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TRANSACTIONS

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Contents

Photography
Alfred Charles Bonanno

The viewer will quickly recognize that Bonanno has the rare ability to capture universal moments. His photographs are used by major teaching centers, appear in national publications, and are held in private and public collections in several countries.

A New Station in Door County, Wisconsin, for the Rare *Iris lacutris* Nutt. (Dwarf Lake Iris)
Charles R. Hart

The *Iris lacustris* Nutt. is known only from Michigan, Ontario and Wisconsin, and has recently been designated as a ''threatened species'' on state and national levels. Recently an extensive population of this threatened plant was discovered in southern Door County.

Diel Periodicity of Movement and Feeding of Yellow Perch (*Perca Flavescens*) in Lake Mendota, Wisconsin
John P. McCarty

Diel activity cycles have been reported for a variety of freshwater fishes, yet the degree to which individual behavior affects population phenomena is not clear. Analysis of the spatial distributions of yellow perch in Lake Mendota, Wisconsin, indicate that diel movement patterns are more variable than previously reported.

Poetry

Some of Wisconsin's best-known poets and some of our most promising new poets are represented in the poetry section.

Voles and Bog Lemmings of Wisconsin
Charles A. Long

This is a report on the taxonomy as well as the geographical and ecological distributions of Wisconsin's voles and bog lemmings. There is also a summary of the environmental status of the animals.

Interspecific Associations of Some Wisconsin Lake Plants
Stanley A. Nichols

This paper is another in the major studies being conducted into the quality of and changes in Wisconsin lakes. The primary purpose of these detailed macrophyte surveys is to design lake management strategies and to collect benchmark limnological data. The lakes being studied represent a broad range of Wisconsin lake types with regard to geographic distribution, chemical and physical parameters, and human impact.

From the Editor

As the editor of *Transactions* it is my pleasure to introduce our readers to the 1990 volume. This issue reflects not only a broad range of topics, but readers will be happy to see the return of the photography section which this year features the work of Alfred Charles Bonanno. This volume presents subjects as diverse as Wisconsin lakes, hummingbirds, tornadoes of fire, and the discovery of a new station for a rare plant. Of course the regular poetry section has been included. Once again I think readers will appreciate the high quality of the work about Wisconsin and by Wisconsin authors.

It is hoped that future volumes of *Transactions* or some other component of the Academy will reflect the work being done by the recipients of the awards given at the annual meeting. We are currently exploring ways to present work dedicated specifically to poetry and photography. The anthology of Wisconsin poets that was announced in the 1989 volume will be published early in 1991. People who attended the 1990 meeting of the Academy held in Platteville were introduced to some of the poems at an afternoon reading by our poetry editor, Bruce Taylor.

For over a hundred years the Wisconsin Academy of Sciences, Arts and Letters has presented the vigorous intellectual life of people in our state. We who currently work on *Transactions* are dedicated to continuing that tradition, and in that spirit are happy to commend this volume to our readers.

Comments, suggestions, and submissions should be addressed to the Editor.

Carl N. Haywood

Announcement

Transactions will be featuring in its next issue a section called "Minority Voices" and especially encourages submission of five to ten pages of previously unpublished poetry from Wisconsin poets who represent as wide and diverse a scope as possible of racial, cultural, ethnic, and esthetic diversity.

A Quantitative Survey of the Submersed Macrophytes in Devil's Lake, Sauk County, with a Historical Review of the Invasion of Eurasian Watermilfoil, *Myriophyllum spicatum* L.

Richard A. Lillie

Abstract. *Quantitative surveys of the aquatic macrophytes of Devil's Lake, Devil's Lake State Park, Sauk County, were conducted July 29–31, 1987, in an effort to assess historical changes in the lake's macrophyte community. Above-ground biomass and frequency of occurrence data were obtained from 28 transects spaced 200 m apart. Biomass samples (0.1 m² quadrats) were collected and frequencies of occurrence (0.8 m² quadrats) were recorded at 5 m intervals along transects from shore to a water depth of 9 m. Macrophytes occupied 78% of the 0–9 m littoral zone at an average biomass of 187 g/m² (within vegetated areas). Potamogeton robbinsii Oakes and Elodea canadensis Michx. were dominant, accounting for almost half of the 39,000 kg of total plant biomass. Myriophyllum spicatum L., an introduced species that accounted for an additional 22% of the total biomass, formed three distinctive surface canopy beds 25–50 m wide by up to 300 m long in water 1.5–3.0 m deep. Milfoil distribution increased dramatically between 1979 and 1987 but showed some indication of declining in 1988 and 1989. Native macrophytes also increased in abundance and distribution. Mechanisms responsible for the growth dynamics of milfoil in Devil's Lake were not identified, but climatic fluctuations and insect disturbances may be significant.*

D evil's Lake State Park, Sauk County, has a rich and diverse flora that has received attention by botanists since the mid-nineteenth century (Lange 1984). However, most botanical collections were of terrestrial species, and relatively little is known about the aquatic flora of Devil's Lake (exceptions include Baker 1975; Lillie 1986). Recently, the Wisconsin Department of Natural Resources (WDNR) conducted a series of lim-

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nological investigations to identify possible causes and mechanisms responsible for deteriorating water quality (Lillie and Mason 1986; Lillie 1986; WDNR 1988). Because some rooted submersed macrophytes can effectively translocate nutrients from sediments to the surrounding water column (Barko and Smart 1980; Nichols and Keeney 1976; Prentki 1979; Smith and Adams 1986), changes in the abundance or community composition of submersed macrophytes may influence lake water quality (Landers 1982; Carpenter 1983; Carpenter and Lodge 1986). Consequently, the WDNR conducted macrophyte surveys in Devil's Lake in 1984 and 1987. Specific objectives of these surveys were: (1) to document the composition,

standing crop biomass, and distribution of the submersed macrophytes in Devil's Lake and (2) to compare current distributions with available historical data. These data, compiled and summarized in this paper, represent a significant contribution to the knowledge of the flora of Devil's Lake and should serve as the basis for monitoring future long-term changes in the lake's aquatic plant community. Likewise, the documented history of the introduction, expansion, and growth dynamics of *Myriophyllum spicatum* L. in Devil's Lake may provide information useful in the management of this exotic invasive species.

Methods

Devil's Lake is a relatively small (151 ha), moderately soft water (total alkalinity 22 mg/L), thermally stratified (maximum depth 14 m), seepage lake with generally very good water quality (Lillie and Mason 1986). Surveys of the submersed macrophytes of Devil's Lake were conducted July 30–August 1, 1984 and July 29–31, 1987. Methods employed in the 1984 survey were described earlier (Lillie 1986) and were generally similar to those used in 1987 as described here. In 1987, macrophyte surveys were conducted via SCUBA along 28 transects spaced 200 m apart around the shoreline (Fig. 1). Two dive-teams, consisting of one diver and two topside assistants each, were required to complete the field collections. Presence or absence of all macrophyte species were recorded from 644 (646 in 1984 survey) circular quadrats (0.8 m²) spaced at 5 m intervals (linear distance) along each transect from shore to a water depth of 9 m. These data were used to compute frequencies of occurrence for each macrophyte species. Divers also visually classified total macrophyte, aboveground, standing crop biomass at each quadrat as either absent, rare, sparse, or dense. Above-ground biomass samples were collected for dry weight determinations from a representative number of each subjective biomass class (i.e. rare, sparse, or dense) by harvesting all plant shoots and stems within

0.1 m² quadrats (three-sided aluminum frame) at the sediment-plant interface (Table 1). In some dense stands, sampling intervals were extended to 10 m (linear distance); standing crop data were interpolated for intermediate quadrats. Biomass samples were collected from every fourth sparse and rare quadrat beginning with the first encounter of each day of field collections. All samples were bagged, labeled, placed in a iced-cooler, and transported to the laboratory where they were sorted by species and dried at 106°C for 48 hours. A spikerush, *Eleocharis acicularis* R. & S., was harvested with roots intact. Because it was not possible to distinguish between *Potamogeton illinoensis* Morong and *Potamogeton amplifolius* Tuckerm. in the field, data for these two species were combined (*P. illinoensis* was the more common species based on laboratory examinations). Likewise, *Nitella* spp. and filamentous algae (*Cladophora* spp.) were often physically intertwined and impossible to separate; hence data for these taxa were also combined.

Taxonomy was based on Fassett (1972) and Voss (1972). Voucher specimens were prepared and taxonomy verified by T. Cochran and H. Iltis of the University of Wisconsin-Madison Herbarium and, in the case of pondweeds, by S. G. Smith of the University of Wisconsin-Whitewater.

Average dry weight biomass for each plant taxon was computed for each 1.5-m depth interval along each transect. Average biomass was multiplied by the area of each representative cell (inshore and offshore boundaries of cells were defined by water depth limits; lateral boundaries were defined by common boundaries half-way between adjacent transects. (See Fig. 1 to obtain areal-weighted biomass values.) These values were summed to derive estimates of total standing crop of each taxon by transect, region, depth zone, and entire lake. For purposes of discussion, results will be presented in terms of these four areas, or combinations thereof.

Inasmuch as this method of calculating standing crop biomass did not permit an un-
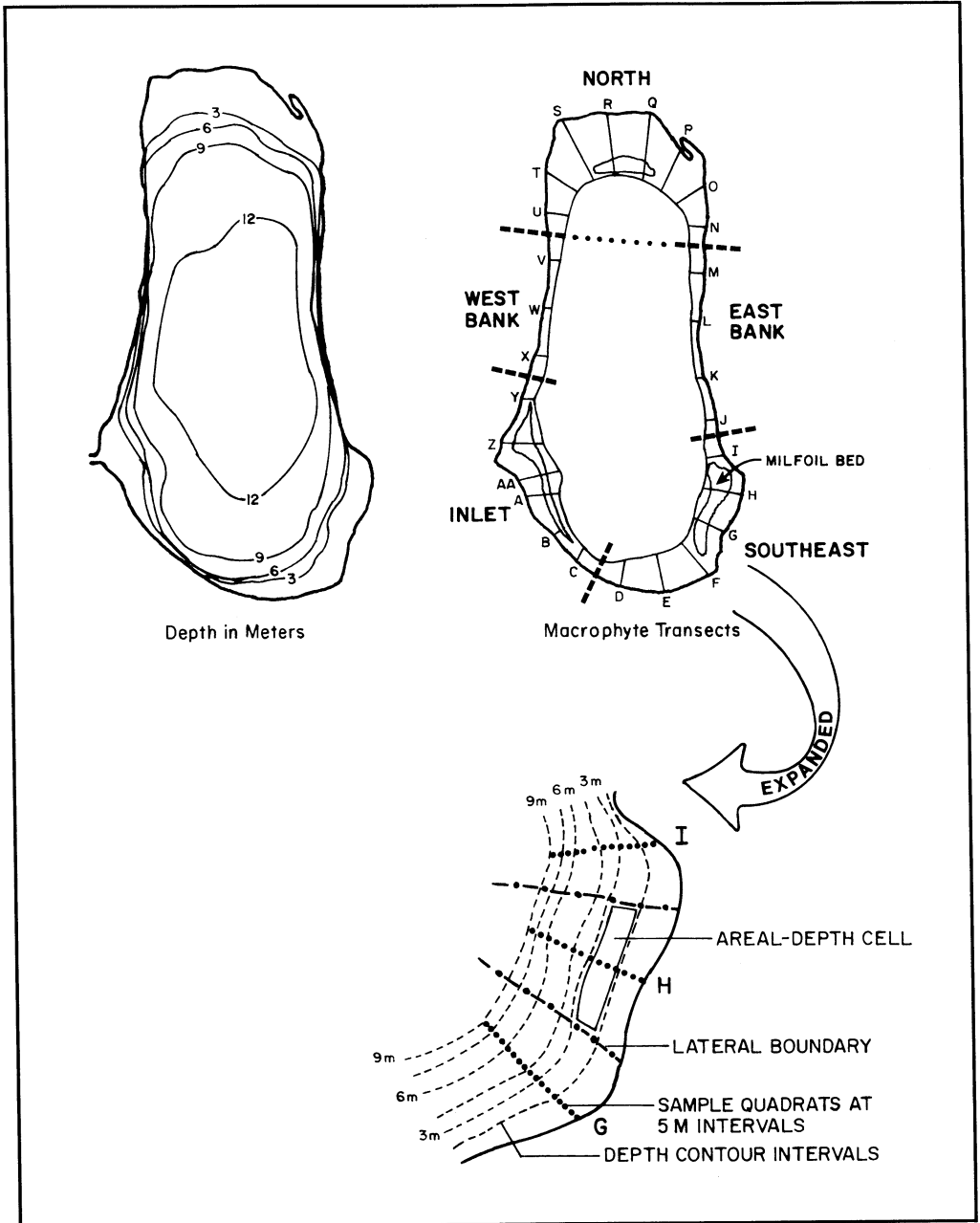
Fig. 1. Hydrographic map of Devil's Lake, Sauk County, Wisconsin with accompanying maps depicting the locations of macrophyte survey transects and boundaries used in estimating plant biomass (see text for further explanation).

biased computation of variance (values were interpolated for intermediate quads and un-sampled sites; a few cells contained only 1 quadrat), a second estimate of total standing crop was made using only the data from the rare, sparse, and dense quads that were ac-tually sampled (see Table 1). Average bio-mass of each subjective plant-biomass class

Table 1. Distribution of biomass samples by visual biomass class. Data represent the percent of quadrats in each visual biomass class within which plants were collected for dry weight measurements.

Visual Biomass Class	1984	1987
"Dense"	79%	84%
"Sparse"	4	24
"Rare"	1	25
"None"*	-	-
All vegetated sites	47	61
All quadrats	56	68

*by definition - No plants; total biomass zero; no collection necessary.

was multiplied by the area occupied by each class (based solely on frequency of occurrence) to derive estimates of standing crop for each region. This latter method of calculation overestimated standing crop biomass by about 33% but permitted an estimation of biomass variance. Coefficients of variation of total standing crop using this second method of calculation were 6.8% and 6.3% for 1984 and 1987 data, respectively. These variances may be roughly applied to the more accurate areal-weighted biomass data.

Actual dry-weight biomass data were compared with the subjective plant-biomass classes as assigned by divers to derive objective plant-biomass classification (Table 2). Dense stands of macrophytes were defined as areas with standing dry-weight crops exceeding 30 g/m^2; sparse biomass ranged from 15 to 29 g/m^2, and quads classed as rare had < 15 g/m^2. A fifth class, very dense, was arbitrarily set at > 99 g/m^2.

Aerial photographs were taken each summer from 1984 to 1989 and, in conjunction with ground-truth measurements, snorkeling surveys, and the transect data, were used to map the distribution of macrophytes.

Subtle differences in the placement of transects and water level changes occurring between the 1984 and 1987 surveys influenced sample sizes and areas surveyed (see Table 3). These differences compromised the validity of detailed statistical analyses of biomass data between regions and depth-zones between years but did not seriously affect direct comparisons of summary data for each species. Changes in frequencies of occurrence of the major species were evaluated using chi-squared tests. Plant associations and community structure of the 1987 data were explored uti-

Table 2. Plant biomass distribution in Devil's Lake based on (A) subjective plant classification assigned by divers (visual estimates) and (B) objective dry weight biomass measurements (quantitative). Data represent percent of total quadrats in each classification. 1984 N = 646; 1987 N = 644.

(A): Subjective Relative Plant Biomass Classification		Year	
		1984	1987
"Dense"		48%	51%
"Sparse"		23%	19%
"Rare"		12%	13%
"Absent"		17%	17%

(B): Objective Plant Biomass Classification	Biomass (g/m²)	Year	
		1984	1987
Very Dense	> 99	29%	29%
Dense	30-99	14	19
Sparse	15-29	26	14
Rare	1-15	14	21
Absent	0	17	17

lizing principal component analysis, Pearson correlation coefficients, and similarity indices. The degree of association between species was based on common co-occurrences (Marvan and Komarek 1978) adjusted for random chance co-occurrence. The later analysis was more informative than chi-squared tests in elucidating plant associations.

Results and Discussion

General distribution in 1987

Macrophytes occupied 78% of the 0–9 m littoral zone of Devil's Lake at an average dry weight biomass of 83 g/m² (Table 3). Dense macrophyte stands covered 21 ha (48–51% by frequency of occurrence; see Table 2) at an average biomass of 187 g/m². Another 16 ha of lake bottom was sparsely vegetated (14–19% frequency of occurrence). Ninety-

eight percent of the total biomass of submersed vegetation in Devil's Lake (39,000 kg dry wt) was contained in dense beds. Eighty-five percent of the total plant biomass was confined to water less than 4.5 m deep; virtually no plants grew at depths deeper than 9 m. Highest average total biomass (313 g/m²) within a particular depth-region zone was in the 1.5–3 m Inlet region. Sixteen species of plants were recorded (Table 4). *Potamogeton robbinsii* Oakes and *Elodea canadensis* Michx. were dominant in water less than 4.5 m deep, and a mixture of *Nitella* spp. and filamentous algae (mostly *Cladophora* spp.) was dominant in deeper water. *Myriophyllum spicatum* L. was less common but still comprised 22% of the lake's total biomass (Table 5). *Ceratophyllum demersum* L., *Vallisneria americana* Michx., *Potamogeton diversifolius* Raf., and a mixture of *Pota-*

Table 3. Regional macrophyte distribution within 0-9 m depth in Devil's Lake during 1987. Comparable data for 1984 are given in ()s (recomputed from Lillie 1984[e]).

Parameter	Inlet	North	Southeast	Total
Bottom area* in hectares	10.3 (9.4)	22.3 (21.1)	14.7 (15.0)	47.4 (45.5)
Densely Vegetated area** in hectares	5.2 (4.3)	10.1 (9.8)	5.7 (7.2)	21.0 (21.4)
Coverage[a] % of total area	50 (46)	45 (47)	39 (48)	44 (47)
Standing Crop[b] in thousands of kg	15.3 (10.0)	12.7 (12.3)	11.1 (11.9)	39.2 (34.2)
Average Biomass[c] g/m²	148 (106)	57 (58)	76 (79)	83 (75)
Average Stand Biomass[d] g/m²	289 (257)	132 (140)	188 (177)	187 (174)

* excludes 2.9 ha of unvegetated, steeply–sloped, rocky, bottom area adjacent to the east and west shorelines. Differences between 1984 and 1987 bottom areas arise from slight positional differences in placement of transects and subsequent definition of cell boundaries.
**frequency of occurrence of quadrats with total biomass > 30 g/m² within each regional depth zone multiplied by the total area within the zone.
[a] total densely vegetated area divided by total bottom area within region.
[b] average total dry wt biomass (g/m²) within each transect-depth zone (cell) multiplied by the area of each cell; products summed within each region; data represent all vegetation.
[c] total standing crop dry wt biomass within region divided by total area; data represent all sites, including unvegetated areas within regions.
[d] sum of dry wts of all quadrats with biomass > 30 g/m² within a region divided by number of quadrats.
[e]Data in Lillie 1986 were computed using WDNR's 1955 hydrographic map; these data were recomputed and are summarized for this publication using the more detailed hydrographic base map prepared from depth soundings made in January 1985 (see Lillie and Mason 1986).

Table 4. Macrophyte community composition of Devil's Lake (1987) listed in order of relative importance.

Taxa	Freq. of Occurrence		Relative Importance		Rank
	Absolute* %	Relative %	Abundance (% Biomass)	Value (IV)** (as %)	Order[a]
Potamogeton robbinsii Oakes	34.1	18.3	34.5	26.4	1 (1)
Elodea canadensis Michx.	34.6	18.5	15.5	17.0	2 (3)
Myriophyllum spicatum L.	19.0	10.2	21.5	15.8	3 (2)
Nitella & *Cladophora* (mixed)	32.1	17.2	12.0	14.6	4 (6)
Ceratophyllum demersum L.	18.1	9.7	8.4	9.0	5 (5)
Vallisneria americana Michx.	9.0	4.8	2.6	3.7	6 (8)
Potamogeton diversifolius Raf.	8.3	4.4	1.1	2.8	7 (10)
Potamogeton illinoensis Morong mixed with *Potamogeton amplifolius* Tuckerm.	8.2	4.4	0.8	2.6	8 (4)
Others/unidentified**	5.7	3.1	0.7	1.9	9 (14)
Eleocharis acicularis (L.) Rostk. & Schmidt	4.0	2.1	1.5	1.8	10 (7)
Najas flexilis (Willd.) R. & S.	5.5	3.0	0.6	1.8	11 (12)
Isoetes echinospora Durieu	4.0	2.1	0.5	1.3	12 (9)
Chara sp.	2.0	1.1	0.1	0.6	13 (13)
Potamogeton crispus L.	2.0	1.1	0.1	0.6	14 (11)
Megalodonta[b] *beckii* (Torr.)	0.1	tr.	tr.	0.1	15 (—)

* Absolute frequency of occurrence based on presence/absence at 601 quadrats within 0–9 m (excludes rocky, unvegetated, east and west quartzite-talus slopes); Relative Abundance represents % of total dry wt biomass; IVs computed by averaging Relative Frequency of Occurrence and Relative Abundance.
**Others include *Ranunculus* spp., *Potamogeton pusillus* sensu lato, and *P. gramineus*.
[a]( )s indicate 1984 ranking.
[b]now *Bidens beckii* Torr.

mogeton illinoensis and *Potamogeton amplifolius* (hereafter referred to as *P. ill/amp.*) were also relatively common. Biomass distribution of most taxa was depth dependent (Figs. 2 and 3). Based on depth distribution, co-occurrences (Fig. 4), and visual observations, four relatively distinct communities were distinguishable. A diverse assemblage of relatively small, short-stemmed plants consisting of *Najas flexilis* (Wild.) R. & S., *E. acicularis*, *Potamogeton crispus* L., *P. diversifolius*, *Chara* spp., *Isoetes echinospora* Durieu, and *V. americana* comprised the shallow-water community. A mixture of *P. robbinsii* and *E. canadensis*, with lesser amounts of *P. ill/amp.* and *V. americana*, formed a distinct community at 2–3 m. *Myriophyllum spicatum*, often accompanied by *C. demersum* at edges of beds, formed very dense beds at the outer edge of the littoral shelf in 2.5–3.5 m (the lake bottom descends sharply beyond this point). A mixture of *Nitella* spp. and *Cladophora* spp. formed the deep-water community.

Distribution of major taxa in 1987

Potamogeton robbinsii, or Robbin's pondweed, was the dominant macrophyte in Devil's Lake, accounting for 34% of the total standing crop biomass. Dense stands, averaging 173 g/m², occupied 7.2 ha (18% of all quadrats sampled). *Potamogeton robbinsii* was distributed in relatively broad, primarily monotypic, distinct bands at 1.5–4.5 m adjacent to the North and Southeast shorelines (Fig. 2 and Appendix A). However, highest average stand biomass (280 g/m²) was located in shallow water (1–3 m) adjacent to the Inlet region. Frequency of occurrence (56–70%) was similar in all three regions. The

largest areal distribution of *P. robbinsii* (2.8 ha) was in scattered beds located off the North shore. *Potamogeton robbinsii* was most commonly associated with *E. canadensis* (Fig. 4). At the time of the survey, *P. robbinsii* appeared to be at the peak of its growth, with strong, well-rooted plant stems. *P. robbinsii* harbored many aquatic fauna, particularly large numbers of dragonfly and caddisfly larvae. Despite its extensive distribution and dense growths, *P. robbinsii* was relatively unnoticed by the average park user due to the plant's low growth form (<1 m height) and moderately deep-water habitat (the beds in the Inlet region were an exception). *Potamogeton robbinsii* has a much narrower ecological niche than that of *C. demersum* or *M. spicatum* (Pip 1988), and hence its dominance in Devil's Lake reflects the relatively low concentration of inorganics present.

Elodea canadensis, or waterweed, was equally as common but less abundant than *P. robbinsii* (16% of total plant standing crop), ranking second in overall relative importance. Where abundant (4.0 ha), *Elodea* stand biomass averaged 142 g/m². *Elodea* formed weakly continuous patches (relatively irregular clumps less than 10 m across) with average biomass up to 152 g/m² in the North

and Inlet regions. *Elodea* co-occurred primarily with *P. robbinsii* and *C. demersum* (Fig. 4). *Elodea* leaves were very short and confined to the margins of the stems (<1.5 m in length), which were weakly rooted. Very dense stands of *Elodea* may interfere with fishing, but generally the plant does not create a problem in Devil's Lake.

Myriophyllum spicatum, or milfoil, comprised 21.5% of the total standing crop. While less extensive in coverage than *P. robbinsii* or *E. canadensis* (only 3.1 ha of dense beds), average milfoil stand biomass (270 g/m²) was more than 50% higher than either competitor. A maximum biomass of 1100 g/m² was recorded at 1 quadrat. Milfoil distribution was concentrated in three distinct beds, 50 m wide by 300 m long, located 50–70 m directly offshore from high-recreation-use areas (Fig. 2). Average biomass in the Southeast and Inlet beds were identical (314 g/m²) and higher than that of the North bed. Milfoil beds generally were confined to 1.5–3 m with deeper extensions to 4.5 m in the Southeast and Inlet beds (Appendix A). Frequencies of occurrence were highest in the Inlet region (60–73%) and lowest in the North bed (15–21%). Milfoil was commonly associated with *C. demersum* (Fig. 4); however, biomass was not significantly correlated within milfoil beds

Table 5. Regional distribution, average biomass, and total standing crop of the five major plant taxa in Devil's Lake. Total biomass (kg dry wt*) estimates include sparsely vegetated sites. Average densities (g/m²; = sum of dry weights/number of quads) and distributional area are given for densely vegetated sites only (i.e., those quads with biomass in excess of 30 g/m²).

Taxa	Inlet			North			Southeast			All Regions		
	Dist. Area ha**	Aver. Biomass g/m²	Total Mass 10³k	Dist. Area ha	Aver. Biomass g/m²	Total Mass 10³k	Dist. Area ha	Aver. Biomass g/m²	Total Mass 10³k	Dist. Area ha	Aver. Biomass g/m²	Total Mass 10³k	# Quads
P. robbinsii	2.0	280	6.5	2.8	127	3.3	2.4	139	3.7	7.2	173	13.5	116
E. canadensis	1.5	146	2.2	2.1	152	3.6	0.5	66	0.2	4.0	142	6.1	62
M. spicatum	1.0	314	3.2	0.7	106	0.7	1.5	314	4.5	3.1	270	8.4	52
Nitella/Cladoph.	1.1	55	0.9	3.0	84	2.6	1.5	49	1.2	5.6	69	4.7	72
C. demersum	0.6	160	1.1	0.7	136	1.0	0.4	232	1.2	1.7	168	3.3	31

* derived by multiplying average biomass (g/m²) within each transect-depth zone cell by the area of each cell; products summed to derive total biomass within each region.
** sum of totals exceeds that given in Table 3 due to overlap between species.
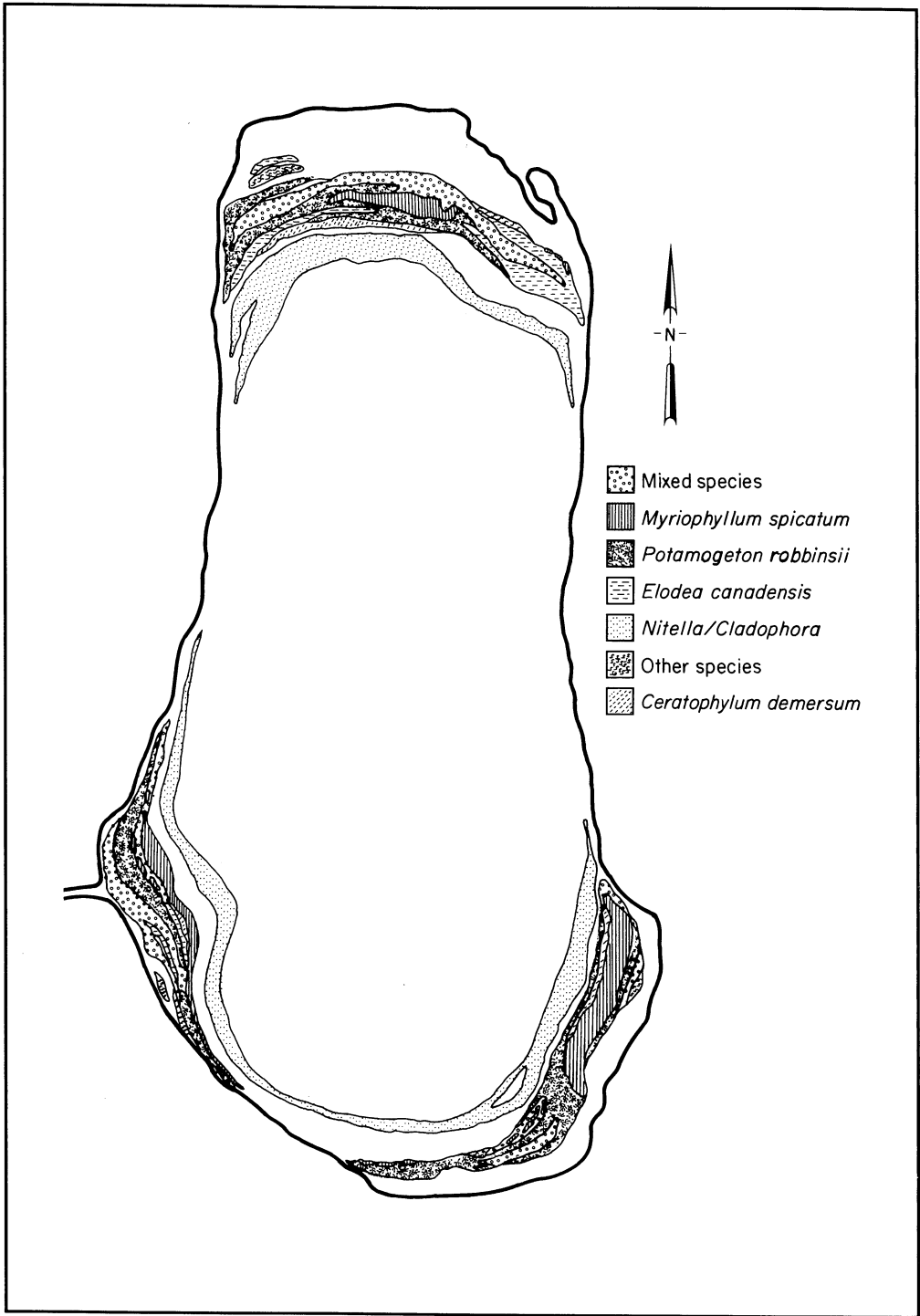
Fig. 2. *Generalized distributional map of submersed macrophytes in Devil's Lake. The map denotes areas dominated by particular species; other species may be present as well, but in lesser amounts.*
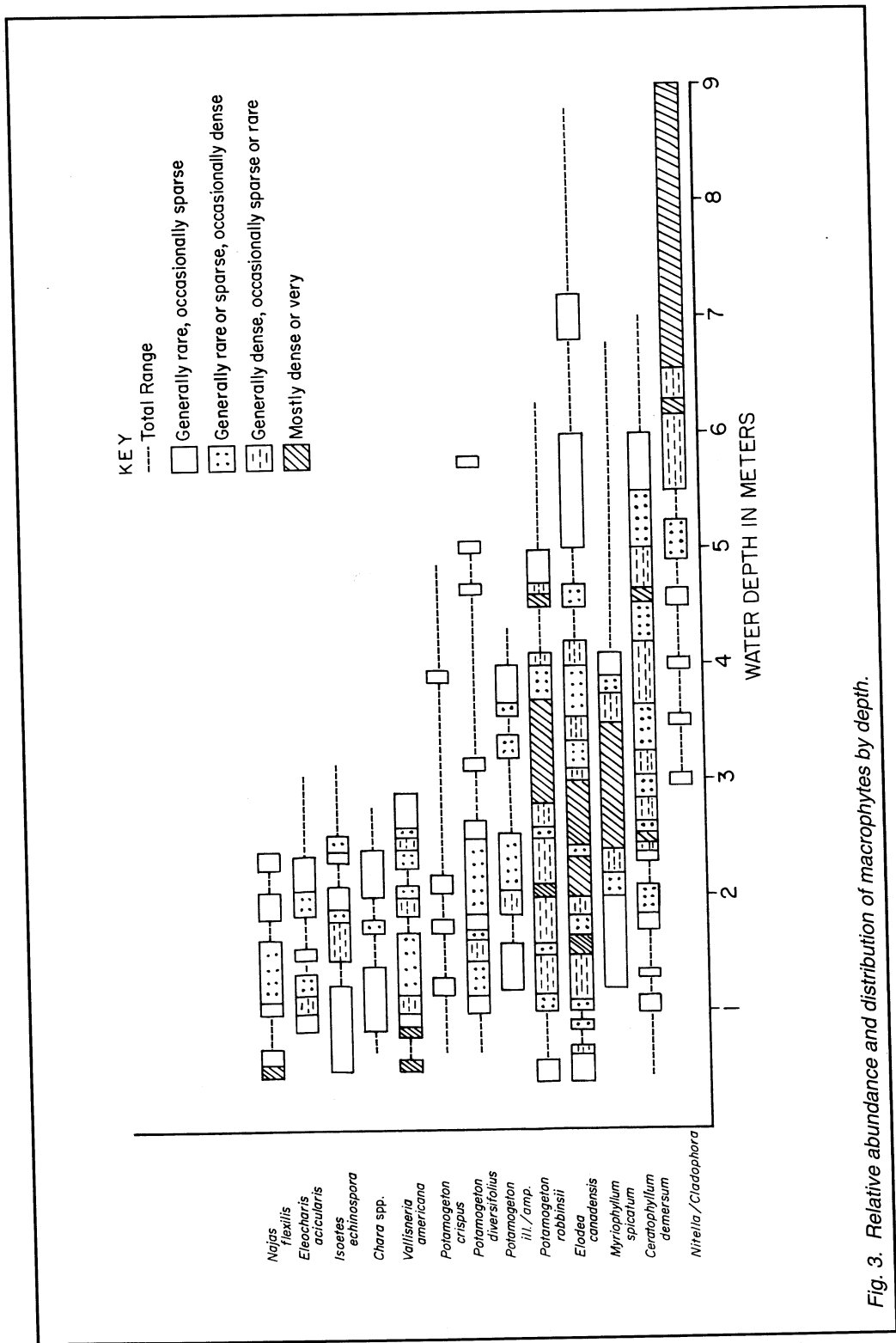
Fig. 3. Relative abundance and distribution of macrophytes by depth.
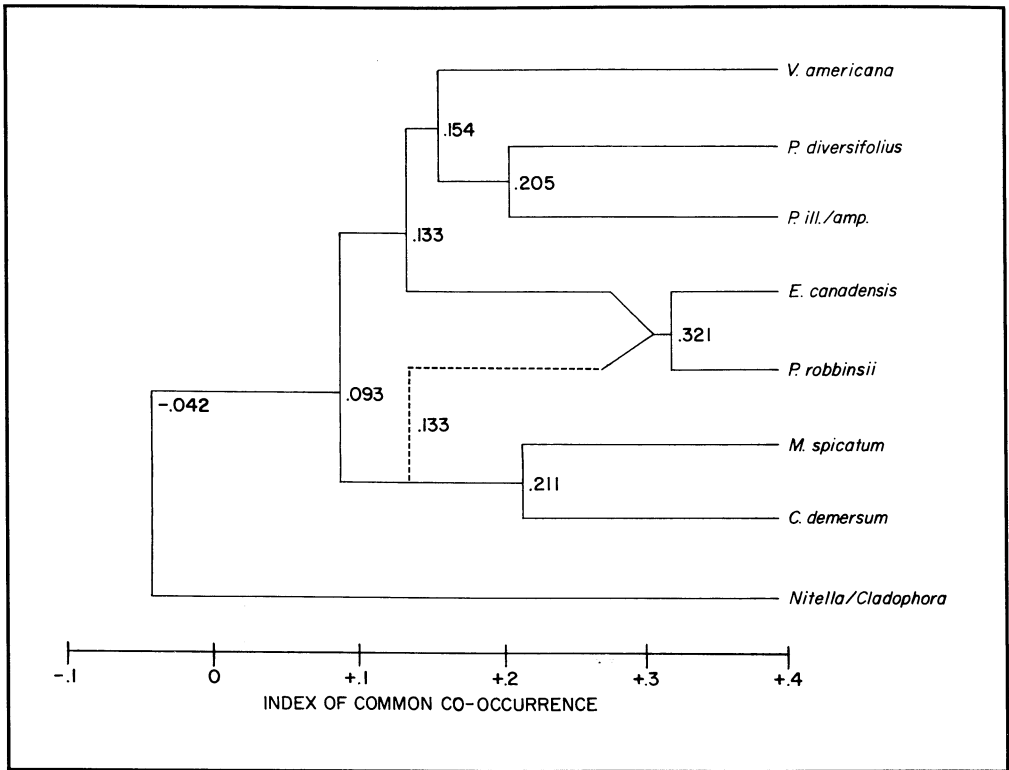
Fig. 4. Plant associations of the more abundant plant taxa based on common co-occurrence.

(p>.05). Milfoil biomass was inversely related to *E. canadensis* biomass within milfoil beds (p = .05), but the standing crop of *P. robbinsii* (the other species from inhabiting similar depths) was not significantly affected (p>.50). Milfoil stems often exceeded 3 m in length, and dense stands formed nearly impenetrable masses at the lake's surface. As such, the beds created a severe nuisance to all users and a particularly dangerous threat to swimmers. Other than small beds of *P. ill/amp* and *Ranunculus* spp., milfoil was the only submergent plant in Devil's Lake that was commonly visible from shore.

Nitella spp., a muskgrass or member of the Characeae, and *Cladophora* spp., a filamentous green algae, formed the dominant deep-water community accounting for 12% of the total standing crop in Devil's Lake (82% of the biomass of all plants at 4.5–9 m). Distribution was continuous to patchy, with highest biomass (84 g/m²) off the North shore in 7.5–9 m where frequencies of occurrence were close to 90% (Appendix A). Few macrophytes were associated with the *Nitella/Cladophora* community. Because these plants grow in relatively deep water and their stems are narrow and weak, they do not present a nuisance to people fishing on the lake. Most filamentous algae problems in Devil's Lake are due to other algae that develop on plants or other substrates in shallower water. Little is known of the fauna associated with the deep-water *Nitella/Cladophora* community in Devil's Lake.

Ceratophyllum demersum, or coontail, had a total standing crop of over 3,000 kg that was relatively evenly distributed among all three regions. Average stand biomass was relatively high (168 g/m²), approaching that of milfoil in the Southeast bed. The irregular distribution of coontail in Devil's Lake (Fig. 3, Appendix A) may be related to this species' close association with milfoil (Fig. 4); coon-

tail and milfoil were most strongly correlated at the margins of milfoil beds (p = .008). While coontail develops rootlets, it does not become firmly attached to the sediments. Hence, coontail may drift about until it becomes entangled within the inner and outer edges of the milfoil beds.

The distributions of the remaining, less common species were primarily patchy. *Vallisneria americana*, *P. diversifolius*, *P. ill/ amp.*, *P. crispus*, and *I. echinospora* were commonly found at 1.5–4.5 m mixed with *P. robbinsii* and *E. canadensis*. Interspecific competition between many of these ecologically similar species was reduced via spatial (depth) separation or by virtue of life-form structure (see Pip 1988). The rosulate quillwort, *I. echinospora*, was almost exclusively restricted to a very narrow band between 1.5– 2.1 m. *Potamogeton ill/amp.* occasionally formed relatively dense beds with plant stems reaching to the lake surface. Other plants were of relatively short stature and formed a varied understory. *Najas flexilis*, *Chara* spp., *E. acicularis*, and *Ranunculus* spp. formed the bulk of the shallow-water community that undoubtedly received a great deal of human disturbance. *Eleocharis acicularis* was extremely short and often formed contiguous, grass-like mats in the interstitial spaces on the lake bottom between the larger macrophytes. *Megalodonta beckii* (Torr.) (= *Bidens beckii* Torr.) is a relatively rare plant in Devil's Lake (only found in one biomass quadrat) and could easily be mistaken for milfoil or coontail. This species was confined to a few widely scattered patches in 3–4.5 m off the North shore.

