Am. Midl. Nat. 159:298–320

Distribution, Population Structure and Habitat Use of the Endangered Saint francis Satyr Butterfly, Neonympha Mitchellii Francisci

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ABSTRACT.—The endangered St. Francis Satyr (*Neonympha mitchellii francisci*) is a small sedentary butterfly and one of the rarest in North America. Our study examined various quantitative aspects of this butterfly's biology, including the distributional range, habitat associations, population size and trends, demographic parameters and spatial aspects of population structure. The range of *N.m. francisci* distribution is restricted to DoD lands at Ft. Bragg, North Carolina, where the butterfly utilizes wetland habitats, predominantly those that have previously been impounded by beaver. In situ habitat associations and captive rearing experiments indicate that multiple sedges in the genus *Carex*, particularly *C. mitchelliana*, may be important larval food plants. Subpopulation estimates range between 49–739 individuals at any one site, while cumulative population estimates range between 700–1400 individuals for all accessible areas on Ft. Bragg. Habitats occupied by *N.m. francisci* are frequently subject to burning or flooding and thus butterfly subpopulations are extremely dynamic, fluctuating in response to these disturbances. This regular disturbance regime dictates that dispersal is necessary for population persistence. Several inter-colony movements were measured during capture-recapture studies and we observed both subpopulation extinctions and colonization of new habitat through the period of our studies. Conservation of *N.m. francisci* depends on accommodating unique aspects of its populations, including its dependence on beaver and its multi-tiered metapopulation structure.

INTRODUCTION

St. Francis' satyr, *Neonympha mitchellii francisci,* is one of the most imperiled butterflies in North America. First discovered in 1983, its range is restricted to Ft. Bragg, North Carolina (NC), where several small subpopulations persist in glades along streams (Parshall and Kral, 1989; Hall, 1993; Hall and Hoffman, 1994).

Neonympha mitchellii francisci is currently considered a subspecies of Mitchell's satyr (*N. mitchellii mitchellii*), which is also endangered. *Neonympha m. mitchellii* populations in the Great Lakes region have been the subject of detailed investigations (McAlpine *et al.*, 1960; Ledge and Rabe, 1996; Shuey, 1997; Darlow, 2000; Kost, 2000; Szymanski *et al.*, 2004; Barton and Bach, 2005). Since 1988 southern populations of *N.m. mitchellii* have also been discovered in Virginia, Alabama and Mississippi (Roble *et al.*, 2001; Hart, 2004). A phylogenetic analysis indicates that these southern populations are more closely related to the nominate *N.m.mitchellii* than to *N.m.francisci* (Goldstein *et al.*, 2004).

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Neonympha mitchellii francisci exhibits several morphological and behavioral similarities with *N.m. mitchellii* (Parshall and Kral, 1989). These butterflies share similar wingspans, coloration and flight behavior, and both utilize wetland grasses or sedges as larval food plants. Like *N.m. mitchellii*, *N.m. francisci* appears to be imperiled due to habitat loss (Hall, 2003; Szymanski *et al.*, 2004). However, they differ markedly in terms of their ecology and life history, reflecting adaptations to very different environments (Table 1). In particular, northern populations of *N.m. mitchellii* in the Great Lakes region occupy relatively long-lasting fen habitats, are relatively sedentary and often have large populations with little or no evidence of subdivision (MacAlpine *et al.*, 1960; Szymanski *et al.*, 2004). In contrast, *N.m. francisci* inhabits a shifting mosaic of early successional wetland habitats and occupies relatively small subpopulations across the landscape. More specifically, *N. m. francisci* persist in a multi-tier metapopulation structure that appears to be influenced by disturbance dynamics associated with beaver activity. This complicated population structure and association with beavers is novel in studies of Lepidoptera and provides a unique case study in butterfly conservation.

Understanding the population structure, population dynamics, habitat requirements, and basic life history of *Neonympha mitchellii francisci* is critical for its management and potential delisting. To accomplish this objective, we have taken two separate lines of investigation. Along one line, between 1993–2005, we conducted reconnaissance surveys to determine the species' distribution and botanical assays to obtain a quantitative description of the butterfly's habitats. Concurrently, between 2002 and 2005 we conducted detailed demographic studies of *N.m. francisci* populations. The main purpose of the demographic studies was to determine the size, spatial structure and trends of butterfly populations. A secondary purpose was to determine the variability of demographic parameters with respect to butterfly sex, relative age, predation threats and environmental characteristics. Additionally, we report here on key aspects of its habitat requirements, as well as larval food preferences based on the results of experiments with reared larvae. Combined, these studies fill critical gaps in our understanding of *N.m. francisci* life history and habitat requirements. This paper complements several unpublished studies (available in full from the authors) that report on *N.m. francisci* from the time of first discovery and provide additional detail on the butterfly's distribution (Hall, 1993; Hall and Hoffman, 1994), its habitat associations (Hall *et al.*, 2001; Hall, 2003; Hall and Haddad, 2005) and its population size and trends (Haddad *et al.*, 2003, 2004, 2005).

METHODS

STUDY SITE

The only known population of *Neonympha mitchellii francisci* exists on Department of Defense lands at Ft. Bragg, NC. Created in 1918, Ft. Bragg is an active army installation comprising roughly 65,000 ha. This army installation is located in the Fall-Line Sandhills physiographic region and is completely contained within the Cape Fear River Basin. The topography of the Sandhills is quite hilly compared to the rest of the Coastal Plain and the portion within Ft. Bragg includes the highest ridges and some of the most dissected terrain located within this region in North Carolina. Despite its hilly terrain, the installation supports a biota typical of the Southeastern Coastal Plain. Approximately 40% of the installation is covered with longleaf pine communities. The installation also supports bottomland hardwood forests along stream floodplains, which are of particular importance as habitat for *N.m. francisci*, especially where modified by beaver activity.

TABLE 1.—Comparisons between *N.m. mitchellii* and *N.m. francisci* populations and potential conservation strategies. * The taxonomic status of these populations have not been confirmed, but preliminary studies indicate that they are likely more closely related to the nominate *N.m. mitchellii* than to *N.m. francisci* (Goldstein *et al.*, 2004)

Species	Known locations	Annual phenology	Habitat types	Range of habitat sizes	Number of subpopulations	Range of Sub/Population sizes	Potential conservation strategies
Neonympha mitchellii mitchellii	MI	Univoltine	Tamarack/Prairie Fens Sedge meadows Shrubby meadows	0.8–12.1 ha	17	6–1858 Individuals	Habitat Protection and Restoration Establishment of Movement Corridors Rearing and Future Reintroduction
Neonympha mitchellii mitchellii	IN	Univoltine	Tamarack/Prairie Fens Sedge meadows	0.6–4.75 ha	2	5–150 Individuals	Habitat Protection Habitat Maintenance
*Neonympha mitchellii mitchellii**	AL	Bivoltine	Shrub/sedge forested wetland complex Old Beaver Ponds	0.2–14.5 ha	17	350 Individuals	Habitat Protection Habitat Maintenance
*Neonympha mitchellii mitchellii**	MS	Bivoltine	Sedge Glades Old Beaver Ponds	0.1–0.2 ha	2	5–12 Individuals (not extensive surveys)	Habitat Protection Habitat Maintenance
*Neonympha mitchellii mitchellii**	VA	Univoltine	Wet Open Patures	0.1–1.5 ha	10	2–338 Individuals	Landowner Education Conservation Easements
Neonympha mitchellii mitchellii	NJ	Extinct	n/a	n/a	n/a	n/a	n/a
Neonympha mitchellii francisci	Ft. Bragg, NC	Bivoltine	Old Beaver Ponds Pocosin Ecotones Wet Sedge Meadows	0.11–1.08 ha	13	50–750 Individuals	Habitat Restoration Establishment of Movement Corridors Rearing + Reintroduction

Approximately 13,000 ha of the installation are included within artillery impact areas that are off-limits to most forms of human intrusion. These areas differ somewhat compared to the surrounding installation in that fire is more frequent (annual return interval in many places) on the impact areas than on the surrounding installation (3 y return interval). Most entry for biological work in these areas was curtailed after 1995. Consequently, despite the discovery of several populations within these areas prior to 1995 (described below), our detailed studies were all conducted outside of these impact areas.

SURVEYS FOR DISTRIBUTION

Between 1992–94 we conducted broad surveys for the butterfly across the Inner Coastal Plain physiographic region of the Carolinas to determine the distributional limits of *Neonympha mitchellii francisci* (Hall, 1993; Hall and Hoffman, 1994). Within North Carolina, these surveys covered 33 sites at Fort Bragg, 17 sites in the neighboring Sandhills region of NC and four Carolina bays in the adjoining, lower portion of the Inner Coastal Plain. In South Carolina, we surveyed six sites in the Sandhills National Wildlife Refuge and seven sites at Fort Jackson. All of these surveys targeted shallow, graminoid-dominated wetlands, based on a habitat profile initially described by Parshall and Kral (1989). These habitats included both natural community types such as swamp forest glades, Carolina bays and vernal pools and artificial impoundments such as old mill ponds. Special attention was given to abandoned beaver ponds and shallow depressions, since they most closely matched the habitats at the original colony sites.

