Short communication

Do substitute species help or hinder endangered species management?

Erica Henry[*], Elizabeth Brammer-Robbins, Erik Aschehoug[1], Nick Haddad[2]

Department of Applied Ecology, North Carolina State University, Box 7617, Raleigh, NC 27695, United States of America

ABSTRACT

Substitute species (common species used to represent endangered species) are used to evaluate a range of conservation strategies globally. However, the effectiveness of this approach has not been empirically evaluated. We leveraged a large-scale habitat restoration experiment to test the validity of the substitute species concept. We selected a common butterfly, *Satyrodes appalachia*, that is on first inspection as near a substitute as possible - it is closely related to, overlaps in distribution, habitat requirements, host use, and life history with *Neonympha mitchellii francisci*, an endangered butterfly. We integrated small-scale measures of behavior, habitat preference, and demography of both species in our test, demonstrating that subtle differences between two species cause the substitute relationship to fail. Despite nearly identical habitat requirements, we found the endangered butterfly used different host plants, had higher larval survival in restored sites, and was found in more open habitat than the common butterfly. These differences added up to differences in abundances; the endangered species was more abundant than the common species in restored sites, the opposite was true in un-restored sites. Management decisions based on unvalidated substitute species run the risk of doing more harm than good for endangered species conservation. Instead, using experiments to evaluate a target species' response to management will result in effective recovery strategies.

1. Introduction

Substitute species (common species used to represent at-risk species; Caro et al., 2005) are often at the heart of efforts that cut across a range of conservation goals. They have been used to test habitat restoration strategies (Himes Boor et al., 2018), predict reintroduction success (Parlato and Armstrong, 2018), test effects of toxic substances (Rowe et al., 2009), and model stressor response (Banks et al., 2010). The great risk associated with this strategy is that if substitute species do not respond to actions the same way as at-risk species, they provide false conclusions about the effects of such actions (Murphy et al., 2011). Despite the vast literature published on various types of surrogate species (*e.g.* Lindenmayer et al., 2015), there are no empirical tests of substitute species demography in a restoration context. Without mechanistic tests of the substitute species approach in habitat management, the utility or danger of this approach cannot be understood. We aim to fill this gap by using a common-endangered butterfly pair to test the primary hypothesis that substitute and endangered species populations respond to habitat manipulation in the same direction.

The strongest justifications for use of substitute species are based on demographic and behavioral mechanisms that underlie population viability. If demographic rates of substitute and endangered species respond in similar ways to disturbance, substitutes can inform whether populations of endangered species will shrink or grow in response to conservation actions (Caro et al., 2005). Likewise, if species behave in similar ways (i.e., residence time within and dispersal between degraded or restored habitats), substitutes can be used to identify conservation strategies that will increase population viability and landscape connectivity (Breckheimer et al., 2014). Key to successful deployment of substitute species, therefore, is to evaluate similarities in behavior and demography between substitute and endangered species. This is rarely done.

The question remains: how broadly can one species substitute for another, if at all? We use criteria based on demography and behavior to choose a substitute species that is closely related to, overlaps in habitat requirements and life history with, and occupies the same habitat patches as an endangered species (Johnson et al., 2010; Wahlberg et al., 2002). Working in a large experiment, we test whether two butterfly

species respond in the same direction to restoration. Because local factors ultimately affect population persistence or extinction, we integrate small-scale measures of behavior, habitat preference, and survival rates to assess whether a common species can, in fact, be a good substitute for a rare species. The high degree of similarity between our substitute and endangered species makes for a conservative test of the utility of substitute species to inform conservation decision making for endangered species and therefore has implications for the use of substitute species broadly.

2. Methods

2.1. Study species and site

Neonympha mitchellii francisci (Satyrinae, USA federally endangered) and *Satyrodes appalachia* (Satyrinae, common) occupy sedge-dominated wetlands where larvae feed on sedges, primarily *Carex mitchelliana*. *S. appalachia* ranges across eastern North America. In eastern North Carolina, populations of *S. appalachia* are largely restricted to Ft. Bragg army base where they exhibit strong overlap with the global distribution of *N. m. francisci*. Both butterflies are threatened by lack of disturbance. Historically, open, sedge-dominated wetlands in the southeastern United States were maintained by beaver activity and frequent fires. These two disturbances were nearly eliminated with European colonization, and with them the habitat on which these butterflies depend.

