

Delayed population explosion of an introduced butterfly

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Summary

1. The causes of lagged population and geographical range expansions after species introductions are poorly understood, and there are relatively few detailed case studies.
2. We document the 29-year history of population dynamics and structure for a population of *Euphydryas gillettii* Barnes that was introduced to the Colorado Rocky Mountains, USA in 1977.
3. The population size remained low (< 200 individuals) and confined to a single habitat patch (~2.25 ha) to 1998. These values are similar to those of many other populations within the natural geographical range of the species.
4. However, by 2002 the population increased dramatically to > 3000 individuals and covered ~70 ha, nearly all to the south of the original site. The direction of population expansion was the same as that of predominant winds.
5. By 2004, the butterfly's local distribution had retracted mainly to three habitat patches. It thus exhibited a 'surge/contraction' form of population growth. Searches within 15 km of the original site yielded no other new populations.
6. In 2005, butterfly numbers crashed, but all three habitat patches remained occupied. The populations within each patch did not decrease in the same proportions, suggesting independent dynamics that are characteristic of metapopulations.
7. We postulate that this behaviour results, in this species, in establishment of satellite populations and, given appropriate habitat structure, may result in lagged or punctuated expansions of introduced populations.

Key-words: dispersal, *Euphydryas*, invasion dynamics, Nymphalidae, population structure.

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Introduction

Introduced species suffer one of several fates: extinction; immediate population and geographical expansion; or stasis followed possibly by expansion (reviewed in Sakai *et al.* 2001). The factors determining what occurs and what allows successful invasion remain

poorly understood (e.g. Ehrlich 1989; Sakai *et al.* 2001). Stasis/expansion presents the largest problem for identification of invasion status, and is attributed generally to lag effects in the population dynamics (reviewed in Crooks & Soulé 1999). These can be due to a need for multiple infusions of propagules (e.g. Wing 1943), slow growth or Allee effects at low population sizes (e.g. Lewis & Kareiva 1993; Grevstad 1999; Memmott *et al.* 2005), changes in habitat structure allowing expansion (e.g. Lonsdale 1993; Essink & Dekker 2002; Rilov, Benayahu & Gasith 2004), invasion of a critical mutualist (e.g. Parker 2001) or hybridization (reviewed in Ellstrand & Schierenbeck 2000) or other genetic change (Thomas *et al.* 2001). However, stasis/expansion patterns could also occur in species that normally exhibit episodic outbreaks, such as ungulates (Caughley 1970) or forest pest insects (Myers 1998).

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The traditionally envisioned pattern of geographical range expansion is a travelling wave converging on a constant rate of expansion across space, defined by a combination of the dispersal parameters and the population growth rate of the organism (e.g. Neubert & Parker 2004). Modelled expansion speeds differ between scenarios with constant environments and with periodic or stochastic environments affecting the dispersal and/or population growth parameters (Neubert, Kot & Lewis 2000b; Neubert & Parker 2004). In periodically fluctuating environments spread may not be constant, but rather the organism may invade new areas in one generation and retreat the next generation in a 'surge/contraction' pattern, depending on model parameters (Neubert *et al.* 2000b). Further, in both constant and variable environments, the shape of the dispersal kernel (distribution of movement distances) influences whether the population's expansion rate converges to a constant rate. If there is an excess of long-distance dispersers, the expansion rate may accelerate with time (Kot, Lewis & Van den Driessche 1996; Neubert & Caswell 2000a; Neubert *et al.* 2000b). In the extreme, populations experiencing episodic outbreaks have large fluctuations in both their demographic and dispersal parameters and potentially also in the shape of the dispersal kernel. Such populations may exhibit outward migration from what is, in effect, a temporary source population, resulting in temporally and/or geographically staggered pulses of expansion surges across a landscape. Depending on the details of variation in demographic and dispersal parameters, these expansion surges may result in the establishment of new viable populations and permanent range expansion. Alternatively, the surges may be followed by total or partial contraction of populations to the original geographical distribution in a pulsed surge/contraction pattern. This alternative scenario may also be responsible for the establishment of satellite populations around an original core population.

These alternative scenarios will determine the rate and pattern of range expansions. Understanding these patterns is a precursor to insight into the processes associated with successful catastrophic invasions. Such patterns may also elucidate the dynamics of range expansions unaided by humans, via establishment of new populations.

Here we document the 29-year history of the population size and structure of an introduced population of the butterfly *Euphydryas gillettii* (Barnes) (Nymphalidae) in Colorado, USA. This population, located in the southern Rocky Mountains, lies to the south of the butterfly's natural range, which extends from Wyoming north to southern Alberta. A large number of propagules was introduced intentionally into habitat that matched the habitat of the donor population as closely as possible (Holdren & Ehrlich 1981), yielding maximal chances for population establishment and expansion. Here we report that the introduced population remained small for about 2.5 decades, expanding recently by

more than an order of magnitude and then contracting. Placed in the context of our current understanding of invasion biology, this relatively detailed case study illuminates both invasion dynamics over an intermediate time-scale of decades and patterns associated with range expansion from suitable habitat.

