



Population Loss and Gain in the Rare Butterfly *Euphydryas gillettii* (Nymphalidae)

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POPULATION LOSS AND GAIN IN THE RARE BUTTERFLY *EUPHYDRYAS GILLETTII*
(NYMPHALIDAE)

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ABSTRACT. Fourteen populations of the montane butterfly *E. gillettii* Barnes were surveyed initially during 1982–1984 and again during 2002–2006 to assess reasons for decline, extirpation, and colonization. Surveys were conducted by counting egg masses at each site soon after the flight period. Seven of the 14 populations disappeared between the two surveys because of vegetative succession, drying of meadow habitats, and isolation from other colonies. Populations at low elevations and low latitude were more likely to die out; colonies that were part of a metapopulation were more likely to survive. One population reestablished at a high elevation site where the habitat remained moist. The vegetation had changed conspicuously at all sites where the butterflies were extirpated, with climate change being implicated in the drying of the habitats. Given the modest number of known populations, continued attention to the status of the species is warranted.

Additional key words: extirpation, colonization, metapopulation, climate change, succession

Butterfly populations fluctuate in size from year to year because of variability in resources, weather, predators, competitors, and human activities, as well as distinct events such as storms and fires (Ehrlich 1984; Roy et al. 2001; Hanski 2003; Hanski et al. 2004). Small, localized colonies are especially subject to extirpation, and the likelihood of dying out increases with greater fluctuations in population size (Pollard & Yates 1992) and habitat quality (Ehrlich & Murphy 1987; Hanski et al. 2004). Losses have been reported from sudden catastrophic events such as late snowstorms (Ehrlich et al. 1972) as well as longer-term, more gradual habitat modification (Hanski 2003). The current decline in overall biodiversity (Wilson 1999) has heightened attention to the causes and rates of loss of local populations.

Because it lives in small and highly localized populations in open meadows, the checkerspot butterfly *Euphydryas gillettii* Barnes is sensitive to modification of its habitat by succession and changing climate. This butterfly occupies moist meadow patches and fens (Williams 1995; Kondla 2005) in the central and northern Rocky Mountains, ranging from western Wyoming through Montana and Idaho to southwestern Alberta (Williams 1988). The latitudinal range extends from about 42° to over 51° N, with an elevational range of 1100 m. to over 2700 m. *E. gillettii* often occurs in metapopulations in which individual colonies are connected by occasional dispersal, thus enabling colonization and growth of new populations. As with other species of *Euphydryas* (Wahlberg et al. 2002; Singer & Hanski 2004; Wang et al. 2004), however, *E. gillettii* shows limited movement. For example, Boggs et al. (2006) reported average distances between recaptures of *E. gillettii* to be only 44 + 39m for males and 51 + 44m for females. The lack of measurable

allozyme variation that Debinski (1994) found in a comparison of specimens from western Idaho, western Wyoming, and northern Montana likely results from recent, post-glacial separation rather than from gene flow. Populations can expand explosively when conditions are favorable (Boggs et al. 2006), but the rates and causes of extirpation and colonization remain unexplored. Checkerspots form a model system for population studies (Ehrlich & Hanski 2004), and a study of populations of *E. gillettii* over time can enhance our understanding of the biology of this system.

The goals of this study were to describe the factors that lead to population loss or gain. A survey of 15 populations from the early 1980s (Williams 1988) provided the basis for a repeated survey during 2002–2006, and that comparison forms the core of the results reported here. These sites represent the full latitudinal and elevational ranges known for the species. In addition, two populations were surveyed annually most years from 1981 to 2011. My goal was to evaluate how many of these populations still existed 20 years later and to look for change in their habitat characteristics. I expected to find drier meadows if climate change were affecting the habitats and greater vegetative biomass if succession were taking place, but I had no expectation about how many populations would still exist.

