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FIRE-BURNED HABITAT AND REINTRODUCTIONS OF THE BUTTERFLY *EUPHYDRYAS GILLETTII* (NYMPHALIDAE)

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ABSTRACT. The butterfly *Euphydryas gillettii* (Barnes) lives in moist mountain meadows connected by riparian corridors, thus forming metapopulations in which local extinctions and recolonizations occur infrequently. Following the 1988 fires in the Greater Yellowstone Ecosystem, I chose 8 unoccupied patches of suitable habitat, 4 of which had been burned, and introduced a single eggmass into each. Larvae survived to diapause in at least 4 of the 8 sites, but only one introduction led to the establishment of a new colony the next year. This was at a burned site. The new population increased rapidly for 2 years but then declined and disappeared. These results suggest that: (1) a single, isolated eggmass is sufficient for colonization of open habitat; (2) most single, isolated eggmasses do not survive to produce adults the following year; and (3) recently burned sites provide acceptable habitat for this scarce butterfly.

Additional key words: transplants, fugitive species, dispersal, metapopulation, colonization.

Many organisms live in habitat that is unpredictable in time and space, and for them natural selection is likely to increase rates of dispersal and subsequent colonization of uninhabited areas (Southwood 1962, den Boer 1990). Even in stable habitats there is an advantage to dispersal because individuals then leave copies of their genes in new areas (Hamilton & May 1977, McPeek & Holt 1992). Many dispersive species occur in metapopulations in which individual colonies periodically go extinct while others are newly established, producing a mosaic of occupied and unoccupied habitat patches (Gilpin 1987).

Some butterfly species have such a metapopulation structure. In these insects, dispersing males rarely help found new colonies because they are unlikely to encounter unmated females away from existing populations. Dispersing females, on the other hand, are likely to have already mated, and if they pass through suitable habitat with acceptable hostplants, they may establish new populations with the eggs they leave behind. Females sometimes disperse at higher rates than males due to behavioral interactions between the two sexes (Shapiro 1970), thereby increasing the likelihood that new sites are colonized. For butterflies that produce eggs in clusters, the existence of a refractory period after ovipositing one large eggmass (Williams in prep.) makes it unlikely that a dispersing female will leave more than one egg cluster in any one new habitat. Thus, each new colony of a cluster-laying species is probably established by a single eggmass.

Euphydryas gillettii (Barnes) (Nymphalidae) is an uncommon, cluster-laying nymphalid butterfly of the northern Rockies which inhabits moist montane meadows. It lives in extended metapopulations along riparian corridors, with low frequency of dispersal up and down stream (unpubl. data) or over longer geographic distances (Holdren & Ehrlich 1981). Its population structure is similar to that of other butterflies (Harrison et al. 1988, Pollard & Yates 1992, Warren 1994) that live in distinct colonies, undergo local extinction, exhibit low levels of dispersal, and occasionally recolonize empty habitat.

Most meadows occupied by *E. gillettii* exist because of disturbance, and the most common form of disturbance is forest fire (Williams 1988). By removing the canopy, fires reduce evapotranspiration and increase sunlight on hostplants and nectar sources. The extensive 1988 fires in the Greater Yellowstone Ecosystem opened up new patches of habitat that are likely suitable for occupancy by *E. gillettii.* To assess colonization in this butterfly, I chose 8 unoccupied sites in this ecosystem, introduced a single eggmass into each, and followed the fate of each transplant. I expected to find that: (1) a single eggmass is sufficient to give rise to a new colony; (2) the probability is small that any single, isolated eggmass will actually give rise to a new colony; and (3) the Yellowstone fires of 1988 produced suitable habitat for *E. gillettii.*

METHODS

To make it likely that the butterflies could survive and reproduce, I chose transplant sites with features that characterize the habitat of *E. gillettii.* The most important features (Williams 1988) are, in order of importance, presence of: (1) the hostplant, *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae); (2) open, sunlit meadows; (3) an abundance of nectar sources; (4) water, usually a small stream; (5) trees for roosting; and (sometimes) (6) south-facing exposure for warmth. Despite occasional use of additional hostplants (e.g., Williams & Bowers 1987), *L. involucrata* is the primary hostplant at every population known. I used field surveys based on U.S.G.S. topographic maps to identify sites in the northern Yellowstone region that provided the above habitat features, including sites burned during the 1988 fires, and for which there

TABLE 1. Summed results of reintroductions of *Euphydryas gillettii*. Reintroductions were made 9–19 July 1989 into patches of open habitat, and the status of each transplant was assessed in August 1990 and July 1991.

