Behavior, Habitat Usage and Oviposition of the Mitchell's Satyr Butterfly, *Neonympha mitchellii mitchellii*

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Summary

1) The behavior, habitat usage and oviposition of the endangered Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii* **FRENCH** was studied using detailed behavioral observations at two sites in Southwest Michigan, USA during the 2000 flight season.

2) Observations focussed on the response of individuals at habitat interfaces, the interactions with woody structures and on female oviposition behavior. Eighty-seven adults were followed for a total of 2760 minutes.

3) 15 oviposition events were observed. Detailed observations indicate that there are two stages in the selection of suitable oviposition locations: (1) the selection of a general location probably chosen via structural attributes; and (2) selection of a suitable hostplant. Behavioral observations indentify potential oviposition cues which should be studied further. Logistic Regression indicates that *Carex lasiocarpa* cover is a significant predictor of oviposition sites.

4) The behavior of individuals at habitat interfaces suggest that contiguous corridors composed of open-sedge or woody-sedge habitat types, lined by thick woody-sedge or woody habitat types are likely to increase interpatch dispersal. The interaction of individuals to woody structures indicates that the size of structure is important.

5) Nectaring was observed for the first time in the two populations studied. Nectaring substrates included Mountain Mint (*Pycanthemum virginianum*), and Black-Eyed-Susan (*Rudbeckia hirta*) at BCF and Swamp Milkweed (*Asclepias incarnata*) and Black-Eyed-Susan at SNC, all events occurred during the latter half of the flight season.

Key words: boundary reaction, habitat selection, nectaring, oviposition cue.

Introduction

The Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii* **FRENCH**, is one of the most imperiled butterflies protected under the Endangered Species Act of 1973. Where the species is historically known from five states it now occupies just 18 isolated sites (Hyde, Rabe and Cuthrell 2000) located in Southern Michigan and extreme Northern Indiana with a mere five sites considered viable (U.S. Fish and Wildlife Service, 1998). Despite the fact that *N.m.mitchellii* was first described over one hundred years ago (French 1889), and has long been known to amateur lepidopterists there is a paucity of knowledge concerning the species ecological requirements which seriously hampers the design of effective conservation strategies (U.S. Fish and Wildlife Service 1998). Only in the last decade, since Federal listing, have resources become available for the scientific study of the *N.m.mitchellii*. Research is still in its early stages and can be described as in an information collecting stage rather than a hypothesis testing stage.

Detailed autecological studies are a critical part of the conservation of any threatened butterfly species (Bergman 1999) and examples exist in which conservation efforts not based on ecological studies have failed (Thomas 1984) and *N.m.mitchellii* is no different. To date the emphasis has been on the use of applied ecological studies to design and implement sound conservation strategies

Background Information on *N.m.mitchellii*

PHYSICAL DESCRIPTION AND SYMPATRIC SPECIES

N.m.mitchellii is a member of the family *Nymphalidae*, and the subfamily *Satyrinae*, the satyrs and wood nymphs (Opler and Krizek 1984). Satyrids are medium-sized, brown butterflies with ocellii on the ventral wing margins. (Szymanski 1999a). *N.m.mitchelii* adults are 33-44mm from wing tip to wing tip and have a dark warm-brown coloration (Opler and Malikul 1992). Males are darker than females both above and below (French 1889). Sexual dimorphorphism is not pronounced however the male forewing is somewhat smaller than in females (Opler and Krizek 1984).

Sympatric species that may be confused with *N.m.mitchellii* include *Satyrodes eurydice, S.appalachia* and *Megisto cymela*. Both the *Satyrodes* are larger than *N.m.mitchellii,* and are both light tan. *M.cymela* (39-47mm) is somewhat larger than *N.m.mitchellii* and the wing patterns are markedly different.

In addition, *N.m.mitchellii* is distinguished from these sympatric species by its slow bobbing flight. The flight patterns of the *Satyrodes* species are noticeably faster and more erratic, and *M.cymela* has a bouncing flight that is more energetic than the flight of *N.m.mitchellii* (McAlpine, Hubbell and Pliske 1960). Males are often found patrolling at the level of, or just below, the upper level of the sedge understory, whereas females are rarely seen in undisturbed flight (Shuey 1997).

The flight period of *N.m.mitchellii* spans a three week period from mid-June to late July with the peak flight usually in the first week of July (Shuey 1997). The species is protandrous, with males emerging a few days before females (Shuey *et al.* 1992). Populations occur at low densities making them vulnerable to environmental stochasticity and human disturbance (Szymanski 1999a).

DISPERSAL TENDENCIES

N.m.micthellii is a relatively sedentary butterfly with most range movements less than 50m (Szymanski 1999a). Although assumed to be strongly tied to its habitat, some observers have suggested that *N.m.mitchellii* frequently flies into non-suitable habitat (Sferra and Aguiar 1993), thus calling into question the usefulness of traditional habitat corridors to increase inter-patch dispersal.

HABITAT REQUIREMENTS

N.m.mitchellii inhabitat a variety of habitat types including open fen, wet prairie, prairie fen, sedge meadow, wet meadow, shrub-carr, tamarack savanna, and numerous variations and combinations of these community types (Shuey 1997). Common to all occupied habitat are a variety of structural components (see Szymanski 1999a).

ASSOCIATIONS WITH WOODY STRUCTURES

Almost all studies of *N.m.mitchellii* have referred to an association with woody structures. Szymanski (1999a) showed that 51% of butterfly observations were in woody-sedge habitat as opposed to just 22% in open-sedge. The importance of these associations have profound management implications. Managers tend to aggressively manage against invasion by woody structures and indiscriminately remove shrub cover, especially when linked to exotic species control. Such activities could be severely detrimental to *N.m.mitchellii*. The role that woody structures play in *N.m.mitchellii* ecology is far from clear however Szymanski (1999a) suggests that *N.m.mitchellii* may be selecting the open-sedge/woody-sedge interface for niche segregation.

The behavior of species at habitat boundaries (for example between open sedge and woody-sedge habitat types or between woody-sedge and thick woody-sedge types) is crucial for the design of habitat corridors (Andreassen, Halle and Ims 1996; Sutcliffe and Thomas 1996; Tischendorf and Wissell 1996; and Haddad 1999). Individual based studies should allow these subtle, but potentially critical habitat requirements to be observed and this may provide us with clues as to their importance. Not only would this allow the formulation of testable hypotheses but the results may also have important consequences for the development of detailed site management plans and in the design of conservation strategies.

SATYRID ECOLOGY AND LIFE HISTORY

Little is known of the life history of *N.m.mitchelii*. Satyrids almost never visit flowers (Opler and Krizek 1984). Females lay single eggs on the leaves of the hostplant or on the ground near the host (Opler and Krizek 1984). The larvae feed mostly at night on grasses and sedges, and are often catholic in their choice of foodplant (Shreeve 1992)

Oviposition Behavior in Butterflies

Factors influencing egg-laying in butterflies vary greatly between individual species (Chew and Robbins 1984), and thus comparisons between species are difficult. Many researchers have argued that female butterflies choose those plants for oviposition which are most suitable for larval growth and survival (Smiley 1978, Rauscher 1979). However, others have noted that the determinants of larval foodplant suitability and determinants of oviposition specificity need not be the same (Courtney 1982). Nylin and Janz (1993) argue that factors causing such poor correlations include (a) selection for enemy-free space; (b) the rarity of the preferred plant; (c) the poor host plant may be a recent addition to the habitat, and selection may not have had time to eliminate oviposition on the poor plant species; and (d) a favorable host may grow in unfavorable habitats.

Stanton (1982) suggests that oviposition choice is a multi-step process, including: (a) encounters with potential foodplants; (b) recognition and orientation towards plants from short distances; and (c) assessment of plant characteristics after contact with foliage many of which vary within each species such as the chemical, textural, developmental, or microsite variation. Both Courteney (1980) and Stanton (1980) argue that since butterflies possess a number of sensory modalities, they may utilize different plant characteristics as oviposition cues at different distances from the plant, or during successive parts of an oviposition sequence. Studies of oviposition site choice should then focus not only on the final substrate but also on the process of selection.

The oviposition of Satyrids has been described as unusual amongst butterflies (Legge and Rabe 1996). Wiklund (1984) found that unlike most butterfly species who attach their eggs to larval foodplants, there is a gradation of oviposition behavior in the satyrids from species that attach eggs directly to the grass species consumed by the larvae, to those that sometimes attached eggs to unsuitable foodplant material; to species who dropped their eggs in flight.

OVIPOSITION BEHAVIOR OF *N.M.MITCHELLII*

Oviposition was first recorded *in situ* during Szymanski's 1999 study. Since that time several other researchers have also observed egg-laying. Szymanski observed seven oviposition events during a three year period all of which occurred on the underside of small forb or sedge leaves, within 5cm of the ground. McAlpine *et al.* (1960) reared *N. m. mitchellii* from egg under controlled conditions. One female layed nearly 100 eggs on the stems of sedges. Legge and Rabe (1996) conducted cage studies at two sites during 1993 and 1996. Unlike most satyrids, *N. m. mitchellii* laid egg clusters varying in size from one to 11 eggs, and averaging 4.7 per cluster. The oviposition substrate (n=7) varied with egg clusters laid on the undersurface of leaves of five different plant species. All eggs were laid on the underside of the leaves of very young herbaceous species. The average height of oviposition sites was 6cm above the thatch but varied considerably. The most commonly used larval substrate was fine sedge leaves.