We tested the effects of habitat restoration on demography of *N. m. francisci* and *S. appalachia*, within a habitat restoration experiment. The goal of the experiment was to mimic disturbance created by beavers by removing trees and installing temporary dams (see Aschehoug et al., 2015 and Appendix for details). Tree removal resulted in a four-fold increase in total sedge cover (Aschehoug et al., 2015). Therefore, we pooled data from all tree removal plots which we refer to as restoration plots, and pooled data from plots with no tree removal which we refer to as controls. From 2012 to 2015, we released captive-reared *N. m. francisci* adults into one experimental block. This combination of restoration and reintroduction has resulted in a stable population of ~600 butterflies (Cayton et al., 2018).

2.2. Larval host use and survival

We measured *N. m. francisci* larval survival following methods used for *S. appalachia* survival studies detailed in Aschehoug et al. (2015). We released first instar larvae into experimental field arenas (57 cm tall × 37 cm diameter ring), allowed them to develop, and counted adult butterflies that emerged from arenas. We used a generalized linear model to test whether larval survival differed among treatments and species (for details of data collection methods and statistical model structure for this and other responses, see Appendix). By releasing *N. m. francisci* larvae into arenas, we tested for similarities in host choice. We checked arenas daily, counting larvae and recording the species of sedge on which each larva was feeding.

2.3. Larval foraging height and microhabitat

We measured larval behavior and microhabitat with captive individuals. To measure foraging behavior, we measured height above soil level for 20 larvae of each species twice a week for four weeks. We also measured sedge canopy cover by dropping a pin through the sedges to each larva and counting the number of sedge blades that contacted the pin. To test for differences in foraging height, we used a linear model. To test differences between sedge canopy cover above the two species, we used a chi-square test.

2.4. Adult locations

To test whether adult butterflies select habitat within wetlands based on host resources, microclimate, or some combination of the two, we walked transects and marked with a pin flag the location where we first detected each adult butterfly. At each location, we estimated canopy cover, total sedge cover, *C. mitchelliana* cover and distance to structural boundary. We used linear models to compare each environmental variable between the two species and the two treatments.

2.5. Adult behavior

To understand how vegetation structure affected movement of both butterfly species, we focused on butterflies that we first detected flying. We recorded vegetation type at the initial detection location for each butterfly and at the last detection point where it was lost or landed. We defined three structural vegetation types as follows: 1) Sedge: open, meadow-like, and sedge-dominated with little to no canopy; 2) Shrub: shrubs and vines; and 3) Forest: closed tree canopy. We compared the vegetation types at initial detection locations, as well as transitions between vegetation types across the two butterfly species, with chi-square tests.

2.6. Index of abundance

Each demographic and behavioral response to restoration we measured has the potential to result in differences in relative abundances between treatments. We estimated an index of abundance in each plot using a modified Pollard walk survey (Haddad et al., 2008) and compared indices for both species across plot types, analyzing data from the second flight period in 2015. To compare abundances across plot-type, we conducted a chi-square test.

3. Results

3.1. Larval host use and survival

Sixty-seven percent (± 27%) of *N. m. francisci* fed on *C. atlantica* until they reached fourth instar, after which all *N. m. francisci* larvae fed on *C. mitchelliana*. In prior experiments in these same arenas (Aschehoug et al., 2015), we never observed *S. appalachia* feeding on *C. atlantica*.

Larval survival did not differ between species (Wald's chi-square = 0.65, df = 1, p = 0.42) or treatments (Wald's chi-square = 0.30, df = 1, p = 0.58). The interaction term, however, indicates a trend toward differential survival between *S. appalachia* and *N. m. francisci* across treatments (Wald's chi-square = 2.66, df = 1, p = 0.10; Fig. 1a), especially in the context of small sample sizes. Survival rates of *N. m. francisci* larvae in restoration sites were almost double those in controls, while survival rates of *S. appalachia* larvae in control plots were 10% higher than restoration.

