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NATURAL HISTORY AND CONSERVATION STATUS OF THE ENDANGERED MITCHELL'S SATYR BUTTERFLY: SYNTHESIS AND EXPANSION OF OUR KNOWLEDGE REGARDING *NEONYMPHA MITCHELLII MITCHELLII* FRENCH 1889

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ABSTRACT. The Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii* French 1889 is a federally-listed endangered species found in parts of the eastern United States of America. Because of its endangered status, considerable research efforts have been devoted to understanding its biology, ecology, and its conservation. Despite these efforts, information about *N. m. mitchellii* has not been summarized for more than a decade. Here we summarize and expand upon the work conducted by governmental and not-for-profit agencies that have produced reports that are not easily accessible to researchers or interested lepidopterists. In addition to summarizing the literature, we present data from feeding trials and also demonstrate that microclimates exist that may be exploited by larvae. We conclude by identifying key areas of needed research and describe steps imperative to the recovery the Mitchell's satyr.

Additional key words: endangered species, Satyrinae, Lepidoptera

The Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii* French 1889 (Nymphalidae: Satyrinae) is a federally-listed endangered species found in parts of the eastern United States of America. As one of only 60 endangered insects, and one of only 20 federally endangered Lepidoptera in the US, it is of particular interest to conservation organizations and butterfly enthusiasts alike (US Fish and Wildlife Service 2011). As a result, a considerable amount of research effort has been devoted to understanding its biology and ecology, as well as studies that inform its conservation. Adding to the uniqueness of *N. m. mitchellii* as a target of conservation, is the fact that its sister taxon, the Saint Francis' satyr, *N. m. francisi*, is also endangered in the US. Morphologically similar to Mitchell's satyr, *N. m. francisi* is known from only one small region of North Carolina on the Fort Bragg Military Reservation. While the Saint Francis Satyr has recently received a thorough treatment of its natural history and population biology by Kuefler et al. (2008), information about *N. m. mitchellii* has not been summarized for more than a decade (Shuey 1997). In that time, considerable new findings have emerged that fundamentally shift our understanding of the species and the prospects for its long-term conservation.

One key discovery that has changed the way we perceive Mitchell's Satyr is the discovery of new populations that greatly expand its known geographic range and habitat use patterns. Discovered in Virginia, Alabama and Mississippi in 1998–2004 (Roble et al. 2001, Hart 2004), these new populations are designated as *N. mitchellii* but are extended the same federally endangered status of *N. m. mitchellii* populations found in Michigan and Indiana [hereafter we use *N. mitchellii* to refer to the species in the broad sense, i.e. including both the northern, and southern populations but excluding the Saint Francis' satyr, and *N. m. mitchellii* to refer specifically to the protected northern populations]. These new populations offer unique opportunities to explore the natural history of the Mitchell's satyr throughout a larger portion of its historic range and to conduct new investigations that may inform its conservation more broadly. While the new populations may increase options for recovery, within Michigan and Indiana there is evidence that *N. m. mitchellii* populations are being lost at an alarming rate, emphasizing the pressing need for effective recovery plans based on sound conservation science (Landis et al. 2011).

Given its protected status, governmental and not-for-profit conservation organizations have spent thousands of person hours investigating aspects of *N. mitchellii* biology. Unfortunately, many of the reports generated by these efforts enter the so-called "grey literature," and are not easily accessible to academic researchers or lepidopterists. During many conversations with both researchers and butterfly enthusiasts it has become clear that much confusion surrounds the biology of Mitchell's satyr, sometimes with little distinction between lore and published data. As such, one goal of this paper is to synthesize and update the literature surrounding *N. mitchellii*. In addition, by pointing to critical gaps in our knowledge, we hope to prioritize future research needs for effective conservation of this endangered species.

Physical Description. The following physical descriptions represent those typical of *N. mitchellii* and are not absolute descriptions. All traits are variable and when there are major deviations from the typical forms they are noted as such. The eggs of *N. mitchellii* appear light to pale lime green (see McAlpine et al. 1960 for detailed line drawings of all immature stages) with their color imparted by the developing embryo, since the chorion itself is transparent (C. Hamm pers. obs). The egg is spherical in shape with a diameter between 0.7 and 1.0 mm and covered with an alveolate sculpturing (Harris 1979). Within two days before hatching, the developing head capsule is visible as a dark spot within the egg (McAlpine et al. 1960, Legge & Rabe 1996, C. Hamm pers. obs.).

First instar larvae have a conspicuous dark brown head capsule and bilobed projections that are common to satyrine larvae (Wagner 2005). First instars range in length from 3 to 4 mm (McAlpine et al. 1960, Szymanski 1999) and are cylindrical in shape, with the tip of the abdomen terminating abruptly. All subsequent instars (total of 5) have a green head capsule and retain the bilobed shape, with the abdomen terminating in a bifurcated process. These later instars, which are 6–12 mm in length, also possess two raised white ridges on the dorsum that traverse the antero-posterior axis from the prothoracic segment to the tip of the abdomen. Additionally, later instars are covered with irregular white papillae. Larvae are cryptic and extremely difficult to locate in the field (Darlow 2000). Observations on the size of *N. mitchellii* larvae may be upwardly biased since they were based on individuals reared in captivity under conditions that may not approximate those in nature (McAlpine et al. 1960, Wilsman & Schweitzer 1991, Legge & Rabe 1996, Darlow 2000; B. Bergman pers. comm., M. Nielsen pers. comm.). The pale green chrysalis is suspended from the cremaster in the head down orientation typical of many satyrine butterflies (Mosher 1916, DeVries 1987), and is between 10 and 15 mm in length. As with the egg, it is the developing imago that imparts color to the pupa, the actual integument being translucent and smoky in color (McAlpine et al. 1960, C. Hamm pers. comm.). Approximately 48 hrs prior to eclosion the chrysalis begins to transition its color from light green to medium brown.

