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Experimental management and mark-release-recapture methods fill critical knowledge gaps for an at-risk butterfly

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Abstract
Understanding how management actions affect target species is crucial for designing conservation strategies that meet recovery goals. In the context of Oregon silverspot butterfly (*Speyeria* = *Argynnis zerene hippolyta*) conservation, we used experimental habitat manipulations and mark-release-recapture methods to measure the effects of habitat restoration and population augmentation on butterfly vital rates. To understand the butterfly's response to management, we (1) measured larval survival in response to invasive grass and thatch removal, and (2) used mark-release-recapture methods to estimate phenology, adult survival, and female egg laying of both wild and captive-reared butterflies. We found that reducing the density of invasive grasses and associated thatch, increased larval survival by up to 50%. We also found that wild butterflies emerged, on average, three weeks before captive butterflies were released and lived up to a week longer than captive butterflies. This mismatch in timing resulted in observations of only 15% of captive females laying eggs as opposed to 45% of marked wild females, suggesting that captive-reared females are contributing very little to the overall population. For Oregon silverspot recovery efforts to succeed, continued management of invasive grasses is key, as is further work to match the timing of releases of captive butterflies with flight of wild butterflies.

Implications for insect conservation Through hands-on manipulation of habitat and markingat-risk butterflies, we identified specific ways to improve current management actions to meetrecovery goals. These techniques are necessary for developing conservation strategies that willsave species from extinction

Keywords Butterfly · Mark-release-recapture · Restoration · Captive rearing · *Speyeria (Argynnis) zerene hippolyta*

Introduction

Amid ongoing insect declines, the importance of directly addressing the negative effects of habitat loss, fragmentation, and degradation is paramount to butterfly conservation (Wepprich et al. 2019; Wagner et al. 2021; Forister et al. 2021). With the aim of creating resilient butterfly populations, conservation efforts typically focus on two main strategies, (1) habitat restoration, and (2) captive rearing and reintroduction programs (Dennis 2010; Samways et al. 2010; Bladon et al. 2022). For these actions to succeed, conservation decision-makers need to understand how actions affect population dynamics of the target species, yet studies rarely assess the demographic response of target species to conservation actions (Schultz et al. 2019; Henry et al. 2019). Here we focus on the Oregon silverspot butterfly (*Speyeria* = *Argynnis zerene Hippolyta*), a threatened species that continues to decline despite years of active management, and assess the effects of habitat restoration and population augmentation on butterfly vital rates.

For many endangered butterflies, habitat restoration is grassland restoration (e.g. Balmer and Erhardt 2000; Fiedler et al. 2017; Joubert-van der Merwe et al. 2019; Bussan 2022). Half of grasslands in the United States have been converted to agriculture and development since European settlement and only small fragments remain (Lark 2020). A coincident loss of historic disturbance regimes caused shifts in grassland plant communities such that remaining fragments do not contain sufficient host plant and nectar resources to maintain butterfly populations (Brunbjerg et al. 2017; Haan and Landis 2019; Kral-O'Brie et al. 2019; Ubach et al. 2020). Restoration strategies, therefore, focus on restoring historic disturbance, using surrogate approaches

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– prescribed fire, grazing, mowing, herbicide applications and direct seeding/planting of key resources (Schultz 2001; Moranz et al. 2012; Bubova et al. 2015; Henry et al. 2020; Bladon et al. 2022). In addition to increasing densities of important butterfly resources, restoration actions may also improve habitat quality by altering microclimate and predator communities to which both larvae and adult butterflies are exposed. The process of restoring habitat always has the potential to have both costs and benefits to butterfly populations (Jellinek et al. 2014; Schultz and Ferguson 2020). By measuring population response to these actions, decision-makers can focus on methods that mitigate the costs, enhance the benefits, and maximize effectiveness of restoration actions (Warchola et al. 2018; Cayton et al. 2023).