On Fort Bragg, we conducted two additional sets of surveys with increasing resolution. In 2000–2001 we surveyed 110 sites excluding the artillery impact areas but including most of the perennial stream drainages (Hall, 2003). In these surveys, we first identified suitable habitat using aerial photography and maps, giving special attention to abandoned beaver ponds and other herbaceous wetlands. We then visually inspected each site during butterfly flight periods to verify whether *Neonympha mitchellii francisci* were present. During the course of these surveys, it became clear that many potential sites could not be identified from aerial photographs alone, as many consisted of small glades deeply imbedded within dense growths of riparian forest or pocosin shrubs. So, employing a finer-scale technique, we walked the lengths of watersheds, looking for small open glades by laboriously penetrating through the thick riparian vegetation.

Butterfly subpopulations were identified on the basis of both consistent presence during the flight periods and the presence of suitable habitat. Additionally, transitory sites were identified where butterflies were irregularly seen in low numbers (often a single individual), typically at sites supporting lower-quality habitat.

HABITAT DESCRIPTION

From 2001 to 2004 we conducted quantitative vegetation sampling at 33 of the sites identified during reconnaissance surveys (Hall, 2005). We surveyed all six subpopulations that were active in 2002, one abandoned subpopulation site, six sites where transients had been observed and 20 unoccupied sites supporting a range of potentially suitable habitat types.

We sampled vegetation at each study site using a series of 3 × 3 m quadrats. At the first nine sites we surveyed, we used two intersecting 50 m transects with eight to ten quadrats laid along them. Subsequently, we employed a single 50 m transect with five quadrats laid along it. At four smaller sites, we used a shorter transect and fewer quadrats. Within each of the quadrats, we estimated cover classes for all plant species using methods developed by the NC Vegetation Survey (NCVS) for ease of visual estimation (Peet *et al.*, 1998). For woody species, height was also recorded in three classes following NCVS conventions.

In 2005 we conducted additional sampling on a much smaller scale to fortify our detailed studies on population trends and habitat quality. To do this, we randomly placed 15–23 1 × 1 m plots in each of the four primary sites where we monitored subpopulations during 2002–2005. We visually estimated the cumulative percent cover of all *Carex*-genus sedges and also the total percent cover of *C. mitchelliana* in each 1 × 1 plot.

LARVAL FEEDING EXPERIMENTS

We intensively searched for larvae at active colony sites on numerous occasions, primarily during the interval between the two adult flights. Special attention was given to *Carex* species, particularly to *C. mitchelliana*, since circumstantial evidence suggests its use as a host plant (*see* below). Also given special attention were any graminoid clumps showing signs of insect feeding damage.

To further identify likely larval food plants, we conducted a laboratory rearing study to test larval growth on several different potential food plants. Late in the 1st flight period of 2004, we collected 45 eggs from three worn adult females. The 28 larvae that hatched were reared at the NC State University Insectiary, with temperature, light cycle and humidity set to reflect average ambient conditions. We reared larvae on fresh clippings of plants in 4 oz glass containers with tight fitting lids. We replaced clippings with fresh plant material when they became dry and withered, and we provided a small amount of additional moisture by placing a moistened disc of filter paper on the bottom of each jar. Larvae were all housed separately, allowing growth and molt records to be kept of each individual.

We tested seven different species of sedges known to occur within *Neonympha mitchellii francisci* subpopulation sites, including: *Carex mitchelliana*, *C. stricta*, *C. glaucescens*, *C. turgescens*, *C. atlantica*, *C. lurida* and *C. lonchocarpa*. We initially tested four larvae per plant species. Larva that failed to feed on their initial host or showed physiological duress by shriveling were transferred to *C. mitchellina* after 2 d if they were still alive. To compare the suitability of potential host plants, we recorded neonate acceptance, growth rates, and instar transitions until death or successful emergence of adults.

DATA COLLECTION FOR ESTIMATING SUBPOPULATION SIZE

We conducted detailed population studies primarily at the four largest subpopulation sites outside restricted areas. As these four subpopulations occur on three different streams, we henceforth labeled the sites A1, D1, D3 and E2 (letter = stream, and number = site within stream). The total area occupied by these four sites is approximately three ha, with individual sites ranging in sizes between 0.5 ha and 1 ha. Sites D1 and D3 are situated on the same drainage roughly 800 m apart. Sites A1 and E2 are isolated on two additional drainages and are roughly 2.5 km and 5 km from the nearest neighboring subpopulations, respectively.

Because these habitats can be damaged by repeated trampling, we prepared each site for surveys prior to the first adult flight period. This preparation included establishing a system of transects in each site using 5 × 15 cm planks to minimize disturbance to wetlands. An attempt was made to position planks across high points (dry soil, exposed roots or rocks) in wetlands to elevate researchers and to prevent vegetation trampling. Transects were not continuous, were placed in several openings throughout sites so that we could visually survey most of the site and totaled approximately 300 m in length per ha. At some areas along transects, thick shrubby vegetation obscured views of butterflies. Because of our concern to avoid impacts to the butterfly's habitat and our attempts to maximize visibility in shrubby wetlands, we were unable to locate transects randomly or uniformly through our sites. We were also unable to determine the area over which butterflies were uniformly distributed.

These aspects of our design precluded our use of a common technique for population estimation, distance sampling (Buckland *et al.*, 2001).

At these four sites, we conducted two types of population studies of *Neonympha mitchellii francisci* each year, modified Pollard-Yates transect counts in the first flight period (Pollard, 1977) and mark-release-recapture (MRR) in the second flight period. For both the observational and MRR studies, we began visiting each site roughly one week before emergence was expected and continued until no butterflies were seen at a site for three consecutive days. We attempted to survey each site daily, with exceptions occurring on rainy days, and on some weekend days at the beginning and end of flight periods when abundances were low.

During a survey, two observers walked neighboring transects within a site at a rate of 200 min per ha, with a minimum survey time of 20 min per observer. When walking transects, we made an attempt to flush butterflies from vegetation by gently swishing 2 m nets one time across the top of the vegetation. Surveys were conducted between 09:00 and 18:00 with an emphasis on sampling after noon.

Although MRR methods are more precise for population estimation, we attempted to capture endangered butterflies as little as possible. We observed butterflies after marking and did not notice any change in behavior compared to unmarked butterflies. We tested for the effects of handling on recapture rates of butterflies using Manly's test (Manly, 1971; Gall, 1984). Manly's test evaluates the likelihood of recapturing individuals on subsequent dates given that an animal was marked on the focal date or some previous date. We applied Manly's test on two dates during peak activity of each year from 2002–5. We found no evidence that handling had negative effects. In 2005 we were more likely to recapture butterflies on days after they had been marked. A non-significant trend in the direction of higher capture probabilities immediately after being marked was observed in all other years. This trend may have two causes. Most importantly, the natural mortality rate of *Neonympha mitchellii francisci* is high, making the most likely recapture the day following marking. This bias is accounted for in our capture-recapture statistics. Second, we have observed butterflies to be sedentary immediately following marking, and this may increase their recapture rate the following day. Because the handling effect was rarely important and probably due to high natural mortality rates, we did not incorporate handling effects in our estimates of population size.

PHENOLOGY AND POPULATION COUNTS

In the first adult flight period each year, we counted butterflies at each site daily while taking care not to double-count adult individuals. A team of two observers worked together to identify the largest number of unique butterflies that were either observed simultaneously within a site, or were clearly unique based on information about condition, sex, and location of individuals. As these data were collected on fixed transects using fixed survey times, we used a modified Pollard-Yates count approach to analyze data. Pollard-Yates counts are standardized transect counts with strict limits on observation area and conditions (Pollard, 1977). An index of population size is generated by summing average weekly counts for the duration of the flight period. We also used these data to catalogue adult flight phenology at each site. This phenology included the emergence dates for both flight periods, the duration of each flight period and the date of peak activity (highest daily count) during each flight period. Additionally, we examined how butterfly counts were influenced by the time of day and the daily climatic conditions during which surveys were conducted. We did this by first calculating an expected count by fitting a standard model of butterfly phenology using a time series of insect counts to produce estimates of population size and survivorship

(Longcore *et al.*, 2003). This modeling approach has been incorporated into user-friendly, open-access software (http://www.urbanwildlands.org/INCA/), the INsect Count Analyser (INCA). We then calculated the difference between the predicted and observed numbers of butterflies in each site each day to account for changes in butterfly counts attributable to changes in population size throughout the season. Using a General Linear Model procedure in SAS v.8.2, we tested for the effects of time of day and weather conditions on daily observed population counts. The time variable was included as minutes after 09:00 and weather variables included as cloud cover, temperature and humidity. We also tested a time-squared term and weather by time interactions. These interaction terms were initially included in the model, but were subsequently removed because they were not significant.