Materials and methods

STUDY SITE AND INSECTS

The study population is located at Gothic, Gunnison County, Colorado, USA [38°57'5" N, 106°59'6" W, 2912 m above sea level (asl)] (Fig. 1). The introduction site, referred to hereafter as the origin patch, is an east–north-east sloping area of ~2.25 ha at the base of an avalanche run-out zone on Gothic mountain, with small streams and active beaver ponds (Holdren & Ehrlich 1981). Beaver and avalanche activity are disturbances that help maintain the habitat, which reverts otherwise to tall willows and/or spruce forest with time. The origin patch is a meadow with clumped spruce [*Picea engelmannii* Parry ex Engelm. (Pinaceae)], willow [*Salix* spp. (Salicaceae)], bog birch [*Betula glandulosa* Michx. (Corylaceae)], abundant larval host plants [primarily *Lonicera involucrata* Banks ex Spreng. (Caprifoliaceae), but also *Valeriana occidentalis* Heller (Valerianaceae)] and adult nectar plants [e.g. *Senecio triangularis* Hook., *Erigeron* spp. (Compositae) and *Heracleum lanatum* Michx. (Umbelliferae)]. Casual observations in this patch indicate increases in height of spruce and height and coverage of willows, and decreases in channelization of some streams over the course of the 29-year study.

Two other habitat patches, Barclay (~0.6 ha) and avalanche (0.3 ha), lie 400 m and 565 m, respectively, to the south-east of the centre of the origin patch, downstream along the East River. These patches were initially unoccupied. Both are on east–south-east sloping areas at the base of avalanche run-out zones, and contain small streams and active beaver ponds. Barclay is the steepest site of the three and contains abundant willows and old avalanche debris, along with larval host plants and adult nectar plants. Avalanche is the most open patch with most vegetation under 0.5 m, except for scattered spruce and a boundary of willows > 1 m tall.

Euphydryas gillettii is univoltine, flying for 3–4 weeks in late June–late July. Males locate female mates either by searching or by perching on tall spruce or willow (Kulahci & Boggs in preparation). Females lay eggs in clusters on the underside of the host plant leaves near the top of the plant, exposed to morning sun (Williams 1981; Carrillo & Boggs in preparation). Pre-diapause larvae spin webs that incorporate sequentially more basal leaves as they are eaten. Larvae generally diapause over the winter in the 4th instar, and have been reported to diapause as early as the 2nd instar elsewhere (Williams, Holdren & Ehrlich 1984).



Fig. 1. Topographic relief map of the study area in Gunnison County, Colorado, USA. The three habitat patches, origin, Barclay and avalanche, are marked.

Post-diapause larvae feed individually after snow melt and pupate near the host plant.

POPULATION SIZE ESTIMATION

Population estimates were carried out using a combination of mark–release–recapture (mrr) of adults and counting of egg clusters and/or larval webs. Due to the length of the study and fluctuating opportunities to spend time monitoring the population, methods used to estimate population size varied among years. We attempted mrr on adults each summer from 1978 to 1989, and again from 2002 to 2005. Butterflies were captured and a number marked on the wings. The butterfly's number, subsite of capture (for 1984–89, 2003–05), sex and wing wear (on a scale of 1–3: a surrogate for age) were recorded, and the butterfly was released at a central point within the subsite. Subsites used for movement analysis were located in the origin patch only (Fig. 2). Marking was carried out at intervals ranging from every day to once a week throughout the adult flight season, except in 2002, when two sets of 2-day marking sessions were conducted, 10 days apart from each other.

We estimated population sizes in the origin patch for adult females and males separately in years with sufficient recaptures and frequency of marking (1981–86, 2003–05). We used the Jolly–Seber (Jolly 1965; Seber 1982) algorithm to estimate daily population sizes from mrr data, then interpolated daily population sizes for days on which mrr was not performed. The estimated total population size for each sex is the sum of all daily population sizes multiplied by $(1 - \phi)$, where ϕ is

the daily survivorship rate. We used a recapture–decay procedure to estimate ϕ (Watt *et al.* 1977), except for females in 1981 and 1983, when we used Scott's average ϕ (Scott 1973; Watt *et al.* 1977). This was performed because the recapture–decay estimates of ϕ for females were very low in these years, considerably lower than that of males, and because Scott's average ϕ is somewhat less sensitive to gaps in sampling (Watt *et al.* 1977). The total population size is then the sum of that for males and females. The 1980s data meet the Jolly–Seber assumption of a closed population. For 2003 and 2004 there was < 2.5% movement into the origin patch based on recapture records. No movement among patches was detected in 2005.

