2018-05-10

Lethal trap created by adaptive evolutionary response to an exotic resource

Singer, MC

<http://hdl.handle.net/10026.1/11598>

10.1038/s41586-018-0074-6

Nature

Nature Publishing Group

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

1 **This is an Accepted Manuscript of an article published by Nature Publishing Group, a**
2 **division of Macmillan Publishers Limited, in the journal *Nature* on May 10, 2018**
3 **available at: 10.1038/s41586-018-0074-6**
4

5 **Full citation:** Singer, MC, C Parmesan (2018). Lethal trap created by adaptive evolutionary response
6 to exotic resource. *Nature* **557**:238-241. doi:10.1038/s41586-018-0074-6
7

8
9
10
11
12 **Lethal trap created by adaptive evolutionary response to exotic resource**
13
14
15

16 Michael C. Singer,^{1,3}

17 Camille Parmesan^{1,2,3}
18
19

20 ¹Biological and Marine Sciences, University of Plymouth, Drake Circus PL4 8AA, UK

21 ²Dept. of Geological Sciences, University of Texas at Austin, Austin, Texas 78712, USA

22 ³Station d'Ecologie Théorique et Expérimentale, UMR 5321, CNRS, Univ. Paul Sabatier, F-
23 09200 Moulis, France

Global transport of organisms by humans provides novel resources to wild species that often respond maladaptively. Native herbivorous insects have been killed feeding on toxic exotics, which acted as "ecological traps"¹⁻⁴. We document a **novel** trap stemming from the opposite effect, high fitness on an exotic resource despite lack of adaptation to it. *Plantago lanceolata* was introduced to Western North America by cattle-ranching. Feeding on this exotic plant released a large, isolated population of the native butterfly *Euphydryas editha* from a longstanding tradeoff between maternal fecundity and offspring mortality. Because of this release, and despite reduced insect developmental rate on the exotic, *Plantago* immediately supported higher larval survival than the insects' traditional host, *Collinsia parviflora*⁵. Prior work in the 1980's documented evolving preference for *Plantago* by ovipositing adults⁶. We predicted that, if this trend continued, the insects could endanger themselves, since availability of *Plantago* to butterflies is controlled by humans, and humans change management faster than butterflies evolve⁶. Here we report fulfillment of this prediction. The butterflies abandoned *Collinsia* and evolved total dependence on *Plantago*. The trap was set. In 2005 humans withdrew their cattle, springing the trap. Grasses grew around the *Plantago*, cooling the thermophilic insects, which went extinct. This extinction could have been prevented if the population had retained partial use of *Collinsia*, which occupied drier microhabitats unaffected by cattle removal. The flush of grasses abated quickly, rendering the meadow once again suitable for *Euphydryas* feeding on either host, but no butterflies were observed from 2008-2012. In 2013-4 the site was naturally recolonized by *Euphydryas* feeding exclusively on *Collinsia*, returning the system to its starting-point and setting the stage for a repeat of the anthropogenic evolutionary cycle.

Subject terms: *Euphydryas*, eco-evolutionary dynamics, anthropogenic evolution, conservation, exotic host, ecological trap, insect diet, host shift, oviposition preference, evolutionary trap.

Main The late Gary Polis described *Homo sapiens* as a "ubiquitous keystone pest"⁷. And so we are⁸. Although adaptation to human activities allows some wild species to coexist with us⁹, many fail to adapt to human land management and suffer in consequence. An example is the setting by humans of "ecological traps"^{10,11}, defined as follows: "in an environment altered suddenly by human activities, an organism makes maladaptive habitat choices based on formerly reliable environmental cues, despite availability of higher quality habitat"¹¹.

Most ecological traps result from preference by wild organisms for novel resources that are unsuitable or toxic. Australian monitor lizards suffered population crashes after feeding on toxic exotic cane toads¹². Bees maladaptively preferred crops grown from seed treated with neonicotinoid insecticides¹³. Several examples involved insect herbivores feeding on exotic hosts that reduced insect fitness¹⁻⁴ but fell short of causing population extinctions, because traditional hosts were still used alongside the exotics.

In the "ecological trap" scenario the novel resource is accepted as food, but is initially detrimental¹¹, with the expectation that evolution should lead either to behavioural avoidance of the resource or physiological ability to use it³. Here, we describe a different type of trap formed by a novel resource that immediately supported such high fitness that a butterfly population evolved complete dependence on it, causing local extinction when humans withdrew our apparent gift. This paradoxical phenomenon is previously undescribed and doesn't fit published definitions, either of "ecological trap" or "evolutionary trap"^{1,11}.