MARK-RELEASE-RECAPTURE METHODS

Mark-release-recapture studies were conducted in the second flight period each year, and in both the first and second flight periods in 2005 when we attempted to determine differences in survivorship and fecundity among flight periods. MRR surveys were conducted using the same general technique as was used for modified Pollard-Yates counts, with several additional protocols. Captured individuals were marked on both hind wings using a fine-tip Sharpie™ pen with a unique alpha-numeric code and immediately released at the location of capture. We added three minutes of additional survey time at the end of each survey for each butterfly caught and marked to account for time spent handling butterflies and recording information, up to a maximum of 15 min added per observer (or 10 butterflies in total). We reached this maximum only twice in 4 y. Using close-focus binoculars, observers were often able to record information about marked and unmarked individuals without physically capturing them. With this technique, we also included individuals that were too far from transects to catch. If an individual butterfly was not physically captured, but was uniquely distinguished by physical characteristics, we collected information on these characteristics and recorded the individual as being captured during that survey. With this approach, we also surveyed smaller peripheral sites to observe potential movements of marked individuals from larger sites.

ESTIMATION OF DEMOGRAPHIC PARAMETERS

We analyzed MRR data using program MARK v.4.2 (White and Burnham, 1999). Within MARK, the subprogram POPAN provides a parameterization of the Jolly-Seber model (Schwartz and Arnason, 1996) using individual capture histories to estimate population size and variance. This approach generated population estimates of the number of adults in the population over the entire, non-overlapping flight period. We used POPAN to derive annual population estimates for each of the four sites we surveyed during 2002–2005.

We also used MRR data to calculate differences in butterfly demography between each of the four sites. For each site, we used Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly 1965; Seber, 1965) embedded in program MARK to estimate apparent survival and detection probabilities. Apparent survival is a daily survival probability that does not distinguish mortality from individuals that have permanently left the survey area, and thus underestimates actual survivorship. Detection probability is a daily probability of capture given the animal is alive and in the study area.

We compared these parameters between sites for each year during 2002–2005, using capture histories from all individuals. Additionally, we compared these two parameters between years by using specific information on marked individuals. We also compared the effect of age and sex on detection and survival probability using the following approach. For each individual caught during MRR studies, we recorded its sex and a relative age class of 1–

3 (from freshly emerged to badly worn). Compiling data from the three largest subpopulations and including data from physically captured individuals only, we pooled individual capture histories for each year between 2003–2005. Then, for each year, we ran four different CJS models in program MARK in which survival and detection probabilities were: (1) constant, (2) varied daily, (3) varied by sex and (4) varied by age. Finally, using a model selection criterion based on AIC values (Burnham and Anderson, 2002), we evaluated whether butterfly sex or relative age or day within a flight period, influenced apparent survival or detectability.

MOVEMENT AND COLONIZATION

Because *Neonympha mitchellii francisci* live in a shifting mosaic landscape where habitat is created and destroyed by fire, beaver activity and succession, movement is necessary to maintain their metapopulations. To enhance our understanding of butterfly distributions and colonization events, we used several types of data from MRR and observational studies. While conducting MRR studies, we recorded the transect location where each individual was first seen. We used a Trimble® GeoXM™ handheld with ArcGIS 9.0 (ESRI, 2004) to determine the length and location of transects used for population studies within sites. Movement distances within sites were categorized by the distances between transects from which the individuals were observed. Movement distances of individuals between sites were calculated as the straight-line distance between the two sites. We also used observational data of individuals occurring at previously unoccupied wetlands and of *N.m. francisci* found at areas distant from occupied wetlands to draw inferences about their colonization ability.

RESULTS

DISTRIBUTION

Our surveys show that the distributional range of *Neonympha mitchellii francisci* appears to be completely confined to Ft. Bragg. The absence of this species in other likely tracts of habitat throughout NC, including the Green Swamp, Holly Shelter Game Land, Camp Lejeune and the Croatan National Forest, has been confirmed by lepidopteron surveys conducted by the NC Heritage Program.

Even within Fort Bragg, the butterfly is highly restricted in its distribution. The total area of known, occupied habitat for *Neonympha mitchellii francisci* is about 10 ha. All observations have been made within just eight headwater drainages. These drainages are concentrated in just one area, with either their headwaters or mouths adjacent to one another across short divides. Including the two sites originally discovered by Parshall and Kral (1989) *N.m. francisci* have been observed at 31 sites within these drainages.

We have recorded *Neonympha mitchellii francisci* at 16 sites outside of restricted, military training areas (Table 2). Of these, only four have been occupied by subpopulations over the entire course of our study. The other 12 sites currently do not support subpopulations of *N.m. francisci,* although individuals have been occasionally seen at several of them over the last ten years. These include degraded sections of peripheral wet habitats near existing sites that once supported subpopulations, potential high-quality sites where the butterfly had never been previously recorded and sites where known populations have gone extinct. In restricted areas, we know of 14 subpopulation sites on five different watersheds. These 14 sites were all discovered during the original status survey for this species, but have been rarely visited since.

TABLE 2.—Summary of *N.m. francisci* sightings and dynamic population events outside of restricted areas. For each site and each year, numbers reflect the maximum number of individuals observed in a year. A '+' denotes sightings without quantitative records. An 'ns' denotes a site that was not surveyed in a particular year. Asterisks denote an area that was burned. Finally, grey shading denotes an area that was subject to beaver activity. For the largest subpopulation sites (A1, D1, D3 and E2), numbers reflect the Pollard-Yates population estimates. For 2003–2005 these population estimates were for the first and second flight periods, respectively, are separated by a comma

Site	Distance to nearest subpopulation	Year						
		<2000	2000	2001	2002	2003	2004	2005
primary								
A1	0 m	+	6	+	17	18,30	24,30	12,24
D1	0 m	+	7	5	19	14,19	16,43	37,42
D3	0 m	ns	ns	ns	11	24,21	18,67	20,42
E2	0 m	ns	ns	ns	8	10,12	7,18	6,7
transitory								
A2	350 m	>50 (1983)	0	0	3	3	0	0
A3	125 m	+	1	0	0	0	0	0
B1	2300 m	+	30	ns	23	*6*	3	2
C1	7400 m	ns	ns	ns	ns	1	0	0
D4	200 m	ns	ns	ns	49	17	5	3
D6	175 m	+	3	ns	ns	0	0	0
D8	650 m	ns	ns	ns	1	0	0	0
D9	475 m	+	6	2	1	0	0	0
E1	750 m	+	5	3	12	13	3	0
E3	100 m	+	ns	ns	ns	7	0	0
E4	1300 m	+	3	ns	ns	2	0	0
E5	1900 m	ns	ns	ns	5	0	0	1

HABITAT ASSOCIATIONS

All populations that we studied are associated with successional wetlands located in the floodplains of small headwater streams. Although quite wet, these habitats are only intermittently flooded. Vegetation consists of a mixture of shrub thickets dominated by alders (*Alnus serrulata*) and transgressive swamp blackgums (*Nyssa biflora*), red maples (*Acer rubrum*) and open areas dominated by sedges, grasses, rushes, sphagnum and other wetland herbaceous species

Several species of *Carex* are common to abundant in these sites and are suspected to be larval food plants for *Neonympha mitchellii francisci.* Wetland grasses, particularly cane *Arundinaria tecta,* rice-cut grass *Leersia oryzoides* and witch-grasses *Dichanthelium* spp., are also common at these sites. While grasses are not suspected to be food resources, they do provide a large amount of herbaceous structure and can dominate the herbaceous community, particularly in drier sites.

Virtually all *N.m. francisci* sites are the result of past episodes of impoundment, which both opened up the canopy and produced deep deposits of organic sediment. Nearly all of the impoundments harboring subpopulations are located on the sites of abandoned beaver ponds. Abandoned beaver dams and beaver-felled tree trunks are present in the majority of sites where *N.m. francisci* occur. Outside of restricted areas, evidence of past beaver activity is missing only at the original two colony sites known to Parshall and Kral (1989). Within restricted areas, several sites lacked explicit evidence of beaver activity, (*i.e.*, beaver-chewed stumps), although almost all showed signs of historical impoundment. Not all abandoned beaver ponds are occupied, however, even when located in close proximity to active colonies of the butterfly.

Another important factor related to habitat suitability appears to be the presence and abundance of *Carex* species, with *C. mitchelliana*, *C. glaucescens*, *C. atlantica*, *C. lurida* and *C. lonchocarpa* all regularly occurring as dominant members of herbaceous openings within occupied sites. Interestingly, *C. stricta*, a larval host plant used by northern populations of *Neonympha mitchellii mitchellii*, is absent from most of the sites occupied by the butterfly.

The sedge with the highest correlation to butterfly abundance is *Carex mitchelliana*, a relatively rare species that appears to have its largest populations in the state within Fort Bragg. From sampling across a variety of habitats at 33 sites (n = 184 plots), we observed that occupied sites have between 6–21% cover of *C. mitchelliana*, and that there appeared to be a positive relationship between its abundance of *C. mitchellina* and butterfly abundance. From further sampling across our four primary study sites (n = 75 plots) we found a perfect relationship ($R^2 = 1.0$) between the average percent cover of *C. mitchelliana* and butterfly population size. Additionally, we confirmed a positive relationship between *C. mitchelliana* abundance and habitat area ($R^2 = 0.43$). Because of the small number of occupied sites, we could not separate the effects of site area and *C. mitchelliana* percent cover on *Neonympha mitchellii francisci* abundance. Virtually all other sedge species found in conjunction with *N.m. francisci* have much wider distributions on Ft. Bragg and across the Southeastern U.S. We note that *C. mitchelliana* appears to be essentially absent at one colony site and very scarce at another (the two sole active colonies in one watershed). These findings indicate that multiple host plants are likely used by *N. m. francisci*.

