Habitat Restoration as a Recovery Tool for a Disturbance-Dependent Butterfly, The Endangered St. Francis' Satyr

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Abstract Habitat restoration is a key management strategy for species that experience loss, fragmentation or degradation of their habitat. The St. Francis' satyr is a federally endangered butterfly found only on Ft. Bragg Army Installation in North Carolina that depends on frequent disturbance to maintain its preferred habitat, ephemeral wetlands. Over the course of 4 years, we restored and maintained critical habitat for the St. Francis' satyr through a combination of hardwood removal and inundation via artificial dams to mimic natural beaver and fire disturbance. Here we present our insights into the challenges of creating and maintaining restored habitat for a species dependent on frequent disturbance, the results of experimental testing of demographic success, and the complexities in carrying out a captive rearing program. We discuss how species that are dependent on disturbance created habitat pose a unique challenge in creating and implementing a long-term plan to maintain a dynamic landscape.

Introduction

The destruction and degradation of native habitat caused by human activities represents the single greatest threat to biodiversity world-wide (Wilcove et al. 1998). To counter the loss of habitat, practitioners are increasingly turning to restoration as a key management strategy for the recovery of imperiled species. Restoration can be a strong tool for creating high quality habitat for a target species, while at the same time improving overall ecosystem health. However, habitat restoration actions have resulted in few successes (Suding 2011). In some cases, a lack of success is because there is no post-restoration monitoring program to assess recovery

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(Bernhardt et al. 2007). In other cases, poorly defined restoration goals make it impossible to evaluate success (Zedler 2007). Restoration actions can also fail (Zedler et al. 2003; Holl and Hayes 2006), or even worse, create habitat that reduces rather than restores biodiversity (Breininger and Carter 2003; Robertson et al. 2013). Here, we present challenges and opportunities for the recovery of rare butterflies focused on restoration experiments.

A commonality shared by many rare butterfly species is the dependence on habitat created by disturbance. Restoration actions can be complicated when disturbance is required for the creation and maintenance of the desired habitat, as is necessary for many butterflies in need of protection. For example, the Schaus' swallowtail (*Heraclides aristodemus ponceanus*) is a federally endangered butterfly endemic to Florida that is subject to frequent tropical storms and hurricanes (Emmel 1995); although hurricanes may initially harm butterflies, they actually benefit from plant growth stimulated at the edge of hardwood hammocks. Fender's blue butterfly (*Icaricia icarioides fenderi*), a federally endangered taxon endemic to Oregon, lives in native grasslands where frequent fire is critical to stimulate growth of its host plant (Schultz and Crone 1998). What becomes immediately evident in any of these cases is that the same process that is required for butterfly persistence has the short term effect of reducing butterfly populations where the disturbance occurs.

In general, restoration programs focus on the creation of habitat with a single management action resulting in long-term, high quality habitat. Dynamic, disturbance dependent habitats present a challenge for managers because they require continued intervention in order to maintain high quality habitat. The integration of disturbance into restoration plans creates a unique challenge for managers, who must balance creating and maintaining habitat sufficient for recovery while also allowing for landscape scale processes, such as plant community succession, to continue.

Here we present our efforts to restore habitat and assess recovery success for the disturbance-dependent St. Francis' satyr (Neonympha mitchellii francisci), a federally endangered butterfly restricted entirely to Fort Bragg Military Installation in central North Carolina. Its primary habitat is herbaceous wetlands dominated by sedges (e.g. Carex spp.) along small riparian corridors. In North Carolina, this habitat is created when beavers abandon ponds, or by fires that reverse the rapid transition from open wetlands to closed canopy riparian forest (Kuefler et al. 2008; Bartel et al. 2010). However, the extirpation of most beavers from the region by humans a century ago, the suppression of fire, and increased human activity in the form of agriculture, development, roads and foot traffic, has eliminated or isolated much of the historic habitat. Because the habitat is naturally shortlived in space and time across the landscape, the St. Francis' satyr exhibits classic metapopulation structure, with small subpopulations that are distributed patchily within the landscape to form a single large population. The largest known subpopulations of St. Francis' satyrs are in artillery ranges on Fort Bragg, where a lack of roads, frequent small fires, and beavers have allowed for the persistence of high quality habitat. Little is known about the size of these subpopulations because highly restricted access to the sites precludes rigorous data collection. Outside of these areas, the number of subpopulations has been reduced from 5 to 2 in the last 15 years. In total, the remaining St. Francis' satyr habitat is thought to comprise 2-5 ha with an overall population size in the low thousands.

