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**BIOGEOGRAPHY OF THE BOG COPPER BUTTERFLY (*LYCAENA
EPIXANTHE*) IN SOUTHERN RHODE ISLAND PEATLANDS: A
METAPOPOPULATION PERSPECTIVE**

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BIOGEOGRAPHY OF THE BOG COPPER BUTTERFLY

(LYCAENA EPIXANTHE)

IN SOUTHERN RHODE ISLAND PEATLANDS:

A METAPOPOPULATION PERSPECTIVE

BY

JOANNE M. MICHAUD

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

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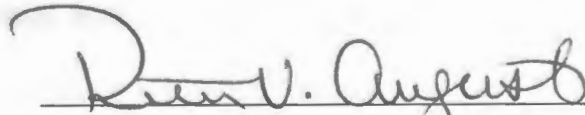
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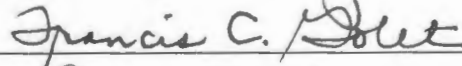
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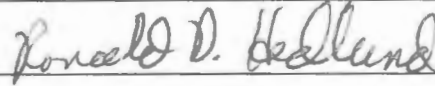
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ABSTRACT

The bog copper butterfly (*Lycaena epixanthe*) (Lepidoptera: Lycaenidae) inhabits patchily distributed open peatlands throughout the northeastern United States and southeastern Canada. To examine the relationship between habitat patch geometry and occupancy by *L. epixanthe* in southern Rhode Island, I surveyed 37 apparently suitable bogs and fens for adult butterflies, and measured various aspects of habitat quality related to patch size and isolation. Host plant patch size, size of the nearest occupied host plant patch, and distance to the nearest occupied host plant patch contributed significantly to the discrimination of occupied from unoccupied sites. During the two-year study period, I recorded deterministic and stochastic extinctions as well as colonizations of vacant patches; these observations suggest a metapopulation structure for *L. epixanthe* in the study area.

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I extend my sincere appreciation to the members of my thesis committee, Drs. Peter August, Francis Golet, and Patrick Logan, for their meticulous instruction and guidance, and for setting lasting examples of true scientific credibility. Dr. Howard Ginsberg kindly agreed to serve as chairperson of my defense committee, and offered many thoughtful comments and suggestions.

Dr. David Wright provided invaluable background on the morphology, behavior, ecology, and distribution of *Lycaena epixanthe*, as well as many stunning photographs of the butterfly and a critical review of this manuscript. Special thanks go to Richard Enser for his contagious interest in field entomology and for many illuminating discussions.

I thank the staff and graduate students at URI's Environmental Data Center, who always offered cheerful help and advice over the past three years. Anthony Davis, in a previous study, painstakingly delineated and classified all wetlands in the town of Richmond, a monumental task which made it possible for me to locate my study sites with relative ease. I acknowledge the cooperation of the many landowners in Richmond who graciously allowed me to study wetlands on their properties.

Most importantly, I am grateful to my husband, Stefan Michaud, and my parents, Gloria and Henry Tribble, for their unwavering confidence in my abilities.

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PREFACE

This study reflects a growing personal interest in both entomology and metapopulation dynamics. It is my hope that any conclusions generated from my work will be applied to the conservation of our native insects, increasingly threatened by popular prejudice, uninformed neglect, and the unabated destruction of natural habitats.

This document will be submitted for publication in *Conservation Biology*, and thus is written in a manuscript format suitable for that journal.

TABLE OF CONTENTS

	Page
ABSTRACT	ii
ACKNOWLEDGEMENT	iii
PREFACE	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
INTRODUCTION	1
METHODS	3
Study Animal	3
Study Area	4
Selection of Study Sites	5
Butterfly Surveys	8
Analyses	9
RESULTS	10
DISCUSSION	13
LITERATURE CITED	19
APPENDIX: Raw Data	36
BIBLIOGRAPHY	37

LIST OF TABLES

	Page
Table 1. Spearman rank correlations among habitat and landscape characteristics at host plant patches.	25
Table 2. Habitat and landscape characteristics of occupied and unoccupied sites.	26
Table 3. Standardized canonical coefficients from discriminant analyses.	27

LIST OF FIGURES

	Page
Figure 1. Locations of 37 host plant patches in the town of Richmond, Washington County, Rhode Island	28
Figure 2. Size distribution of host plant patches	30
Figure 3. Incidence function of occupancy rate versus host plant patch area	32
Figure 4. Relationship of host plant patch area and isolation to occupancy by <i>Lycaena epixanthe</i>	34

Introduction

Fragmentation and isolation of natural areas pose increasing threats to a region's native biota. Populations of plants and animals in small, isolated habitats may be particularly vulnerable to extirpation (Harris 1988; MacArthur & Wilson 1967; Wilcove et al. 1986). Gilpin and Soule (1986) describe extinction vortices where a decrease in effective population size brought about by the loss and division of habitat heightens the threats of inbreeding, demographic stochasticity, and environmental catastrophe.

If an organism's habitat is distributed patchily on the landscape, patch size, patch dispersion, and the organism's dispersal powers determine the extent of local populations (MacArthur & Wilson 1967). Many animals exist in metapopulations, or aggregations of local populations connected by dispersing individuals (Hanski & Gilpin 1991). Although the dispersing individuals may experience a higher risk of mortality by leaving the natal area, dispersal behavior favors the long-term persistence of the metapopulation as a whole (den Boer 1990). As local populations are periodically extirpated due to chance events, dispersal allows formerly occupied habitat patches to be recolonized; dispersal also enables newly created patches to be populated.

However, extreme isolation of habitat patches or alteration of the matrix environment can make successful dispersal impossible (MacArthur & Wilson 1967; Fahrig & Merriam 1994). Under these conditions, the establishment of new colonies cannot compensate for local extinctions; over time, a species may become increasingly rare throughout its range, and loss of peripheral populations may cause the range to contract.

Lycaena epixanthe (Boisduval and Le Conte) (Lepidoptera: Lycaenidae), the

bog copper butterfly, is a small, habitat-specific, relatively sedentary insect with poor dispersal capabilities. As such, it is well-suited for a study of the effects of habitat size and isolation. In southern Rhode Island, the larval host plants, large and small cranberry (*Vaccinium macrocarpon* Ait. and *V. oxycoccos* L.), grow in discrete patches of bog and fen habitat within a matrix of upland and other wetland types; the preponderance of these habitats on the landscape raises the possibility that local populations of *L. epixanthe* exist in a metapopulation context.