OVIPOSITION SITE CHOICE IN *N.M.MITCHELLII*

The pre-oviposition behavior of *N.m.mitchellii* has never been described before in detail. However Hyde *et al.* (2000) noted that “all females flew below the sedge and grass canopy just before ovipositing”, similarly Szymanski (1999b) noted “a short, direct move to a tiny forb”. There is a clear need for a detailed description of oviposition behavior. Its’ study should give us clues as to how females perceive their environments and the factors which are likely to be important in oviposition site choice, thereby allowing the development and testing of hypotheses in future studies.

Nothing is known of the relationship between oviposition site choice and larval performance. Thus it is difficult to say whether females are selecting sites which are good for larval success, for egg survival or other factors. The variety of oviposition substrates observed so far suggests that hostplant specificity is not a factor; similarly visually apparent hostplants have never been observed being used as substrates. It is likely then that gravid females are selecting sites based on other attributes such as shade, microclimate, humidity, or temperature of sites which may themselves be provided by some structural feature of the microhabitat. The method of using Logistic Regression to explore the predictability of microhabitat variables used here should then be useful.

Research Aims

1) Quantitatively describe the behavior of *N.m.mitchellii* at two sites in Southwestern Michigan. Including:
    - document and describe the behavior of *N.m.mitchellii* at habitat interfaces
    - document and describe the interactions of *N.m.mitchellii* with woody structures
2) To describe in detail the pre-oviposition and oviposition behavior of female *N.m.mitchellii*.
3) To test the hypothesis that females select oviposition sites using microhabitat cues.

Methodology

STUDY SITES

Field research was conducted at two sites in Berrien County, Michigan during summer 2000. Blue Creek Fen (BCF) and Sarett Nature Center (SNC) are located approximately 3km apart within the Paw Paw River drainage. Both sites occur on peat, clay, and sandy soils in oak-forested river valleys. BCF is a 10.42 ha linear wetland system with seven distinct vegetation communities (Szymanski 1999). Whilst *N.m.mitchellii* was known to inhabit eight habitat patches in the early 1990s (Shuey, Reznicek and Rogers 1994) patch occupancy during the three years of Szymanski's (1999a) study was reduced to just three of these. During this study (N Darlow, unpublished results) patch occupancy has increased and *N.m.mitchellii* is now known to occupy at least four patches, thus showing some characteristics of a dynamic spatial population structure. SNC is a 6.8 ha preserve with suitable habitat limited to two distinct areas. One patch is approximately 1.4 ha, and is characterized as open fen grading into thick shrub carr. The second patch, which is separated from the first by 290m, is a small (0.21 ha) sedge opening in an otherwise close canopy forested wetland. The two patches function as separate demographic units (Szymanski 1999a). Habitat management experiments over the past two winters have now increased the area of suitable habitat to approximately 0.29 ha.

DATA COLLECTION

Data was collected by walking through all types of suitable habitat using existing trails wherever possible to minimise trampling. To make behavioral observations as random as possible, the first individual encountered was followed. At the beginning of each observation the environmental conditions and time of day were noted. Conditions noted include: wind speed, cloud cover, temperature and the presence or absence of precipitation. The sex of the individual was determined through a combination of size of forewing, depth of colour and size of abdomen. Where sex was ambiguous behavioral observations were not used in data analysis. Each individual was followed from a minimum distance of 2m to avoid affecting behavior. Binoculars were used when necessary to view inconspicuous behaviors (such as sipping and nectaring) and a record of behavior made with a portable cassette recorder and later entered into a spreadsheet. The initial habitat type and any subsequent changes in habitat type, including movement in and between interfaces were noted. Habitat types were defined as follows:

Open Sedge (os) : area dominated by a Carex understory with scattered shrubs, not exceeding 10% cover.
Woody-Sedge (ws): Understory dominated by Carex spp. but with shrubs cover between 10 and 75%.
Thick-Woody Sedge (thws): Sub-canopy dominated by shrubs with cover >75% with subcanopy closed or nearly closed. Graminoid understory still present.
Woody: Sub-canopy closed with little or no graminoid understory.

Interfaces were defined as the area buffered 2m on either side of a line between two habitat types. For analysis, interfaces were considered as aggregated (termed 'interface') and individually (for example 'os/ws' meaning the interface between open-sedge and woody-sedge habitat types).

The behavior of the insect was timed to the nearest second using a stopwatch. Behaviors noted include: Flying, Resting, Basking, Fluttering, Interactions, Dispersal flight, Abdominal Curling, Abdominal Touching, Oviposition, Mating, and Nectaring. A distinction was made between Dispersal flights and Inspection flights by females: dispersal flights consist of short, often direct movements whereas Inspection flights are characterised by flight just below or at the level of the vegetation and an inspection of the general area by a circling, or spiraling flight, at the level of the vegetation and/or flying low in the vegetation. Wherever possible, additional data was collected including the resting substrate to species (however Dogwood and Goldenrod substrates were identified to Genus). Resting height both above the ground and below the level of the vegetation was estimated to the nearest 10cm using a 150cm rule with 10cm gradations. Resting locations were recorded as either on the upperside or underneath of the substrate, in the sun, shade or partial sun/shade.

RESPONSE TO WOODY STRUCTURES

Woody structures were classified into three types based on their height:
(1) small (<1m tall)
(2) medium (1-1.5m tall)
(3) large (>1.5m)

The behavioral responses of individual *N.m.mitchellii* were recorded and placed into four categories:

(1) individuals flew **around** the structure
(2) individuals flew **between** structures
(3) individuals flew **into** woody structures
(4) individuals flew **over** woody structures

N.M.MITCHELLII BEHAVIOR AT HABITAT INTERFACES

The behavioral responses to habitat interfaces were placed into three categories. Whether the individual flew:

(1) into the interface and then back out into the original habitat type
(2) through the interface into the second habitat type
(3) and stayed within the interface for extended periods of time and/included periods of resting

OVIPOSITION

When an oviposition event was observed a uniquely labeled wire and vinyl flag was placed at the oviposition site. Females were followed for as long as practicable and oviposition sites were returned to at the end of observations for data collection. The number of eggs laid, their distribution (singly or clumped), the position on the plant (upper or underside of leaf, or on the stem) and the presence of con- or hetero-specific eggs were noted. The substrate height and the height of eggs above the thatch were recorded. 0.25 m^2 plots were centered over each oviposition site and 50 random sites and 11 vegetation and structural variables variables were measured at each site (Table 1.). Random locations were determined using a random number

Table 1. Structural Microhabitat Variables measured at oviposition locations and 50 random locations at BCF and SNC. $0.25m^2$ plots were centered over locations. Visual cover estimates are ranked on a scale of 0-5, with 0-absent, 1=1-5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-100%. Percent shade cover was measured with a spherical densiometer. As Szymanski (1999) with additions.

Variable	**Description**	**Possible Relevance to *N.m.mitchellii***
DTW	Distance to woody cover	Habitat heterogeneity, niche segregation & foodplant quality
Shade	% woody & herbaceous shade cover at 0.5m height	Habitat heterogeneity, niche segregation & foodplant quality
Woody	% cover of woody species, any height	Habitat heterogeneity, niche segregation & foodplant quality
Tussock	% cover of tussocks	Overwintering habitat, niche segregation & foodplant quality
Sedge	% cover of sedge species	Foodplant density
Short forb	% cover of forbs <0.1m in height	Hostplant density
Intermediate Forb	% cover of forbs 0.1-0.5m in height	Inidicative of hostplant density
Tall forb	% cover of forbs >0.5m in height	Inidicative of hostplant density
Shoot Density	% cover of sedge shoots	Inidicative of foodplant density
Carex stricta	% cover	Foodplant density
Carex lasiocarpa	% cover	Foodplant density

generator and a grid superimposed over a map of the site. Percent shade cover was measured with a spherical densiometer.

Oviposition site locations were recorded using a Trimble GeoExplorer Global Positioning System (GPS) receiver. A minimum of 120 data points were collected for each location and the mean location taken. Data points were corrected via post-processing Differential GPS using Trimble Pathfinder software and base-station files from the University of Michigan Forestry GIS lab (42º 43' 20.55020" North, 84º 28' 42.49902" West and 242.326 m (HAE)). Differential correction decreased receiver error to +/- three meters. Locations were added into the Mitchell's Satyr butterfly GIS held by the U.S. Fish and Wildlife Service, Region 3 office.

Data Analysis

BEHAVIOR OF *N.M.MITCHELLII*

Data analysis was carried out at the population level by aggregating individual behaviors. Descriptive statistics were calculated for each behavior grouped by sex and site. Each dataset was tested for normality using a Kolmogrov-Smirnov test and for equality of variances using Levene's test. Where data was normally distributed and had equal variances, parametric tests were used to test for significant differences between groups. Where data was non-normally distributed, it was either transformed or non-parametric statistical tests used.

HABITAT USAGE

Selection for habitat types was tested using Ivlev's (1961) Electivity Measure which provides an index of the use of a community compared with its availability and is calculated as:

$$\boldsymbol{E_i = r_i - n_i / r_i + n_i} \qquad \text{(Equation 1.0)}$$

Where r_i is the proportion of observations in vegetation community i and n_i is the proportion of the study area that is occupied by community i. E_i then varies between –1 to +1 with –1 to zero indicating avoidance and zero to +1 indicating selection. Habitat type abundance was calculated from color infra-red photographs using ArcView's Image Analysis spectral radiometric classification (ArcView© ver 3.2, ESRI, Redlands, California) using an unsupervised classification. The resulting vegetation community map was smoothed so that community boundaries were more clearly visible and the boundaries were then delineated and buffered using a distance of 2m. Buffered regions were denoted as habitat interfaces. The areal extent of each habitat type at both sites was then calculated.