In order to maintain and increase the subpopulations of butterflies outside of the artillery target zones, we initiated a long-term restoration project in 2011 near remaining or historic St. Francis' satyr sub-populations. Through a combination of hardwood removal and inundation via artificial dams, we attempted to mimic the natural process of herbaceous wetland creation using a factorial experiment framework. Within our experimentally restored sites, we were restricted in the ways we could assess the response of St. Francis' satyrs to restoration because of its endangered status. Instead, we conducted detailed experiments on a closely related surrogate species to estimate butterfly population growth rates in different restored habitat types as a way to assess successful recovery. We also released captive reared adult butterflies into restored sites, and conducted transect surveys to track natural colonization of our restored sites over time. In this chapter, we present our insights into the challenges of creating and maintaining restored habitat for a species dependent on frequent disturbance, the results of experimental testing of demographic success, and the complexities in carrying out a captive rearing program.

Natural History

The St. Francis satyr is a small, brown butterfly that is a subspecies of *Neonympha mitchellii* (Fig. 1). The St. Francis' satyr is bivoltine, with adults emerging in late May through early June, and in late July through early August (Fig. 2). Extensive searching has determined that St. Francis' satyrs occur only on Fort Bragg military base, located in central North Carolina. Ft. Bragg is in the Sandhills region, and supports mostly longleaf pine forest with bottomland hardwood forests along stream floodplains. These streams dissect much of the terrain, but drainages are often interrupted by dirt roads used as fire breaks spaced every ≈ 200 m. Historically, fire played a large role in suppressing woody undergrowth along stream corridors and maintaining open herbaceous meadows. However, fire suppression is now common throughout the region. Current management plans at Fort Bragg include burning the pine understory approximately every 3 years, and largely exclude fire from riparian zones.

This stream network is also often modified by beavers, which dam portions of a creek to create flooded ponds that usually kill most standing hardwoods. Once these dams are abandoned and flood waters subside, the habitat is ideal for supporting wetland plants such as sedges in the *Carex* family. This includes *C. mitchelliana*, which is thought to be the main host plant for St. Francis' satyr larvae based on its successful use in captive rearing and its ubiquity in sites where St. Francis' satyrs are found. Other potential host plants that could support St. Francis' satyr larvae include *C. lurida* and *C. atlantica*, which larvae will eat in captivity, and *C. turgenscens*, which is widespread throughout the wetlands in artillery ranges.



Fig. 1 St. Francis' satyr (*Neonympha mitchellii francisci*), female, Fort Bragg, North Carolina (Photo by Melissa McGaw, North Carolina Wildlife Resources Commission)

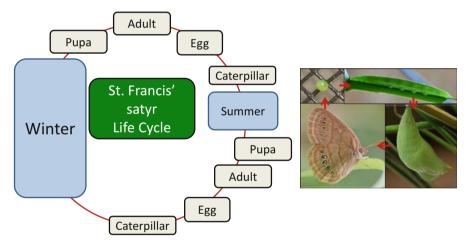


Fig. 2 Life cycle of the St. Francis' satyr (Neonympha mitchellii francisci)

Habitat Restoration

Our short-term goals upon starting restoration were threefold: (1) to document how restoration work impacted the plant communities in the wetlands, in particular sedge species; (2) to test whether hardwood removal, inundation, or a combination of both would best support St. Francis' satyr population growth; and (3) to establish populations of adult St. Francis' satyrs through the release of captive-reared individuals.

Long term data will better determine if restoration sites support growing or declining subpopulations, and how this may affect the fate of the overall population.

We focused restoration on two separate creeks outside the artillery ranges where St. Francis' satyrs have been found historically. Both creek systems are subject to woody encroachment, dry soils, and human activity that can quickly reduce the abundance of sedges. Historically, these two creeks supported two of the largest St. Francis' satyr subpopulations outside of artillery ranges, although numbers were low and in decline due to drought and woody encroachment when restoration began in 2011. As of 2014, no butterflies had been detected outside of restoration areas at either creek, indicating a need for urgent management.