Historical Perspective

Milfoil invasion

The pattern of invasion of Eurasian watermilfoil in other lakes has been characterized as one of introduction, rapid expansion, subsequent die-off, and resurgence, not necessarily to previous maxima (Carpenter 1979;

Nichols and Shaw 1986). While the invasion and subsequent expansion of milfoil in Devil's Lake have been fairly well documented (Lillie 1986), it has not been possible to identify the mechanism responsible for the introduction nor the exact year that the introduction occurred. Best estimates place the time of the infestation around the early 1960s (Lillie and Mason 1986), although Meier and Ensign (1967) make no mention of milfoil in their field notes during two fish survey seine hauls of the Southeast beach area during 1967. Baker (1975) described milfoil (possibly misidentified as *M. verticillatum*) in the Southeast bed area during a 1974 SCUBA survey as "very scattered, at 1.2 to 4.5 m depth contributing little to the population of the total community." The distribution and area of the three milfoil beds changed dramatically from 1979 to 1983 based on rake-survey data (Southeast bed shown in Fig. 5a) collected by the WDNR (Bale and Molter 1979, 1980, 1981; Schlesser et al. 1982; Molter and Schlesser 1983). In 1979, the North milfoil bed was quite extensively developed, while the Southeast bed was just becoming established. The Inlet bed appeared to be slightly smaller than at present (referring to 1987). By 1983, the Inlet bed was similar or slightly larger than at present, and the North-shore bed extended slightly farther to the west than its present distribution. The Southeast bed extended considerably farther to the west along the south shoreline, but it was much less abundant along its northern extension than at present. Despite a significant decrease in frequency of occurrence of milfoil between 1984 and 1987 (p<0.05), the general configuration of the three milfoil beds remained relatively stable. Transect data suggest that the North-shore milfoil bed decreased in both size and average biomass; the Inlet bed biomass increased 140%, primarily due to increases in both size and stand biomass within the 1.5–4.5 m zone; and the Southeast bed remained stable except for a moderate increase in biomass.

Aerial photography suggests that the distribution of milfoil in the Inlet bed expanded

75% from 1984 to 1987, the Southeast bed expanded very slightly, and the North-shore bed declined slightly (Table 6, Fig. 5b). However, during the 1987 survey, tops of milfoil stems were 0.5 and 1 m below the lake surface at the Inlet and North beds, respectively, and at the surface in the Southeast bed. Because milfoil growth had not reached the surface at the North and Inlet beds, other submersed plants may have been mistaken for milfoil; thus milfoil distribution may have been overestimated in those two beds. Biomass estimates presented in Table 5 are believed to be the more accurate, suggesting that milfoil biomass increased by approximately 20% between 1984 and 1987.

While the transect data (1984 and 1987) suggest an overall increase in milfoil biomass (frequency of occurrence decreased), changes in biomass within individual beds were asynchronous; the Inlet bed expanded and the North-shore bed contracted. It appears that the North-shore milfoil bed reached a peak in size in 1983 or 1984 and then experienced a gradual die-off. The expansion of the Inlet bed in 1987 may have represented a reestablishment following a period of decline experienced in the early 1980s. The size of the Southeast bed increased substantially from 1974 to 1984 and then remained relatively stable through 1987. However, continued aerial photography and snorkeling surveys revealed a dramatic die-off of milfoil in the northern half of the Southeast bed between 1987 and 1988 (Fig. 5b). Part of this bed recovered in 1989, but the major portion of the bed remained unvegetated (except for some very scattered sparse growths of native species). While such asynchronous variations in milfoil have been observed in other lakes (Carpenter 1979), the mechanism responsible for these fluctuations has not been clearly identified.

While historical records of milfoil invasions in some lakes suggest that milfoil outcompetes and displaces native macrophytes (Nichols and Mori 1971; Adams and Prentki 1982), some data suggest that milfoil invades disturbed areas or denuded sediments (Keast 1984). While milfoil now occupies areas in Devil's Lake that were formerly occupied by *E. canadensis* and *P. robbinsii*, the historical record is inadequate to determine whether milfoil aggressively displaced the native species or whether milfoil simply filled the void created when the native species succumbed to some other disturbance (Lillie 1986). Of particular note in this respect is the recent report by Devil's Lake State Park staff of an unusual amount of native macrophytes accumulating along the park's beaches during the summer of 1989. Further investigations by the author revealed that an enormous number of caddisfly *(Trichoptera: Leptoceridae)* larvae had constructed their cases from *Elodea* plant fragments. Whether the large masses of free-floating *Elodea* resulted from the mechanical fragmentation by the caddisfly larvae or from increased wave-action intensity accompa-

Table 6. Estimated distributional coverage (ha) of *Myriophyllum spicatum* in Devil's Lake 1984–1989 based on aerial reconnaissance photography.

Bed Location	1984	1985	(*)	1986	1987	1988	1989
Southeast	1.3	1.4	(1.6)	1.3	1.5	0.5	0.7
North	1.1	0.8	(0.8)	0.9	1.0	0.6	0.4**
Inlet	0.7	1.1	(1.2)	0.9	1.3	0.7	0.9
Totals	3.1	3.4	(3.6)	3.1	3.8	1.8	2.0**

*based on ground-truth data collected August 1985.
**much of the North shore milfoil bed was hand-harvested on 24 September 1988 by teams of SCUBA-divers.
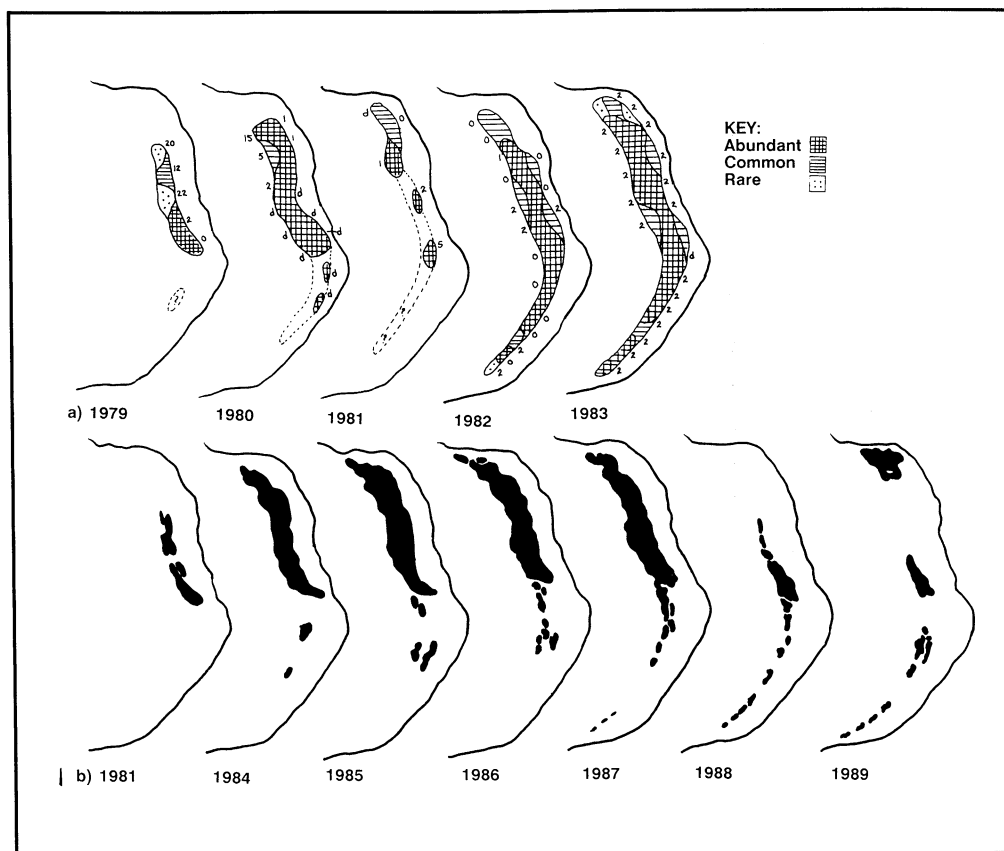
Fig. 5.(a) Generalized configuration and extent of SE milfoil bed based on summer WDNR rake surveys 1979–83 (unpublished WDNR studies—Bale and Molter 1979, 1980, 1981; Schlesser et al. 1982; Molter and Schlesser 1983). Numbers indicate distance (cm) from lake surface to top of plant beds (d = deep, not measured).
(b) Configuration and extent of SE milfoil bed based on aerial photography taken in mid-summer 1981, 1984–1989.

nying a moderately severe drop in lake water level (0.75 m since 1984) was not determined. However, it was clear that large areas formerly occupied by *Elodea* were rapidly becoming denuded. Whether milfoil invades these areas in the future remains to be seen.

Native plant community

In addition to the recent changes in *Elodea* noted above, other changes have occurred in the native plant community of Devil's Lake. Biomass of *P. robbinsii* and *P. ill/amp.* decreased and *E. canadensis*, *C. demersum*, and *Nitella/Cladophora* biomass increased during the short period from 1984 to 1987.

Excluding the deep-water *Nitella/Cladophora* community, the combined standing crop of all native plants increased only 4% from 1984 to 1987. *Nitella/Cladophora* biomass doubled and frequency of occurrence increased significantly during the same time span. Coverage (area) of dense macrophytes (all species combined) differed very slightly from 1984 to 1987 based on visual observations by divers and biomass measurements (Table 2). Total standing crop increased 15–16% during the same period (including milfoil). With the exception of a possible decline in *Elodea* and an increase in coontail, the distributions and biomass of native species

in the Southeast bed during 1984 and 1987 were generally similar to that described by Baker (1975) in his 1974 survey (Baker's 1974 survey was restricted to only the Southeast area; no other quantitative biomass data exist for other beds or other years). The rake-surveys conducted by the WDNR during 1979–1983 documented an increase in the distribution of *E. canadensis* from 1979 to 1982 (down slightly in 1983), and a decline in the distribution of *P. robbinsii* from 1979 to 1983. Apparent fluctuations in distribution and relative abundance of *Nitella* and filamentous algae may have resulted from changes in sampling methodology.

Prior to the 1974 Baker survey, only a few scattered records exist. Perhaps most important are comments from WDNR fish management surveys: 1967 — "Aquatic vegetation, primarily *Anacharis (= Elodea) canadensis,* was growing profusely in the area (Southeast) of the lake seined." *Potamogeton robbinsii* was also listed as common (Meier and Ensign 1967); and 1945 —"There is a weed bed (North shore) that apparently is a feeding spot for perch," and "there is little vegetation" (Wis. Cons. Dep. 1945). While it may be safely assumed that the first of these comments refers to plants hauled up in the seines, the basis for the latter and other records is less certain. Many comments simply may reflect casual observations made from shore or boat, perceptions that may be grossly inaccurate. However, the consensus of opinion among people who have trolled the lake on a regular basis for many years is that submersed vegetation has increased greatly during the past 30 years. Other subjective observations, such as the milfoil expansion and the water lily disappearance off the entrance to the North shore boat landing, have been substantiated by hard data. This data further supports the short-term scientific record and conclusion that submersed vegetation has increased substantially in Devil's Lake during the last 30 years.

Acknowledgments

Appendix A: Part 1

Total plant biomass (kg) distribution of major plant species in Devil's Lake by year, region and depth (in meters).

Species	Region	DEPTH ZONES						SUM
		0-1.5	*1.5-3*	*3-4.5*	*4.5-6*	*6-7.5*	*7.5-9*	
ALL PLANTS								
1984	Inlet	3,842	5,214	549	114	97	137	9,953
	North	684	7,277	2,982	714	272	342	12,270
	SE	448	6,818	2,701	884	758	328	11,938
								34,161
1987	Inlet	6,482	5,959	1,958	36	70	814	15,319
	North	759	5,496	3,187	890	665	1,736	12,733
	SE	286	5,895	3,449	429	491	593	11,143
								39,195
M. spicatum								
1984	Inlet	15	896	421	50	11	0	1,393
	North	128	1,756	14	0	0	0	1,898
	SE	63	3,231	84	210	0	0	3,588
								6,879
1987	Inlet	0	1,815	1,362	0	2	0	3,220
	North	10	734	4	0	0	0	748
	SE	19	3,131	1,306	10	5	0	4,471
								8,439
P. robbinsii								
1984	Inlet	2,614	3,220	0	2	7	0	5,843
	North	15	4,172	1,495	18	28	0	5,728
	SE	76	3,044	2,005	103	1	0	5,229
								16,800
1987	Inlet	3,790	2,553	130	16	0	0	6,489
	North	24	1,765	1,462	50	0	0	3,301
	SE	12	1,828	1,804	82	4	0	3,730
								13,520
E. canadensis								
1984	Inlet	767	718	5	12	5	0	1,507
	North	121	343	852	447	1	0	1,764
	SE	97	395	168	47	26	0	733
								4,004
1987	Inlet	1,304	872	18	0	0	1	2,195
	North	285	1,885	1,425	20	11	0	3,626
	SE	76	143	20	1	5	3	248
								6,069
C. demersum								
1984	Inlet	4	128	63	36	0	1	232
	North	1	67	379	155	25	8	635
	SE	0	44	360	67	32	31	534
								1,401

cont.

Appendix A: Part 1

Species	Region	DEPTH ZONES						
		0-1.5	1.5-3	3-4.5	4.5-6	6-7.5	7.5-9	SUM
1987	Inlet	8	661	444	19	4	0	1,136
	North	21	136	255	566	2	0	980
	SE	3	665	298	229	0	0	1,195
								3,311
Nitella-Cladophora community								
1984	Inlet	0	0	0	0	71	137	208
	North	2	0	0	66	217	334	619
	SE	0	1	1	459	700	297	1,458
								2,285
1987	Inlet	0	0	0	0	64	812	876
	North	0	1	12	248	652	1,736	2,649
	SE	0	0	0	101	477	591	1,169
								4,694

Appendix A, Part 2

Frequency of occurrence (% quadrats present*) of major plant species in Devil's Lake by year, region, and depth (meters)..

Species	Region	0-1.5	1.5-3	3.4-5	4.5-6	6-7.5	7.5-9	SUM
ALL PLANTS								
1984	Inlet	84%	92%	77%	71%	73%	71%	81%
	North	69	99	94	95	97	83	91%
	SE	45	95	97	83	87	96	85%
1987	Inlet	89	98	82	50	61	96	89%
	North	56	95	94	91	92	93	88%
	SE	42	97	97	93	95	87	87%
M. spicatum								
1984	Inlet	24	49	77	29	14	0	31%
	North	50	42	20	0	0	0	30%
	SE	21	65	39	8	0	0	32%
1987	Inlet	0	60	73	0	6	0	26%
	North	8	21	15	0	0	0	11%
	SE	15	41	50	7	9	0	26%
P. robbinsii								
1984	Inlet	52	62	0	7	9	0	30%
	North	7	68	69	26	12	0	42%
	SE	10	60	81	12	4	0	38%
1987	Inlet	67	56	11	25	0	0	34%
	North	23	59	58	9	0	0	33%
	SE	15	59	70	27	4	0	36%
E. canadensis								
1984	Inlet	56	67	15	7	4	0	33%
	North	37	56	74	37	3	0	43%
	SE	14	25	52	25	17	0	23%
1987	Inlet	56	56	11	0	0	4	31%
	North	51	73	79	26	3	0	47%
	SE	19	25	30	7	14	7	19%
C. demersum								
1984	Inlet	20	20	54	43	0	5	20%
	North	2	12	29	63	38	8	18%
	SE	0	15	39	42	30	22	21%
1987	Inlet	15	47	27	38	11	0	24%
	North	13	12	51	52	3	0	17%
	SE	4	13	50	27	0	0	15%
Nitella-Cladophora community								
1984	Inlet	0	0	0	0	50	71	19%
	North	2	1	3	26	84	83	19%
	SE	0	2	3	58	74	96	29%
1987	Inlet	0	0	0	0	56	96	27%
	North	0	1	12	87	92	93	35%
	SE	0	0	0	53	91	87	29%

*allocation of quadrats by regions and years:
        1984 (I=134, N=289, SE=182) total N = 605;
        1987 (I=137, N=278, SE=186) total N = 601.

Appendix A, Part 3

Mean dry weight biomass (g/m²) distribution of major plant species in Devil's Lake by year, region, and depth zones (in meters).

Species	Region	0-1.5	1.5-3	3-4.5	4.5-6	6-7.5	7.5-9	Avg.
TOTAL PLANTS								
1984	Inlet	164	281	63	17	7	6	106
	North	11	116	174	43	12	11	58
	SE	13	157	154	71	48	13	79
1987	Inlet	254	313	210	4	5	33	148
	North	12	85	175	50	26	50	57
	SE	8	137	213	33	32	23	76
M. spicatum								
1984	Inlet	<1	48	48	7	<1	0	15
	North	2	28	<1	0	0	0	9
	SE	2	74	5	17	0	0	24
1987	Inlet	0	95	146	0	<1	0	31
	North	<1	11	<1	0	0	0	3
	SE	<1	73	81	<1	<1	0	30
P. robbinsii								
1984	Inlet	111	173	0	<1	<1	0	62
	North	<1	66	87	1	1	0	27
	SE	2	70	115	8	<1	0	35
1987	Inlet	149	134	14	2	0	0	54
	North	<1	27	80	3	0	0	15
	SE	<1	43	111	6	<1	0	25
E. canadensis								
1984	Inlet	33	39	<1	2	<1	0	16
	North	2	5	50	27	<1	0	8
	SE	3	9	10	4	2	0	5
1987	Inlet	51	46	2	0	0	<1	21
	North	5	29	78	1	<1	0	16
	SE	2	3	1	<1	<1	<1	2
C. demersum								
1984	Inlet	<1	7	7	5	0	<1	2
	North	<1	1	22	9	1	<1	3
	SE	0	1	21	5	2	1	4
1987	Inlet	<1	35	48	2	<1	0	11
	North	<1	2	14	32	<1	0	4
	SE	<1	15	18	18	0	0	8
Nitella-Cladophora community								
1984	Inlet	0	0	0	0	5	6	2
	North	<1	<1	<1	4	9	11	3
	SE	0	<1	<1	37	44	12	10
1987	Inlet	0	0	0	0	4	33	8
	North	0	<1	<1	14	25	50	12
	SE	0	0	0	8	31	23	8

* derived by summing total kg in each cell (transect by depth) and dividing by total area in each region.

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Tornadoes of Fire at Williamsonville, Wisconsin, October 8, 1871

Joseph M. Moran and E. Lee Somerville

Abstract. *A small Door County park northeast of Brussels, Wisconsin, is a memorial to sixty people who lost their lives when a wildfire destroyed the tiny village of Williamsonville on the night of October 8, 1871. The tragedy was compounded by what eyewitnesses described as "tornadoes of fire" that accompanied the inferno. Today, we know that large wildfires often spawn intense vortices that resemble Williamsonville's tornadoes of fire. The Williamsonville fire was one of several major wildfires on the same day that claimed more than seventeen hundred lives and destroyed millions of hectares of forest land in the upper Midwest. A dry summer coupled with a general disregard of fire prevention strategies contributed to the disaster. In southern Door County, the fires meant the end of lumbering and shinglemaking as major industries and served as an impetus for development of agriculture.*

On the night of October 8, 1871, a wildfire swept through the tiny village of Williamsonville in Brussels township, southern Door County, Wisconsin (Fig. 1). All but seventeen of the settlement's seventy-seven inhabitants perished. The Williamsonville tragedy was one of many that night when fires swept into lumber and shinglemill towns located on both sides of the bay of Green Bay; in all, perhaps thirteen hundred lives were lost and seventy-five hundred people were left homeless. Most victims were either lumberjacks or homesteaders. In addition to the tragic loss of life and human suffering, wildfires so devastated the forests—more than a half million hectares were burned—that the historical course of the region's economy

changed significantly. In southern Door County, the fire that destroyed Williamsonville and other settlements was a singular event that marked the end of lumbering and shinglemaking and spurred the region's transition to agriculture.

Geographic Setting

In 1871, the Door County peninsula was thickly forested and sparsely populated. The glacial era had shaped a gently rolling terrain that was covered by northern mesic forest species (maple, hemlock, and yellow birch). Cedar swamps and tamarack and black spruce bogs occupied moist lowlands. The southern half of the county (south of Sturgeon Bay) had been settled in the mid-1850s primarily by Belgian immigrants. They were mainly farmers but the densely forested condition of their new homeland forced them into logging as their primary occupation at least for a time (Friedman 1989).

Settlers built small dwellings in isolated

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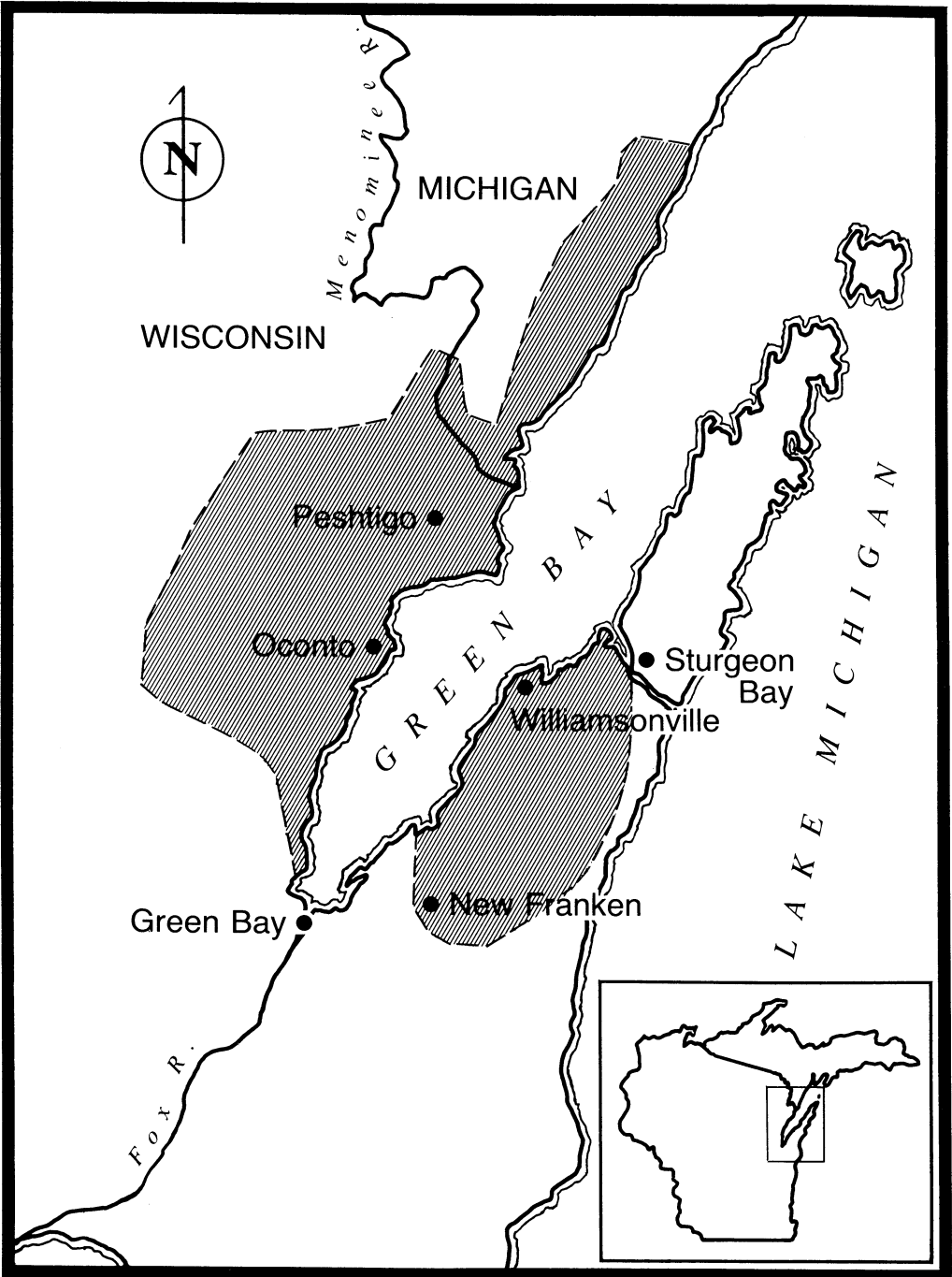
Fig. 1. Wildfires burned over large areas of northeastern Wisconsin on the night of October 8, 1871. Shading indicates the approximate location of the burned-over region based on maps by Tilton (1871) and Wells (1968).

settlements in the woods and survived by shinglemaking, lumbering, and some farming and fishing. At first, poor roads limited the marketing of logs, and no doubt much valuable timber was wasted during slash-and-burn clearing of land for crops. Eventually, markets opened for wood products including lumber, railroad ties, and shingles. Shingles were split from pine and cedar logs, shaved by hand, and transported via ox carts or sleighs to Green Bay or to boats on the Bay for eventual transport to Milwaukee or Chicago. Later, shinglemills were built.

Williamsonville, site of one of Door county's largest shinglemills, occupied a clearing of about 4 hectares. A sketch map of Williamsonville (Fig. 2) shows a linear pattern of settlement along the original stage road that linked Sturgeon Bay and Green Bay. The mill and a large storage barn were located well away from other buildings presumably as a fire safety measure. Roadside buildings consisted of a boarding house, store, blacksmith shop, and eight dwellings (C. I. Martin 1881). The present highway on the map was built in the late 1920s and is now State Highway 57.

Today, the former site of Williamsonville is marked by a small roadside park on land purchased by the county in 1927 at the suggestion of the Door County Historical Society (Holand 1931). Tornado Memorial Park (Fig. 3) is located 6.6 kilometers northeast of Brussels, Wisconsin. Bronze tablets commemorate the sixty victims who on the night of October 8, 1871, burned to death in the "tornado of fire" that "blotted out" the village.
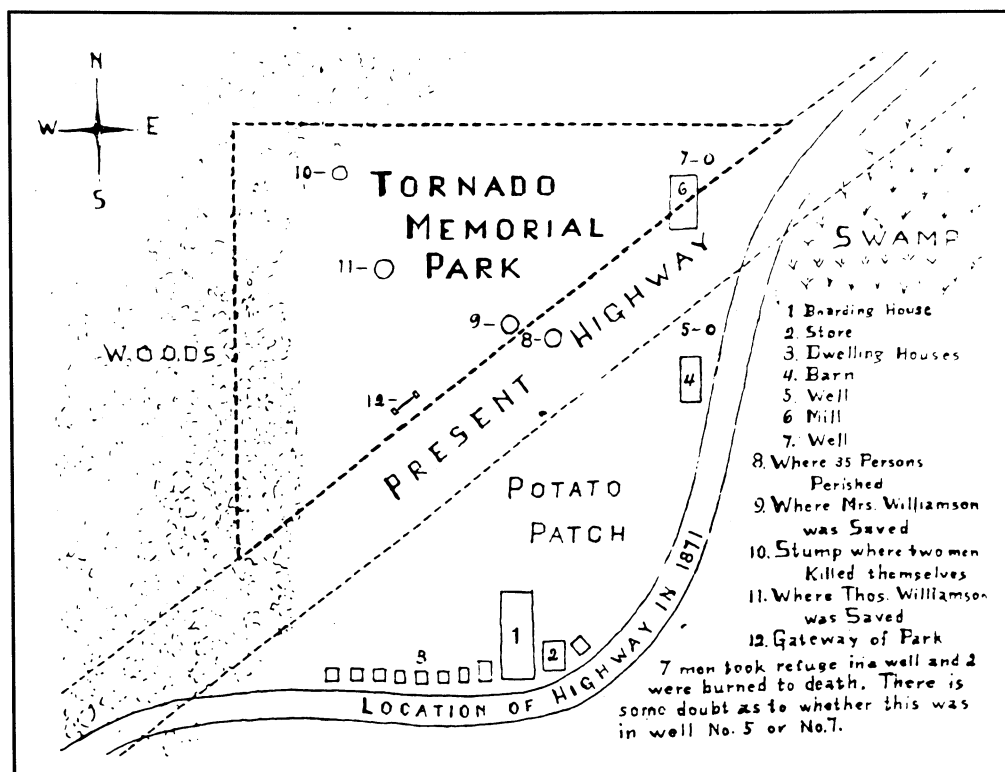
Fig. 2. Sketch map of Williamsonville, Wisconsin. On October 8, 1871, this shinglemill village was destroyed by a wildfire; only seventeen of its seventy-seven inhabitants survived. (From Holand 1931.)

Fig. 3. Tornado Memorial Park is the former site of Williamsonville, Wisconsin, and commemorates the sixty people who lost their lives to a "tornado of fire" on the night of 8 October 1871. The park is 6.6 kilometers northeast of Brussels, Wisconsin, on State Highway 57. (Photograph by J. M. Moran)

The Fire

Although the Williamsonville fire is often considered part of the same conflagration that destroyed Peshtigo, Wisconsin, actually separate fires engulfed the two settlements. According to Wells (1968), at least two major wildfires ravaged the west side of the bay of Green Bay—one spread from near the Green Bay city limits to just south of Oconto and another burned north of Oconto into Peshtigo and then on to Michigan's Upper Peninsula (Fig. 1). On the less populated east side of the Bay, another wildfire spread from south of New Frankin northeastward to near Sturgeon Bay. By far, the greatest loss of life was in Peshtigo and neighboring settlements.

The Peshtigo and Williamsonville fires occurred on the same night as the great Chicago fire, which claimed more than two hundred lives and destroyed 17,450 buildings. Between October 8 and 10, 1871, other major

wildfires burned over perhaps one million hectares of woodland in lower Michigan and may have claimed another two hundred lives. In all, these were the most destructive wildfires in United States history.[1]

We are fortunate in having a detailed eyewitness account of the Williamsonville fire. Thomas Williamson, one of the owners of the mill and village, was startled by the rapid approach of flames. He reported that as he sat with several relatives on the stairs of his family home

> there came a heavy puff of wind, the trees fell in all directions, and I saw the reflections of a big fire south of us. I thought it was a mile and a half off. In less time than it takes to write this, there came another heavy gale, and the flames came rolling through the woods up to the back of the barn. . . . Then the sparks came down like a heavy snow-storm. . . . (Holand 1931)

Williamson then describes how he and his family tried to save themselves and their possessions, but their efforts were to little avail. The next day, the bodies of thirty-five victims were found huddled together in a potato patch located about one hundred meters from the charred forest. Two of seven persons who sought refuge in a well perished. Of the eleven members of the Williamson family, only Thomas and his mother survived. Williamsonville was literally erased off the map. On a Door County map published only seven years after the fire, Williamsonville was replaced by Tornado, which apparently consisted of nothing more than a post office and saloon (Fig. 4).

Why it Happened

Although wildfires are largely random and unpredictable events, fire specialists cite fuel, ignition, and weather as key contributing factors. No one of these ingredients alone usu-

Fig. 4. On this 1878 map of Door County, "Tornado" marks the former site of Williamsonville, Wisconsin. Tornado apparently consisted of nothing more than a post office and saloon. (Map from Historical Atlas of Wisconsin, *Milwaukee: Snyder, VanVechten and Co., 1878, p. 101; courtesy of the American Geographical Society Collection, The University of Wisconsin-Milwaukee Library.)*

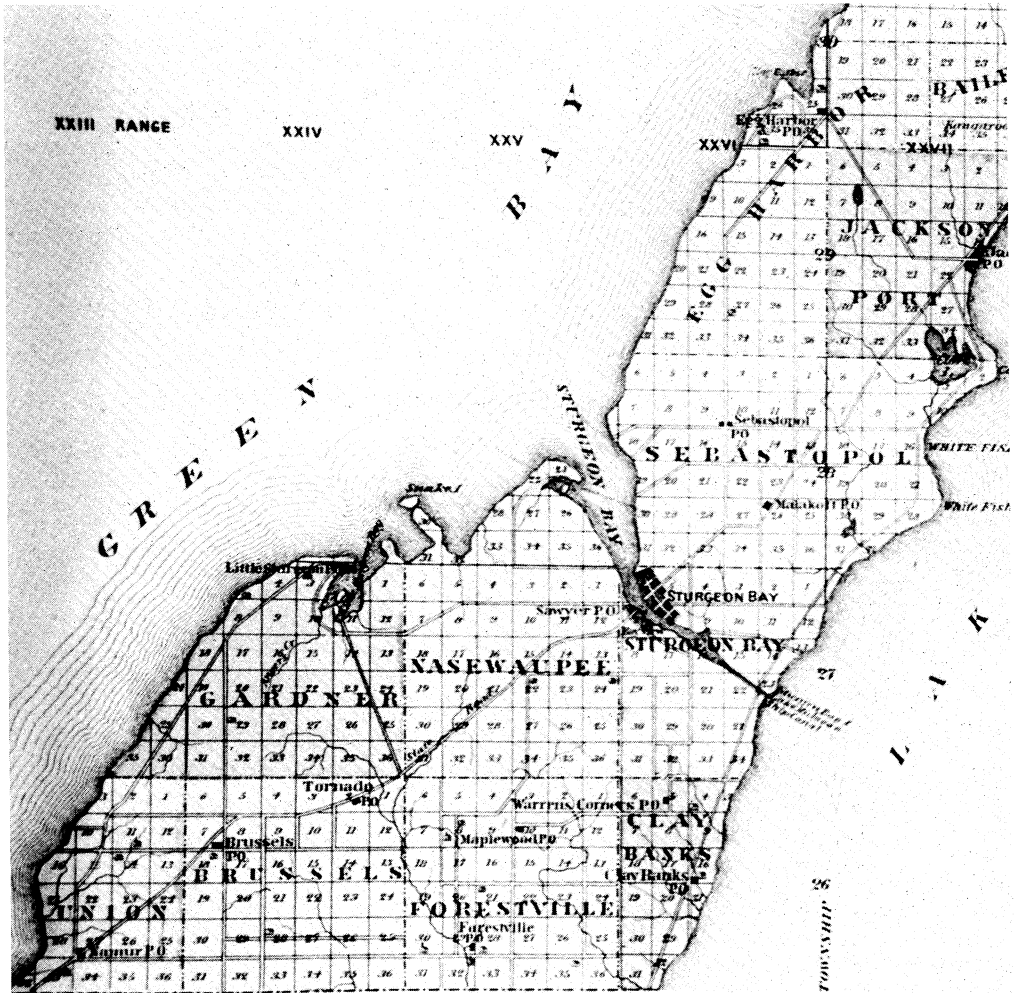ally is sufficient to trigger major wildfires. For example, even if the weather is unusually dry for a lengthy period, wildfires are unlikely unless sufficient fuel (e.g. humus, woody debris) has accumulated.

In his review of wildland fire behavior, Albini (1984) notes that wildfires are loosely classified on the basis of the type of fuel through which they burn. Ground fires slowly consume the subsurface organic materials that compose peat bogs and swamps; surface fires engulf forest litter, fallen trees, and other vegetation; and crown fires rapidly burn through tops of standing (usually coniferous) trees. Eyewitness accounts (e.g. Tilton 1871) indicate that the northeastern Wisconsin wildfires were unusually intense and involved all three sources of fuel. For example, Williamsonville survivors described a "sheet of fire that rolled along over the tree tops," probably indicating a crown fire (C. I. Martin 1881). Also, eyewitnesses noted that the fire was so intense that stumps were burned out and roots were gone (Holand 1931).

By early October 1871, the fire danger had become acute over much of the upper Midwest partially because of the wasteful logging practices of the day. Lumbering, clear-cutting for farming, and the railroad right-of-way (then under construction between Green Bay and Menominee, Michigan) left behind considerable residue and slash accumulation in the woods. The debris fueled numerous small fires that broke out frequently throughout the summer. In fact, newspapers reported that smoke blown from the smoldering woods often obscured the midday sun and sometimes was so thick over the Bay that it slowed ship traffic. The week before the wildfires, fog horns were sounded continuously and navigation was done by compass (Pernin 1971).

Numerous small fires burning in the woods of northeastern Wisconsin in the days prior to the main conflagrations meant many points of ignition, which is one reason why fire burned so rapidly over such huge areas (Haines and Sando 1969). Today, wildfires usually burn over much smaller areas because modern fire prevention practices mean that wildfires typically originate from only a few ignition points. Back then, wildfire was a tolerated hazard, and as long as winds were light, workers were able to contain the flames whenever they drew close to settlements. Residents of Williamsonville, for example, vigilantly controlled small fires that flared up around their clearing in the woods, and, if winds permitted, they would set protective backfires confident that fire would not burn over the same area twice (Holand 1931).

One obstacle in reconstructing the weather conditions on the day of the wildfires as well as the months preceding is a lack of reliable data. Weather-observing practices were not standardized as they are today, instruments were less reliable, and weather stations were few and far between. Nonetheless, available data indicate that the summer of 1871 was very dry throughout northeastern Wisconsin (Haines and Sando 1969; Haines and Kuehnast 1970). Precipitation records at Embarrass (about 58 kilometers northwest of Green Bay) and Sturgeon Bay indicate that rainfall was below average during June, July, August, and September of 1871.

Although summer dryness likely contributed to the wildfires of early October, we would be remiss in assuming that the area was in the grip of a drought of unparalleled severity. Lorimer and Gough (1982) computed a drought index for northeastern Wisconsin for each day, May 1 through October 31, 1864–1979, and tabulated the number of days per month of moderate and severe drought. From May through September of 1871, moderate drought occurred on 33 days and severe drought characterized only one day. In the 116 years of record, 22 years had a greater frequency of moderate drought and 29 years had a greater frequency of severe drought. Furthermore, March and April of 1871 were relatively wet at both Embarrass and Sturgeon Bay (Haines and Sando 1969). But what may be more important than summer drought in contributing to the fire weather of early October was the very low relative
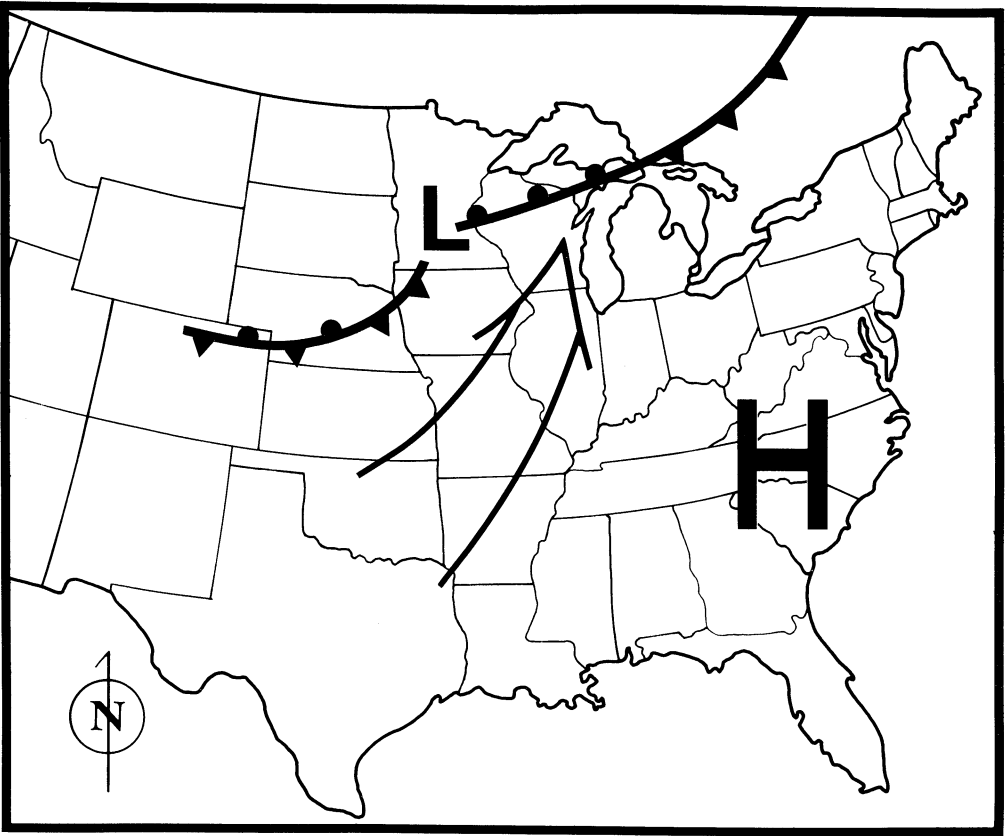
Fig. 5. Reconstruction of the major features of the synoptic weather pattern on the evening of 8 October 1871 based on a study by Haines and Kuehnast (1970). Low pressure (L) over southwest Minnesota coupled with a slow-moving high pressure system (H) over the mid-Atlantic states meant a south to southwesterly flow over the upper Midwest. Fronts stretch northeast and southwest of the low center.

humidity that persisted during the week or so prior to the wildfires (Haines and Kuehnast 1970). Low relative humidity is known to significantly elevate the fire danger by reducing the moisture content of dead logs and branches.