The rate of change of habitat usage for each observation was calculated by dividing the total observation time by the number of habitat type transitions and then the average calculated. The average was then reciprocalled to give a rate.

RESTING SUBSTRATES

Selection or avoidance of resting substrates was determined using Ivlev's (1961) Electivity Measure as described above. Resting Substrate abundance was determined by assessing the relative cover of each substrate in fifty 0.25 m^2 random quadrats at each site. Random locations were determined using a random number generator and a grid superimposed over a map at each site. Both the relative cover (by taking the mid-point of each cover class) and relative frequency of resting substrates were calculated.

NECTARING SUBSTRATES

Curtis's (1959) Index of Commonness was calculated for all nectaring substrates by multiplying the relative cover by the relative frequency. This provides an index whereby widespread dominants are given high scores and small, uncommon species a low score. Both mean cover and relative frequency were determined using random quadrats at each site as discussed above.

OVIPOSITION SITE CHOICE

Logistic Regression using SPSS ver 9.0 (SPSS inc, Chicago, Illinois) was used to test whether the 11 microhabitat variables differed between oviposition sites and the 50 random sites at both SNC and BCF.

Results

Results shown here are based on 2760 minutes of observation time of 87 *N.m.mitchellii* adults, 345 minutes for SNC males, 1120 minutes for SNC females, 170 minutes for BCF males and 974 minutes for BCF females .

BEHAVIOR

Fig 1. shows the total percentage time individuals were seen to engage in different behaviors. SNC males spent 64% of their time resting and only 34% of their time flying, however BCF males spent a larger proportion of their time in flight (67%) than resting (32%). SNC females at both sites spent most of their time resting (72%) and shorter periods flying (8%). Behavior of BCF females is similar, spending 53% of their time resting and 14% of their time flying. Females spent approximately 10% of their time actively engaged in oviposition (SNC females,12%; BCF females, 10%), whilst pre-oviposition fluttering occupied between just 3% and 4% of their time respectively. Nectaring accounted for a substantial part of female observations (SNC, 5%; BCF, 17%).

FLYING

There were significant differences in the proportions of observation times flying between sexes at each site (Sarett: Mann-Whitney U test, Z = -3.771, p <0.001; BCF: M-W U, Z = -2.817, p = 0.004) however there were no significant differences between individuals of the same sex between sites (Males: M-W U, Z = -2.008, p = 0.45; Females: M-W U, Z = -1.798, p = 0.076).

RESTING

There were no significant differences between sexes at either site in the proportion of observation times seen resting (SNC: M-W U, Z = -1.159, p = 0.246; BCF: M-W U, Z = -1.973, p = 0.051) but there were significant differences for each sex between sites (Males: M-W U, Z = -3.109, p = 0.001; Females: M-W U, Z = -2.440, p = 0.014).

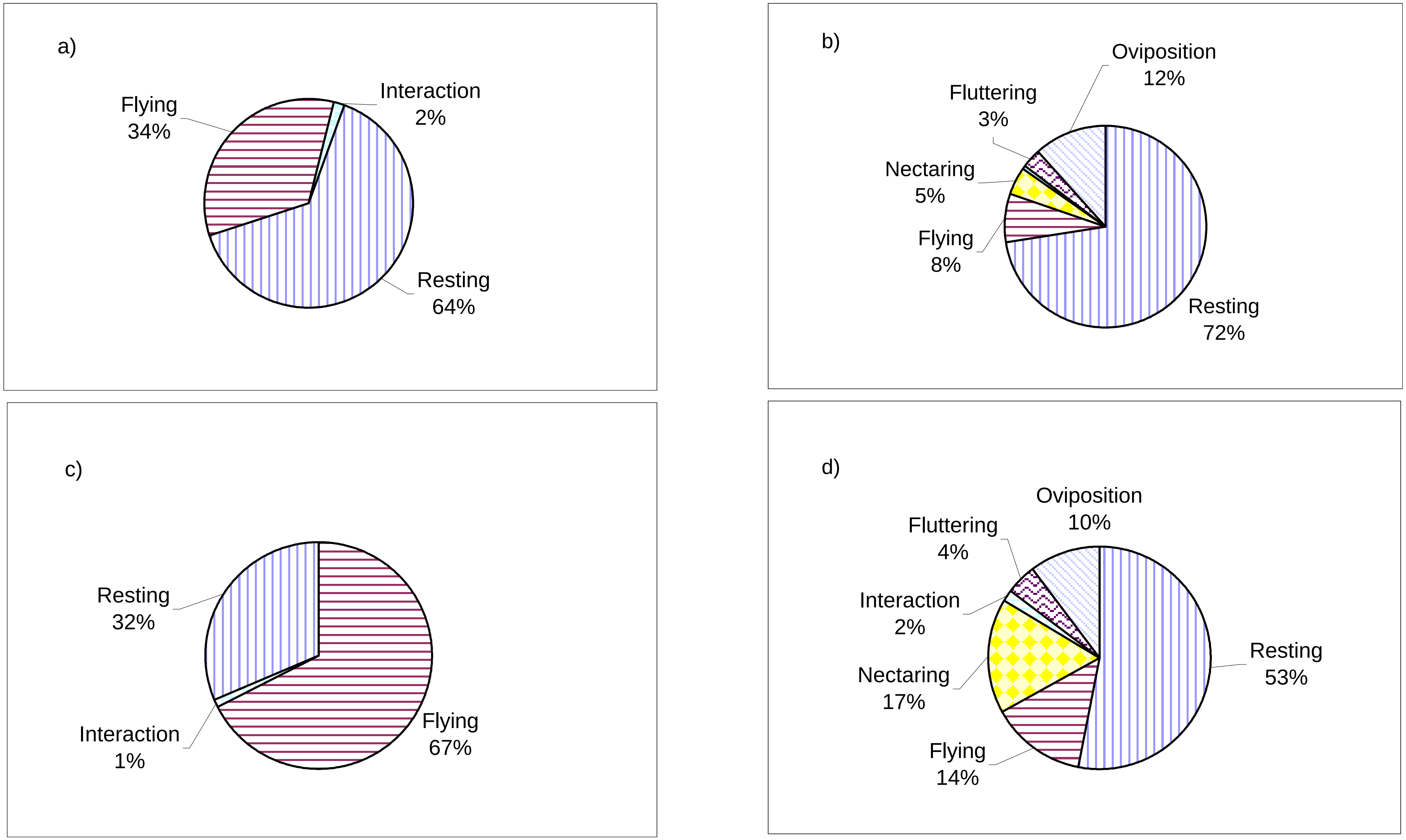

Fig 1. Behavior of Adult *N.m.mitchellii* . Shown are the total percentage times individuals were observed engaged in each activity. Shown are results for (a) SNC males, (b) SNC females, (c) BCF males, and (d) BCF females.

FLUTTERING

There were no significant differences in the proportion of observation time that females were observed fluttering (t-test, t = -0.311, d.f. = 17, p = 0.759)

INTERACTIONS

There were no significant differences between sex or site in the proportion of observation time that individuals spent in either con- or heterospecific interactions (Kruskall Wallis, χ^2 = 1.364, d.f. = 3, p = 0.714)

Resting Substrates

Adults rest upon a large number of different substrates but spend most of their resting time on a small proportion of these, for example, whilst Sarett males were seen to rest on 17 different substrates, they spent over 75% of their time on just three different species. All adults spent the majority of their time resting upon *Carex stricta*, except BCF males who rested predominantly on *Typha angustifolia*.

Ivlev's (1961) Electivity Measure shows that some substrates are positively selected for, however there appears to be no clear pattern of selection (Tables 2. and 3.). All but BCF males showed selection for *C.stricta* (SNC males, E = 0.40; SNC females, E = 0.27; BCF females, E = 0.59). Males at both sites showed varying levels of selection for *Dryopteris thelypteris* (SNC males, E = 0.48; BCF males, E = 0.11).

RESTING HEIGHT

Both the resting height above the ground (referred to as 'above', n=326) and below the top of the sedge level (referred to as 'below', n=294) were estimated. Both sexes at SNC rested half-way up in the middle of the vegetation (males: mean above = 40 cm, mean below = 40 cm; females: mean above = 50cm, mean below = 50cm) whereas at BCF both sexes rested in the top half of the vegetation (males: mean above = 60 cm, mean below = 30 cm; females: mean above = 60cm, mean below = 50cm). Comparisons between groups were all non-significant except that females rested at different heights above ground between the two sites (t-test, t = -3.992,

Table 2. Electivity Measure values for *N.m.mitchellii* resting substrates at SNC. A negative value indicates avoidance and a positive value indicates selection. Positive selection is highlighted in bold. Scientific names are as Swink and Wilhelm (1994) Shown are results for (a) Sarett Males, and (b) Sarett Females.