Reintroduction or population augmentation is often critical to increase occupancy and enhance connectivity between habitat patches (Schultz et al. 2008). Many butterfly conservation programs use captive rearing and breeding to produce individuals for release into the wild (Grow et al. 2015; Daniels et al. 2020). However, local adaptation of source populations and adaptation to captivity can result in captive-reared individuals that are the wrong size, genetic bottlenecks, and behavioral/habitat mismatches (Saccheri et al. 1996; Lewis and Thomas 2001; Heidinger et al. 2009; Aardema et al. 2011; Turlure et al. 2013), all of which have the potential to influence the fitness of captive-reared individuals and their ability to contribute to (or establish) self-sustaining wild populations. Simple measurements comparing captive and wild butterflies in-situ are necessary to evaluate if these measures are having intended effects, and if they are not, to re-design rearing and release strategies to meet conservation goals (Crone et al. 2007).

The Oregon silverspot butterfly was listed as Threatened under the United States Endangered Species Act in 1980; it was the second invertebrate species to be protected under the law. The coastal grassland habitat the butterflies rely on was historically maintained by annual indigenous burning practices (Wall Kimmerer 2013) and spanned from southern Washington to northern California. Now only six occupied grassland complexes remain (five in Oregon and one in California; (USFWS 2020). All remaining Oregon silverspot butterfly habitat has been invaded by non-native grasses and native shrubs due to the removal of fire from the system and planting of pasture grasses for livestock forage by settlers. Habitat management (primarily mowing, host and nectar plantings, and occasional prescribed fire) has been ongoing for decades, and captive rearing of Oregon silverspots began in 1998 with butterflies released into the wild every year since. Still, Oregon silverspot populations continue to decline, raising questions about the effectiveness of current management strategies (USFWS 2020). To understand effects of management and how to improve current practices, we measured larval survival in a targeted habitat restoration experiment seeded with larvae from a zoo-based captive rearing program and used mark-release-recapture methods to compare phenology, apparent survival, and egg laying between wild and captive-reared butterflies.

Methods

Study system

Butterfly lifecycle

Female Oregon silverspot butterflies lay eggs in late summer/early fall on dry vegetation after violets have senesced and before fall rains and cool temperatures end the adult flight season. First instar larvae overwinter. Larvae emerge from diapause in the spring, typically in mid-late April, when temperatures begin to rise, aligning with the reemergence of their larval host plants, early blue violet (*Viola adunca*). Larval development is unusually long (3–4 months to develop through 6 instars), as larvae take advantage of short bursts of sunshine that punctuate characteristic cold, grey, rainy spring weather on the Oregon coast (Sims 2017; USFWS 2020). The timing of adult emergence is largely dependent on spring weather; in warm years adults begin eclosing by late June while cool, wet springs result in longer larval development and later adult eclosure (2021 vs. 2022, Henry unpublished data). Depending on when adults emerge, females may enter reproductive diapause for much of the summer to delay egg laying and reduce exposure of overwintering first instars to desiccation. This is an unusual aspect of Oregon silverspot life history and is thought to be a major contributor to the decline of many silverspot species (Sims 2017).

Distribution and habitat

We focused our research at Rock Creek and Bray Point, which together form one of the three occupied historic meadow complexes in Oregon (we use the word meadow to refer to grassland fragments; it is the term land managers in this system use for Oregon silverspot habitat patches). The ownership and management of the meadows in this complex is split between Siuslaw National Forest (USFS) and Oregon Parks and Recreation Department (OPRD). Depending on the agency, recent management of these meadows includes annual mowing (USFS), targeted herbicide application (OPRD), intermittent prescribed burning (OPRD) and planting of violet host plants and native nectar sources (OPRD and USFS). These efforts are aimed at reducing the density of invasive grasses, accumulated thatch, and slowing woody shrub (primarily salal (*Gaultheria shallon*)) encroachment into meadows. The underlying hypothesis for this work is that increasing resources for larval and adult butterflies and restoring the open vegetation structure characteristic of historic meadows will increase larval survival and oviposition of Oregon silverspot butterflies.