The population size in the origin patch in 2002 was determined by using two Lincoln indices to estimate population size at two time-points 10 days apart. These daily estimates were then compared with daily and total estimates for other years with longer-run mrr, and total population size was inferred.

In some years, egg cluster or larval web counts are more reliable than adult population estimates, because mrr was performed on an infrequent basis or not at all (1989, 1998) or few to no adults were seen (1978–80, 1987–89). We marked and counted egg clusters and/or larval webs in the origin patch in 1978–89 and counted them in mid-August 1998 and in 2002, 2004 and 2005. We also counted egg clusters in the Barclay patch in 2003, in the avalanche patch in 2004 and in both of those patches in 2005. In all years except 1998, egg cluster counts were performed throughout the season. In 1998, counts are based on 1.5-h search time on each of

2 consecutive days. We then regressed the number of egg clusters or webs on number of adults in years when good estimates were available for both adults and eggs (1981–86) and used that regression to estimate number of adults in years with unreliable adult mrr data, and in the Barclay and avalanche sites. We used a natural log transformation of number of egg clusters and number of adults to achieve normality prior to regression.

Finally, we visited the origin site in mid-flight season on 1 day in 1990–93, to assess whether the population was still extant.

POPULATION STRUCTURE AND LOCAL GEOGRAPHICAL DISTRIBUTION

We calculated adult movement distances for 1984, 1985, 2003 and 2004 based on subsite capture/recapture data gathered in the course of estimating adult population size in the origin patch. In each of these years, we recaptured more than 20 individuals. Distances were measured between subsite centres. In 2003–04, subsite mapping was carried out using Trimble global positioning system (GPS) units, with an accuracy of ± 3 m (Fig. 2). Origin patch subsites used in the 1980s were taken from maps drawn in the 1980s that incorporated local landmarks. Subsites 1, 2, 4, 6 and 8 are identical among all years; subsites numbered 3, 5 and 7 in 2002–04 were treated as one subsite in the 1980s.

To examine movement propensity within the origin patch only, we divided the total distance moved by an individual across all its recaptures by the number of recapture events. Because the resulting individual distances per recapture event were not normally distributed, we used Kolmogorov–Smirnov two-sample tests to examine differences among years and sexes. Differences in the intensity of the recapture effort, which might influence measured distances, were examined by testing for differences among years and sexes in the number of days between recaptures and the number of recaptures per individual, again using Kolmogorov–Smirnov two-sample tests.

Differences in movement propensity may have been influenced by weather conditions or population size. The closest weather station to the site did not start operating until 1989 (see below); therefore, we used data from the National Weather Service Cooperative Network Station at Crested Butte, Colorado, 12 km from the site ($38^{\circ}52' N$, $106^{\circ}58' W$, 2726 m asl). Adult flight occurs predominantly in July. Hence we regressed total July precipitation or mean maximum temperature on distance moved per recapture.

Areas surrounding the origin patch were searched annually from 1978 to at least 1987 for egg masses or larval webs. During these years, the search was concentrated in areas along the East River to the south and north of the origin patch (see Fig. 1).



Fig. 2. Aerial photograph showing origin patch subsites used in butterfly mark–release–recapture studies in 2003–05. Subsites 3, 5 and 7 were combined into one subsite for mark–release–recapture work in 1978–89; all other subsites were the same in all years. Dark patches in subsites 1 and 3 are beaver ponds.