MATERIALS AND METHODS

Surveys of *E. gillettii* populations were conducted by counting egg masses around the end of the flight period and using these counts to estimate population sizes. Eggs are laid in clusters on the host shrub *Lonicera involucrata* (Rich.) Banks on leaves that are among the highest and most likely to intercept sunlight (Williams 1981; see Bonebrake et al. 2010 for factors that influence this behavior). The eggs require about three

weeks to hatch (Williams et al. 1984) and form conspicuous feeding webs after hatching, so significant time is available to find and count egg masses (generally, the month of August). Plants other than *L. involucrata* are used only rarely for oviposition (Williams 1990). Following the same procedures, from 2002 to 2006 I repeated the survey that I had conducted from 1982 to 1984 (14 of the original 15 sites); late in the flight period, I revisited the sites where adults or eggs had been observed during 1982–1984 (Williams 1988) and surveyed the core of the habitat of each to count all egg masses and any lingering adults and to record characteristics of the habitat. Habitat patches were

defined as discrete meadows with the host plant *L. involucrata*; descriptions of the sites are given in Williams (1988). For each survey, I examined every host shrub in the entire open area where the butterflies were found, areas that ranged up to 3 ha, and counted every egg mass I could find. In addition, at each site I searched surrounding areas for nearby colonies, going up and down stream or valley up to 1 km in each direction and investigating likely habitats (open, moist meadows) within about 5 km, as indicated on USGS topographic maps.

All 14 sites are in the central and northern Rocky Mountains of North America, including two in the

TABLE 1. Characteristics of 14 *E. gillettii* populations, including seven that died out. The numbering follows the descriptions of these sites in Williams (1988) (site 3 was not resurveyed). Counts of egg masses were from a 30m × 30m core of the habitat. The first letter of the site name refers to the state or province (Wyoming, Montana, Idaho, Alberta), while metapop indicates whether or not there were nearby satellite colonies.

Site No.	Site Name	Lat. (deg)	Elev. (m)	Egg masses (adults) 1980s	Egg masses (adults) 2000s.	Meta-pop	Vegetative change at the site by 2006
1	WBC	44.93	2621	94 (185)	0	yes	denser; larger trees near the stream; open meadow drier
2	WGC	43.37	2164	16 (53)	113 (209)	yes	no perceptible change
4	WTP	43.83	2362	2 (13)	52 (122)	yes	no perceptible change
5	WSC	42.52	2576	4 (20)	0	no	all parts of meadow drier; <i>L. involucrata</i> scarce and over-topped by <i>Salix</i> spp.
6	MMP	48.32	1707	10 (39)	109 (204)	yes	a recently logged area adjacent to an older area filling in by succession
7	MLM	48.53	1494	9 (45)	24 (71)	no	expanded habitat from beaver activity
8	MCC	48.62	1152	21 (65)	0	no	site now dominated by <i>Salix</i> spp. and <i>P. contorta</i>
9	AOR	50.10	1814	22 (59)	7 (30)	yes	no perceptible change
10	WBG	44.93	2713	11 (41)	38 (98) ^a	yes	no perceptible change; many <i>L. involucrata</i> and many nectar sources
11	MSL	47.19	1305	7 (26)	0	no	meadow drier; <i>L. involucrata</i> gone, now dominated by <i>Salix</i> spp.
12	MSC	48.32	1609	3 (14)	3 (14)	no	no perceptible change
13	ARH	49.83	1448	1 (8)	0	no	over-grown by <i>Salix</i> spp.; little nectar available
14	WCV	42.10	1911	1 (8)	0	no	meadow hotter and drier; little <i>L. involucrata</i> left
15	IWL	44.59	1634	25 (73)	0	no	meadow drier; no <i>L. involucrata</i> left

^aThe population at site 10 disappeared in 1992 and then reestablished in 2005

Beartooth Mountains, Wyoming, where I have conducted annual surveys of adults and egg masses most years from 1981 through 2011 (all except 1985, 1997, 2003, 2004). These annual surveys provided the opportunity to record the gradual loss of one Beartooth population (site 1 in Table 1) and the loss and then reappearance of the other Beartooth population (site 10). Plants were identified with Hitchcock & Cronquist (1973).