Our study insects, the thermophilic¹⁴ Edith's checkerspot butterflies, *Euphydryas editha*, formed a sedentary, isolated population around the margins of a spring-fed meadow, Schneider's Meadow, at 1800m elevation in Carson City, Nevada. They have one generation per year. Their novel host was the exotic perennial, *Plantago lanceolata*, and their traditional host the ephemeral native annual *Collinsia parviflora* (Extended data Fig. 1).

The geographically closest *E. editha* populations of the same ecotype as Schneider, but where *Plantago* had not arrived, used *Collinsia* as their sole host⁵. When neonate larvae from one of these "ancestral" populations were transplanted to Schneider, their survival on *Plantago* was identical to that of the local Schneider insects⁵. The "ancestrals" were ready to use *Plantago* from the moment of its introduction. It is not surprising, then, that this exotic has been colonized twice by other North American *Euphydryas*^{15,16}. Oregon *E. editha taylori* are now

dependent on the exotic, though it is not clear if this is due to evolution of the butterfly, since the original host(s) have disappeared¹⁶.

During the 1980's, survival of *E. editha* at Schneider was consistently higher on the exotic than on the traditional host (Table 1), despite larval growth being c.18% slower on *Plantago*⁵. Where the principal host is ephemeral, as is *Collinsia*, female *E. editha* face a trade-off between maternal fecundity and offspring survival. Prolonging larval development can increase fecundity, but the resulting delay in adult emergence augments the risk of offspring mortality from host senescence¹⁷. The evolutionary response to this trade-off has been to delay emergence to the point where many offspring routinely starve from phenological asynchrony with their hosts¹⁷. The stage is set for the time constraint to be released and fitness increased by host-switching to the longer-lived *Plantago*, despite slower larval growth on it. Indeed, the majority of larval mortality observed on *Collinsia* was from host senescence, while *Plantago* did not senesce during the seasons of larval activity.

No adult females sampled from "ancestral" populations preferred *Plantago* over *Collinsia* for oviposition, but around 20% accepted both hosts equally⁵. In contrast, by 1982 *Plantago* was already preferred for oviposition by a minority (c.7%) of preference-tested adults at Schneider⁶. Evolution of *Plantago* preference had begun.

Given natural selection for oviposition on *Plantago*, and given that oviposition preferences at Schneider were both heritable (estimated heritability 0.9) and correlated with offspring performance¹⁸, we expected to see rapid evolution of preference. We did: the proportion of insects preferring *Plantago* increased to around 50% by 1990⁶. This change was heritable. Laboratory-raised, *Collinsia*-fed offspring of field-caught 1990 butterflies were significantly more *Plantago*-preferring than similarly-raised offspring of field-caught 1983 insects⁶.

Here, we report that the bout of anthropogenic evolution continued until monophagy on *Plantago* was achieved. In 2005 and 2007, all tested females preferred to oviposit on the exotic (Fig. 1a) and in 2007 all larvae found in the field were on *Plantago* (Fig. 1b). The insects had abandoned both their traditional host, *Collinsia*, and the minor host, *Penstemon rydbergii*, that had been incorporated into their diet during the host shift (Extended data Table 1, Extended data Fig. 2).

In 1993 we wrote that this episode of anthropogenic evolution was “foreshadowing a new problem in Conservation Biology. By adapting genetically to human-induced changes, the insects risk becoming dependent on continuation of the same practices. This is a serious risk, because human cultural evolution can be even faster than the rapid genetic adaptation that the insects can evidently achieve.”⁶

This prediction was fulfilled. In late 2005, following the death of "Uncle Harry" Schneider, the meadow was sold and cattle-grazing ceased. Grasses grew freely. By March 2007, 96% of *Plantagos* had become embedded in grass (Table 2, Extended data Figs. 3,4a) and *E. editha* larvae wandered among dense vegetation, no longer able to bask in sunlight on bare ground adjacent to their hosts.

The conspicuous communal webs spun by gregarious young larvae render *E. editha* easy to census (Extended data Fig. 4b) and population extinction feasible to establish. Searches for larval webs, eggs and adults found no *E. editha* in 2008, 2009, 2010 or 2012 (Fig. 1c, Extended data Table 1). The population was extinct.

By analogy with known cause-effect relationships involving other thermophilic butterflies, we attribute this extinction to the flush of lush vegetation caused by cattle removal. Lushness is associated with high rates of predation on butterfly larvae¹⁹ and increased lushness caused by abandoning of traditional management in Europe has caused ground-level cooling resulting in butterfly declines and local extinctions²⁰⁻²². The UK extinction of the Large Blue butterfly was attributed to lushness-caused microclimatic cooling, following myxomatosis-related reduction of grazing by rabbits²². Restoration of grazing and re-warming of ground-level microclimate were essential for this butterfly's successful re-introduction²².