We are indebted to Haines and Kuehnast (1970) for their reconstruction of the synoptic weather pattern of the day of the wildfires (Fig. 5). On the evening of October 8, 1871, a slow-moving high pressure system was centered over Virginia and the Carolinas, and a deepening Alberta-type low pressure system was over southwestern Minnesota. A nearly stationary front stretched northeastward from the low center across northwestern Wisconsin to just north of Lake Michigan.

The relatively steep pressure gradient between the two weather systems gave rise to south to southwesterly winds over portions of Iowa, northern Illinois, and most of Wisconsin and Michigan. The strongest winds were over southeastern Wisconsin and northern Illinois; at 2 PM winds at Chicago and Milwaukee were from the south/southwest at a brisk 37 and 52 kilometers per hour respectively. Winds were weaker over northeastern Wisconsin with Embarras and Sturgeon Bay reporting winds of only 19 kilometers per hour at 9 PM. Nonetheless, winds were sufficiently strong to fan many small blazes into larger conflagrations. By late on the evening of October 8, southwesterly winds were driving major wildfires to-

ward Peshtigo and Williamsonville. By about 2 AM on October 9, the wildfires were over and the burned-over region lay in smoldering ruin.

Fire Vortices

Although regional winds were only light to moderate over northeastern Wisconsin, by many eyewitness accounts, wildfires were accompanied by winds strong enough to twist and uproot large trees and rip the roofs off barns and other buildings. Also, some survivors reported that wind and fire whirled about like a tornado and produced a roar similar to the sound that often precedes a tornado. In his fascinating report of the fire, Tilton (1871), a Green Bay newspaper man, quotes two residents of Sugar Bush, a small settlement near Peshtigo, who witnessed "tornadoes of fire."

Says Alfred Griffin, of the lower Sugar Bush, "When I heard the roar of the approaching tornado I ran out of my house and saw a great black, balloon-shaped object whirling through the air over the tops of the distant trees, approaching my house. When it reached the house it seemed to explode, with a loud noise, belching out fire on every side, and in an instant my house was on fire in every part."
G. H. Brooks makes a similar statement. He went out of his back door to see the approaching storm, saw a similar cloud or ball approaching, and then ran into the house and with difficulty closed the door, so strong was the wind. The ball had by this time reached the house and exploded with a loud noise, filling the air with great sheets of flame. A stream of fire entered his house through the crack under the back door, and swept through the house to the front door. Of course the house was ablaze in an instant from foundation to roof, the family barely escaping with their lives, supremely happy to do that. We visited the place afterwards. The house stood at a considerable distance from the woods—so far, that in any ordinary fire, it would have been perfectly safe. But here were remaining but the stone walls of the cellar, dilapidated stoves, melted stove-pipe and broken crockery. . . . (Tilton 1871)

Tornadoes of fire were actually fire vortices, which are frequently spawned by large wildfires (Graham 1955; Haines and Updike 1971; Albini 1984). Development of fire vortices was probably the principal reason for both the rapid pace and destructiveness of the wildfires. Fire vortices are of two general types: fire whirlwinds and horizontal roll vortices. The Wisconsin wildfires likely generated both types of vortices.

Fire whirlwinds are the more common vortices. They are vertically oriented and vary in diameter (1 to more than 100 meters) and height (1 to more than 1000 meters) and range in intensity from weak dust-devil–like whirls to severe tornado-like disturbances. Whirlwinds develop both within and immediately downwind of a wildfire and are made visible by swirling smoke and masses of burning embers.[2] Horizontal roll vortices, whirls that rotate about a horizontal axis, are less common and rotate more slowly than fire whirlwinds (Haines and Smith 1987). If either type of fire vortex develops at the downwind leading edge of a wildfire, they can hasten the spread of fire by scattering firebrands (burning embers) and igniting spot fires well beyond the perimeter of the main body of fire. In controlled burns, for example, fire whirlwinds are known to ignite spot fires many kilometers downwind from the main inferno. This is likely what happened as regional southwesterly winds steered wildfires toward Williamsonville and Peshtigo, for it explains how objects situated some distance downwind of the main body of the wildfire were quite suddenly consumed by fire.

In some respects, wildfires that scorched northeastern Wisconsin in October 1871 may have resembled the huge fire storms that engulfed hundreds of city blocks during Allied bombing raids on cities in Germany and Japan during World War II. In those fire storms, violent updrafts formed over the fire center and strong cyclonic (counterclockwise) winds developed at the surface. For example, on July 27–28, 1943, heavy incendiary bombing of Hamburg, Germany, set off a fire storm

that engulfed an area of about 12 square kilometers. Surface winds likely exceeded hurricane strength and the fire storm was accompanied by intense local vortices (Ebert 1963).[3]

Models and experimental burns provide some insight on the genesis of fire vortices. For example, Church et al. (1980) attempted to model fire whirlwinds during experiments at the Meteotron facility in southern France near the central Pyrenees. The Meteotron is a 140 by 140 meter square array of 105 fuel oil burners which, when ignited, produces fires that merge into a highly energetic inferno. A network of weather instruments and cameras continually monitors the fire plume, a hot and buoyant mixture of combustion gases and entrained air. Church and his colleagues found that vortices of varying intensity develop within the fire plume, and some travel downwind and away from the fire perimeter. Apparently surface winds interact with the fire plume in such a way that vorticity (a measure of the rotational tendency of the fluid) is concentrated in a series of anticyclonic (clockwise) and cyclonic (counterclockwise) vortices.

Haines and Updike (1971) point out that, once formed, a fire whirlwind feeds itself. A fire whirlwind occupies an air column that is heated intensely by the underlying burning ground cover. Intense heating destabilizes the air, especially close to the ground, and gives rise to a strong updraft that draws surface winds radially inward toward the whirlwind. In this way, horizontal surface winds transport fuel (burning logs and other debris) into the whirlwind. Burning fuel further heats the air enhancing its buoyancy and thereby whirlwind circulation strengthens.

Historical Significance

In many of the devastated settlements, including Peshtigo, survivors of the wildfires stoically tried to put their lives back together. Some saw and shingle mills destroyed by fire were rebuilt but not in southern Door County where the wildfires had permanently altered the landscape and the local economy. The thick forests were gone, replaced by burned-over vegetation and tree stumps; the lumbering era had ended.

Clearing trees and stumps had always been a slow and arduous task for settlers living independently on isolated plots of land and relying on their own muscle power and that of their sluggish oxen. Ironically, the devastating wildfires of 1871 helped farmers to clear the forest and open the land to crops. Furthermore, when news of the wildfires reached the rest of the state and nation, an enormous relief effort began which brought food, clothing, money, and farm implements to the area. Xavier Martin, a prominent Green Bay politican and real estate dealer, observed that by 1874, only three years after the fire, the Belgian immigrants of Door County were in better condition and circumstances than ever before (X. Martin 1895).

In effect, the fire was a catalyst that accelerated the transition to agriculture in southern Door County, a conclusion that is supported by area census data that bracket the 1871 fire. Censuses of 1870 and 1880 indicate sharp increases in population, number of farmers, and land area in cultivation in the five southern Door County townships most severely affected by fire (Tables 1 and 2). In fact, the rate of development was much faster than statewide trends during the same period. While population more than doubled and cultivated land area almost tripled in the five southern Door townships, statewide population increased 25% and farm acreage increased 31% (Ebling et al. 1948). Census data also tell us that the number of sawmill or shinglemill workers in the five townships declined from thirty-nine in 1870 to none in 1880.

Farming in Door County in the 1870s was largely of the mixed or subsistence type with an emphasis on livestock (Ebling et al. 1948). That is, farmers produced primarily for their family's essential needs (food, fiber, and shelter). Nonetheless, this stage in the region's agriculture was a key step in the even-

Table 1. Percent change in population and farm statistics between 1870 and 1880 for the five southern Door County townships most severely affected by the 1871 wildfires.

	Brussels	*Forestville*	*Gardner*	*Nasewaupee*	*Union*
Population	+146%	+197%	+ 50%	+120%	+108%
Households	+141%	+181%	+ 53%	+ 87%	+ 87%
Farmers	+145%	+269%	+100%	+115%	+ 98%
Farm land*	+167%	+341%	+ 25%	+129%	+156%

*Tilled plus permanent meadow
Source: U.S. Census, 1870 and 1880. Population and Agricultural Schedules, Door County, Wisconsin. Wisconsin State Historical Society, Madison, Wisconsin.

Table 2. Change in population and farm statistics between 1870 and 1880 for the combined five southern Door County townships most severely affected by the 1871 wildfires.

	1870	*1880*	*Percent Change*
Population	1800	4016	+123%
Households	328	692	+111%
Farmers	273	673	+147%
Farm land (acres)*	6614	17755	+168%

*Tilled plus permanent meadow
Source: U.S. Census, 1870 and 1880. Population and Agricultural Schedules, Door County, Wisconsin. Wisconsin State Historical Society, Madison, Wisconsin

tual development (after 1890) of dairy farming, which remains important today. In 1895, Xavier Martin wrote that "it is a beautiful sight to see fine crops of wheat, rye, barley, and oats covering fenceless and stumpless fields with an even height along the highways. The wilderness of 40 years ago begins to look like the fields of Belgium. . . ." (X. Martin 1895).

Conclusion

Several factors contributed to the outbreak of wildfires that destroyed Williamsonville and other villages in northeastern Wisconsin on October 8, 1871: wasteful logging practices, summer drought, low relative humidities just prior to the fires, and, on the day of the fires, a weather pattern that favored the region with moderate southwesterly winds.

But perhaps the most devastating aspect of the wildfires was the spawning of intense fire vortices. Based on vivid eyewitness accounts, it appears that fire vortices set spot fires ahead of the main infernos, thereby accelerating the progress of the wildfires and producing isolated pockets of destruction. From an historical perspective, the wildfires altered the economy of the region— especially in southern Door County where the fires meant the end of lumbering and spurred the development of agriculture.

Acknowledgments

Endnotes

[1]During the summer of 1988, in perhaps the worst wildfires since 1872 (Romme and Despain 1989), more than two million hectares of U.S. forest land burned including about 290,00 hectares in Yellowstone National Park. By contrast, in an average year, 130,000 wildfires burn over about one million hectares of U.S. land (Albini 1984).

[2]The North Central Forest Experiment Station (East Lansing, Michigan), has produced an excellent videotape, "Vortices in Wildland Fires," which includes dramatic footage of a variety of vortices spawned by wildfires.

[3]An important difference between urban fire storms and forest fires is the fact that the former tends to be stationary while the latter are in motion.

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Spectral confusion by Hummingbirds and the Evolution of Red Coloration in their Flowers: A New Hypothesis (Müllerian mimicry/wavelength discrimination/shade/color name)

Robert Bleiweiss

Abstract. *Red is the predominant color among mimetic hummingbird-pollinated flowers in North America. Recent experimental studies suggest that the ability of hummingbirds to discriminate among different wavelengths is poorest in the long (red) end of the spectrum. I propose that red is the best signal for the mimetic flowers precisely because the hummingbirds' poor discrimination of long wavelengths makes them more likely to mistake flowers of slightly different shades of red as being subjectively similar; spectral confusion favors both the initial convergence and subsequent maintenance of mimicry. Since the effectiveness of floral color in attracting pollinators is a function of both the probability that the flower will be seen (conspicuousness) and that it will be recognized as a good food source (mimetic advantage), the relative conspicuousness of red against green foliage may complement red's mimetic advantage. The hypotheses that red hummingbird flowers have evolved because of an innate preference by hummingbirds for red, or because red is inconspicuous to insects, are not supported by available evidence. Poor discrimination of long-wavelength signals may also explain why red predominates among other mimetic prey of birds, such as in mimicry rings of noxious butterflies.*

T he convergent flower structure and red coloration of the North American hummingbird-pollinated flora presents an evolutionary puzzle because it provides an exception to the general pattern that interspecific competition for the services of pollinators leads to character divergence and pollinator specificity among sympatric plant species (Brown and Kodric-Brown 1979). Grant (1966) proposed that North American hummingbird-pollinated flowers are analogous to Müllerian mimics and have evolved convergent structures and red color because often than to 590 nm (yellow-orange). They tors, hummingbirds, outweigh the advantages of pollinator specificity. Hummingbirds must learn what plants provide a nectar reward. Grant suggested that the migratory habits of temperate hummingbirds make floral convergence beneficial for both bird and plant; a common color would increase the rate at which hummingbirds learn appropriate food sources in new areas and hence, the probability that any plant with flowers of the same color will be visited and pollinated by a hummingbird (Grant 1966; Grant and Grant

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1968). Brown and Kodric-Brown (1979) have provided convincing evidence for Grant's hypothesis that the similar appearance of the North American hummingbird-pollinated flora is due to mimetic convergence.

It is less clear why these plants have evolved red as their typical color. Hummingbirds have excellent color vision (Stiles 1976; Goldsmith and Goldsmith 1979). All previous explanations of why red is the predominant floral color in North America incorporate in some way the notion that hummingbirds more readily discriminate red, but each presents some difficulties. The hypothesis that hummingbirds are innately attracted to red because of a special property of their neural apparatus (Faegri and van Der Pijl 1979) has been disproved by experimental evidence that hummingbirds learn color preferences through their experience with the best food sources (Grant and Grant 1968; Stiles 1976; Bené 1945; Wagner 1946; Lyerly et al. 1950; Collias and Collias 1968; Miller and Miller 1971). The hypothesis that red is a good attractant color because hummingbirds perceive it as conspicuous (i.e. contrasting) against green foliage (Grant 1966) is based on human perceptions, which may not apply to hummingbirds. The currently favored hypothesis that red color prevents nectar-robbing insects, (which do not pollinate the flowers), from finding the plants (Grant 1966; Raven 1972) is based on the fact that red is inconspicuous to most insects. However, insects may in fact frequent red hummingbird-flowers (Lyon and Chadek 1971; Feinsinger 1977; Carpenter 1978; Snow and Snow 1980; Gill et al. 1982; Page and Whitham 1985), which often possess other structures that appear designed to limit the foraging efforts of insects (Faegri and Van Der Pijl 1979; Gill et al. 1982; Bolton and Feinsinger 1978; Stiles 1981; Feinsinger 1983). Such features would be superfluous for red hummingbird flowers if insects could not find them. Furthermore, at least some of these visitors, namely butterflies, are obligate nectar-feeders that can distinguish long wavelengths as a distinct hue (Swihart

1963, 1965, 1967; Swihart and Gordon 1971).

In this report, I suggest a new "confusion hypothesis" for the evolution of common red color based on a previously unconsidered property of color vision: wavelength discrimination. I summarize evidence that hummingbirds actually discriminate poorly *among* long (red) wavelengths, and I argue that poor discrimination of long-wavelength signals facilitates the mimetic advantage of the common color because hummingbirds are more likely to mistake red flowers of slightly different shades as being subjectively similar. I assume, as have others (possible reasons given in Brown and Kodric-Brown 1979), that the relative benefits of mimetic convergence outweigh any costs associated with lack of pollinator specificity. My explanation addresses the more specific question: given that the plants are selected to converge, what floral color will be favored? Data available from studies of hummingbird visual physiology and behavior supports my "confusion hypothesis."

Wavelength Discrimination by Hummingbirds

Color discrimination ability is usually measured based on some criterion of reliability of discrimination, which, when applied for all wavelengths throughout the spectrum, generates a characteristic function that describes how discrimination varies with wavelength. Goldsmith et al. (1981) generated a spectral discrimination function for black-chinned hummingbirds (*Archilochus alexandri*) by first training them to receive a nectar reward at feeders illuminated by a monochromatic light, and then testing their ability to distinguish this light from another such light of equal brightness but with a spectral separation of 10 nm. They tested the response over the range of the human visual spectrum (410 nm to 650 nm) to generate a discrimination function. Although the function does not give information about the minimum wavelength difference that the birds can de-
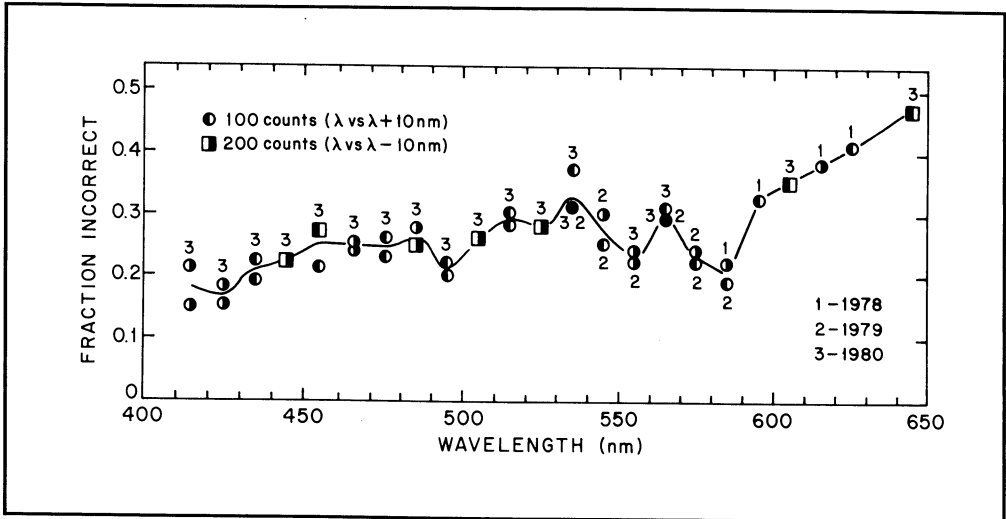
Fig. 1. Goldsmith et al's (1981) wavelength-discrimination function for the black-chinned hummingbird (Archilochus alexandri). Birds were trained to feed at bottles containing 25% sucrose mounted in front of a glass disc illuminated by the training wavelength (λ). Birds were then presented with two bottles illuminated by the training wavelength, and two bottles illuminated by the test wavelength (λ ± 10 nm). The function measures the fraction of incorrect choices for the two stimuli of monochromatic light separated by 10 nm. In the function, the points along the abscissa are plotted midway between the training and test wavelengths. The training wavelength lay 5 nm to the shaded side of the data symbol.

tect (the so-called just-noticeable difference), it does provide a relative measure of wavelength discrimination; where the birds make more errors, their wavelength discrimination is poorer.

Surprisingly, Goldsmith et al. (1981) found that the birds' ability to discriminate two stimuli was best at shorter wavelengths and decreased roughly monotonically toward longer wavelengths (Fig. 1). In particular, the birds' ability to discriminate two stimuli decreased dramatically for wavelengths longer than 585 nm, the region in which the human sensation of orange-red begins (Jacobs 1981). Thus, hummingbirds' poorest powers of color discrimination are in the orange to red range of the spectrum. Data on discrimination also make it possible to evaluate whether hummingbirds see as a single hue, i.e. a "color name," the range of wavelengths that we call red. Hues, and the range of wavelengths they encompass, are perceptual categories rather than objective physical standards. Thus, the

common color "red" would not be of evolutionary significance if hummingbirds distinguished two or more hues within the region of the spectrum we perceive as red (Table 1). Although by definition color-naming functions cannot be described for non-human animals, Goldsmith and Goldsmith (1979) found that, in making spontaneous choices, the hummingbirds' experience with 620 nm (red) was generalized to 650 nm more often than to 590 nm (yellow-orange). They

Table 1. Spectral limits of human hue "color names"[1]

Color Name	Wavelengths (nanometers)
Violet	400–440
Blue	440–500
Green	500–570
Yellow	570–590
Orange	590–610
Red	610–700

[1]See Begbie, G. H. 1973.

concluded that 590 nm probably falls close to a hue border and that hummingbirds delimit hues at long wavelengths in a manner similar to primates, whose hue border for orange begins at 590 nm (Table 1).

In summary, it appears that human "red" corresponds to a sensation that hummingbirds also perceive as a single hue category, and that discrimination among "red" wavelengths by hummingbirds is poorer than that among wavelengths of other hues. These results are most likely to apply to all of the hummingbird genera that regularly breed in North America (*Archilochus, Selasphorus, Calypte, Stellula*) because all of them are closely related (Zusi and Bentz 1982).

Consequences for the Evolution of Mimicry

In Müllerian complexes of distasteful prey, mimicry is advantageous because the probability that any given individual will be sampled decreases as the number of mimetic species increases. Hummingbird flowers differ from classical Müllerian mimics, of course, in that the flowers advertise their palatability so they can be sampled more often. The selective basis for mimicry among either noxious or palatable prey is the same, however. In both contexts, convergence increases the rate at which the animal learns to associate the signal with a stimulus. A hummingbird that has sampled a nectar-ladened flower of a particular shade will seek out and pollinate similar-looking flowers. Thus, mimicry benefits the plant by increasing their reproductive success and benefits the bird by reducing their costs of seeking out and testing potential food sources.

I propose that poorly discriminated phenotypes will be favored to evolve as mimics, both during the initial phase when mimetic resemblance is first evolving, and during subsequent evolution of the complex. In mimicry, the mimics gain some advantage through their resemblance to another organism, the model, by exploiting the learning capacities of some animal, usually termed the "signal

receiver" (Turner 1977). Fisher (1927, 1958) pointed out that the mimetic advantage can depend on the subjective perceptions of the signal receiver. I argue that discrimination ability is the key subjective element driving the evolution of mimetic color among the hummingbird-pollinated plants.

According to standard models for the evolution of mimicry (Turner 1977), a mimic can evolve initially if a mutant phenotype arises that achieves sufficient resemblance to the model such that it overcomes any counterselection for other functions (in the present case, distinctness of floral display that might serve to reduce competition with other plants for the services of pollinators). It is evident that the mutant does not have to be an exact physical replica, but only that it must fall within the range of phenotypes that the signal receiver considers subjectively similar. For hummingbird-pollinated plants, this stage will be influenced by the visual discrimination capacities of the hummingbirds. As phenotypes (wavelengths) are more likely to be confused at the long (red) end of the spectrum, the production of a mimetic mutant is more likely to occur for red models. In other words, there are more mutant phenotypes that would confer a mimetic advantage in the region of poor discrimination. Conversely, the production of mimetic mutants of non-red models is less likely.

Alternatively, two plants might by chance alone already resemble each other sufficiently well that a major mutation would not be necessary to confer some mimetic advantage (Turner 1977). The chance of being confused will be greater where the range of suitable mimetic phenotypes is greater, namely, in the region where the signal receiver's powers of discrimination are poorest. Thus, for hummingbird-pollinated plants, the chance for this fortuitous resemblance will again be greater in the long (red) region of the spectrum.

As the Müllerian advantage increases in direct relation to the abundance of the mimics (Turner 1977; Fisher 1927, 1958), then the actual advantage conferred through Müllerian resemblance will be inversely related to

the discriminatory powers of the signal receiver. Poor discrimination leads to the confusion of more spectral phenotypes, which therefore make up a greater proportion of the total population, and hence should gain proportionately in mimetic advantage at any stage in the evolution of mimicry. By these arguments, red facilitates the mimetic function of the common color and should be favored when the plants are under selection leading to a convergent appearance.

Discussion

The "confusion hypothesis" predicts that hummingbirds will learn food sources associated with slightly different shades (wavelengths) of red faster than with a similar array of shades centered in a different hue. Goldsmith and Goldsmith (1979) observed that red (620 nm) and green (546 nm) stimuli were learned with equal rapidity. This finding does not refute my prediction because confusion should favor rapid learning only among slightly different shades; single shades of any hue should be learned with equal speed. The hypothesis also predicts that variation in shade (wavelength) among the mimetic flowers will not be reduced below what hummingbirds can discriminate, so red flowers should vary greatly in their physical wavelengths. I am unaware of any data in the literature that pertain to these two predictions, which I am endeavoring to test.

The effectiveness of floral color in attracting pollinators is no doubt a function of both the probability that the flower will be seen (conspicuousness) and the conditional probability that the bird will recognize it as a good food source (mimetic advantage). Since hummingbirds are able to discriminate green (560 nm) from orange (590 nm) and red (620 nm) lights almost completely (Goldsmith and Goldsmith 1979), they no doubt perceive red as conspicuous against green. Therefore, the hypothesis that red is favored because it is easy to discriminate from the background of middle wavelength (green) foliage, i.e., conspicuousness, may complement the mimetic advantage.

Evidence that insects visit red flowers does not by itself refute the hypothesis that red has evolved to limit nectar-robbing by them, as the device need not be completely effective to be selectively favored. Thus, red may be a particularly good advertisement for hummingbird flowers under selection to converge just because it is conspicuous against green, inconspicuous to insects, and easily confused with other shades of red. Given the suitability of hummingbirds to experimental manipulations of behavior, it should be possible to dissect the relative contributions of these potential benefits.

Should poor discrimination of long wavelengths prove to be typical for insectivorous birds, then the "confusion hypothesis" may also explain the predominance of red among aposematic avian prey such as butterflies that are Müllerian mimics (Rettenmeyer 1970). This would indicate that red's primary value is as a mimetic signal.

Acknowledgments

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Glaciated Karst Terrain in the Door Peninsula of Wisconsin

Carol J. Rosen and Michael J. Day

Abstract. *Glaciated karst terrain, which is poorly documented in the United States, is well developed in the Door Peninsula of northeastern Wisconsin. The peninsula is a southeastward-dipping cuesta developed on the Silurian Niagaran dolomite. Wisconsinan glacial plucking east of the escarpment produced glaciokarst features including alternating steps and risers (schichttreppenkarst) and extensive dolomite pavements. Pre- and post-glacial karst landforms include enlarged crevices (grikes), sinkholes, and caves. Staircases and pavements are predominantly south- and east-facing and are particularly well developed on the Brussels Hill outlier. Their distribution is as predicted by the general model of northwest-southeast ice movement. Many of the smaller karst landforms are postglacial, although shallow features may have an important inherited component, and the larger sinkholes and the caves may antedate Wisconsinan glaciation. Much of the postglacial karst development is in the Burnt Bluff Formation on the western side of the peninsula where the hydraulic gradient is steepest, joints are dilated, and the drift is thinnest. Regional joint sets at 25, 70, and 155 degrees have strongly influenced cave and sinkhole development.*

Although large areas of carbonate bedrock in the United States experienced the effects of Pleistocene glaciation, glaciokarst—characteristic terrain developed through glaciation of karst landscape—is poorly documented. In many areas glaciokarst is limited because the limestones or dolomites are mantled by thick, often carbonate-rich glacial deposits. These mask any preglacial karst, as well as the effects of glacial erosion, and hinder postglacial karst development. Nevertheless, glaciokarst is present in some areas, particularly where drift deposits are thin. In this paper we call attention to one major area of glaciated karst terrain developed on dolomites in northeastern Wisconsin and present some initial results of studies of the karst landforms.

The Regional Setting

The Door Peninsula, which extends some 100 km into Lake Michigan and ranges from 5 to 30 km wide (Fig. 1), is a cuesta developed on the Silurian-aged Niagaran dolomite (Sherrill 1978). The Niagaran Series is approximately 107-m thick and consists dominantly of light gray, medium to coarse-grained, thin-bedded, fossiliferous dolomites. Bioherms are common and are expressed topographically in outliers such as Brussels Hill, the highest point on the peninsula at 260 m (Thwaites and Bertrand 1957).

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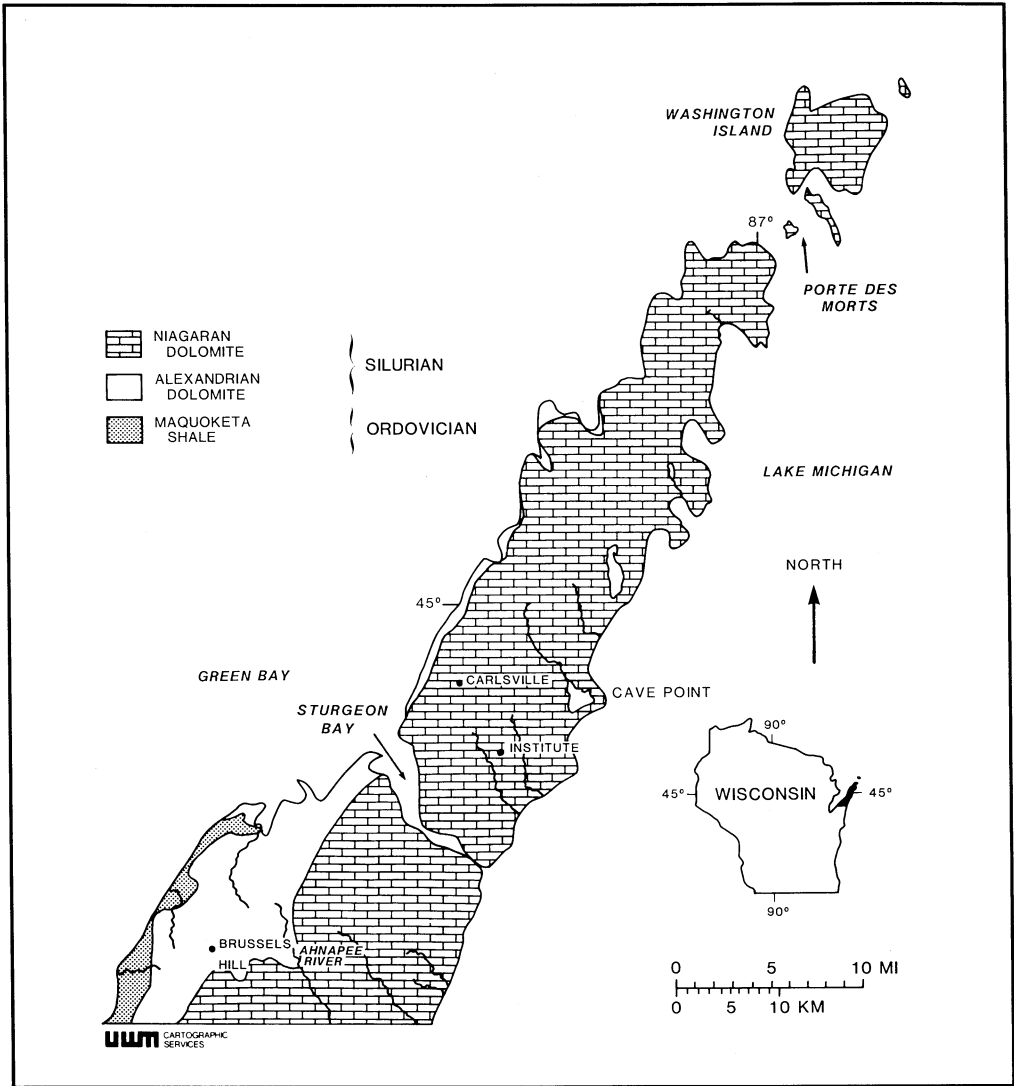
Fig. 1. Map of Door County (adapted from Sherrill 1978).

On the western, Green Bay side of the peninsula the Niagara Escarpment rises up to 79 m above present lake level; the cuesta backslope, sloping to the southeast at generally less than one degree, forms the main body of the peninsula. Headlands, talus-strewn bluffs, and island outliers characterize the west coast; the eastern coast is gently sloping and has sandy beaches and dunes.

The peninsula is traversed by a series of five northwest-southeast-trending lowlands, the most conspicuous being Sturgeon Bay,

the Porte des Morts channel, and the Ahnapee River Valley (Fig. 1). These probably represent preglacial river valleys modified by glacial and meltwater erosion (Deller and Stoelting 1986; Johnson 1987).

The Door Peninsula was glaciated extensively during the Pleistocene, latterly by two major advances of the Green Bay Lobe during the Wisconsinan Stage: the Port Huron advance during the Woodfordian Substage (22–13ka) and, following the Twocreekan Interstade, a subsequent advance during the
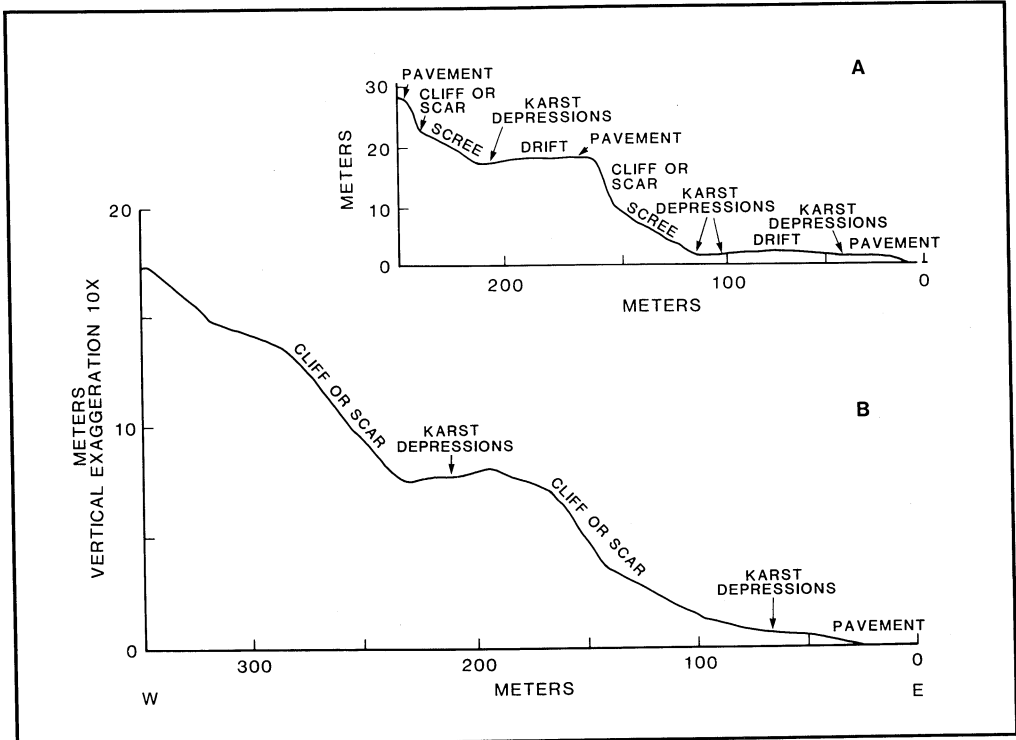
Fig. 2. Stepped glaciokarst profiles. A in Yorkshire, England, after Sweeting (1972), B on the east side of Brussels Hill.

Greatlakean Substage (11.5–10ka) (Schneider 1981, 1986, 1989). Ice movement was predominantly north-south or northwest-southeast (Thwaites and Bertrand 1957; McCartney and Mickelson 1982; Schneider 1981, 1986, 1989; Need 1985). The peninsula is covered by a thin veneer, mostly less than 1 m thick, of unstratified sandy till, much of which contains more than 25% calcium carbonate (Thwaites and Bertrand 1957). The drift thickens towards the southeast, where there is a cover of red clayey till and where there are moraines and some drumlins. Locally there are lacustrine and fluvial deposits, plus some outwash, beach, and dune sands (Deller and Stoelting 1986).

Mean annual precipitation is 690 mm, and mean annual daily maximum and minimum temperatures are respectively 11.6 and 1.3 degrees Celsius (Link et al. 1978). Surface water infiltrates into the dolomite aquifer very rapidly, giving rise to serious groundwater

contamination (Sherrill 1975, 1978; Wiersma et al. 1984; Johnson 1987). Groundwater is calcium-magnesium-bicarbonate dominated, with a mean total hardness (as $CaCO_3$) of 299mg/l (s = 66.1, n = 23) (Sherrill 1978).

The Glaciated Karst Terrain

The Door Peninsula glaciokarst is similar to that developed on the Niagaran dolomite in the Bruce Peninsula of Ontario (Cowell 1976; Cowell and Ford, 1980, 1983) and has many of the characteristics of the "classic" glaciokarst of western Europe (Williams 1966; Sweeting 1972). The principal diagnostic features are the numerous nearly horizontal ledges and benches alternating with steep steps, or risers (Fig. 2). The ledges are developed on bedding planes that have been accentuated by intense glacial scouring and plucking on the down-ice side of the cuesta. East of the escarpment, the main body of the peninsula

decreases in elevation via a series of large benches that attain widths of over 1 km and cover areas up to 10 km². The benches are drift mantled, and bedrock is exposed usually only where drift has collapsed into widened joints, locally giving rise to sinkholes. Between the benches, the steps, although generally obscured by drift, are as much as 10 m high.

Superimposed upon the large benches, and most evident on steeper east-facing slopes, are smaller ledges and steps that together make up distinct staircases—the *schichttreppen-karst* of Bögli (1964). These ledges range typically from 5 to 20 m in width, and steps range from 0.5 to 10 m high. On ledges where the drift cover is thin, there are exposed bedrock pavements, some with striations, others bearing well-defined, dissolutionally-molded clints and grikes (Rosen 1984; Johnson 1987). The ledges also carry a variety of karstic depressions, which have been documented by Rosen et al. (1987) and by Johnson (1987), and in overall morphology the staircase assemblages bear a striking resemblance to European examples (Fig. 2).

The staircases are predominantly south- and east-facing and are best developed on the south- and east-facing sides of hills and valleys. This distribution provides independent evidence that supports the theory that ice movement was predominantly from northwest to southeast. Particularly well-developed staircases occur on the eastern flanks of the Brussels Hill outlier, along the western margin of Sturgeon Bay, and on the eastern coast of the peninsula, for example at Cave Point (See Fig. 1 for locations). At Brussels Hill well-defined pavements occupy areas up to 0.75 km² and achieve widths over 50 m (Rosen 1984). Risers, in part near-vertical but mostly veneered by talus, are 5 to 10 m in height (Fig. 2B). Pavements on the western side of Sturgeon Bay are up to 20 m wide, with risers 1 to 5 m high.

Glacier basal bulldozing, plucking, and abrasion erases shallow karst features (Ford 1987) and, since the staircases and pavements themselves are of glacial origin, the crevices and sinkholes developed on them are essentially postglacial in age. Most grikes terminate at the level of the first or second bedding plane beneath the surface, but perhaps 25% are deeper, suggesting that in part they may have been initiated prior to Wisconsinan glaciation. A certain proportion of grikes, at least in the master joint set, may survive glacial scouring (Ford 1987), and thus the postglacial pavements may have an important inherited component.

Larger karst landforms may also have survived glacial action, although the majority of sinkholes are small enough to have developed entirely during the Holocene. Some larger sinkholes may antedate the last glaciation, and some may have originated as glacial scour holes, although there is no firm evidence of this. Caves too probably antedate recent glaciations, although it seems unlikely that they are strictly preglacial, i.e. developed prior to all episodes of Quaternary glaciation. As yet there has not been sufficient analysis of cave deposits to provide a chronological framework.

Postglacial karst development on the stepped surfaces is influenced strongly by three major regional joint sets oriented at 25, 70, and 155 degrees (Sherrill 1978; Rosen 1984). Consistent joint sets throughout the Michigan Basin are attributed by Holst (1982) to Paleozoic folding and more recent tectonic stresses. The 25-degree joint set is expressed only rarely on the eastern side of the peninsula. At Brussels Hill 71% of all sinkholes (n = 61) follow a joint trace. Fifty-eight percent of sinkholes occur at three-way joint intersections, 21% at two-way intercepts, and 21% are on a single joint (Rosen et al. 1987). Caves also show this structural control, especially by the 70- and 155-degree joint sets. Paradise Pit Cave, at 554 m long, and Horseshoe Bay Cave, at 945 m long, are among the longest in Wisconsin (Hennings et al. 1972; Barden 1980). Brussels Hill Pit Cave, the deepest in the state at −28 m, is currently yielding a rich suite of Holocene faunal remains (Kox 1988).