Site	Habitat	Eggmass (no. eggs)	Elevation (m)	Fate of eggs	Adults in 1990
1	burned	107	2195	prediapause feeding	no
2	burned	146	2045	prediapause feeding	yes
3	burned	202	2015	unknown	no
4	open	110	2440	prediapause feeding	no
5	burned	104	2445	prediapause feeding	no
6	open	210	2380	unknown	no
7	open	196	2470	browsed	no
8	open	165	2350	browsed?	no

was no evidence of *E. gillettii* being already present. I surveyed more than 25 possible sites before choosing 8 for transplants. Of the 8 sites chosen (Table 1), 4 experienced canopy burns in 1988, while the other 4 had not burned within recent decades. The eight sites, found within 109°30′ to 110°40′W longitude and 44°50′ to 45°10′N latitude, occur within the Greater Yellowstone Ecosystem (Marston & Anderson 1991). While there was some variation in the size of the 8 sites chosen, what is most important for the survival of *Euphydryas* butterflies is the quality of the habitat, not its extent (Ehrlich 1992). Both limited habitat and restrictions on experimenting in Yellowstone National Park prevented me from increasing the number of sites for transplants as I had planned.

Prior absence of *E. gillettii* was judged by lack of indicators—butterflies, eggs, or evidence of characteristic feeding on the hostplant *Lonicera involucrata*—during two or more visits at each site during the height of the flight period (mid July) in 1989, when all surveys and subsequent introductions were made. Extensive field work with this species (Williams et al. 1984, Williams 1988) has shown that wherever a population occurs, even a small one, evidence of its presence is easily found.

Eggmasses for transplantation were collected from one of the few large populations known (Valley Co., Idaho, 400 km distant) and transported on ice to the study area. At each site, using adhesive tape, I attached one randomly-chosen eggmass-bearing leaf by its petiole to a small twig in the upper middle of a large *L. involucrata* shrub in an open meadow near water. Each site and eggmass was marked and photographed. Eggmasses for the 8 transplants averaged 155 eggs (Table 1). The eggmasses used in this study came from a population at a lower elevation (1615 m), where the adults fly 10 days earlier. Thus, the transplanted eggs may have been developmentally ahead of those ex-

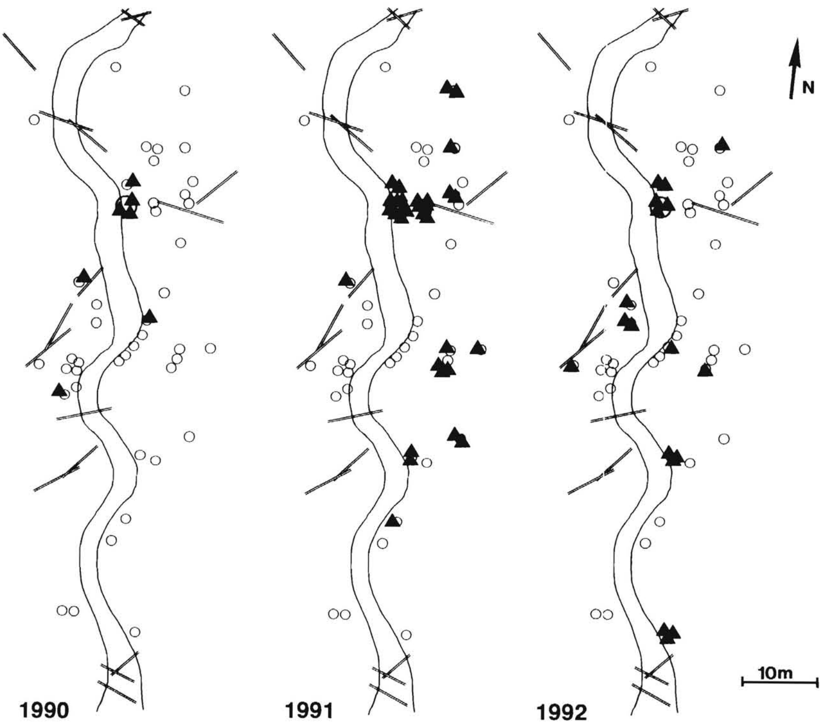

FIG. 1. Eggmass distribution for 1990–1992 at the site with the successful introduction. The stream is shown through the middle of the site, while straight lines represent burned, fallen trees. Triangles show locations of eggmasses. Open circles represent hostplants, *Lonicera involucrata*, with the large circle being the shrub that received the introduced eggmass in 1989. No additional eggmasses could be found within another 100 m up or down stream or to either side (no hostplants occurred away from the stream) in any year.

pected at the transplant sites, yielding a little more feeding time for transplanted larvae to prepare for winter (R. R. White pers. comm.).