3.2. Larval foraging height and microhabitat

S. appalachia larvae foraged at heights twice as great as *N. m. francisci* ($F_{1,353} = 149.3$, $p < 0.0001$); *S. appalachia* foraged at 12.6 ± 5.2 cm off the soil and *N. m. francisci* at 6.5 ± 3.7 cm. This difference was consistent across larval development, species ∗ date interaction was not significant ($F_{8,346} = 0.25$, $p = 0.98$). The difference in foraging height translated to a difference in sedge canopy cover under which the two species were found, with *S. appalachia* foraging in the open and *N. m. francisci* under cover ($\chi^2 = 134.87$, df = 4, $p < 0.0001$).
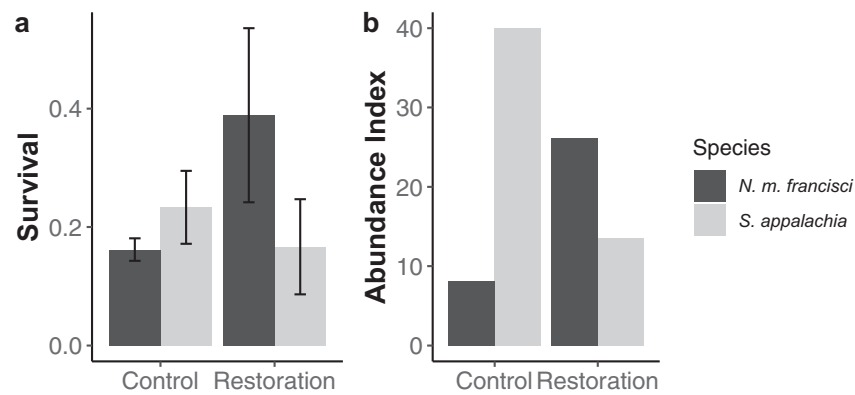
Fig. 1. a) Means and standard error of *N. m. francisci* and *S. appalachia* larval survival. b) Population indices measured for *N. m. francisci* and *S. appalachia*.

3.3. Adult locations

We marked locations of a total of 148 *N. m. francisci* and 135 *S. appalachia* adults. Canopy cover was the only variable that differed between the two species ($F_{1,301}$ = 114.3, p < 0.0001; Table A1). *S. appalachia* butterflies were found under an average of 70 ± 12% canopy cover, whereas *N. m. francisci* were found under only 53 ± 16% canopy cover.

3.4. Adult behavior

We recorded the flight behavior of 230 *N. m. francisci* and 370 *S. appalachia*. The two species differed in initial vegetation type (χ^2 = 93.94, df = 2, p < 0.0001; Fig. A1a), and probability of changing vegetation type, regardless of initial location (starting in sedge:χ^2 = 8.88, p = 0.005; starting in shrub: χ^2 = 7.01, p = 0.03; Fig. A1b, c). Eighty-four percent of *N. m. francisci* were first observed in sedge; 58% of which stayed in sedge and 26% flew into shrubs. *S. appalachia* were almost equally likely to be found in sedge and shrub and most stayed within the vegetation type in which they were initially observed; 17% changed vegetation type.

3.5. Index of abundance

In 2015, *N. m. francisci* abundance in restoration plots was twice that of *S. appalachia* and *S. appalachia* abundance in control plots was five times that of *N. m. francisci* (χ^2 = 23.6, df = 3, p < 0.0001, Fig. 1b).

4. Discussion

We demonstrate that two species that are nearly identical in broad and specific ways (e.g. same subfamily, overlapping habitat, overlapping host use, same life history, same phenology) are not suitable substitutes to guide conservation. *N. m. francisci* and *S. appalachia* differed in resource use, habitat selection, behavior, and survival, ultimately resulting in differences in relative abundances following restoration (Fig. 1, Table 1). Given the tight relationship between our study species in every aspect typically used to choose substitutes across taxa (not just for butterflies), our results call into question the use of substitute species without thorough evaluation.

Our findings are consistent with predictions from niche theory – that even very similar species will occupy different spaces (MacArthur, 1958). Sympatric species are expected to exploit different resources and/or occupy different physical locations at local spatial scales (Schoener, 1968). Therefore, it is not surprising that the two butterflies we studied differed in subtle ways (Table 1). Niche differences, however, do not *a priori* predict differences in response to habitat alteration. Substitute work **does** predict *a priori* that the pair of species will not

Table 1
Subtle differences between *N. m. francisci* and *S. appalachia* butterflies.