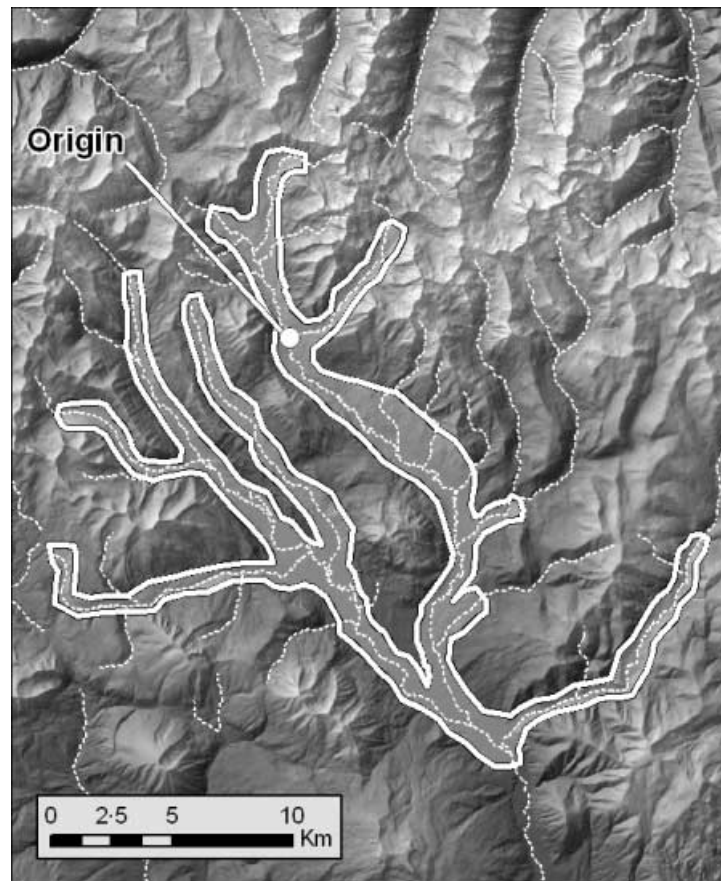


Fig. 3. Topographic relief map of the region surrounding the study area. Shaded areas outlined in white indicate river valleys searched in the 2000s for new *Euphydryas gillettii* populations. The origin patch is marked for reference.

In 2002–05 all butterflies caught outside the origin patch, whether in the course of mrr or as incidental encounters, were marked and released. Locations of adult capture or of egg masses found outside the three habitat patches in 2002–05 were located on an aerial photograph. Additionally, we searched a broader area (Fig. 3) for new populations in 2002–05, including the area surrounding a second (failed) introduction at Pioneer Resort in 1979 (Holdren *et al.* 1981). Areas searched included possible habitat, defined as exposed to morning sun, wet, containing larval host plants and adult nectar plants, and below 3200 m asl (Williams 1981; Williams 1988; Bonebrake & Boggs in preparation).

To test whether the geographical direction of the population expansion followed the prevailing wind direction, we used wind data from an EPA CASTNET weather station located at Gothic (<http://www.epa.gov/castnet/metdata.html>), 800 m from the origin patch and 500 m from the avalanche patch. Continuous data from this site are recorded on hourly intervals. We used data from 9 : 00–16 : 00 MST, 15 June–24 July 2002, which covers the adult flight period. Histograms of hourly wind direction were used to split wind direction into categories based on count frequencies. We examined differences in hourly wind speed among these categories using an analysis of variance (ANOVA).

Results

POPULATION SIZE

Adult population size (n) showed a significant positive relationship with number of egg clusters (EC) in the origin site ($\ln N = 2.044 + 0.698 * \ln EC$, $F_{1,4} = 19.42$, $P = 0.01$, $r^2 = 0.83$). This equation was used to estimate population size in years prior to 2002 with inadequate or no adult mark–release, and to estimate population sizes in the avalanche and Barclay patches.

Yearly changes in population size for the origin patch are shown in Fig. 4. The number of egg clusters released was demographically equivalent to a founding population of 169 individuals, although those eggs came from roughly 40 females, which laid eggs in the laboratory (Holdren *et al.* 1981). The population went through a bottleneck in 1979, when five egg clusters but no adults were seen (Holdren *et al.* 1981). We can now estimate that the bottleneck population size was 24 individuals, based on the number of egg clusters. The population recovered in the early 1980s, shrinking again in the late 1980s. Few adults were seen during a partial day visual survey in each of 1990 and 1991, and only one adult was marked in the patch in the partial day spent catching in each of 1992 and 1993. This

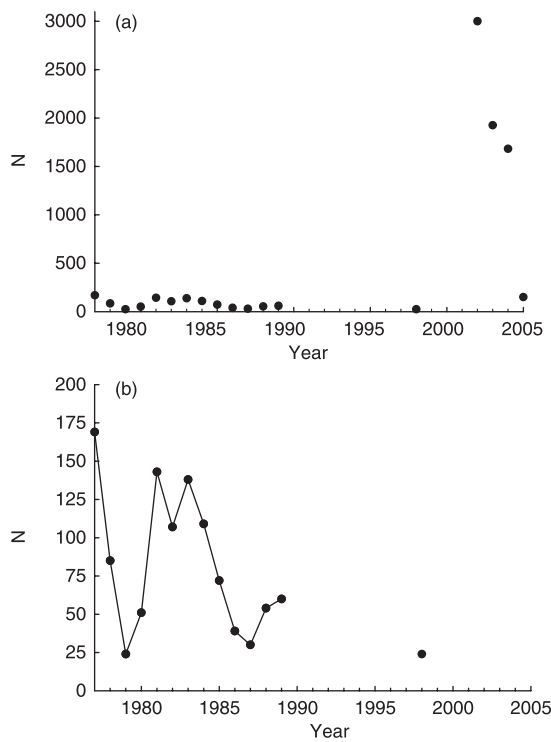


Fig. 4. (a) Adult population trajectory with time in the origin patch. The population size in 1990–93 was low, but values were not determined. (b) Expansion of the graph for 1977–2000.

suggests that the population was not notably larger or smaller than during the 1980s. The egg cluster survey in 1998 gave an estimated population size of 24, suggesting another bottleneck.