For the next three years I revisited the sites near the end or after the flight period. Estimates of brood size were based on the number of eggmasses at each site that could be found from surveying every *L. involucrata* shrub within a 100 m radius (Fig. 1). With this survey technique, I missed long distance dispersers; however, few *E. gillettii* move away from regions of high concentration, and eggmass counts accurately reflect the relative size of each year's population (unpub. data). The most accurate censusing is done at the end of the flight period or soon thereafter, because, unlike adults, eggmasses and larval webs are easily found and censused during periods of variable weather.

RESULTS

In 1990, there was conspicuous evidence at 4 of the 8 sites that the eggs introduced in 1989 had hatched successfully and that prediapause larvae had fed (Table 1). At all 4 of these sites, the twig that received the transplant was leafless or dead the following year, a characteristic result of *E. gillettii* oviposition on *L. involucrata* (Williams et al. 1984). In addition, a partial feeding web remained on the transplant twig at 2 of the 4 sites. Three of these 4 sites had burned in 1988. Judged by evidence of browsing, moose had consumed the transplanted eggs or first instar larvae at a fifth site and possibly a sixth. Such a fate is not uncommon for *E. gillettii* early stages within this ecosystem (Williams et al. 1984). There was no evidence to assess the fate of the final 2 transplants.

I could find surviving *E. gillettii* at only one of the eight sites in 1990, however, despite extensive searching for eggs, larvae, adults, or characteristic feeding on *L. involucrata* (a success rate of about 0.12). Searches of all eight sites again in 1991 and 1992 gave the same results. The site with the successful transplant (near 45°N, 110°30′W) burned extensively in the 1988 fires and as a result provided newly open, sunlit patches of meadow. The introduced eggmass at this site had 146 eggs, fifth largest of the 8 transplanted eggmasses. Flowers were abundant here, including the following common nectar-sources for *E. gillettii*: *Arnica* spp., *Aster occidentalis* (Nutt.) T.&G., *Geranium richardsonii* Fisch. & Trautv., and *Senecio serra* Hook (identification from Hitchcock & Cronquist 1973).

Based on annual counts (1990–1993) of eggmasses after the flight period, the population at the successful site grew rapidly for two years, declined in the third year, and disappeared in the fourth (Fig. 2). The distribution of eggmasses and larval feeding webs indicated that the butterflies remained remarkably close to the transplant site (Fig. 1): (1990) mean distance 9 m, range 0–29 m; (1991) 12 m, 0–46 m: and (1992) 23 m, 0–62 m. No eggmasses or signs of larval feeding were evident more than 20 m from the stream (no hostplants grow away from the stream) or 100 m up or down stream (where the canopy is more closed).

DISCUSSION

The recolonization of empty habitats within a metapopulation structure has been infrequently observed. These results show clearly that a single eggmass can give birth to a new population; thus, with the oviposition of one eggmass, a single dispersing female of *E. gillettii* can colonize a new habitat patch, at least for the short-term. The introduced

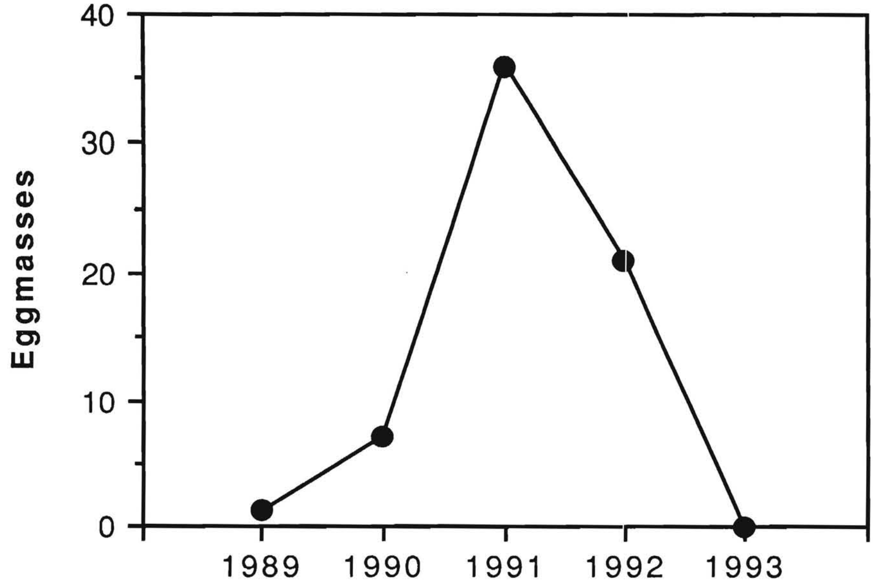

FIG. 2. Growth and decline of the introduced population of *Euphydryas gillettii*. The number of eggmasses found after the flight season is shown for each year since the introduction of a single eggmass in 1989. Population size is proportional to the number to eggmasses.

eggs would have hatched at the same time or slightly ahead of those expected at the transplant elevations, thereby ensuring that the larvae would have enough food of sufficient quality to prepare for diapause. Also, though few introductions were attempted, the probability of a single eggmass surviving and producing a new colony is small, as expected. The number of eggs in the eggmass is probably of secondary importance to the overall fate of the mass itself in determining whether any adults emerge the following year; random events such as browsing by moose exert strong impact on the survival of an eggmass, whereas other factors lead to the survivorship of some but not all eggs within an eggmass.