(a)

Common name	Scientific name	Electivity
Dogbane	*Apocynum cannibinum*	-0.10
Red-stem Aster	*Aster puniceus*	**0.57**
Bog-birch	*Betula pumila*	-0.02
Narrow-leaved woolly sedge	*Carex lasiocarpa*	-0.47
Fen star sedge	*Carex sterilis*	-0.25
Tussock sedge	*Carex stricta*	**0.40**
Swamp Thistle	*Cirsium muticum*	-1.00
Marsh Shield Fern	*Dryopteris thelypteris*	**0.48**
Joe Pye Weed	*Eupatorium maculatum*	-0.84
Boneset	*Eupatorium perfoliatum*	-0.99
Blue Flag Iris	*Iris virginica*	-0.08
Dogwood		-0.16
Unid. Forb		-0.54
unid. Goldenrod		-0.89
unid grass		-0.15
unid. Sedge		**0.48**

(b)

Common name	Scientific name	Electivity
New England Aster	*Aster novae-angliae*	-1.00
Bog-birch	*Betula pumila*	-0.35
Narrow-leaved woolly sedge	*Carex lasiocarpa*	-0.89
Fen star sedge	*Carex sterilis*	**0.63**
Tussock sedge	*Carex stricta*	**0.27**
Marsh Shield Fern	*Dryopteris thelypteris*	-0.66
Joe Pye Weed	*Eupatorium maculatum*	**0.27**
Boneset	*Eupatorium perfoliatum*	-0.92
Blue Flag Iris	*Iris virginica*	-0.88
Sensitive fern	*Onoclea sensibilis L.*	-0.96
Nine-Bark	*Physocarpus opulifolius*	-0.97
Swamp Rose	*Rosa palustris*	**0.17**
Willow	*Salix spp.*	-0.81
Tall Meadow Rue	*Thalictrum polygamum*	-0.07
Dogwood		-0.19
Unid. Forb		-0.94
unid. Goldenrod		**0.31**
unid grass		**0.76**
unid. Sedge		**0.50**

Table 3. Electivity Measure values for *N.m.mitchellii* resting substrates at BCF. A negative value indicates avoidance and a positive value indicates selection. Positive selection is highlighted in bold. Scientific names are as Swink and Wilhelm (1994) Shown are results for (a) Blue Creek Males, and (b) Blue Creek Females.

(a)

Common name	Scientific name	Electivity
Tussock sedge	*Carex stricta*	-0.74
Silky Dogwood	*Cornus ammonum*	-0.16
Gray Dogwood	*Cornus racemosa*	-1.00
Red-Osier Dogwood	*Cornus stolonifera*	**0.52**
Marsh Shield Fern	*Dryopteris thelypteris*	**0.11**
Joe Pye Weed	*Eupatorium maculatum*	**0.53**
Mountain Mint	*Pycanthemum virginianum*	-0.98
Glossy buckthorn	*Rhamnus frangula*	**0.30**
Willow	*Salix spp.*	-0.06
Narrow-leaved Cattail	*Tyha angustifolia*	**0.70**
Dogwood		**0.41**
Unid. Forb		-0.80
unid. Goldenrod		**0.18**
unid. Sedge		-0.21

(b)

Common name	Scientific name	Electivity
Narrow-leaved woolly sedge	*Carex lasiocarpa*	-0.90
Fen star sedge	*Carex sterilis*	**0.86**
Tussock sedge	*Carex stricta*	**0.59**
Red-Osier Dogwood	*Cornus stolonifera*	-0.79
Marsh Shield Fern	*Dryopteris thelypteris*	-0.81
Joe Pye Weed	*Eupatorium maculatum*	**0.31**
Sensitive fern	*Onoclea sensibilis L.*	-0.73
Nine-Bark	*Physocarpus opulifolius*	-0.41
Mountain Mint	*Pycanthemum virginianum*	-0.35
Glossy buckthorn	*Rhamnus frangula*	**0.14**
Black Eyed Susan	*Rudbeckia hirta*	**0.18**
Narrow-leaved Cattail	*Tyha angustifolia*	-0.97
Dogwood		-0.84
Unid. Forb		-0.50
unid. Goldenrod		-0.70
unid. Sedge		**0.22**

df = 224, p<0.001). Males rested at different heights than females at each site (M-W U: SNC, Z = -4.148, p<0.001; t-test: BCF, t = -3.149, df = 75, p = 0.006) and there were no differences between sites for each sex (Males: M-W U, Z = -0.776, p = 0.438; Females: t-test, t=-0.658, df = 199, p=0.511).

EXPOSURE OF RESTING LOCATION

245 resting locations were analysed for whether the butterfly rested in direct sunlight, in the shade or in partial sun/shade. Results are given in Fig 2. Approximately half of all resting locations were in the sun, 31% in the shade and 18% in partial sun/shade. Males at both sites rested most often in the sun. SNC females showed little preference for resting locale however BCF females showed a strong preference for resting locales in the sun.

NECTARING

Nectaring was observed for the first time at BCF and SNC during this study. Nectaring substrates included Mountain Mint (*Pycanthemum virginianum*), and Black-Eyed-Susan (*Rudbeckia hirta*) at BCF and Swamp Milkweed (*Asclepias incarnata*) and Black-Eyed-Susan at SNC. All nectaring substrates started to flower after July 11th, after most males had died, thus most observations were of females nectaring. Nectaring was so prevalent that between July 11th and the last day of the flight season (July 19th at SNC and July 20th at BCF) nectaring was observed at least once at each site every day. The duration of nectaring events varied from several seconds to 120 minutes with events occurring on multiple flowers and multiple plants, often interspersed with short periods of resting.

HABITAT USAGE

Fig 3. shows the total percentage observation time within each habitat type. At each site there are differences in the use of different habitat types by each sex. At SNC whilst males partitioned their time between most habitat types fairly evenly, females spent nearly half their time at the interface of different habitat types and nearly one third of their time in woody-sedge habitat. Ivlev’s (1961) Electivity Measure shows that SNC males showed positive selection for Open Sedge (E = 0.48) and Thick-Woody Sedge (E=0.07) habitat types. SNC females, however, showed positive selection for Open Sedge (E = 0.09) and the Interface between habitat

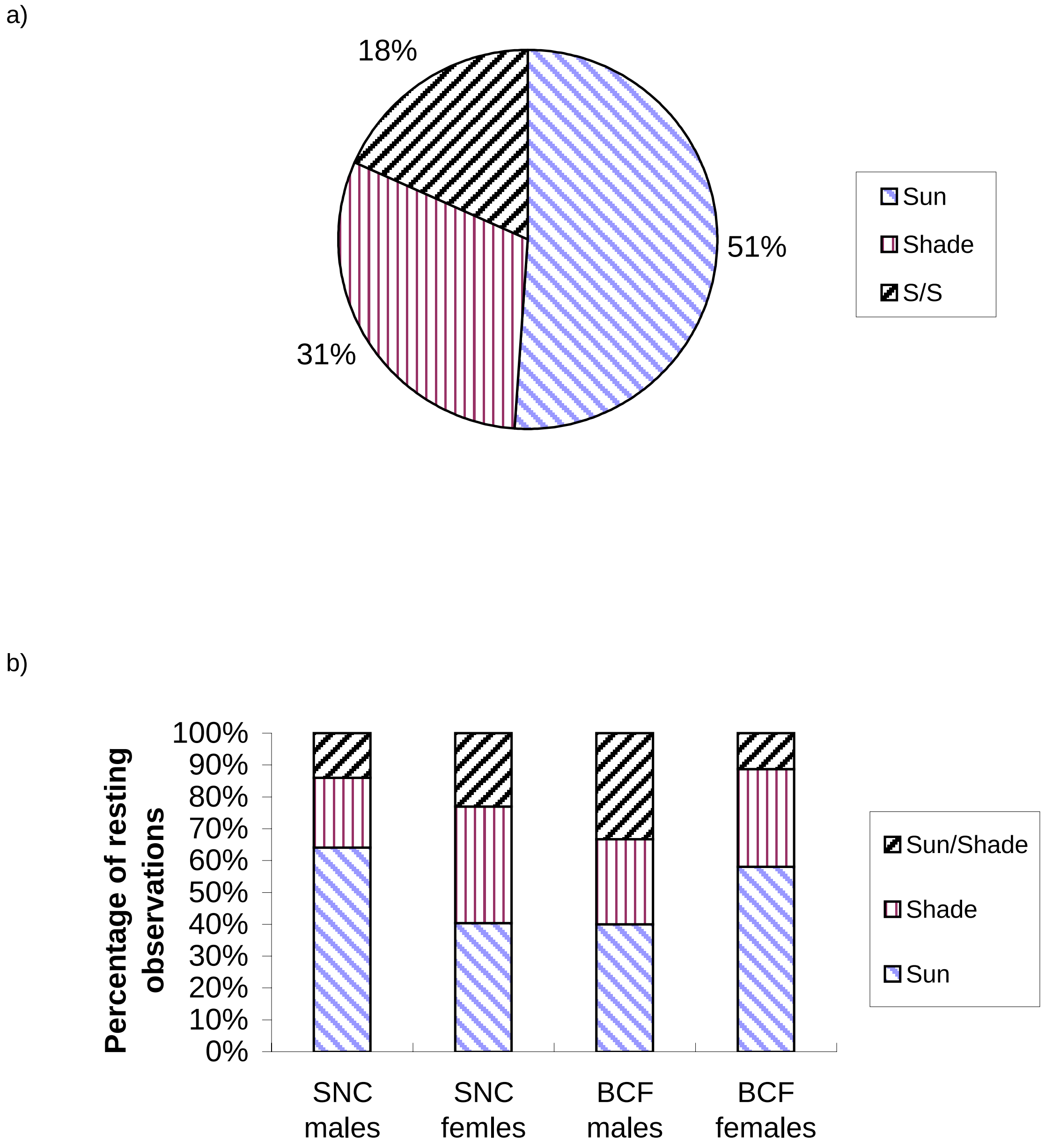

Fig 2. Exposure of resting locations. Shown are (a) results for entire data-set and (b) results grouped by sex and site.