LARVAL FEEDING EXPERIMENTS

We did not find any *Neonympha mitchellii francisci* larvae in the field, despite intensive searches. Occasionally, we observed other insects feeding on the plants, including larvae of the Appalachian eyed brown butterfly (*Satyrodes appalachia*), which is known to be a generalist feeder on *Carex*.

Our larval feeding experiments support the hypothesis that *Carex mitchelliana* is an important larval food resource. They also indicate, however, that other species may be used. In a test of initial acceptance, all neonates (n = 4) offered *C. mitchelliana* fed upon it immediately. In contrast, acceptance rates for the other species offered varied from 3 out of 4 on *C. atlantica*, 2 out of 4 on *C. lurida* and *C. stricta* and only 1 out of 4 on *C. glaucescens*, *C. lonchocarpa* and *C. turgescens*. Three larvae that failed to eat these other species were subsequently transferred to *C. mitchelliana*. All four larvae started on *C. mitchelliana* survived to the 6th instar and two survived to adulthood, the only ones to do so. Two of the three larvae transferred to *C. mitchelliana* also survived to the 6th instar. In contrast, only a single larvae feeding on *C. stricta, lurida* and *glaucescens* survived to the 6th instar, with none entering pupation.

Although these results are consistent with the habitat correlations we have observed, growth rates were much slower in the lab than they must be in the wild, as the larvae that reached adulthood took weeks longer to do so than their wild cohort. We suspect that food quality may have been a factor – we fed the larvae on cut leaf segments rather than on whole plants – and we cannot rule out the possibility that this biased our results in other ways as well.

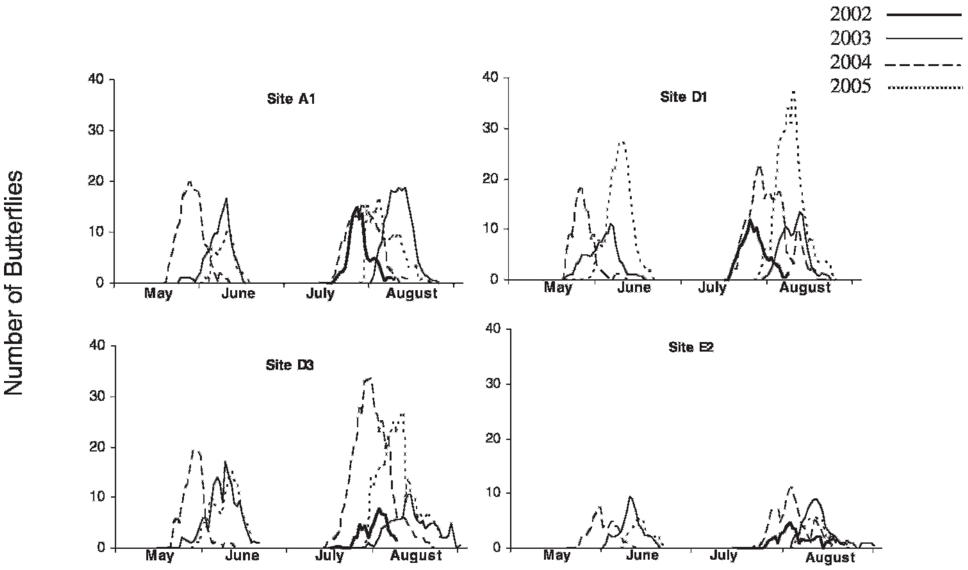

FIG. 1.—Annual flight phenologies based on count data, in the four largest subpopulation sites outside restricted areas at Ft. Bragg, NC

PHENOLOGICAL PATTERNS

Butterflies were consistently more active in the afternoons than in the mornings and less active on sunny days. We observed an additional butterfly for every 3 h later a survey was conducted between 09:00 and 17:30 ($F = 14.8$, $P > 0.002$, $df = 159$). Temperature did not influence butterfly counts ($F = 2.3$, $P = 0.147$, $df = 159$). However, fewer butterflies were observed on sunny days than on overcast or partly cloudy days ($F = 3.44$, $P = 0.035$, $df = 159$). The mean difference between observed-expected butterfly counts was -1.4 (+/− 0.11 SE) on sunny days, 0.04 (+/− 0.024 SE) on overcast days and 0.21 (+/− 0.064 SE) on partly cloudy days.

Seasonal flight phenologies differed in their onset and duration between sites and from year to year (Fig. 1). In four years of study, *Neonympha mitchellii francisci* emerged between May 18 and May 26 in the first flight period, and between Jul. 12 and Jul. 28 in the second flight period. On average, the time span between emergence of the first flight period and the second was 61 (4.8 s.d.) d. The date on which we recorded highest counts in the first flight period ranged between May 28 and Jun. 8, and in the second flight period between Jul. 24 and Aug. 10. On average, there were 61 (4.4. s.d) d between the peak of the first flight and the peak of the second flight. The first flight period lasted 19 (4.3 s.d.) d within a site and 24 (4.4 s.d.) d among all sites. The second flight period lasted 24 (5.4 s.d.) d within a site and 33 (4.2 s.d.) d among all sites.

For each of the seven flight periods we monitored during 2002–05, we used publicly available environmental data from the National Climatic Data Center (http://lwf.ncdc.noaa.gov/oa/ncdc.html) to estimate the beginning of the first flight period. Given the variation in the start of the first flight period, we presumed emergence was controlled not by photoperiod but by temperature. We used measures common to the agriculture literature (*i.e.*, Vittum *et al.*, 1965) that sum heat input into the environment, and started the measure on Mar. 1, when sedge species that are presumed hosts would begin active production. We summed "Growing Degree Days" (GDD), which accounts for

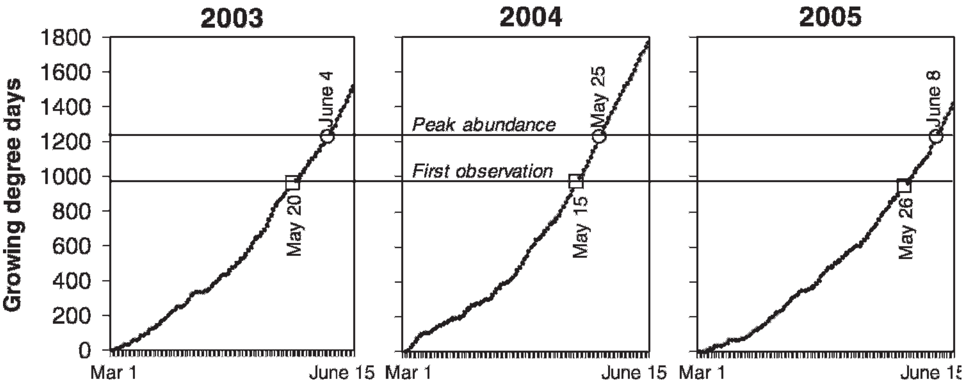

FIG. 2.—Accumulation of Growing Degree Days over the year from May 1 through Jun. 15. The first and peak days of the flight period are marked

minimum temperatures for larval development (50F) and maximum temperatures above which temperature does not increase growth rates (86F). GDD is calculated as the cumulative sum of the average of the maximum and minimum daily temperature minus 50 degrees Fahrenheit (where the maximum cannot be above 86 degrees and the minimum can not be below 50 degrees). When we plotted this value over time for 2003–2005, we found that we could accurately predict the time of emergence, with the first butterfly being observed around 984 GDD, and the peak of the emergence occurring at 1245 GDD (Fig. 2). Given these data, we can predict the first day of emergence and the start of the peak abundance ±1 d. The second flight period is then best predicted by days from the first flight period (*see* above). These results can aid future monitoring efforts by focusing sampling regimes.

DEMOGRAPHIC VARIATION

In the second adult flight periods of 2002–2005, we marked a total of 1210 individual *Neonympha mitchellii francisci* in the four large subpopulation sites. Of those marked, we were able to determine the sex and age of 930 individuals. Model comparisons using these individuals indicate that, overall, parameter estimates vary by sex (Table 3). Males consistently have higher detectability. Furthermore, the model including sex classes was the best fit to MRR data for 2003 and very close to the best fit model in other years (within one criterion unit; *see* Burnham and Anderson, 2002). In the field, we observed behavioral differences whereby males actively search for mates and, hence, are more easily detected. Females, conversely, tend to be more sedentary and are more difficult to find. Males accounted for ~2/3 of all butterflies captured.

In 2003–04 model comparisons indicate that male survivorship tends to be lower than females, however this pattern did not hold for 2005 (Table 3). One explanation for increased male mortality is that males are exposed to more predation threats while searching for females (via spider webs or dragonflies). We found no support for differences in detectability by age, however oldest butterflies consistently show a trend toward lowest survivorship (Table 3).