Particularly in sparse vegetation, sunshine creates thermal stratification with microclimate hotter close to the ground²³, speeding insect development²⁴. We used prior observations of natural oviposition sites at Schneider to measure "eggspace" temperatures. Eggspaces on exposed *Plantagos* were augmented by 13.4°C above ambient, compared to 6.0°C on embedded *Plantagos*, leaving "eggs" on embedded plants >7°C cooler, on average, than those on exposed plants (Extended data Table 2). In light of the high proportion of plants embedded in 2007 (Table 2), and of the known adverse effects of host embedding^{16,19} and

microclimatic cooling²⁰⁻²² on other butterflies, it is not surprising that this cooling was followed by extinction.

As anthropogenic nutrients were used up, the flush of grasses abated naturally in 2008, since when *Plantagos* exposed to full sunlight have again been available (Table 2, Extended data Fig. 5). In 2013-4 butterflies recolonized: an exhaustive search in 2014 revealed nine *E. editha* larval webs, all on the ancestral host, *Collinsia* (Fig. 1b,c, Extended data Fig. 4b). Recolonization had occurred from a population resembling the starting condition, prior to the anthropogenic evolution.

The distance from Schneider's Meadow to the nearest known population of the subspecies, *E.e. monoensis*, at Simee Dimeh summit, is 37.7km. How far is this to a *Euphydryas*? Harrison²⁵ measured colonizations of empty habitat patches by the Bay Checkerspot (*E. editha bayensis*) and found that the greatest cumulative distance travelled in ten years was 4.5km. Given this sedentary nature of the butterfly and the physical isolation of the meadow, we did not consider the possibility of rapid recolonization. Our mindset in 2014 was simply to reconfirm the extinction and we were astonished to find larvae. After the event, we discovered that the "Carter Springs" fire in September 2012 had positively impacted the Simee Dimeh butterflies, dramatically extending size and lifespan of *Collinsia* (Extended data Fig. 6), resulting in a population boom of *E. editha* similar to previously-documented response to fire²⁶ and providing a plausible source of *Collinsia*-feeding *E. editha* despite the distance.

Could the original population have survived if it had retained its traditional diet of *Collinsia* alongside *Plantago*, as it did from 1982 to 2002? *Collinsia* was both most abundant and most used by the insects in dry sagebrush around the meadow edge (Extended data Figs. 1,2,3), where removal of cattle did not result in embedding of *Collinsias*, even at peak lushness in 2007 (Table 2, Extended data Fig. 3). If the butterflies had adopted the exotic less completely, they would likely have survived the change of land use. Conversely, if they had remained monophagous on *Collinsia* they may not have survived the bottleneck in 1988-9⁶, when, after record-breaking frost without insulating snow (-25°C at Minden on January 1, 1988), the population was spatially restricted to a small, sheltered, south-facing area from which *Collinsia* was coincidentally absent (Fig. 1b,c; discussion with extended data Fig. 2).

Evolution of *E. editha* at Schneider illustrates the process by which, long ago, European grassland butterflies evolved widespread dependence on human haymaking and grazing, rendering themselves vulnerable to abandonment of traditional management techniques²⁰⁻²². However, *E. editha* as a species is not threatened by the trap we document. Its ecotypic variation and rapid evolution augur well for resilience to environmental fluctuations, whether natural or anthropogenic²³. In contrast, substantial perturbation occurred at the subspecies level, since *E. e. monoensis* is currently restricted to four known sites: two isolated populations and two metapopulations distributed along 235km of the eastern Sierra Nevada from McGee Creek at latitude 37.29 to Schneider at latitude 39.11.

Unless the Schneider population sent out successful propagules, which we judge unlikely, the lineage we observed from 1982-2007 is extinct. At the population level, the changes we observed exemplify dramatic, oscillating anthropogenic evolution of a species not directly targeted by humans. This example of small-scale oscillating diet evolution oddly mimics repeated recolonizations of abandoned hosts detected across millions of years by phylogenetic analysis of the butterfly family Nymphalidae, to which *E. editha* belongs²⁷.

Attempts at "evolutionary rescue" of wild species^{28,29} may be compromised when anthropogenic traps such as that documented here remain undetected. These traps may be cryptic to humans, but understanding them may become increasingly important to species conservation in the Anthropocene.

Data availability. Raw data are included in the Figure, Tables and Extended data.