Invasive grass removal experiment

To test the effect of invasive grass and thatch removal on post-diapause larval survival, we established 10, 1.5-meter x 1.5-meter experimental plots at both Rock Creek and Bray Point. We selected locations at each site representative of typical meadow habitat where violets are growing in competition with invasive grasses and associated thatch. At each site, we randomly selected five plots as treatments leaving the other five as no-treatment controls. To simulate management, we hand trimmed invasive grasses and pulled thatch out of experimental plots. We trimmed grasses and thatch as close to ground level as possible, being careful to leave violets and other native grass and forb species unharmed. We trimmed plots once in mid-May, once violets had begun growing. This was later in the growing season than mowing generally occurs, but was necessary to avoid trimming newly emerging violets in our study plots. Once trimming was completed, we built mesh enclosures over each plot; we used white, polyester mosquito netting that would allow sun and airflow into the plot but keep larvae from escaping (Figure S1a). We released seven third-instar captive-reared Oregon silverspot larvae into each enclosure ($n = 140$ larvae in total) by placing each larva on a centrally located violet plant. On many occasions we watched released larvae immediately begin to feed. We checked enclosures 3–4 times per week, fixing any holes in the mesh and looking for signs of larval feeding. We did not search for larvae because we were just as likely to harm a larva as find one in the process of searching. Once butterflies began eclosing, we checked enclosures daily, marking (see mark-release-recapture methods below) and releasing butterflies on the day they emerged. For each butterfly that eclosed, we recorded the sex, date, and enclosure ID.

In addition to monitoring larval survival, we placed one iButton temperature logger in the center of each enclosure approximately 10 cm above the ground tucked into the vegetation (roughly the location where we observed larval feeding in enclosures). We set loggers to record temperature every 90 min throughout the summer.

We compared larval survival across treatment types and sites by fitting generalized linear models with binomially distributed errors. We included predictor effects of treatment (trimmed vs. untrimmed), site (Rock Creek vs. Bray Point), and their interaction and tested for significance using Wald's chi-square tests. We compared daily maximum, minimum, and mean temperatures across treatments and types with linear mixed effects models. Each temperature model included fixed effects of treatment, site, and their interaction, and random effects of date and enclosure to account for repeated measures in the same location. Data management, statistics, and visualizations were done using R 4.3.0 (R Core Team 2023) and the *tidyverse* (Wickham et al. 2019), *lme4* (Bates et al. 2015), *emmeans* (Lenth 2023), and *car* (Fox and Weisberg 2019) packages.

Captive vs. wild butterflies

We used mark-release-recapture methods (Lebreton et al. 1992; Haddad et al. 2008; Schtickzelle et al. 2012) at Rock Creek to compare phenology, apparent survival, and egg laying rates between butterflies that were: 1) captive-reared larval releases (described above in grass removal experiment, 2) captive-reared pupal releases, and 3) wild. In addition to the larvae we released into experimental plots, we also released 42 larvae, 7 each into 6 mesh enclosures in violet plantings at Rock Creek in coordination with USFWS 2021 release objectives. We marked all adult butterflies that emerged from these enclosures as described above and included them in analyses. In coordination with the Oregon Zoo and USFWS we released 100 captive-reared pupae at Rock Creek. These individuals came from the same cohort as the larval releases but were raised to pupation and prepared for release at the Oregon Zoo according to the Zoo's husbandry protocol (Anderson et al. 2010). Pupae were released in mesh cages (four cages total – 25 pupae per cage, two cages each tucked into the shade at the edge of two meadows; Figure S1b). We checked pupal-release cages daily, recording the date and sex of each butterfly that eclosed and marking its wings with a unique number before release (Figure S2).