POPULATION SIZES AND TRENDS

Between 2002 and 2005, the combined population estimates from MRR ranged from 502–1400, with a peak of 1400 in 2004. Subpopulation sizes totaled 49–739 adults per brood. The

TABLE 3.—Demographic model outputs and estimates of apparent survivorship (phi) and detectability (pi) for MRR data. In 2003 data are pooled from Sites A1, D1, and D3. In 2004–2005 data are pooled from sites D1 and D3

Year	Model	AIC	*phi*	SE	*pi*	SE
2003	constant	343.4	0.645	0.042	0.262	0.046
	daily var	364.4	.	.	.	.
	by sex (m)	340.9	0.613	0.050	0.354	0.237
	by sex (f)	.	0.733	0.078	0.128	0.058
	by age (1)	350.0	0.654	0.069	0.245	0.072
	by age (2)	.	0.661	0.056	0.260	0.060
	by age (3)	.	0.417	0.164	0.505	0.299
2004	constant	506.5	0.709	0.029	0.284	0.039
	daily var	507.9	.	.	.	.
	by sex (m)	507.0	0.663	0.042	0.296	0.055
	by sex (f)	.	0.762	0.039	0.279	0.055
	by age (1)	507.2	0.769	0.038	0.316	0.058
	by age (2)	.	0.681	0.045	0.255	0.054
	by age (3)	.	0.541	0.121	0.396	0.18
2005	constant	451.7	0.672	0.033	0.350	0.045
	daily var	487.2	.	.	.	.
	by sex (m)	451.7	0.684	0.035	0.388	0.290
	by sex (f)	.	0.652	0.079	0.239	0.117
	by age (1)	450.6	0.63	0.059	0.497	0.100
	by age (2)	.	0.701	0.038	0.323	0.051
	by age (3)	.	0.591	0.354	0.071	0.110

peak in 2004 may have been caused by weather conditions; however, we do not have a long enough time series of data to understand fully how weather affects population size. In 2005 we generated MRR estimates for both flight periods for A1, D1 and D3 (Fig. 3). We observed an increase in numbers between the first and second broods at sites A1 and D3, which is consistent with the general increase between broods shown by modified Pollard-Yates counts (Table 2). One explanation for an increase in numbers between broods is that there is a much longer diapause between the second and first broods and thus greater possible larval mortality. The difference in population sizes between sites may be partially attributed to the size of each subpopulation site. Across sites, MRR estimates were positively correlated ($R^2 = 0.95$) with the area of wetland habitat at each site (Fig. 4). Even the four largest subpopulation sites are subject to frequent changes in habitat size, which can result in rapid fluctuations in population size. At site D1, the population responded favorably to the removal of a beaver dam and pond downstream in 2003. Uniformly higher counts after 2003 are attributable to a three-fold increase in wetland area. Differences in population sizes may also be due to habitat quality, as butterfly abundances are highly correlated with the abundance of potential host plants. Because there are only four sites, we cannot currently separate the effects of area and site quality on population size.

MOVEMENT, COLONIZATION AND METAPOPULATION STRUCTURE

Neonympha mitchellii francisci is generally a sedentary butterfly. During MRR studies, we commonly observed individuals that did not move during a survey lasting 30–45 min, whether captured or not. Of the 536 recapture events we recorded over 4 y of study, fewer than half of the recaptures resulted in a movement from the transect location of previous

TABLE 4.—Estimates of apparent surviviorship (phi), detectability (pi) and population size (N) for second flight period, in each the four largest subpopulation sites outside restricted areas at Ft. Bragg, NC. In 2005 MRR estimates were derived for both adult flight periods

Subpopulation site	2002	2003	2004	2005 (1st)	2005 (2nd)
Site A1 (0.66 ha)					
#marked	46	67	47	24	36
phi	0.58	0.61	0.43	0.69	0.78
±	(0.06)	(0.05)	(0.08)	(0.07)	(0.04)
pi	0.38	0.35	0.48	0.48	0.40
±	(0.09)	(0.07)	(0.15)	(0.09)	(0.06)
N	140	289	233	60	134
±	(22.9)	(35.2)	(54.1)	(7.6)	(12.5)
Site D1 (0.96 ha)					
#marked	51	35	94	71	101
phi	0.56	0.54	0.70	0.65	0.74
±	(0.06)	(0.07)	(0.03)	(0.04)	(0.03)
pi	0.59	0.51	0.34	0.38	0.36
±	(0.09)	(0.11)	(0.05)	(0.05)	(0.05)
N	97	90	349	274	254
±	(10.6)	(13.5)	(31.5)	(24.8))	(20.6)
Site D3 (0.86 ha)					
#marked	22	48	118	15	56
phi	0.64	0.61	0.64	0.64	0.54
±	(0.16)	(0.07)	(0.04)	(0.09)	(0.06)
pi	0.08	0.27	0.26	0.25	0.42
±	(0.07)	(0.08)	(0.05)	(0.11)	(0.09)
N	331	295	739	232	330
±	(223.9)	(56.9)	(101.0)	(63)	(46.3)
Site E2 (0.51 ha)					
#marked	15	28	34	6	16
phi	0.59	0.75	0.49	0.30	0.63
±	(0.14)	(0.05)	(0.11)	(0.10)	(0.11)
pi	0.29	0.35	0.29	1.0	0.54
±	(0.16)	(0.08)	(0.13)	(/)	(0.16)
N	64	91	182	28	49
±	(25.4)	(12.5)	(61.0)	(/)	(8.8)

capture (Fig. 5). Females were particularly sedentary; males were between 2–3 times more likely to move than females and they were more likely to move longer distances. Although both sexes occasionally traversed the extent of a site throughout an entire flight period, incremental movement distances between recaptures were generally small (<50 m) (Fig. 5).

Neonympha mitchellii francisci occasionally move between subpopulations, especially if subpopulations are located along a single watershed. During our MRR studies, we recorded five dispersal events between subpopulations. Between 2002 and 2003, we observed the movements of three marked individuals between two sites separated by a distance of 350 m along the same watershed. In 2005 we observed the movements of two marked individuals between two sites that are on different forks of a shared watershed. While the minimum

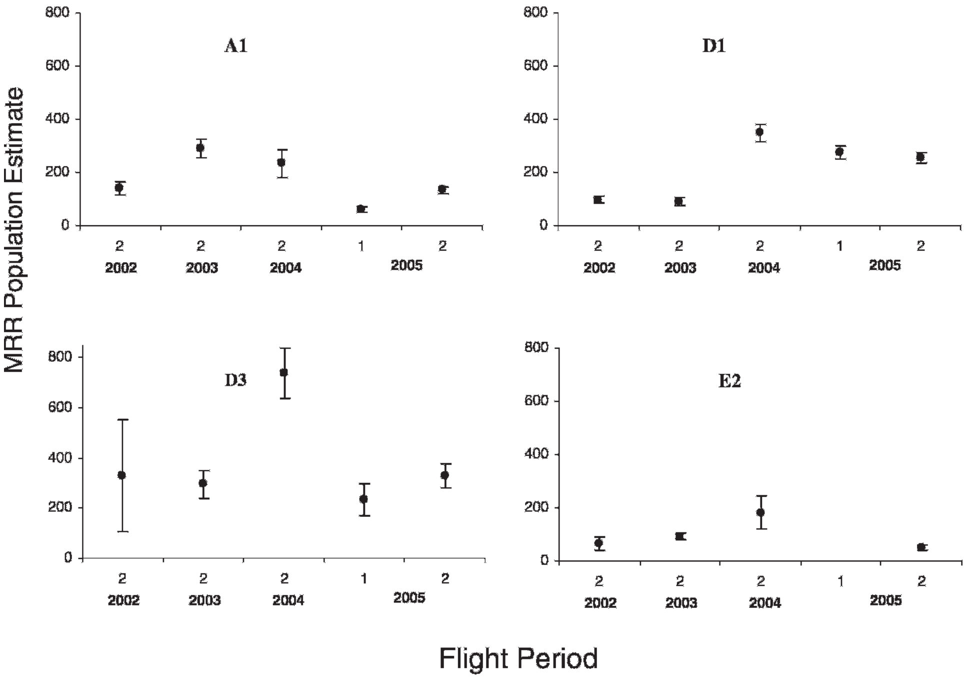

FIG. 3.—MRR Population Estimates, second flight period, in the four largest subpopulation sites outside restricted areas at Ft. Bragg, NC. In 2005 MRR estimates were derived for both adult flight periods

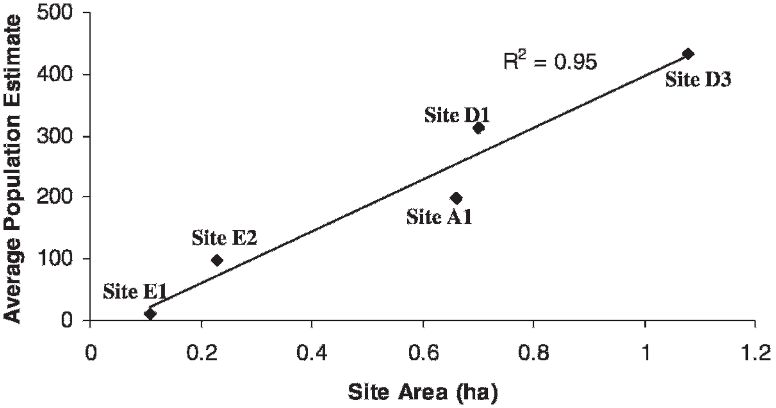

FIG. 4.—*N.m. francisci* subpopulation sizes, second flight period 2002–05, in the four largest subpopulation sites outside restricted areas at Ft. Bragg, NC. Population estimates are averaged across the four years of study. For site D1, only population estimates from 2004–2005 are included, for which time the site area was stable. Additionally, one smaller site (E1) is included for 2002–03, after which flooding resulting in a local extinction. The regression line illustrates the relationship between population estimates and site areas