Although bogs and fens are numerous in southern Rhode Island, these wetland types currently make up only a small fraction of the state's total land area. However, in the period following the last Pleistocene deglaciation, open peatlands occupied most of southern New England (Pielou 1991). Davis' (1969) study of pollen deposition at Rogers Lake in southern Connecticut indicates the prevalence of a post-deglaciation open tundra community dominated by sedges (Cyperaceae) until about 12,000 years ago; gradual climate change and northward migration of tree species from southern refugia brought about the eventual transition to open spruce (*Picea*) woodland and finally mixed forest. Thus, present host plant patches suitable for *L. epixanthe* in Rhode Island may be the naturally fragmented remnants of a vegetation community formerly widespread and nearly continuous in the early Holocene.

In this study, I investigate the present-day distributions of both suitable habitat patches and colonies of *L. epixanthe* in the town of Richmond, Rhode Island. I use various measures of habitat patch size and isolation to formulate an occupancy model for *L. epixanthe*, and examine the implications of this model in the context of metapopulation theory.

Methods

Study Animal

Lycaena epixanthe ranges from Manitoba and Minnesota east to Newfoundland and south to the Great Lakes region, West Virginia and southern New Jersey (D. Wright, in litt). The traditional habitat is open acid peatlands where one or both of the obligate larval foodplants, *Vaccinium macrocarpon* and *V. oxycoccos* (Ericaceae), are present (Opler 1992).

Permanent saturation of the wetland substrate is considered to be a habitat requirement for *L. epixanthe*, as saturation helps maintain substrate temperatures within a range suitable for first instar larval development and diapause which occur within the egg (D. Wright, personal communication). Although *L. epixanthe* eggs are morphologically adapted to cope with periods of inundation (Wright 1983), prolonged flooding may destroy larvae or pupae (D. Wright, personal communication).

The life history of *L. epixanthe* has been described by Wright (1983). Cranberry flowers serve as the principal nectar source for *L. epixanthe* adults, and the period of cranberry flowering closely parallels the flight period of the butterfly. Basking, perching, feeding, courtship, and mating all occur on or in the immediate vicinity of the host plant. Following mating, the adults oviposit directly on cranberry leaves. The insect winters in the egg stage; eggs hatch as early as mid-April in New Jersey, and probably around the end of April in Rhode Island. The first three larval instars feed solely on cranberry leaves; the fourth larval instar may also feed on cranberry stems and immature flower parts. During the pupal phase, chrysalids lie attached to the undersides of cranberry leaves near the *Sphagnum* moss surface.

Adults eclose up to 60 days after the date of egg hatching. Adults have been observed in Rhode Island from 21 June to 24 July.

Study Area

The township of Richmond, Washington County, Rhode Island encompasses a land area of 106 km² (Rhode Island Geographic Information System database, see August et al. 1995), and is located at approximately 41° 30' N latitude, 71° 40' W longitude.

The temperate, humid climate is influenced by Washington County's close proximity to the Atlantic Ocean and Narragansett Bay. At Kingston, Rhode Island (10 km east of Richmond), the average January and July temperatures for the years 1951 to 1980 were -0.2° C and 21.2 °C, respectively; the average annual precipitation was 1,213 mm (National Oceanic and Atmospheric Administration 1992).

Richmond lies at the confluence of the Pawcatuck and the Wood Rivers, whose combined watersheds cover about 785 km² (Rhode Island Geographic Information System database, see August et al. 1995). Meadow Brook, White Brook, Taney Brook, the Beaver River, and the Usquepaug River flow through the town in discrete north - south valleys; all of these tributaries feed directly into the Pawcatuck River.

The bedrock underlying the study area is predominantly gneissose, composed of somewhat metamorphosed igneous material of Devonian age or older. Primary constituents include Hope Valley alaskite gneiss, Ten Rod granite gneiss, and Scituate granite gneiss (Moore 1958, 1959, and 1964; Power 1959). In addition, a substantial portion of eastern Richmond as well as smaller areas throughout the township are underlain by rocks of the Blackstone series, probably formed during Precambrian

metamorphism of sedimentary material into schists and quartzite (Moore 1958, 1959, and 1964).

Although small amounts of bedrock are exposed in some places, most of the study area is covered with a thick layer of surficial deposits of glacial origin. These deposits in southern Richmond are largely stratified glacial drift, especially sandy outwash, whereas those of the northern portion of the town are generally loamy till (Wright & Sautter 1988). Land surface elevations (above sea level) range from 15 m at the Wood/Pawcatuck confluence in the southwestern corner of the town, to 155 m along the ridge of Pine Hill near the northeastern corner.

Aerial photographs from 1988 show the land use/land cover in Richmond to be 63% upland forest or brushland, 15% wetland or open water, 12% developed, and 10% agriculture (Rhode Island Geographic Information System database, see August et al. 1995). The single most abundant wetland type in the town is wooded swamp, representing about 61% of the total wetland area; the remainder of the wetland area is made up of shrub swamp, open water, deep marsh, fen, meadow, bog, shallow marsh, and seasonally flooded basin, in decreasing order of abundance (Golet & Davis 1982).

Selection of Study Sites

To locate potential habitat patches for *L. epixanthe*, I used the wetlands database for the town of Richmond produced in 1980 by the University of Rhode Island's Department of Natural Resources Science (Golet & Davis 1982). This database describes all wetlands occurring within the town boundaries, as well as portions of those wetlands that extended into neighboring towns. Wetland patches over 0.04 ha

were delineated and classified by Golet and Davis using 1:12,000-scale panchromatic aerial photographs taken on 14 April 1975. Wetland classification followed a modified version of the Golet and Larson (1974) system. Roughly 50% of the wetlands identified through photointerpretation were field-checked by Golet and Davis for accuracy in delineation and classification. These data were digitized and stored in a Geographic Information System (GIS) at the University of Rhode Island.

Fernald (1950) describes the respective habitats for *V. macrocarpon* and *V. oxycoccus* as "open bogs, swamps, and wet shores" and "boggy or peaty soil." I have also seen *V. macrocarpon* growing in Rhode Island on the seasonally damp sands of roadsides, open fields, and abandoned gravel pits, and in temporarily flooded basins (vernal pools) within upland forests. Because of *L. epixanthe*'s reported requirement for a permanently saturated substrate and open, sunlit exposure, I selected shrub and emergent bogs and fens as delineated by Golet and Davis (1982) for potential study sites.