The adult Mitchell's satyr butterfly was described based on a series of six males and four females collected by J.N. Mitchell, a professor at the University of Michigan (French 1889). The type series was collected in Cass County, Michigan from an "upland dry meadow," but these butterflies likely originated from the nearby prairie fen (French 1889, McAlpine et al. 1960, Shuey 1997). Over the years *Neonympha* Hübner has been synonymized into *Euptychia* Hübner and *Cissia* Doubleday, but is currently recognized as valid (Dyer 1902, Hemming 1937, Lewis 1974, Hamm 2007, Pelham 2008).

Imagos of *N. mitchellii* are medium-sized brown butterflies that resemble many of the other members of the Satyrinae. Male *N. mitchellii* have a wingspan of roughly 2.5 cm while females are larger, with a wingspan of approximately 3.0 cm (Hamm et al. 2010). The Mitchell's satyr was originally described with a medium brown dorsal wing surface and lighter brown ventral wing surface, with females darker than males (French 1889). Subsequent research has noted that both sexes are darker when they first emerge from the chrysalis and may even have a 'sheen' to them, which wears off within hours of eclosion (Barton & Bach 2005). In addition, *N. mitchellii* color appears to vary throughout its range, may be polyphenic (from tan to a dark brown) and associated with the hydrology of sites (Brakefield 1996, Hamm 2009). We have observed that, in general, sites with high levels of water are associated with darker butterflies (Hamm 2009), although this observation remains to be quantified. Similar observations have been made for other butterflies, including satyrs (Brakefield 1996). Color polyphenism is thought to provide an advantage by correlating the color of the butterfly more closely with its habitat (Brakefield 1996). High water levels support more lush plant growth, against which a light colored butterfly would stand out. By being darker when there are higher levels of ground water, the butterfly is presumably able to blend in more effectively. Adult *N. m. mitchellii* are rather short lived, with the average male living between two to five days

Fig. 1. Dorsal (left) and ventral (right) wing pattern from the right wing of a male *N. mitchellii* specimen collected at the Kellogg Biological Station in 1953. This population was extirpated in the 1960s.

and the average female two to four days (Szymanski et al. 2004).

One of the most conspicuous characters noted in the descriptions of *N. mitchellii* is the prominent border ocelli on the ventral surface of the wings. Border ocelli, sometimes mistakenly referred to as eye spots (Nijhout 1991), are situated in cells between wing veins in the postmedial area of the wings (Fig 1). Females have the same number of border ocelli as males but they tend to be larger (C. Hamm unpub. data). On the forewing, border ocelli may be found in the cells M_1, M_2, M_3 and Cu_1, and on the hindwing the border ocelli may be found in the cells R_5, M_1, M_2, M_3, Cu_1 and Cu_2. Based on preliminary data from over 300 museum specimens, each *N. mitchellii* male forewing usually has three and each hindwing has six ocelli (Fig. 1).

Each ocellus appears as two concentric rings of pigment, with an outer ring of buff yellow and an inner ring of black, centered on a silver focus (Fig. 1). In contrast to the original description, which holds that all border ocelli are circular (French 1889), ocelli actually range in shape from circular to oval (C. Hamm unpub. data). A pair of bands surrounding the border ocelli often converge at the leading and trailing edges of the wings. These bands correspond to the proximal and distal bands of the central symmetry system (Nijhout 1991) and range in color from light orange to brown. The thorax and walking legs of *N. mitchellii* are densely covered with setae and scales similar in color to that of the wings, though the setae projecting off of the prolegs are often a dark brown.

Distribution. Our understanding of the range of Mitchell's satyr has continued to evolve over time. After French's description was published, the Mitchell's satyr was subsequently found in fens throughout the Battle Creek-Kalamazoo and Jackson glacial interlobate regions (areas where ice sheets were in contact) of Michigan (Fig 2) (Wolcott 1893, Siepmann 1936, Moore 1939; 1960, Landis et al. 2011). The influential Butterfly Book (Holland 1898) also noted the Mitchell's satyr in Morris and/or Sussex Counties of northern New Jersey. The Mitchell's satyr was next confirmed in Portage County in eastern Ohio (Pallister 1927) and LaGrange County of northern Indiana (Badger 1958).

Several subsequent reports of *N. mitchellii* have been called into question for various reasons. One such report is that of *N. mitchellii* from Anne Arundel County, Maryland. During World War II two brothers collected a butterfly from a "military marsh" in the vicinity of Fort Meade and shipped the specimens home, where they were subsequently lost (Opler & Malikul 1998, P. Opler pers. comm.). The lack of a voucher specimen should warrant skepticism, but in this case some authors are convinced that the sighting was accurate (P. Opler pers. comm.). Arnett (2000) referenced Mitchell's satyr from Pennsylvania but no details were given beyond the state level reference. Rutkowski (1966) stated that it was highly likely the butterfly existed in Pennsylvania and he encouraged lepidopterists to search for it, no specimen of Mitchell's satyr from Pennsylvania is known to exist.

In 1983, a single population of butterflies, which appeared phenotypically similar to the Mitchell's satyr, was discovered on the Fort Bragg Military Reservation in North Carolina. Further exploration uncovered a

Fig. 2. Map highlighting the locations of *N. mitchellii* including both extant and extirpated populations. Extirpated populations are found in Wisconsin, Ohio, and New Jersey.

number of additional occupied sites, all were restricted to Fort Bragg (Parshall & Kral 1989; Kuefler et al. 2008). Citing phenotypic differences, such as the shape of the male valvae, and ecological differences, such as voltinism (these populations are bi-voltine), the *N. mitchellii* in North Carolina were described as a new sub-species, *Neonympha mitchellii francisi*, the Saint Francis' satyr (Parshall & Kral 1989).