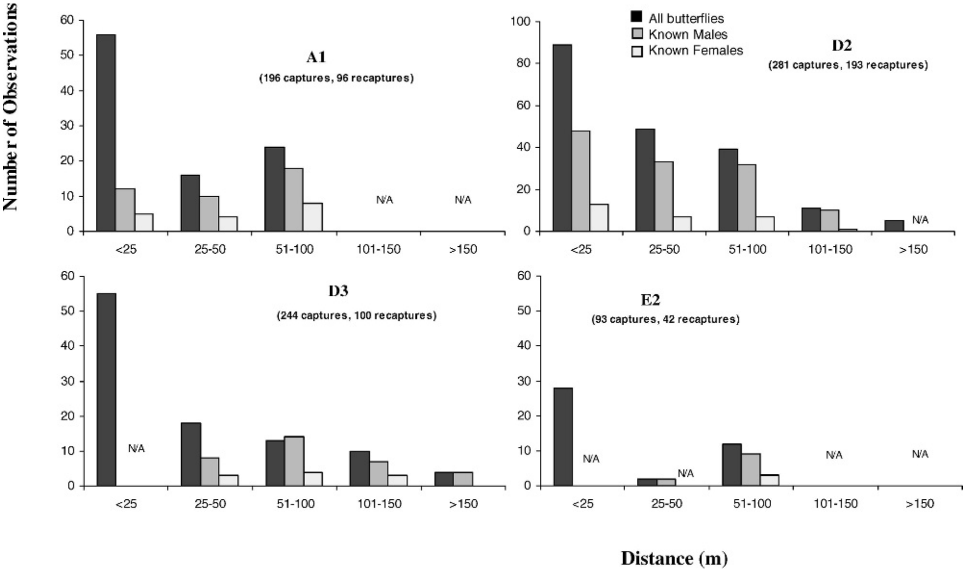

FIG. 5.—*N.m. francisci* movement distance sizes, within each of the four largest subpopulation sites outside restricted areas at Ft. Bragg, NC. The cumulative observations of recaptured individuals (ALL) are illustrated by the darkest bars, and movement distances for individuals of a known gender are categorized by the lighter bars. For all sites between 2002–05, the average time span prior to recapture is 2 d (1 d s.d.)

linear distance between these sites is roughly 1 km through the forest, the along-stream distance between these sites is roughly 2 km.

Additionally, we have observed 36 occurrences of solitary individuals found in areas away from known subpopulations (Table 2). All of these movements except one were recorded along streams where subpopulations occur. Twenty-three observations were located <500 m (straight-line distance) from a subpopulation and 12 other observations were <2 km from a subpopulation. The exception was an individual found on an isolated watershed 2.6 km (straight-line distance) from the nearest known subpopulation. If stream-wise distance is considered, the shortest distance this individual could have moved from the nearest subpopulation is over 7 km.

In general, the spatial arrangement of occupied habitats is constantly shifting on the landscape. During 2002–05 we observed two rapid subpopulation extinctions that occurred within one year following habitat disturbance (E1 and D4), one gradual subpopulation extinction that occurred over a decade or more, as the (suitable) wetland habitat succeeded into an (unsuitable) drier, shaded, hardwood forest stand (A2) and the sharp decline of a fifth population immediately after the habitat experienced a thorough burn (B1). Through our ongoing monitoring of unoccupied sites, we have also directly observed the colonization of new habitat. Following the removal of a beaver dam in the winter of 2002, a large pond adjacent to site D1 succeeded into a sedge-dominated meadow, expanding the D1 habitat area by a factor of three. Beginning in the second adult flight period of 2003, we recorded the colonization of this new habitat by individuals that were marked in the older D1 habitat, >100 m away.

DISCUSSION

THE IMPORTANCE OF BEAVERS

On Fort Bragg, wetland glade habitats are created and maintained through regular disturbances. Our observations clearly point to the important role of beaver activity (*Castor canadensis*), at both a site level and over the landscape, as *Neonympha mitchellii francisci* appear to be most strongly associated with habitats created by beavers. These habitats are similar to the northern fens used by *N .m. mitchellii* in that they support a high diversity and abundance of *Carex*-genus and other sedges (Shuey, 1997). However, beaver-wetlands are more clearly maintained by recurrent disturbance than are northern fens. Wilsmann and Schweitzer (1991) and Shuey (1997) observed that succession in fens is very slow due to the hydrological regime and edaphic factors, allowing these types of open communities to persist for perhaps hundreds of years. In contrast, succession of the open, sedgy habitats occupied by *N .m. mitchellii* is typically fairly rapid. Gerald (1994) found that the graminoid-rich habitats that develop on the sites of abandoned beaver ponds may persist only for as long as 20 y in the North Carolina Sandhills.

Historically, the extirpation of beavers and inhibition of fire has drastically reduced the area of suitable habitat, and is potentially responsible for the small total population size of *Neonympha mitchellii francisci* (Hall, 1993). Beavers were last trapped in NC in 1897 and they were not reintroduced into the state until 1939, at a site near Ft. Bragg (Woodward and Hazel, 1991). Fire has been uniformly suppressed, particularly since the 1950s, to prevent loss to agriculture or dwellings (Frost, 1993). However, within the last several decades, both beavers and fire have been restored to the landscape, providing opportunities for population restoration. Since the early 1970s, Ft. Bragg has housed an active program of prescribed burning that accounts for its retention of one of the finest long-leaf pine communities in the southeastern U.S. Due to the contiguous extent of undeveloped landscape, beavers generally thrive on Ft. Bragg with minimal population control or intervention. Acting together, these disturbances are critical for shaping this particular landscape, where wetland habitats exist in a constantly shifting mosaic of patches at the right stage of succession to support colonies of *N m. francisci.*

POPULATION STRUCTURE AS A MULTI-TIERED METAPOPULATION

The overall population size of *Neonympha mitchellii francisci* has remained relatively constant throughout the duration of our study. The relative constancy of the overall population is the sum of fairly dynamic subpopulations, where some sites have decreased to extinction at the same time that others have increased. To that end, the *N.m. francisci* populations is best characterized as having a hierarchical structure, whereby multiple subpopulations comprise a metapopulation within a watershed, and a network of watershed-specific metapopulations comprise a rangewide metapopulation. Within this hierarchical structure, habitat dynamics and population dynamics vary at a site (or subpopulation), intra-watershed and inter-watershed levels.

Metapopulations have become paradigmatic in butterfly population ecology, especially for rare species on conservation concern. They show up virtually anywhere a species is subject to localized but potentially extirpating environmental perturbations (*e.g.*, Harrison *et al.*, 1988; Hanski *et al.*, 1994; Thomas, 1995; Neve *et al.*, 1996; Wahlberg *et al.*, 2002). However, the population structure of *Neonympha mitchellii fransisci* at Fort Bragg appears to be particularly complex, having a multi-tiered structure. While a hierarchical, nested structure has been previously noted for butterfly metapopulations, at least descriptively (*e.g.*, Neve *et al.*, 1996), the complexity of the structure of the *N. m. fransici* population appears to be particularly related to the nature of the prevailing disturbance regime, not just a side-effect of regular dispersal.

At the site level, butterfly habitats are relatively unstable. Fires and flooding may temporarily reduce the quality or amount of habitat available (*e.g.*, sites E1 and B1). Conversely, foraging activity by beavers or pond abandonment can increase the amount of available habitat (*e.g.*, site D1). These types of disturbances can affect habitat sites quickly, and can change habitat quality from year to year. As such, the size of individual subpopulations can fluctuate substantially from year to year. Butterflies readily move 100+ m within high-quality habitat and individuals of both sexes will colonize new habitats quickly if the new habitat is created adjacent to an existing subpopulation. Although we have witnessed several extinction events and one colonization event, the inevitable succession toward unsuitable habitat makes the viability of individual subpopulations low.

Within watersheds, individual sites are separated by distances of 700 m–1300 m along streams and are connected by relatively contiguous riparian habitat. Although infrequent, dispersal occurs between subpopulations connected by streams; out of >1200 individuals marked during MRR studies, we recaptured only five individuals in a different subpopulation (on the same stream) from the one where they were marked. We also have observed solitary, adult butterflies in pockets of high quality habitat separated from subpopulations by distances of >75 m to 2 km.