References

1. Schlaepfer, M. A., Sherman, P. W., Blossey B. & Rynge M. C. Introduced species as evolutionary traps. *Ecol. Lett.* **8**, 241-246 (2005).
2. Nakajima, M., Boggs, C. L., Bailey, S., Reithel, J. & Paape, T. Fitness costs of butterfly oviposition on a lethal non-native plant in a mixed native and non-native plant community. *Oecologia* **172**, 823-832 (2013).
3. Morton, T. A. L., Thorn, A., Reed, J. M., van Driesche R. G., Casagrande R. A. & Chew, F. S. Modeling the decline and potential recovery of a native butterfly following serial invasions by exotic species. *Biological Invasions* **17**, 1683-1695 (2015).
4. Yoon, S. & Read, Q. Consequences of exotic host use: impacts on Lepidoptera and a test of the ecological trap hypothesis. *Oecologia* **181**, 985-996 (2016).
5. Thomas, C. D., Ng, D., Singer, M. C., Mallet J. L. B., Parmesan, C. & Billington, H. L. Incorporation of a European weed into the diet of a North American herbivore. *Evolution* **41**, 892-901 (1987).
6. Singer, M. C., Thomas, C. D. & Parmesan, C. Rapid human-induced evolution of insect-host associations. *Nature* **366**, 681-683 (1993).
7. Polis, G. A. Address to the Ecological Society of America (1999).
8. Gotanda K. M., Hendry, A. P. & Svensson, E. I. Human influences on evolution, and the ecological and societal consequences. *Philos Trans Roy Soc B* **372**, 20160028 (2017).
9. Thomas, C. D. *Inheritors of the Earth: How Nature Is Thriving in an Age of Extinction*. Penguin/Allen Lane Books (2017).

10. Robertson, B. A., Rehage, J. S. & Sih, A. Ecological novelty and the emergence of evolutionary traps. *Trends Ecol Evol* **28**, 552-559 (2013).
11. Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. Ecological and evolutionary traps. *Trends Ecol Evol* **17**, 474-480 (2002).
12. Jolly, C. J., Shine R., & Greenlees, M. J. The impacts of a toxic invasive prey species (The cane toad, *Rhinella marina*) on a vulnerable predator (the lace monitor, *Varanus varius*) *Biological Invasions* **18**, 1499-1509 (2016).
13. Kessler S. C. *et al.* Bees prefer foods containing neonicotinoid pesticides. *Nature* **521**, 74-76 (2015).
14. Weiss, S. B., Murphy, D. D., & White, R. R. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* **69**, 1486-1496 (1988).
15. Brown, L. M., Breed, G. A., Severns P. M. & Crone, E. E. Losing a battle but winning the war: moving past preference-performance to understand native herbivore-novel hostplant interactions. *Oecologia* **183**, 441-453 (2017).
16. Severns, P. M. & Warren, A. D. Saving an imperiled butterfly, *Euphydryas editha taylori* (Taylor's checkerspot), by selectively conserving and eliminating exotic plants. *Animal Conserv* **11**, 476-483 (2008).
17. Singer, M. C. & Parmesan, C. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philos Trans Roy Soc B* **365**, 3161-3176 (2010).
18. Singer, M. C., Ng, D. & Thomas, C. D. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* **42**, 977-985 (1988).
19. Wiklund, C. & Friberg, M. Enemy-free space and habitat-specific host specialization in a butterfly. *Oecologia* **157**, 287-294 (2008).

277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295
296
297
298
299
300
301
302
303
304
305
306
307
308
309
310

20. WallisDeVries, M. F. & van Swaay, C. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Glob Chang Biol* **12**, 1620–1626 (2006).

21. Warren, M. S. & Bourn N. A. D. Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. *J Insect Conserv* **15**, 321-326 (2010).

22. Thomas, J. A., Simcox, D. J. & Clarke, R. T. Successful conservation of a threatened *Maculinea* butterfly. *Science* **325**, 80-83 (2009).

23. Bennett, N. L., Severns, P. M., Parmesan, C. & Singer, M. C. Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos* **124**, 41-53 (2015).

24. McBride, C. S. & Singer, M. C. Field studies reveal strong postmating isolation between ecologically divergent butterfly populations. *PLoS Biology* **8**, Issue 10 Article Number: e1000529 DOI: 10.1371/journal.pbio.1000529 (2010).

25. Harrison, S. Long-distance dispersal and colonization in the Bay Checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* **70**, 1236-1243 (1989).

26. Thomas, C. D., Singer, M. C., & Boughton D. A. Catastrophic extinction of population sources in a butterfly metapopulation. *Amer Natur* **148**, 957-975 (1996).

27. Nylin, S., Slove, J. & Janz, N. Host plant utilization, host range oscillations and diversification in Nymphalid butterflies. *Evolution* **68**, 105-124 (2014).

28. Gonzalez, A., Ronce, O., Ferriere, R. & Hochberg, M. E. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philos Trans Roy Soc B* **368**, 20120404 (2012)

29. Carroll, S. P. et al. Applying evolutionary biology to address global challenges. *Science* **346**, 313+ DOI: 10.1126/science.1245993 (2014).

30. Singer, M. C. Butterfly-host relationships: host quality, adult choice and larval success. Pp 81-88 in *The Biology of Butterflies, Symp. Roy. Ent. Soc.* **13**, (1984).