We sampled the Oregon silverspot butterfly population at Rock Creek using mark-release-recapture methods. We visited the site every day, unless it was foggy or actively raining, from July 2 – September 14, 2021. In addition to marking captive-reared butterflies as they eclosed, each day we also marked every wild butterfly we could capture and resighted previously marked individuals, both captive-reared and wild. Each time we marked or resighted a butterfly we recorded its GPS location using Avenza maps. For new captures, we also recorded the butterfly's sex. To understand potential differences in the number of females laying eggs between wild and captive-reared females, we recorded when butterflies exhibited oviposition behaviors (i.e. dragging abdomen on the ground and probing vegetation with abdomen).

We used Cormack-Jolly-Seber models to compare apparent daily survival probability (Lebreton et al. 1992) between captive-reared and wild butterflies using the *marked* package (Laake et al. 2013) in R (R Core Team 2023). Apparent survival is the probability of an animal surviving between capture events. In our case, it is impossible to distinguish between mortality and emigration, therefore, apparent survival is the probability that an individual survives *and* does not emigrate from the site between capture events. We estimated survival for each sex and butterfly source (wild, captive larval release, and captive pupal release) combination to better understand similarities between captive and wild butterflies.

The meadows at Bray Point are 10 km north of Rock Creek and are on a steep coastal headland which precluded us from conducting regular mark-release-recapture surveys at the site. Given these constraints, we excluded butterflies released at Bray Point from this analysis.

Results

Invasive grass removal experiment

Of the 140 larvae released, a total of 50 survived to adults – 30 at Bray Point, 20 at Rock Creek. Post-diapause survival was nearly 50% higher in trimmed plots than in untrimmed plots (X^2 = 4.618, df = 1, p = 0.032; Fig. 1). There was no significant effect of site (X^2 = 3.232, df = 1, p = 0.072) or site by treatment interaction (X^2= 0.043, df = 1, p = 0.84).

Maximum, minimum, and mean daily temperatures were all warmer at Bray Point than at Rock Creek (Fig. 2). Only minimum temperatures differed between treatments; trimmed plots were significantly cooler than untrimmed

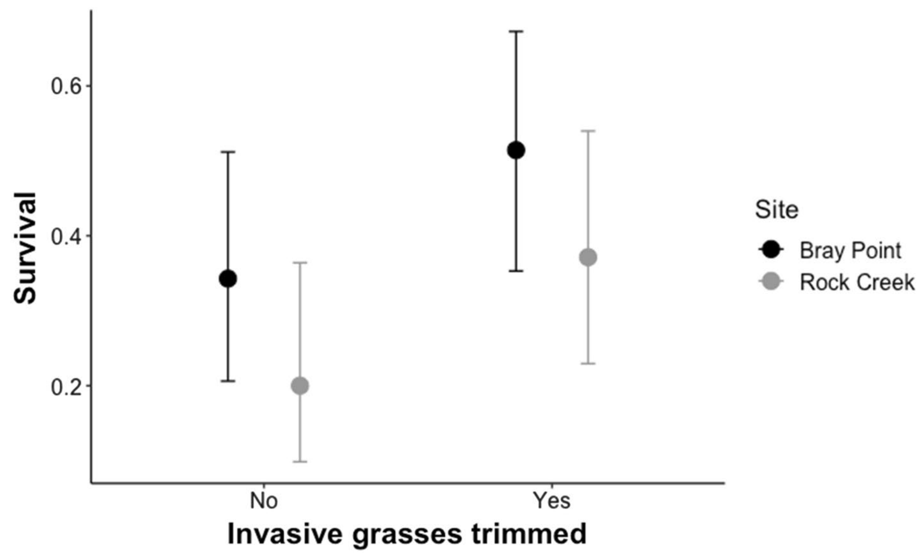

Fig. 1 Model-estimated mean larval survival (survival from 3rd instar to adult) in plots where invasive grasses and thatch were trimmed and untrimmed control plots. Survival in trimmed plots was significantly higher than in untrimmed plots, but there was no significant effect of site. Error bars are model-estimated standard errors