At the intra-watershed level, riparian habitats may serve as corridors and pockets of ephemeral high-quality habitat along streams is important to facilitate the movement of individuals between larger subpopulation sites (Kuefler and Haddad, 2006). Here, the role of beavers as ecosystem engineers is critical (Wright *et al.*, 2004), and their populations must be maintained on streams where *Neonympha mitchellii francsici* occurs. It is important to note that while disturbances will potentially improve or create new habitats throughout a watershed, the immediate, deleterious effects of disturbances may threaten existing butterfly subpopulations.

The range-wide metapopulation outside of restricted areas is composed of three watersheds that are known to support *Neonympha mitchellii francisci* subpopulations. Watersheds are separated by distances of 1–15 km, with large tracts of pine forest, dry fields, and areas manicured for military training in between them. One watershed metapopulation (A) now appears to consist of a single active subpopulation, and there is no nearby beaver population to regenerate wetlands. Dispersal between watersheds is probably extremely rare; we did not directly observe any movements between different watersheds. Thus, with continued succession of this subpopulation and no possibility of disturbance, the local extinction of the butterfly on this watershed is likely. However rare, the colonization of new watersheds is not impossible. Our observation of one individual female in 2003 in a watershed where *N.m. francisci* has not otherwise been observed suggests dispersal at this scale does indeed occur.

The likelihood of metapopulation extinction is the product of the probability of extinction in individual subpopulations (Morris and Doak, 2002) and, thus, metapopulation viability is dependent upon the number, viability, and interaction between component subpopulations. Given that there is some non-zero extinction probability within a watershed, then some degree of connection between the watershed metapopulations also is necessary for the persistence of *Neonympha mitchellii francisci.* To that end, the larger constellation of watershed populations at Ft. Bragg likely serves to maintain the stability of the entire system even as the smaller watershed subpopulations are colonized and go extinct over time.

The metapopulation viability for the butterfly, then, is greatly enhanced by reducing extinction probabilities in each watershed. While occupancy of individual colony sites has varied greatly during the past 15 y, occupancy of specific stream valleys has been essentially constant during that period. The close proximity of these headwater streams allows for at least occasional dispersal to occur between them. If this population structure is required to cope with a constantly shifting mosaic of habitat suitability, then Ft. Bragg may be one of the few places left within the butterfly's range that is large enough to support such structure.

IMPLICATIONS FOR MANAGEMENT

The tiered population structure of *Neonympha mitchellii fransisci* necessitates a novel, tiered strategy for restoration and recovery. Considering the rarity and instability of subpopulation sites, habitat protection and maintenance at the site level should be high conservation priorities. Most subpopulation sites are small enough that temporary maintenance of habitat quality may be achieved directly by hand-thinning encroaching shrubs and trees, and possibly by planting *Carex* sedges. Prescribed burns help maintain site quality by preventing encroachment of shrubs and grasses. Fire appears to be beneficial when site quality is already high. In degrading habitats, however, fire can have disastrous impacts on small, isolated subpopulations and should be used carefully. In numerous cases, we have observed prescribed fires burn up to, but not penetrate, butterfly habitats. Between 2002–05 we observed only one site (B1) that was burned through completely, which coincided with a sharp decline in the butterfly population at that site. Inevitably, the current subpopulation habitats will mature into lower-quality riparian habitat. Thus, successful conservation planning must consider habitat maintenance at larger spatial and temporal scales in the population hierarchy.

One conservation approach at the inter-watershed level involves the translocations of adult butterflies. It appears individuals may be reared in captivity successfully and translocated to suitable habitats. However, firm evidence of a primary host plant preference is needed before manipulation of *Neonympha mitchellii francisci* is undertaken. Also, translocation involves a number of considerations including the size and genetic composition of the introduced population (Conant, 1988; Griffith *et al.*, 1989). Furthermore, Allee effects may hamper successful reintroduction attempts, whereby if too few butterflies are released they may leave the site, as a low population density may be perceived as an indicator of poor site quality (Menendez *et al.*, 2002).

Another approach would involve restoring or creating suitable habitats on unoccupied watershed located between occupied watersheds. Planting of *Carex mitchelliana* (or other important host plants) may help provide stepping stones, if not important colony sites, favoring the dispersal of the butterfly into new areas. Such an approach has, in fact, been employed for species of European satyr, *Lopinga achine* (Bergman, 2000). This approach would be especially effective if coupled with a translocation of reared individuals to newly created habitats, reducing the dispersal distance for an inter-watershed exchange. Habitat manipulation, however, imposes the challenge of recreating the structure, composition, and stability of suitable *Neonympha mitchellii francisci* habitat. Future work should consider these details of inter-watershed management initiatives.

As *Neonympha mitchellii francisci* subpopulations are incredibly dynamic, management initiatives for this species should include an ongoing monitoring regime. Annual monitoring can be used to catalogue immediate changes in population sizes caused by habitat disturbances and, thus, give insight into how to better manage those disturbances. Additionally, longer-term monitoring is needed to understand population responses to larger-scale disturbances, such as climatic changes and the spatial variation in habitats. Monitoring through observational counts is a simple, cost-effective way for managers to track changes in subpopulations. Furthermore, this simple approach may be integrated with occasional intensive sampling (*e.g.*, MRR) to produce reliable estimates of demographic variability (Gross *et al.*, 2007; Haddad *et al.*, 2007).

NEONYMPHA MITCHELLII FRANCISCI VS. N.M. MITCHELLII

Neonympha mitchellii francisci and *N.m. mitchellii* provide interesting case studies of how management approaches can be tailored to match a species' unique population structure. While northern *N.m.mitchellii* occupy large, relatively stable habitat units that are regionally disconnected, *N.m.francisci* occupy small patches of dynamic habitat that are connected by streams. These habitat differences mirror differences in butterfly population structure. The fen-inhabiting *N.m. mitchellii* in the Great Lakes region are consistently described as sedentary, with little or no evidence of movements between populations. Szymanski *et al.* (2004) observed maximum movement distances of <500 m within the two sites they studied and they observed no movements between the sites, which were located only 3 km apart in the same stream valley. In contrast, we observed individuals at distances of over 500 m from the nearest colony site, with distances of 2–3 km being observed on at least three occasions. Hence, management approaches for *N.m. francisci* should promote an active disturbance regime and facilitate the exchange of individuals at multiple scales. By contrast, management approaches for northern *N.m.mitchelli* focus on preserving the stability of large habitats and facilitating movement only at subpopulation scales (Szymanski *et al.*, 2004; Barton and Bach, 2005).

Improvement of habitat conditions across Ft. Bragg and in nearby areas could facilitate a range expansion of *Neonympha mitchellii francisci.* Other butterflies with similar habitat preferences and dispersal capabilities rapidly expand across entire regions within just short period of time (Baguette and Neve, 1994; Neve *et al.*, 1996). Future research directions that enable range expansion will verify specific habitat requirements and factors that facilitate dispersal. More generally, the rarest butterflies will often have unique environmental or life history features that cause their endangerment. In the case of *N.m. francisci,* unique attributes population dynamics, namely their dependence on beaver, and population structure, namely their multi-tiered metapopulation structure., will be critical to conservation. These aspects of Nmf population biology may provide more general insights for other butterfly species. A challenge for butterfly conservation is managing those unique features to enhance population viability in fragmented landscapes.

Acknowledgments.—This work was funded by support from Ft. Bragg through the Department of Defense, Department of the Army, Director of Public Works (DPW)-ESB. We also thank the many professional biologists on staff: Brian Ball, Jackie Britcher and others at the Endangered Species Branch and Natural Resources for their willingness to facilitate our work at Ft. Bragg. At North Carolina State University, we thank Ken Pollock for his feedback and advice on MRR analyses and we thank the Insectiary for facilitating larval rearing experiments. Bruce Sorrie participated in all the reconnaissance surveys as well as in some of the quantitative sampling that followed. Nora Murdock (USFWS) also played a key role in both the status surveys and in the initial recovery project. Carrie Tansy (US Fish and Wildlife Service) provided correspondence regarding northern *Neonympha mitchellii mitchellii* research. Finally, we would like to credit the expert help of many invaluable research technicians who have sweated with us in the field. Administrative support for funding was graciously provided by the North Carolina Cooperative Fish and Wildlife Research Unit, particularly by Wendy Moore.

LITERATURE CITED

BAGUETTE, M. AND G. NEVE. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology*, **19**:1–5.

BARTON, B. J. AND C. E. BACH. 2005. Habitat use by the federally endangered Mitchell's satyr butterfly (*Neonympha mitchellii mitchellii*) in a Michigan prairie fen. *American Midland Naturalist*, **153**:41–51.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS AND L. THOMAS. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.

BURNHAM, K. AND D. ANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Ed. Springer-Verlag New York, Inc.

CONANT, S. 1988. Saving endangered species by translocation: are we tinkering with evolution? *Bioscience*, **38(4)**:254–257.

CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika*, **51**:429–438.

DARLOW, N. 2000. Behavior, habitat usage and oviposition of the Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii*. Master's Thesis. University of York, United Kingdom. 43 p.

DEPARTMENT OF THE ARMY. 1997. Fort Bragg Endangered Species Management Plan. 90 p.

ESRI. 2004. ArcGIS Version 9.0 Redlands. CA, USA.