Trait	*N. m. francisci*	*S. appalachia*
Larva		
Host plant	*C. atlantica/C. mitchelliana*	*C. mitchelliana*
Microhabitat	Under cover	Exposed
Height on plant	6 cm	12 cm
Survival	Highest in restoration	Highest in control
Adult		
Microhabitat	Sun	Shade
Movement	Prefers open sedge	Equally likely in sedge and shrub
Abundance	Highest in restoration	Highest in control

respond differently to management actions, which we tested explicitly. The differences we measured between butterfly species in terms of host plant use and behavior, added up to differences in abundances; the endangered species was more abundant than the common species in restored sites, and the opposite was true in un-restored sites (Fig. 1b). We show that local differences in the mechanisms of movement and demography, ultimately drive differences in population level response to habitat alteration. Thus, the substitute species approach will fail to support conservation actions if these mechanisms are even slightly different among species pairs.

Improper selection of substitute species can be catastrophic for endangered species recovery. Like other researchers who use substitute species, we assumed the high degree of similarity between the two butterflies and their vulnerability to the same ecological process would result in the same response to habitat restoration (Banks et al., 2010; Himes Boor et al., 2018; Rowe et al., 2009). This was not true (Fig. 1). Restoration strategies based solely on *S. appalachia* responses might have incorporated habitat elements unfavorable to *N. m. francisci*, such as maintaining canopy cover, potentially resulting in local extinctions of *N. m. francisci*. Instead, by studying *N. m. francisci* directly, we learned key aspects of the species' natural history, and how behaviors at a small-scale may promote survival. This kind of detailed information is the cornerstone of successful endangered species recovery efforts (Lindenmayer et al., 2015). Without such information, conservation practitioners are left to make decisions based on gut feelings and expert opinions, which has the potential to do more harm than good for endangered species recovery.

Our test focused on the efficacy of substitute species, but our results call into question the validity of other types of surrogates. Tests of umbrella, focal, and indicator species are faced with the same limitations as those we identified for substitute species: species overlap is not adequate for predicting conservation outcomes. For example, Carlisle et al. (2018) found management strategies designed for Greater Sage Grouse, an umbrella for sagebrush communities, had detrimental effects on populations of other rare, sage-obligate songbirds. This was

despite strong overlap in habitat use. Focal species can be a useful conservation shortcut at the local scale when they are carefully chosen based on life history traits (Nicholson et al., 2013). However, Lindenmayer et al. (2014) found that the most vulnerable species in a landscape are actually not effective focal species, and in fact, can be "antisurrogates". Our results further call into question the ability of one species to substitute for another or a suite of species.

If substitute species are problematic, what is the alternative? First, study the endangered species directly. This is especially important in terms of understanding demographic mechanisms. Had we not released endangered larvae into field experiments, we would still be blind to the essential need for multiple hosts in *N. m. francisci* restoration sites. We recognize that manipulating listed species and their habitats directly carries with it inherent risk; however, those risks are almost always lower than the risk of inaction (Martin et al., 2012). Second, conduct conservation actions in an experimental context. Carefully designed restoration experiments provide the clearest path toward validating or rejecting hypothesis about threats a species is facing (Bradshaw, 1987). Our experimental test revealed that restoration actions improved endangered species habitat through its effects on key resources, and that differences in resource requirements between the two butterflies resulted in the failure of our substitute species. When restoration experiments are incorporated into an adaptive management framework, each experiment will update knowledge, reduce uncertainty, and refine management actions to those that best promote the endangered species (Canessa et al., 2016). Third, center data collection on small-scale habitat selection, movement, and demographic parameters. Our previous studies at large scales supported surrogates (Hudgens et al., 2012); our small-scale studies did not. A small-scale focus places the emphasis on mechanisms that drive population level responses to conservation actions. Finally, incorporate variability into habitat management. Embracing variability in management plans has the potential to accommodate various aspects of an endangered species' life history and behavior, even those that remain unknown (Hiers et al., 2016; Lawler et al., 2015). Incorporation of these elements will redirect a potentially misguided focus on substitute species and improve outcomes of conservation actions for endangered species recovery.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.01.031.

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