31. Newcombe, R. G. Two-sided confidence intervals for the single proportion: a comparison of seven methods. *Statistics in Medicine* **17**, 857-872 (1998).

Acknowledgements Paul Ehrlich introduced MCS to *E. editha* in 1967; Chris Thomas, Helen Billington, David Ng, and Jim Mallet helped initiate the project. Dennis Murphy performed the 2010 census. Carol Boggs, Rachel Steward, Jim Mallet & Carolyn McBride critiqued the MS. The 2013 Integrative Biology Faculty Merit Review Committee, University of Texas at Austin, provided incentive to complete the study and publish it here. Joe and Becky Schneider, the Drudge family, Clear Creek Tahoe Inc. and The Nature Conservancy allowed access to the site.

Reprint and permissions information is available at www.nature.com/reprints

Correspondence and requests for materials should be addressed to michael.singer@plymouth.ac.uk

Author Contributions Both authors participated in field censuses and writing. MCS performed oviposition preference tests and statistical analyses.

Competing Financial interests The authors declare absence of financial interests, whether competing or not.

Figure 1. Changes of *E. editha* oviposition preference (a), larval diet (b) and population density (c). The two preference graphs (a) are not mirror-images because insects without preference are not shown. Changes in strength of preference are shown in Extended data Fig. 7. (b) absence of larvae on *Collinsia* in 1988-89 caused by temporary spatial restriction during and after bottleneck; in those two years larvae were restricted to *Plantago* and *Penstemon* (extended data Table 1 and extended data Fig. 2). Numbers within graphs represent biologically independent sample sizes; individual adult insects (a) or larval groups (b,c). Error bars = 95% c.i. calculated according to Newcombe³¹, with continuity correction; source data in Extended data Table 3. No error bars for larval diet in years of inadequate sampling (1982, 1983, 2015) or total census (1988,1989, 2014).

346 **Table 1. Survival of *E. editha* placed in the field on *Collinsia* and *Plantago* at**
347 **Schneider's Meadow in the 1980's.** Proportions of groups surviving analyzed as 2x2
348 contingency tables by Fisher's exact test, two-tailed.

Year And reference	Life Stages measured	Group Survival <i>Collinsia</i>	Group Survival <i>Plantago</i>	Individual survival <i>Collinsia</i>	Individual survival <i>Plantago</i>	Statistical significance (group survival)
1980 (previously unpublished)	Oviposition to second instar	33% (n = 15)	70% (n = 20)	Not recorded	Not recorded	P = 0.044
1982 ³⁰	Oviposition to second instar	17% (n = 58)	55% (n = 86)	4% (n = 1810)	24% (n = 2764)	P = 0.000011
1985 ^{5,18}	Larval survival for ten days from hatch	62% (n = 63)	84% (n = 62)	19.9% (n = 1260)	27.1% (n = 1240)	P = 0.0085 (combining data from both references)
1986 (previously unpublished)	Oviposition to second instar	29% (n = 28)	80% (n = 25)	Not recorded	Not recorded	P = 0.00028

349

350 **Table 2. Estimated host densities and percentages of each host embedded and exposed.**

Year	<i>Plantago</i> density, plants/m ²	<i>Collinsia</i> density, plants/m ²	Percent <i>Plantago</i> embedded	Percent <i>Collinsia</i> embedded
1984	2.3 (50 in 244x 30cm quadrats)	103 (2266 in 244x30cm quadrats)	<10%	<5%
2005	9.4 (317 in 15 x 2.25 m ² quadrats)	27.5 (330 in 12 x 1m ² quadrats)	<10%	<5%
2007	0.21 (18 in 85 x 1m ² quadrats)	35.2 (528 in 15 1m ² quadrats)	96.4% (189/196)	10.5% (69/657)
2008	2.8 (44 in 16 x 1m ² quadrats)	26.1 (418 in 16 x1m ² quadrats)	18.6% (43/231)	13.8% (77/559)
2009	2.5 (48 in 19 x 1m ² quadrats)	45.7 (869 in 19x 1m ² quadrats)	11.8% (251/2115)	11.7% (114/975)
2014	3.4 (173 in 50 x 1m ² quadrats)	52.4 (472 in 9 x 1m ² quadrats)	8.5% (28/328)	18.0% (150/833)

Methods

Statistics. All tests are two-tailed. Error bars on Figures, given only where justified by sampling techniques, are 95% c.i., calculated by vassarstats.net, using methodology of Newcombe³¹ for c.i. of proportions, with continuity correction. Figure 1a does not explicitly depict insects without preference but they can be deduced by subtracting the depicted percentages from 100%. Otherwise no relevant data have been omitted from any experiment or set of observations. Sample sizes were largely limited by feasibility.