In the classification system used by Golet and Davis (1982) for wetlands in Richmond, a bog is characterized by a virtually continuous *Sphagnum* moss cover, a quaking substrate of poorly decomposed organic matter, a permanently saturated water regime, and an extremely low soil pH. A fen is characterized by a *Sphagnum* cover of up to 75%, a quaking substrate of moderately to poorly decomposed organic matter, a permanently saturated water regime with possible seasonal or temporary flooding, and a slightly to moderately low soil pH. Emergent bogs and fens are dominated primarily by sedges (Cyperaceae) including *Carex rostrata*, *C. lasiocarpa*, *C. exilis*, and *Cladium mariscoides*; shrub bogs and fens have a cover of low, compact woody species, usually

Chamaedaphne calyculata, *Myrica gale*, and *Gaylussacia baccata*.

The Golet and Davis (1982) GIS coverage contains 109 wetland polygons, each over 0.04 ha in size, classified as emergent or shrub bogs or fens, for a townwide total of 37.6 ha of these wetland types. I produced a map from the GIS which graphically combines polygons that are immediately adjacent to one another to yield 87 potentially suitable wetland areas, some of which are composed of both bog and fen elements. Of these 87, I was not able to locate 21, including four which had succeeded to young forested wetlands, three destroyed by sand and gravel operations, two severely degraded through apparent anthropogenic hydrologic manipulation, and one reportedly completely flooded by beaver activity. Of the remaining 66 areas, 25 did not support cranberry, and three, although they supported cranberry, were underlain with mineral or sapric (well-decomposed organic) soils indicative of nonsaturated water regimes (Moore & Bellamy 1974). Twelve of the 38 suitable peatlands were less than 20 m from their nearest neighbor; I combined these areas with their nearest neighbor to yield six sites. Finally, during the course of field work, I found five additional bogs and fens with saturated soils and cranberry cover which had been misclassified in the Golet and Davis study, resulting in a total of 37 sites available for inventory.

While in the field, I sketched onto base maps the areal extent of cranberry at each site. I made no attempt to quantify cranberry density. At most sites, cranberry plants occurred in single, continuous, often irregularly-shaped patches. Using PC-ArcInfo software version 3.4D (Environmental Systems Research Institute, Redlands, CA), I digitized the distributions of these cranberry patches into a GIS database. At five sites, areas of cranberry occurred as two to four separate patches per site, but

because the within-site inter-patch distances would be easily traversed by *L. epixanthe*, I considered the assemblage of within-site patches functionally connected and digitized them as such. The locations and relative sizes of the 37 cranberry patches are shown in Figure 1.

For several sites at or near Richmond's western, southern, and eastern boundaries, the distance from each site to the town boundary was shorter than the respective distance from each site to the nearest occupied site within the town. I drew a circle around each of these sites with a radius equal to the distance to the nearest occupied site. Using topographic maps, the statewide wetlands GIS coverage (see August et al. 1995), 1:24,000 scale panchromatic aerial photographs taken in April, 1988, and field reconnaissance, I examined all land area in the neighboring towns falling within these circles. Two apparently suitable wetlands located within these radii were visited during the *L. epixanthe* flight season, and data from these two areas were used only to evaluate the isolation of Richmond sites.

Butterfly Surveys

Of the 37 subject sites, I visited 35 in 1993, and all 37 in 1994 to search for *L. epixanthe* adults. In addition, I visited two wetlands in the neighboring town of Hopkinton in 1994 to assess the degree of isolation of some of the Richmond sites (see above). I did not visit sites during heavy rainfall, but I conducted many searches throughout extended periods of exceptional heat and humidity (27.3° C average daily maximum temperature, 59.8% average daily minimum relative humidity during the 1993 and 1994 flight seasons), and occasionally during periods of light mist. In every

case but one, I took a voucher specimen from each occupied site; specimens are deposited in the Lepidoptera collection of the Smithsonian Institution in Washington, DC.

In nearly all surveys, I searched the entire bog or fen for butterflies. However, at a few sites I ended my search after I encountered individuals, and did not continue to survey the entire bog or fen. Because I did not have sufficient time to completely search all possible locations in the larger sites, or revisit every site every few days throughout the flight season, I did not attempt to estimate *L. epixanthe* population sizes. I did, however, record the total number of individuals seen at each site.

During the flight season of 1993, I visited three sites known to support *L. epixanthe* (herein termed the "verification sites") a total of five times each during the flight season as a reliability check. Successful and expedient reconfirmation of the presence of the butterfly at these sites during each subsequent visit constituted an assurance of my ability to determine presence or absence at the other sites.

Analyses

I used ArcView software, version 1 (Environmental Systems Research Institute, Redlands, CA), for area and proximity measurements. I measured the following variables for each site, using bog or fen boundaries as site limits: site area, area of nearest site, distance to nearest site, total area of sites within 500 m, total area of sites within 1000 m, area of nearest occupied site, distance to nearest occupied site, total area of occupied sites within 500 m, and total area of occupied sites within 1000 m. I repeated this suite of measurements using cranberry patch boundaries as site limits to

yield a second dataset on habitat characteristics.

I used PC-SAS software (SAS Institute, Cary, NC) on a 80486-based microcomputer to perform Shapiro-Wilk tests for normality, F-max tests for homoscedasticity (equal variances), Spearman rank correlations, Wilcoxon signed-rank tests, regression analyses, discriminant analyses, and cross-validation classification tests (Shapiro & Wilk 1965; Sokal & Rohlf 1981; Krebs 1989). Presence/absence and proximity data from the 1994 inventories only were used in the statistical analyses.

Results

Although the 37 bogs and fens ranged in size from about 0.05 ha to just over 9 ha, only seven were larger than 1 ha (see Appendix). The density of cranberry cover varied among and within sites, from nearly pure, lush open stands to scattered plants beneath compact shrubs. The spatial extent of cranberry growth at each bog or fen varied from five percent to over 80%. The 37 cranberry patches ranged in size from just over 0.01 ha to nearly 7 ha, with 29 of the 37 patches smaller than 0.3 ha, and only two larger than 1 ha (Fig. 2).