The number of egg masses enables one to estimate population sizes. During 1981 and 1982, I conducted a mark-release-recapture (MRR) study of the population at site 1, analyzed with the Jolly-Seber method (Jolly 1965; Seber 1982), and this yielded estimates of 298 and 238 adults for those two years (unpublished); the egg mass counts for those years were 165 and 135. A larger regression of population size on egg mass counts was determined by Boggs et al. (2006), who also used MRR analysis to determine population estimates. Their regression was: $\ln N = 2.044 + 0.698 \cdot \ln EC$, where EC is the number of egg clusters. This equation yields estimates of 273 and 237 adults for the Beartooth population in 1981 and 1982, estimates that are remarkably close to the Beartooth MRR results. For this study, I used the Boggs et al. equation to approximate sizes of all populations from egg mass counts.

RESULTS

Colony Loss. The repeated surveys from 2002–2006 for *E. gillettii* two decades after the initial surveys yielded only seven extant populations (50%). The characteristics of all 14 sites are given in Table 1. A conspicuous pattern of these sites apparent in Fig. 1 is that the butterflies disappeared from sites that were characterized by a combination of low elevation and low latitude (sites 8, 11, 14, 15); in particular, a population did not survive if its location were such that $\text{latitude}(\text{deg}) + 10 \cdot \text{elevation}(\text{km}) < 62$. Three additional populations disappeared: one at low latitude (site 5), one at low elevation (site 13), and one other (site 1, considered in detail below).

Sites 8, 11, and 15 had supported substantial colonies in the 1980s (Table 1), so their disappearance was unexpected. The loss from site 15 was particularly surprising because that population had been large and had served as the study population for a previous analysis of host plant usage (Williams 1990) and as the source of egg masses for a colonization study (Williams 1995). Habitat characteristics changed conspicuously at site 15 in the intervening 20 years, however; a survey in 2002 showed that the meadow was much drier than it had been, and no *L. involucrata* host plants remained.

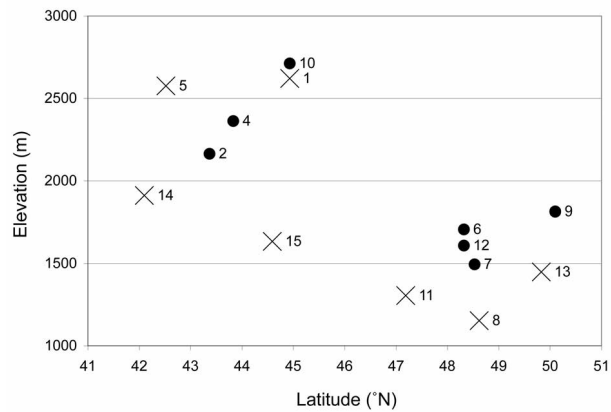


FIG. 1. The fate of 14 populations of *E. gillettii* initially examined during 1982–84 (sites 1–2 and 4–15 from Williams 1988) and then resurveyed in 2002–06. Each population is plotted by its latitude and elevation. When resurveyed, seven had disappeared (marked by an X), while seven continued (marked by solid circles).

In contrast, more than 20 clumps of *L. involucrata* had been present in the core area in 1984. Three other sites (5, 11, and 14) were also conspicuously drier after 2000 than they had been in the 1980s and had fewer nectar sources and a reduced abundance or complete loss of host shrubs.