Data availability. Raw data are included in the Figure, Tables and extended data.

Blind preference testing. Oviposition preference tests to estimate heritability¹⁸ were performed blind, in the sense that the tester did not know which insects were sibs or offspring of particular parents. The high heritability estimate from this blind testing (0.9) gave confidence that the tests were not subject to severe observer bias; repeated blind testing of the same butterfly by different observers has also given confidence. However, in the present MS the appropriate blind test would require the tester to not know which year it was, and we were not able to achieve this without compromising the quality of the data.

Figure 1a. Butterflies were captured in the field and their oviposition preferences tested by a standardized technique, in which encounters are staged between the tested insect and each plant in alternation. Plants were undisturbed in their natural habitats or freshly transplanted into pots in their own soil. Acceptance of plant taste was judged from full abdominal curling and extrusion of the ovipositor for 3 sec³². Acceptance and rejection were recorded at each encounter, but oviposition was not allowed³². Videos showing acceptance in such staged encounters are in reference 24. During each test the range of plants that would be accepted, if encountered, expands over time with increasing motivation to oviposit. Therefore, acceptance of plant A followed by rejection of plant B is recorded as preference for A over B. Testing of assumptions underlying this technique described in reference 32. Because insects without preference are not shown in the Figure, percentages do not sum to 100% except in 2005 & 2007, when preference for *Plantago* was unanimous among tested butterflies. Raw data are in Extended data Table 3. A more detailed comparison between early and late periods, showing strength as well as direction of preferences, is given in Extended data Fig. 7. The assumption

that these insects' preferences are not influenced by prior experience, either as larvae or as adults, is supported by prior observation and experiment^{18,32,33}.

Figure 1b. Percentages of egg clutches/larval groups found on *Plantago*. Raw data in Extended data Tables 1 and 3. Low sample sizes in 1988 and 1989 were total counts, reflecting bottleneck. High proportion of larvae on *Plantago* in 1989 reflects lag in recolonization of *Collinsia* after spatial restriction in bottleneck, shown in Extended data Fig. 2. In 2002-2007 we searched a larger area for larvae on *Collinsia* than for larvae on *Plantago*. For those years the Figure, showing the proportion of larvae found on the two hosts, overestimates the overall proportion on *Collinsia*; the areas searched are in Extended data Table 1. To be conservative we indicated data for 2002 and 2005 as "published" although neither sample sizes nor confidence limits were given previously³³. The graph shows that in 2015 we found a single group of hatching eggs on *Collinsia*. However, we performed no census in 2015, our visit was too early.

Figure 1c. Estimates of density of larval webs, on all hosts combined, per 10,000m². Raw data in Extended data Table 1. In each census, individual host plants of all species were searched for eggs, larvae, larval webs and typical damage. Very different scales of census were conducted in different years. For small patches, every individual host plant could be searched, for larger patches, stratified line transects were used. Confidence limits are not given, but the log scale of the Y-axis makes clear the dramatic scale of population changes; for example, the raw data (Extended data Table 1) include the finding of 34 groups in only 70m² in 1982 and 4 groups in 20,000m² in 1988. No density estimate is given for 2007, because, although 38 groups were found (Fig. 1b), at the time of the last census some were still eggs, so harder to find than larvae. Sample calculation for 2002, (see methods for Extended data Table 1): estimated number of webs on *Plantago* = 67 x 4,000/170 = 1576. Total number on *Collinsia* = 3 (all were counted). Estimated total number webs in entire area of 20,000m² = 1579; density per 10,000m² = 789.

Table 1. Effects of oviposition host on fitness: eggs were placed out on randomly-chosen hosts in the field, by manipulating butterflies to lay (videos in ref. 24). Gregarious neonate larvae were placed out with a sable brush in groups of 20-35. After ten days of larval life, just before diapause, each group was gathered in. It is in pre-diapause life that the principal

effects of oviposition on fitness are manifest, since post-diapause larvae are mobile and can switch between host species.

Table 2. Host densities estimated from quadrats along line transects placed randomly within the strata of the ecotone where each plant was concentrated (Extended data Fig. 1). Early rough estimates of percent embedded from photographs, memory and anecdotal observation, since embeddedness was uncommon and its value as a trait was not anticipated prior to the sudden embedding of *Plantago* in 2007. A plant was classed as "embedded" if surrounded for > 50% of circumference by vegetation taller than itself. In most cases the differences between "embedded" and "exposed" plants were striking (Extended data Fig. 3); in the March census in 2007 some embedded plants were hidden and not found, pressed under thatch from winter snow, inaccessible to post-diapause larvae feeding in March but reappearing and, if no longer completely embedded, accessible to ovipositing butterflies in May. Extended data Fig. 4a has a photo of eggs naturally laid on such a reappearing *Plantago*, emerging from winter thatch, in May, 2007.