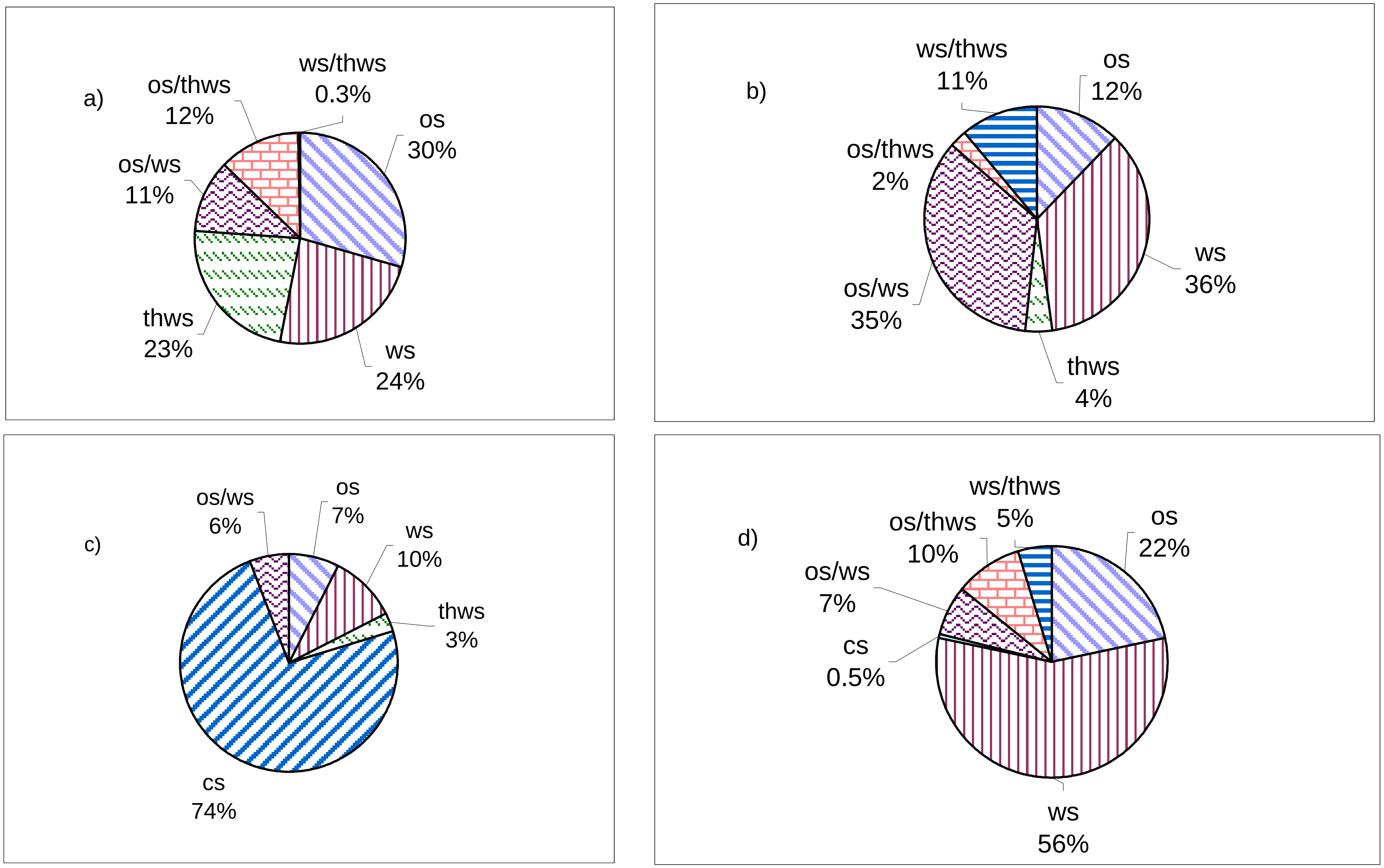

Fig 3. Habitat Usage by adult *N.m.mitchellii* . Data shown represents the total percentage observations time in each habitat type. Results shown are for (a) SNC males, (b) SNC females, (c) BCF males, and (d) BCF females

Key:

os - Open Sedge thws - Thick Woody Sedge os/ws-interface between os and ws
ws - Woody Sedge cs - Cattail Sedge os/thws - interface between os and thws ws/thws - interface between ws and thws

types (E=0.21). In contrast, BCF males showed selection for the Cattail-Sedge habitat type (E=0.50) whilst BCF females showed selection for both Open Sedge (E=0.37) and Woody-Sedge habitat types (E=0.30). Results for BCF males may be biased due to the small amount of observation time.

The electivity measure indicates that different interface types were differentially selected by the sexes at each site. SNC males showed positive selection for the os/ws interface (E=0.25) and the os/thws interface (E=0.71). BCF did not show positive selection for any interface types. SNC females showed positive selection for the os/ws (E=0.65), os/thws (E= 0.01) and ws/thws interfaces (E-0.26). BCF females showed positive selection for os/ws (E=0.21) and the ws/thws interface (E=0.73) (Table 4.).

RESPONSE TO WOODY STRUCTURES

Fig 4. shows the categorised interactions between *N.m.mitchellii* and woody structures grouped by sex and site. The data presented are based on a total of 149 interactions. It is clear that the response to woody structures varies based on shrub size and butterfly sex. In general for males with increasing shrub size there is a decreasing likelihood of flying around the structure, an increasing likelihood to fly into larger structures, and a decreasing proclivity to fly over larger structures. The low number of observations of females interacting with woody structures makes any generalisations difficult.

Observations suggest that females frequently rested higher when in woody structures than when on other substrates (N Darlow, personal observation). Using a subset of the resting height dataset an analysis of the height at which individuals rest in woody structures reveals that males do not rest significantly higher in woody structures than other resting substrates (M-W U, Z = -1.667, p = 0.096) whereas females do rest at a greater height (M-W U, Z = -3.495, p=<0.001).

BEHAVIOR AT HABITAT INTERFACES

The behavior of *N.m.mitchellii* at habitat boundaries was grouped into three categories:

(1) the individual moved into the interface and then returned to the original habitat type
(2) the individual moved through the interface into the second habitat type

Table 4. Electivity Measure values for habitat usage by N.m.mitchellii at two sites in Southwesten Michigan. A negative values indicates avoidance and a positive value indicates selection. INT refers to the aggregation of interface types.

	SNC		BCF	
Vegetation Community	Male	Female	Male	Female
Open-Sedge	**0.38**	-0.04	-0.31	**0.22**
Woody-Sedge	-0.11	**0.10**	-0.55	**0.95**
Cattail-Sedge			**0.50**	-0.96
Thick Woody-Sedge	0.00	-0.72		
INT	**0.12**	**0.45**	-0.44	**0.18**
os/ws interface	**0.25**	**0.65**	-0.41	**0.21**
ws/thws interface	**0.71**	**0.01**		
thws/woody interface	-0.89	**0.26**		**0.73**

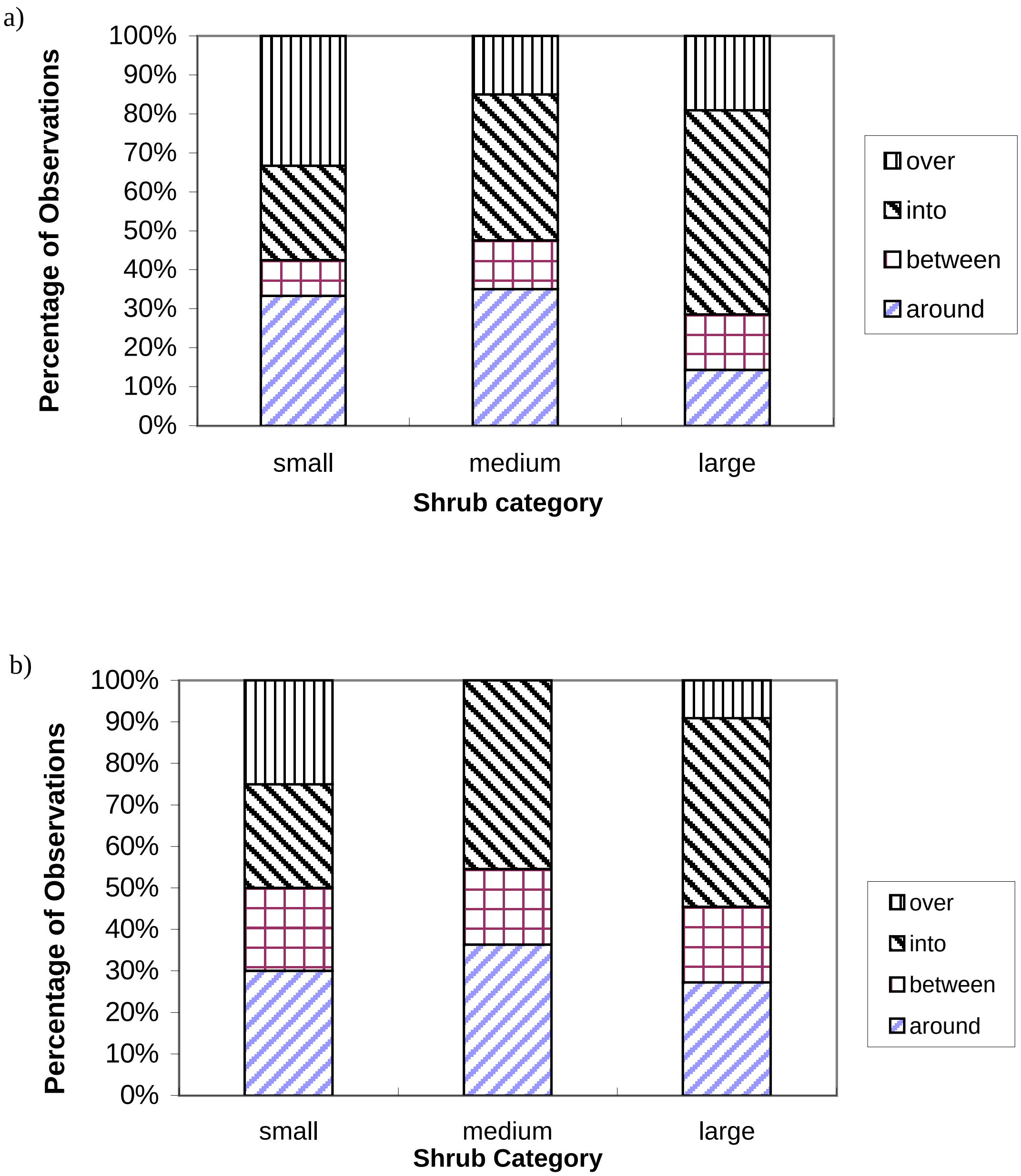

Fig 4. Behavioral responses to woody structures. Shown are the total percentage of observations for each response. Shrub size categories are small (<0.5m tall), medium (0.5-1.5m tall) and tall (>1.5m tall). Shown are results for (a) SNC males, and (b) BCF males.