In 1994, *L. epixanthe* was present at 23 sites and absent from 14. Numbers of individuals seen varied from one to 105. I suspect that a complete search of the largest habitat patch would yield a population estimate many times larger than 105 individuals. Butterflies were active throughout the hot and humid conditions which pervaded southern New England in July 1994. However, *L. epixanthe* activity was diminished during periods of light mist, and individuals were usually seen perched on sedge stems rather than in flight under these conditions.

Two sites (numbers 6 and 16) unoccupied in 1993 supported butterflies in 1994. Conversely, three sites (numbers 4, 19, and 26) occupied in 1993 were vacant in 1994. I was able to quickly locate *L. epixanthe* individuals during each of the five replicate visits at the three "verification sites".

A Shapiro-Wilk test for normality showed that none of the variables were normally distributed. Log transformation normalized the distributions for the area variables used in the discriminant analysis (see below); distance measurements were not normalized by the log transformation. An F-max test on the raw data indicated significant heteroscedasticity (unequal variances) between occupied and unoccupied sites for most variables, although raw data for distance variables were homoscedastic. Log transformation equalized the variances for all variables among the two groups. Thus, for the statistical analyses I used raw values for distance measurements, and log transformed values for area measurements.

Habitat data based on bog or fen boundaries were consistently and significantly ($p < 0.001$) correlated (positively) with habitat measurements based on cranberry patch boundaries (mean Spearman's $r = 0.86$). Thus, all subsequent analyses use only those measurements based on cranberry patch boundaries. The intimate spatial association between *L. epixanthe* and the host plant in New Jersey (Wright 1983) and in Rhode Island support this decision. There was a moderate amount of redundancy among habitat measurements as evidenced by the number of variable pairs exhibiting significant correlations (Table 1).

Occupied cranberry patches were significantly larger than unoccupied patches (Table 2). Occupied and unoccupied sites did not differ significantly in the other

habitat parameters. The incidence function (*sensu* Peltonen & Hanski 1991) showed that the proportion of occupied sites steadily increased with the size class of the cranberry patch (Fig. 3). Incorporation of distance to nearest occupied cranberry patch further distinguished occupied from unoccupied sites (Fig. 4). The line that best distinguished these two groups in Figure 4 was derived using a linear regression model (*sensu* Lomolino et al. 1989) of the form:

$$O = B_0 + B_1 (\log \text{ area}) + B_2 (\text{distance}),$$

where the dependent variable *O* is a dummy variable for presence (*O*=1.0) and absence (*O*=0.0). The line separating occupied from unoccupied sites is obtained by setting *O*=0.5 and solving for cranberry patch area and distance to nearest occupied cranberry patch.

I used discriminant analysis to develop a linear model that distinguished occupied from unoccupied sites. The habitat variables chosen for the discriminant analysis were those which exhibited as little redundancy as possible: cranberry patch area, area of nearest occupied cranberry patch, and distance to nearest occupied cranberry patch. Examination of the magnitudes of the standardized canonical coefficients (Table 3) showed that cranberry patch area dominated the model, with lesser but significant contributions by the remaining variables. The signs of the coefficients indicated a positive relationship between occupancy and the variables cranberry patch area and area of nearest occupied cranberry patch; and a negative relationship between occupancy and distance to nearest occupied cranberry patch. Cross-validation of the discriminant function using a jackknife procedure showed that for the 14 sites lacking *L. epixanthe*, the model correctly predicted absence 86% of the

time; for the 23 sites supporting *L. epixanthe*, the model correctly predicted presence 74% of the time. The overall classification accuracy was 78%.

Discussion

The accuracy of this habitat use model hinged on the correct assessment of butterfly presence or absence in a given wetland. There were two potential sources of error in the determination of this variable. First, despite my complete success at locating individuals at the three "verification sites", I could have failed to observe adults at other sites because of butterfly inactivity during adverse weather conditions, seclusive behavior of butterflies, or early/late visits outside of an exceptionally brief flight period. Conversely, I could have erroneously interpreted the presence of one or two stray individuals as a *bona fide* colony. To eliminate these ambiguities, the study would have required more intensive field checking of habitat patches, complete with behavioral observations to confirm reproduction.

A second potential source of error in this study was the completeness of the identification of suitable habitat patches. Because the smallest host plant patch studied was about one-fourth the size of the minimum wetland polygon area delineated by Golet and Davis (1982), it is possible that small yet suitable host plant patches existed within larger areas of wetland of some other type. Only a thorough on-the-ground search of all wetlands in the township would have eliminated this source of error.

The presence of butterflies in 1994 in two patches not occupied in 1993 provided evidence that *L. epixanthe* is capable of dispersing from patch to patch in the study area, and that butterfly dispersal can result in the founding of new local

populations. In addition to these colonizations, I also observed evidence of local extinctions in the study area. These observations confirmed that *L. epixanthe* exists here in a metapopulation context. Although there are very few suitable habitats directly to the west and south of Richmond, I am aware of many in nearby areas to the north and east; thus, the Richmond colonies may represent a portion of a metapopulation, many separate metapopulations, or some intermediate structure.

To understand the metapopulation dynamics in the study area, stochastic extinctions must be considered separately from deterministic losses (Thomas 1994). Three sites occupied in 1993 were vacant in 1994, with no visible changes in habitat quality; these disappearances were probably due to stochastic forces in habitats which remained suitable for recolonization. In comparison, I also observed the extinction of a colony due to deterministic habitat change: In 1993, a colony of *L. epixanthe* occupied a small patch of cranberry in a dry, shrubby fen; a year later, no butterflies were seen, and the host plant had disappeared amidst a dense stand of *Spiraea* sp., *Rhus vernix*, and sapling *Acer rubrum*. A comparison of Golet and Davis' (1982) observations with current conditions showed that deterministic losses of potential *L. epixanthe* habitats in Richmond are not uncommon in recent history: Over the last 15 years, ten bogs and fens were lost or severely altered through vegetative succession, excavation, anthropogenic hydrologic manipulation, and flooding by beaver.

Although the 37 sites used in this analysis may eventually succumb to some type of permanent alteration, they all appeared suitable for habitation by *L. epixanthe* in 1994, based on the presence of the host plant and evidence of permanent saturation. As the smallest cranberry patch in the study area was occupied in both 1993 and 1994,

I assume that all patches studied were large enough to accommodate the behavioral and physiological needs of the butterfly. However, all 37 patches were still subject to non-persistent perturbations which may have affected occupancy.