Extended data Table 1. Table contains counts over wider areas including lower host densities than the "core areas" censused in Table 2. Total area where suitable *Plantago* might be found was around 4,000m²; total area that might contain suitable *Collinsia* was larger, maximally about 17,000m² (1982 map in Extended data Fig. 2) but less in dry years. About 1,000 m² overlapped between the two distributions. Wider areas were searched in 1988 and 1989 to check whether we had missed part of the population in prior work. We had not, so since we found no habitat in wider search, subsequent searches were restricted to meadow margins and adjacent sagebrush, approximately 20,000m² (Extended data Figs.1 & 2).

In 2002, 2005 and 2007 the entire area where larvae might have been found on *Collinsia* was searched, but *Plantago* areas were not searched in entirety, merely sufficiently to get an estimate of plant density and occupancy by the butterflies. After the extinction in 2007-8, the entire habitat was searched in each census. In most years, more plants were searched for *E. editha* than were included in censuses to estimate plant density reported in Table 2.

The Table shows data from areas censused in which plants with and without larvae were counted. Where maps in Extended data Fig. 2 show more insects than the Table, as in 1982,

the insect distribution in the map is derived from rapid assessment in which insects were observed and counted but plants were not.

Extended data Table 2. Eggspace temperatures were measured with a fine thermocouple (MT-29/1B insect probe, type T, copper-constantan). After measuring each exposed *Plantago* we measured one or two adjacent (within 1m) embedded plants growing in the same position within the ecotone; we took care that embedded plants were not systematically growing in more humid microsites. When two embedded plants were measured, we used the mean value of the two for analysis.

We found three errors in our prior publications: (1) number of groups found on *Collinsia* in 1990 is here corrected to 18 from 6⁶; (2) number of butterflies preference- tested in 1986 is corrected from 31 to 36^{5,6}; (3) misleading early reference to population as feeding on *Plantago* in 1969³⁴ stemmed from initial visit in June, after *Collinsia* had senesced and disappeared. Faster-growing larvae on *Collinsia* had entered diapause and were not found, while some still remained feeding on *Plantago*. Next visit in 1971 made clear that, although *Plantago* was already being used, *Collinsia* was the principal host. No censuses were performed in 1969-71.

References

32. Singer, M.C., Vasco, D. A., Parmesan, C., Thomas, C. D. & Ng, D. Distinguishing between preference and motivation in food choice: an example from insect oviposition. *Animal Behaviour* **44**, 463-471 (1992).

33. Singer, M. C., Wee, B., Hawkins, S. & Butcher, M. Rapid natural and anthropogenic diet evolution: three examples from checkerspot butterflies. Pp. 311–324 in K. J. Tilmon, ed. *The evolutionary ecology of herbivorous insects: speciation, specialization and radiation*. Univ. of California Press, Berkeley, CA (2008).

34. Singer M. C. Evolution of food-plant preference in the butterfly *Euphydryas editha*. *Evolution* **25**, 383-389 (1971).

Extended data Figure 1. **Habitat and host distributions at Schneider's Meadow.** **a:** Butterfly habitat is a single, isolated, spring-fed wet meadow in the centre of the picture, surrounded by non-habitat for the butterflies: dry sagebrush scrub and coniferous forest. **b:** Distribution in the meadow-edge ecotone of the principal hosts, *Plantago lanceolata* and *Collinsia parviflora*, plus the minor host *Penstemon rydbergii*. **c:** Typical difference in phenology between *Plantago* and *Collinsia* in May 2014. In the foreground are red, senescent *Collinsia* plants that are edible to the insects but will die within a few days; behind them is a single green, budding *Plantago* that will remain edible until after all *E. editha* larvae have entered diapause. **d:** Hatching egg clutch on *C.parviflora* cotyledon in hot, dry microhabitat.

Extended data Figure 2. **Changes in distribution of early stages of *E. editha* (eggs or larvae) from 1982-2007.**

Data added by hand to GoogleMaps image. Most stars represent several groups. For example, in 1989, 23 groups were found on *Plantago* and one on *Penstemon*. The restricted distribution in that year followed a bottleneck in 1988 after record-breaking cold in January, without the usual insulating snow cover. Schneider's Meadow is at 1700m elevation. Nearby towns at lower elevations recorded -25C on January 1 1988 (Minden, 1444m elevation) and -20C on January 18 (Carson City, 1424m). Note recolonization of *Collinsia* as the insects expanded back into the distribution of *Collinsia* in 1990 and 1993. Larval groups recorded in 1988 and 1989 were clustered around an attractive nectar source (*Wyethia* sp.); it is possible that adults attracted to this nectar in 1988 had survived as larvae on *Collinsia* in 1987-8, then laid eggs in 1988 on *Plantago* adjacent to nectar. This possibility prevents us from making a definite conclusion that the population would have become extinct if eggs in 1987, prior to the bottleneck, had been laid only on *Collinsia*. Data for 2005 exist, and closely resemble those for 2002.