Annual counts of *E. gillettii* egg masses at site 1 revealed continuous decline from 1980 through 1992 and disappearance in 1993 (Fig. 2) without subsequent recolonization. Mark-release-recapture studies at this site gave adult population sizes of 539 in 1980, 298 in 1981, and 238 in 1982; egg mass surveys in following years showed a decline to extirpation 12 yr later,

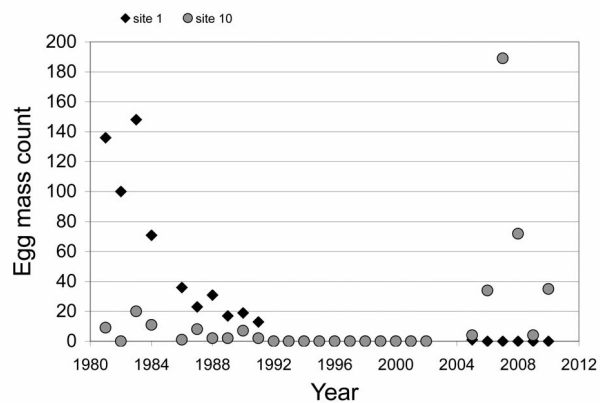


FIG. 2. Annual counts of egg masses late in or after the flight season at site 1 and site 10 through 2011. The counts are from the core area at each site; additional egg masses may have existed outside the core areas. At site 1 the population declined and disappeared by 1992, with a single egg mass seen since (2005). At site 10, the population disappeared from 1992 through 2002 but was present again in 2005; the population then increased greatly, peaking in 2007.

resulting in an average annual growth rate (λ) of 0.823 (s.d. = 0.577, $n = 10$). Loss of this population was confirmed by thorough observation in 1993 and 1994 and by additional yearly observations thereafter (note that the absence in 1992 was not because it was the off year in a biennial life cycle; Williams et al. 1984).

The vegetation at site 1 changed conspicuously over this time (Fig. 3). The *L. involucrata* shrubs that had received the largest numbers of egg masses in the early 1980s were conspicuously smaller than they had been 20 years earlier: 0.7–0.9 m tall in the 1980s and 0.3–0.5 m tall in 2006. In the intervening years, other vegetation, including *Salix* spp. shrubs and graminoids, grew luxuriantly and overtopped many *L. involucrata*, making the host plants less accessible to ovipositing females. Based on fire records of the U.S. Forest Service (C. Dawson, Shoshone National Forest, pers. comm.) and the age of the largest trees in the burned area as determined from cores, site 1 burned extensively in the 1890s. Succession has taken place since then, and open meadows near the stream have filled in with trees, primarily *Pinus contorta* Doug. ex Loud. and *Picea engelmannii* Parry ex Engelm. Small trees observed in 1980 are now larger, and the herbaceous vegetation is taller with fewer nectar sources in the habitat. In the early 1980s, adults nectared most frequently on the abundant *Geranium richardsonii* Fisch. & Trautv. (Geraniaceae) but also on *Agoceris glauca* (Pursh) Raf. and *Senecio* spp. (both Asteraceae). These species are now much less abundant; counts of *G. richardsonii* flowers from photographs of a central 8 m \times 8 m plot yielded 410 in 1980 (24 Jul) and 360 in 1982 (29 Jul) but only 74 in 2010 (31 Jul). The only appearance of *E. gillettii* at this site since its disappearance in 1992 has been a single egg mass found during the annual survey on 28 Jul 2005. Regular egg mass surveys each year at least 200 m up and down stream from the core area have revealed no evidence of the butterflies. These areas provide little usable habitat, and formerly open patches are now more closed in. The population did not move; it simply disappeared.

Metapopulations. Surveys to more than 2 km around all sites revealed the persistence of satellite populations around sites 2, 4, 6, and 9 (the satellites around sites 2, 4, and 9 were small and unnumbered; site 6 had site 12 as a satellite). It is noteworthy that these four sites sustained *E. gillettii* colonies over the 20-yr observation span, whereas no satellite colonies could be found near six of the seven populations that disappeared (the seventh was site 1; its loss through succession is described above). The structure of the metapopulations varied among locales, while no more than four nearby patches were occupied around any of

the known sites, with fewer than 20 egg masses found in any one satellite. Site 2 presents classic metapopulation structure (Levins 1970), with four habitat patches of approximately equal size and abundance, with patches separated by only 0.3 to 0.5 km. Site 9 has a linear structure, with four habitat patches distributed in sequence along a river, with separation distances ranging from 1.0 to 2.4 km. Sites 4 and 6 are best described as having a core-satellite structure, with separation distances of 0.6 and 1.7 km between the larger core and smaller satellite colonies. Surveys around each of these areas revealed no additional colonies.