In all analyses, habitat size (defined as host plant patch size) was the primary predictor of occupancy. Eleven of the 14 unoccupied habitat patches were in the two smallest of six size classes (Figs. 1, 3). Small populations, typically in smaller patches, may be more susceptible to crashes caused by stochastic environmental and demographic effects (Gilpin & Soule 1986). Decreased fitness through inbreeding and genetic drift may also contribute to the loss of small populations, but these factors are probably inconsequential for butterflies in most cases (Thomas 1984).

Small patches may be less likely to support *L. epixanthe* populations because of increased vulnerability of small habitats to environmental catastrophe (Soule and Simberloff 1986). The major class of natural catastrophe in the study area is occasional seasonal flooding. Although this form of environmental stochasticity is climate-induced, and thus regional in scope, topographic and hydrologic conditions of individual wetlands determine the degree of flooding and thus the extent of synchrony, or correlation, of the perturbation in the patch array. In Richmond, five fens adjacent to the largest rivers in the study area (the Wood and Pawcatuck Rivers) were flooded in the spring of 1993. These five patches occurred over a broad range of size classes; thus, large habitat size appeared not to confer an advantage with regard to flooding as an environmental perturbation. Stream gauge data from two stations along the Pawcatuck and Wood Rivers showed that mean flows for April 1993 were 150% and 137%, respectively, of the mean historical April flows (United States Geological

Survey 1993). Direct observation of hydrologic conditions at these fens in 1993 confirmed that all five were inundated with up to two feet of water well into late April and early May; established *L. epixanthe* populations (in the larval stage at this time of year) would have perished under these conditions. Predictably, no adult butterflies were found in any of the five fens in June or July 1993. However, river flows approximated the historical means during April 1994 (United States Geological Survey 1994), and one of the five sites (number 6) supported *L. epixanthe* in July 1994.

In addition to habitat patch size, characteristics of neighboring occupied patches also contributed to site occupancy. The positive relationship between occupancy and size of nearest occupied patch, and the negative relationship between occupancy and distance to nearest occupied patch, suggested that habitats experiencing periodic extirpation may be recolonized from neighboring patches if the nearest occupied patch is large (presumably supplying more dispersers than a small patch) and/or close (within dispersal distance). A strict dependence of occupancy on patch area would have indicated selective extinction without recolonization, or faunal relaxation (Lomolino et al. 1989). However, the additional importance of proximity further suggested a dynamic system of extirpations and recolonizations.

L. epixanthe is generally considered a sedentary butterfly with a very limited dispersal ability. Throughout this study, I only once observed an individual away from its host plant. On this occasion, as I approached, I flushed the butterfly out of a cranberry patch, and watched it fly up, out of the fen, and across an unpaved road in the direction of more wetland habitat. Scott (1975) has shown that butterflies using perennial woody hosts as larval foodplants generally disperse shorter distances than

those dependent on early successional or highly disturbance-adapted plants. *V. macrocarpon* and *V. oxycoccus* are both perennial and woody, and, although succession may eventually displace these plants, they are not considered early successional or disturbance-adapted. Thus, *L. epixanthe* is not regularly required to move over large areas in search of food plants in a rapidly succeeding habitat mosaic. Although maximum dispersal distance has not been directly measured for this species, observations of the recolonization of a habitat patch in southern New Jersey yielded an indirect estimate of about 400 m, based on the distance to the nearest source of colonists (D. Wright, personal communication). One of the habitat patches in Richmond apparently colonized during my study (site number 6) was 2,212 m away from the nearest known source of colonists. It is probable that I failed to detect closer, occupied habitat patches; alternatively, the location of the site along a major river raised the possibility that *L. epixanthe* was able to disperse longer distances along a waterway than over upland. Wright (in litt) has directly observed *L. epixanthe* moving along streams.

Two exceptionally large sites (numbers 17 and 18) dominated the patch array. These two sites were likely sources, or reservoirs, of dispersers to smaller satellite patches. Protection of these reservoirs may be critical to the maintenance of the metapopulation as a whole (Ehrlich & Murphy 1987), especially in light of a central location (site number 17) or location along a waterway which may facilitate dispersal (both sites) (Fahrig & Merriam 1994). Site number 18 (2.4 ha) is included in a 95-ha wildlife management area owned and managed by the State of Rhode Island, and is thus considered safe from anthropogenic threats. However, site number 17 (6.9 ha) is

privately owned; this fen may at some time succumb to alteration or conversion.

The balance of temporary extirpations and subsequent recolonizations which characterize a metapopulation is affected by a background of permanent habitat losses and the creation of new habitat patches. If habitat losses exceed gains, the remaining patches become increasingly isolated, lessening the probability of recolonization. In the densely settled northeastern United States, human population pressures continue to intensify; anthropogenic habitat conversion is inevitable, especially in the event that wetland protection laws are weakened. Natural succession of fens and bogs is normally exceedingly slow, but may be accelerated in small patches (Thomas & Harrison 1992), in sites experiencing nutrient enrichment (Benforado 1981), and in cases where fen/wet meadow systems maintained by mowing or grazing are allowed to revert to forest. Beaver (*Castor canadensis*) was completely extirpated from Rhode Island prior to 1968 (Cronan and Brooks 1968), but subsequently repopulated the state from the west; beaver impoundments have been observed at various locales in the Wood/Pawcatuck watershed. Although beaver reportedly caused the flooding of one bog in the study area since 1975, the animal may also contribute to the development of new patches, through the creation of open water bodies in areas of poor drainage which may eventually support *Sphagnum*/cranberry mats (Naiman et al. 1988). New habitat patches may also form in other depressions, such as abandoned stream meanders, but only long-term monitoring will show if these gains are sufficient to balance losses.

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Table 1. Spearman rank correlations among habitat and landscape characteristics at host plant patches.