In 1998, during a 4th of July Butterfly Count, observers discovered a population of what appeared to be *N. mitchellii* in Floyd County, Virginia, approximately 200 km from Fort Bragg, North Carolina (Roble et al. 2001). Subsequent searching revealed additional sites that harbored *N. mitchellii* populations within Virginia, athough only within Floyd County. In June of 2000, a population of *N. mitchellii* was discovered in the Oakmulgee Ranger District of the Talladega National Forest in central Alabama (Glassberg 2000; 2001). Since this discovery, researchers have identified approximately 20 sites within the Oakmulgee Ranger district as well as sites along the Natchez Trace Parkway in northeastern Mississippi that contained *N. mitchellii* (Hart 2004, Hamm 2008). As noted earlier, the recently discovered populations (Virginia, Alabama and Mississippi) are treated as *N .mitchellii* and not as either the Mitchell's (*N. m. mitchellii*) or the Saint Francis' satyr (*N. m. francisi*), hence they have no subspecies designation. Research is underway to determine the taxonomic status of these recently discovered populations.

A number of *N. m. mitchellii* populations have apparently been extirpated leading to the elimination of the species in parts of its former range. The Mitchell's satyr was extirpated from Ohio sometime in the 1950's and it was last seen in New Jersey in 1988 (Shuey 1997, Hamm 2008). High collecting pressure has been implicated in the extirpation of at least one New Jersey population due to a collector returning daily over successive seasons to the site (Glassberg 1999). While examining the Strecker collection in the Field Museum of Natural History, a part of the entomology collection not accessioned with the rest of the material, the first author found *N. mitchellii* with collection labels indicating they were taken from Wisconsin. These specimens were donated by E.T. Owen, who removed Strecker's original labels and replaced them with his own (J. Boone pers. comm.); any date or locality information have apparently been lost, though southeastern Wisconsin has a number of the prairie fens that may provide suitable habitat. We are unaware of any surveys in Wisconsin that have searched for *N. m. mitchellii*, but we suspect that it may be extirpated from Wisconsin and the surrounding region.

Habitats. With the discovery of these new populations of Mitchell's satyr, our understanding of its habitat usage patterns has also expanded. *Neonympha mitchellii* was first described from specimens collected near a "bog" (French 1889), although we now know that this habitat was a prairie fen (Spieles et al. 1999, Kost et al. 2007). Prairie fens are groundwater fed, sedge-dominated wetlands, whereas a "bog" is a basin that has no net outflow of water (Pielou 1991). Conditions leading to the formation of fens were a result of the Pleistocene glaciation (Pielou 1991) and prairie fens are concentrated in the interlobate regions of the Laurentide ice sheet (Landis et al. 2011). All *N. m. mitchellii* sites in Michigan and Indiana were subsequently determined to be prairie fens (Shuey 1997). Previous workers have suggested that these wetlands provide microhabitat which allows Mitchell's satyr to escape the high heat that characterizes these sites during the summer (Darlow 2000). Indeed, recent evidence suggests that there are significant differences between the ground level and air temperatures (Fig 3; C. Hamm unpub. data). During the winter (Fig. 3a) the ground is significantly warmer than the air (t-test, $P < 0.01$), likely due to insolation of the sedge tussocks. In the early spring there is no significant difference

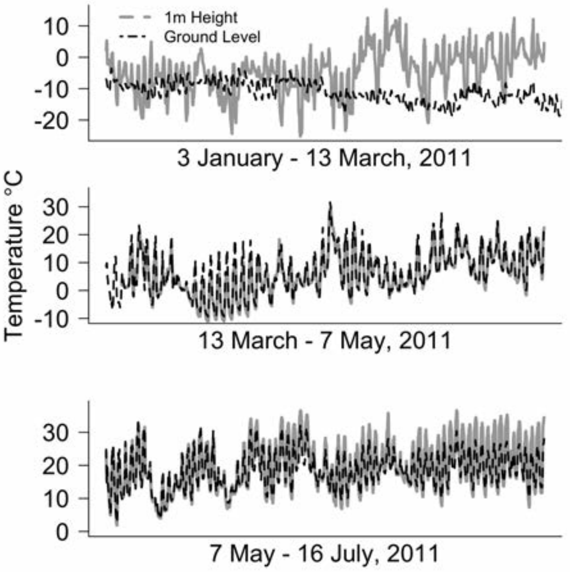

FIG. 3. Temperature data depicting ground level and air temperature in a Michigan prairie fen. A: during the winter (top plot) the ground (black dotted line) was significantly colder than the air (grey dotted line) (t-test, $P < 0.01$), B: during the spring (middle plot) the temperatures were not significantly different (t-test, $P = 0.28$), C: during the early summer (bottom plot) the air was significantly warmer than the ground (t-test, $P < 0.01$).

between the ground and air temperatures Fig. 3b) (t-test, P = 0.28), while during the early summer the ground is significantly cooler than the air Fig. 3c) (t-test, P < 0.01).

Neonympha mitchellii populations located south of the glacial maximum are not found in prairie fens, but rather in other sedge dominated wetlands such as the edges of beaver ponds and groundwater seepage slopes (Roble 2001, Hart 2004). Sites with *N. mitchellii* in Alabama and Mississippi tend to occur on the periphery of beaver ponds, on the edge of pocosin swamps, in areas where roads culvert create a buildup of water, or in proximity to seepage slopes (Hart 2004). In these habitats, it appears that hydrological disturbance creates the necessary conditions for a sedge-wetland to exist, if even for a short time (Hart 2004, Bartel 2010). The Alabama and Mississippi sites were initially surveyed for *N. mitchellii* in 2002 and 2003, during which time sites on the periphery of beaver ponds had high numbers of *N. mitchellii* (Hart 2004). However, when revisited in 2008 and 2009 *N. michellii* was absent from all such sites (Hamm 2008, Hamm and Hart, unpub. data). After the beavers abscond the pond filled with silt, which allowed shrubs to encroach on the banks, and left few sedges (Hamm 2008). Immediately upstream from these ponds (approx. 800 m) were recently constructed beaver ponds (approx. 2–3 y.o.; C. Ragland pers. comm.) that had a high number of *N. mitchellii*. This scenario of site loss and colonization was observed at five sites in Alabama and one site in Mississippi (C. Hamm and B. Hart; pers. obs.). This pattern fits into the metapopulation model of Hanski (1994) and suggests that, in Alabama and Mississippi, *N. mitchellii* historically existed in a metapopulation structure with regular movement along riparian corridors. This pattern of utilizing temporally available habitats has also been suggested as the population structure that describes Saint Francis' satyr populations (Hall 1993, Shuey 1997, Kuefler et al. 2008, Barel et al. 2010).