Reestablishment. The population at site 10, the second location in northwest Wyoming, which is 1.9 km by air from site 1, died out in 1992 but then reestablished in 2005. This site has an abundance of needed resources (Williams 1995), including many large *L. involucrata* host plants and a high density of nectar sources. Up to 11 egg masses (population size 41) were present from 1981, when observations began, until 1991 (Fig. 2), but then *E. gillettii* disappeared from 1992 through 2002, a loss confirmed by yearly surveys. Observations were resumed in 2005, and four egg masses (representing approx. 20 adults) were present that year; in 2006, the numbers had expanded to 38 total egg masses (98 adults), and in 2007 to 189 egg masses (297 adults). The explosion of 2007 was reflected in dense egg clusters on host shrubs and expansion to all parts of the surrounding meadow, from approximately 0.4 ha occupied in previous years to 0.9 ha occupied in 2007. These totals far exceeded the numbers seen in the 1980s. Over the 30-year period of observation, little change in the vegetation took place. This meadow is higher in elevation, moister, and more open than site 1, and that appears to be why the vegetation has not changed as it did at site 1. Trees have not invaded the meadow. The population at this site grew exponentially from 2005 to 2007 ($N = 0.14 e^{1.82}$) but declined afterward (Fig. 2).

DISCUSSION

Population Loss. The repeated survey showed that half of the sites at which *E. gillettii* existed in the early 1980s no longer supported a population 20 years later. Periodic loss of isolated colonies is not surprising, however, because of habitat change, inbreeding (Saccheri 1998), Allee effect (Kuussaari et al. 1998), and chance events; furthermore, small populations may represent only temporary expansions from nearby colonies (Lewis & Hurford 1997). What is surprising is that two of the populations that disappeared were among the largest known of the species in 1980.