Karst depressions on the stepped surfaces range from 0.6 to 12.0 m wide and from 0.15 to 3.0 m deep. At Brussels Hill, mean depression depth is 0.28 m (s = 0.07, n = 61). Large scattered depressions are evident in farm fields, where many have been filled in. In less-altered woodland areas most depressions are grouped in high-density lattice networks that reflect the closely spaced joint sets. At Brussels Hill densities are up to 8.7/100 m², and at Ledge Woods, west of Carlsville (Fig. 1), depressions occupy 95% of the surface of a 170 m² area.

Other karst features developed throughout the peninsula include swallets, which take runoff primarily from farm fields, and various types of karren (grooves, runnels, and solutional basins) (Rosen 1984; Johnson 1987). Enlarged joints, which are common where surficial deposits are less than 0.6 m thick, range up to more than 10 m in length and 0.8 m wide. Near Institute (Fig. 1) dissolution-widened crevices occupy about 0.4 km². Mean spacing of joints on the 70-degree azimuth is 3.1 m and that on the 155 azimuth is 5.1 m.

Many of the sinkholes, swallets, caves, and other karst landforms of the Door Peninsula are developed on the western side of the peninsula. This distribution reflects several factors (Rosen 1984):

1. Some karst features are developed preferentially in the Burnt Bluff Formation (Barden 1980), which outcrops at an elevation of about 190 to 215 m.

2. The hydraulic gradient is steepest close to the escarpment (see Cowell and Ford 1983).

3. Close to the escarpment, joints are dilated as a result of glacial unloading or ice-wedging (e.g., see Stieglitz et al. 1980).

4. The drift cover is thinnest on the western side of the peninsula. 96% of exposed karst features are in areas with less than 1.2 m-thick drift and 73% are developed where drift is less than 0.6 m thick (Rosen 1984).

Conclusion

The Door Peninsula is possibly the most impressive glaciated karst landscape in the United States. It contains a characteristic suite of glaciokarst landforms, including staircases and pavements, together with postglacial crevices and sinkholes, and probably preglacial caves. Development of the karst merits further study particularly because its environmental implications are now being fully realized. Distribution of the glaciokarst agrees with predictions based upon previous models of Wisconsinan ice movement. Most of the surface landforms are postglacial in age, although some may have characteristics inherited from karstification antedating the Wisconsinan glaciation. Caves and larger karst landforms may have been initiated prior to the last glaciation, but like the smaller features they too are oriented preferentially along the regionally dominant joints.

Acknowledgments

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The Photography of Alfred Charles Bonanno

"A genuine Artist with the compassionate eye" is how Studs Terkel has described Al Bonanno. The fifteen photographs that follow demonstrate not only that artistry and compassion, but the versatility and range of subject as well. Bonanno has long been known for his photographs of American Indians, and no collection of his work would be complete without some of them. Sixty-seven of these photographs have been selected by the International Center of Photography (New York) for use in its teaching program. Other of his photographs are in private collections in Japan, France, Kuwait, and the U.S. In addition, viewers can find his work in virtually every regional publication, many national newspapers, and in such magazines as *Time, Parade,* and *Sports Medicine.*

Bonanno's work is an intellectual and emotional tour de force. Irony, beauty, joy, love, celebration, dignity, loneliness, isolation, contentment, struggle, and rejection are leitmotifs throughout his photography making it complex and difficult to categorize. The emotional range of his work is seen when the joy of children playing with a wheelbarrow, or two brothers, or a grandfather with his granddaughter, is followed by the enormous emotions swirling around autistic children. And the love of a young girl for a woman in a nursing home is a stark contrast to the newly admitted resident who has not been able to remove his hat. When a child with a bouquet stands by the three-hundred-mile fence separating the Hopi and Navajo reservations, what is captured is more than what many words have conveyed.

Perhaps it is best to allow the viewer to venture into Bonanno's world with only this brief introduction. It is a journey well worth making, and *Transactions* is happy to make it possible.
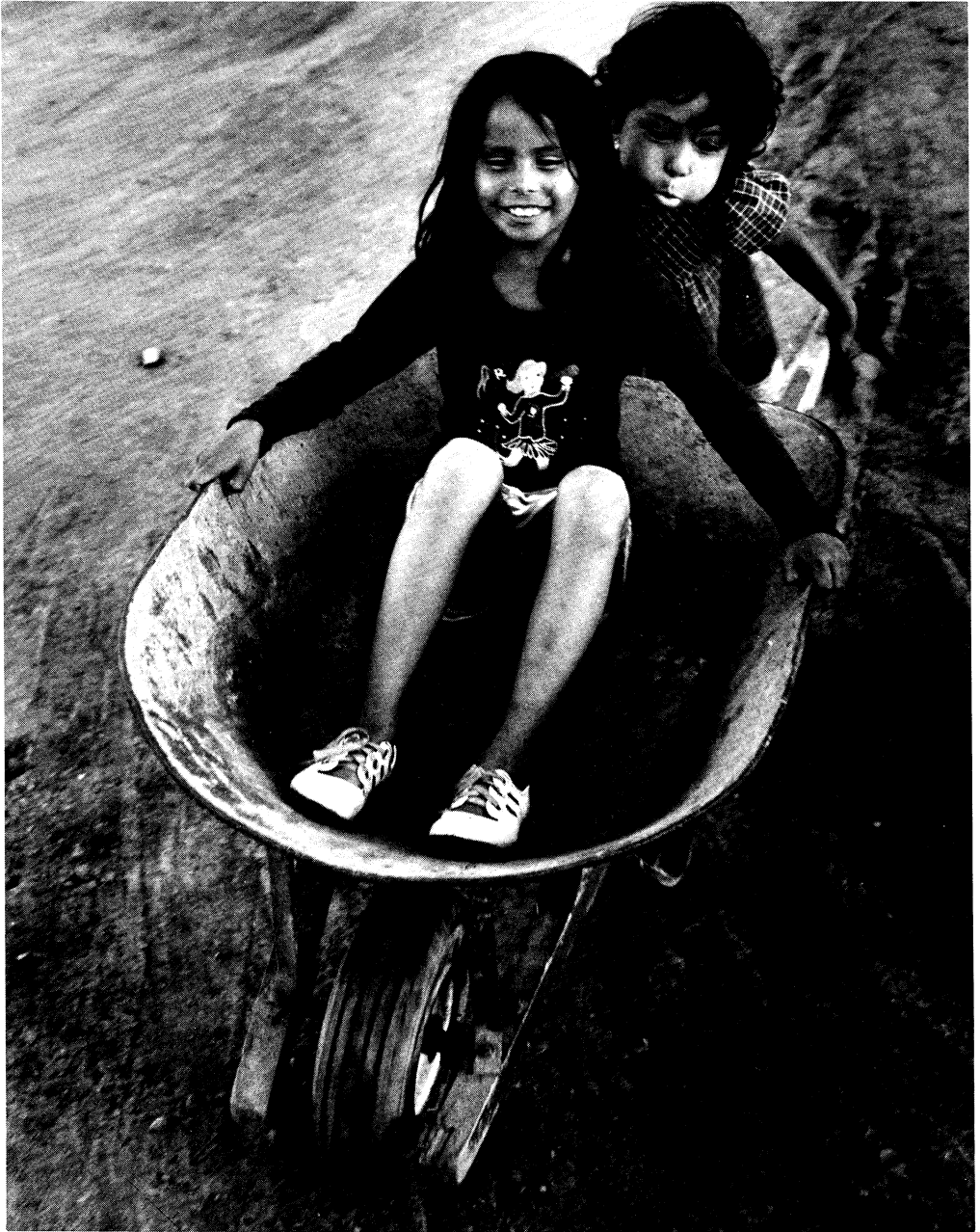
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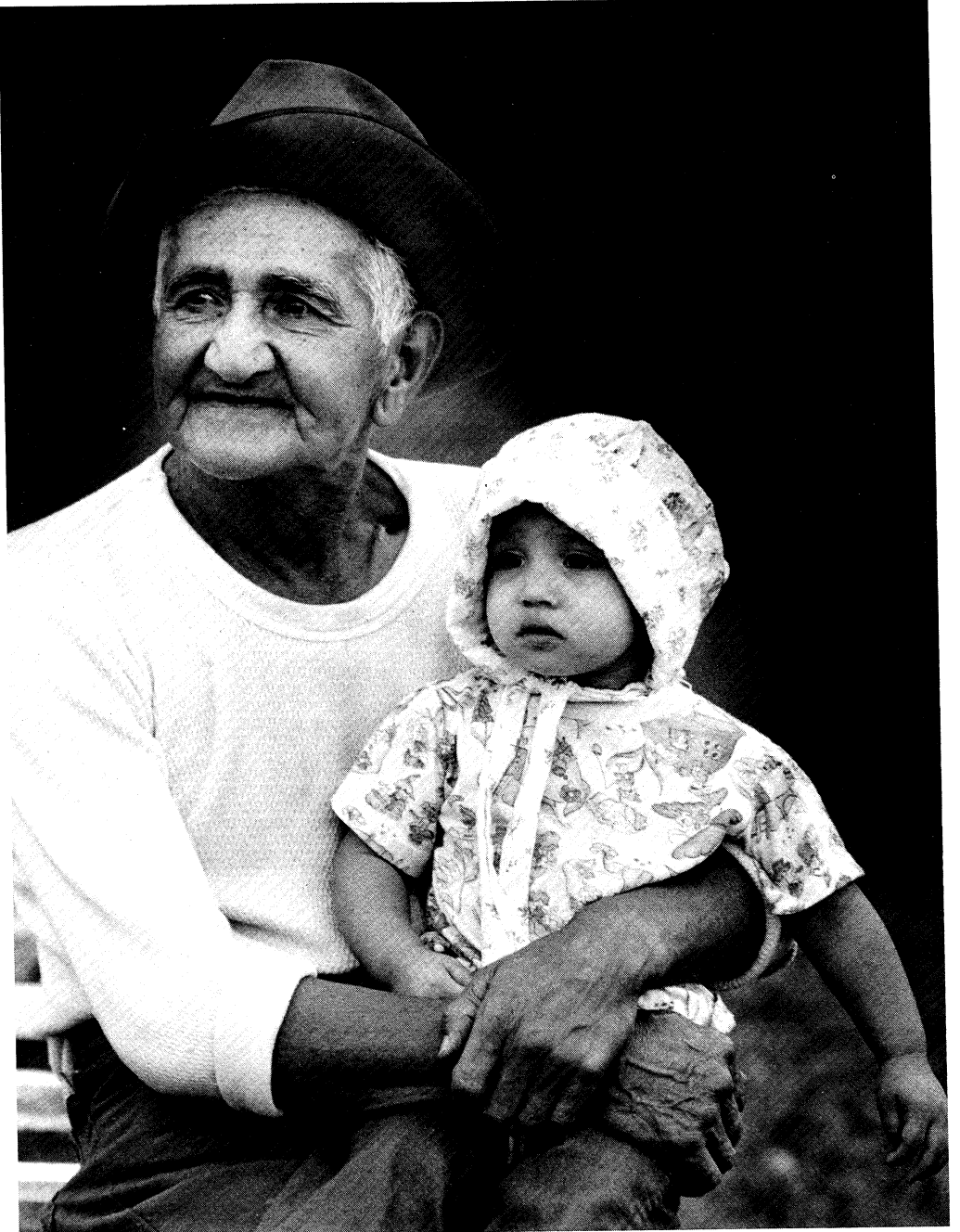
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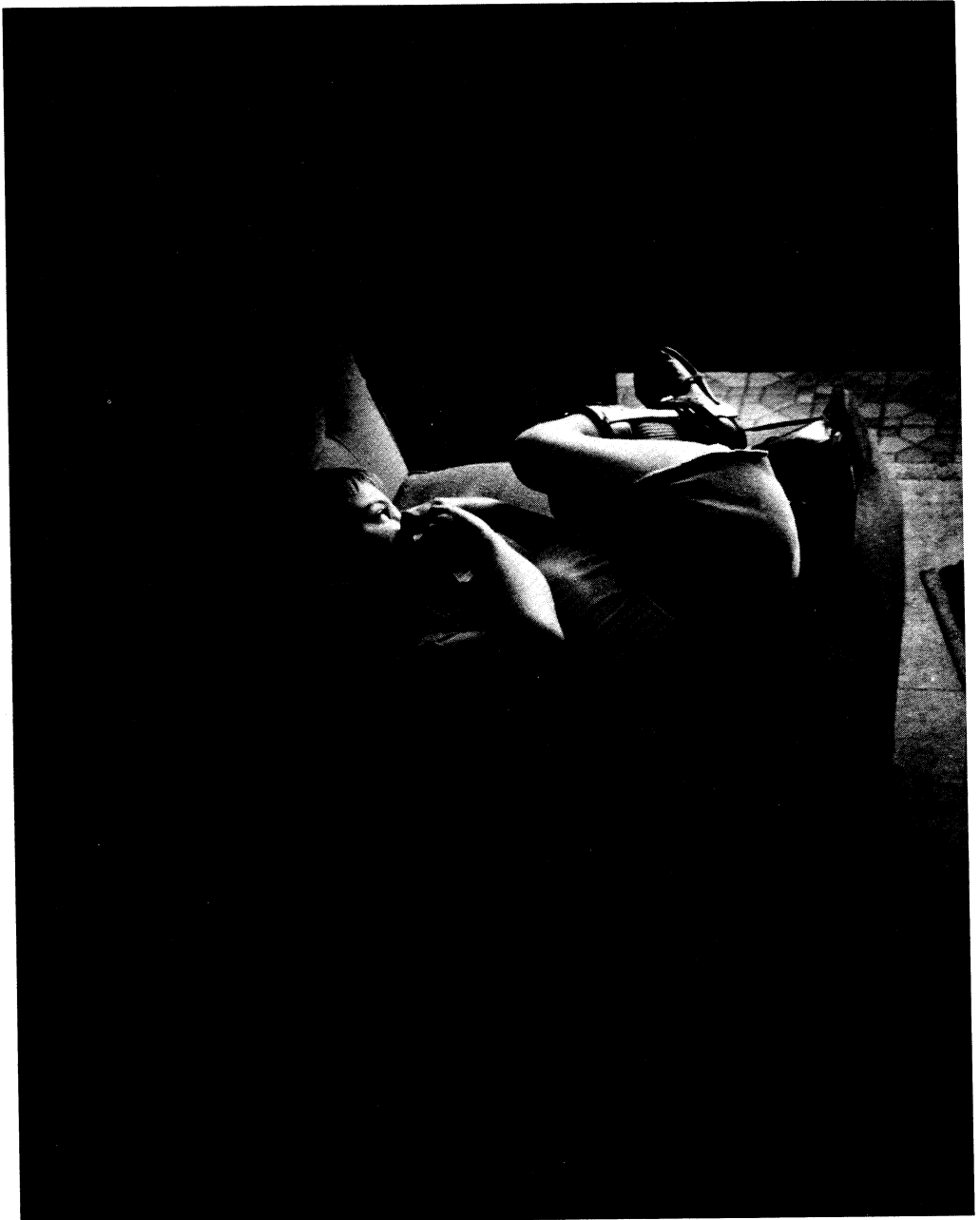
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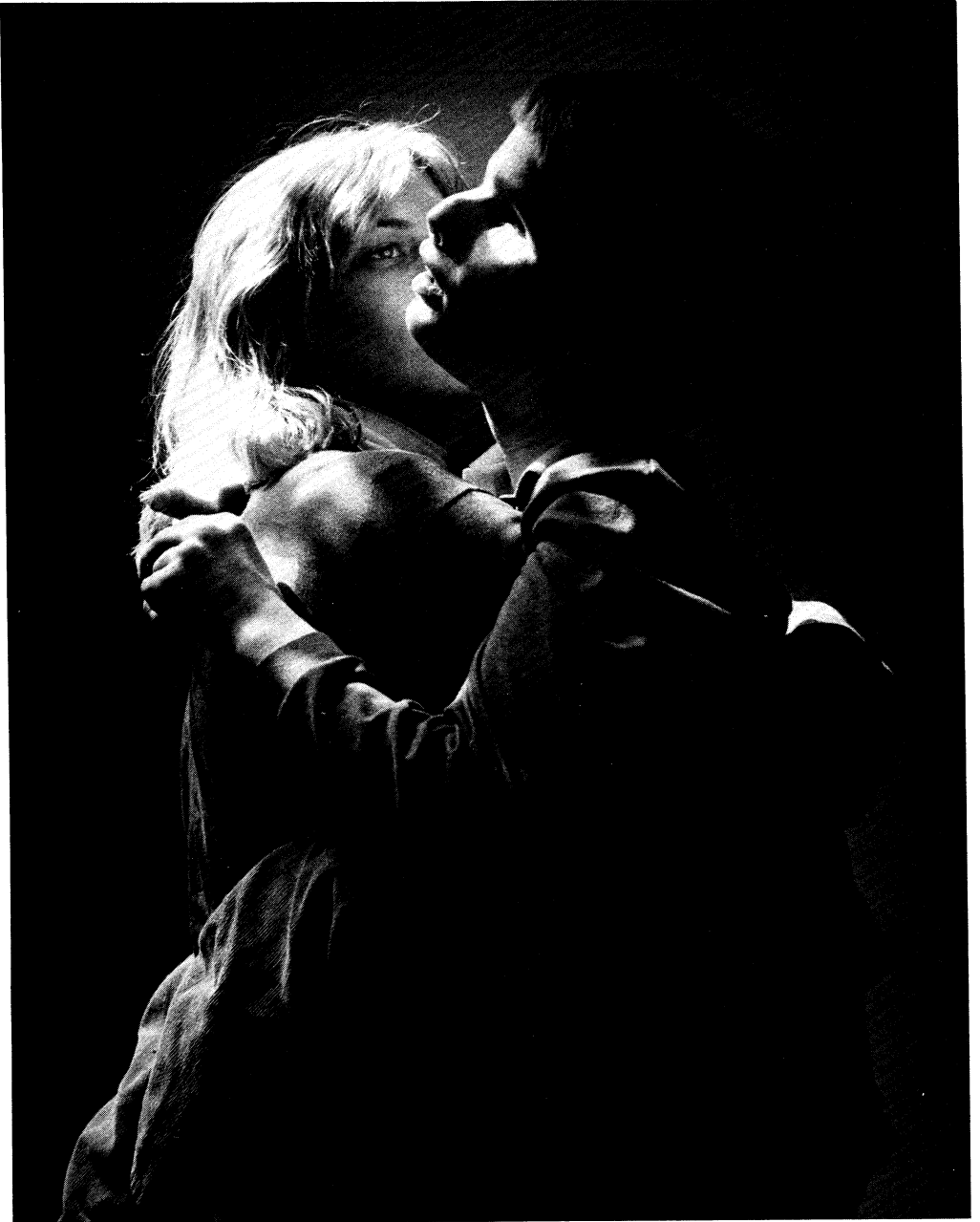
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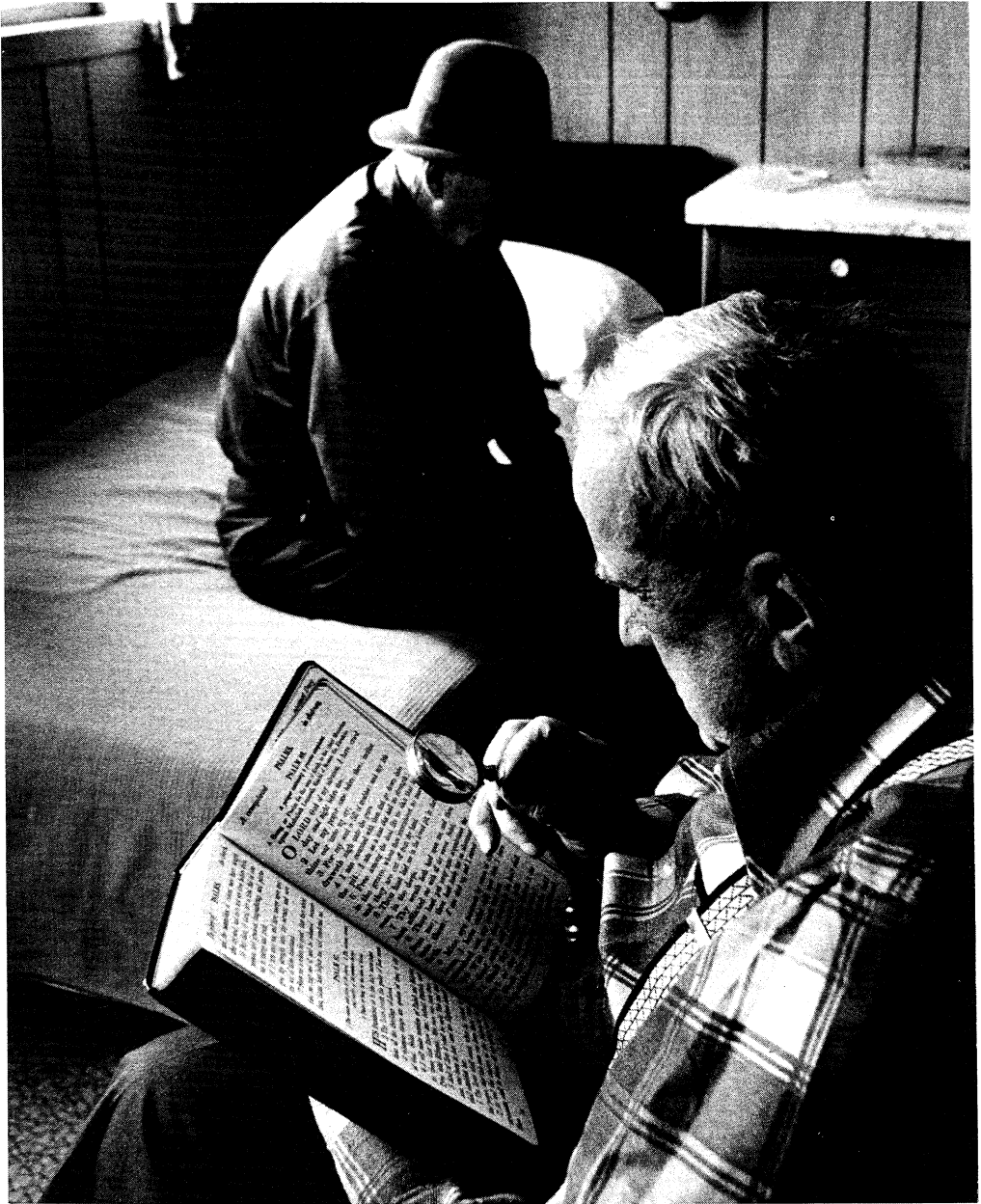
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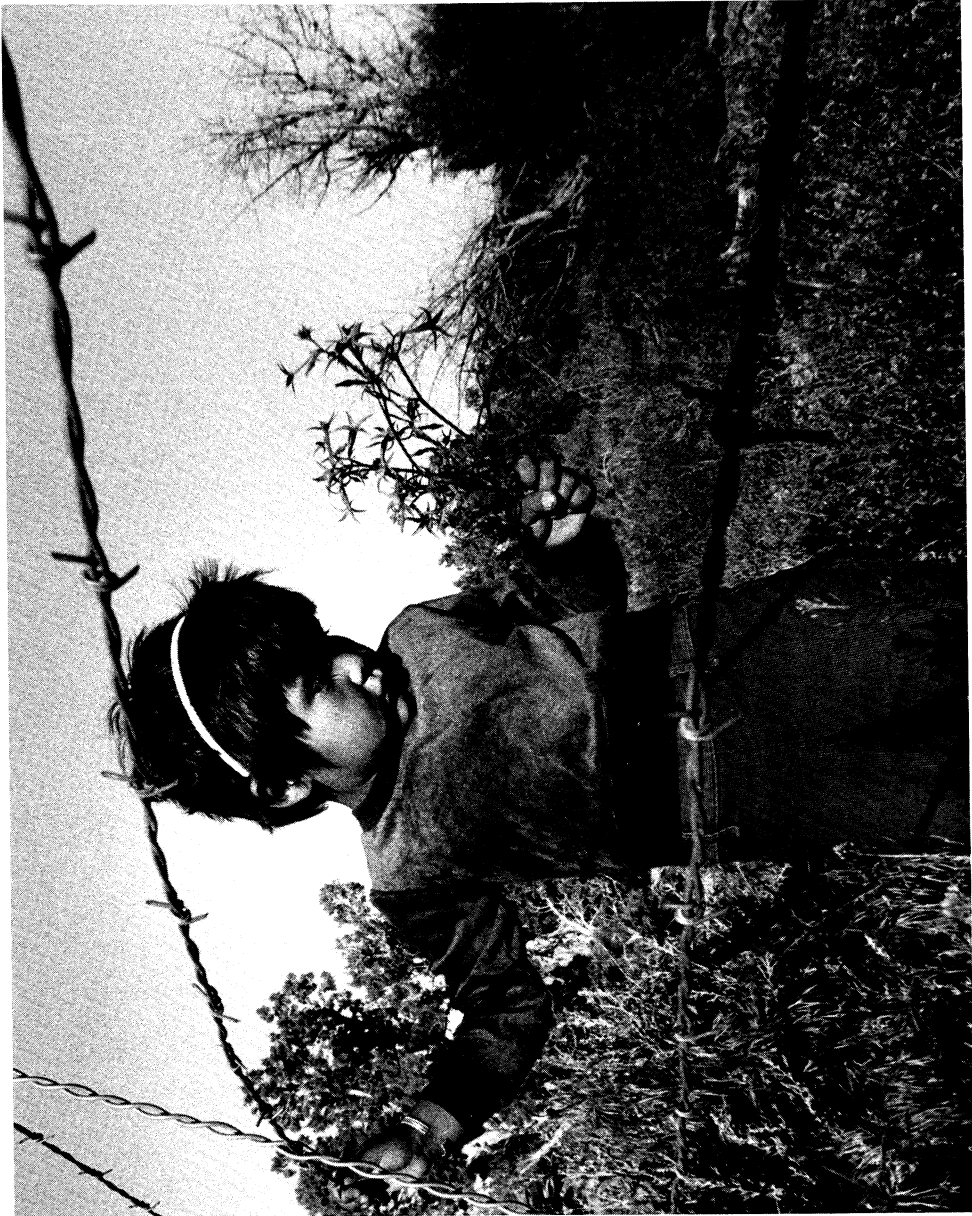
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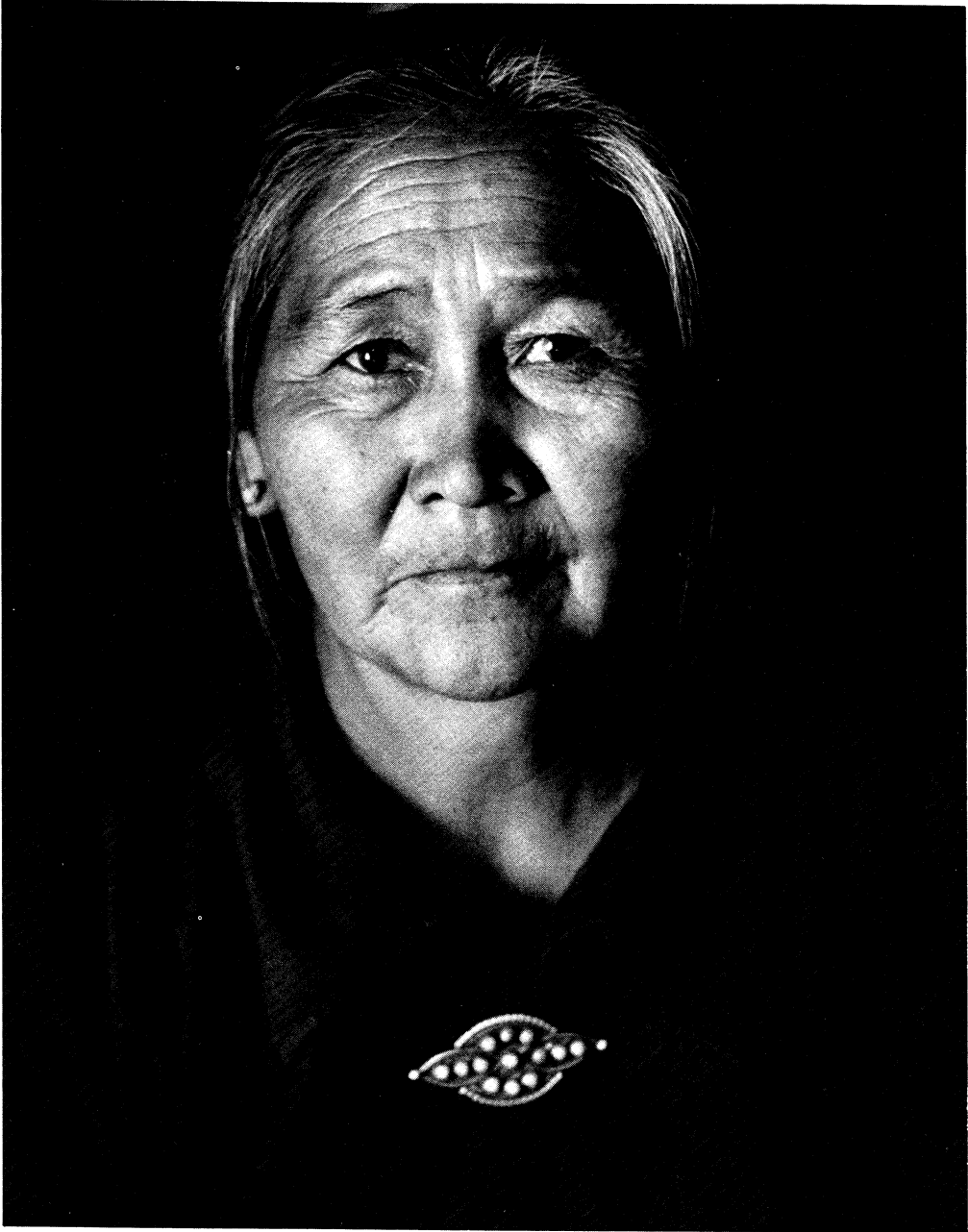
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The Bridegroom

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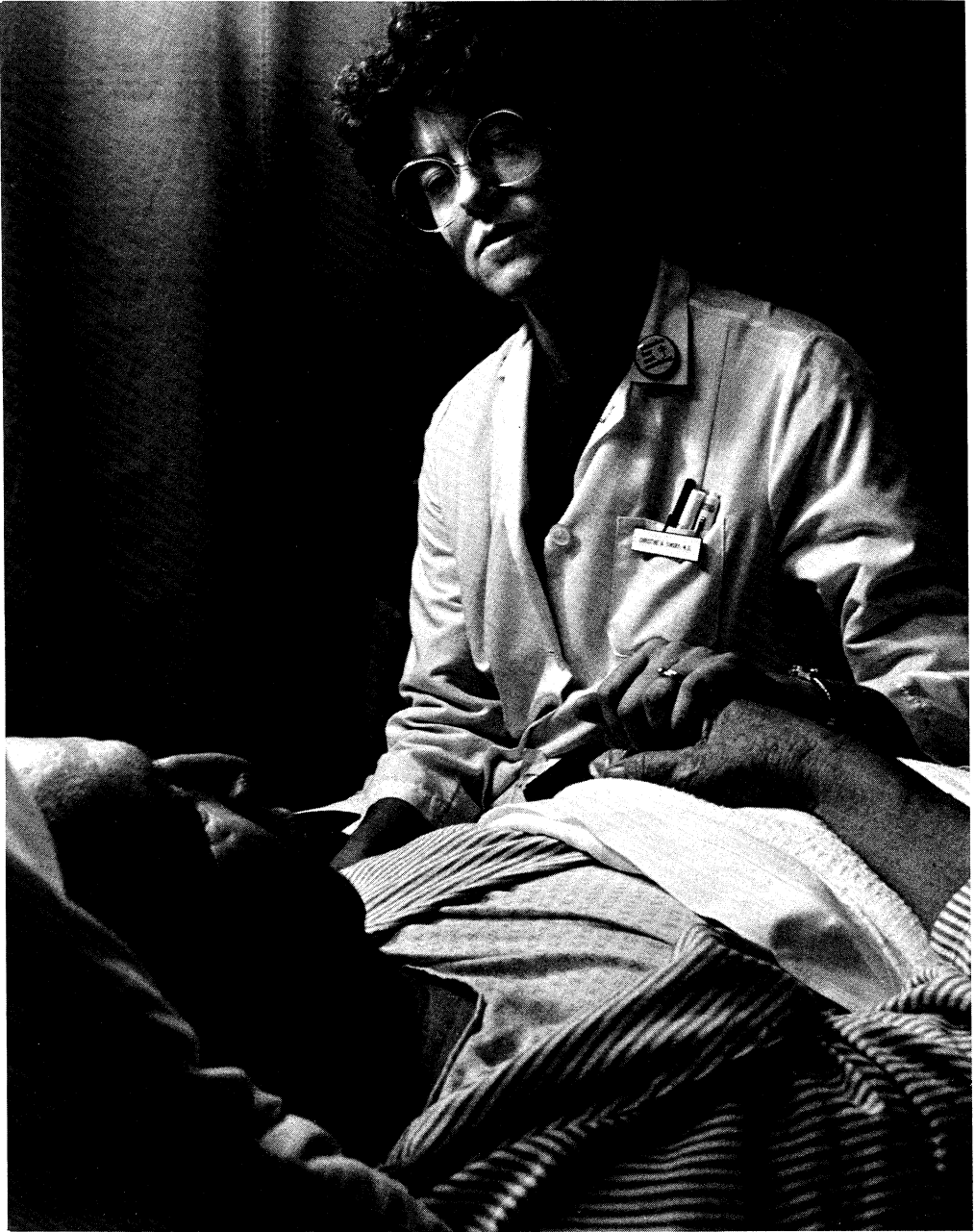
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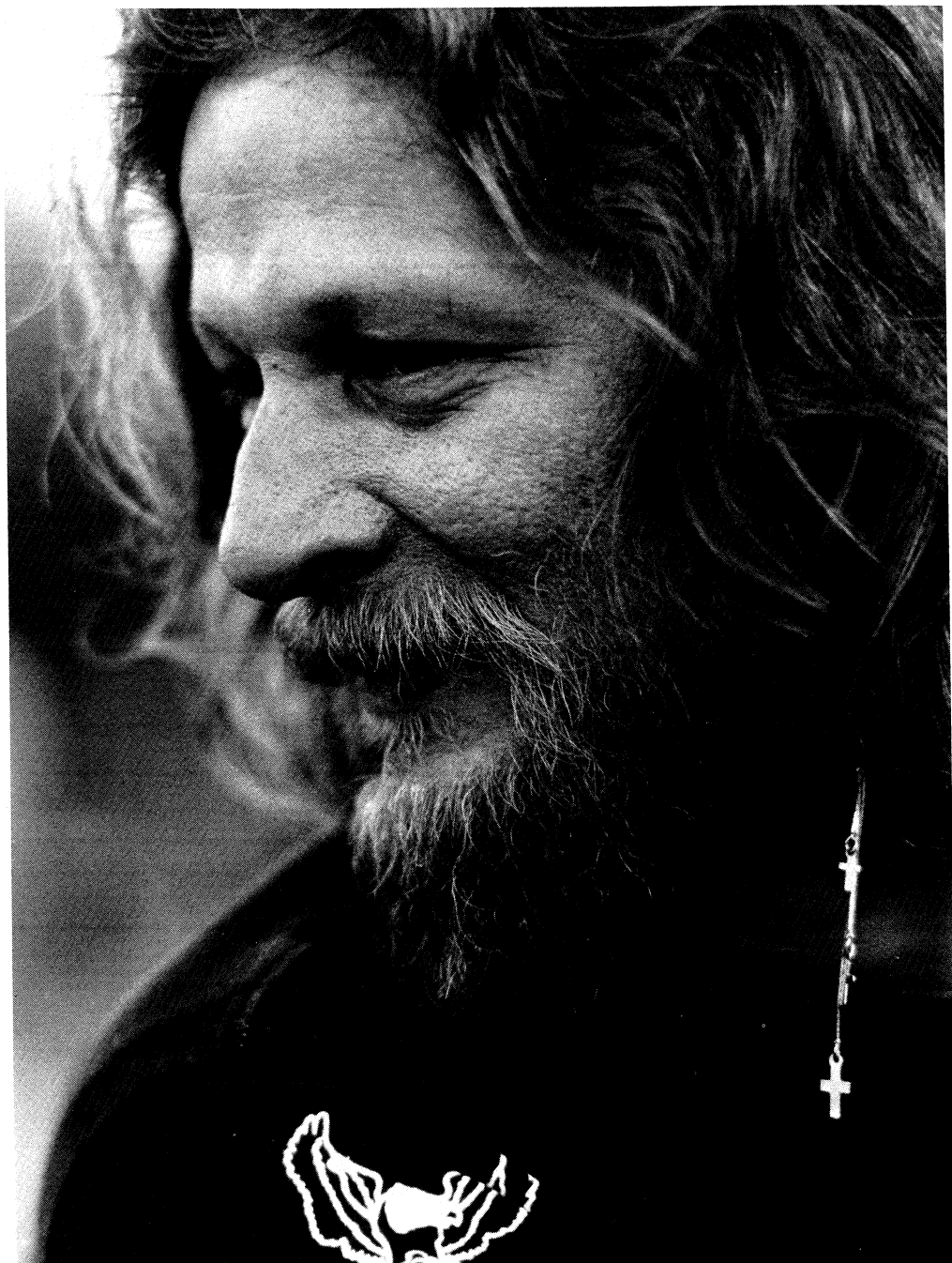
Ear Ring

Flag with 30,000 Miles on it

A New Station in Door County, Wisconsin, for the Rare *Iris lacustris* Nutt. (Dwarf Lake Iris)

Charles R. Hart

Abstract. *A new site for* Iris lacustris *Nutt., the rare Dwarf Lake Iris, in Door County, Wisconsin, is described.*

Recently, a fairly extensive population of *Iris lacustris* Nutt. was discovered in southern Door County, Wisconsin. Heretofore, the known range for this species in northeastern Wisconsin was somewhat disjunct, occurring to the south in Brown County and then reappearing north of Sturgeon Bay, Wisconsin, in Door County.

Iris lacustris Nutt., a Great Lakes endemic, is known only from Michigan, Ontario, and Wisconsin (Guire and Voss 1963; Voss 1972, p. 431). In Wisconsin this species is considered to be threatened and was recently elevated to the same status at the federal level as well (Harrison 1988). Prior to the discovery of the new site, the Dwarf Lake Iris had been found at a total of fifteen sites in two counties on Wisconsin's Door Peninsula (Harrison 1988). The southerly most site, in Brown County, was reported by Trick and Fewless (1984). The other extant sites are scattered to the north of Sturgeon Bay and were recorded by Makholm in 1986. For indigenous species as rare and local as this

one, any and all new stations are of significance in terms of recommending habitat management or other protection measures.

The newly discovered population is located in secs. 27 and 28 of T28N R25E in the Township of Nawewaupee. It occurs approximately 15 miles southwest of the nearest reported northerly Door County population and approximately 17 miles northeast of the southerly Brown County population. Representative voucher specimens of this population were taken (15 June 1989, Hart-13-89) and are housed in the herbarium/greenhouse at the University of Wisconsin Center—Manitowoc County.

At this locality, the *Iris* is closely associated with *Toxicodendron radicans*. The densest growth occurs in the preferred habitat for this *Iris* species, which is sandy or gravelly soil (underlain by Niagara dolomite) and open, although the plant occurs in partial shade of coniferous trees *(Thuja occidentalis)*, in mesic areas at the forest edge and along township roads or right-of-ways. The geological location of this population is in keeping with the prior documentation of Dwarf Lake Iris colonies occurring on land previously occupied by the postglacial Lake Nipissing (Makholm 1986).