It is unknown whether the successful site could have supported a population of *E. gillettii* without a recent forest fire (their absence suggests not), but with the canopy burn and felling of a number of trees, the fires of 1988 opened up this habitat conspicuously. Recycled nutrients may have increased plant growth, and tree loss likely reduced evapotranspiration, but the most immediate change in habitat quality as a result of the fires was reduction in tree canopy cover. *Euphydryas gillettii,* like most butterflies, depend on solar warming to remain active, and they avoid shaded areas (Williams 1981). Larvae of other *Euphydryas* have been shown to bask both to facilitate digestion and growth (*E. aurinia*, Porter 1984) and to develop more rapidly through a limited growing season (*E. editha*, Weiss et al. 1988). It is the presence of hostplants and nectar sources in open, moist meadows that attracts the butterflies, and fire is the most common producer of such conditions. There is a significant history of fire throughout the Greater Yellowstone Ecosystem (Romme & Despain 1989, Despain 1990) as well as the rest of *E. gillettii*'s range. The successful colonization of a recently burned habitat patch supports the expectation that fires produce acceptable habitat for *E. gillettii*. Natural colonization of fire-burned areas have yet to be reported, however.

The introduced population grew rapidly over the first two years (Fig. 2), and though exponential growth cannot continue for long, the decline in numbers in the third year did not appear to result from exhaustion of resources at that site. More likely, rainy weather during the normal flight period of 1992 decreased the opportunity for oviposition, so fewer eggmasses were produced (egg shortfall). Weather is known to limit brood size by restricting oviposition (Courtney & Duggan 1983). The same 1992 reduction in population size was seen in another *E. gillettii* population 80 km east (unpubl. data), and synchronous responses of different populations point to more general controlling factors such as weather (Pollard 1991). Furthermore, the establishment of a colony from a single eggmass produces limited genetic variability that, without subsequent gene flow, diminishes the long-term survival of the colony. The disappearance of the population in 1993 was surprising; a significant factor was that heavy spring flooding led to the collapse of some of the streambank and washed away the shrubs on which there had been the heaviest oviposition. Once it had been established, I did not expect to lose this colony so soon, but the loss reinforces the notion that chance events can exert strong impact on the survival of small colonies that make up metapopulations of this species.

A few introductions of this and related butterflies have been attempted. Holdren and Ehrlich (1981) introduced *E. gillettii* into two sites in Colorado, and while their transplants were successful for a few years, they used nearly 10,000 eggs each (up to 83 eggmasses) to ensure successful colonization. Harrison (1989) introduced propagules of 100 larvae of *Euphydryas editha* to each of 38 empty sites and found only a 6% chance of persistence for two years. Her results are in accord with the low probability of survival I found in *E. gillettii*.

No introduction can be undertaken lightly, however. My study was based on introducing eggs to empty habitat patches within the historic range of the species (Yellowstone National Park is also the source of the type specimen). *Euphydryas gillettii* is known from sites 24 km to the southwest and 80 km to the east of the transplant sites, for example. Thus, these introductions may be more accurately characterized as "re-establishments" (New 1991) into known range, and they therefore are not fraught with the risks associated with making introductions into non-endemic areas. Nevertheless, genetic variation does occur among populations in sedentary species, and Debinski (1994) has documented low level genetic differences among *E. gillettii* from Idaho, Montana, and Wyoming. I did not regard this variation as a deterrent to attempting re-establishment of a scarce butterfly in its native range.

Even with low rates of success, *E. gillettii* is able to colonize patches of habitat newly opened by disturbance. For animals that vary widely in abundance, such as insects, dispersal and recolonization of new patches are necessary for the longterm maintenance of a metapopulation (den Boer 1990). For insects that occupy disturbed sites, such as *E. gillettii*, the production of newly opened habitat by fire or other means is necessary for their survival. The results reported here provide an example of colonization in *E. gillettii*, illustrate how the Yellowstone fires of 1988 recreated habitat for this scarce butterfly, and, importantly, show how infrequent such re-establishment may be.

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