A crucial aspect of restoration experiments is that they represent management actions that are practical. To insure this, we worked with local land managers to develop restoration treatments and methods that could easily be incorporated into future management actions at our study site. We restored wetlands using two techniques: manual removal of hardwoods and inundation. Both of these techniques represent a difficult trade-off for restoring habitat, as both are the result of natural disturbance and last for only a short time. In the case of the St. Francis' satyr, there is a relatively short period of time where habitat conditions are optimal. After disturbance, grassy wetlands quickly transition to hardwood forest, eventually reducing habitat quality for the butterfly. The inconsistent and random nature of disturbance in our system means that within a few seasons, the habitat must be re-evaluated to determine if disturbance is needed again. In light of these challenges, we planned our restoration activities with the knowledge that the effects of restoration were likely to be short-lived.

To create restoration sites, in the spring of 2011 we established four restoration areas, each containing four 30 m×30 m experimental plots. In each area, plots were randomly assigned to one of four treatments in a factorial design: (1) manual removal of most trees; (2) installation of temporary dams; (3) both tree removal and installation of dams; and (4) no manipulation. Tree removal was intended to increase light availability within wetlands to encourage herbaceous plant growth. We intentionally left ≈ 10 % of the trees in order to mimic the canopy structure found in beaver-created wetlands in our area. We maintained tree removal treatments by cutting back the re-sprout of trees and shrubs in 2012 and 2013 to suppress hardwood canopy regeneration. Damming was intended to increase soil moisture and the amount of standing water, a key requirement for sedges. In dammed plots, we installed 0.5 m high and 1 m wide water-filled temporary coffer dams (Aquadam Inc., Scotia, CA, USA) across the length of the downstream edge of the plot, which inundated ≈ 10 m of the downstream portion of the plot. Within each plot we established vegetation subplots that were surveyed for percent cover of all sedge species and the major vegetation types (e.g. grasses, forbs, and shrubs) prior to restoration in Spring 2011, as well as in Fall 2011, Spring 2012, and Spring 2013.

Restoration of wetland habitat via the removal of trees had strong effects on the plant community. Tree removal had a significant positive effect on sedge populations, with the average percent cover of *Carex mitchelliana*, an important host plant for St. Francis' satyr, more than doubling (from 3 to 7 %) and the percent cover

of all sedge species combined more than quadrupling (from 7 to 31 %) from 2011 to 2013. The percent cover of all understory vegetation also increased significantly in tree removal plots, with an increase from 34 to 73 %. In contrast, damming did not have a significant positive effect on the percent cover of *C. mitchelliana*, all sedges, or all understory vegetation.

By experimentally testing each restoration treatment independently, we were able to identify tree removal as the most important factor determining host plant size and abundance in our system. The increases in sedge and understory cover are likely due to increases in light availability. It is important to note that increases in host plants do not guarantee butterfly population recovery success, but do create a favorable landscape for individuals to become established.

The disturbance-dependent nature of these herbaceous wetlands means that our results, while positive, do not necessarily represent a long-term, stable change to the plant community. Without continued intervention, restoration sites are likely to revert back to original conditions, with woody encroachment reducing the herbaceous understory. There is a challenging balance between constant maintenance of host plant dominated communities, and allowing natural regeneration of trees to occur. Ultimately, the amount and frequency of management actions can only be determined by understanding the population dynamics of St. Francis' satyrs over time.

Assessing Restoration Success

Deciding how to measure the success of restoration is as critical as determining what the restoration actions will be. While presence/absence counts of a target species are easy to conduct with minimal time and effort, they give little indication of whether the dynamics within the restored area are favorable to long-term success. Even population counts, which superficially give a measure of success by showing quantitative changes in population size, provide little information on whether populations are growing due to recruitment via immigration or reproduction within the site. Thus, it is vital to measure demography in addition to population size. Demographic rates provide information on whether a population is growing (i.e. the number of births exceeds the number of deaths) without the complication of considering immigration from outside areas. The ultimate goal of restoration is to create stable, increasing populations; therefore, success can only be determined by explicitly measuring population growth rates independent of immigration and dispersal.

To understand more about the population growth rates of St. Francis' satyrs in our restoration plots, we experimentally estimated the survival rates of eggs and juveniles of the closely related surrogate species Appalachian Brown butterfly (*Satyrodes appalachia*). The Appalachian Brown is a locally rare, bivoltine butterfly that prefers *Carex* species as a host plant, and is found in the same herbaceous wetlands as St. Francis' satyrs (Hudgens et al. 2012) at our study site. We chose to use a surrogate species because of the limited population size of St. Francis' satyr, and because of the tremendous risks restoration experiments conducted with an endangered species pose to individuals and the population as a whole. However, the use of a surrogate species, no matter how similar in behavior and biology, runs the risk of not accurately representing how the imperiled species will respond to restoration. Therefore, experiments using a surrogate species should be, when possible, coupled with additional measures of success that relate directly to the target species such as population counts via detailed surveys.