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Acknowledgments

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Diel Periodicity of Movement and Feeding of Yellow Perch (*Perca flavescens*) in Lake Mendota, Wisconsin

John P. McCarty

Abstract. *Analysis of the spatial distributions of yellow perch in Lake Mendota, Wisconsin, indicated that diel movement patterns are more variable than previously reported. A series of gill-net samples from several different stations in the lake showed that a significant movement onshore at dusk and offshore at dawn occurs. The movement was more directed in the morning, and closer to the surface. This movement appears to be the result of a dispersal, biased towards the offshore areas, from nocturnal concentrations of perch in shallow water. Periods of directed movement are interspersed with feeding bouts and forays deeper into the water column. In the evening the direction of the movement is reversed and perch tend to concentrate inshore, where they can rest on the bottom at night. Diet analysis indicated that perch found offshore fed exclusively on* Daphnia *and* Leptodora, *but that perch captured in littoral areas consumed both planktonic and benthic prey.*

D iel activity cycles have been reported for a variety of freshwater fishes, including such well-studied species as yellow perch (*Perca flavescens*; Helfman 1981, Hanson and Leggett 1986), golden shiner (*Notemigonus crysoleucas*; Hall et al. 1979, Helfman 1981), walleye (*Stizostedion vitreum*; Helfman 1981), and bluegill and pumpkinseed sunfish (*Lepomis macrochirus* and *L. gibbosus*; Keast and Welsh 1968, Bauman and Kitchell 1974, Werner et al. 1977, Helfman 1981, Hanson and Leggett

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1986), yet the degree to which individual behavior affects population phenomena is not clear. For example, observed diel changes in the spatial distribution of a fish population could be due to a small portion of the population undergoing a highly directed, large scale movement or to a large portion of the population moving in a less directed manner. Diel migrations have been reported for many populations of yellow perch (Scott 1955, Emery 1973, Engel and Magnuson 1976) including the population in Lake Mendota, where fish move inshore at dusk and offshore at dawn (Hasler and Bardach 1949). Yellow perch travel in schools during the day. As in many freshwater fish species, these schools break up at dusk and reform at dawn the following day (Hergenrader and Hasler 1968, Helfman 1981). These patterns are based on observations made in a variety of ways, including direct observations by divers (Hasler and Bardach 1949, Helfman 1979), data from echosounding (Hasler and Villemonte 1953, Engel and Magnuson 1976), and from spatial

Fig. 1. A simple model of the daily behavior patterns of yellow perch in Lake Mendota, Wisconsin, summarized from the work of Hasler and Bardach (1949). This model includes a rapid, population-wide migration from nocturnal resting areas to day-time feeding areas. Dashed lines represent water depth contours. See Figure 2 for approximate horizontal scale.

distributions derived from gill-net sets (Hasler and Bardach 1949, Scott 1955, Engel and Magnuson 1976). In addition to movement patterns, feeding activity cycles are well known in yellow perch, with peaks generally reported before sunset and after sunrise (Keast and Welsh 1968, Helfman 1981, Hanson and Leggett 1986).

The general picture of perch behavior that emerges from this literature is that perch feed offshore, in schools, on zooplankton during the day with a feeding peak after dawn and another feeding peak before dusk. At dusk these schools move rapidly inshore, where the schools break up, and the perch settle to the bottom and remain inactive until dawn. At dawn the schools reform and move offshore again before the fish resume feeding. This activity pattern (Fig. 1) is commonly reported in books and reviews of yellow perch biology (Maclean and Magnuson 1977, Ney 1978, Brock 1985). There is, however, considerable variability in activity found both

between and within populations (Helfman 1979, Helfman 1981). In addition to finding groups of migrating perch, Hasler and Bardach (1949) and Scott (1955) both found non-migrating groups of perch. Tonn and Paskowski (1987) reported non-migrating subpopulations and indicated that some perch were migrating offshore at dusk. In addition, some groups of yellow perch are consistently found inshore feeding during the day (Engel and Magnuson 1976, Sandheinrich and Hubert 1984).

In this study I examined the daily behavior cycles of yellow perch in Lake Mendota by catching perch in gill-nets at several stations in the lake at different times of the day. Specifically, I have addressed three questions: 1) Is there evidence that the perch are undergoing a daily migration? 2) Is segregation by sex and age occurring? 3) Are these movement patterns reflected in the diet? My results indicate that perch behavior in Lake Mendota is more complex than is indicated

by the classic descriptions by Hasler and Bardach (1949) and Hasler and Villemonte (1953).

Methods

The study site for this project was Lake Mendota, Wisconsin (43° 4'37" N, 89° 24' 28" W), a large (area = 39.4 km²) eutrophic lake with an average depth of 12.4 m and a maximum depth of 25.3 m (Brock 1985). The physical and biological characters of this lake have been described in detail by Brock (1985).

Temperature and Oxygen. Vertical temperature profiles were obtained with a thermistor at 1-m intervals, and oxygen concentrations were determined using the Winkler method on water samples collected every 2 m. Samples were taken at the Deep Hole station in 23-m of water. Secchi disk depths (a measure of water clarity) were also recorded at these times (Richard Lathrop, Wisconsin DNR, unpubl. data).

Perch Distribution. Fish samples were taken from four stations in the lake: in 23 m of water (Deep Hole), in 13 m of water (intermediate), in 6 m of water, and in 3 m of water (inshore) (Fig. 2). Fish were caught using vertical gill-nets with a variety of mesh sizes (mesh sizes = 19 mm, 25 mm, 32 mm, 38 mm, 52 mm, 64 mm, 89 mm, 127 mm), set parallel to shore, during the weeks of 6 July, 30 July, 4 August, and 17 August, 1987. The two largest mesh sizes were eliminated from some August samples, because the maximum size of perch in Lake Mendota were not vulnerable to these mesh sizes (Regier and Robson 1966, Hamley and Regier 1973). A horizontal net with a similar series of mesh sizes was also used at the shallow station for the August sets. Nets were set between two and four hours before sunset and emptied between one and two hours after sunset for the evening samples. The nets were left set overnight after the evening samples and were emptied between two and four hours after sunrise for the morning samples. Nets were set between 0900h and 1400h CDT for the day samples.

Fish were removed from the nets and sep-
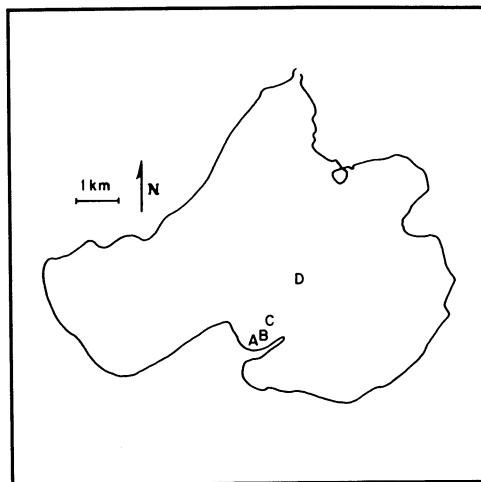
Fig. 2. Lake Mendota, Wisconsin, with locations of sampling stations used in this study. A = 3-m (inshore) station, B = 6-m station, C = 13-m (intermediate) station, D = 23-m (Deep Hole) station.

arated according to which direction they were traveling when caught and the depth at which they were caught. Total length was later measured to the nearest 1 mm and weighed to the nearest gram. Stomachs were collected from between 20 and 40 individuals from each sample and were preserved in a 10% formalin solution.

Data from all samples were pooled for diet and movement analysis. Catches were expressed in catch per unit effort (fish·m^{-2}·h^{-1}) where the time was determined for the evening sets from the time the nets were set until they were pulled and for the morning sets from thirty minutes before sunrise until the nets were pulled. Area was considered the area of the gill-net in the water above 13-m depth. Depths below 13 m at the 23-m site were not considered since the water below the thermocline was anoxic and catches below this level were negligible. For determining the direction and magnitude of dispersal the following vector was calculated:

$$DISPERSAL\ VECTOR = \frac{(\#\ OFF - \#\ IN)}{(\#\ OFF + \#\ IN)} \times 100\%$$

where # OFF is equal to the number of perch caught moving towards the offshore areas and # IN is equal to the number of perch caught moving towards inshore areas. This gives a vector where the sign indicates the direction of movement and the magnitude gives the strength of that movement, relative to the total catch.

Perch Diets. Stomach contents were examined using a dissecting microscope at 25x. The contents were identified to genus and counted. When large numbers of prey organisms were present, two or three 4% subsamples were used to estimate total numbers present.

Zooplankton prey available to perch were collected from three stations in the lake, at the 23-m (Deep Hole), 13-m (intermediate), and 3-m (inshore) stations, using transverse tows of a Clark-Bumpus metered plankton sampler affixed with an 80 μm net. Samples were preserved in a 10% buffered formalin solution and later identified to species using a dissecting microscope at 25x. Samples were collected on several dates over the period of gill-netting. Mean abundances of zooplankton per liter over all sample dates are reported.

Results

Temperature and Oxygen. The thermocline during the period of this study varied between 7 m on 3 August, 1987, and 12 m on 18 August 1987. During the early sampling dates the thermocline was between 9 m and 10 m. The hypolimnion was anoxic during the entire study (Fig. 3). Secchi disk depth during the period of this study ranged from 1.7 m to 2.7 m (Richard Lathrop, Wisconsin DNR, unpubl. data).

Perch Distribution. Catch per unit effort ranged from 0 for the day samples at the 6-m station to 265 for the morning samples at the 13-m station (Table 1). At the 13-m station significantly more fish were moving offshore in the morning and inshore in the evening (Table 2, $X^2 = 6.62$, P<0.025). The magnitude of the dispersal vector is higher in the morning (15%) than in the evening (7%, Table 2). When the water column is divided into shallow (0–5 m) and deep (6–12 m) portions, directionality is much higher in the shallow portion than in the deep portion (Table 3). This difference between the total catches in the shallow portion is highly significant ($X^2 = 7.87$, P<0.01), whereas in the deep portion the Dispersal Vector did not differ from random expectations ($X^2 = 0.07$, P>0.09). This trend was especially strong in the morning sets where the Dispersal Vector equalled 22% in the shallow portion and 0% in the deep portion of the water column.

Comparisons between depth distributions of 23-m and 13-m stations indicate that the horizontal movement between deep and shallow water is accompanied by only minor change in depth. Perch at the 6-m station were located below 4 m (Fig. 4). Perch passed through the 13-m station moving towards the 23-m (Deep Hole) station at an average depth of 4.9 m (SE = 0.17) in the morning (Fig. 5), while at the Deep Hole station they were located at an average depth of 5.5 m (SE = 0.31) (Fig. 4). When passing through the 13-m station in the evening towards shallow water, perch moved at an average depth of 6.1 m (SE = 0.19) (Fig. 5).

The size distribution of perch was similar

Table 1. Number of yellow perch caught at each station and sample time, expressed as catch per unit effort, with sample dates combined. Catch per unit effort equals fish•h^{-1}•m^{-2}·1000. Level of effort for each station (h•m²) given in parentheses.

		Station		
Sample Time	*23-m*	*13-m*	*6-m*	*3-m*
AM	19 (468)	265 (1404)	172 (180)	178 (342)
PM	no sample	138 (1560)	19 (216)	169 (414)
DAY	126 (546)	no sample	0 (288)	172 (198)
TOTAL	77 (1014)	198 (2964)	51 (684)	173 (954)
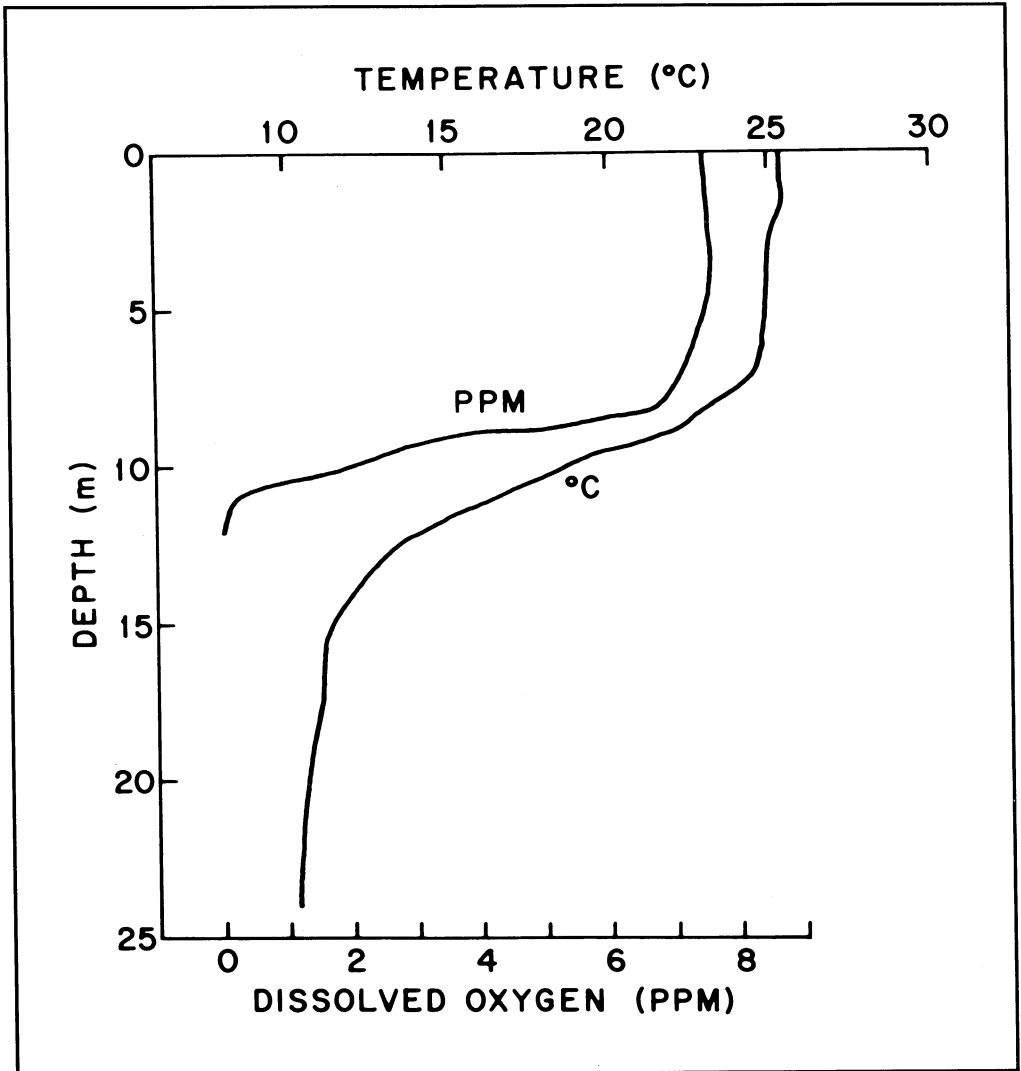
Fig. 3. Sample temperature and oxygen profile for Lake Mendota taken vertically through the water column at the Deep Hole station on 20 July 1987. Water deeper than approximately 10-m depth was anoxic throughout the period of the study.

at all but the 3-m station where a large number of young-of-year perch were captured (Fig. 6). The mean lengths of perch caught at the 6-, 13- and 23-m stations were 192, 192, and 195 mm respectively. The length distribution of perch at the 3-m station was bimodal. The mean length of perch greater than 150 mm at the 3-m station was similar to the other sites, but a large number of perch less than 150 mm was present as well. A Kolmogorov-Smirnoff test (Sokal and Rohlf

1969) indicated that the length distribution of perch at the 3-m site was significantly different from the other sites (D = 0.25, P<0.01; D = 0.25, P<0.01; D = 0.29, P<0.01; when compared to the 23-, 12- and 6-m stations respectively). The absence of young-of-year perch at the offshore stations indicates that these fish do not participate in the diel offshore migration observed for the older age classes (Fig. 6).

No differences were found to indicate mi-

Table 2. Number of yellow perch caught at the 13-m (intermediate) station. The dispersal vector is as defined in the text (1). A positive vector indicates movement directed offshore, and a negative vector indicates movement directed inshore. $X^2 = 6.62$, $P<0.025$.

| Sample Time | Direction of Movement | | Total | Dispersal Vector |
	Inshore	Offshore		
AM	159	213	372	+15
PM	116	100	216	−7
Total	275	313	588	

Table 3. Number of yellow perch caught at the 13-m (intermediate) station, separated by time of day, depth, and direction of movement when caught. Dispersal vector is defined in the text (1). $X^2 = 7.87$, $P<0.01$ for depth $= 0 - 5$ m. $X^2 = 0.07$, $P>0.09$ for depth $= 6 - 12$ m.

| Sample Time | Direction of Movement | | Total | Dispersal Vector |
	Inshore	Offshore		
Depth = 0m-5m				
AM	96	150	246	+22
PM	60	49	109	−10
Total	156	199	355	
Depth = 6m-12m				
AM	63	63	126	0
PM	56	51	107	−5
Total	119	114	233	

gration was selective in regard to sex. Sex ratios at all stations did not deviate significantly from 1:1. The ratios of males to females at the station were: Deep Hole 38 males: 39 females; 13-m (intermediate) 34 males: 41 females; 6-m 12 males: 22 females; inshore 70 males: 72 females (Table 4).

Perch Diets. Copepods and other small zooplankton were the most numerous taxa sampled from the lake at all three stations (Table 5). *Daphnia* ranged from 3% at the 3-m station to 13% at the 23-m station. *Leptodora* made up less than 1% of the sample at the 23-m and 13-m stations and 1% at the 3-m station.

Although there is a trend for the proportion of *Daphnia* in the lake to decrease from deep to shallow water, the proportion increases in the perch diets (Table 6). *Daphnia* make up 34% of the contents of stomachs of perch caught in the Deep Hole, 72% of the diet at the 13-m station, and 87% of the stomach contents from fish from the 3-m station. Because of high variability between individuals within the groups, differences in diet between sub-groups were not statistically significant (Table 6).

In addition to *Daphnia* and *Leptodora*, other organisms (primarily chironomid fly larvae and copepods) increased in importance from 0% at the Deep Hole station, to 4% at the 13-m station, and 6% at the 6-m and 3-m stations (Table 6). The diversity of organisms also increased from deep to shallow water. The stomachs of fish from the Deep Hole contained primarily *Daphnia* and *Leptodora*, with only three chironomids and one copepod. Stomachs from the 13-m station held organisms from seven categories, and stomachs from the 3-m station contained organisms from ten categories (Table 7).

The percent of empty stomachs increased from deep to shallow water. All the stomachs from the Deep Hole station contained prey, while 2% were empty at the 13-m station, 12% were empty at the 6-m station, and 33% were empty at the 3-m station (Table 6).

Discussion

These results support a more variable view of perch behavior than is commonly presented. While there are many reports of perch migrations (Hasler and Bardach 1949, Scott 1955, Engel and Magnuson 1976, Helfman 1979), only Scott (1955) gives a comparison of the numbers of perch moving in each direction, while the others imply that the migration is a population-wide phenomenon, with schools moving en masse in a certain direction. My results correspond to those of Scott, who found a significant directional movement but also reported that a large proportion of the individuals were headed in the "wrong" direction. The difference in results

found may be due to a difference in the method used in the studies. This study followed a method similar to that of Scott (1955), putting gill-nets across the presumed path of
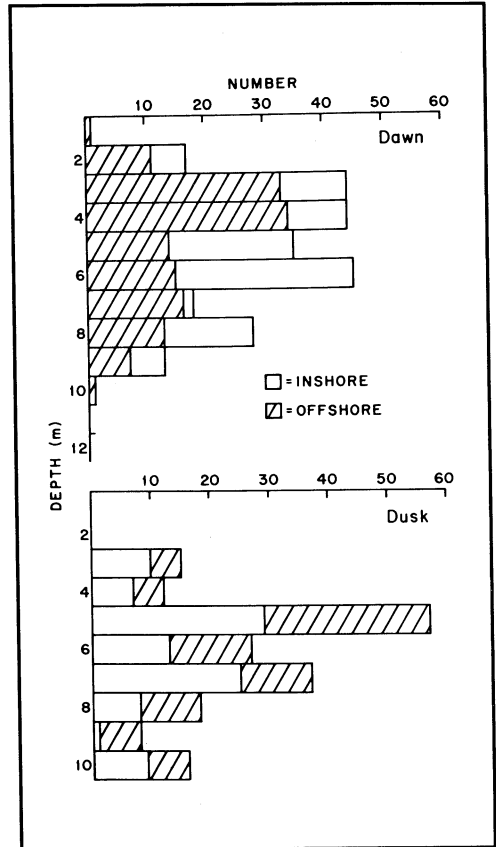
Fig. 5. Top panel: Depth distribution of perch from the 13-m (intermediate) station, morning samples only, with all sample dates combined. N = 246 fish, $\overline{D}$ (mean depth) = 5.1 m (SE = 0.13). Cross-hatched areas indicate perch moving offshore, with N = 145 fish, $\overline{D}$ = 4.9 m, and SE = 0.17. Non-crossed-hatched areas indicate perch moving inshore, with N = 101, $\overline{D}$ = 5.6 m, and SE = 0.19.
Bottom panel: Depth distribution of fish from the 13-m (intermediate) station, evening samples only, with all sample dates combined. N = 190 fish, $\overline{D}$ = 6.2 m, and SE = 0.14. Cross-hatched areas indicate perch moving inshore, with N = 101, $\overline{D}$ = 6.1 m, and SE = 0.19. Non-cross-hatched areas indicate perch moving offshore, with N = 89, $\overline{D}$ = 6.3 m, and SE = 0.20.

Fig. 4. Top panel: Depth distribution of perch from the 23-m (Deep Hole) station with all sample dates and times combined. N = 75 fish, $\overline{D}$ (mean depth) = 5.5 m (SE = 0.31). Bottom panel: Depth distribution of perch from the 6-m station with all sample dates and times combined.
N = 35 fish, $\overline{D}$ = 4.3 m (SE = 0.08).

Table 4. Sex ratios of yellow perch caught at each station with all sample dates and times combined.

Station	Number of Males	Number of Females	χ^2
23-m	36	39	0.12 P>0.50
13-m	34	41	0.66 P>0.10
6-m	12	22	2.94 P>0.05
3-m	70	72	0.01 P>0.90

Table 5. Composition and abundances of zooplankton in Lake Mendota. Samples pooled over three sampling dates. % = percent of sample by number, $\bar{x} \pm SE$ = mean number per liter plus or minus one standard error.

	Daphnia % ($\bar{x} \pm SE$)	*Leptodora* % ($\bar{x} \pm SE$)	other % ($\bar{x} \pm SE$)
23-m	13% (4.25±2.09)	<1% (0.04±0.04)	87% (27.96±4.28)
13-m	11 (3.44±3.69)	<1 (0.03±0.03)	89 (26.77±5.36)
3-m	3 (0.90±0.82)	1 (0.25±0.43)	96 (25.05±29.4)

Table 6. Diet summary of yellow perch for each sample station and time, with all sample dates combined. N = total number of stomachs examined for each group and % empty = percent of stomachs with no prey organisms. Results are expressed as percent by number of *Daphnia*, *Leptodora* and "other". Prey Items per Stomach = mean number of items found per stomach (standard error). Taxa present in the "other" category are listed in Table 7.

Station	Time	N	% Empty	% Daphnia	% Leptodora	% Other	Prey Items/Stomach
23-m	Day	11	0	34	66	0	170 (161)
13-m	AM	57	2	73	24	3	263 (287)
13-m	PM	48	2	80	15	5	505 (449)
6-m	AM	23	13	79	8	13	11 (13)
6-m	PM	4	0	42	56	2	61 (73)
3-m	AM	35	43	33	2	65	9 (31)
3-m	PM	37	30	54	29	17	64 (127)
3-m	Day	26	23	99	0	1	318 (517)

Table 7. Diversity of organisms found in yellow perch stomachs at each sampling station. % Occurrence = number of stomachs where taxa was present/total number of non-empty stomachs in sample. N = total number of non-empty stomachs in sample.

	% Occurrence			
Type of Organism	23-m N=11	13-m N=103	6-m N=24	3-m N=66
Daphnia	100%	96%	83%	74%
Leptodora	100	82	42	27
Chironomidae	27	38	25	21
Copepoda	9	24	25	21
Ceriodaphnia		3		
Pontoporeia			13	23
Diaphanosoma				3
Bosmina		1	4	1
Chydorus				2
Nematoda			2	21
Acanthocephala				1
Fish sp.				1
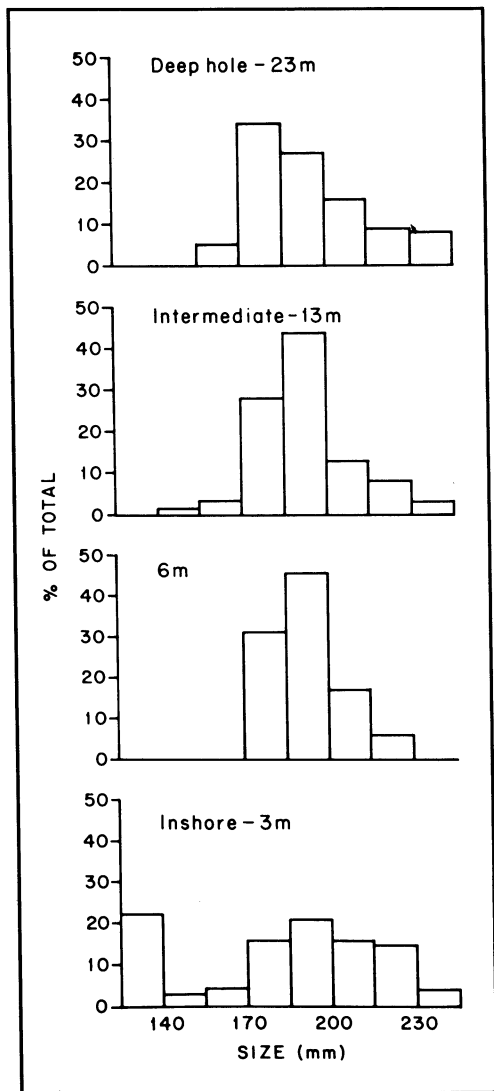
Fig. 6. Size distribution of fish with all sample dates and times combined, for each station. N = 77 and $\overline{TL}$ (mean total length) = 195 mm for the 23-m (Deep Hole) station, N = 583 and $\overline{TL}$ = 192 mm for the 13-m (intermediate) station, N = 35, $\overline{TL}$ = 192 mm for the 6-m station, and N = 164 and $\overline{TL}$ = 175 mm for the 3-m (inshore) station.

movement, while the others were based upon nets set in deep water and in shallow water and a migration inferred from the differences in total catches at different times of the day. The large percentage of fish moving in the opposite direction in this study, 44% of the total, indicates that the movement does not occur as a rapid, population-wide migration, but is a more gradual dispersal.

The extreme variability of individual diets made comparisons between the groups in Table 6 difficult. Variability of this magnitude is found in other populations and is explained as being due to either an ontogenetic change, a learned, individual preference for certain prey types (Helfman 1979, Mills et al. 1987), or unknown, complex behavioral patterns (Chabot and Maly 1986). A comparison of the proportion of different zooplankton in the lake with the proportion found in stomachs reveals that the perch are feeding selectively on certain prey types, primarily zooplankton. *Daphnia* made up between 33% and 99% of the diets of perch but accounted for only 3% to 13% of the zooplankton in the lake. Likewise *Leptodora* accounted for up to 66% of the diets of the perch but made up 1% or less of the lake's zooplankton (Table 5 and 6). At the two inshore stations (3-m and 6-m) where perch had access to the sediments, diet consisted of both planktonic and benthic prey. Feeding habits at the inshore stations are similar to those reported for perch in lakes with an oxygenated hypolimnion (Keast 1977, Hanson and Legget 1986, Mills et al. 1987).

The picture of perch behavior that emerges from this study indicates more variation among individuals than previously cited models have included. It is unlikely that a population-wide migration occurs but rather that the perch start to disperse from their inshore areas at dawn. The dispersal is in the form of short periods of movement alternating with periods of feeding, with changes in direction along the way. This "random walk" has a vector biased towards the offshore areas. The revised conceptual model presented (Fig. 7) accounts for both the offshore movement and the large number of fish moving in the opposite direction. This model also accounts for the presence of fish at the intermediate and 6-m stations during the day. If the choice of direction vector after a feeding bout has only a slight bias towards offshore areas, some
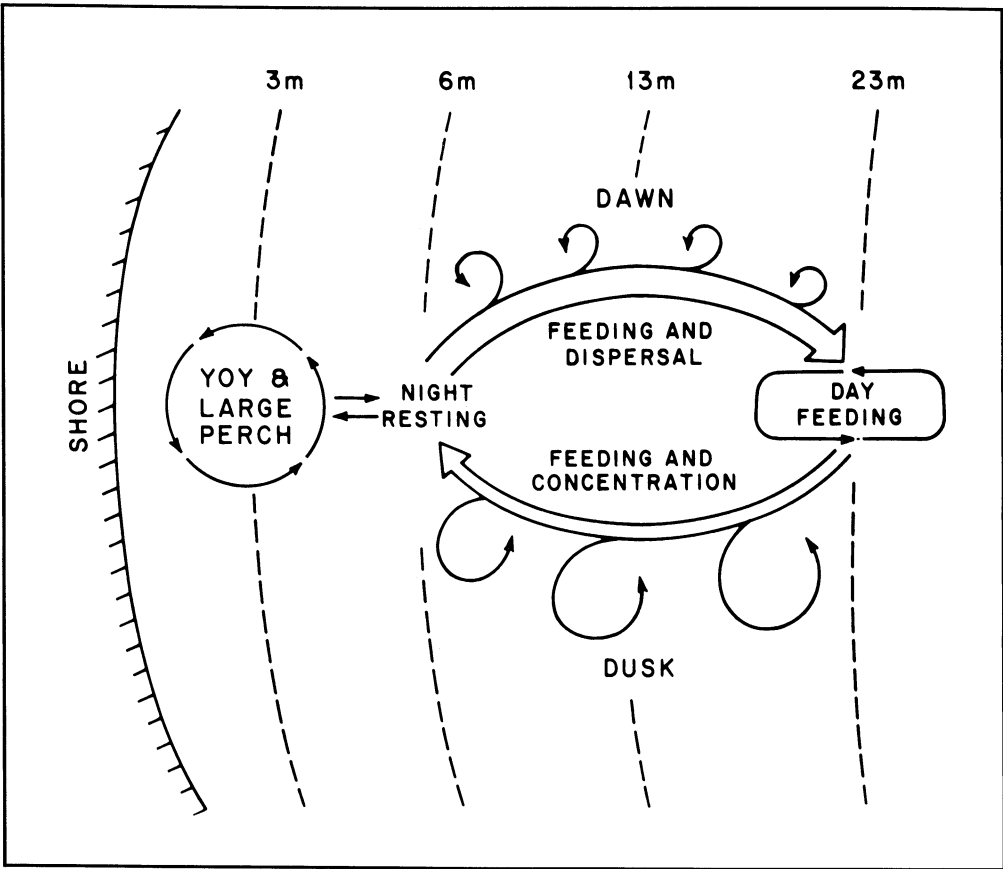
Fig. 7. Revised model of diel behavioral patterns of yellow perch in Lake Mendota, Wisconsin. This model includes a random feeding dispersal at dawn from nocturnal concentrations of perch inshore and movement directed towards the shore at dusk to reach night-time refugia on the bottom, inshore. Large perch (>230mm) and young-of-year perch remain inshore during the day. Movements between inshore and offshore include feeding and may include feeding forays to deeper water up to approximately the 13-m contour. Dashed lines indicate water depth contours.

fish will end up in the inshore areas due to chance alone. This effect would be accentuated if some individuals are biased to turn inshore. An inshore bias could occur if the preferred prey of some individuals was more abundant or accessible inshore, as is the case for those individuals feeding on benthic organisms.

Two groups of perch do not take part in this diel migration. These are the young-of-year perch and perch larger than 215 mm. Yearling perch may be influenced by predation pressure to remain close to shore where cover is available as a predation refuge, and

the largest perch may be influenced by an ontogenetic shift in diet towards larger benthic organisms (i.e. amphipods, insect larvae) and small fish (including young-of-year perch), both of which are more accessible inshore (Crowder and Cooper 1982).

Most studies point to the change in light intensity at dawn and dusk as the proximate cause of diel changes in yellow perch behavior (Hasler and Bardach 1949, Scott 1955, Werner et al. 1977). It is likely that perch use the reduced light level around dusk as a cue to direct their movements inshore. As individuals move horizontally they intersect

the bottom at approximately the 6-m contour line and settle for the night. The process is reversed with increasing light levels near dawn.

The ultimate causes of these diel migrations in perch are less certain. The benefits of dispersing long distances on a daily basis must be high enough to balance the energy expenditure of swimming between the littoral and the pelagic zones. A variety of factors influencing the change in distribution can be identified, including variation in local food availability (Hasler and Bardach 1949), avoidance of interspecific (Engel and Magnuson 1976, Werner et al. 1977) and intraspecific competition (Mittelbach 1981, Sandheinrich and Hubert 1984, Paszkowski 1985), and avoidance of predation (Maclean and Magnuson 1977, Werner et al. 1977;1983, Tonn and Paszkowski 1987). It is likely that a combination of these factors are influencing the perch in Lake Mendota, including inability to forage efficiently at low light levels, and predation risk from nocturnal walleye.

Whatever the mechanisms involved in this change in perch distribution, the movements between the littoral and pelagic zones will have profound effects on the ecosystem. In terms of biomass, perch are the most important fish in Lake Mendota (Brock 1985), and their movements will influence both zooplankton and piscivore populations through predation effects and may affect primary producers through both cascading trophic interactions and the transfer of nutrients between pelagic and littoral zones of the lake.

Acknowledgments

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About the Poets

Shirley Anders *is writer-in-residence at the University of Wisconsin-Fox Valley. Her poetry has been published in* Michigan Quarterly Review, Poet and Critic, Kansas Quarterly, Prairie Schooner, *and* Southern Poetry Review, *among others. Her chapbook* The Bus Home *was published in 1986 (University of Missouri Press). Anders received a North Carolina Arts Fellowship in 1985 and a Devins Award from the University of Wisconsin Press in 1986.*

Howard Frederick Ibach *is currently a writer/producer for a Milwaukee advertising agency. His poems have appeared in numerous publications.*

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Laurel Yourke, *a native of New York City, received her PhD from UW-Madison and is currently working as a research associate through UW-Madison extension and as a teaching assistant in the Women's Studies program at UW-Madison. She also teaches English at an alternative high school in Madison. Her poetry has appeared in* Cypress Review II, Cypress Review III, *and* Day Tonight/Night Today.

Chris Halla *has had his work published in* Northeast, Poetry Now, Pembroke, Wisconsin Review, Blue Cloud Quarterly, *and* Abraxas. *His chapbooks include* River Bottom, *(Broken Arrow Press),* Adventures of a Freelance Farmer *(River Bottom Press), and* River Boy, River Town, River *(Wolfsong). Previously, Halla was the managing editor of* Wisconsin Trails/ Wisconsin Weekend; *currently, he is working as a product development manager for J. J. Keller and Associates and as a freelance writer, editor, and illustrator.*

A former editor of the Hayden Ferry Review, **John Graves Morris** *currently teaches English at Cameron University in Lawton, Oklahoma. His poetry has appeared in numerous publications.*

Spring Again

Startled by the bird's sharp call, little
flycatcher whose exultation
caught my ear, I turned in time to see it
fly straight for the window, the pane
smack its sharp smack, bird drop,
jerk in the dirt, be gone,
despite my moving its slack
being from the sunny flag it struck
to rain-fresh earth among white violets
massed at the late-leafing catalpa's
trunk. In minutes, drawn back to verify
the fledgling's wing bars, its mandible,
I watched an ant drink from the open eye.

      Lawrence, behind the Guest House,
        May 1989.

                —Shirley Anders

Three Sensations

1. "It is still beautiful to feel the heart beat."
—Tomas Tranströmer

You,
grey premonition,
emerged
between two pulsations,
a vibration
wearing the rain
around your neck;
a heaving
under the cloth
so deep
and consuming
you frightened away
the tentacles
of a candle.

2. "To die a tiny noise will do."
—Vicente Aleixandre

Yes, it is true
hesitation rises with the dawn

Your name is a throb
throwing itself against a wall

You were absolute morning
caught in my throat

3. "Quiet, for we too are of the night."
      —Yves Bonnefoy

Cat,
how can I name
the sensation
of touching you?
It could be so many things

When I touch you
I hide
in the deepness
of your teeth

I hide
in the clarity
of your extended claw

I wrap myself
in the suddenness
of your white forehead

I hide in you
and we chant together
as your shadow
licks its paw

The evening,
quivering in my hand
would have felt just right
beneath us
if only
I could hold you
the way evening
tilts its head

   —Howard Frederick Ibach

The Wasp and the Secretary

Split in the thorax by the fat hand
Of the manila-envelope wielding man,
Master of rote, who loves his mother:
"Did you see that?
Its head flew one way, its body another!"
I hated you, too, I admit to that,
But I gathered your parts on a yellow sheet
And in horror saw you were still moving,
Digging, chewing,
As if your life were a thing worth saving.

One long wing, shiny and crisp,
Remained, a veined, stained-glass wisp,
The color of smoke, resembling
A quartz chip,
Iridescent, transparent, trembling.

Your legs, hollow broomstraws bent,
Were signalling without intent.
On their edges, saw-toothed ridges
Dragged half of you
Toward headless dreams of screens and ledges.

Far away two blister eyes stared,
Lidless, prehistoric, bare
As river-bed stone, bone ovals set
On either side
Of molded shoulders, clay epaulets.

Your pieces lay like a broken bowl,
A brittle little artifact, a ceramic soul,
The color of dry things, of locust, or carob,
Of chalcedony,
Every curve an ivory carving, a scarob.

A fallen flower crisply pinched,
The overturning of a turtle trenched,
The shell belly, flown apart.
Grasping, drinking,
And nothing but air sucked through the heart.

Your schismed self, your self apart,
Your tigery abdomen, glossy and fat,
Squirmed, a waspish waste, lame
As a worm in rain,
The stinger searing for someone to blame.

—*Beth H. Roney Drennan*

Weeding: Flowers and Friendships

Wild greens love all weathers, lap torrents
that drown more fragile seedlings
stretch boldly toward the hottest sun
plunge deeper through the sparsest soil
erect against the shrillest wind.

They own territories: miniature suns border
trumpeting morning glories
friendly but not encroaching
into wild but neighborly places
each knowing its soil, its home.

But the cultivated, no matter how
loved, fear imaginary enemies
seek constant tending. Heat shrivels
sculptured leaves. Rains rot the roots.
Strangeness settles on the stem, nips
the fruit, steals every empty space till
you no longer know which flowers were your own.

—Laurel Yourke

Compulsories

A fine, long, looping line
etched, then traced
by a single, sharp, silver
blade slowly slicing the surface
of perfect ice made
more perfect
by the figure
skater.

Her legs are perfect,
in black tights, black
leg warmers.
Her back a study in
perfect posture.
Her whole form perfect
in baggy
black and blue and red and
yellow ski
sweater.

No crowd,
no sound.
Just eyes to the ice
and blessed, perfect
silence.

—Chris Halla

Epithalamion
for Betty & Steve: 28 July 1990

On a day like today, the sunlight
High in the maples startles us awake.
Praise is our native tongue, but we say
Little, too numbed by the sales pitch,
The stock quotation, the body count.
Even the poet tells us that dark comes down
On all we do, but the Mockingbirds' natter
Reminds us that we were made to shine,
To sing. Brightness rifts through pear trees,
& wind redeploys it on many walls,
A movable feast of dappled light.
The world comes clean, & everywhere grackles,
Elms, & Oklahoma give themselves away.
On a day like today, the sky is
A blue so effortless that love
Becomes more than a possibility, blackbirds
Rising in pairs, in waves, undulating
Toward the reeds in Lake Helen to roost.

—John Graves Morris

Voles and Bog Lemmings of Wisconsin

Charles A. Long

V oles and bog lemmings of Wisconsin are field mice belonging to the rodent subfamily Arvicolinae (formerly Microtinae). Their resemblances to one another prevent easy identifications and they remain an enigma in the well-known fauna of Wisconsin. They have not been appraised taxonomically since Hall and Cockrum's regional study (1952) summarized by Jackson (1961). Approximately 960 new Wisconsin specimens were studied in this collection (University of Wisconsin Museum of Natural History). Forty-eight Arvicolines (or "Microtines" according to some workers) were borrowed from neighboring museums. All the Wisconsin species (except the muskrat) are taxonomically revised herein. The characteristics of each kind are described. Some natural history information, such as breeding data, is reported. The chief aims of this paper are to report information on the taxonomy, geographical and ecological distributions, and to summarize in condensed form some information on the environmental status of all the Wisconsin voles and bog lemmings. Where relevant, findings from specimens in closely adjacent areas in Illinois, Minnesota, and Michigan are also included.