(3) the individual stayed within the interface for extended periods of time and/or included periods of resting

When interfaces were aggregated, results indicate that males at both sites show a strong proclivity for behaviors (1) and (2) whilst females very clearly stay within the interface for extended periods of time (Fig 5. (a). Results are consistent between sites.

A separate analysis was carried out in which interface types were treated separately. The low number of observations mean that only results from SNC males and BCF males are given in Fig 5. (b). Males at both sites show little change in behavior at the os/ws interface (i.e. there were very few boundary reactions) (behavior type (1)), additionally there is a strong predilection for males to enter the ws habitat type rather than the os habitat. Strong boundary reactions were seen at the ws/thws interface with most males returning to the first habitat type although there was no preference shown for ws over thws. Females at SNC showed a strong affinity for all interface types in which they were observed although the low number of observations mean that results should be treated with caution.

HABITAT TRANSITION RATE

Results are based on a total of 45 observations. Males had a high rate of habitat transition (SNC males: mean = 0.66, s.d. = 0.99; BCF males: mean = 0.92, s.d = 0.37) whereas females had a low rate (SNC females: mean = 0.01, s.d. = 0.13; BCF females: mean = 0.21, s.d. = 0.16). There are significant differences between sexes and sites in the rate of movement between habitat types (Males between sites: M-W U, Z = -2.301, p=0.021; Females between sites, M-W U, Z=-2.028, p=0.045; between the sexes at SNC: M-W U, Z=-3.524, $p<0.001$; between the sexes at BCF: M-W U, Z= -3.098, p=0.001).

PRE-OVIPOSITION BEHAVIOR

The results shown here are based on a total of 2040 minutes of behavioral observations of 41 females. The first female at SNC was observed on June 29th, four days after the beginning of the flight season. At BCF the first female was observed on July 7th, eight days after the beginning of the flight season. Although females were observed to be active between 09:30 and 19:30, all oviposition events occurred between 14:00 and 17:45 (Eastern Standard Time).

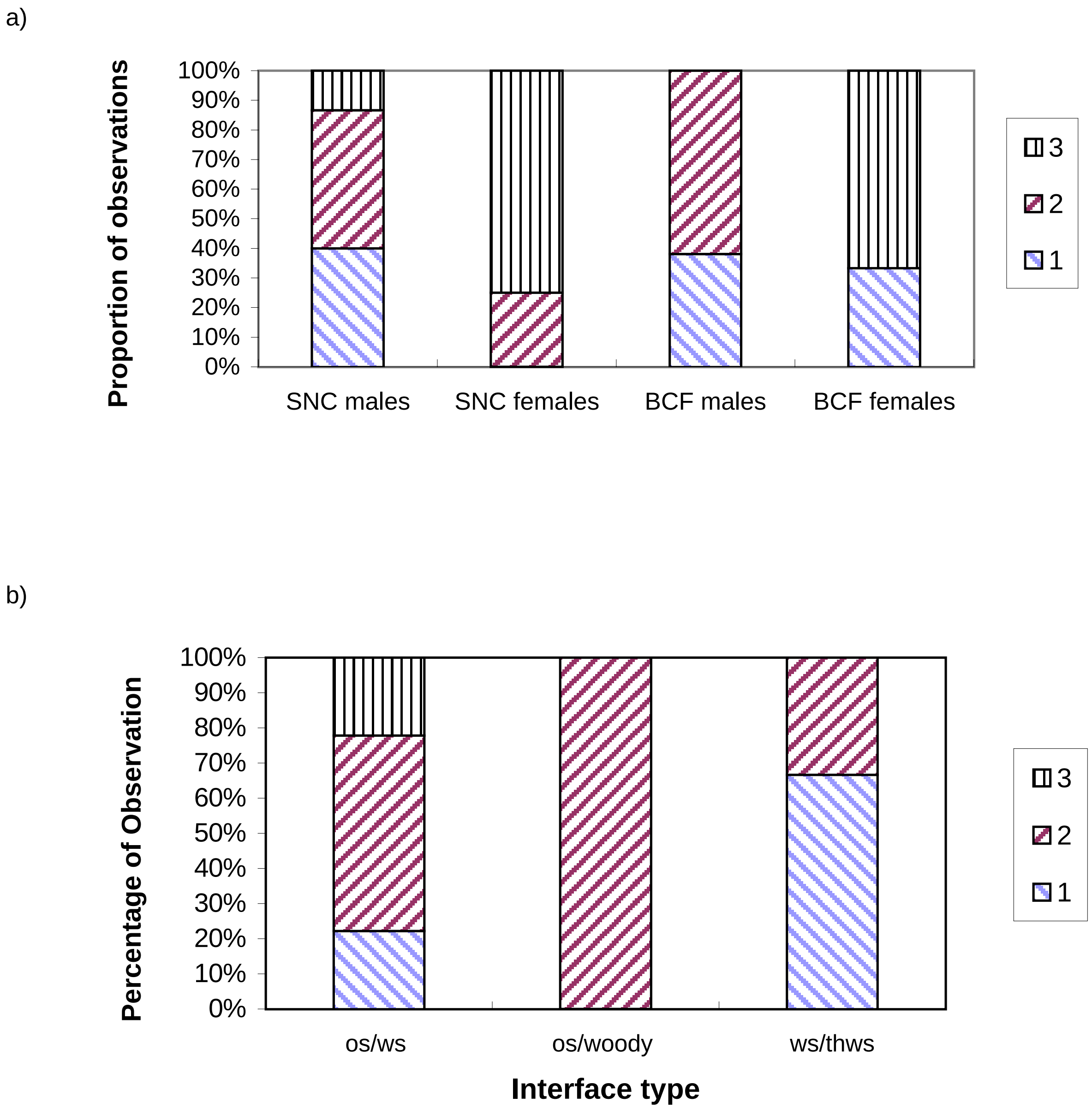

Fig 5. Behavior of *N.m.mitchellii* at habitat interfaces. Shown are (a) aggregated interfaces, and (b) interface behavior of Sarett males at each interface.

Key to Interface Behaviors:
1) Upon interface contact, individual returns to previous habitat type
2) Upon inteface contact, individual proceeds through, into next habitat type
3) Inidivual remains within interface

As with other studies, the behavior of egg-laying females varied considerably between individuals but in general there appear to be two stages to hostplant selection: After an extended period of resting (mean = 11.1 minutes, s.d. = 11.7) individuals engaged in a dispersal flight which then changed to an inspection flight (stage 1) consisting of a flight just below or at the level of the vegetation and an inspection of the general area by circling at the level of the vegetation and/or flying low in the vegetation. Most inspection flights were of short duration. In all observations, females then rested for several minutes before making a short, direct hop down low in the vegetation. Individuals either landed directly on a forb and began ovipositing or began "fluttering" low in the vegetation (stage 2), resulting in either substrate acceptance or rejection. If the substrate was rejected the female would rest nearby, high in the vegetation (resting time mean = 4.9, s.d. = 4.6), or engaged in a dispersal flight. Fluttering events were usually short (time = 0.37, s.d. = 0.36). Because of small numbers of observations data was pooled from both sites.

OVIPOSITION BEHAVIOR

Once a suitable site was found, females alighted on the edge of a leaf, curled their abdomen below the leaf surface to lay an egg before uncurling again (average = 15 secs). No tarsal pawing, antennal touching or abdominal touching was observed (i.e. all abdominal movements resulted in egg-laying). This was repeated until a cluster of eggs had been layed; the female then immediately made a direct hop to a resting position, high in the vegetation but usually close to the oviposition site and rested for an extended period of time before pre-oviposition behavior would recommence. Actual egg-laying lasted, on average, 14.5 minutes (s.d. = 14.0).