A number of Alabama sites were also found on the edges of seepage slopes or along the margins of impoundments created by road culverts (Hart 2004). Unlike the populations associated with beaver ponds, these sites had maintained *N. mitchellii* populations when surveyed six and seven years later (Hamm 2008; Hamm and Hart unpub. data). It appears that these sites avoid shrub encroachment though hydrological disturbance, though again, we have only observational data to support these postulations. The culverts and seepage slopes were imbedded within a matrix of fire dependent habitat, often a considerable (3 km) distance from the nearest actively populated beaver pond, which indicates the possibility that these sites may experience other forms of disturbance. Sites with *N. mitchellii* in Virginia are all found in close proximity to groundwater seepage slopes. These sites are very open compared with other *N. mitchellii* sites and are often used as pasture for cattle and other livestock (Roble et al. 2001). Management of the sites for cattle (i.e. the removal of shrubs and prevention of overgrazing) appears to simultaneously manage for *N. mitchellii* as these sites had high population density estimates (C. Hamm, unpub. data).

While there are many apparent differences among sites with *N. mitchellii* there are a number of commonalities that unite these habitats. All habitats, whether beaver pond, seepage slope, pasture or prairie fen, are sedge-dominated, early successional wetlands. Another commonality is that changes in hydrology and shrub encroachment are commonly associated with population extinctions, although the process by which this occurs remains unclear. The postglacial radiation of sedge wetlands northward from what is now the southern US following the Pleistocene glaciation provides a plausible explanation for the current distribution of *N. mitchellii* (Landis et al. 2011). Initially postulated based on distribution maps (Shapiro 1970; 1977, Metzler et al) researchers have only recently begun to test these hypotheses (Emerson et al. 2010).

Vagility and Dispersal. *Neonympha mitchellii* exhibits low vagility relative to many other butterflies. As has commonly been reported for most Satyrinae, *N. mitchellii* has a low and jerky flight with an up and down bobbing motion for each wingbeat (Scott 1986). Males tend to fly through the habitat (between sedges and grasses) rather than over it and they generally fly below the height of the dominant vegetation, perhaps to avoid predators (see below). Individual male flights are short, lasting an average of ten seconds (range: 1 sec to 1 min) (Sferra & Aguiar 1993). Female flight is even shorter, averaging five seconds though this distribution is extremely skewed (range: 1 sec to 19 min). When ovipositing, females approach potential sites and hover a few seconds before alighting (Sferra & Aguiar 1993). Males appear to spend the majority of time (~70%) patrolling, whereas females spend much of their time resting (~60%) early in the flight period, but later females spent 70% of their time flying in search of oviposition sites (Sferra & Aguiar 1993, Barton & Bach 2005).

As with most butterflies, male *N. m. mitchellii* fly with high frequency they appear to have small home ranges (Brussard et al. 1974). After examining two sites in southwest Michigan, Szymanski et al. (2004) reported that *N. m. mitchellii* did not disperse long distances. The mean daily distance moved for males was 18 m and for females was 11 m (Szymanski et al. 2004). Concordant with these observations, the mean minimum home range for the butterflies were small, with males occupying ~0.04 ha and females occupying ~0.01 ha (Szymanski et al. 2004). However, the sites where these data were recorded were relatively small (2.3 ha and 1.6 ha) and suffered from shrub encroachment, which may have biased the estimates. The size of surveyed habitats can produce a downward bias because habitat size may constrain movement. Using similar protocols at a larger site (12 ha), Barton & Bach (2005) reported larger home ranges for males (0.22 ha) and females (0.07 ha) and higher means for the daily distance moved (males: 35 m; females: 33 m). Overall, the data from both Szymanski et al. (2004) and Barton & Bach (2005) suggest that *N. m. mitchellii* does not disperse very far and thus falls into the sedentary mobility class of Pollard &Yates (1994). Sedentary butterflies are categorized by a movement rate between 10 and 200 m per day with colonization occurring up to 1 km away from natal habitat (Thomas 2000). At present there are no data on the vagility of *N. mitchellii* populations in Virginia, Alabama and Mississippi and studies are needed to examine vagility among these populations.

Individual dispersal events for individual *N. mitchellii* are not well characterized. Habitat corridors of 200 m and 400 m length have been created to connect prairie fens at two sites in Michigan and *N. m. mitchellii* have been observed in both. However, without mark-release-recapture (MRR) studies it is not clear if these individuals were transiting or were resident in the corridor. The longest distance recorded between subsequent captures in MRR studies was recorded by Barton & Bach (2005) and was 510 m for a male and 344 m for a female. A male in Virginia was observed at two different sites along a creek that were 1 km apart (S. Roble, pers. comm.), and this stands as the longest recorded distance for *N. mitchellii* dispersal.

Population Structure. The population structure of Mitchell's satyr is influenced by habitat isolation, flight phenology and within-habitat spatial preferences. In Michigan and Indiana today, prairie fens are typically highly isolated from one another and there is no evidence for *N. m. mitchellii* dispersal among them. In contrast, analysis of historic data on the distribution of prairie fens indicated that these habitats may once have been contiguous along geologic fomrations and would have allowed for increased dispersal among sites (MacKinnon & Albert 1996, Landis et al. 2011), but see Andreas (1985) and Swinehart & Parker (2002). Mitchell' satyr occupied sites in Virginia, Alabama, and Mississippi are typically much closer together, and dispersal among sites in these states has been observed (Roble 2002; 2003, Hart 2004, Hamm unpub. data).