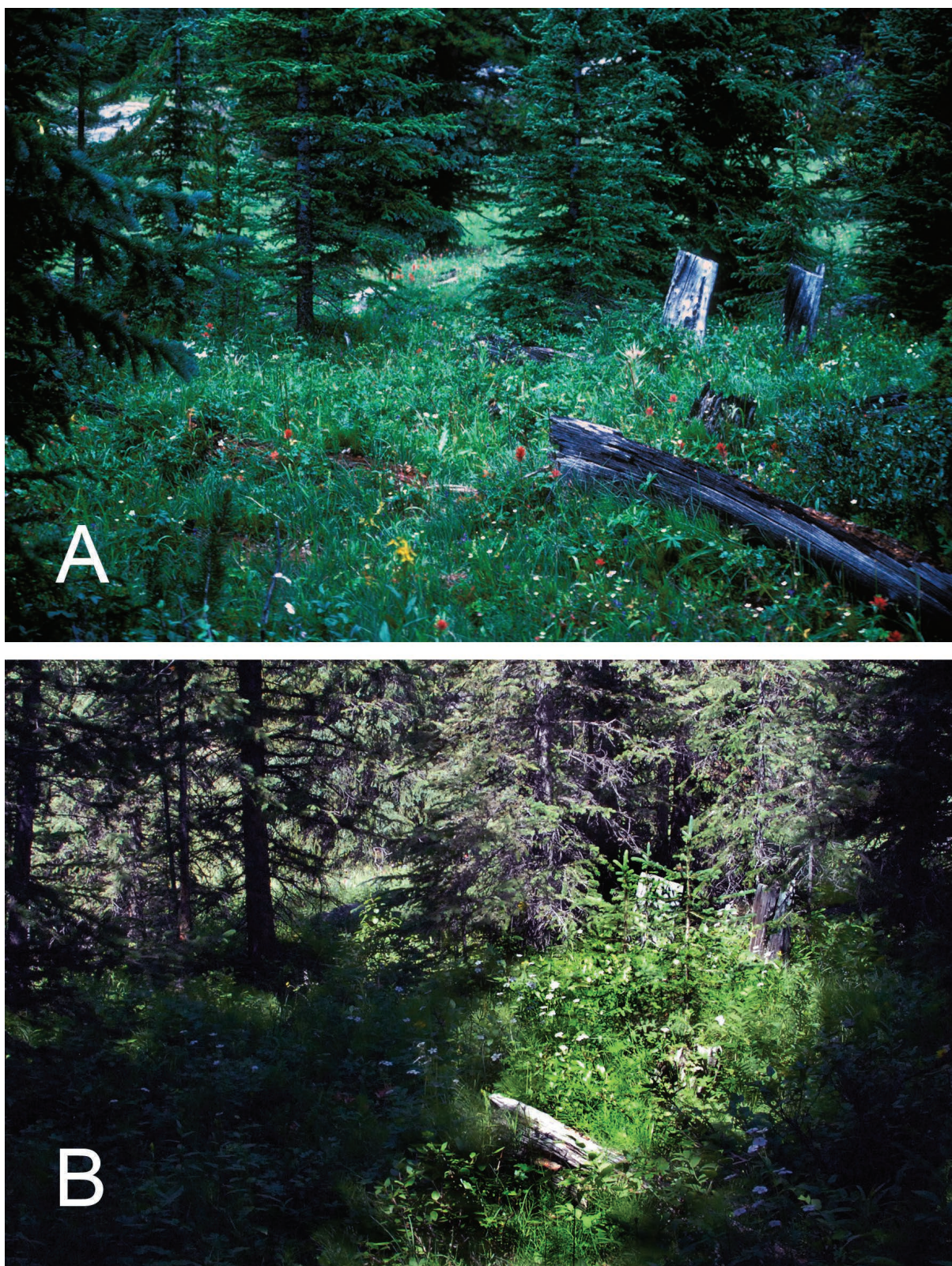


FIG. 3. Views of the same location from the same perspective in the middle of Beartooth site 1 from 29 July 1987 (**A**) and 31 July 2010 (**B**). Note the two stumps to the right. Over time, spruce, herbaceous vegetation, and willows have filled in what had been an open, flower-dominated site.

The disappearance of populations at low latitudes and low elevations, coupled with drying of the habitat and the decline or disappearance of host plants and nectar sources, implicates climate change as a causal agent. The hydrology of the western U.S. has already been altered by climate change (Barnett et al. 2008), leading to shifts in the distribution of plants (Kelly & Gouliden 2008). Data from the NOAA National Climate Data Center illustrate the trend of rising temperatures and increasing frequency of drought (Weather Perspectives 2011). In this study, four sites that had appeared as lush meadows in the early 1980s had become dry meadows by 2004. Based on surveys from 1992 to 1996, Parmesan (1996) reported similar losses in California, with local extinction of *E. editha* populations from historically known sites at low latitudes (70% disappeared) and low elevations. With the losses reported here, the range of *E. gillettii* has contracted and is now, on average, farther north. In 1983, the lowest latitude of a known population was 42.10°N, but by 2005 it was 43.37°N. If new habitat has appeared farther north through climate change and been colonized, it has thus far gone undetected.

Global climate change is known to have affected the distribution and abundance of many organisms (Parmesan & Yohe 2003; Root et al. 2003; Parmesan 2006; Rosenzweig et al. 2008). Populations of some butterfly species have died out (McLaughlin et al. 2002), while the ranges of others have shown reductions in size and shifts upward in latitude and altitude (Dennis 1993; Parmesan 1996, 2003, 2006; Parmesan et al. 1999; Warren et al. 2001; Hill et al. 1999, 2002, 2003; Forister et al. 2010). Insects in general and butterflies in particular are especially sensitive to climate change because of their dependence on multiple resources within their habitats (Dennis et al. 2003) as well as their short generation time and ectothermic physiology (Hill et al. 2003).