Extended data Figure 3. **Effects of cessation of grazing: *Plantagos* embedded, *Collinsias* unaffected.** Data in Table 2. Panel **a** shows a *Plantago* at Schneider in 1984, exposed to full sunlight and physically acceptable to ovipositing *E. editha*. Panel **b** shows the meadow edge in May 2007, after cattle removal. In the foreground is *Plantago* habitat with thick grasses; in the background is *Collinsia* habitat not grassed-in, with barren spaces between the sagebrush. Panel **c** shows *Collinsia parviflora* in May 2007, unaffected by the embedding that simultaneously affected the *Plantagos* shown in panels **d** and **e**. Embedding in grasses not

only cooled the *Plantagos* (Extended data Table 2) but rendered them hard to find, both by butterflies seeking oviposition sites and by larvae seeking food.

Extended data Figure 4. **a. Natural egg clutch laid in May 2007 on *Plantago***

The plant is pushing through winter thatch, and would have been unlikely to be acceptable to ovipositing butterflies prior to cattle removal, when plants like the one in Extended data Fig 3a were available. **b. Communal web spun after recolonization.** Second-instar larvae on *Collinsia* at Schneider in May 2014. This is a single group of larvae probably stemming from a single oviposition event; there were 9 such groups, all on *Collinsia*. Oddly, this group is not on the most exposed *Collinsia* available.

Extended data Figure 5. **The return of mostly-exposed *Plantagos* after anthropogenic lushness abated.** Photos taken in 2014, but Table 2 shows that they could have been taken in 2008 or subsequently.

Extended data Figure 6. **Effect of fire on size and longevity of *Collinsia parviflora*.**

A single fire-enhanced *Collinsia parviflora* individual at McGee Creek (East of Bishop, California) is still blooming. There is a small web of *E. editha* larvae at its base from a naturally-laid egg clutch. The fifteen senescent individual *C. parviflora* lying on the ground are a haphazard sample gathered from unburned microsites within 2m of the enhanced individual.

Extended data Figure 7. **Strength and direction of oviposition preferences of butterflies sampled at Schneider in 1983 and (2005+2007).**

The number over each bar is the sample size of biologically independent samples: individual butterflies captured in the field. The "discrimination phase" is the length of time for which the insect would search, during which it would consistently accept the preferred host and consistently reject the second-ranked host. At the end of this phase, if it does not succeed in ovipositing, the insect enters an "acceptance phase," after reaching the level of oviposition motivation at which either host would be accepted, whichever were next encountered.

Insects in the blue 1-4 column on the left of the Figure would search for 1-4 hours during which only *Collinsia* would be accepted. If they failed to find *Collinsia* within 4 hours, they would subsequently accept either host, until actual oviposition occurred. Green central bar

shows butterflies without preference. Sample size for 2005-7 is smaller than in Fig. 1a because we include on Fig. 1a (and here omit) 5 butterflies for which we determined the direction of preference, but not the strength.

Extended data Table 1. **Census results: areas searched and numbers of egg clutches or larval webs found on each host.** Data for 1982-1993 from reference 6. These are not the same data shown in Extended data Fig. 2; see Methods. Extension of survey to 50,000m² in 1989 did not reveal additional habitat, so density in Fig. 1c for that year is calculated using the estimated maximum habitat area of 20,000m², giving a higher estimate than reported in reference 6.

Extended data Table 2. **Measurements of temperature excess over ambient air at 1m height at three potential types of oviposition site at Schneider's Meadow: embedded *Plantago*, exposed *Plantago* and exposed *Collinsia*.**

Measures taken at egg space height (2-4cm) between noon and 15:00 in May 2015. Each measure of exposed *Collinsia* or *Plantago* came from a different, haphazardly chosen habitat patch. On occasion we measured two embedded *Plantagos* in the same patch; when this occurred we show the mean of the two values and used those means in analysis, treating the two plants as a single sample. Consequently, each data point in the Table represents a biologically independent sample, and the independent sample sizes are 12, 18 and 18 as indicated at the base of each cell.

Comparison between exposed *Plantago* (mean excess 13.4) and embedded *Plantago* (mean excess 6.0) by two-sided t-test: $t = 7.55$, $df = 28$, $p < 0.0001$

Comparison between exposed *Collinsia* (mean excess 11.46) and exposed *Plantago* by two-sided t-test: $t = 1.77$, $df = 28$, $p = 0.09$

Extended data table 3. **Source data for means and confidence limits of adult preference and larval diet, shown in Fig. 1a,b.** Statistical test described in caption to Fig. 1.