The mean annual adult population size (\pm SD) from 1978 to 1998 was $72 (\pm 41)$. By 2002, however, the population exploded, with an estimated 3000 adults in the origin patch, and remained above 1500 adults in this area in 2003 and 2004. In 2005, the population in the origin patch crashed to 150 adults.

In 2002–05, the population also expanded south to include two other habitat patches, Barclay and avalanche (Fig. 1). Adult densities in these two newly occupied patches were about half that of the origin patch in 2003 and 2004, based on extrapolations from egg cluster counts (2003: origin 851 adults/ha, Barclay 274 adults/ha; 2004: origin 743 adults/ha, avalanche

343 adults/ha). The decline in population densities observed in 2005 was not uniform across patches, with the avalanche patch retaining a higher density of adults (2005: origin 67 adults/ha, Barclay 13 adults/ha, avalanche 153 adults/ha). These data suggest independent population fluctuations among the patches, which is characteristic of metapopulations.

POPULATION STRUCTURE: DISPERSAL WITHIN THE ORIGIN PATCH

Dispersal distance per recapture within the origin patch did not vary between the sexes (Table 1; K–S, $P = 0.67$). However, the distance was greater in 2003 and 2004 (after the population outbreak) than in 1984 and 1985 (before the population outbreak) (Table 1; $P < 0.001$ for 1984 + 1985 vs. 2003 + 2004; pairwise comparisons show the same pattern). This difference pre- and post-population outbreak cannot be explained by differences in the total number of recaptures per individual. That number did not differ among years, except that it was significantly lower in 2003 than in 2004 (K–S, $P = 0.006$). Additionally, the pattern of differences among years in the mean number of days between recaptures did not break down to pre- and post-population outbreak, as the values for 2003 were not different from those for 1985 (K–S, $P = 0.10$).

Dispersal distance per recapture within the origin patch was not significantly affected by mean maximum July temperature ($F_{1,2} = 0.91$, NS). However, movement increased significantly with decreasing total July rainfall, even when total population size was included in the regression (rainfall coefficient = -16.14 , $t = -20.9$, $P = 0.03$; regression $F_{2,1} = 2427$, $P = 0.01$). This suggests that time available for flight influenced movement within the origin patch.

POPULATION STRUCTURE: CHANGES IN LOCAL GEOGRAPHICAL DISTRIBUTION

Euphydryas gillettii adults were caught outside the origin patch only once between 1978 and 1980 (Holdren *et al.* 1981) and never between 1981 and 1989. No egg masses or larval webs were found during searches outside the origin patch during this time, with the sole exception of an egg cluster found 165 m downstream

Table 1. Dispersal distance (in metres) per recapture event within the origin patch. Data are means \pm standard deviation, with sample size in parentheses

Sex	Year				
	1984	1985	2003	2004	All
Male	21.4 \pm 25.7 (20)	14.0 \pm 22.6 (12)	48.2 \pm 44.2 (34)	54.0 \pm 36.8 (68)	44.1 \pm 39.0 (134)
Female	11.7 \pm 20.7 (11)	48.8 \pm 57.0 (11)	62.8 \pm 50.3 (44)	49.8 \pm 38.4 (88)	50.7 \pm 44.3 (154)
Both	18.0 \pm 26.4 (31)	30.6 \pm 45.2 (23)	56.5 \pm 48.0 (78)	51.6 \pm 37.6 (156)	

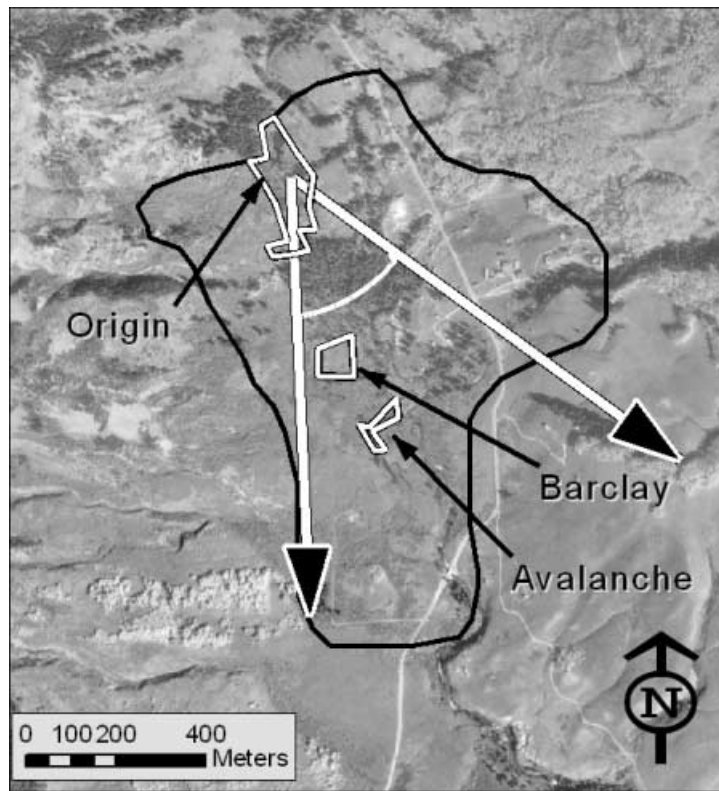


Fig. 5. Aerial photograph with the primary area occupied by the expanding *Euphydryas gillettii* population in 2002 outlined in black. The predominant wind direction (Table 2) is indicated between the two arrows.