Flight phenology and patterns of within-patch habitat preference may also contribute to population structure. Overall, *N. mitchellii* is protandrous with males emerging one to two days before the first female. As a result, during the first week of flight the sex ratio is male biased, after which there is a three to four day period of approximately equal sex ratio followed by a female biased sex ratio as the flight progresses (Barton & Bach 2005). This pattern of shifting sex ratios within the flight season is often used to infer the progress of the flight period. The detection probability of males is generally higher than that of females and is probably due to patrolling behavior making males more conspicuous (Szymanski et al. 2004, Barton & Bach 2005). Within sites, *N. m. mitchellii* are not uniformly distributed throughout the available habitat but the location of these aggregations fluctuates from year to year (Szymanski et al. 2004). For an as yet unknown reason, *N. m. mitchellii* are often found near habitat margins, especially at the interface of prairie fen and upland areas (Barton & Bach 2005, Hamm unpub. data).

Several techniques have been used to attempt to estimate the population size of *N. m. mitchelli*. In 1997, Pollard walks were conducted at three sites in southern central Michigan, but the data generated from these walks were not analyzed and may not have had enough samples to generate parameter estimates (Summerville & Clampitt 1997). Mark release recapture (MRR) methods have also been used in several instances. In all cases, the pattern of *N. mitchellii* adult distribution within habitats is complex, which complicates population size estimates. For two sites in southwestern Michigan, Szymanski et al. (2004) used MRR techniques to estimate population size in 1997 and 1998. They found that each site contained no more than 80 *N. m. mitchellii* per day and had a total population of no more than 380 individuals. MRR studies were also conducted at one site in southern central Michigan during the 2003, 2005, 2007 flight periods of *N. m. mitchellii* (Barton 2008). During the 2003 survey, the maximum daily population estimate was approximately 1100 individuals and was approximately 3000 during 2007. That population estimates varied a great deal from year to year is indicative of the stochasticity inherent with insect populations (Hamm 2013, Brown & Boyce 1998). In addition, short-lived study organisms complicate the use of MRR based methods for population estimation and may have influenced the results. In Michigan, the total population of Mitchell's satyr is informally estimated to be less than 10,000 individuals (Barton & Bach 2005; D. Cuthrell and D.

Hyde pers. comm.) but the uncertainty around this estimate reveals the need for standardized methods to more accurately assess the size of Mitchell's satyr populations (Hamm 2013).

Population size estimates are also poorly known for the southern populations of *N. mitchellii*. Sites with *N. mitchellii* outside of Michigan and Indiana have only been the focus of attention since 2000 (Roble et al. 2001, Hart 2004) with approximately 20 known *N. mitchellii* sites in Virginia, 15 in Alabama, and four in Mississippi. The estimates of total population size have been compiled from governmental reports, biological surveys, and our own experience. No statewide survey has been conducted on Mitchell's satyr or *N. mitchellii* in Virginia, Alabama or Mississippi (but see Haddad et al. 2008). Estimates of the total population size of Virginia *N. mitchellii* are roughly 8,000 individuals (Roble 2005). Researchers in Virginia have irregularly visited sites with *N. mitchellii* in Alabama and Mississippi since Hart (2004), but in that time many of these sites have become overgrown by shrubs since they were first surveyed and no butterflies have subsequently been observed (Hamm 2008). At least 15 sites are extant in the Talladega National Forest and are estimated to contain 1,500 individuals total (B. Hart pers. comm.). The three sites in the Natchez Trace Parkway of Mississippi have been surveyed for *N. mitchellii*, and were only found at one of these sites (the others having been overgrown by shrubs). We estimate fewer than 100 individuals occur at this occupied site (C. Hamm and B. Hart pers. obs.). Recently, additional populated sites have been discovered in the same area of Mississippi and there are unconfirmed reports of additional sites in Alabama (S. Surette and P. Hartfield pers. comm., Turner 2007).

The populations of *N. mitchellii* in Alabama and Mississippi are bivoltine. The first flight begins in early June and the second flight in mid August, and all flights last approximately three weeks. In contrast, all populations of *N. m. mitchellii* are univoltine and begin flying in late June in Michigan and Indiana. The *N. mitchellii* in Virginia are also univoltine and their flight begins in late July. Voltinism in *N. mitchellii* appears to be controlled by accumulated degree-days as a second generation can be induced in Michigan and Indiana populations by rearing them at higher temperatures (Shuey 1997, P. Tolson & C. Ellsworth pers. comm., C. Hamm unpub. data). Similarly, a single generation can be induced in Alabama populations of *N. mitchellii* by rearing them under cool conditions (C. Hamm unpub. data).

Host Plants. A variety of host plants have been associated with the Mitchell's satyr, but there are surprisingly few records of observed larval feeding. Based largely on the work of McAlpine et al. (1960) the sedge *Carex stricta* Lam. (Cyperaceae) was assumed to be the host of *N. mitchellii* because it was found at all Michigan and Indiana sites. Further observations, in both the field and artificial conditions, have demonstrated that *N. mitchellii* feeds on Cyperaceae and some graminoids as well (Table 1). It also appears that *N. mitchellii* rarely oviposits onto its sedge host plants (Table 2). One common observation among all oviposition reports is that female *N. michellii* generally deposit eggs near to ground level (Hyde et al. 2000; Darlow et al. 2000). We have observed eggs that were deposited singly and in groups of up to six (C. Hamm, unpub. data), which contradicts the commonly accepted theme that satyrs only lay eggs singly (Opler & Krizek 1984).