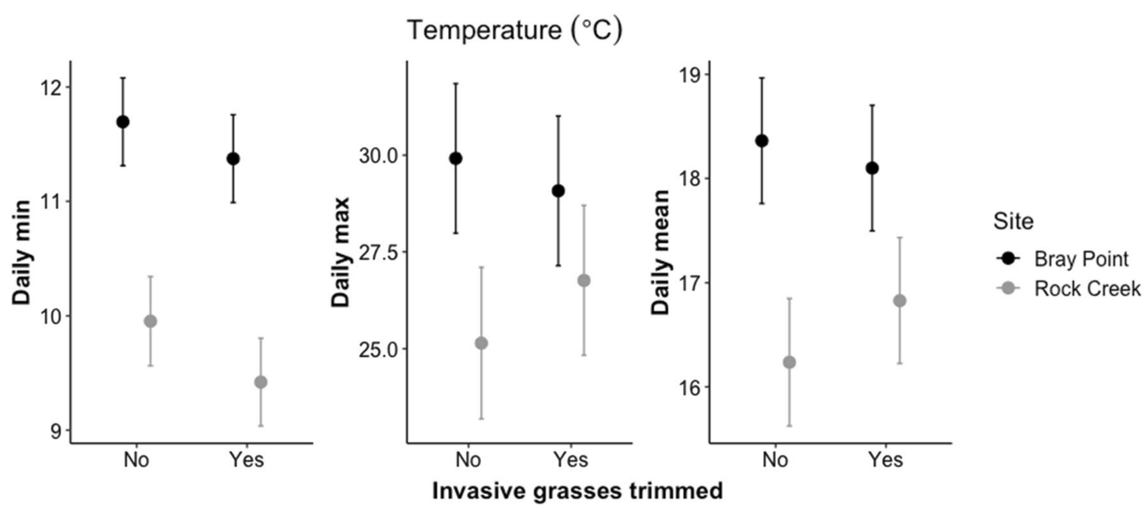

Fig. 2 Temperature by site and treatment (model-estimated means and standard errors). Bray Point was significantly warmer than Rock Creek. Trimming only affected minimum temperatures, which were significantly lower in trimmed plots than untrimmed. Mean and maximum temperatures were not significantly different

plots ($X^2 = 12.0$, df = 1, $p < 0.001$), maximum and mean temperatures were not significantly different between treatments (Maximum: $X^2 = 0.893$, df = 1, $p = 0.765$, mean: $X^2 = 0.165$, df = 1, $p = 0.684$).

Captive vs. wild butterflies

We marked a total of 175 wild butterflies at Rock Creek. Of the 100 pupae we released, 66 eclosed as adult butterflies and were marked. These butterflies along with 55 adults that eclosed from larval releases at Rock Creek (20 from trimming experiment, and 35 from violet plantings), combine for a total of 296 marked butterflies. From these marked butterflies we had a total of 654 resights (Table 1).

We detected the first wild butterflies at Rock Creek on June 25. The first adults eclosed from larval survival enclosures on July 12, 2021, two weeks behind the wild butterflies, and the last butterfly eclosed in an enclosure on August 15, 2021. Pupae were placed in the field on August 2, following Oregon Zoo and USFWS protocol, and butterflies began eclosing on August 7, six weeks after the first wild butterflies were seen at Rock Creek, and continued until August 18. Despite the late release of the pupae, these butterflies did not persist at the site later than wild butterflies. Our last detection of a pupa-release butterfly was on August 31, two weeks before our last observation of a wild butterfly (Fig. 3).