Table 2. Wind direction hourly counts and hourly speed. Direction is in degrees, and is the direction from which the wind is blowing. Wind speed is mean hourly speed \pm standard error. With the exception of categories 1 and 2, all pairs of wind speed are significantly different at $P = 0.03$ or better (*post-hoc* Bonferoni pairwise comparisons; see text)

	Wind direction category			
	1	2	3	4
Degrees	15–90	90–150	150–300	300–15
Counts	18	84	52	122
Speed (m/s)	2.21 \pm 0.23	1.66 \pm 0.11	1.19 \pm 0.14	3.07 \pm 0.09

(south-east) from the edge of the origin site in 1 year. Additionally, in the course of fieldwork on other projects in the vicinity of the origin patch during the 1990s, neither Ehrlich nor Boggs saw adult *E. gillettii*, egg masses or larval webs.

As defined by presence of egg masses or larval webs, the local geographical distribution of the population expanded 30-fold, from 2.26 ha in the 1980s to 70.4 ha in 2002 (Fig. 5), concurrent with the population size explosion. The furthest adult capture event was 6.5 km south-east of the origin patch and was a female who, after release, continued moving south-east away from the origin patch. However, searches in 2002–05 of possible habitat have not yet yielded any disjunct populations of *E. gillettii* within the areas shown in Fig. 3.

Although *E. gillettii* was spread over a broad area in 2002, locations in which adults were captured contracted towards the three habitat patches in 2003–05 (Fig. 5). The number of larval webs found in areas to

the north, east or south of the origin, Barclay and avalanche patches also decreased (91, 13, 5 and 1 in 2002, 2003, 2004 and 2005, respectively), and anecdotal evidence suggests that the same pattern occurred on the west side of the origin patch (upslope along Gothic Mountain) (CLB, TCB, IGK personal observations). These data indicate an initial generalized expansion, followed by a retreat into more suitable habitat.

Counts of mean hourly wind direction allowed us to define categories of wind direction, with winds down-valley from north to south predominant (Table 2). Mean hourly wind speed differed among these direction categories (Table 2; $F_{3,272} = 59.5$, $P < 0.001$). The predominant wind direction had a greater speed than that of other wind directions (Table 2).

The two newly colonized habitat patches lie within the 20° arc describing the predominant wind direction out of the origin patch (Fig. 5). Additionally, only one egg mass and no adults were found during searches

Table 3. For origin and avalanche patches, proportion of recaptured individuals within a patch that originated in the alternative patch and resulting Nm. Population size estimation is based on mark–release–recapture in the origin patch, and on number of larval webs in the avalanche patch in 2004. No reliable population size estimate is available for the avalanche patch in 2003

Sex	Year			
	2003		2004	
	To origin	To avalanche	To origin	To avalanche
Male	0/36 (0.0%)	0/3 (0%)	0/68 (0%)	1/5 (20.0%)
Female	1/44 (2.3%)	2/14 (14.2%)	2/90 (2.2%)	0/9 (0.0%)
Nm	22		21	8

north of the origin patch in 2002, and none were found in 2003–05.

POPULATION STRUCTURE: DISPERSAL AMONG PATCHES

Dispersal in 2003 and 2004 between the two furthest patches, origin and avalanche, ranged from 0 to 2.3% of recaptures in the origin patch coming from avalanche and 0–20% of recaptures in the avalanche patch coming from origin, among sexes and years (Table 3). The overall proportion of recaptured individuals that moved between patches was not significantly different among sexes ($\chi^2 = 0.974$, 1 d.f., NS) or years ($\chi^2 = 0.042$, 1 d.f., NS). There was no directionality of movement among patches for recaptured individuals. Two individuals moved from the origin to the avalanche patch, two moved from avalanche to origin and one moved from the origin to avalanche patch and back to the origin patch. These dispersal frequencies translate to an estimated Nm (effective population size times the proportion of the population migrating) greater than 1 (Table 3) for each patch, indicating that the patches are linked genetically at least at large population sizes.

Discussion

The introduced population of *Euphydryas gillettii* maintained a relatively small and localized population for at least 21 (and probably 25 or 26) years, before increasing by more than an order of magnitude in numbers of individuals and 30-fold in local geographical distribution and then crashing abruptly. The population size observed at Gothic in 2002–04 is large in comparison with many known native *E. gillettii* populations. For example, Williams (1988) records only four of 15 surveyed populations within the native range as having greater than 30 individuals.