To address questions of host plant specialization an experiment was conducted using sedges from different regions of the *N. mitchellii* distribution. *Carex mitchelliana* M.A. Curtis, *C. lurida* Wahlenb., and *C. stricta* were collected from North Carolina, Alabama, and Michigan, respectively. These species were selected because they were endogenous to one or two sites but not present at all three. After collection, plants were grown in a 90:10 mixture Fafard 3B soilless potting medium (Conrad Fafard Inc., Agawam, MA) and calcined clay (Diamond Pro, Dallas, TX) in thee quart pots. Sedges were initially grown under greenhouse conditions at Michigan State University and were watered *ad libidum* using a 19-4-23-2 Ca fertilizer (Greencare Fertilizers, Chicago, IL) with H_2SO_4 added to counteract the high alkalinity of the well. Plants were then transferred to environmental growth chambers (Percival I-35LLVL) to simulate environmental conditions in Michigan and Alabama. Two females from Alabama and two from Michigan were collected for oviposition. The females were moved to 0.5 m^3 mesh cages with potted sedge (*C. lurida* for AL females and *C. stricta* for MI females) and allowed to oviposit for 48 hrs, each female laid 30–35 eggs. Eggs were then placed into treatment groups based on the experimental design outlined in Table 3.

Environmental conditions in growth chambers were set to simulate those encountered at *N. mitchellii* sites when the eggs were collected. Temperature, humidity and photoperiod were adjusted weekly based on data acquired from weather stations nearest the appropriate collection sites. Plants were placed in environmental chambers one week before the addition of *N. mitchellii* larvae. Once larvae were added, the plants were enclosed is mesh cages to prevent escape. Individuals were moved by hand to new plants as needed and

TABLE 1. Plant species fed upon by *Neonympha mitchellii* with literature reference and type of observation (field or artificial conditions).

Food plant	Family	Reference	Field
Carex alopecoidea	Cyperaceae	1	N
Carex atlantica	Cyperaceae	5	Y
Carex cephalophora	Cyperaceae	1	N
Carex lasiocarpa	Cyperaceae	2	Y
Carex leptalea	Cyperaceae	7	N
Carex lurida	Cyperaceae	6	Y
Carex mitchellii	Cyperaceae	8	N
Carex stricta	Cyperaceae	2, 3, 4, 5, 7, 9	Y
Carex tetanica	Cyperaceae	3, 7	Y
Cyperus esculentus	Cyperaceae	8	N
Rhynchospora capillaceae	Cyperaceae	7	N
Scripus atrovirens	Cyperaceae	1	N
Poa pratensis	Poaceae	8	N

References: [1]McAlpine et al. 1960; [2]Legge and Rabe 1996; 2; [3]Szymanski and Shuey 2002; [4]Roble 2005 [5]Roble 2006; [6]Hart 2006; [7]Tolson 2008; [8]B. Bergman, unpub. data;

[9]Hamm, unpub data.

TABLE 2. Plants on which *Neonympha mitchellii* oviposited, listed by family and reference (nomenclature follows Reznicek et al. 2011).

Plant species	Family	Reference
Eupatorium maculatum	Asteraceae	2
Solidago spp.	Asteraceae	2
Symphyotrichum ontarionis	Asteraceae	1
Carex bromoides	Cyperaceae	3
Scripus expansus	Cyperaceae	4
Juncus effusus	Cyperaceae	3, 5
Pycnanthemum virginuanum	Lamiaceae	1
Thalictrum dasycarpum	Ranunculaceae	1, 2
Galium boreale	Rubiaceae	1
Thelypteris palustris	Thelypteridaceae	2
Viola nephrophylla	Violaceae	1, 5

References: [1]Legge and Rabe 1996; [2]Darlow 2000; [3]Hart 2004; [4]Roble, 2005; [5]Hamm unpub. data.

TABLE 3. Experimental design for larval rearing experiment. All treatments began with 10 larvae, the data presented here indicate the number of survivors for each treatment. Treatments are listed by environmental conditions and the state of origin for Carex (L to R): *C. mitchelliana* (NC), *C. lurida* (AL), and *C. stricta* (MI).

		Environmental Conditions					
		Alabama Conditions Sedges from:			Michigan Conditions Sedges from:		
		NC	**AL**	**MI**	**NC**	**AL**	**MI**
Larvae from:	AL	5	4	4	5	5	3
	MI	3	5	4	4	4	5

Table 4. Observed predators of *Neonympha mitchellii*

Taxon	Common Name	Family	Notes
Erythimis simplicicolis	Eastern Pondhawk	Odonata :Libellulidae	Aerial predation
Asilus sericeus	Robber Fly	Diptera: Asilidae	Aerial predation
	Ambush bug	Homoptera: Reduviidae	Nymph on *Rudbeckia*
Formica spp	Wood ant	Hymenoptera: Formicidae	Landed on aphid tended plant
Bombycilla cedorum	Cedar Waxwing	Aves: Bombycillidae	Attempted aerial predation
Tyrannus tyrannus	Eastern Kingbird	Aves: Tyrannidae	Aerial predation

mortality noted daily. The total number of survivors to pupation, by treatment, was noted. Survivors from Michigan grown under Alabama conditions were allowed to mate and produce a second generation while the remaining individuals were sampled for DNA extraction. Voucher specimens were deposited in the Albert J. Cook Arthropod collection at Michigan State University. Logistic regression was used to compare all survival against all two-way interactions in the statistical program R (R Core Development Team 2011) against a significance value of $\alpha = 0.05$.

Adults emerged after approximately 2000 degree days (base 50) accumulated. Michigan collected individuals reared under Alabama conditions went through a second generation after an additional 900 degree days accumulated post eclosion. The photoperiod in Alabama was shorter than that of Michigan, which suggests that photoperiod does not play a role in voltinism for *N. mitchellii*. Logistic regression revealed no difference among treatment for survival. Due to permitting restrictions, only two females were sampled. As a result, this experiment did not have high genotypic diversity among treatments. Lastly, this study did not quantify growth rates among treatments, though the final size of adults is not significantly different from other wild caught specimens (C. Hamm unpub. data). These results, while preliminary, indicate no difference in host plant performance, and serve as proof of concept that such rearing experiments can be successfully undertaken.