FROST, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem, p. 17–23. *In:* S. H. Herman (ed.). Proceedings of the 18th Tall Timbers Fire Ecology Conference. Tall Timbers Research Station. Tallahassee, FL.

GALL, L. F. 1984. The effects of capturing and marking on subsequent activity in Boloria acrocnema (Lepidoptera : Nymphaliedae), with a comparison of different numerical models that estimate population size. *Biological Conservation*, **28**:139–154.

GERALD, L. T. 1994. Characterization and classification of wetlands created or converted by beavers in the Sandhills region of North Carolina. M.S. Thesis. UNC-Wilmington, Wilmington, NC.

GOLDSTEIN, P. Z., S. P. HALL, B. HART, S. M. ROBLE AND J. SHUEY. 2004. Evaluation of relationships and conservation status within the *Neonympha mitchellii* complex (Lepidoptera: Nymphalidae). Report to the U.S. Fish and Wildlife Service, Raleigh Field Office. Raleigh, NC.

GRIFFITH, B., M. SCOTT, J. CARPENTER AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. *Science*, **245**:477–480.

GROSS, K., E. J. KALENDRA, B. R. HUDGENS AND N. M. HADDAD. 2007. Robustness and uncertainty in estimates of butterfly abundance from transect counts. *Population Ecology*, **49(3)**:191–200.

HADDAD, N. M. 1999. Corridor use predicted by behaviors at habitat boundaries. *The American Naturalist*, **153**:215–227.

———, D. KUEFLER AND B. HUDGENS. 2003. Evaluating population viability, and potential restoration of the St. Francis Satyr butterfly. Report to the Endangered Species Branch, Ft. Bragg, NC.

———, ——— AND ———. 2004. Developing techniques and protocols for monitoring St. Francis Satyr Report to the Endangered Species Branch, Ft. Bragg, NC.

———, ——— AND ———. 2005. Monitoring protocol for the St. Francis Satyr butterfly. Report to the Endangered Species Branch, Ft. Bragg, NC.

———, ——— AND ———. 2006. Ongoing monitoring of St. Francis Satyr butterfly populations. Report to the Endangered Species Branch, Ft. Bragg, NC.

———, B. HUDGENS, C. DAMIANI, K. GROSS AND D. KUEFLER. 2007. Optimal sampling for rare insect populations. *Conservation Biology* (in press).

HALL, S. P. 1993. A rangewide status survey of Saint Francis' satyr (Lepidoptera: Nymphalidae). Report to the U.S. Fish and Wildlife Service, Region 6 Endangered Species Office, Asheville, NC.

——— AND E. L. HOFFMAN. 1994. Supplement to the rangewide status survey of Saint Francis' satyr, *Neonympha mitchellii francisci*, (Lepidoptera: Nymphalidae); 1993 field season. Report to the U.S. Fish and Wildlife Service, Region 6 Endangered Species Office, Asheville, NC.

———, ——— AND N. MURDOCK. 2001. Preliminary studies for the recovery of Saint Francis' satyr, *Neonympha mitchellii francisci*. Report to the U.S. Fish and Wildlife Service, Region 6 Endangered Species Office, Asheville, NC.

———. 2003. Survey for the Saint Francis' Satyr (*Neonympha mitchellii francisci*) and Associated Ecosystems at Fort Bragg Exclusive of Artillery Impact Areas. Report to the Endangered Species Branch, Fort Bragg. Fort Bragg, NC.

——— AND N. M. HADDAD. 2005. Rearing studies of larval *Neonympha mictchellii* francisci and *N. areolata.* Report to the Endangered Species Branch, Ft. Bragg, NC.

HANSKI, I., M. KUUSSAARI AND M. NIEMEN. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinixia. Ecology,* **75**:747–762.

HARRISON, S., D. D. MURPHY AND P. R. EHRLICH. 1988. Distribution of the Bay Checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist,* **132**:360–382.

HART, B. 2004. A survey for the Mitchell's satyr (*Neonympha mitchellii* French) in the national forests in Alabama (final report). Report to the US Fish and Wildlife Service, Daphne Field Office; Daphne, AL.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration – Stochastic model. *Biometrika,* **52**:225–247.

KOST, M. A. 2000. Vegetation characteristics of Mitchell's satyr (*Neonympha mitchellii mitchelii*) habitat. Report to the U.S. Fish and Wildlife Service, Region 3 Office, Fort Snelling, Minnesota., 97 p.

KUEFLER, D. AND N. M. HADDAD. Landscape versus local determinants of butterfly movement behaviors. *Ecography,* **29**:549–560.

LEDGE, J. T. AND M. L. RABE. 1996. Observations of oviposition and larval ecology in caged Mitchell's satyr butterflies (*Neonympha mitchelli mitchellii*) (Lepidoptera: Nymphalidae). Report to the U.S. Fish and Wildlife Service, Region 3 Office, Fort Snelling, Minnesota. 17 p.

LONGCORE, T., R. MATTONI, C. ZONNEVELD AND J. BRUGGEMAN. 2003. INsect Count Analyzer: a tool to assess responses of butterflies to habitat restoration. *Ecological Restoration,* **21**:60–61.

MCALPINE, W. S., S. P. HUBBELL AND T. E. PLISKE. 1960. The distribution, habits, and life history of *Euptychia mitchellii* (Satyridae). *Journal of the Lepidopterists Society,* **14(4)**:209–225.

MENENDEZ, R., D. GUTIERREZ AND C. D. THOMAS. 2002. Migration and Alle effects in the six-spot moth Zygaena filipendulae. *Ecological Entomology,* **27(3)**:317–325.

MANLY, B. F. J. 1971. Estimates of a marking effect with capture-recapture sampling. *Journal of Applied Ecology,* **8(1)**:181–189.

MORRIS, W. F. AND D. F. DOAK. 2002. Quantitative conservation biology: theory and practice of population viability analyses. Sinauer Associates, Sunderland, Massachusetts, USA.

NEVE, G., B. BARASCUD, R. HUGHES, J. AUBERT, H. DESCIMON, P. LEBRUN AND M. BAGUETTE. 1996. Dispersal, colonization power and metapopulation structure in the vunerable butterfly, *Proclossiana eunomia* (Lepidoptera, Nymphalidae). *J. Appl. Ecology,* **33**:14–22.

PARSHALL, D. AND T. KRAL. 1989. A new subspecies of (French) Satyridae from North Carolina. *Journal of the Lepidopterists' Society,* **43(2)**:114–119.

PEET, R. K., T. R. WENTWORTH AND P. S. WHITE. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea,* **63**:262–274.

POLLARD, E. 1977. Methods for assessing changes in abundance of butterflies. *Biological Conservation,* **12(2)**:115–134.

ROBLE, S. M., C. T. KESSLER, B. GRIMES, C. S. HOBSON AND A. C. CHAZAL. 2001. Biology and conservation status of *Neonympha mitchellii,* a globally rare butterfly new to the Virginia fauna. *Banisteria,* **18**:3–23.

SCHAFALE, M. P. AND A. S. WEAKLEY. 1990. Classification of the natural communities of North Carolina, 3rd approximation. Department of Environmental and Natural Resources, Division of Parks and Recreation, NC Natural Heritage Program, 325 p.

SHUEY, J. 1997. Conservation status and natural history of Mitchell's satyr (*Neonympha mitchellii mitchellii*). *Natural Areas Journal,* **17(2)**:153–163.

SCHWARTZ, C. AND N. ARNASON. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics,* **52**:860–873.

SEBER, G. A. 1965. A note on the multiple-recapture consensus. *Biometrika,* **52**:249–259.

SZYMANSKI, J., J. SHUEY AND K. OBERHAUSER. 2004. Population Structure of the endangered Mitchell's satyr, *Neonympha mitchellii mitchellii* (French): implications for conservation. *American Midland Naturalist,* **152**:304–322.

THOMAS, C. D. 1995. Ecology and conservation of butterfly metapopulations in the fragmented British landscape, *In:* A. S. Pullin (ed.). Ecology and Conservation of Butterflies. Chapman and Hall, London.

VITTUM, M. T., B. E. DETHIER AND R. C. LESSER. 1965. Estimating growing degree days. *Proceedings of the American Society for Horticultural Science*, **87**:449–455.

WAHLBERG, N. T., T. KLEMETTI AND I. HANSKI. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography*, **25**:224–232.

WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimates from populations of marked animals. *Bird Study*, **46**:120–139 Suppl.

WILSMANN, L. E. AND D. F. SCHWEITZER. 1991. A rangewide status survey of Mitchell's satyr, *Neonympha mitchellii mitchellii* (Lepidoptera: Nymphalidae). Report to U.S. Fish and Wildlife Service, Region 3 Endangered Species Office; Fort Snelling, MN.

WOODWARD, D. K. AND R. B. HAZEL. 1991. Beavers in North Carolina: ecology, utilization, and management. Publication number AG-434. North Carolina State University, Cooperative Extension Service, Raleigh. 21 p.

WRIGHT, J., W. GURNEY AND C. JONES. 2004. Patch dynamics in a landscape modified by ecosystem engineers. *Oikos*, **105(2)**:336–348.

SUBMITTED 26 MARCH 2007 ACCEPTED 8 OCTOBER 2007