The results here contrast with those of Williams (1995), who conducted introduction experiments with *E. gillettii* within the species' range in the Greater Yellowstone Ecosystem after the Yellowstone fires in 1988. He evaluated the likelihood that a single egg cluster could result in colony establishment in newly disturbed habitat. Of eight suitable habitat patches (four burned

and four open), a population established at only one site (a burned site). This population expanded within 2 years to ~35 egg clusters (Fig. 2 in Williams 1995), which is in the range of that observed in Colorado during the 1980s. The population also expanded along a stream, occupying an area of about 1.5 ha (based on Fig. 1 in Williams 1995), yielding population densities similar to those seen in Colorado during the 1980s. The fates of the experimental Yellowstone and Colorado colonies differed, however. The Yellowstone colony's population size dropped in the third year and went extinct in the fourth year, due probably to flooding that destroyed particular host plants favoured for oviposition (Williams 1995).

POTENTIAL CAUSES OF THE POPULATION EXPLOSION

The causes of the Colorado population outbreak remain to be determined, but several hypotheses are plausible which are not mutually exclusive. First, the outbreak occurred after several years of dry winter weather with low avalanche activity and early snow-melt dates, which began in 1999 (W. Barr, unpublished snowfall and avalanche data for Gothic). Such conditions might increase larval over-winter survival and/or the time available to larvae to feed prior to diapause. A second possibility is evolutionary change in the Colorado population. Over ~25 generations, selection may have operated on traits that allow greater survival or higher fecundity in the new habitat. A third possibility is that the habitat quality or structure changed since the introduction, reaching a threshold quality that allowed the population outbreak. However, casual observations suggest that nectar or host plant availability have not improved dramatically over this time period. Finally, non-linear population dynamics resulting from an interaction with generalist pupal parasitoids could have played a role in the butterfly's population dynamics (e.g. Blarer & Doebeli 1999).

IMPLICATIONS FOR POPULATION STRUCTURE

The increase in the area covered by the expanding *E. gillettii* population was remarkable for its directionality.

Patches to the south of the origin patch were colonized and almost no adults or egg masses were discovered to the north, despite repeated searches. Because at least a few suitable habitat patches occur north of the origin patch, we did not expect the strong southerly bias in distribution of adults and egg masses. However, this bias was in the direction of the prevailing winds, which may have a strong influence on movement direction, given the generally sedentary nature of the butterfly and indeed of other members of the genus (Ehrlich & Hanski 2004).

Nonetheless, movement between patches in 2003 and 2004 was not directional, at least with the small sample sizes observed. This suggests that prevailing winds may not explain fully the expansion's southerly bias, but that some aspect of the habitat to the north may be a barrier to movement or some aspect of the habitat to the south may serve as a corridor.

Given that checkerspots as a group include classic examples of different types of metapopulation structure (Ehrlich & Hanski 2004), the question arises as to whether we have observed the birth of a metapopulation or whether the Colorado *E. gillettii* simply are now a larger, patchy population. Based on movement patterns the patches are linked genetically, at least at the population sizes seen from 2002 to 2004. The population decline of 2005 was not synchronous in intensity among patches, however. Dynamics in patches in equally close proximity were also correlated poorly for *E. editha* Boisduval at Jasper Ridge, Stanford University, San Mateo County, California (Ehrlich & Mason 1966; Hellmann *et al.* 2003). In that case, the independence was due to differences among patches in topography, which differentially mediated effects of climate on population dynamics. In the present case, differences in hydrology or disturbance regimes (e.g. avalanche frequency or beaver activity) contribute most probably to differences in patch dynamics.

Nonetheless, the 'surge/contraction' form of population expansion observed in 2002–05 suggests that exchange among subpopulations within a metapopulation, or colonization of empty patches, does not always occur as a continuous process. Rather, in species such as this, colonization probabilities vary due to changes in demographic and/or dispersal parameters over time and/or space. Both genetic structure and patch occupancy patterns would be affected. In cases of large numbers of subpopulations within a metapopulation, the effect of variation in demographic or dispersal parameters may be detectable only if that variation is correlated temporally among sets of subpopulations. However, in populations with a core-satellite structure, the effect of such variation on observed occupancy patterns and genetic structure, and on longer-term extinction probabilities, may be more dramatic.

Finally, this work again indicates the great value of long-term experiments and monitoring, even if not pursued intensively (Ehrlich, Hanski & Boggs 2004).