Predators. An eclectic group of predators has been observed to prey on Mitchell's satyr. In the course of various oviposition studies researchers have reported numerous accounts of larval predation by spiders (Arachnida: Araneae) (C. Ellesworth and B. Barton, pers. comm.). During an experiment to test the effects of fire on larval survival, a group of researchers collected gravid females and placed them in enclosures that covered *C. stricta* tussocks. The experiment was quickly abandoned due to high levels of predation by spiders (Barton 2008). Additionally, we have observed a number of predators attack adult *N. mitchellii* (Table 4) in the course of research. When a male *N. mitchellii* patrols an area he tends to fly through the sedges rather than over them. All aerial predation events (birds and insects such as flies and dragonflies) we observed occurred when a male flew over sedges and was thus exposed.

Other factors affecting conservation. Effective conservation of *N. mitchellii* into the future depends on a combination of biological, ecological and social factors. For example, the taxonomic uncertainty of *N. mitchellii* in Virginia, Alabama, and Mississippi will impact the federal conservation status of *N. m. mitchellii* more broadly. Currently, these populations are not included in the endangered species listing but they are protected by other measures. The State of Virginia considers their populations of *N. mitchellii* to be endangered at the state level and many of the sites are protected by conservation easements (S. Roble, pers. comm.). Many of the *N. mitchellii* sites in Alabama and Mississippi are located on U.S. Forest Service and National Park Service lands, thus affording them some level of protection.

The future of the northern protected populations of *N. m. mitchellii* and prairie fens on which they depend is also uncertain (reviewed in Landis et al. 2011). Preliminary data based on the study of >100 sites suggest that the water feeding these sites may enter the aquifer many kilometers away from the fen decades ago (H. Abbas unpub. thesis). For example, the water coming out of the ground today may have entered the aquifer 50 years ago. We do not know the impact that contemporary levels of water consumption and groundwater extraction will have on the future of these sites. Field observations have noted that when fens dry out shrubs move in and as a result the biodiversity is apparently reduced (C Hamm pers. obs.).

The reproductive parasite *Wolbachia* in both *N. m. francisi* and *N. m. mitchellii* raises serious issues for conservation (Hamm et al. in review). *Wolbachia* is a common intracellular bacterium that is found in 20% of arthropods and 66% of insects (Hilgenboecker et al.

2008). This bacterial endosymbiont manipulates its host's reproduction to facilitate its own and can be of major importance for the management of insects (Nice et al. 2009). *Wolbachia* can feminize males, kill male embryos, induce parthenogenesis or, in its most common form, induces cytoplasmic incompatibility (Werren et al. 2008). Cytoplasmic incompatibility only results in successful mating between the same strains of *Wolbachia*, of which there are currently over 200 known strains (Baldo et al. 2006, Stahlhut et al. 2010). *Wolbachia* imparts a reproductive advantage to infected individuals and is spread through maternal transmission, so when a population becomes infected it will pass through a bottleneck until infection rates are high (Werren et al. 2008, Nice et al. 2009, Hamm et al. in review). While the identity of a strain may be deduced from molecular sequence data, the induced phenotype can only be determined by controlled breeding experiments. Demographic models suggest that if differently infected individuals are mixed the consequences for small populations will be catastrophic (Nice et al. 2009, Hamm et al. in review).

Federal Actions. The Mitchell's satyr was first petitioned for listing under the endangered species act in November of 1974 by a private citizen; however in May of 1975 the USFWS judged that listing was not warranted due to insufficient data (49 FR 2485). In 1984 the USFWS listed *N. mitchellii* within category 3C in their Animal Notice of Review (49 FR 21664), indicating that it was considered too abundant to be considered for protected status. However, in 1989, the USFWS upgraded the species to category 2 and thus made *N. mitchellii* a candidate for listing under the Endangered Species Act (ESA) (54 FR 554). In 1989 a new subspecies was recognized that altered the taxonomic status of *N. mitchellii*. The newly discovered Saint Francis' satyr was found on the Fort Bragg military reservation in North Carolina and given the trinomial *Neonympha mitchellii francisi* (Parshall & Krall 1989). With this split, the Mitchell's satyr became the nominate subspecies *Neonympha mitchellii mitchellii* (Parshall & Krall 1989).

A 1991 report issued to the USFWS described the rangewide status of *N. m. mitchellii* (Wilsmann & Schweitzer 1991). The authors noted that the Mitchell's satyr was once known from approximately 30 sites in four states (Michigan, Indiana, Ohio, and New Jersey) but at the time of the report, was known from only 15 sites in two states (Michigan and Indiana) (Wilsmann & Schweitzer 1991). This report recommended that the USFWS list *N. m. mitchellii* as endangered, which led to an emergency listing on 25 June 1991 (56 FR 28825). The emergency listing provided 240 days of protection and on 11 September 1992, the USFWS formally proposed a rule to fully protect the Mitchell's satyr under the ESA (56 FR 46273). The final ruling that listed the Mitchell's satyr as an endangered species was published in May 1992 (57 FR 21564). Note that while the ESA considers a "species" to be any taxonomically recognized subspecies, this does not apply to insects (section 4.(15) of the ESA). Cited among the reasons that the Mitchell's satyr deserved protection were: destruction and modification of its habitat, overutilization for commercial purposes, inadequacy of existing regulatory mechanisms, and other man-made factors affecting its continued existence (i.e. habitat loss due to anthropogenic forces).