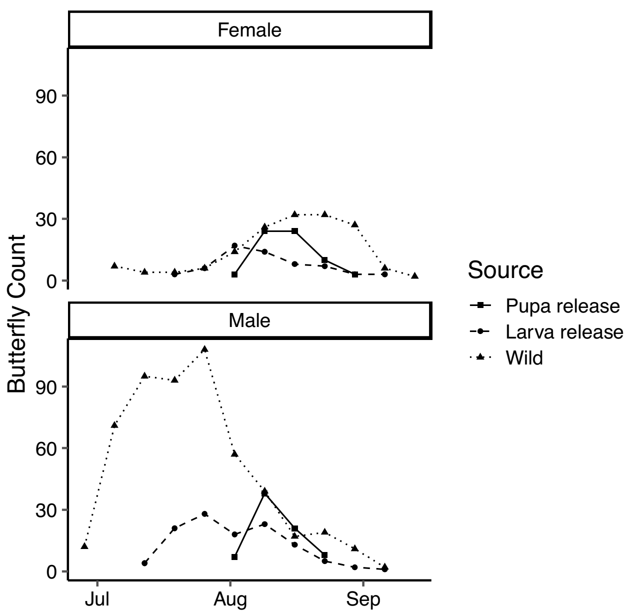

Fig. 3 Phenology of adult butterflies by butterfly source and sex. Y-axis count is total weekly detections of butterflies of each source/sex, this includes newly marked/eclosed butterflies and resights

In the first month of the adult flight season we observed very few female butterflies; only 27 of our 283 female observations occurred before August 1, 2021 (Fig. 3). After August 6, our detections of female butterflies increased dramatically, quickly outnumbering male detections and remaining high until the end of the flight season on September 14, 2021.

We estimated apparent survival for each combination of butterfly source (wild, captive larval release, captive pupal release) and sex (Table 1). Wild female butterflies had the highest mean daily survival estimate (0.959) which translates to the longest lifespan (24 days). Mean lifespan of larval-released females was 4 days shorter than wild females, and 3 days shorter for males. Pupal-released butterflies had the lowest daily survival, and therefore the shortest mean lifespans.

One notable difference between wild butterflies and those that came from the captive rearing program was the proportion of females that we observed laying eggs at Rock Creek. Of the 52 wild female butterflies that we marked, we observed 46% (24 females) of them performing oviposition behaviors. That ratio was considerably lower for both pupal (4 of 31; 13%) and larval (5 of 23; 22%) releases, suggesting that captive females played a small role in total reproduction at Rock Creek in 2021. We first observed wild females exhibiting oviposition behaviors on August 7, 2021. We did not see a captive-reared butterfly lay an egg until August 20, when we observed both larval and pupal released butterflies oviposit.

Table 1 Mark-release-recapture results

Sex	Source	# marked	# resighted	total resights	daily survival	lifespan
M	Wild	123	96	397	0.939 (0.927–0.950)	16 (13–19)
F	Wild	52	33	110	0.959 (0.937–0.973)	24 (15–36)
M	Larva	32	13	51	0.928 (0.894–0.952)	13 (9–20)
F	Larva	23	13	35	0.951 (0.914–0.972)	20 (11–35)
M	Pupa	31	16	38	0.818 (0.744–0.874)	5 (3–7)
F	Pupa	35	15	33	0.873 (0.809–0.918)	7 (5–12)

The number of marked and resighted individuals and total number of resights are summarized by sex-source groupings. Daily survival estimates from mark-recapture analyses, and their corresponding lifespans, are given with 95% confidence intervals in parentheses

Discussion

We demonstrate the importance of evaluating conservation actions through a population dynamics lens. Our tests of current management practices indicate mixed results on the effectiveness of current conservation actions; invasive grass removal nearly doubled larval survival, but captive-reared butterflies (both larval and pupal releases) had lower survival rates than wild butterflies and fewer than 25% of captive-reared female butterflies laid eggs. These results suggest that habitat management that accomplishes the goal of reducing invasive grasses is having intended positive effects (at least in the short-term), but captive rearing and releases fall short of their full potential to benefit the population.