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References

- Blarer, A. & Doebeli, M. (1999) Resonance effects and outbreaks in ecological time series. *Ecology Letters*, **2**, 167–177.
- Caughley, G. (1970) Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology*, **51**, 53–70.
- Crooks, J.A. & Soulé, M.E. (1999) Lag times in population explosions of invasive species: causes and implications. *Invasive Species and Biodiversity Management* (eds O.T. Sandlund, S.J. Schei & A. Vikens), pp. 103–125. Kluwer Academic Publishers, the Netherlands.
- Ehrlich, P.R. (1989) Attributes of invaders and the invading processes: vertebrates. *Biological Invasions: a Global Perspective* (eds J.A. Drake, H.A. Mooney, F.D. Castri, R.H. Groves, F.J. Kruger, M. Rejmnek & M. Williamson), pp. 315–328. Wiley, Chichester.
- Ehrlich, P.R. & Hanski, I., eds. (2004) *On the Wings of Checkerspots: a Model System for Population Biology*. Oxford University Press, Oxford, UK.
- Ehrlich, P.R., Hanski, I. & Boggs, C.L. (2004) What have we learned? *On the Wings of Checkerspots: a Model System for Population Biology* (eds P.R. Ehrlich & I. Hanski), pp. 288–300. Oxford University Press, Oxford, UK.
- Ehrlich, P.R. & Mason, L.G. (1966) The population biology of the butterfly *Euphydryas editha*. III. Selection and the phenetics of the Jasper Ridge colony. *Evolution*, **20**, 165–173.
- Ellstrand, N.C. & Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences*, **97**, 7043–7050.
- Essink, K. & Dekker, R. (2002) General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetous worm. *Biological Invasions*, **4**, 359–368.
- Grevstad, F.S. (1999) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biological Invasions*, **1**, 313–323.
- Hellmann, J.J., Weiss, S.B., McLaughlin, J.F., Boggs, C.L., Ehrlich, P.R., Launer, A.E. & Murphy, D.D. (2003) Do hypotheses from short-term studies hold in the long-term? An empirical test. *Ecological Entomology*, **28**, 74–84.
- Holdren, C.E. & Ehrlich, P.R. (1981) Long range dispersal in checkerspot butterflies: transplant experiments with *Euphydryas gillettii*. *Oecologia*, **50**, 125–129.
- Jolly, G.M. (1965) Explicit estimates from capture–recapture

- data with both death and immigration-stochastic models. *Biometrika*, **52**, 225–247.
- Kot, M., Lewis, M.A. & Van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.
- Lewis, M.A. & Kareiva, P. (1993) Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, **43**, 141–158.
- Lonsdale, W.M. (1993) Rates of spread of an invading species *Mimosa pigra* in northern Australia. *Journal of Ecology*, **81**, 513–521.
- Memmott, J., Craze, P.G., Harman, H.M., Syrett, P. & Fowler, S.V. (2005) The effect of propagule size on the invasion of an alien insect. *Journal of Animal Ecology*, **74**, 50–62.
- Myers, J.H. (1998) Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. *Ecology*, **79**, 1111–1117.
- Neubert, M.G. & Caswell, H. (2000a) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.
- Neubert, M.G., Kot, M. & Lewis, M.A. (2000b) Invasion speeds in fluctuating environments. *Proceedings of the Royal Society London B*, **267**, 1603–1610.
- Neubert, M.G. & Parker, I.M. (2004) Projecting rates of spread for invasive species. *Risk Analysis*, **24**, 817–831.
- Parker, M.A. (2001) Mutualism as a constraint on invasion success for legumes and rhizobia. *Diversity and Distributions*, **7**, 125–136.
- Rilov, G., Benayahu, Y. & Gasith, A. (2004) Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. *Biological Invasions*, **6**, 347–364.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.
- Scott, J.A. (1973) Convergence of population biology and adult behaviour in two sympatric butterflies, *Neominois ridingsii* (Papilionoidea: Nymphalidae) and *Amblyscirtes simius* (Hesperioidea: Hesperioidea). *Journal of Animal Ecology*, **42**, 663–672.
- Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. Macmillan, New York.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.
- Watt, W.B., Chew, F.S., Snyder, L.R.G., Watt, A.G. & Rothschild, D.E. (1977) Population structures of pierid butterflies 1. Numbers and movements in some montane *Colias* species. *Oecologia*, **27**, 1–22.
- Williams, E.H. (1981) Thermal influences on oviposition in the montane butterfly *Euphydryas gillettii*. *Oecologia*, **50**, 342–346.
- Williams, E.H. (1988) Habitat and range of *Euphydryas gillettii* (Nymphalidae). *Journal of the Lepidopterists' Society*, **42**, 37–45.
- Williams, E.H. (1995) Fire-burned habitat and reintroductions of the butterfly *Euphydryas gillettii* (Nymphalidae). *Journal of the Lepidopterists' Society*, **49**, 183–191.
- Williams, E.H., Holdren, C.E. & Ehrlich, P.R. (1984) The life history and ecology of *Euphydryas gillettii* Barnes (Nymphalidae). *Journal of the Lepidopterists' Society*, **38**, 1–12.
- Wing, L. (1943) Spread of the starling and English sparrow. *Auk*, **60**, 74–87.

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