Determining population growth rates, whether using a surrogate or not, is complicated by the cascading effect restoration can have on the environment. Changes can occur in both biotic factors, such as host plant abundance or quality, and abiotic factors, such as temperature and light conditions. These changes can directly impact the target species by creating high quality habitat for development and breeding; however, these changes can also have unintended indirect effects, for example by improving habitat conditions for predators. For St. Francis' satyrs and Appalachian Browns, an open canopy provides additional light for *Carex* growth, but also makes it easier for known aerial predators such as dragonflies to prey on adult butterflies, and for ants and spiders, which prey on eggs and small larvae, to move and hunt. Therefore, it is important to determine how restoration activities both directly and indirectly impact different life stages of the target species, and strike a balance between habitat that supports butterflies but does not encourage predators to proliferate.

To estimate the direct and indirect effects of restoration treatments on *S. appalachia* demography, we estimated egg survival and larval to adult survival independently. To estimate egg survival, we placed greenhouse raised, potted *C. mitchelliana* plants with a known number of eggs into our established experimental restoration plots and counted the number of eggs that remained after 48 h. We first caged wild-caught *S. appalachia* females on potted sedge plants in a greenhouse at Fort Bragg, and counted the number of eggs laid. Each restoration plot received one pair of potted sedges, one randomly assigned to a predator exclusion treatment and a second that was accessible to all predators. Plants in the predator exclusion treatment were enclosed in a cage constructed from a 20 L fine mesh fabric paint strainer and bent wire. A 15-cm band of Tanglefoot[®] insect barrier was applied to pots to exclude crawling predators. Paired plants were placed in the center of each restoration plot on dry ground within 5 m of each other. All plants were removed from the field after 48 h and we counted the number of eggs remaining.

To estimate survival over the larval and pupal stages, we deployed a known number of larvae into experimental arenas created in each plot and counted the number of butterflies that emerged. We constructed larval arenas by removing the ends of a standard 55 gal polyethylene food grade drum and cutting the remainder into thirds, resulting in an approximately 57 cm diameter \times 35 cm tall ring. At six randomly chosen locations in each plot, rings were buried approximately 10 cm into the ground surrounding naturally occurring, mature *C. mitchelliana*. In one block with low sedge abundance, field cages were placed around greenhouse raised and transplanted *C. mitchelliana* plants. We randomly assigned each arena to a predator-free or predator-accessible treatment. Predator-free arenas were enclosed with tulle

netting that was secured to the outside of the rings using nylon straps and tied at the top of a vertical support structure to hold the fabric off the plants. All potential predators were manually removed from predator-free arenas prior to addition of larvae. Arenas accessible to predators remained open during larval development, but once pupae were observed, arenas were enclosed with tulle netting to facilitate capture of emerging adults. Five larvae varying in age from first to third instars (most commonly second instars) were placed into each arena in a block on the same day. Larvae were left to develop in the field. After the observation of pupae, arenas were checked daily for newly emerged adults until no butterflies were found for five consecutive days.

Despite the fact that our restoration treatments had strong, differential effects on our wetland systems, such as increases in sunlight, water, and host plants, we found that these differences did not affect the survival of eggs, larvae or pupae when protected from predation. This suggests that common mortality factors in early stage development like egg desiccation and plant quality are likely not important drivers of population growth rates of *S. appalachia*. It also suggests that the location of a host plant is not as important as the presence of the host plant. *S. appalachia* appear to be robust to a wide range of water and temperature regimes as they develop, and potentially can be successful as long as they have access to their host plant without excessive predation.

Another important finding from our experiments is that restoration treatments had different effects on the levels of predation experienced by eggs and juveniles. When eggs were exposed to predation, survival in the three types of restored plots was about one-third the survival in control plots, meaning our manipulation of tree cover and standing water appears to have substantially increased predation of butterfly eggs. In contrast, when juveniles were exposed to predation, survival rates were different depending on the type of restoration. Survival in dam only plots was twice that of both control plots and plots where both trees were removed and dams installed, and five times that of tree removal only plots. The differences in predation among restoration treatment types appear to be driven by changes in access to juveniles by ground predators. The installation of dams increased the amount of standing water within our plots and likely reduced the ability of ground predators, such as ants and spiders, to gain access to juveniles.