Invasive grass removal

As with other at-risk butterflies, reducing invasive grasses and associated accumulated thatch is key to maintaining habitat that supports populations of Oregon silverspot butterflies (Severns 2008; Cayton et al. 2023; Demarse et al. 2023). There are three key mechanisms that could explain the increase in larval survival we measured in trimmed plots. First, clearing dense vegetation and thatch may have allowed larvae to move between and encounter host plants more easily, increasing the rate of feeding and likelihood of completing development (Bierzychudek and Warner 2015). Second, creating more open and variable habitat structure may have increased microclimatic heterogeneity and therefore the ability of larvae to find warm locations suitable for basking and feeding (Fey et al. 2019; Logan et al. 2019; Rytteri et al. 2021). Finally, reducing vegetation complexity may have reduced predator pressure directly and indirectly (Wiklund and Friberg 2008). We may have physically removed potential invertebrate predators during trimming, and/or altered the abundance and diversity of predators by reducing vegetation complexity (Langellotto and Denno 2004). Regardless of the mechanism, it is clear that restoring open meadow structure will increase Oregon silverspot larval survival.

Captive vs. wild butterflies

To our surprise, captive-reared butterflies and wild butterflies were markedly different in their apparent survival and egg laying. Wild butterflies had higher survival rates and a higher proportion of wild females laid eggs than both larval and pupal-released captive-reared butterflies. The simplest explanation for these patterns is the late timing of captive (particularly pupal) releases which resulted in phenology differences between cohorts. Butterflies eclosed from captive releases two (larval-release) and six (pupal-release) weeks after the first wild butterflies eclosed, but the flight period ended for all butterflies on September 14 when cool, foggy weather returned to the Oregon coast. This reduced the number of days available for captive butterflies to mate and lay eggs relative to wild butterflies. It is also possible that captive-reared females lacked the time necessary to complete oogenesis and begin egg laying before the end of the flight season. Because female *Speyeria* butterflies emerge with undeveloped eggs, they need up to two weeks for eggs to mature after mating (Sims 1984; Kopper et al. 2001) and captive-reared releases timed too late in the summer will reduce egg laying capacity of these individuals. Finally, late releases may contribute to reproductive asynchrony between wild males and captive females, resulting in unmated females who fail to reproduce (Calabrese et al. 2008).

We are unable to differentiate whether increased mortality or emigration rates are the mechanism behind the lower survival rates of captive-reared butterflies that we measured. It is possible that captive-reared butterflies are simply less fit and had lower within-patch survival rates (Lewis and Thomas 2001). Alternatively, high emigration rates of captive-reared butterflies may drive the differences we measured. Butterfly movement is generally more directed and faster in landscapes individuals perceive as "non habitat" (Brown et al. 2017). If captive-reared butterflies did not perceive the habitat at Rock Creek as "high quality", this fast, directed movement may have facilitated their dispersal away from the site soon after eclosing (Schultz 1998; Schultz et al. 2012). In both observational studies and experimental tests of environmental drivers of dispersal, low habitat quality consistently predicts high emigration rates from low resource patches (Baguette et al. 2011; Legrand et al. 2015). In the case of Oregon silverspots at Rock Creek, it is unclear why captive-reared butterflies might perceive the meadows to be "non habitat". It could simply be a translocation effect (Heidinger et al. 2009) or adaptation to high quality host plants fed to larvae in captivity (Turlure et al. 2013).

Implications for insect conservation

We demonstrate that (1) mark-release-recapture of rare butterflies, and (2) experimental habitat manipulation are powerful methods to fill knowledge gaps that often stymie butterfly conservation efforts. These activities can be perceived as too dangerous given the potential to injure individuals and/or damage habitat. However, in this study, through careful experimental design and training of field technicians, we were able to answer key questions with minimal impact to the study population. Identifying differences between captive-reared and wild butterflies can help managers redesign release protocols to increase the contribution of captive butterflies to the wild population. Having quantitative estimates of how habitat management affects survival rates empowers land managers to refine their restoration strategies to maximize benefits to the butterfly population. Neither of these insights are possible without hands-on manipulation and assuming some risk to the focal population. Despite the risks, the lessons we learned help decision-makers make informed, cost-effective decisions to put rare species on the road to recovery.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by E.H. and B.S. The first draft of the manuscript was written by E.H. and B.S. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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