceptible to disturbance and extinction.

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