	Area of nearest patch	Distance to nearest patch	Total area of patches within 500 m	Total area of patches within 1000 m	Area of nearest occupied patch	Distance to nearest occupied patch	Total area of occupied patches within 500 m	Total area of occupied patches within 1000 m
Patch area	-0.13	0.08	-0.07	-0.19	-0.26	0.16	-0.09	-0.20
Area of nearest patch	--	-0.18	0.40*	0.47**	0.25	-0.39*	0.43**	0.43**
Distance to nearest patch		--	-0.73***	-0.64***	0.02	0.56***	-0.54***	-0.46**
Total area of patches within 500 m			--	0.82***	-0.01	-0.72***	0.92***	0.78***
Total area of patches within 1000 m				--	-0.02	-0.61***	0.78***	0.83***
Area of nearest occupied patch					--	0.06	0.02	-0.09
Distance to nearest occupied patch						--	-0.84***	-0.85***
Total area of occupied patches within 500 m							--	0.89***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2. Habitat and landscape characteristics of occupied and unoccupied sites.¹

<i>Variable</i>	<i>Occupied (n = 23)</i>	<i>Unoccupied (n = 14)</i>	<i>Z</i>
Cranberry patch area (m ²)	1817 (3150)	445 (728)	3.24*
Area of nearest cranberry patch (m ²)	628 (808)	1073 (1814)	0.60
Distance to nearest cranberry patch (m)	287 (827)	578 (930)	0.11
Total area of cranberry patches within 500 m (m ²)	628 (3339)	577 (2105)	0.57
Total area of cranberry patches within 1000 m (m ²)	1173 (3134)	1966 (2962)	0.47
Area of nearest occupied cranberry patch (m ²)	1739 (6984)	1817 (3214)	0.00
Distance to nearest occupied cranberry patch (m)	419 (1109)	1199 (1488)	0.96
Total area of occupied cranberry patches within 500 m (m ²)	365 (3339)	0 (2105)	1.04
Total area of occupied cranberry patches within 1000 m (m ²)	1173 (3339)	0 (2182)	0.61

¹ For each variable, I provide the median value followed by the inter-quartile range in parentheses. Wilcoxon two-sample statistics were used to test if variable values for occupied sites were significantly different from those for unoccupied sites. A normalized approximation (Z) of the Wilcoxon score is reported.

* $p < 0.01$

Table 3. Standardized canonical coefficients from discriminant analysis.

<i>Independent variable</i>	<i>Coefficient</i>
Cranberry patch area	1.27
Area of nearest occupied cranberry patch	0.52
Distance to nearest occupied cranberry patch	-0.66
Eigenvalue	0.61

Figure 1. Locations of 37 host plant patches in the town of Richmond, Washington County, Rhode Island. Filled circles represent patches occupied in 1994; empty circles represent patches vacant in 1994. Actual patch areas are uniformly smaller than areas covered by circles. The six circle sizes correspond to the six logarithmic host plant patch size classes used in Figure 3. Site numbers are shown for patches specifically discussed in text.

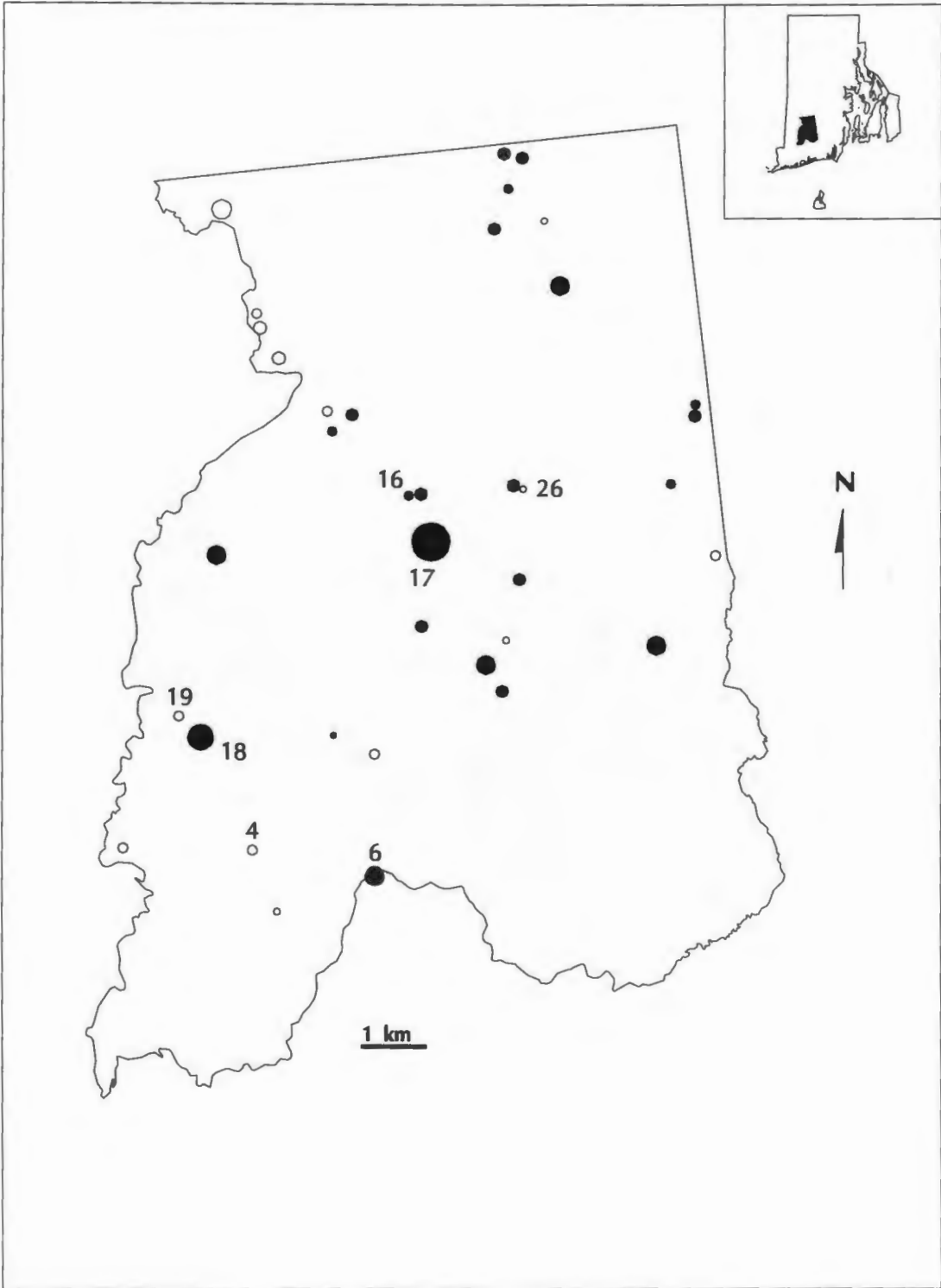


Figure 2. Size distribution of host plant patches.