Interestingly, these predation effects appeared to outweigh any potential benefit butterfly populations might gain from the restoration of plant communities. Tree removal treatments tripled potential host plant cover, but also led to the highest rates of predation for both eggs and juveniles. The addition of dams decreased predation of juveniles, but did not increase the abundance of host plants. Most importantly, we found that no single restoration treatment both increased host plant abundance and egg or juvenile survival. These results highlight the need for experiments that carefully measure the recovery potential of different restoration methods across all life stages of butterflies. In our case, because of the conflicting effects we found, further work is needed to fully understand how our restoration treatments impact population growth rates. Only when this is complete can we expect to guide management decisions for restoration.

Population Expansion: Natural Colonization

Even if restoration actions result in the creation of habitat that supports growing populations of butterflies, the establishment of new populations first requires successful colonization. Ideally, individuals are able to reach restored habitat via natural dispersal because this allows the overall population to both grow at a sustainable rate, and ensures that individuals can move freely between subpopulations, which is important for maintaining genetic diversity. Where restored habitat is in close proximity to existing populations, or can be connected via corridors, the likelihood of natural colonization may be high. Detections of natural colonization are a critical first measure of success, and support the need for close monitoring to determine where and when individuals arrive.

In May 2012, the first flight period after restoration activities were completed, we detected the first St. Francis' satyr adult in a restoration plot. This individual was undoubtedly a wild individual, because St. Francis' satyr were not present in restoration sites prior to restoration and no captive reared individuals were ever released into this restoration site. However, there is no way to distinguish whether it emerged in the restoration plots as a result of a prior colonization event or dispersed there as an adult from the historic colony that is located less than 250 m away. This natural colonization event was followed by several other detections of individuals during that flight period and in subsequent flight periods. The continued detection of individuals over time confirms that natural colonization by St. Francis' satyrs is possible between our restoration sites and existing subpopulations.

Following these colonization events, we were able to use daily transect surveys to assess the overall population trend across multiple years (Fig. 3). While populations in non-restored areas remained relatively stable, populations in restored areas showed an increase each year. This information was a valuable first step in determining whether restoration is successful in sustaining a growing population,

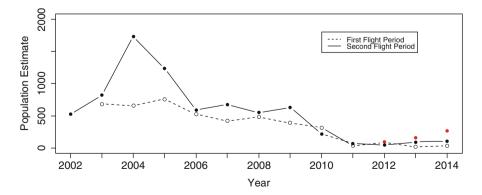


Fig. 3 Population size of St. Francis' satyrs outside of artillery ranges on Fort Bragg from 2002 to 2014. *Red points* in years 2012–2014 represent the overall population size when individuals from restoration sites are included

and represents more than we could have determined with simple presence/absence surveys. When combined with demographic data from the surrogate species, it allows us to gain a much broader view of overall population dynamics. We are now in a position to not only measure success in a quantitative way, but also have a better sense of what future population trends will look like.

Population Expansion: Captive-Reared Releases

Although natural colonization is ideal, in many cases it is unlikely or even impossible. Impediments such as low population size, limited dispersal, human development, or poor surrounding habitat conditions may prevent individuals from moving into restored areas on their own. In such cases, artificially colonizing sites through the release of captive-reared individuals may be the best strategy to populate a restored area. For the St. Francis' satyr, restoration on one creek allowed for natural colonization. However, the restoration area on the second creek was so isolated from other existing populations that natural colonization was not possible. We considered the release of captive-reared St. Francis' satyrs to be critical to the success of restoration in this scenario, so we began a captive-rearing program to create new subpopulations and augment the existing overall population.

In 2012, we expanded our captive-rearing program into a large greenhouse on Fort Bragg in order to control temperature, exclude predators, and ensure a constant population of host plants. We maintain the greenhouse at approximately ambient temperature year-round, and keep a continuous stock of mostly C. mitchelliana available for larval growth and adult breeding. To generate a captive stock, we collect 3–5 females from artillery ranges during both flight periods, when possible. Females were kept for up to 72 h in small oviposition chambers in order to collect eggs before being released at one restoration site. All eggs were placed in a small dish at the base of a *C. mitchelliana* plant. We allowed newly hatched caterpillars to crawl onto the plant unassisted. This process was closely monitored; we manually assisted caterpillars that were unable to find a leaf on their own. Once on the plant, caterpillars developed without further assistance. Captive rearing enclosures were monitored daily for the presence of predators and to ensure all C. mitchelliana plants were healthy. Because we carefully controlled the greenhouse temperature to match our site conditions, captive-reared adults emerged at approximately the same time as the wild population. We marked all individuals with a unique ID and released them at a restoration site within 24 h of emergence.