A total of 15 oviposition events (10 separate individuals) were observed between July 3rd and July 17th, nine at SNC and six at BCF. Table 5. gives details for each oviposition event. All ovipositions occurred on a variety of forbs: seven on Marsh Shield Fern (*Dryopteris thelypteris*), two on Tall Meadow Rue (*Thalictrum polygamum*), two on Joe-Pye Weed (*Eupatorium maculatum*), one on a Goldenrod (*Solidago* spp.) and three on unidentified forbs. The oviposition substrate height ranged between 35mm and 400mm (mean = 136 mm, s.d. = 90) and there were no significant differences between sites (t-test, t=-0.529, df=13,p=0.606). All eggs were placed on the underside of leaves in clumps ranging in size from two to nine (mean =

Table 5. Oviposition events observed at SNC and BCF. 'Height - thatch' refers to the height of the egg cluster. Position refers to the location of the egg cluster on the substrate. For example, '3rd leaf' refers to the third leaf from the base of the substrate. Time is Eastern Standard Time. Results are given for (a) SNC, and (b) BCF.

a)

Number	Date	Time	Temp	Substrate	Height - substrate (mm)	Height - thatch (mm)	Position	# of eggs
1	03/07/2000	14:00	78	Forb	80	50	lower leaf	9
2	03/07/2000	15:17	82	MSF	70	35	lower leaf	6
3	03/07/2000	15:58	82	TMR	300	100	3rd leaf	6
4	08/07/2000	14:34	78	Goldenrod	300	70	lower leaf	3
5	08/07/2000	16:05	78	TMR	35	20	top leaf	3
6	12/07/2000	16:02	85	tiny forb	40	15	lower leaf	5
7	12/07/2000	16:27	85	tiny forb	50	30	lower leaf	6
8	12/07/2000	17:07	/	MSF	150	70	2nd leaf	5
9	12/07/2000	17:42	/	MSF	100	100	3rd leaf	3

b)

Number	Date	Time	Temp	Substrate	Substrate height (mm)	Height above duff (mm)	Position	# of eggs
1	07/07/2000	16:03	/	MSF	200	120	lower leaf	5
2	07/07/2000	17:30	/	MSF	100	50	lower leaf	4
3	07/07/2000	17:45	/	young JPW	120	40	lower leaf	6
4	11/07/2000	16:10	78	MSF	200	80	2nd leaf up	2
5	13/07/2000	16:23	/	young JPW	250	125	4th leaf up	4
6	17/07/2000	16:15	82	MSF	40	20	lower leaf	3

Key:

MSF	Marsh Shield Fern (*Dryopteris thelypteris*)
TMR	Tall Meadow Rue (*Thalictrum Dasycarpum*)
JPW	Joe Pye Weed (*Eupatorium maculatum*)

4.7, SD = 1.3); again there were no significant differences in clump size between sites (t-test, t=1.189, df=13, p = 0.256). The height of clumps above the thatch ranged from 15 to 125 mm (mean = 62 mm, s.d. = 36); there were no significant differences in the height of clumps between sites (t-test, t=-0.927, d.f.=13, p = 0.371).

All oviposition events occurred at the interface of habitat types when the ambient temperature was between 78 and 85F (average = 81F, s.d. = 3.0). Temperature close to the oviposition site was not taken for fear of disturbing oviposition behavior. All ovipositions occurred after the daily peak in solar radiation intensity, air and vegetation temperatures (N Darlow, personal observation). No con- or heterospecific eggs were found at any oviposition site and no behavior was noted which suggested that females were searching the oviposition substrate or surrounding area for such eggs. At SNC, all ovipositions were recorded within one meter of clumps of mature shrubs. The species composition of shrub clumps used varied from single species to multi-species clumps, however no trend in usage was apparent. At BCF, all ovipositions were recorded within one meter of shrubs, however their growth form and age varied from young, individual shrubs to clumps of mature shrubs. Again, species composition did not seem important.

Table 6. (a) and (b) give the results of the logistic regression at SNC and BCF respectively. The microhabitat variables have little predictive capability. At SNC the only significant variable was *C.lasiocarpa* cover whilst at BCF no variables were significant. At both sites there are several variables which are nearly significant; these include Sedge cover at SNC, Shade cover, Sedge cover, Intermediate forb cover and *C.stricta* cover at BCF.

Table 6. Logistic regression results for testing the effects of microhabitat variables on oviposition presence. Shown are results for (a) SNC, and (b) BCF Significant variables are shown in bold.

a)

Analysis of deviance likelihood ratio tests

Predictor	df	Deviance[1]	*p*
Distance to Woody Cover	1	8.79	0.58
Shade cover	1	2.05	0.16
Tussock cover	1	1.08	0.34
Sedge cover	1	3.95	0.07
Woody covr	1	0.14	0.71
Tall forb cover	1	0.01	0.93
Intermediate forb cover	1	1.55	0.22
Short forb cover	1	0.89	0.35
Shoot Density	1	2.11	0.71
C.stricta cover	1	1.70	0.20
C.lasiocarpa cover	1	4.15	**0.05**

[1] change in deviance compared to model with a constant variable

b)

Analysis of deviance likelihood ratio tests

Predictor	df	Deviance[2]	*p*
Distance to Woody Cover	1	0.35	0.55
Shade cover	1	9.90	0.06
Tussock cover	1	0.67	0.42
Sedge cover	1	4.44	0.09
Woody covr	1	0.18	0.67
Tall forb cover	1	0.11	0.74
Intermediate forb cover	1	3.36	0.07
Short forb cover	1	0.02	0.91
Shoot Density	1	1.97	0.64
C.stricta cover	1	3.95	0.07
C.lasiocarpa cover	1	0.31	0.58

[2] change in deviance compared to model with a constant variable

Discussion

As with many short-term studies of threatened and endangered species with such restricted phenology the amount of data recorded is small and thus any conclusions drawn should be tempered with this in mind. In addition it is difficult to make comparison with results from previous years as the data presented here is only based on one field season. Despite this, the information presented here represents the largest data-set so far collected for both behavioral observations and oviposition events in *N.m.mitchellii*. To see this study in context the results of Sferra and Aguiar (1993), the only other scientific study of *N.m.mitchellii* behavior, were based on just nine hours of observations.

As noted by Szymanski (1999a) individuals are difficult to observe, follow and capture as the density of shrubs or cattails increase. Therefore it should be noted that all studies of *N.m.mitchellii* are biased towards data in open-sedge habitat types, and this study is no different. Results should then be interpreted carefully and the significance of any associations with woody structures should be more patent.

RESPONSE TO WOODY STRUCTURES

The behavioral responses of *N.m.mitchellii* to shrubs clearly depends on their structure, and this is related to the age of individual shrubs. Habitat heterogeneity has been implicated as an important component of *N.m.mitchellii* habitat (Kost 2000; Szymanski 1999a) and the variety of woody structures should be seen as enhancing such heterogeneity.

BEHAVIOR AT HABITAT INTERFACES

The behavioral responses of individuals to habitat boundaries are clearly implicated as one of the most important, if not the most important determinants of the success of habitat corridors in increasing dispersal between habitat patches (Haddad, 1999). The use of habitat corridors has been identified as an important component of the site management at BCF (Szymanski 1999a; Shuey *et al.* 1994) since *N.m.mitchellii* rarely disperse more than 50m (Szymanski 1999a). The results gained here should prove useful in the design of such corridors.

There are two basic types of habitat corridors which have been proposed. The most common of these are the contiguous corridors, composed of a stretch of suitable habitat, usually lined with unsuitable habitat. The second type, 'stepping stones' are thought to be useful for species which regularly move out of suitable habitat in search of suitable habitat patches (Schultz 1998). This study indicates that contiguous corridors composed of ws whose sides are composed of thws are likely to be the most effective at increasing dispersal rates. Additionally since individuals were rarely seen moving into woody habitat types then it is also likely that corridors whose sides are composed of woody habitat types would also be effective. These results imply that ‘stepping stone’ corridors are likely to be ineffective.

OVIPOSITION BEHAVIOR

Results of this study are in general agreement with previous observations of *N.m.mitchellii* oviposition. In all previous cases, events occurred close to the ground on a variety of small and intermediate forbs during the afternoon (Hyde, Rabe and Cuthrell 2000, Szymanski 1999). In this study all events occurred on a variety of forbs, at an average height of 6cm, occurring late in the afternoon. Differences with previous work include the use of intermediate, rather than just short forbs.

Almost no scientific studies have been done on the oviposition behavior of North American satyrids and so comparisons between related species are difficult to make. It is known however, that the sympatric species *Satyrodes eurydice* has been shown to lay its eggs indiscriminantly on many plants (Scott 1986).

The oviposition behavior of European satyrids, on the other hand, have been more closely studied. Wiklund (1984), examined the oviposition habits of 51 European butterflies and found that unlike the majority of butterflies, the satyrids (subfamily *Satyrinae*) almost exclusively oviposit on substrates other than their hostplants, arguing that since satyrid hostplants are usually superabundant, newly hatched larvae should find no difficulty in finding suitable foodplants. As Legge and Rabe (1996) note, the oviposition behavior of *N.m.mitchellii* does not neatly fit into this category described by Wiklund since oviposition does, rarely, occur on sedge leaves (Szymanski 1999b). *N.m.mitchellii* ovipositon behavior does, however, fit into the gradation of site fidelity described. The results shown here are in agreement with those of Wiklund (1984) and Legge and Rabe (1996) as none of the oviposition substrates reported here have been shown to be suitable foodplants for newly hatched larvae. Legge and Rabe further suggest that *N.m.mitchellii* choose sites that offer some requirement not found on the sedges that larvae consume. The behavioral observations shown here suggest, or at least allow us to initially reject, some of those possibilities. Requirements which may be important include partial shade (for buffering of environmental extremes), humidity, predator avoidance, foodplant availability and density, and niche segregation. It is then suprising that the 11 microhabitat variables used in the Logistic Regression are not more predictive. It is not clear whether such a lack of predictability is due to the low number of oviposition events observed (causing a Type II error) or whether the variables are simply not good predictors. The importance of these significant variables is then even more patent because of the small number of observations. Indeed *C.lasiocarpa* is the only sedge species which Legge and Rabe (1996) found suitable for newly-hatched larvae although other fine-leaved sedges have also been shown to be utilised (Szymanski 1999). *C.lasiocarpa* although not the dominant sedge species at either site was found to be an important component of the graminoid cover (SNC relative cover = 0.08, relative frequency = 0.17, Index of Commonness = 1.44). Suprisingly, the regression co-efficient for *C.lasiocarpa* is negative, indicating that gravid females choose sites with less *C.lasiocarpa*, contrary to what one would expect. It may be then that gravid females are selecting oviposition sites which are a compromise between larval foodplant resources (and likely first-instar success) and some other factor, likely egg survival.