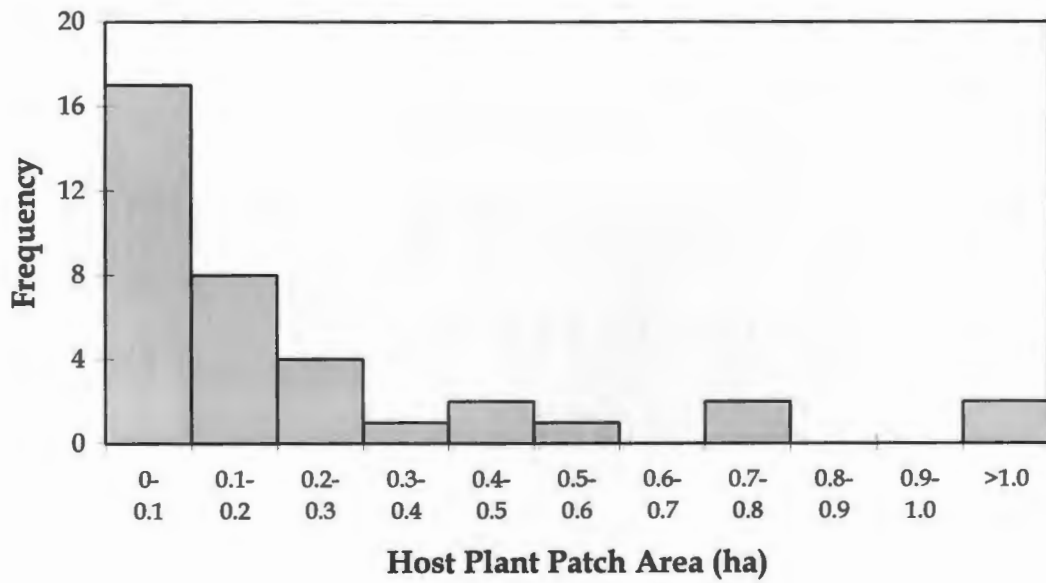


Figure 3. Incidence function of occupancy rare versus host plant patch area. The total number of patches in each size class is indicated at the top of each column.

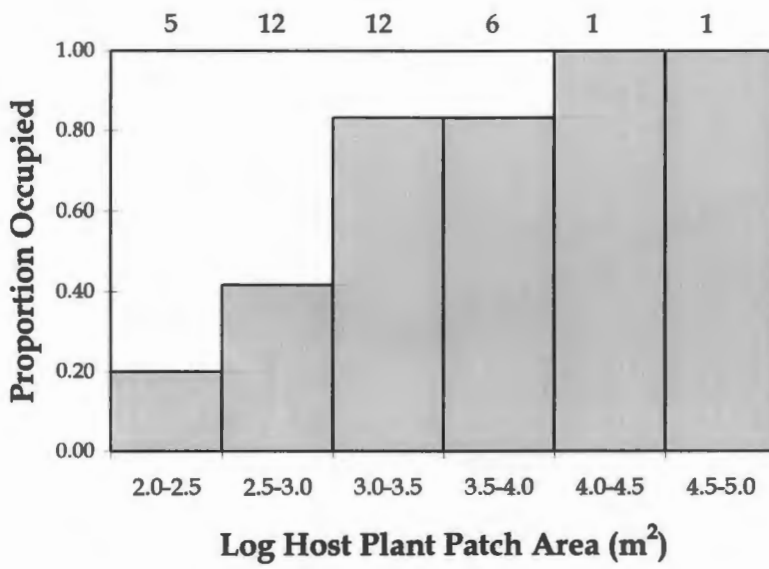
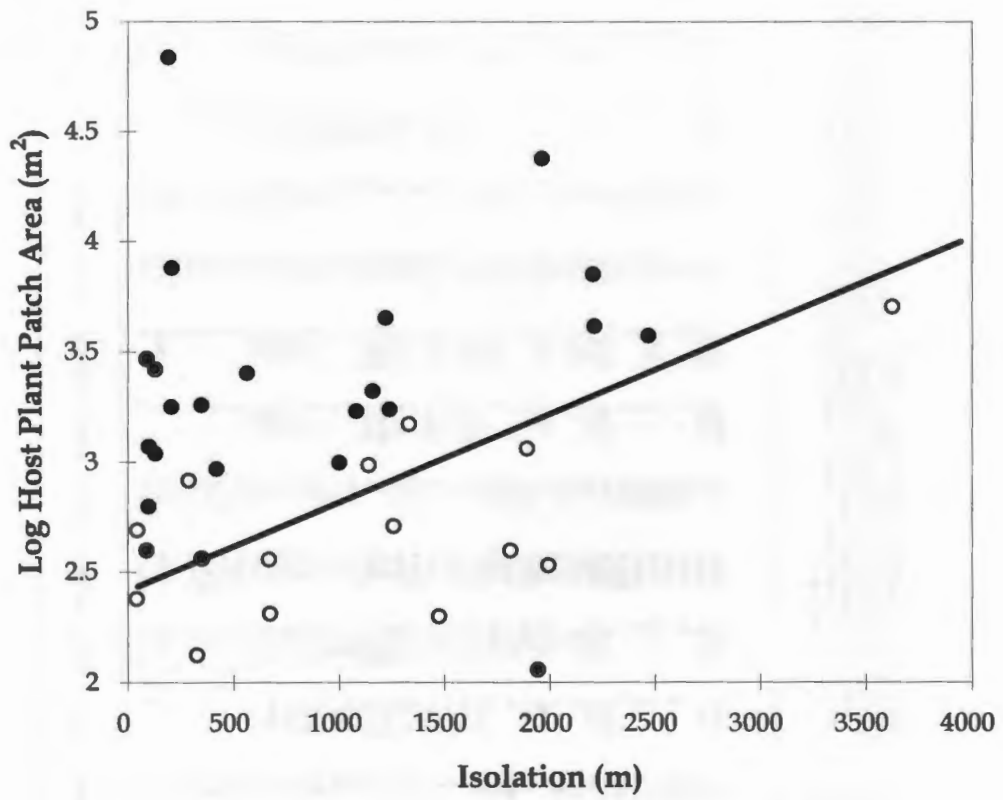


Figure 4. Relationship of host plant patch area and isolation to occupancy by *Lycaena epixanthe*. Isolation is defined as the distance to the nearest occupied host plant patch. Filled circles represent patches occupied in 1994; empty circles represent patches vacant in 1994. The method used to calculate the line separating occupied and unoccupied sites is described in the text.