We successfully raised St. Francis' satyrs from egg to adult stage for every flight period where we were able to collect wild eggs (Table 1). Wild females collected from artillery ranges laid an average of 16 eggs per female, although not all females laid eggs, indicating that we captured some females prior to mating. Although the success rate for eggs transitioning to caterpillars was variable, our success rate for obtaining viable adults once individuals survived to the caterpillar stage averaged 56 % when years when no eggs were laid are excluded.

Year	Flight period	Captured females	Eggs	Caterpillars	Adults	Survival rate
2011	1	3	60	10	9	0.90
	2	5	142	86	32	0.37
2012	1	4	65	59	27	0.46
	2	0	0	0	0	0.00
2013	1	4	102	76	47	0.62
	2	0	0	0	0	0.00
2014	1	5	122	62	28	0.45
	2	4	88 ^a	70 ^a	NA	NA

Table 1 Results of captive-rearing of St. Francis' satyrs from 2011 to 2014

Eggs were collected from wild females captured in artillery impact areas. Years with no eggs were a result of no trips taken into artillery impact areas during the flight period ^aIncludes eggs and caterpillars from one captive female who successfully mated

Table 2Population estimates based on Pollard-Yates indices of four restoration plots from 2012to 2014

		Captive adults	Wild females	P-Y index	P-Y index (unmarked	Population
Year	Flight	released	released	(unmarked)	and marked)	estimate
2012	1	0	0	0	0	NA
2012	2	27	0	0	1.3	11
2013	1	0	4	0.45	0.45	NA
2013	2	47	0	5.42	9.07	106
2014	1	0	5	3.00	3.00	32
2014	2	28	4	12.25	14.65	175

Some flight periods had too few individuals to estimate population size

We released captive-reared individuals into the same site each flight period beginning in the second flight period of 2012 (Table 2) and detected unmarked individuals there during each subsequent flight period. These unmarked individuals represent wild individuals that are almost certainly the result of successful breeding within the restoration site because the only existing subpopulations are too far away to have such a large and immediate effect via dispersal and colonization. We detected an increase in population size during each successive year through the use of transect surveys. Our most recent estimate is of almost 200 individuals across our restoration site, which is approximately 1/2 ha in size.

In the 3 years since restoration began, we have noticed a distinct increase in the overall St. Francis' satyr population, owing mostly to individuals seen in restored sites (Fig. 3). This increase follows several years of decline in historic sites, where populations still continue to decline due to dry conditions and woody encroachment. Without the additional restoration undertaken in 2011, it is possible that St. Francis' satyrs may have gone extinct at all sites outside of the artillery ranges. Our current positive trend shows great promise for the successful restoration of St. Francis' satyrs, although long term data will be needed to determine how long habitat persists after intervention, and whether the overall population will continue to grow naturally.

Summary and Key Points

- Restoration can be an important step in managing for rare and endangered species that encounter habitat loss or fragmentation, especially when conducted within a factorial experimental framework. Without a clear structure for determining which specific restoration activities are effective, it is difficult to fully understand which actions contribute to population growth.
- Species that are dependent on disturbance created habitat pose a unique challenge in creating a long-term plan to maintain a dynamic landscape.
- Disturbance-dependent species such as the St. Francis' satyr can be managed with multiple restoration techniques such as inundation and hardwood removal, but long term success requires monitoring to determine the continued effective-ness of the restoration actions.
- Captive-rearing can be a highly effective method of augmenting existing populations and artificially colonizing restored sites that may otherwise see little or no dispersal from already established populations.
- Success is best determined by closely measuring the population growth rates of butterflies in restored sites. However, other measures, such as adult survivorship, breeding capacity, or vegetation growth may serve as a suitable proxy. Importantly, goals should be clearly outlined at the start of a restoration program so that the appropriate measures of success can be implemented.
- Restoration requires several years of monitoring to determine its effectiveness, especially with rare or endangered butterflies, where a short time span of only one flight period or one season is unlikely to accurately assess population trends. Continuous monitoring over several seasonal cycles is the only way to determine population trends, which are the best indication of whether restoration has been successful.

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