Materials and Methods

The kinds of voles and bog lemmings were identified by their external and dental char-

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acters. Specimens were aged by fusion of the basioccipital-basisphenoid suture and by other useful evidences of maturity (size, breeding, angularity of the cranium). Specimens of both sexes were combined because no significant differences between them were noted. Specimens of like age were compared from place to place to ascertain geographic variation in size, cranial characters, and color. Localities were plotted on range maps, and by comparison with Jackson's (1961) records it was possible to document some expansion or contraction of geographic ranges. University of Wisconsin-Stevens Point (UW-SP) specimens are listed without reference. Specimens from the following museums were listed with these abbreviations: United States National Museum (Nat. Hist.), USNM; Chicago Natural History Society Museum (CNHS); University of Michigan at Ann Arbor (UM); University Wisconsin-Madison (UWM); and University of Illinois (UI).

Cranial measurements were obtained by dial calipers in millimeters. In mice that all have protruberant upper incisors, the *greatest length* of the skull, measured between the anteriormost extension or projection of the incisors and the posteriormost extensions of the exoccipital condyles, is the greatest longitudinal dimension. The supraoccipital occasionally projects slightly posterior to the condyles, in which case its posteriormost point is the posterior measure. The *condylobasal length* is the comparable distance between the condyles and the anteriormost extension or projection of the premaxillary bones (not

including the incisors). The breadths of the skull are the *zygomatic breadth,* being the greatest distance between the outer borders of the zygomatic arches (at right angles to the longitudinal axis of the skull) and the narrowest constriction, the *interorbital breadth* between the orbits. The *lambdoid breadth* is the distance across the posterior face of the skull, including the lambdoid crests bordering the exoccipitals. The *length of the nasals* is measured from the anteriormost extension as the longer distance to either posteriormost extension. The *maxillary tooth-row* is the alveolar length of the three cheek teeth measured along the maxillary bone. Since there is no sagittal crest in voles, the *cranial depth* measures from the highest point of the cranium to either the base of the cranium or to a transverse line tangent to the ventral projections of the auditory bullae. When possible, arithmetic means are accompanied by the observed range of variation and in bog lemmings by the standard error.

Most cheek teeth are persistent in growth (rootless) and develop as prisms of dentine enclosed by angular borders of enamel. The projecting salients are salient angles, and the indentations between are termed re-entrant angles. More circular enclosures are called loops or islands. The patterns are extremely useful in identification of Arvicoline mice.

Accounts of Species and Races

Genus *Pitymys* McMurtrie, 1831

In *Pitymys* the teeth are primitive, especially lower first and upper third molars; the M/1 has the anterior island slightly constricted, with only two to three salient angles between it and the posterior loop; the upper third molar has only two islands (two closed salient angles) between the anterior and posterior loops.

The best treatment I could give the woodland (pine) voles and the prairie voles to emphasize the similarity in dental characters was to combine them in the genus *Pitymys.* This arrangement implies a close evolutionary relationship not as evident when including these voles in the genus *Microtus,* as is often done.

Pitymys pinetorum (LeConte)

1830. *Psammomys pinetorum* LeConte, in Ann. Lyc. Nat. Hist., New York, 3:133, type from Georgia.

1831. *Pitymys pinetorum* McMurtrie. In The Animal Kingdom . . . by Baron Cuvier, vol. 1, p. 434, footnote.

1896. *Microtus pinetorum,* Miller. N. Amer. Fauna, 12:9.

The scientific binomen *Pitymys pinetorum* refers to a mouse taken in pines. It is seldom taken in pines, and now it is sometimes called the woodland vole. It is as often referred to by the name *Pitymys* as by any common name, but by some workers referred to as *Microtus.*

Description: This vole has slightly *reddish* or *walnut brown fur,* hair even, short and dense as in moles. The venter is grayish overlain with ochraceous or buff. The tail is *exceptionally short.* The foreclaws are often white, *exceptionally large* (elongated for digging) and much longer than the hind claws. The *skull is broad,* especially the posterior extensions of the nasals, the adjacent premaxillaries, and the interorbital region. The post-rostral part of the skull is rather circular, the brain case encroaches into the orbits, and the nasals are short and broad. The upper third molar consists of an anterior loop, two enclosed prisms, and a posterior portion with a salient bulge confluent with a lingual loop. The lower first molar has nine angles, but only four closed prisms, with the anteriormost part constricted, but not pinched together. The teeth are similar to those of *Pitymys ochrogaster,* except the first inner prism of the middle upper molar tends to be quadrate and sharply angled.

Comparisons: Whereas the prairie vole has a high, narrow skull, the woodland or pine vole has a low broad skull. The woodland vole has short, dense, fleecy fur of even brown or reddish brown color, instead of coarse fur in the prairie vole. The hands are broad, the foreclaws robust. The very short tail is seen only in this vole and the more grizzled bog lemmings. The acromion process of the scap-

ula flares abruptly, so that it diverges from the glenoid socket, and bends terminally toward the head of the humerus. In *Microtus pennsylvanicus* and *Pitymys (Pedomys) ochrogaster* the acromion is delicate and the fossa between it and the scapula narrow, with the opening at less of an angle. The clavicle in *Pitymys pinetorum* is more robust.

The tunnels and dirt piles, unlike those of other mammals, are usually found below the tough, dense, and deep leaf litter, rather than standing above.

Measurements: According to Jackson (1961) *P. p. scalopsoides,* referred to herein as *kennicotti,* had weights ranging up to 36 grams in old adults. External measurements in mm of six specimens from early day Chicago (listed under Cook County, Illinois), four adult specimens from Clark County, three from Wood County, and one from Klondike

Pond, Sauk County, are given in Table 1. The type specimen of *P. p. schmidti,* not seen by me, measured 128, 24, 18, which resembles the specimens seen in Clark County.

The single specimen of *P. p. nemoralis* from Lynxville in western Wisconsin was much larger (133, 22, 19), resembling four topotypes of *nemoralis* from Stillwell, Oklahoma: 137 (127–144), 24 (20–27), 18.5 (18–19). Skull dimensions of the Lynxville pregnant female are also larger than Wisconsin and Illinois *kennicotti,* measuring 27.1 in greatest length, 16.0 zygomatic breadth, and 6.8 maxillary tooth row.

Cranial measurements of a subadult specimen from Wolf Lake, Cook County, the type of *schmidti* from Clark County, three adults from Wood County, one from Dane County, and three adults from Canton, Illinois are given in Table 2.

External Measurements in mm for P.p. scalopsoides (or kennicotti)					
	Jackson (1961)	Specimens from these Counties:			
		Cook, Ill	Clark, WI	Wood, WI	Sauk, WI
Number		6	4	3	1
Length	110-133	110-126	119-127	110-126	109
Tail	18-25	14-23	20-23	14-16	17
Hind Foot	16.5-18	16-18	16.5-18	16-18	15

Table 1

Cranial Measurements in mm for P.p. kennicotti					
	Specimens from these Counties:				
	Cook, WI	Clark, WI	Wood, WI	Dane, WI	Canton, Ill
Number	1	1	3	1	3
Length Mean	25.1	25.5	(23.1-26.2) 25.1	25.6	(24.8-25.0) 24.9
Zygomatic Breadth Mean	13.9	——	(13.7-16.0) 14.1	15.4	(14.8-15.1) 14.95
Inter-Orbital Breadth Mean	4.05	4.6	(4.5-4.75) 4.6	4.5	(4.2-4.5) 4.35
Nasals Mean	7.5	——	(7.8-8.0) 7.9	7.4	(7.3-8.0) 7.7
Maxillary Tooth Row Mean	5.8	5.9	(5.6-6.2) 5.9	——	(5.9-6.0) 6.0

Table 2

Distribution: Southern Wisconsin. See Figure 1.

Habitats: The pine or woodland vole occurs in a wide variety of habitats outside Wisconsin (Paul 1970). It is most commonly taken in hardwood (maple, hickory, oak) forests (Jackson 1961; Schmidt 1931). In southwest Wisconsin numerous burrows were found on a dry grassy hillside, and in Clark County, burrows ran under maple leaf litter, in the gray sandy-clay loam soils that roofed the burrows without caving in. Abundant meadow voles may replace *Pitymys* in competition (Paul 1970).

Remark: Litter size varies from 1 to 5, and there are only four teats.

Western Woodland Vole

Pitymys pinetorum nemoralis V. Bailey

A single large female is the only specimen reported from Wisconsin. Its size, massive teeth and chestnut-reddish brown color are the only distinguishing features. The type of *nemoralis* is from Stillwell, Adair County, Oklahoma, where the color is dark rufescent, and the topotypes are large and wide across the zygomata. Specimens from Minnesota and Iowa have been assigned to *nemoralis*, and in size and color the Lynxville specimen agrees with the type and topotypes.

Specimen examined: Lynxville, 1 (USNM).

Kennicott's Woodland Vole

Pitymys pinetorum kennicotti
Baird, new combination

1858. *Arvicola kennicotti* Baird. Mammals of the Pacific R. R. Survey, p. 547. This available name was applied to Illinois voles, and they are inseparable from *P. p. schmidti* Jackson, but distinctive from reddish *P. scalopsoides* found eastward of Illinois.

1941. *Pitymys pinetorum schmidti* Jackson. Proc. Biol. Soc. Washington, 54:201, December 8.

1912. *Microtus pinetorum scalopsoides* (Audubon and Bachman). In Cory,

Mammals of Illinois and Wisconsin Field Mus. XI. p. 222, Also, Hall and Cockrum, 1952; Jackson 1961, and others.

Description: Dark brownish, almost purplish brown, slightly ochraceous in unworn pelage, and decidedly less reddish than either *P. p. nemoralis* or *P. p. scalopsoides*. The voles are smaller than in *nemoralis,* but are rather large from Wood County. The dark color is constant throughout the vole's range in Wisconsin and northern Illinois.

Specimens examined: Wisconsin, 12. Illinois, 20. See Table 3. Jackson (1961) re-

Kennicott's Woodland Vole **Pitymys pinetorum kennicotti**	
Specimens Examined:	
Wisconsin:	**Total - 12**
County:	**Number**
Clark County:	
Worden Twsp.	4 USNM
	1 UWM
Dane County:	
Town of Vermont	1 UWM
Westport	1 UWM
Sauk County:	
Klondike Pond	2
Wood County:	
Powers Bluff	3
Illinois:	**Total - 20**
County:	**Number**
Cook County:	
Palas Park	3 CNHS
Elk Grove	1 CNHS
Wolf Lake	2 CNHS
Orlando Park	1 CNHS
No Specific Locality	2 CNHS
Crawford County:	
Flatrock	2 CNHS
DeKalb County:	
Somonauk	1 CNHS
DuPage County:	
Lemont	1 CNHS
Fulton County:	
10 miles N.W.	
Canton	4 UI
Massoe County:	
Metropolis	2 CNHS
Will County:	
New Lennox	1 CNHS

Table 3
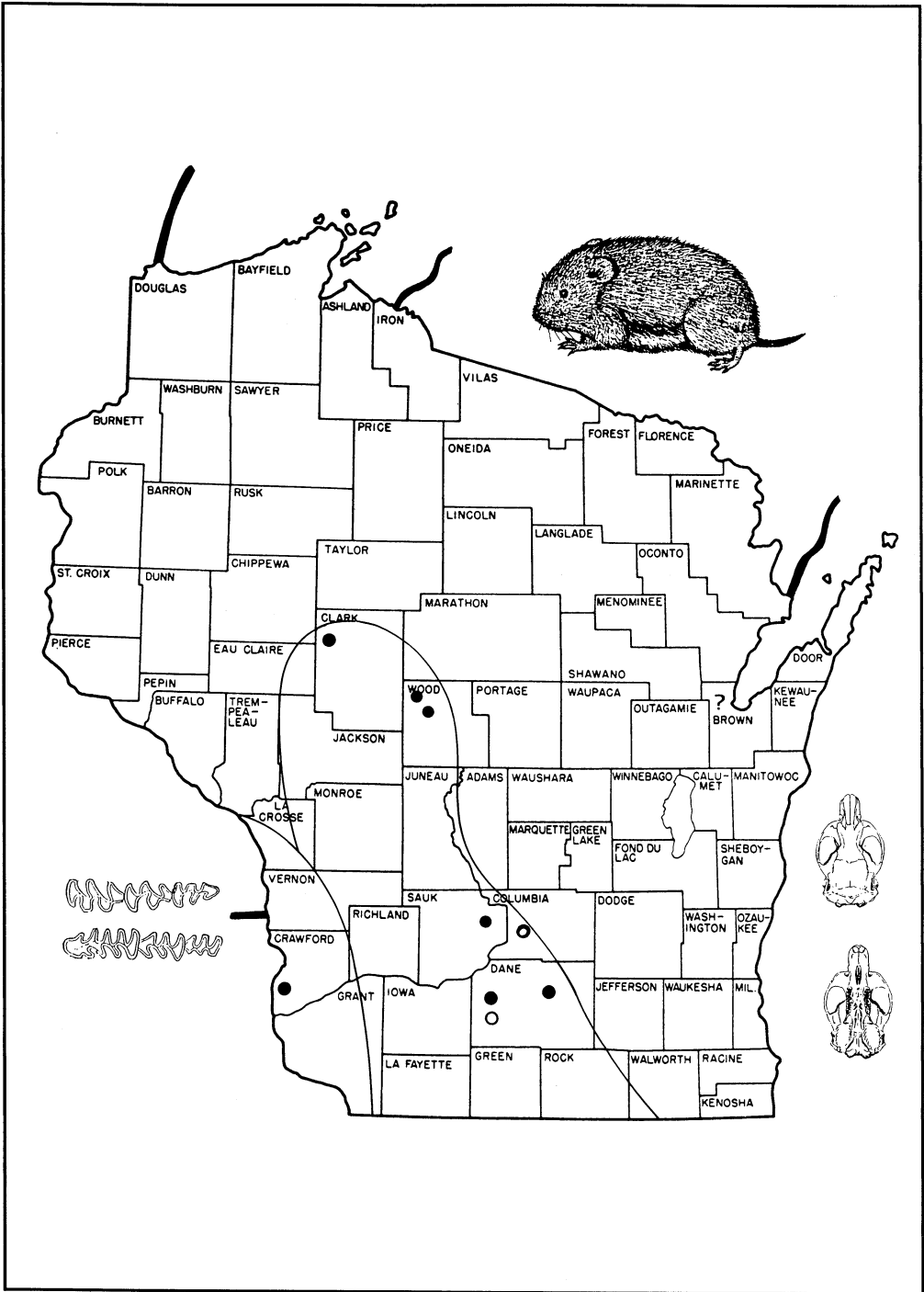
Fig. 1. Distribution of Pitymys pinetorum. *P. p.* nemoralis *is known from Crawford County and west of the Mississippi. The other race is here regarded as* P. p. kennicotti *and the record from Brown County needs to be confirmed. Upper and lower molar tooth-rows. Open circles, Jackson's (1961) records.*

ported a specimen from Green Bay, Wisconsin, in the Neville Public Museum, but it was destroyed by insects. Unfortunately no skull seems preserved, and the locality is now drastically disturbed. The record is questionable, but any specimens from northern Wisconsin may be assigned on geographic grounds to *kennicotti*.

Prairie Voles

Pitymys ochrogaster (Wagner)

1842. *Hypudaeus ochrogaster* Wagner. In Schreber, Die Saugethiere . . ., Supple. 3:592, type from America, probably New Harmony, Indiana (Bole and Moulthrop, Publs., Cleveland Mus. Nat. Hist., 5:157, 1942).

1853. *Arvicola austerus* Le Conte. Proc. Acad. Nat. Sci. Philadelphia, 6:405, type from Racine, Wisconsin. This name is a junior synonym.

1898. *Microtus (Pedomys) ochrogaster,* J. A. Allen. Bull. Amer. Mus. Nat. Hist., 10:459, November 10.

1966. *Pitymys (Pedomys) ochrogaster,* Ellermann and Morrison-Scott. Checklist of Palearctic and Indian mammals. British Mus. Nat. Hist., p. 681.

The scientific binomen of the prairie voles means literally the mouse has an ochraceous belly. Some workers refer the species to the genus *Microtus,* and often it is assigned to the subgenus *Pedomys.*

Description: The prairie vole is brown with a slight mixture of orange or *orchraceous.* On the belly, fur is grayish basally, the tips are *richly ochraceous,* except in the very young. The tail is short in the prairie vole but not nearly so short as in pine (woodland) voles or bog lemmings (in which the tail extends only about as far as the hind feet). The skull closely resembles that of *Pitymys pinetorum.* The upper middle molar has four prisms, lacking any fifth posterior loop, and the last molar has only four prisms, with posterior portion short, narrowing, and hardly invaginated (c-shaped) as seen so clearly in *M. pennsylvanicus.*

Comparisons: The prairie vole is a clean, sociable vole, easier to handle in captivity than *Microtus pennsylvanicus,* and not so vicious with one another. Xeric habits are reflected by less copius urine and drier feces in cage and trap. The fur has an ochraceous intermixture, usually not seen in walnut brown, blackish and reddish tones of *M. pennsylvanicus.* Often taken in prairie with *pennsylvanicus,* the teeth in adults clearly characterize either species. Young prairie voles tend to be remarkable ochraceous-gray whereas young *pennsylvanicus* (which have the characteristic dental patterns often undeveloped) are nearly black, very dark brown, without ochraceous showing in the fur. The feet of adult *ochrogaster* are more reddish tan, whereas they are brown-gray in *pennsylvanicus.*

Measurements: See accounts of subspecies.

Distribution: See Figure 2.

Habitats: Thin, dry, sandy prairies, upland fields, old fields, and railroad rights-of-way. Prairie voles occur primarily in grassland in the south and west, and perhaps in relation to openings in the Southern Deciduous forests. They are not seen in the pine barrens and dunes of northwest Wisconsin, but seem associated in northward distribution to the outwash sands of the Wisconsin glaciers. Perhaps the Northern pine-hardwoods and wooded hills prevent these voles from expanding their geographic range northward. Prairie and pine voles have approximately similar geographic ranges in Wisconsin, but occupy different habitats. There are six mammae and up to seven embryos.

Common Prairie Vole

Pitymys ochrogaster ochrogaster (Wagner)

This vole is large, nearly as large as *Microtus pennsylvanicus.* The skull is larger than in *P. o. minor,* exceeding 26 mm in greatest length in old adults (those with basioccipital-basisphenoid suture closed). The pelage is darker and less grayish than western specimens of *minor,* but not much darker than in the Wisconsin *minor.* The belly is on average
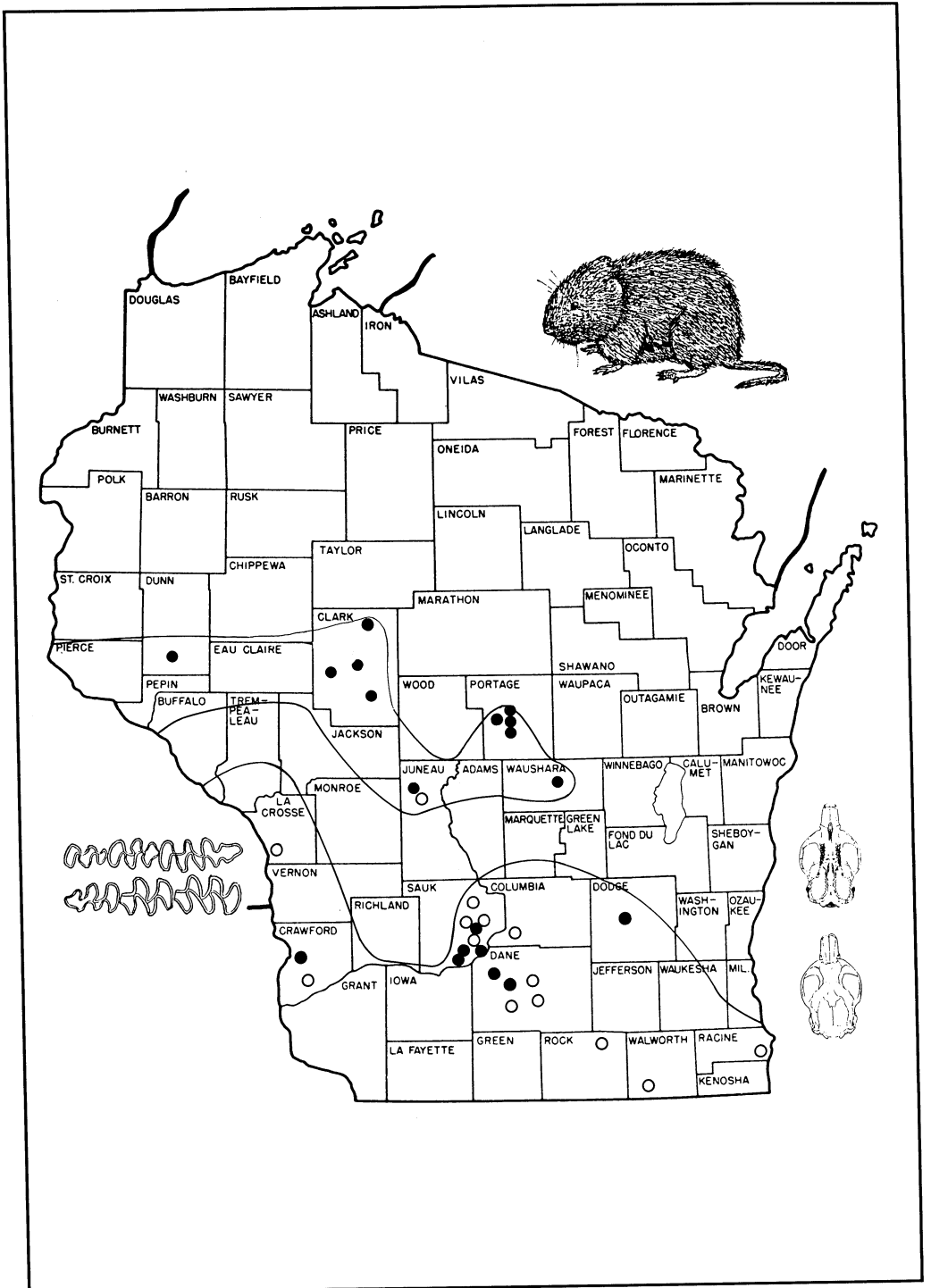
Fig. 2. Distribution of Pitymys ochrogaster. P. o. minor *is known from thin soil glacial sands to the northwestward. The southern race is* P. o. ochrogaster. *Upper and lower molar tooth-rows. Open circles, Jackson's (1961) records. Racine Co. After Amin.*

more richly ochraceous. The most constant difference between the common and minor prairie voles is size, but the common prairie vole has longer and broader nasals, and the auditory bullae tend to be relatively less inflated.

Measurements: According to Jackson (1961), the total length varies up to 160 mm, tail to 40 mm, hind foot to 20 mm, total weight to 50 g, and total skull length to 28.1 mm. The three adult males from Lynxville, in extreme southwestern Wisconsin, are clearly referable to the larger, nominate race in all measurements taken (see Table 4). Specimens from Beaver Dam and Pleasant Valley Road, in southern Wisconsin, are comparably large. Even the oldest and largest specimens from near Stevens Point are smaller than these specimens.

Specimens examined: Total, 23. See Table 5. Other records are in Jackson (1961). See also. Amin (1974) and Amin and Thompson (1974).

Minor Prairie Vole

Pitymys ochrogaster minor (Merriam), 1888, new combination.

Arvicola austerus minor Merriam, Amer. Nat. 22:600; type from Bottineau, North Dakota.

Common Prairie Vole	Pitymys ochrogaster	
Specimens Examined:	**Total - 23**	
County:		
Crawford County:		
Lynxville		3 USNM
Dane County:		
Beeny, Sec. 18, T8N, R7E		1 UWM
5 miles N. Cross Plains		1 UWM
Dodge County:		
Beaver Dam		1
Rock County:		
Milton		5 UWM
Sauk County:		
Pleasant Valley Road, near Sumpter Church		3
1/4 - 3/4 mile S., 2 miles W. Prairie de Sac		2
3 miles W. Prairie de Sac		3
4 miles W. Prairie de Sac		4

Table 5

Long (1976) first reported this diminutive vole in Wisconsin, extending the known range 218 miles eastward, in small local populations living on railroad rights-of-way and thin outwash sands of brushy, grassy fields. Two taxonomists have suggested that *M. o. minor* is a species because of its peculiar and distinctive behavior and small size. In Wisconsin there is no evidence of intergradation of the two prairie voles, but woodlands separate them a distance of 50 miles (between Waushara and Dodge counties) and 40 miles (between Juneau and Sauk counties). The minor vole hardly varies in size from central Wisconsin into North Dakota, but Swanson (1945) reported intergradation with large *M. o. ochrogaster* in Southeast Minnesota. Another thing to keep in mind is the close similarity of skulls and dentitions of *minor* and *ochrogaster*.

Measurements: The decidedly small dimensions of the skull are seen in the means of Old-Adult voles shown in Table 6.

Specimens examined: Total, 29. See Table 7.

Status: This vole was never common in Wisconsin, and in Portage County all known localities of occurrence have been so drastically disturbed by plowing and urban de-

Common Prairie Vole	Pitymys ochrogaster	
3 Specimens From Lynxville, Wisconsin		
External Measurements in mm:		
Total Length	153	(152 - 155)
Tail Length	39	(38 - 40)
Hind Foot	18.7	(18 - 19)
Weight in gm	47	(44-50)
Cranial Measurements in mm:		
Length of Skull	26.8	(25.8 - 26.9)
Condylobasal Length	26	(25.3 - 26.5)
Maxillary Tooth Row	6	(5.6 - 6.5)
Zygomatic Breadth	15	(14.9 - 15.1)
Cranial Depth	9.63	(9.6 - 9.7)
Interorbital Breadth	4	(3.95 - 4.1)
Nasal Length	7.55	(7.5 - 7.6)

Table 4

Measurements of the Minor Prairie Vole			Cranial Measurements in mm		
Old-Adult Vole Specimens From:					
	Goodall, ND	Elk River, MN	Ft. Snelling, Mn	Clark Co., WI	Stevens Point, WI
Number	5	3	2	1	6
Greatest Length Of Skull	24.07	24.33	23.74	25.93	24.6 (24.1 - 25.6)
Zygo-matic Breadth	12.35	13.05	12.88	13.4	13.7 (13.5 - 13.9)
Lamb-doidal Breadth	10.39	10.51	10.31	11.4	11.2 (10.8 - 11.4)
Nasals	6.66	6.73	6.75	7.0	6.59 (6.7 - 7.3)
Inter-Orbital Breadth	3.43	3.42	3.7	3.8	3.95 (3.8 - 4.05)

Table 6

velopment that the subspecies may have been extirpated. No specimens have been obtained for ten years in spite of intensive efforts to find them. Efforts should be made to preserve this species and its habitat, perhaps by introductions onto sandy upland prairie preserves.

Genus *Microtus* Schrank

Teeth elaborate, lower first molar with deep constrictions forming separate islands or prisms, five salient angles between anterior island and posterior loop, upper third molar elaborate, with three closed prisms (salient angles) between anterior and posterior loops.

Meadow Vole

Microtus pennsylvanicus pennsylvanicus (Ord)

1815. *Mus pennsylvanica* Ord. In Guthrie, A new geography, 2nd Amer. ed., vol. 2, p. 292.
1895. M[*icrotus*]. *Pennsylvanicus*, Rhoads. Amer. Nat., 29:940.

1841. *Arvicola fulva*. Audubon and Bachman. Proc. Acad. Nat. Sci. Philadelphia, 1:96. Type from a western state, probably Illinois.

Minor Prairie Vole Pitymys ochrogaster minor	
Specimens Examined	Total - 29
County:	Number
Clark County:	
Brick Creek, near Owen-Withee	1
Foster Twsp.	2 UWM
No Specific Locality	1
Juneau County:	
4 1/2 mile N., 1 mile W. Necedah	2
Portage County:	
Stevens Point	14
Whiting	2
Plover	5
8 miles S. Stevens Point	1
Waushara County:	
Saxeville	1 UWM

Table 7

1858. *Arvicola riparia* var. *longipilis* Baird. Mammals. Reports Expl. Surv. . . . 8(1)1524, type from West Northfield, Illinois or Racine, Wisconsin.

The scientific name *Microtus pennsylvanicus* means the mouse has small ears and was found near ("Meadows south of") Philadelphia. This vole resembles *M. agrestus* of Eurasia.

Description: Usually the largest, darkest vole in Wisconsin, often exceeding 160 mm total length. Long blackish tail, blackish gray-brown feet, and belly overcast with whitish, pale buff (occasionally rust, red, or cinnamon buff). The skull is long, the rostrum and nasals long and narrow, and the braincase well extended posterior to the zygomata. The upper third molar consists of an anterior loop, three closed prisms, and a *distinct* posterior crescentic loop. In the middle upper molar an extra small *posterior loop* is squeezed in, rarely absent in adults. The lower first molar is pinched in anteriorly, so that there are five closed prisms behind the anterior loop. This species is identified with certainty by the loop of the middle upper molar, and the identification confirmed by the extra prisms in upper third and lower first molars. The skull is long (up to 28.6 mm), the yellow incisors projecting beyond the nasals. The incisive foramina exceed 5 mm in length. There is a *slight reddish* (not ochraceous) *cast* in the *dark walnut brown upperparts* (especially in late summer and fall), which are evenly colored and hardly grizzled at all. The dorsal pelage, long and lax in winter, is remarkably constant throughout the state. Little individual variation is shown except in rare albinism in southeastern Wisconsin and a gray specimen with hairs whitish basally from Portage County. The black eyes seem small, and like the ears are fringed by coarse guard hairs.

In ventral coloration the range of whitish to buff to buffy ochraceous varies remarkably, as can be seen by the following values based on a scale of pale to dark ochraceous, one to five. The standards are (1) UW-SP No. 1610 pure silvery white; (2) buffy white No. 377, (3) whitish buff No. 1089, (4) buff No. 947, (5) buffy ochraceous No. 3190 or 2259, all aforementioned specimens from central Wisconsin, and (5) dark ochraceous No. 4579 from Waupaca Co., 4851 from Vernon Co., or 5024 from Clark County. From Marathon, Wood, and Portage counties a large sample was analyzed and fell into these frequencies: pure silvery white 1; buffy white, 16; whitish buff, 37; buffy ochraceous 46; dark ochraceous, 4. The frequencies were hardly dissimilar in other parts of Wisconsin. Of course, all ventral pelages were gray basally. From this it follows that *Microtus pennsylvanicus* cannot always be distinguished from *Pitymys ochrogaster* by the color of the belly for the color is often ochraceous. However, *whitish venters* are characteristic of *pennsylvanicus*.

Jackson (1961:230) described mutants from Wisconsin: yellow from Alderly, Dodge County, and two albinos from Madison and another from Lake Koshkonong. A pink-eyed albino in the UW-SP collection (No. 1792) is from Dodge County, and a partial albino (No. UWSP-6261) is from Horicon Marsh. This vole was normal above except for a faint intermixture of white hairs below the ears and approaching the vibrissae. The left hind foot was normal, the other three feet white. The tail was normal. The venter was pure white without gray at the hair bases.

Measurements: Total length to 188 mm. (but large meadow voles seldom exceed 165 mm), tail 42 to 56 mm, hind foot 20 to 23 mm, ear 20 to 23 mm. Wts. vary to 56 g. Greatest length of skull varies to 28.6 mm, width to 15.8 mm (see Jackson, 1961:231).

Distribution: Statewide, but restricted from most islands in Lake Michigan and Lake Superior, dense forests, and dry, sandy prairies. See Figure 3.

Habitats: Wet, grassy or weedy soils, fields, wet meadows, marshes, bogs, riparian grassy shores, and grassy glades in open woodlands. Occasionally in cultivated fields, often on lawns and gardens, and rarely in houses.
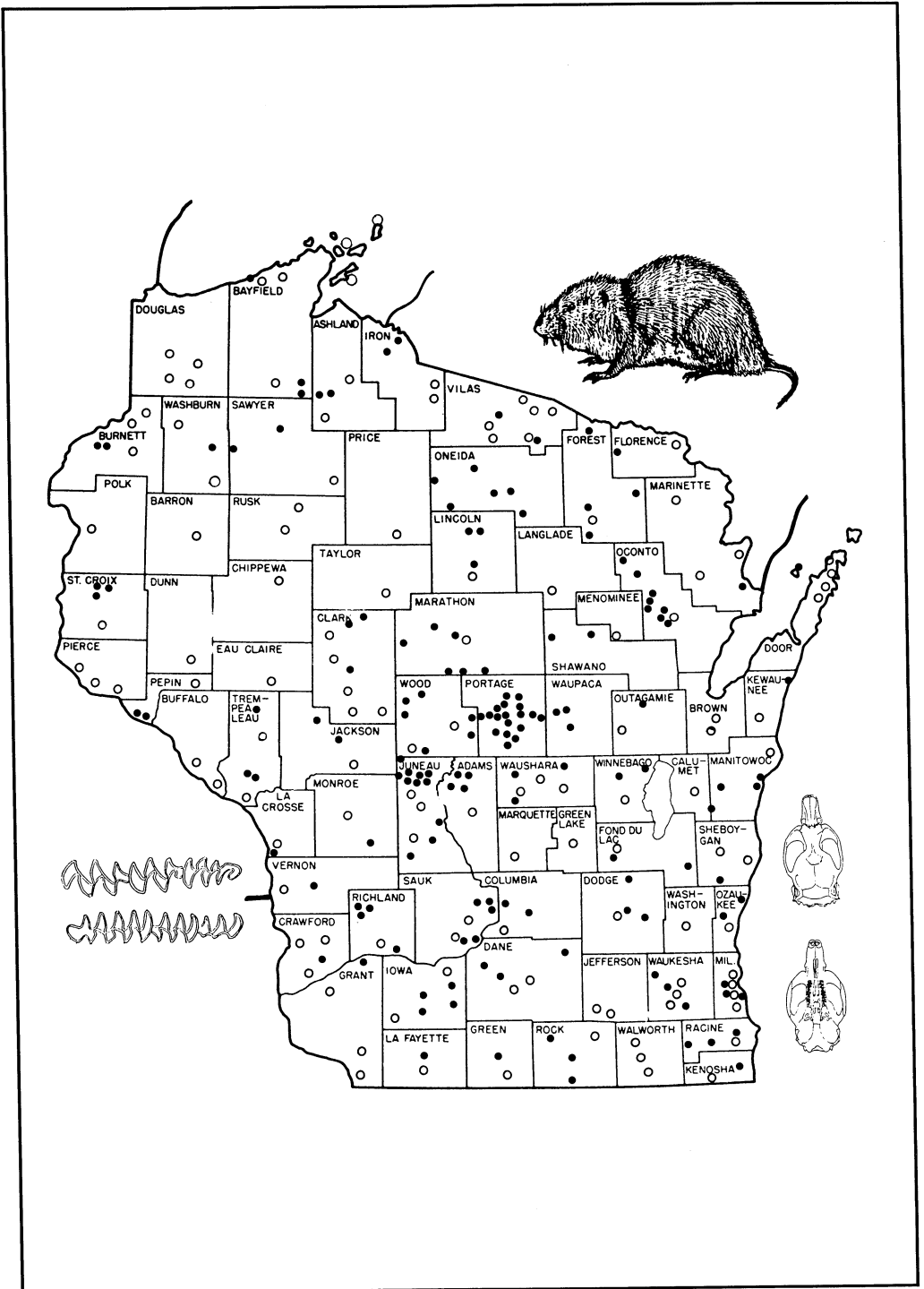
Fig. 3. Distribution of Microtus pennsylvanicus pennsylvanicus, *which occurs in every county in the state. Upper molar tooth-row and lower. Open circles, Jackson's (1961) records.*

Jackson rated the meadow vole as the second most abundant mammal in Wisconsin, exceeded possibly by the short-tailed shrew. In my field work I find the white-footed mouse to outnumber them both, except in dense forest, wetlands, and the northern counties. Probably the meadow vole is most abundant there. The meadow vole is found in every county in Wisconsin. Hamerstrom (1986) discussed the 4–5 year cycle of abundance and its profound effects on harriers *(Circus cyaneus).*

Microtus can breed every month of the year (Jackson 1961:233) and usually continue in central Wisconsin into November, a full month later than in the *Peromyscus.* The litter size varies from two to nine, and is often seven. In 27 pregnant Wisconsin specimens observed, the mean was 5.2; modes 4, 6; observed range was 4–8; the peaks of breeding were April and July; and females were found pregnant from March to October (lactating to 14 November).

The meadow vole prefers black soils and wet environments due to a need for water. It swims well, even diving, and young have been seen running over water surfaces. The nest of grasses and leaves is often on the ground surface, occasionally in a burrow eight or nine inches below ground. Foods include grass, sedges, grains, seeds, and carrion.

Specimens examined: Total, 548. See Table 8. Other records in Jackson 1961: Long 1974. The species is widespread in Upper Michigan as well (Baker 1983).

Genus *Clethrionomys* Tilesius, 1850

Teeth small and primitive, occasionally rooted in adults, salient projections less pointed (more arcuate) then in *Microtus* or *Pitymys,* upper third molar elaborate, posterior palate shelf-like.

Red-Backed Voles

Clethrionomys gapperi (Vigors)

Gappers Red-Backed Vole

1830. *Arvicola gapperi* Vigors. Zool. J.,
5:204. Type from between Toronto and Lake Simcoe, Ontario.
1928. *Clethrionomys gapperi gapperi,* Green. J. Mammal., 9:255, August 9.

The scientific name means a swamp alder mouse, and Gapper was a man's name.

Description: This small vole has a weakly built skull, having delicately and neatly arranged folds and prisms in the cheek teeth, and pale yellow incisors. It is easily recognized by its *russet* or *chestnut reddish-brown dorsum,* set off by ochraceous (almost yellowish)-grayish-tan sides. The sides are usually flecked with dark blackish gray, a false pattern of guard hairs, but actually the gray bases of the hairs show through the coarse pelage. (There are a few brownish guard hairs in dorsal and lateral pelage evident under the microscope.) The ventral surface is *whitish,* either a pure or grayish white, although from place to place up to 40 percent may have pale ochraceous buff or cinnamon buff (e.g., UWSP-1497, 6075, and others). The pale coloration is conspicuous on the throat and lower cheeks and extends often as a ventral line to whitish feet and claws. The general effect is a tri-colored mouse, red-brown, gray-orange, and whitish. The tail is medium in length. There are six tubercles on the hind foot. In juveniles the coloration is not fully developed, so the dorsum and sides are rich rusty brown with just a tinge of russet, and the venter is brownish or gray with just a tinge of white. However, in young mice even the smallest seem to have bright adult coloration in winter. (Apparently the hair protection develops rapidly, much more so than in summer.)

The skull is small and rather circular in profile. No other arvicoline has such a shelf-like or straight posterior border of the palate (actually the anterior border of the pterygoid fossa or posterior nares). The upper third molar has an anterior loop, three closed prisms, and a selenodont or crescentic posterior loop, resembling the pattern in *Microtus.* However, the more *arcuate angles* are more even in linear arrangement, and more delicate, the tiny prisms neatly outlined. The

upper middle molar consists of an anterior loop and three closed prisms (which is ordinary in arvicolines). The lower first molar might be said to terminate with *two* posterior loops in tandem, only two enclosed areas intervene between the complex anterior part and the last loop. The anterior portion is pinched so that a tiny inner salient angle may occasionally be closed off as well. The third lower molar is distinctive in its three similar and large outer salient angles all in a row, and three small inner salient angles neatly arranged opposite. The teeth are narrow and small.

Colors are highly variable, and large samples are essential to compare colors from place to place. Nevertheless, the range of variability is constant geographically. There is only one geographic race in Wisconsin and Upper Michigan.