Climate change isn't the only factor that alters habitats enough to lead to population loss; monitoring of site 1 showed succession also to be a cause. In 1980 the site 1 population was one of the three largest known of this species (Williams 1988), but by 1992 it had disappeared. The loss of this population highlights the vulnerability of isolated colonies. The population disappeared after succession led to diminished habitat quality, as small trees invaded the moist meadow, and grasses, forbs, and other shrubs displaced or overtopped the host *L. involucrata* and what had been abundant nectar sources. Females alight on the highest parts of their host plants in open, sunlit areas (Williams 1981), so *L. involucrata* may be numerous in shady parts of the habitat but not serve for oviposition. The

influence of succession was already apparent during the 1980s survey, when succession was found to have led to loss of one population (reported in Williams 1988). Climate change can affect rates of succession, too, by altering the frequency of forest fire, which opens up patches of meadow habitat (Gavin et al. 2007), so climate change and succession can interact in altering the vegetation of a site.

Colonization. An already mated dispersing female can begin a new population by leaving a single egg mass in an empty patch of habitat (Williams 1995). An egg mass typically contains about 136 eggs (s.d.=54, n=153) (Williams et al. 1984), and although entire clusters usually survive or disappear as a group, both the number of egg masses and the number of eggs per mass influence the success of colonization. Although the source of the colonizing dispersers remains unknown, the colonization of site 10 reported here took place 10 to 12 years after the population had disappeared. Natural colonizations are rarely recorded because observers do not regularly survey empty habitats. Site 10 offers all the resources needed for *E. gillettii* (Williams 1988), and had, in fact, once supported a population, so it was not surprising that the species could reestablish here. Where all the needed resources were available in Colorado, an intentional introduction of *E. gillettii* has been successful (Holdren & Ehrlich 1981).

Once an egg mass has been laid in a previously unoccupied patch, the resultant colony may grow rapidly but with limited genetic variability. In an earlier study, when a single egg mass was introduced to an empty patch of newly disturbed habitat, exponential growth led from 1 to 7 to 35 egg masses in the successive years 1989 to 1991 (estimated adult population sizes 8 to 92) (Williams 1995). In the current study, population growth at site 10 was equally rapid, from 4 to 38 to 187 egg masses in the successive years 2005 to 2007 (adult populations estimated to be 20 to 98 to 297). These populations grew at similar exponential rates ($e^{1.81}$ and $e^{1.82}$) before subsequent decline. The likelihood is low, however, that a growing population develops from a single egg mass in a new habitat patch; seven of Williams's (1995) eight introductions of single egg masses did not succeed, and the one egg mass found at site 1 in 2005 also failed to establish a new colony.

Dispersal occurs through population explosions as well as through occasional emigrants. Explosive increases in the population density of *E. gillettii* led to dispersal that established new colonies in Colorado (Boggs et al. 2006), just as they have with *E. editha* in its range (Murphy & White 1984). Following the 2002

expansion in Colorado, two new colonies remained after subsequent range contraction (Boggs et al. 2006). In this study, the population explosion of 2007 spread adults and egg masses through a much larger area than the butterflies had occupied previously, and some individuals remained in new areas the following year.

Status. The loss of several populations and re-establishment of one colony between 1982 and 2011 provide evidence of metapopulation dynamics in *E. gillettii*. The metapopulations occur in mountain meadows, where the limited distributions of their host plants and nectar sources, both of which grow more abundantly near streams, restrict their movement. The butterflies fly along riparian corridors, rarely in drier habitat 30m or farther from streamside or wet meadows. Like *E. editha* (Singer & Hanski 2004), *E. gillettii* responds behaviorally to features of the surrounding vegetation, and the forest matrix strongly inhibits butterfly movement (e.g., Ricketts 2001). Outward migration from a population may occur as a result of genetically-based unidirectional flight or as simple (“active”) diffusion beyond the edges of the meadows, a movement that prevailing winds can accentuate (Boggs et al. 2006).