Appendix: Raw data*

no	pr	bgar	crar	nrbga	nrbgds	bgar5	bgar10	nrocbgar	nrocbgds	ocbgar5	ocbgar10	nrcrar	nrcrds	crar5	crar10	nroccrar	nroccrds	occrar5	occrar10
1	y	1854	114	2557	643	0	2557	29744	1874	0	0	363	671	0	363	23964	1944	0	0
2	n	2557	363	1854	654	0	1854	1854	654	0	1854	114	666	0	114	114	666	0	114
3	n	9969	968	2179	1140	0	0	2179	1140	0	0	2179	1140	0	0	2179	1140	0	0
4	n	5014	397	735	939	0	735	15490	1731	0	0	199	982	0	199	4142	1815	0	0
5	n	735	199	5014	939	0	5014	15490	1393	0	0	397	976	0	397	4142	1474	0	0
6	y	15490	4142	735	1413	0	0	1854	2177	0	0	199	1474	0	0	114	2212	0	0
7	y	4520	1739	2696	793	0	2696	25064	1176	0	0	133	894	0	133	7612	1239	0	0
8	y	2553	1817	15800	125	17207	17207	1407	308	1407	1407	365	350	1188	1188	365	350	365	365
9	n	15800	823	2553	125	3960	11052	2553	125	3960	3960	365	288	2182	2182	365	288	2182	2182
10	y	1001	628	1849	94	1849	1849	1849	94	1849	1849	1173	100	1173	1173	1173	100	1173	1173
11	y	1407	365	15800	226	18353	18353	2553	308	2553	2553	823	287	2640	2640	1817	350	1817	1817
12	n	7092	1486	3264	302	2520	19389	1407	1299	0	0	1154	489	1154	1494	365	1333	0	0
13	n	2520	1154	1069	36	8161	8161	1407	1873	0	0	340	45	1826	1826	1817	1892	0	0
14	n	1069	340	2520	36	2520	9612	1407	1981	0	0	1154	45	1154	2640	1817	1994	0	0
15	y	3693	2941	8065	61	98915	98915	8065	61	98915	98915	398	90	69099	69099	398	90	69099	69099
16	y	8065	398	3693	61	94543	94543	3693	61	94543	94543	2941	90	71642	71642	2941	90	71642	71642
17	y	90850	68701	8065	166	11758	11758	8065	166	11758	11758	398	191	3339	3339	398	191	3339	3339
18	y	29744	23964	1770	34	1770	1770	1854	1892	0	0	492	46	492	492	114	1963	0	0
19	n	1770	492	29744	34	29744	29744	29744	34	29744	29744	23964	46	23964	23964	23964	46	23964	23964
20	y	5777	2634	1838	94	7157	7157	1838	94	7157	7157	1091	130	2019	2019	1091	130	2019	2019
21	y	1838	1091	5777	94	11096	11673	5777	94	11096	11096	2634	130	3562	3767	2634	130	3562	3562
22	y	5319	928	1838	417	7615	11317	1838	417	7615	10740	1091	419	3725	6461	1091	419	3725	6256
23	y	3125	2531	5319	569	0	5896	5319	569	0	5319	928	563	0	1133	928	563	0	928
24	n	14938	5078	3161	840	0	3161	2553	3619	0	0	3161	840	0	3161	1817	3626	0	0
25	y	6503	2105	553	36	553	553	90850	1123	0	0	240	42	240	240	68701	1160	0	0
26	n	553	240	6503	36	6503	6503	6503	36	6503	6503	2105	42	2105	2105	2105	42	2105	2105
27	y	9100	4526	577	927	0	577	3125	1221	0	0	205	927	0	205	2531	1221	0	0
28	n	577	205	5319	672	0	19382	5319	672	0	19382	928	672	0	9076	928	672	0	9076
29	y	25064	7612	3183	198	5879	5879	3183	198	3183	3183	1779	207	1912	1779	207	1779	1779	1779
30	y	3183	1779	25064	198	25064	27760	25064	198	25064	25064	7612	207	7612	7745	7612	207	7612	7612
31	y	9034	1705	90850	1069	0	0	90850	1069	0	0	7612	1081	0	0	7612	1081	0	0
32	y	7610	3746	1770	2432	0	0	29744	2432	0	0	492	2541	0	0	23964	2469	0	0
33	y	9107	992	1849	1000	0	1849	1849	1000	0	1849	1173	1000	0	1173	1000	0	1173	1000
34	y	22245	7148	695	1389	0	0	4520	2187	0	0	514	1416	0	0	1739	2209	0	0
35	n	695	514	9107	1216	0	0	9107	1216	0	0	992	1258	0	0	992	1258	0	0
36	y	1849	1173	1001	94	1001	10108	1001	94	1001	10108	628	100	628	1620	628	100	628	1620
37	n	2696	133	25064	321	25064	32767	25064	321	25064	32767	7612	327	7612	11130	7612	327	7612	11130

* All area measurements are in m²; all distance measurements are in m.
no = site number; pr = present; bgar = bog area; crar = cranberry patch area; nrbgar = area of nearest bog; nrbgds = distance to nearest bog; bgar5 = total area of bogs within 500 m; bgar10 = total area of bogs within 1000 m; nrocbgar = area of nearest occupied bog; nrocbgds = distance to nearest occupied bog; ocbgar5 = total area of occupied bogs within 500 m; ocbgar10 = total area of occupied bogs within 1000 m; nrcrar = area of nearest cranberry patch; nrcrds = distance to nearest cranberry patch; crar5 = total area of cranberry patches within 500 m; crar10 = total area of cranberry patches within 1000 m; nroccrar = area of nearest occupied cranberry patch; nroccrds = distance to nearest occupied cranberry patch; occrar5 = total area of occupied cranberry patches within 500 m; occrar10 = total area of occupied cranberry patches within 1000 m.

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