Comparisons: The coloration (reddish dorsum, whitish venter) and dentition clearly distinguish this species from all other arvicolines in Wisconsin. The longer tail clearly sets a red-backed vole apart from the short-tailed (woodland) pine vole and southern bog lemming.

Measurements (Jackson, 1961:225): Total length varies to 150 mm, tail only 32–42 in adults, hind foot 18–20, ear 14 to 16. Weights vary to 36 grams. Total length of skull varies only to 24.8 mm, width of cranium 12.0 to 13.6 mm.

Distribution: Northern woodlands and swampy communities. See Figure 4.

Habitats: The red-backed voles occur in boreal forests. In Wisconsin they are found on several islands in Lake Superior and Lake Michigan, and throughout the North Woods (the pine-maple, hemlock, and spruce-fir woodlands), occurring always in the presence of at least a few trees. They dwell in swamps, bogs, and marshes as well as on forested hills and the slopes of valleys. They live in complex burrows usually below a stump or dead-fall tree. On Big Summer Island, Michigan, which is in Green Bay, red-backed voles tunneled as might moles, short-tailed shrews, or *Pitymys* (Long 1978). These voles are less specialized for eating grass, and they feed on nuts, seeds, and small arthropods. In Wisconsin this forest species does not range far into the southern deciduous woods or southern and western prairies. They are thought to be rather solitary, but Pitts (1983) caught six adults in the same tunnel beneath a decayed stump.

Home range is about 1,000 square meters, habits mostly nocturnal, and the females have two to four litters per breeding season, of three to eight young (Jackson 1961). There are eight mammae. In only seven observed breeding females some breeding was noted in winter, pregnant specimens observed from February to late September (lactation and juveniles in November). The mean litter size was 4.75, two modes 3, 6, and the observed range 3 to 6. A female from Poverty Island, Michigan, had six embryos in August.

Status: Abundant in suitable habitats, wide-spread in northern and eastern Wisconsin, and in no peril. Harmless to man.

Remark: One female specimen (UW-SP 1040) from 15 mi. E. Stevens Point was belted with pure white mid-dorsally, nearly all around, the ventral white extending fairly continuously, forward to each manus.

Specimens examined: Total, 296. See Table 9.

Other Records: See Map. Also see Jackson 1961; Pitts 1983 (Monroe Co.); Johnson 1978 (Door Co.); Kewaunee Co., personal corr. Neville Museum; Long 1974. The species is widespread in Upper Michigan as well (Baker 1983).

Genus *Synaptomys* Baird, 1858

Teeth specialized, entrant angles deeper on one side, shallow on the opposite, so that prisms extend as nearly transverse lophs across the tooth surface, the salient angles reduced on outerside of lower molars, inner side of upper molars, upper incisors slightly grooved along outer border.
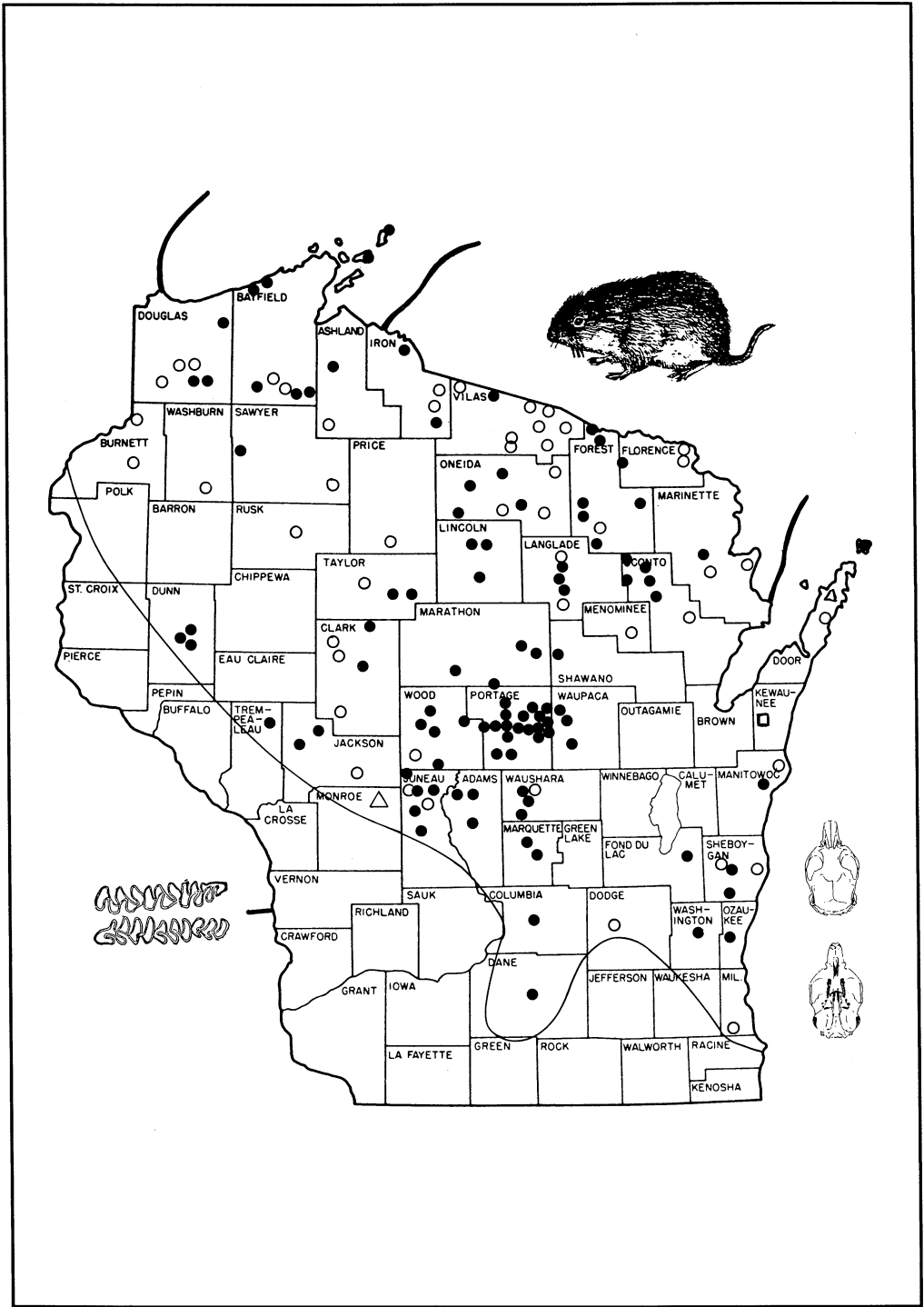
Fig. 4. Distribution of Clethrionomys gapperi gapperi. *Restricted from prairies. Upper and lower molar tooth-rows. Open circles, Jackson 1961; Large triangle, Pitts 1983; small triangle, Johnson 1978. Square, personal report Neville Museum.*

Meadow Vole *Microtus pennsylvanicus* — Specimens Examined - Total 548

County	Number
Adams County:	
Rome Twsp.:	
Sec. 25, T20N, R5E	1
Section 16, T19N, R5E	2
Monroe Center	2
Richfield Twsp.	1
Ashland County:	
Clam Lake	1
6 miles S.E. Clam Lake	111
6 miles E. Ashland	2
Bayfield County:	
Chippewa Lake (at Clam Lake Field Station)	21
Drummond	5
Port Wing, T50N, R8W	1
Burnette County:	
Barrens	1
Crex Meadows	3
Clark County:	
Hixon Twsp.	4
Hoard Twsp.	5
Globe	1
Columbia County:	
Sandhill Wildlife Refuge	1
Hinkes Lake	1
Poynette	2
10 miles S.W. Columbus	1
Crawford County:	
Steuben	1
Dane County:	
Black Earth	5
Section 30, T9N, R11E	3
10 miles W. Madison	1
York Twsp.	3
No Specific Location	1
Juneau County:	
Castle Rock on the Wisconsin River	2
Necedah Wildlife Area:	
Section 3, T17N, R7E	1
Section 4, T18N, R3E	1
Section 12, T19N, R2E	1
Section 13, T20N, R2E	3
2 miles W. Necedah	1
8 miles N. Necedah	2
Union Airport, Section 28	1
Meadow Valley Wildlife Area:	
Section 1, T18N, R2E	2
Section 6, T20N, R2E	1
Lemonweir River	4
Section 3, T17N, R2E	1
Kenosha County:	
5 miles W. Kenosha, Hwy. 50	10
Kewanee County:	
2 miles N. Algoma	1
LaCrosse County:	
Goose Island	1
Lafayette County:	
No Specific Locality	1
Lincoln County:	
Tomahawk	3
1 mile E. Tomahawk	1
Merrill	2
Manitowoc County:	
E. Hwy. 141	1
Kiel	1
Manitowoc	6
Manitowoc River	5
Collins Marsh	1
Ozaukee County:	
3 miles N. Lake Church	2
Cedarburg Bog	1
Pepin County:	
3 miles N.E. Pepin	3
Section 36, T23N, R15W	1
Portage County:	
Stevens Point	49
10 miles N.E. Stevens Point on Plover River	4
Jordan Park & Marsh	13
Haymeadow Creek, 5 miles N. Stevens Point	10
6 miles N. Stevens Point, on Wisconsin River	2
2 miles W. Stevens Point	5
3 miles W. Stevens Point	3
6 miles W. Stevens Point	1
Whiting	5
5 miles E. Stevens Point	3
1-2 mile N. Stevens Point	5
1 1/4-2 miles N.E. Stevens Point	2
8 miles S.E. Stevens Point	5
Isaac Walton Wildlife Area, Stevens Point	1
2 miles E. Stevens Point	4
5 miles E. Plover, Hwy. B	2
Stockton Twsp.	1
Tomorrow River	1
Plover	2
8-10 miles E. Stevens Point	2
8-10 miles S.W. Stevens Point	4
Heigs Farm, near Polonia	1
Sawyer County:	
Stone Lake	1
Lake Chippewa Island	1
Shawano County:	
Gresham	1
Eland	1
Sheboygan County:	
Random Lake	3
St. Croix County:	
4 miles S.E. Star Prairie	1
Section 17, T31N, R17W	1
5 miles S. New Richmond	1
No Specific Locality	1
Trempeleau County:	
2 miles S. Galesville	2
2 miles S.E. Galesville	1
1 miles W. Strum	1
2 miles E. Strum	1
Vernon County:	
Viroqua	1
Vilas County:	
Camp Eagle River	1
Musky Lake near Sayner	1
Walworth County:	
Springfield	1
Washburn County:	
Sarona	1
5 miles W. Stone Lake	1
Washington County:	
4 miles S.E. Hartford	7
3 miles W. Hartford	1
West Bend	1
Waukesha County:	
2.5 miles N.W. Muckwanago	1
North Prairie	2

Table 8

Dodge County:
3 miles W. of Hutisford — 1
Horicon Marsh — 5
2 miles E. of Juneau — 2
Door County:
Lost Lake Bog, Chambers Island in Green Bay — 1
Florence County:
Chipmunk Rapids — 1
Fond du Lac County:
Brandon — 1
1/2 mile S.E. Dundee — 2
Forest County:
Pickerel Lake — 1
Roberts Lake — 4
Alvin — 1
Armstrong Creek, Sec.13 — 3
No Specific Locality — 1
Grant County:
Blue River — 1
Green County:
Monroe — 1
Iowa County:
3 miles E. Hollandale — 2
Mineral Point — 2
Ainslies Pond — 1
Barneveld — 1
No Specific Locality — 1
Iron County:
Hurley — 2
Montreal by Hurley — 1
Jackson County:
Hatfield — 1
2 miles E. Merrilan — 2

Marathon County:
16 miles N. Marshfield — 1
Mead Wildlife Area — 2
Wausau — 2
7.5 miles N. Miladore — 1
Gunther Twsp. — 2
Lake Dubay, Big Island — 2
Johnson Twsp.,Sec. 1 — 1
Marinette County:
8 miles N.W. Marinette — 1
Milwaukee County:
Wauwautosa — 1
Milwaukee — 1
Cudahay — 1
Monroe County:
6 miles S. Wilton — 1
Oconto County:
3 miles W. Oconto Falls — 1
4.5 miles W. Oconto Falls — 3
Mountain — 1
5 miles NE. Oconto Falls — 1
5 miles W. Suring — 4
11 miles NE. Suring — 2
Oneida County:
Willow Flowage — 1
Tripoli — 1
Noisy Creek, 5 miles S. — 1
Rhinelander — 1
Velvet Lake — 1
Section 26, T39N, R11E — 1
1.5 miles W. Hazelhurst, Upper Kanbashire Lake — 2
Outagamie County:
2 miles W. Nichols — 2

2-3 miles S. Stevens Point — 2
8 miles S. Stevens Point — 1
10 miles S. Stevens Point — 1
New Hope Twsp. — 1
Section 28, T24N, R8E — 1
Section 4, T21N, R8E — 1
Buena Vista Marsh — 2
3 miles E., 1 mile S.Stevens Point — 1
Dewey Marsh — 2
6 miles S. Lake Dubay — 1
Junction City — 1
No Specific Locality — 1
Racine County:
5 miles W. Racine — 1
Union Grove — 1
4 miles E. Burlington — 1
Richland County:
1/2 mile W. Gotham — 2
1 mile E. Viola — 1
2 miles E Viola — 1
4 miles E. Viola — 4
Rock County:
3 miles E. Beloit — 4
2 miles W. Afton — 2
5 miles S. Evansville — 2
Sauk County:
Prairie de Sac — 1
Pleasant Valley Road, 1/2 mile S. Hwy. C. — 1
Baraboo Wildlife Refuge — 2
Klondike Pond — 4
Devil's Lake — 1

Oconomowoc — 1
Weyer Road — 1
Waukesha — 4
Waupaca County:
Brekke Lake — 1
Scandanavia — 1
Waupaca — 2
Waushara County:
Section 8, T20N, R8E — 2
Richford Twsp. — 1
Long Lake — 1
4 miles S. Plainfield — 1
Winnebago County:
Menasha — 1
Winchester — 1
Wood County:
2 miles S.W. Kellner — 3
2 miles W. Auburndale — 1
Pittsville — 3
3 miles N.W. Arpin — 4
Sandhill Wildlife Area, near Babcock — 1
Rudolph — 1
10 miles W. Stevens Point in Wood County — 1

Red Backed Voles Specimens Examined - Total 296

County:	Number	County:	Number	County:	Number	County:	Number
Adams County:		Pickerel Lake	2	Mountain	1	1 mile N. Burbank Road, on Hwy. Y	2
5 miles S. Adams, Hwy. 13	1	Crandon	1	7 miles W. Mountain	1	6 miles S. Lake Dubay, Town of Dewey	1
Monroe Center	1	Nelma	2	5 miles W. Suring	1	Sec. 19, T24N, R10E	6
Quincy Twsp., Sec. 14, T16N, R5E	1	**Iron County:**		11 miles N.E. Suring	1	Sec. 24, T25N, R8E	3
Big Flats Twsp., Sec. 28, T19N, R6	1	5 miles S.E. Springstead	1	**Oneida County:**		Sec. 27, T25N, R8E	10
Ashland County:		Hurley	2	Velvet Lake	1	**Sawyer County:**	
Morgan Creek	1	**Jackson County:**		Long Lake, near Rhinelander	1	5 miles S. Stone Lake	1
6 miles S.E. Clam Lake	1	Hixton	2	Lake Tomahawk	6	**Shawano County:**	
Bayfield County:		4 miles E. Merrilan	3	Hazelhurst	1	Eland	1
Apostle Islands:		**Juneau County:**		No Specific Locality	6	**Sheboygan County:**	
Outer Island	1	Mulligan Ridge, Sec. 26, T15N, R2E	1	**Ozaukee County:**		Random Lake	1
Stockton Island	1	Daylight Hill, T14N, R2E	1	Cedarburg Bog	1	Plymouth	1
Drummond	11	8 miles N. Necedah	1	**Portage County:**		**Taylor County:**	
Chippewa Lake	11	2 miles W. Necedah	1	Stevens Point	9	16 miles E. Medford	1
Cable	2	Necedah Wildlife Area: Sec. 12, T9N, R2E	1	Whiting Woods, Stevens Point	1	Roosevelt Twsp.	2
5 miles E. Herbster	1	Lisbon Twsp., Sec. 28, T16N, R3E	1	4 - 6 miles N. Stevens Point	3	**Trempeleau County:**	
Port Wing	2	Meadow Valley Wildlife Area, Sec. 1, T18N, R2E	1	3 miles N. Stevens Point	2	2 miles E. Strum	1
Clark County:		**Langlade County:**		1 - 2 miles N. Stevens Point	5	**Vilas County:**	
Greenwood	1	Summit Lake	1	1 1/2 - 2 miles N.E. Stevens Point	11	Presque Isle, Sec. 32, T43N, R7E	2
Hoard Twsp., Sec. 18 T29N, R1W	4	Camp Susan	1	10 miles N.E. Stevens Point	1	**Washburn County:**	
Columbia County:		Kempster	3	15 miles N.E. Stevens Point	1	Sarona	1
Portage	1	**Lincoln County:**		10 miles W. Stevens Point	1	**Washington County:**	
Dane County:		1 mile E. Tomahawk	1	5 miles W. Stevens Point	1	West Bend	1
Town of Burke, Madison	1	Tomahawk	1	8 miles W. Stevens Point	1	**Waupaca County:**	
Door County:		Merrill	2	10 miles S.W. Stevens Point	1	7 miles N. Iola	1
Washington Island, Pedants Lane	14	Treehaven	1	Jordan Park and Swamp	15	Lake Iola, Iola	2
Douglas County:		**Manitowoc County:**				Waupaca	1
1/2/ mile S. Gordan	1	15 miles N. Manitowoc	1			Peterson Creek, 1/4 mile W. Rollofson Lake	1
8 miles W. Gordan	1	No Specific Locality	1			Town of New Hope	1

Table 9

Table 9 continued

Location	Count
Near Brule, Sec. 22, T47N, R10W	1
Dunn County:	
3 miles E. Menominee	1
5 miles E. Menominee, Elk Mounds Hunting Grounds	
2 miles N., 5 miles E. Menominee	1
Florence County:	
2 miles W. Chipmunk Rapids	2
Fond du Lac County:	
Mt. Calvary	1
Forest County:	
Alvin	6
Roberts Lake	3
Armstrong Creek, Sec. 13, T37N, R16E	2
Marathon County:	
1 1/2 miles S. Elderon	2
Sec. 31, T26N, R9E	4
S.E. Marathon County: 15 miles N.E. Stevens Point	2
Lake Dubay, Big Island	1
20 miles E. Wausau, Hwy. Z	
Guenther Twsp.	1
Marinette County:	
9 miles N.W. Crivitz	1
Marquette County:	
Harrisville	1
John Muir Park	1
Oconto County:	
2 miles E. Lakewood	2
Jct. Hwy. T and 64	2
Dewey Marsh	11
7 miles E. Stevens Point	1
5 - 5 1/2 miles E. Stevens Point	7
Tomorrow River	1
Sunset Lake	2
1 1/2 - 2 miles N. Jordan Pond	4
Lost Creek	1
2 miles N. Town of Hull	1
Amherst	1
8 miles N.W. Stevens Point	1
Sec. 28, T24N, R8E	2
Peterson Creek, 1/4 mile N. Hwy. B	1
2 miles E., 1/2/ mile S. on Hwy. 10	2
Collins Lake	1
Waushara County:	
Plainfield	1
1 mile S. Plainfield	1
4 miles S. Plainfield	2
Rickford, Sec. 33	1
Wood County:	
Pittsville	4
3 miles N.W. Arpin	7
Arpin, Sec. 7, T24N, R4E	1
Vesper	2
Sandhills Area, Babcock	1
Milladore	2

Southern Bog Lemmings

Synaptomys cooperi Baird

> *Synaptomys cooperi* Baird. Mammals. Report Explor. and Surveys Railroad to Pacific, Part 1, Mammals. page 558, 1858.
>
> *Synaptomys fatuus* Bangs. Proc. Biol. Soc. Washington, 10:47, 1896. Type from Lake Edward, Quebec.
>
> *Synaptomys cooperi fatuus,* Cory. The mammals of Illinois and Wisconsin. Field Mus. Nat. Hist. Publ., 153:237, 1912.

The name *Synaptomys* means a mouse link. It links the voles to the boreal lemmings. The name *cooperi* honors William Cooper of New Jersey who gave Fullerton Baird the type specimen. The type locality was fixed at Jackson, New Hampshire.

Description: This chunky mouse has *grizzled, coarse pelage* (except in winter), an *extremely short tail* as in *Pitymys pinetorum,* and ears mostly hidden by the fur. The upper parts are a coarse mixture of gray, pale ochraceous brown and dark brown or black guard hairs. The venter has a whitish, grayish, buffy, or tan ochraceous wash over dark plumbeous gray bases of the hairs. The feet are usually brownish but sometimes gray. There is usually a *faint groove* on the the anterior face of each incisor, along the outer edges. The skull is nearly square (subquadrate) resembling Arctic lemmings, because the braincase protrudes into the orbits, encompassed by the zygomata, and the rostrum is short. The *outer re−entrant angles* of the upper molars are exceptionally *deep,* whereas the *inner angles shallow,* so the upper teeth are zagged, but not zig-zagged. The lower teeth have the deep re−entrant angles on the inner side of the teeth. On the middle lower molar is a small outer prism (Fig. 5).

Comparisons: The *short tail,* coarse *grizzled fur, grooved incisors,* squarish braincase, and *odd re-entrant angles* distinguish this species. Externally the bog lemming resembles *Pitymys pinetorum,* especially in winter pelage. There is a superficial resemblance (breadth) in their skulls as well. There

Fig. 5. Distribution of Synaptomys cooperi. *On Washington and Rock islands, S. c. jesseni. S. c. gossii occurs in Crawford County. In Upper Michigan and most northern counties S. c. cooperi occurs. Upper and lower molar tooth-rows. Open circles, Jackson 1961.*

are three races in Wisconsin, the most distinctive of which is the white-footed insular race *jesseni*.

Measurements: See accounts of subspecies.
Distribution: See Figure 5.
Habitats: In black soils along streams, in bogs, wet forests, and in sedge meadows, red pine plantations, and bouldery ground. Runways are seldom seen. Feces are bright pale green. Irruptions sometimes occur, but are unknown in Wisconsin where this vole seems uncommon.

Cooper's Southern Bog Lemming

Synaptomys cooperi cooperi Baird

As defined by Wetzel (1955), the nominate race for the bog lemming occurs both east and west of Lake Michigan. It is characterized by a rather *narrow, high cranium.* All specimens examined in the University Museum collection, except those from Washington and Rock Islands, proved referable to *S. c. cooperi,* showing little variation in color. Some specimens had a rich reddish chocolate color intermixed with ochraceous, gray, and black. Winter specimens were bleached and less grizzled. Young specimens were darker brown. Specimens examined from the Upper Peninsula of Michigan were likewise referable to *cooperi.*

Using a scale from reddish to grayish brown, the dorsal pelage being lined with dark guard hairs and darkened from below by the underlying basal gray, the most reddish specimen, a rich reddish-chestnut brown was 5742 from Portage County, Wisconsin. A shade paler is 2197 from Crivitz. Next is 5038 from Bayfield County, where the light ochraceous color separates from the dark brown lines of the guard hairs, and finally the ordinary coloration—a grayish, ochraceous brown, as in 5626 from Bayfield County. Scaled from 4 to 1, all the adult and probably mature bog lemmings were compared against this standard, and the color values recorded.

A specimen from Fish Hawk Lake, Gogebic County, Michigan, was reddish (3). From Menominee County, Michigan, four speci-

mens averaged 1.5 (1–2). A vole from Delta County was 3.

From Bayfield County, Wisconsin, five specimens averaged 1.7 (1–2), and another with worn pelage (in June) was dark grayish, perhaps juvenile. Langlade County specimens were 1 and 3, mean 2.0; and an Oconto County specimen from Suring was 2. Two specimens from Crivitz were each 2.

A specimen from Marathon County was 1, Portage County 4, and Douglas County 1.

Specimens examined: Michigan, 6 UM. Wisconsin, 34. See Table 10.

Measurements: External measurements of four adult males from Drummond and cranial measurements of four adults from Gogebic and Taylor counties, Upper Michigan and Bayfield County (2) are given in Table 11.

White-Footed Southern Bog Lemming or Jessen's Bog Lemming

Synaptomys cooperi jesseni Long, 1986

Synaptomys cooperi jesseni Long, Mammalia, 51:324, 1986. Holotype, UW-SP6250, skin and skull from Swenson Road, T. Jessen's Place, Washington Island, Wisconsin.

In dorsal and ventral coloration the specimens from Rock and Washington islands (Long and Long 1988) resemble *S. c. cooperi,* but they have conspicuous white feet. The observed tails and all four feet on the specimens are grayish or plumbeous gray, as is common in juveniles elsewhere, but there is generally *pure white* distally, of the claws and toes. The toes and claws occasionally may be whitish in *Synaptomys cooperi cooperi,* but they are seldom pure white, the whiteness not nearly so extensive, not set off so cleanly by dark pelage of the feet, and not so constant. White toes are even fairly constant on the forefeet in the insular specimens.

Even the hind dew toes are white on the Rock Island specimen. They are white also on UW-SP 6548–49. All ten toes are pure white on these specimens. On Washington

Cooper's Southern Bog Lemming *Synaptomys cooperi* Specimens Examined	
Upper Michigan - Total	**6 UM**
UP Counties:	**Number**
Delta County:	
2 miles N.W. Fairport	1
Gogebic County:	
Fish Hawk Lake	1
Menominee County:	
5 miles N. Menominee	1
10 miles W.	
Stephenson	1
5 miles S.W. Banat	
Meadow	2
Wisconsin - Total	**34**
Wisconsin Counties:	**Number**
Ashland County:	
6 miles S.E. Clam Lake	9
Bayfield County:	
Drummond	12
Burnett County:	
Crex Meadows	1
Douglas County:	
Wascott	2
Langlade County:	
Camp Susan	3
Marathon County:	
7 1/2 miles N.E. Athens,	
on Big Rib River	1
Marinette County:	
9 miles N.W. Crivitz,	
Cnty. A	3
Oconto County:	
11 miles N.E. Suring	1
Portage County:	
Dewey Marsh	1
Taylor County:	
Near Medford	1

Table 10

Cooper's Southern Bog Lemming *Synaptomys cooperi* External Measurements in mm 4 Adult Males From Drummond:		
Total Length	113	(110 - 115)
Tail Length	16	(10 - 19)
Hind Foot	17.6	(17 - 18)
Ear from Notch	9	(5 - 10)

Cranial Measurements in mm 4 Adults from Gogebic and Taylor Counties, Upper Michigan and 2 from Bayfield County:	
Condylobasal Length	25.0+-.23 (24.4 - 25.5)
Nasal Length	7.05+-.05 (7.0 - 7.2)
Zygomatic Breadth	15.23+-.33 (14.6 - 15.7)
Lambdoid Breadth	12.25+-.12 (11.9 - 12.45)
Cranial Depth	
(with Bullae)	8.5+-.13 (8.2 - 8.8)

Table 11

does one specimen from Bayfield County, Wisconsin, but these, the best marked from the mainland, are less distinctive than the least whitish specimens on Washington and Rock Islands.

White toes were seldom observed on any forefeet of Mainland specimens, but all the front toes were pure white on the Rock Island vole, and toes of the front feet were white on seven from Washington Island. Some toes of the forefeet were white on the others also, except two of the eight specimens had only dark toes on the forefeet.

White toes seem a sporadically appearing character in bog lemmings, but on Washington and nearby Rock Islands it is ordinary and in fact constitutes a remarkable and conspicuous difference allowing the large majority of bog lemmings to be identified on sight. The geographic isolation of these bog lemmings from sedge meadows and fields on Washington and Rock Islands, with average differences in several cranial dimensions, leads to their recognition as a distinctive geographic race endemic to these isles. Long ago the Door Peninsula was an archipelago of seven islands, when lake levels were higher, enhancing geographic isolation of the bog lemmings (see Kowalke 1946).

Island, eight distinctively white hind toes (excluding dew toes) were seen in eleven specimens. Seven white toes were seen in the other two, and even in these there was at least a trace of white in all eight. In 22 adult and probably adult bog lemmings from mainland Wisconsin and Upper Michigan, white toes were seen only in five specimens. Some specimens from Menominee County, Michigan, show several white hind toes, as

Cuttings of sedge in the mouth of UWSP-6259 were 3, 4, 5, 5, 6 and 8 mm in length. Pregnant females were taken in April (5 embryos) and late September (3 embryos).

Measurements: External measurements of six adult males and three females from Washington Island and cranial measurements of six adults from Washington and one from Rock Islands are given in Table 12.

Remark: The race is named in honor of Tom Jessen, supervisor of Rock Island State Park, an amateur naturalist who obtained the first specimen and has helped on this and other natural history studies on the aforementioned islands.

Specimens examined: Total, 14. Rock Island Hq., 1; Washington Island, Swenson Road, Door Co., 6; Airport, on Airport Road, 7.

Goss' Southern Bog Lemming

Synaptomys cooperi gossii (Coues), 1877

This vole resembles *S. c. cooperi* also, but it is larger and relatively larger in many dimensions, especially the higher crania. The Wisconsin specimens, referred by Jackson (1961) to *gossii,* have wider incisors (1.9 mm) than in *cooperi* (1.6 mm). Specimens in southeast Minnesota and northeast Iowa have been referred to *gossii.*

This race is known only from Lynxville, Crawford County, and may occur in other places on dry hillsides and fields in southern and southwestern Wisconsin. The habitats seem to be quite different from those in northern Wisconsin.

Measurements (Jackson, 1961:224): No. 249, 769 USNM, adult male from Lynxville: total length 129, tail 22, hindfoot 19, ear from notch 14 mm, wt. 42 g., cranial length 27.7, width, 17.2, height 10.3 mm.

Remark: This race was named after the Kansan naturalist B. F. Goss, and the race occurs southward and westward as far as Kansas.

Specimen examined: Lynxville, 1 (USNM).

White Footed Southern Bog Lemming or Jessen's Bog Lemming
<u>Synaptomys cooperi jesseni</u>

External Measurements in mm
6 Adult Males, 3 Females from
Washington Island:

	Males	Females
Total Length	118	123
	(112 - 122)	(119 - 126)
Tail Vertebrae	17	18
	(15 - 19)	(16 - 20)
Hind Foot	19.4	19
	(18 - 21)	(17 - 20)
Ear from Notch	11	11.3
	(10 - 12)	(11 - 12)

Cranial Measurements in mm
6 Adults from Washington Island,
1 from Rock Island:

Condylobasal Length	24.63+-.2 (23.8 - 25.2)
Nasal Length	6.87+-.14 (6.3 - 7.3)
Zygomatic Breadth	15.67+-.03 (15.6 - 15.8)
Lambdoid Breadth	12.93+-.13 (12.6 - 13.4)
Cranial Depth (with Bullae)	8.62+-.11 (8.3 - 9)

Table 12

Summary

The numbers of specimens and mapping of them reveal that of the five species and nine races of arvicoline mice now recognized in Wisconsin only *Microtus pennsylvanicus* is abundant and widely distributed. It may be considered a pest. *Clethrionomys* is next in abundance, harmless, confined to northern forests. The other species are uncommon or rare, with limited and local distributions. In tolerable numbers they are beneficial and interesting members of Wisconsin ecosystems. The pine (woodland) vole is listed by the Wisconsin Bureau of Endangered Resources as rare enough for "special concern" (Watch List). *Pitymys ochrogaster minor, P. pinetorum, Synaptomys cooperi jesseni,* and *S. c. gossii* seem to be among the rarest of Wis-

consin animals. In this study the pine vole and prairie vole were both assigned to the genus *Pitymys*. Of the nine recognized races, three were not known to Jackson (1961). Two of his Wisconsin names are placed in synonymy.

Acknowledgment

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Key

Key to Wisconsin Voles and Bog Lemmings (Adults) All teeth are comprised of loops and prisms.

1. Upper middle molar with anterior loop, three closed prisms, and *one small posterior loop* or islet; posterior upper molar with anterior loop, three closed prisms and distinct posterior crescentic loop; anterior lower molar deeply constricted with five closed prisms and a posterior loop .... *Microtus pennsylvanicus* Meadow Vole

1.' Upper middle molar with anterior loop and only three prisms; posterior upper molar with two prisms, posterior loop not crescentic; anterior lower molar with fewer than five closed prisms between loop 2

2. Molars with deep re-entrant angles on one side only, opposite side comprised of sinuous arcs; each upper incisor with small groove near outer edge extending the length of the tooth .... *Synaptomys* 3.

3. Lower molars with shallow, sinuous re-entrant angles on outer or labial side; three large and one minute prisms on lower middle molar .... *Synaptomys cooperi* Southern Bog Lemming

3.' Lower molars with hardly any indentation (re-entrant angles) on labial side; three large prisms in lower middle molar. Known in Wisconsin or Michigan only from fossils .... *S. borealis*

2.' Teeth with regular re-entrant angles on both sides; upper incisors lacking grooves 4

4. Teeth small, neatly regular indentations, sometimes more curved than pointed, relatively thick enamel border; teeth rooted in adults, posteriormost loop of upper third molar irregular in shape; lower anteriormost loop deeply constricted as in *M. pennsylvanicus* with only three closed prisms and a posterior loop .... *Clethrionomys gapperi* Red-backed Vole

4.' Teeth large or medium; posterior prism of middle upper molar terminating abruptly in a shoulder or bulge confluent with salient angle, posteriormost loop of upper third molar often spear-shaped (subtriangular), lower anterior molar slightly constricted anteriorly and deeply constricted posteriorly with three closed prisms (and a posterior loop) behind this doubly constricted anterior loop .... *Pitymys* 5.

5. Tail exceptionally short; fur fleecy, walnut or reddish brown, forefeet with robust claws; skull broad, interorbital breadth more than half the distance between the tips of the nasals to posterior extensions of premaxillaries. *Pitymys pinetorum* Pine or Woodland Vole

5.' Tail not exceptionally short; fur coarse, grizzled buff or orange-brown, forefeet normal; skull narrow, interorbital breadth about half the length from tips of nasals to posterior extensions of premaxillaries behind the nasals .... *Pitymys ochrogaster (=Microtus ochrogaster)* Prairie Vole

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Interspecific Associations of Some Wisconsin Lake Plants

Stanley A. Nichols

Abstract. *Interspecific association was used to group 54 aquatic plant taxa found in 68 Wisconsin lakes. Three of the four groups formed could be explained by water chemistry, substrate preference, and turbidity tolerance. The fourth group appeared to be of intermediate preference to the other three groups. A number of species did not commonly associate with other species. They were often found in unique habitats. No significant negative correlation between species pairs was found. This makes it difficult to speculate about the causes of non-association among species.*

Interspecific association provides one method of objectively grouping species. Positive associations may result from similarities of adaptation and response to environmental conditions. They may also result from beneficial interactions such as mutualism or commensalism, favorable to one or both species. Negative associations may result from species preferring different habitats or from detrimental interaction such as resource competition or allelopathy.

Studies that relate species groupings to habitat factors generally fall into two types. One type relates species groups in a single lake to within-lake habitat differences (Mirsa 1938; Spence 1967; Carpenter and Titus 1984; Nichols 1971; Schmid 1965; Sheldon and Boylen 1977; Wilson 1937 and 1941). These studies assumed water chemistry is constant, and inlake variables such as water depth, sub-

strate type, fetch, sediment accumulation, light penetration, and water turbulence explain plant distribution. A second type concentrates on between-lake differences, which generally mean differences in water chemistry (Seddon 1972; Moyle 1945; Swindale and Curtis 1957; Pip 1979; Olsen 1950; Kadano 1982; and Lind 1976). Studies describing resource competition or allelopathy between aquatic plants are more limited and the results are not definitive (Agami and Waisel 1985; Engel and Nichols 1984; Nichols 1984; Seddon 1972; McCreary et al. 1983; Titus and Stephens 1983).

Interspecific association was used to group 54 aquatic plant species found in 68 Wisconsin lakes. This study builds on past studies by using both inlake (ie., substate, depth, and interspecific interaction) and between-lake (i.e., water chemistry and water clarity) habitat variation to interpret species groupings.

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Methods and Analysis

Between 1975 and 1983 detailed macrophyte surveys were completed for 68 Wisconsin lakes (Appendix A). The lakes were sampled by Wisconsin Department of Nat-
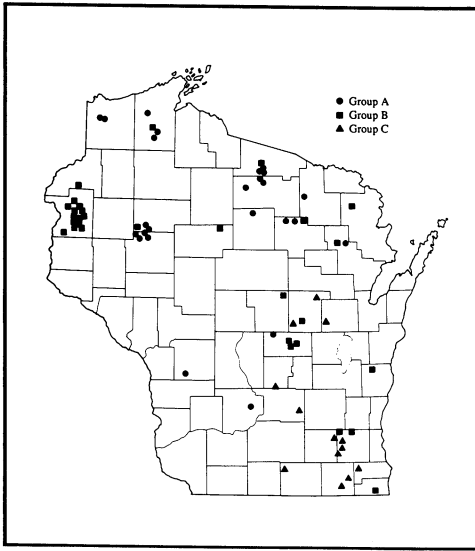
Fig. 1. Location of sampled lakes showing different lake types

ural Resources (WDNR) field staff or by private consultants for the WDNR Office of Inland Lake Renewal. The primary purpose of the surveys was to design lake-management strategies or to collect benchmark limnological data.

The lakes represent a broad range of Wisconsin lake types with regard to geographic distribution (Fig. 1), chemical and physical parameters, and human impact. Physical and chemical data were collected during macrophyte sampling or were collected earlier as part of surface-water resource inventories of each county (Appendix A).

Field methods

To assure geographic coverage of a lake, sampling points were selected using a grid system. Grid size and the number of sampling points per lake varied with lake size; i.e., larger lakes contained more sampling points on a larger grid. All plants within a 2-m diameter circle around the sampling point were recorded and were assigned a 1–5 density rank based on criteria established by Jessen and Lound (1962). Species not identified in the field were collected and sent to the

Wisconsin Geological and Natural History Survey for identification. Specimens were then sent to the University of Wisconsin-Madison herbarium as voucher specimens.

Analysis

Initially all taxa that were not identified to species except for *Chara* spp. and *Nitella* spp. and all taxa that had less than 15 total occurrences in the 8419 quadrats sampled were eliminated from further analysis. For the remaining species the joint occurrence in all quadrats for each species pair was summed, Cole's index (Cox 1967) of association was calculated (Appendix B), and chi-square was used to test the significance of the association. Bonferroni's correction (Snedecor and Cochran 1980) was used to account for random co-occurrence in the data. A chi-square value of 20, corresponding roughly to $p = 0.00001$, was used to determine significance of the association. This ensured an experiment-wise error rate of 0.05. If a species did not have a significant association with at least four species and an absolute sum of Cole's index values of at least 1.5, it was eliminated from further consideration. Ward's minimum variance cluster analysis (SAS 1985) was used to group the remaining 54 species. The absolute value of (Cole's index-1) was the distance measure used for clustering. This facilitated calculations by changing all distances to positive values and by assigning larger numbers to more dissimilar species. An importance value for each species in each lake was calculated by multiplying relative species frequency by average ranked species density. Theoretically, importance values could range from 0 to 500. Only sampling points with vegetation were used when calculating importance value.

Lakes were also clustered using Ward's minimum variance cluster analysis. The parameters compared by cluster analysis were total alkalinity, pH, total phosphorus, specific conductance, water color, secchi depth, chloride, free carbon dioxide, water fluctuation, and whether the water body was a lake

or reservoir. Lake clusters were compared to species clusters to examine patterns that might be attributable to habitat.

Correlation of importance values across lakes for all species pairs with a Cole's index greater than ± 0.5 was used to determine whether there might be species interactions shown by differing species abundances. Both Cole's index and correlation analysis test for association among species. Cole's index tests association based only on the presence or absence of two species in a quadrat; correlation analysis tests association based on the abundance of two species in lakes where they occur together.