A conspicuous feature of the population structure of *E. gillettii* is how few colonies form each metapopulation, usually with a single larger source pool and one to three nearby smaller colonies. The smaller populations may be in poorer quality patches and function as sinks (Pulliam 1988; Dias 1996) or as pseudo-sinks (Boughton 1999) that sometimes endure without immigration. This structure is on a dramatically smaller scale than that of the well-studied checkerspot *Melitaea cinxia*, as described by Hanski et al. (1995), who reported 1502 habitat patches, of which 536 were occupied at one time. The structure is also far more limited than that of its congener *E. editha*, for which many patches are occupied by hundreds of butterflies each (Harrison et al. 1988). The metapopulation structure of *E. gillettii* at the known sites reflects the response of the butterflies to the topological complexity of mountain landscapes and the unpredictable occurrence of disturbance, which creates habitat patches of varying form and orientation. Metapopulations have received extensive study in the last 20 years (e.g., Hanski & Gilpin 1997; Hanski 1999; Ehrlich & Hanski 2004), and that focus is warranted; all surviving populations found in this study were near one or more satellite sites, whereas most of those that died out were isolated.

The distribution of *E. gillettii* is limited, and it is considered imperiled in Montana, Alberta, and British Columbia (insects are not yet ranked in Wyoming or

Idaho; NatureServe 2010). The distribution of the species appears to be a relic from the last glaciation given that its closest relatives are Eurasian (Zimmerman et al. 2000). Furthermore, since 1980 more populations have disappeared than have been discovered (unpubl. data). An added problem is that loss of populations of an uncommon species can occur after a time lag, producing an “extinction debt” (Bulman et al. 2007), which occurs when the abundance of a population is below the equilibrium needed for long-term viability. Dispersal of *E. gillettii* occurs at low rates; its closest relative, *E. maturna*, is the species that moved the shortest distances of five species of checkerspot butterflies studied for movement patterns (Wahlberg et al. 2002). Climate change is altering vegetation at the landscape scale (Romme & Turner 1991; Debinski et al. 2006), and drought produced by warming leads to decreased forbs in *E. gillettii*'s habitat (Debinski et al. 2010). As Boggs and Murphy (1997) emphasized, butterflies like *E. gillettii* that are both montane in distribution and sedentary in behavior are at greater risk in a changing climate because of the fragmented nature of their habitat.

Both the range and abundance of *E. gillettii* have been dynamic over the past three decades. Monitoring is difficult, however, because the species occurs in mountainous regions where access is limited. In contrast to the decline in the number of known colonies, favorable characteristics of the species are that single populations can reach substantial densities (50 or more individuals seen during a single day in a habitat patch of one-half hectare), and populations are found through a wide elevational range (1100m to 2800m), even though the resource needs are specific and moist montane meadows are the most common habitat (Williams 1988). New habitat forms through disturbance, primarily by fire, but also by beaver activity, avalanches, storms, and logging, while a dispersing female may, by ovipositing a single egg mass, initiate a new colony in newly disturbed habitat (Williams 1995). Fire, in particular, is a regular disturbance within the range of *E. gillettii* (Romme 1982). The quality of habitat patches is critical for long-term survival of butterfly populations (Thomas et al. 2001; Wahlberg et al. 2002; Thomas et al. 2008), but habitats are dynamic, with both succession and climate change altering the vegetation. The broad effects of climate change (Parmesan 2006) coupled with *E. gillettii*'s limited habitat (Williams 1988) and the fact that fewer sites with *E. gillettii* are known now than was the case in the 1970s suggest continuing concern for the long-term future of the species and a need for continued monitoring.

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