EDGE EFFECTS

All oviposition events occurred at the interface between habitat types. Such edge-effects are becoming increasingly acknowledged in butterfly oviposition (for example see Dennis 1982, 1985) and have been attributed to (i) use of hostplant margins for rapid conspecific recognition and avoidance and for the purpose of releasing eggs rapidly as determined by low realized fecundities and (ii) the result of differences between edge and central plants, in vigour and age, related to the growth form of patches. The first reason does not apply to *N.m.mitchellii* since they do not use visually apparent hostplants, however since the microhabitat variables are not very predictive then it is possible that females are choosing sites based on (ii).

Pre-oviposition behavior described above is not typical of butterflies but similar behaviors have been noted previously (see Shreeve, 1986). Most butterfly species have been shown to either choose visually apparent host plants, the presence or absence of secondary compounds, or the colour and shape of plants, particularly the leaves (for example *Pieris brassicae* (Ilse 1937) quoted in Chew and Robbins (1984)). The process of fluttering may indicate that secondary compounds may influence the choice of oviposition site and satyrids have been shown to posses chemosensory receptors in their tarsi (Calvert 1974, quoted in Chew and Robbins 1984).

Shreeve (1986) has described the pre-oviposition behavior of the speckled wood butterfly (*Pararge aergeria*) a European satyrid. His account of pre-oviposition behavior is superficially similar to that described here. Shreeve noted four stages in the selection of hostplants: (1) the dispersal flight switching to an inspection flight, (2) orientation towards and landing on leaves of grass plants, (3) rejection or abdominal curling and (4) oviposition or rejection. In *N.m.mitchellii* pre-oviposition behavior is superficially; there is a noticeable switch from a dispersal to an inspection flight and when a suitable locale is found, *N.m.mitchellii* rests for an extended period of time before engaging in either a direct hop down to the oviposition substrate or 'fluttering' leading to eventual rejection of a hostplant or oviposition. However its' behavior differs in that there no discernable orientation towards substrates. Additionally I have included abdominal curling as an integral part of the process of egg-laying whereas Shreeve suggests that this may be part of the hostplant selection process. Such selection is well documented in the literature (Chew and Robbins, 1984) however rejection was never observed after such ‘abdominal touching’ and so it appears that *N.m.mitchellii* does not utilise this stage. Similar behavior has also been noted in other *N.m.mitchellii* populations during the 2000 field season (Daria Hyde, Michigan Natural Features Inventory, personal communication).

N.m.mitchellii appears to select the general oviposition locale during the inspection flight suggesting that at least a component of site choice is structural. The second stage of selection suggests selectivity based on some factor which is not clear at present but could involve differences in moisture content, secondary compounds, shade or other aspects of growth forms in the shade. Thus females seem to respond to several cues in choosing oviposition sites at different stages in its search.

NECTARING

Despite several hundred hours of previous field research, nectaring had only previously been recorded once, during the 1999 field season. It is then suprising that nectaring was observed for the first time at SNC and BCF during this study, especially when it is considered that nectaring was not only observed but was prevalent towards the end of the flight season and accounted for a substantial proportion of female observations.

Whilst the range of nectaring substrates suggests an opportunistic nature to *N.m.mitchellii* nectaring, it is unclear why nectaring was prevalent this year. Szymanski believes that “nectaring could still be a rare event that occurrs only under certain environmental conditions” (J Szymanski, personal communication). There are two possible explanations I can think of:

a) Environmental extremes allow an overlap in the phenology of the flight season with that of the flowering season of nectaring substrates:

All nectaring substrates began to flower on July 11th. In most “normal” years the peak flight is July 1st (Shuey 1997). Thus, in most years the flight season is unlikely to overlap the flowering season of at least the nectaring substrates shown here. It may then be that only in years of environmental extremes do the two seasons overlap, thereby allowing nectaring to occur. However there are many records of flight seasons lasting into late July and nectaring had never been observed during these periods. Additioanlly it has been noted that there are flowering plants available throughout the flight season (J Szymanski, personal communication). This may then reflect some level of specificity for nectaring (see below). We do not know how the phenology of the flowering substrates is affected by these same environmental extremes, therefore this argument is weak but may deserve further attention. In further years the first date of flowering for all nectaring substrates should be recorded, and any overlap in pehnologies noted.

b) Environmental extremes during the spring cause low levels of larval nutrition. Adult females then supplement nutrition to extend egg production and longevity:

The spring of 2000 was unusually cool and wet (C Nelson, Director, Sarett Nature Center, personal communication). This is a critical time for 4th and 5th instar larvae when they feed extensively in preparation for pupal formation (McAlpine *et al.* 1960). Previous work has shown that late-instar larvae are more active on warm days (Szymanski 1999b), thus cool, wet springs may limit the size and nutritional state of late-instar larvae. Hinton (1981) argues that larval nutrition may generally determine reserves available for oogenesis and Chew and Robbins (1984) further suggest that for butterflies whose adults eat nitrogen-rich foods, resources for egg production may not be limited by larval reserves. It is then possible that in years of limited larval nutrition, females could be nectaring to increase egg production or longevity. Such selectivity for nectar sources has been shown in other species (e.g. Colias species, *Watt et al.* 1974). The availability of sugars have been shown to markedly enhance female longevity and number of egg clusters in *Euphydryas editha* (Ehrlich 1984) and so it is also possible that females could be nectaring to increase longevity. At this time it is unclear whether the nectaring substrates observed at SNC and BCF and those observed at other sites by MNFI researchers are nitrogen or sugar-rich. This clearly should be an avenue for further work.

FURTHER IMPLICATIONS OF NECTARING

There may be important implications of such behavior at least in those years when nectaring occurs. Wiklund and Persson (1983) argue that butterfly fecundity is limited by the time available for females to fly and lay eggs. In years when nectaring occurs, this could then increase the life-span of individual females. As noted above, butterflies who nectar on nitrogen-rich substrates are able to extend their production of egg clutches, with the implication of increased fecundity, if not limited by other factors (such as environmental conditions suitable for egg-laying).

MNFI researchers observed more males nectaring than females during the 2000 field season (D. Hyde, MNFI, personal communication). Since the *N.m.mitchellii* flight season is protandrous with males emerging before females, it is conceivable that females who emerge at the tail-end of the flight season have very few, if any, opportunities to mate. If the phenology of nectaring plants overlaps with the tail-end of the male flight period it is possible that the overlap of flight seasons could be increased, thereby increasing mating opportunities. The end result may be an increase in fecundity.

Whether such speculation is true must be left for future researchers to test, however it is clear that the potential of nectaring to increase fecundity should make this behavior a component of future research and of the annual monitoring of *N.m.mitchellii* populations. At the very least, the date of first flowering of the nectaring substrates observed during this study and those by MNFI researchers should be noted at each site wherever possible and any overlap in phenologies noted.

Conservation Implications

As other studies have shown, habitat heterogeneity appears critical to sustain *N.m.mitchellii* through years of environmental extremes. The selection of differing habitats during this study from previous years, likely reflecting differential survival of immature stages, should add weight to this argument. Habitat management should then focus on creating a mosaic of patches, within each should be a diversity of microhabitats.

There is a clear need to increase inter-patch dispersal to prevent inbredding and the loss of vagility tendencies in this species, thus the establishment of interpatch corridors and scientific studies of their effect on dispersal should be made a priority. Information on boundary reactions presented here will aid in the design of such corridors.

The importance of interfaces to *N.m.mitchellii* has been previously noted, and that all oviposition events were observed within interfaces further supports this contention. It may be that shade is critical for egg survival and given that larval foodplant resources appear to decline with increasing cover it seem plausible that gravid females are using the interface as a compromise between egg survival and early instar success. Increasing the amount of ‘interface’ may then benefit *N.m.micthellii*.

The results presented here suggest that several possible oviposition cues are not being used by *N.m.mitchellii*. Experiments to test for correlations between oviposition cues and first-instar larval success should become a focus as they may provide further insights (Chew and Robbins 1984). This work should tie in with that shown here to give a more comprehensive view of female oviposition behavior. Important attributes which should be investigated include microclimate, aspects of the growth form of vegetation grown in the shade (moisture content), the presence or absence of secondary compounds and predator avoidance.

The importance of nectaring in increasing lifespan and fecundity should clearly become an aspect of future research and further behavioral observations should look for other nectaring substrates, noting their phenology. Nectaring, although rare in satyrids, has the potential to increase fecundity which could have important consequences for population viability and enhancement. Follow-up work during the 2001 field season should be done to document whether there are any noticeable effects of nectaring during 2000 on population density in 2001. Additional work should attempt to account for its presence only during certain years.

That environmental extremes can have profound effects on the population dynamics and life-history of *N.m.mitchellii* is becoming clear. For example it has been implicated in the differential survival of immature life stages of *N.m.mitchellii* in different microclimates (Szymanski 1999a) and as being responsible for differing habitat selection between years (Szymanski, 1999a) and in adult nectaring (Darlow, this study). Yet this is an area which has received little attention. Clearly then, in order to aid in the investigation of the autecological studies of *N.m.mitchellii* this area should receive considerable attention in future research.

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