The Mitchell's satyr received additional attention in the early 1990's as preparations to extend the US-31 freeway in southern Michigan through a fen were being put into motion. The original 1981 Final Environmental Impact Statement (FEIS) identified Blue Creek fen as a site where the Mitchell's satyr was present, but a 1991 report by the Michigan Department of Transportation (MDOT) mistakenly reported that the site contained the *Lycaeides melissa samuelis*, the Karner Blue butterfly (Lepidoptera: Lycaenidae) and not the Mitchell's satyr (MDOT 1981; MDOT 2004). With the 1981 FEIS no longer accurate, the USFWS required MDOT to revise the path for the freeway. Negotiations between the USFWS and MDOT, ultimately resulted in the freeway being rerouted around the wetland complex and today an easement has been negotiated that allows biologists access to survey for the Mitchell's satyr.

In 1998 the Mitchell's satyr Recovery Team, a group of key stakeholders representing various state and federal governmental agencies and conservation organizations, submitted a recovery plan to the USFWS. This plan described the sites where extant and historical populations of *N. m. mitchellii* were found and noted that many of the original descriptions of those habitats were inaccurate (USFWS 1998). Additionally, the report outlined conservation measures that should be taken to aid in the recovery of the Mitchell's satyr. These included; range-wide surveys for the satyr, host plant identification and general study of the life history and ecology of the satyr, land acquisition and the development of habitat management plans, and the securing of easements with private property owners. The report also outlined the criteria that must be met for the Mitchell's satyr to be have its status changed (USFWS 1998):

> "1. For reclassification from endangered to threatened a total of 16 geographically distinct and viable populations or metapopulations must exist and these populations may be extant, established via

translocation, or discovered. 12 of these sites must occur in Michigan, two in Indiana, one in Ohio and one in New Jersey and at least half of these sites must be protected in some form (i.e. conservation easement or under the ownership of a conservation organization).

2. For **delisting** to occur a total of 25 distinct and viable populations must be exist and remain viable for five years after delisting. At least 15 of these sites must have legal protection and we should note that the recovery team may modify or change the recovery criteria if new information becomes available."

In March of 2009 the USFWS began a five-year review of the Mitchell's satyr to determine if the species was still in need of protection (74 FR 11600). In April of 2009 the, the Mitchell's satyr was identified by the USFWS as a "Spotlight Species" and an action plan was instituted that brought additional resources to bear on the butterfly's recovery.

Discussion

While much is already known about *N. mitchellii*, this manuscript highlights the need for prioritized research in key areas. One critical need is for the development and use of standardized methods to estimate demographic parameters such as population size. While the currently used method of timed meander surveys is reasonably standardized, it is not quantitative with respect to area and thus does not yield a population density. Such density estimates are critically needed before any management practice can be tested robustly. Without such baseline data we cannot compare treatments let alone determine if populations are in decline. Methods that do not require handling the butterflies, such as distance methods, may be ideal for *N. mitchellii* work and have already been used with butterflies (Brown & Boyce 1998, Isaac et al. 2011).

Natural history forms the foundation for all biological work and without the data contained herein, any inferences based on molecular data could be out of context. Knowledge of the evolutionary history of *N. mitchellii* can aid in the recovery of the species by informing us about the relationship among populations at the regional and state level. Determining if and how the Virginia, Alabama, and Mississippi populations of *N. mitchellii* are related to the northern populations of *N. m. mitchellii* with have an impact on the recovery criteria of the species. These inferences can be made both with morphology and with DNA-based evidence. For example, Parhsal & Krall (1989) cited morphological character differences between the Saint Francis' satyr and Mitchell's satyr. Using methods such as geometric morphometrics we can test if these differences are robust to statistical testing and may serve to distinguish taxa. The use of DNA technology will allow us to directly compare populations when the time since divergence is not great enough to allow morphological characters to diverge. Using two mitochondrial DNA markers, Goldstein et al. (2004) surveyed a number of *N. mitchellii* from throughout its range. Their findings suggested that the Saint Francis' satyr was distinguishable from other *N. mitchellii*, however, the populations from Michigan, Virginia, and Alabama could not be resolved as unique (Goldstein et al. 2004). These results, while interesting, may be compromised by the presence of the reproductive endosymbiont *Wolbachia*, which is transmitted maternally in the same manner as mitochondria (Nice et al. 2009, Hamm et al. in review). Once *Wolbachia* is corrected for, molecular methods will allow us to test proposed routes of post-glacial radiation that these butterflies undertook (Shapiro 1977, Metzler et al. 2005).

New research is also needed to determine the full implications of the recently discovered infections of the reproductive parasite *Wolbachia* (Hamm et al. in review). Examination of the prevalence and strain type of *Wolbachia* should be conducted before any individuals are moved among populations. This is perhaps the single most pressing need for research because the introduction of a new *Wolbachia* strain into a population could result in population extinction. Once the strain is "typed" its effects must be determined experimentally so that any future introductions can be monitored for the effects of *Wolbachia.*

We must also continue to quantify aspects of *N. mitchellii* biology and habitat ecology. Replicated experiments to compare host plant performance among populations could reveal local adaptation, which if found, may counterindicate the movement of individuals among populations. Finally, understanding the hydrology of prairie fen habitat will better allow us to manage these sites by telling us where the groundwater is coming from and thus prevent the loss of these habitats.

The goal of the Endangered Species Act is to recover species that were placed in peril by anthropogenic forces. No insect has ever been removed from the endangered species list due to recovery; rather they have been removed due to extinction. If sustained recovery is the goal, then quantifiable research must be conducted to address the major obstacles that face *N. mitchellii* conservation. Conservation organizations must partner with academic researchers to design critical experiments and research thrusts that will directly benefit *N. mitchellii*. The Mitchell's satyr is at a critical juncture, this butterfly presents an amazing opportunity to successfully recover the first insect species if steps are taken immediately. If these steps are not taken immediately, populations will likely continue to decline and surveys will no longer be necessary.

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