Results

Species commonness

Ceratophyllum demersum is by far the most common species, occurring at nearly twice as many sampling points as the next most frequent species (Table 1). Only six other taxa—*Chara* spp., *Elodea canadensis, Najas flexilis, Potamogeton zosteriformis, Vallisneria americana* and *Myriophyllum exalbescens*—occurred at more than 10% of the sampling points (Table 1). More than one-third or 38 or the 111 taxa identified had less than 15 total occurrences. These species were eliminated from further consideration because their Cole's index could not be adequately tested using chi-square.

Cole's Index of Association

Of the remaining 73 species, Cole's index showed that 19 species did not commonly associate with many species or at a very high level. These species (Table 1) were eliminated from the cluster analysis because they did not meet the arbitrary criteria of associating with four other species and having an absolute sum of 1.5 for Cole's index values. However, it may be significant that they do not associate with other species. Potential causes for low association are discussed later.

As might be expected from the most common species, *C. demersum* was associated

with the greatest number of species (Appendix B). It was associated with 38 other species. *Chara* spp., *Brasenia schreberi,* and *Nymphaea odorata* were associated with 25 or more species. *C. echinatum, Megalodonta beckii, P. berchtoldii, P. diversifolius, P. nodosus, P. oakesianus, P. pusillus, P. strictifolius, P. vaginatus, Ranunculus longirostris, Sagittaria latifolia, S. rigida, Typha latifolia, Utricularia geminiscapa,* and *U. intermedia* showed only positive association with other species. *Chara* spp. was negatively associated with 20 species and had no positive associations greater than 0.5.

Species clusters

An analysis of pseudo F/pseudo t^2 provides a guideline for determining optimum cluster numbers (SAS 1985). This ratio indicates that 45, 32, 11, and 4 clusters might be optimum. It seems reasonable that there is more information about a cluster if the number of clusters is small and the species number per cluster is large. Therefore, for most purposes, four clusters (Fig. 2) were used to determine what adaptations, interactions, or habitat preferences might cause the groups to form. Each cluster could form for different reasons. Because of the individualistic nature of species, each cluster is not a unique entity that requires the rigid faithfulness of each species. Therefore, the clustering dendogram (Fig. 2) is included so that species associations can be examined without the constraint of the four-cluster classification structure.

Analyzing the cause of species groups

Correlation Analysis. No significant negative correlations between species pairs were found. Deciding whether a negative correlation was caused by competition, allelopathy, or unique and very different habitat requirements is, therefore, a moot point.

Because macrophyte community dynamics that appear to be caused by species competition and replacement of *Chara* spp. and *Najas flexilis* have been described (Nichols 1984; and Engel and Nichols 1984), and be-

Table 1. Species Occurrence

Species	% Quads Occur	% Lakes Occur	
SPECIES OCCURRING > 10% OF QUADS			**SPECIES OCCURRING IN >15 QUADS BUT <1% OF QUADS**
Ceratophyllum demersum	34.1%	66.2%	Ceratophyllum echinatum
Chara spp.	18.5%	52.9%	Dulichium arundinaceum
Potamogeton zosteriformis	16.8%	60.3%	Eleocharis acicularis
Elodea canadensis	16.4%	67.6%	* Eleocharis palustris
Najas flexilis	14.0%	61.8%	* Eleocharis robbinsii
Vallisneria americana	13.8%	64.7%	Eriocaulon septangulare
Myriophyllum exalbescens	11.9%	41.2%	* Isoetes echinospora
			Isoetes macrospora
SPECIES OCCURRING IN 1%–10% OF QUADS			
			* Lobelia dortmanna
Potamogeton richardsonnii	8.9%	45.6%	* Myriophyllum tenellum
Myriophyllum verticillatum	8.8%	17.6%	* Nuphar advena
Potamogeton amplifolius	8.4%	64.7%	Potamogeton diversifolius
Potamogeton robbinsii	8.2%	29.4%	* Potamogeton epihydrus
Potamogeton pectinatus	8.0%	47.1%	* Potamogeton filiformis
Potamogeton praelongus	7.4%	30.9%	Potamogeton nodosus
Nuphar variegatum	7.0%	57.4%	Potamogeton oakesianus
Nymphaea tuberosa	6.5%	38.2%	* Potamogeton obtusifolius
Myriophyllum spicatum	5.8%	13.2%	Potamogeton strictifolius
Heteranthera dubia	5.7%	38.2%	Ranunculus longirostris
Brasenia schreberi	5.1%	23.5%	* Ranunculus reptans
Potamogeton gramineus	4.9%	35.3%	* Ranunculus trichophyllus
Potamogeton crispus	4.7%	26.5%	* Sagittaria graminea
Nymphaea odorata	4.4%	25.0%	Sagittaria latifolia
Scirpus validus	4.2%	38.2%	Sagittaria rigida
Potamogeton natans	4.2%	41.2%	* Scirpus americanus
Lemna minor	4.2%	20.6%	* Sparganium chlorocarpum
Lemna trisulca	3.8%	14.7%	Sparganium eurycarpum
Potamogeton pusillus	3.3%	22.1%	Utricularia intermedia
Potamogeton foliosus	2.9%	13.2%	* Zanichellia palustris
Potamogeton illinoensis	2.4%	22.1%	
Megalodanta beckii	2.0%	13.2%	
* Pontederia cordata	1.9%	29.4%	
Myriophyllum heterophyllum	1.7%	2.9%	
* Nitella spp.	1.7%	17.6%	
Wolfia columbiana	1.6%	4.4%	
Typha latifolia	1.5%	27.9%	
Utricularia vulgaris	1.5%	5.9%	
Spirodela polyrhiza	1.4%	8.8%	
Potamogeton berchtoldii	1.4%	7.4%	
Polygonum amphibium	1.3%	8.8%	
* Zizania aquatica	1.2%	13.2%	
Myriophyllum farwellii	1.2%	1.5%	
Utricularia gibba	1.1%	1.5%	
* Najas marina	1.1%	4.4%	
Utricularia geminiscapa	1.0%	2.9%	
Potamogeton vaginatus	1.0%	2.9%	
TOTAL QUADS	8419	TOTAL 68	

* Species deleted from cluster analysis because of low association
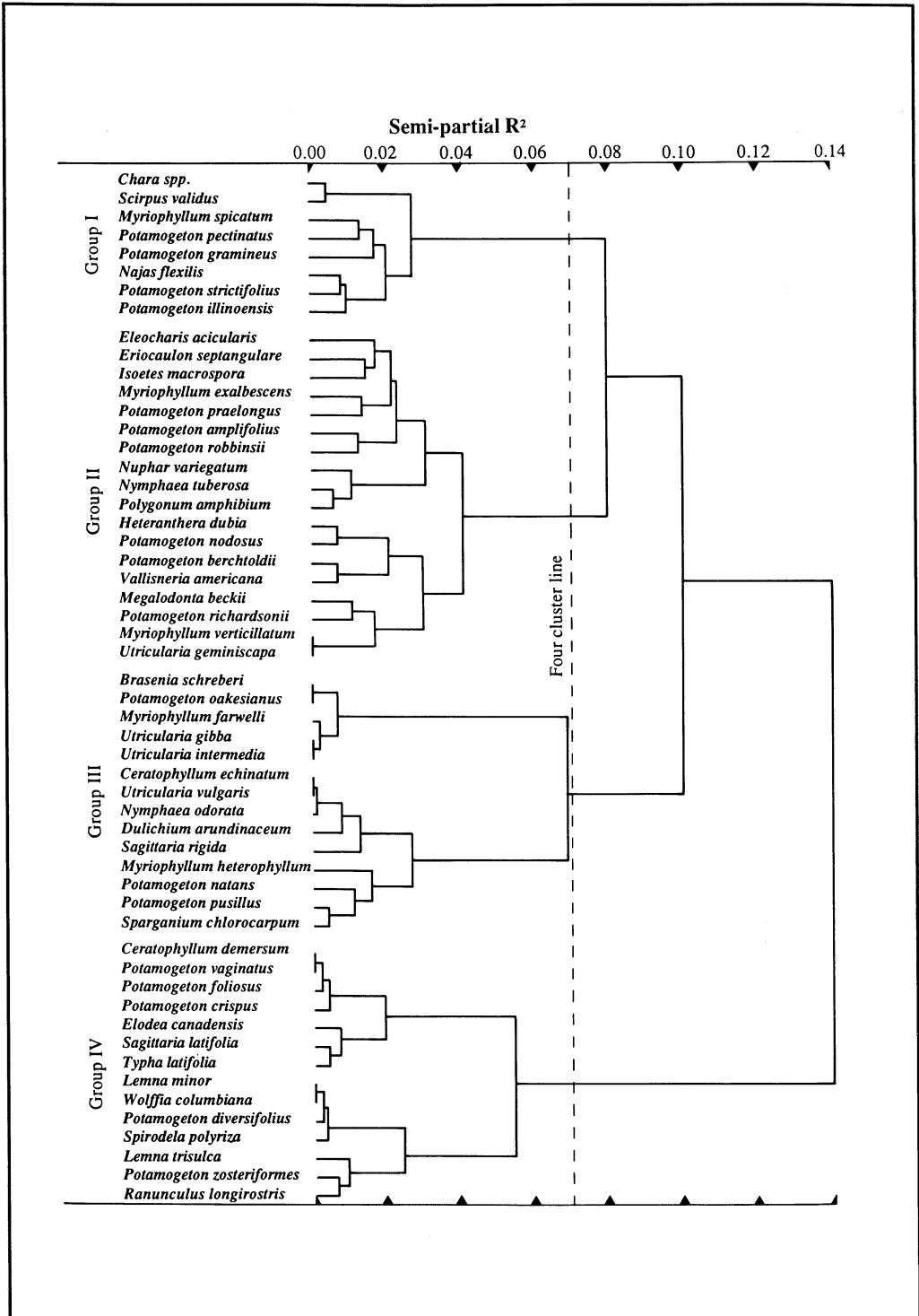
Fig. 2. Dendrogram of Ward's Cluster Analysis

cause there are a great number of negative associations with *Chara* spp. (Appendix B), correlation analysis was further used to test the hypothesis that competition is the result of the combined importance of other species with *Chara* and *N. flexilis* rather than competition between individual species. The correlation between the importance of *Chara* spp. and all other species in a lake was significant (p<0.05) but low (r= −0.29, n=68); the correlation between the importance of *N. flexilis* and all other species was not significant.

Significant positive correlations were found between 23 species pairs (Fig. 3). The majority of the species pairs belong to species Group III. There are no Group II species pairs; one Group I species pair and eight Group IV species pairs showed significant correlation. Most of the Group IV species involve small free-floating plants such as *Lemna* spp., *Spirodela polyrhiza,* and *Wolffia columbiana*. Later discussions will try to establish whether beneficial interactions or similarity in adaptations or habitat preference is the primary cause for positive correlations.

Habitat preference. Median alkalinity, pH, specific conductance, secchi disk, and free CO_2 values were calculated for each species that occurred in five or more lakes. These values were compared across species groups (Fig. 4). In addition, species substrate preference, turbidity tolerance, and median depth of growth (Nichols in prep.) were added to the figure.

Group III species are found in the lowest alkalinity, pH, and conductivity waters of the four species groups. They are also found in the most clear waters. All species except *Potamogeton oakesianus* prefer soft substrate or show no substrate preference. All species are tolerant of turbid water, show no turbidity preference, or the preference is unknown.

Group II species are found in more alkaline water with a higher pH and conductivity. They show little preference pattern for substrate or turbidity tolerance.

There appears to be little difference in the chemical regime between Group I and Group IV species. These groups occupy the most alkaline and the highest conductivity waters. Group I species generally prefer hard substrates and non-turbid water or they show no preference. They are also found in the highest pH water. Group IV species prefer soft substrates, but the turbidity tolerance is mixed. Group IV is found growing in the most shallow water, but the depth range is broad. The growth depth of the other three groups is similar.

Relating species clusters to lake clusters. Various investigators have correlated the distribution of aquatic plant species with single environmental gradients (see introduction). Community type is more likely affected by a complex of interacting factors. However, analyzing and describing a complex habitat is difficult. To approach the problem, multivariate (i.e., Ward's) cluster analysis was used to define three lake groups (Groups A, B, and C, Fig. 5). The lake groups are roughly geographically distributed in the state (Fig. 1). Total alkalinity and specific conductance are the two parameters that show the most unique distribution among the three groups (Fig. 5).

Group A lakes are located in northeast and north-central Wisconsin. They are lowest in total alkalinity and specific conductance. Group B lakes are more scattered geographically, but many are found in northwestern Wisconsin. They are medium in specific conductance and alkalinity. Group C lakes occur most frequently in southeastern Wisconsin. They have higher total alkalinity and specific conductance and lower maximum secchi and free CO_2 levels than the other two lake groups.

The average importance value per species was compared for each species group in each lake group via a t-test (Table 2). Each species group—except for species Group II in lake Groups A and B and species Group III in lake Groups A and C—showed significantly different average importance in each lake group (experiment-wise p<0.05; see previous reference to Bonferroni's correction). The average importance of species in Groups
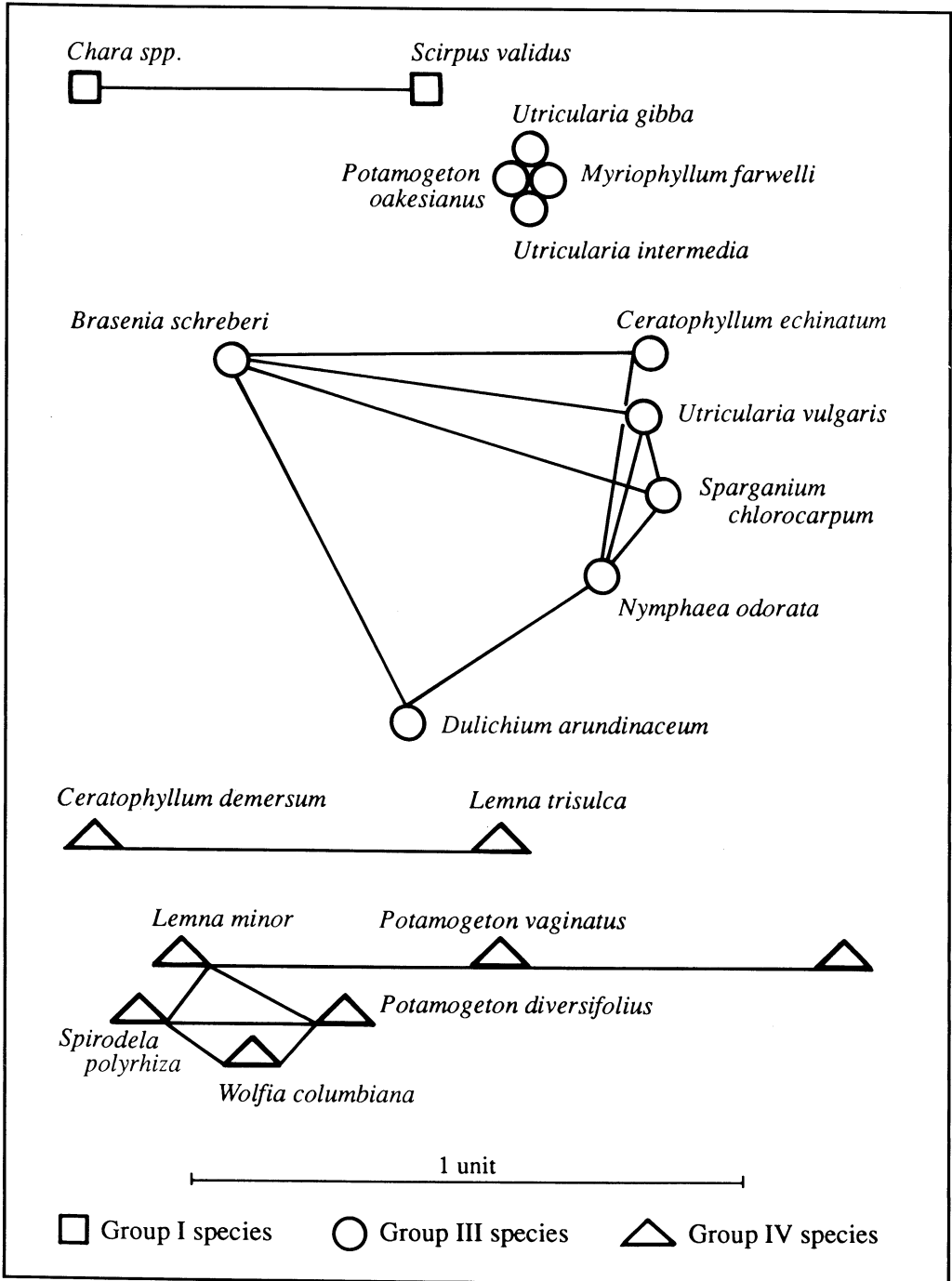
Fig. 3. Species constellations based on positive correlations

```
TOTAL ALKALINITY

GROUP I                            I---------(---[====+=========)]---I
GROUP II        I----------------------(---[+===)===]------I
GROUP III      I----(--[+======)===]-----------------I
GROUP IV        I--------------------(-[+)]-------I

mg/l CaCO₃    I    I    I    I    I    I    I   .I    I    I    I    I    I    I
              10             50                   100                  140

pH

GROUP I                         I--------[(====+==]--)-----------I
GROUP II        I-----------[==(=====+==]--)-----------------I
GROUP III       I-----[(====+]----)I
GROUP IV            I(-[==+========)=====]--------I

UNITS         I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I
              6.8   7.0              7.5              8.0              8.4

SPECIFIC CONDUCTANCE

GROUP I                         I------(----[===+=========)=]----I
GROUP II        I----------------------([====+====)==]-----I
GROUP III       I--(-------[+========)===]-----------------I
GROUP IV             I----------------(--[+==)===]----------I

umhos/cm      I    I    I    I    I    I    I    I    I    I    I    I    I    I
              20             100                 200                  300
25°C

SECCHI

GROUP I                             I-----[(=+==)]-------I
GROUP II                            I-----[==(+)]----------------I
GROUP III                           I-----------(--[=====+====]--)I
GROUP IV     I--------------------[(====+=====)==]I

m            I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I
             1.2                      2.0                          3.0

FREE CO₂

GROUP I       I----(([+)]---------I
GROUP II      I---[=(==+==)]---------------I
GROUP III      I-([=====+=====)====]-----------I
GROUP IV      I----(-[===+====)=]-----------------I

mg/l          I    I    I    I    I    I    I    I    I    I    I    I
              1.0             5.0                 10.0
```
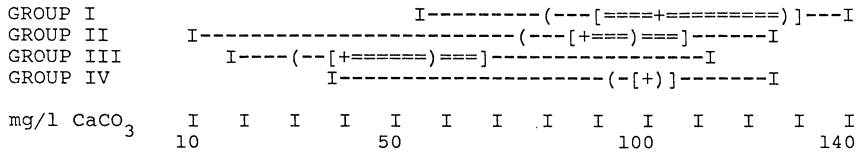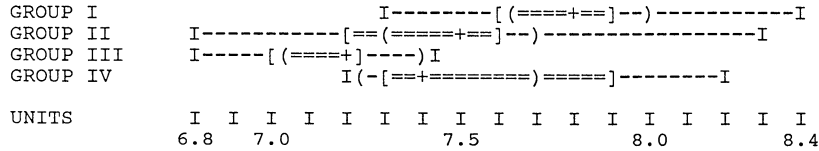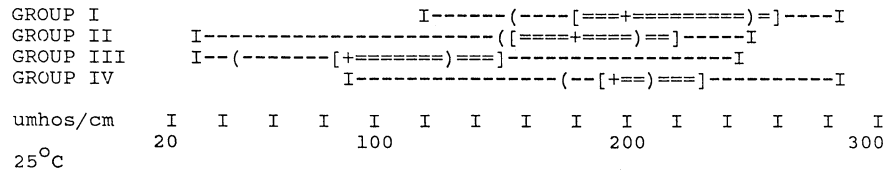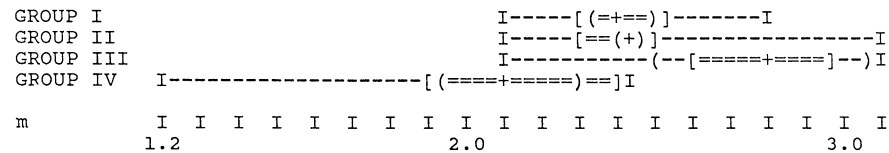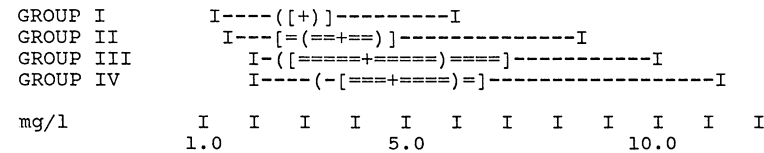
Fig. 4. Habitat values for species clusters

I and IV increased from lake Groups A to C. The average importance for species Group III dropped from Group A to Group B and then increased slightly in Group C lakes. The average importance of Group II species decreased in Group C lakes. Species Group I and IV never showed significant differences between each other within the same lake group. The average importance within Group A lakes is very similar. Group II and Group III species are significantly different only in Group B lakes.

This analysis supports results from the previous section. Group III species prefer low alkalinity, low specific conductance habitats. Group II species prefer medium alkalinity and specific conductance habitats. The water chemistry preference between species Group I and IV are similar. Both prefer the highest alkalinity and specific conductance habitats.

```
DEPTH OF OCCURRENCE

GROUP I                  I-----------(--[==+====)]--------I
GROUP II                      I--[==(==+==)=====]--------I
GROUP III                 I--------[(=+==)==]----------------------I
GROUP IV   I--[(===============+================)]-----I

m          I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I
           0.2      0.5              1.0            1.5            2.0

TURBIDITY

NUMBER OF SPECIES
                         NO
             TOLERANT    PREFERENCE    INTOLERANT

GROUP I       0          2             5
GROUP II      5          4             7
GROUP III     5          1             0
GROUP IV      4          2             2

SUBSTRATE PREFERENCE

NUMBER OF SPECIES
                         NO
             HARD        PREFERENCE    SOFT

GROUP I       4          4             0
GROUP II      6          4             8
GROUP III     1          4             9
GROUP IV      0          3             7
-------------------------------------------
Boxplot definitions follow Reckow and Chapra, 1983
I-Minimum or maximum, [-25% quartile, ]-75% quartile,
()-notch, +-median.
```

Fig. 4, continued

Extreme caution is necessary when interpreting these data. *Chara* spp. is so important in species Group I and *C. demersum* in species Group IV that the average importance of the group is largely influenced by these two species (Table 3). *C. demersum* is so pervasive that it is the most important species in Group A and B lakes even though it does not reach its maximum importance until lake Group C. Table 3 also shows how faithful each species is to the group preference.

Discussion and Interpretation

Non-associating species

Species that meet the criteria for commonness but show low association with other species tend to grow in monotypes or clumps in unique habitats that may not be conducive to more varied plant growth.

Isoetes echinospora, Lobelia dortmanna, Myriophyllum tenellum, Rannunculus reptans, R. trichophyllus, Potamogeton epihydrus, and *P. obtusifolius* are plants of soft, sterile water (Moyle 1945; Swindale and Curtis 1957) and hard bottoms (Nichols in prep.). Because they prefer similar habitats and in some cases have a similar growth form, it is surprising they do not associate with each other. However, it is not unusual for species of comparable growth form and habitat not to be found in the same lake (Seddon 1972) and not to associate with each other when they are found in the same lake (Carpenter and Titus 1984). Colonization pattern, colonial growth, or competition are plausible explanation for this segregation (Carpenter and Titus 1984). Seddon (1972) interprets this group as having a wide habitat tolerance

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```
TOTAL
ALKALINITY

GROUP A        I-[(+=)]--I
GROUP B              I---[(=+)]--I
GROUP C                        I---[(==+===)=]--------I

mg/l       I   I   I   I   I   I   I   I   I   I   I   I   I   I   I
CaCO₃      0              100            200            300

pH

GROUP A        I--------[(=+=)]------------I
GROUP B              I---[(==+===)=====]--------------I
GROUP C                    I------[(+=)]------I

UNITS      I I I I I I I I I I I I I I I I I I I I I I I
             6.0        7.0        8.0        9.0        10.0

SPECIFIC CONDUCTANCE

GROUP A        I-[(+)]-I
GROUP B             I-[=(==+=])----I
GROUP C                      I-([=+==)]--------------------I
umhos/cm   I   I   I   I   I   I   I   I   I   I   I   I   I   I   I
25°C       0         200        400        600        800

SECCHI

GROUP A           I----[======(=====+=====])--------------I
GROUP B         I---------[=(===+===)===]----------------I
GROUP C         I---[(====+=====)]-I

m          I   I   I   I   I   I   I   I   I   I   I   I   I
           0     1.0     2.0     3.0     4.0     5.0     6.0

FREE CO²

GROUP A        I-([=+==)===]-------------------------I
GROUP B        I[=(==+===)====]-----------------I
GROUP C        I[(+)]--------:---I

mg/l       I   I   I   I   I   I   I   I   I   I   I
           0    10     20     30     40     50
        ------------------------------------------------------
Boxplot definitions follow Reckow and Chapra,1983
I-Minimum or maximum, [-25% quartile, ]-75% quartile,
()-notch, +-median.
```

Fig. 5. Limnological characteristics of lake groups

but being excluded from more productive sites by competition rather than physiological limitation. Correlation analysis done in this study could not confirm competition, but these plants are so limited in distribution and have such a low importance value when they are found that correlation analysis does not provide an adequate test of their behavior.

Zizania aquatica, Eleocharis palustris, E. robbinsii, Pontederia cordata and *Scirpus americanus* are emergent species that often grow in monotypes, in shallow water, and

Table 2

Lake Group

Species Group	A	B	C
I	1.1	⌐3.6	⌐7.0
II	1.7	└2.0 ┐	└0.8 ┐
III	1.4	⌐0.2 ┘	└0.6 ┐
IV	1.5	└3.7 ┘	5.1 ┘

Lake Group

Species Group	A	B	C
I	1.1	3.6	7.0
II	1.7	2.0	0.8
III	1.4	0.2	0.6
IV	1.5	3.7	5.1

[⌐─ = Experiment-wise t values significant at p<0.05

---

on beaches. *Najas marina* was found in three southeastern Wisconsin lakes with extremely high alkalinity and conductivity.

It is possible that non-association could also be an artifact of the sampling procedure. Association analysis is sensitive to quadrat size (Grieg-Smith 1964). The sample area (i.e., a 2-m diameter circle) may not be appropriate for studying association in monotypic or colonial growth patterns.

Species interactions

Despite laboratory studies (Agami and Waisel 1985) and field observations (Engel and Nichols 1984; Nichols 1984; Seddon 1972) that support competition among aquatic species, data from this study support observation by McCreary et al. (1983) and Titus and Stephens (1983), who found little competition among selected aquatic species in transplant experiments.

The hypothesis that the positive correlation between species is the result of specific habitat requirements beneficial to both species is favored, especially for Group III species. Growth in soft water, typical of the habitat where Group III species are found, is depauperate and localized to areas of more fertile substrate (Moyle 1945). If all species in a lake are localized to a few areas of suitable substrate, their growth will appear correlated. All but one Group III species prefer soft sediments.

A stronger case for a passive mutualism or commensalism could be made for the positive correlation between *Lemnaceae* and other species. Larger species could provide protection from wind, waves, and current for these small, free-floating plants. However, they are not correlated with species in other plant groups that would offer them as much protection as Group IV species, and they are correlated with each other. One *Lemnaceae* species does not provide much protection to another species, although they could be distributed to the same location by wind or current. Specific habitat requirements, which will be discussed later, is the preferred explanation for the correlation among these species.

Species-habitat groups

The species groups formed appear to be the result of similar habitat preferences. Group III species were found in the lowest alkalinity, pH, and conductivity waters. Their growth is depauperate and is likely due to the infertility of the water where they are commonly found. They generally prefer soft substrate. Except for *Myriophyllum heterophyllum* and *Potamogeton pusillus,* Group III species show their best growth in Group A lakes. The preferred habitat for *P. oakesianus,* the only Group III species to prefer hard bottom, is sandy bottom, low alkalinity ponds (Hellquist 1980). The main difference between Group III species and the soft-water species that show no association is the preference of Group III species for soft substrates. Although pH and water-color data are

Table 3. Average Importance Value (IV) of Species by Lake Group

		Group A Lakes	Group B Lakes	Group C Lakes
Group I Species	Chara spp	1.7	7.8	36.0
	Scirpus validus	0.5	0.5	3.1
	Myriophyllum spicatum	1.9	10.6	6.1
	Potamogeton pectinatus	0.0	1.8	4.9
	Potamogeton gramineus	1.6	0.8	0.0
	Najas flexilis	3.2	6.4	5.5
	Potamogeton strictifolius	0.0	0.1	0.0
	Potamogeton illinoensis	0.1	0.6	0.1
	Group Ave. IV	1.1	3.6	7.0
Group II Species	Eleocharis acicularis	0.3	0.0	0.0
	Eriocaulon septangulare	0.6	0.0	0.0
	Isoetes macrospora	0.5	0.0	0.0
	Myriophyllum exalbescens	4.7	7.1	7.8
	Potamogeton praelongus	0.9	1.4	4.5
	Potamogeton amplifolius	3.4	3.0	0.0
	Potamogeton robbinsii	5.3	4.5	0.0
	Nuphar variegatum	7.8	1.2	1.0
	Nymphaea tuberosa	0.7	1.8	0.6
	Polygonum amphibium	0.2	0.4	0.0
	Heteranthera dubia	0.1	1.7	1.0
	Potamogeton nodosus	0.0	0.0	0.0
	Potamogeton berchtoldii	0.1	0.1	0.0
	Vallisneria americana	4.5	7.2	0.1
	Megalodonta beckii	0.1	0.2	0.0
	Potamogeton richardsonii	1.4	3.8	0.0
	Myriophyllum verticillatum	0.0	4.0	0.1
	Utricularia geminiscapa	0.0	0.0	0.0
	Group Ave. IV	1.7	2.0	0.8
Group III Species	Brasenia schreberi	7.7	0.3	0.0
	Potamogeton oakesianus	0.0	0.0	0.0
	Myriophyllum farwelli	1.5	0.0	0.0
	Utricularia gibba	1.4	0.0	0.0
	Utricularia intermedia	0.8	0.0	0.0
	Ceratophyllum echinatum	0.1	0.0	0.0
	Utricularia vulgaris	1.7	0.0	0.0
	Nymphaea odorata	5.0	0.0	0.1
	Dulichium arundinaceum	0.2	0.0	0.0
	Sagittaria rigida	0.0	0.0	0.0
	Myriophyllum heterophyllum	0.0	1.6	4.7
	Potamogeton natans	0.3	0.9	0.8
	Potamogeton pusillus	0.3	0.2	3.4
	Sparganium chlorocarpum	0.0	0.0	0.0
	Group Ave. IV	1.4	0.2	0.7

too scant to confirm it, Group III species appear more characteristic of bog or dystrophic conditions than the non-associated, soft-water species.

Group I and IV species are found in the highest pH, alkalinity, and conductivity waters. Water chemistry preference between the two groups is similar, but they are the two most dissimilar groups in regard to species association. Substrate preference and

Table 3 (continued). Average Importance Value (IV) of Species by Lake Group

		Group A Lakes	Group B Lakes	Group C Lakes
Group	Ceratophyllum demersum	12.0	25.0	31.9
IV	Potamogeton vaginatus	0.0	0.0	0.8
Species	Potamogeton foliosus	0.2	0.0	9.4
	Potamogeton crispus	0.0	5.8	9.0
	Elodea canadensis	6.2	12.1	2.9
	Sagittaria latifolia	0.0	0.0	0.2
	Typha latifolia	0.1	0.1	0.4
	Lemna minor	0.4	0.4	4.5
	Wolffia columbiana	0.2	0.0	2.8
	Potamogeton diversifolius	0.0	0.0	0.3
	Spirodela polyrhiza	0.2	0.2	0.8
	Lemna trisulca	0.0	1.0	0.8
	Potamogeton zosteriformis	2.0	7.8	7.7
	Ranunculus longirostris	0.0	0.0	0.0
	Group Ave. IV	1.5	3.7	5.1

turbidity tolerance are important differences between the groups.

Lemna minor, L. trisulca, Wolffia columbiana, and *Spirodela polyrhiza* are associated with Group IV species. Their free-floating habit gives them the ultimate turbidity tolerance; they are found in quiet water over fertile bottoms (Moyle 1945).

Marl bottoms frequently have a flora of *Chara* spp., *Najas flexilis,* and *Potamogeton pectinatus* (Moyle 1945). These three species are associated in Group I and may represent the plant community found in the highest pH, alkalinity, and conductivity waters in Wisconsin.

The habitat preference of Group II species are less well defined. They prefer intermediate water chemistries and have mixed substrate and turbidity preference. There is no consistent pattern of habitat or adaptation that provides a good explanation for this group. For example, *Eleocharis acicularis, Eriocaulon septangulare,* and *Isoetes macrospora,* which grow best in Group A lakes on hard substrate, and are often grouped with the unassociated, soft-water species (Moyle 1945; Swindale and Curtis 1957), are closely linked with *Myriophyllum exalbescens* and *Potamogeton praelongus,* which grow best in Group C lakes and prefer soft bottom but

are not turbidity tolerant.

Certainly there are growth-forms, adaptations, or habitat preference that could be used as arguments to subdivide this group. The *Nuphar variegatum, Nymphaea tuberosa, and Polygonum amphibium* are all floating leaved species that prefer soft substrate. *Potamogeton nodosus, P. berchtoldii,* and *Vallisneria americana* prefer hard substrate, but show mixed turbidity preference. Perhaps the best explanation is that Group II is an intermediate group that fits into the continuum concept of plant community structure (Curtis 1959) and is found in other studies of aquatic vegetation (Pip 1979; Moyle 1945).

This study found that only a few taxa were commonly found in sampled lakes; a large number were infrequently found. Species groups can be explained by species adaptation and habitat preference. Many unassociated species are found in low pH, alkalinity, and conductivity water, and on hard substrates. One associated group is also found in low pH, alkalinity, and conductivity water but is common on soft substrates and is turbidity tolerant. Two other groups are found in similar water chemistries. They prefer high pH, alkalinity, and conductivity waters. They appear to be separated by substrate preference and turbidity tolerance. A final plant

group is found in intermediate water chemistries, but further reason for the groups' existence is not clear.

Acknowledgments

Appendix A. Sampled Lakes*

Lake Name	County	Lake Name	County
GROUP A LAKES		*GROUP B LAKES (CONT.)*	
Allequash Lake	Vilas	Little Elkhart Lake	Sheboygan
Amnicon Lake	Douglas	Moon Lake	Marinette
Bear Lake	Oneida	Mount Morris Lake	Waushara
Bear Paw Lake	Oconto	Mud Hen Lake	Burnett
Chain Lake	Chippewa	Okauchee Lake	Waukesha
Clear Lake T39 R7 S16	Oneida	Pearl Lake	Waushara
Decorah Lake	Juneau	Pike Lake	Polk
Devils	Sauk	Pine Lake	Waukesha
Dowling Lake	Douglas	Rib Lake	Taylor
Enterprise Lake	Langlade	Rolling Stone Lake	Langlade
Frank Lake	Vilas	Round Lake	Polk
Half Moon Lake T47 R8 S17	Bayfield	Twin Lake, North	Polk
Island Lake	Rusk	Twin Lake, South	Polk
Little Arbor Vitae Lake	Vilas	White Ash Lake	Polk
Long Lake T20 R09 S17	Waushara	White Ash Lake, North	Polk
Long Lake T32 R8 S8	Chippewa		
McCann Lake	Rusk	*GROUP C LAKES*	
Mid Lake	Oneida		
Muskellunge Lake	Lincoln	Ashippun Lake	Waukesha
Perch Lake T45 R7 S5	Bayfield	Black Otter Lake	Outagamie
Pine Lake	Forest	Como Lake	Walworth
Pine Lake	Chippewa	Ennis Lake	Marquette
Post Lake, Upper	Langlade	Lazy Lake	Columbia
Prong Lake	Vilas	Leota Lake	Rock
Tahkodah Lake	Bayfield	Oconomowoc Lake, Upper	Waukesha
Town Line Lake	Chippewa	Ottawa Lake	Waukesha
		Pigeon Lake	Waupaca
GROUP B LAKES		Pretty Lake	Waukesha
		Silver Lake (Anderson) T22	Waupaca
Anodanta Lake	Bayfield	Tichigan Lake	Racine
Apple River Flowage	Polk	Vienna Lake (Honey)	Walworth
Balsam Lake	Polk		
Big Butternut Lake	Polk		
Big Hills Lake	Waushara		
Blake Lake	Polk		
Bone Lake	Polk		
Cary Pond	Waupaca		
Cedar Lake	Polk		
Chute Pond	Oconto		
Clear Lake	Rusk		
George Lake	Kenosha		
Half Moon Lake	Polk		
Helen Lake	Portage		

* PHYSICAL AND CHEMICAL PARAMETERS AVAILABLE
FROM WISCONSIN DEPARTMENT OF NATURAL RESOURCES
SURFACE WATER INVENTORY FILE

Appendix B. Cole's Index Values*

APPENDIX B. COLE'S INDEX VALUES

Species	no.	1	994	1801	1804	2515	2566	2623	2800	3487	3697	3937	3943	4405	4594	4597	4600	4603	4609	4618	4663	4666	4669	5263	5383
Chara spp.	1	1																							
Brasenia schreberi	994	-0.85	1																						
Ceratophyllum demersum	1801	-0.64	-0.57	1																					
Ceratophyllum echinatum	1804	0	0.58	0	1																				
Dulichium arundinaceum	2515	0	0.52	-1.00	0.39	1																			
Eleocharis acicularis	2566	0	0.15	-0.90	0	0.08	1																		
Elodea canadensis	2623	-0.58	-0.66	0.35	0	0	0	1																	
Eriocaulon septangulare	2800	0	0.46	-0.95	0	0.10	0.08	0	1																
Heteranthera dubia	3487	-0.54	0	0.40	0	0	0	0	0	1															
Isoetes macrospora	3697	0	0	-0.95	0	0	0	0	0.10	0	1														
Lemna minor	3937	-0.97	0	0.83	0	0	0	0.40	0	0	0	1													
Lemna trisulca	3943	-0.80	0	0.71	0	0	0	0.17	0	0.27	0	0.14	1												
Megalodonta beckii	4405	0	0	0.28	0	0	0	0	0	0.28	0	0	0.24	1											
Myriophyllum exalbescens	4594	0	0	0.19	0	0	0	0	0	0	0	0	0	0	1										
Myriophyllum farwellii	4597	-1.00	0.43	-0.64	0	0	0	0	0	0	0	0	0	0	0	1									
Myriophyllum heterophyllum	4600	-0.96	0	0.81	0	0	0	0	0	0	0	0	0	0	0	0	1								
Myriophyllum spicatum	4603	0	-0.88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1							
Myriophyllum verticillatum	4609	0	-0.97	0.35	0	0	0	0	0	0	0	0.27	0	-0.84	0.31	0.27	-0.74	0	1						
Najas flexilis	4618	0.09	-0.61	-0.52	0	0	0	-0.31	0	0.14	0	-0.78	0	0.17	-0.52	0	-1.00	0	0.13	1					
Nuphar variegatum	4663	0	0.17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1				
Nymphaea tuberosa	4666	-0.45	0.16	0.16	0	0	0	0	0.18	0.15	0	0	0.24	0.26	0	0	0	0	0.18	0	0.19	1			
Nymphaea odorata	4669	-0.88	0.34	0	0.96	0.51	0	0	0	0	0	0.14	0	0	0	0	0	0	-1.00	-1.00	-0.75	0	1		
Polygonum amphibium	5263	-0.95	0.60	-0.68	0.27	0.35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.37	0.42	0.27	1	
Potamogeton amplifolius	5383	-0.41	0	0	0	0	0	0	0	0	0	0	0	0	0	0.19	0	0	0	0	0	0	0	0	1
Potamogeton berchtoldi	5386	0	0	0.37	0	0	0	0	0	0	0.11	0	0	0	0	0	0	0	0	0	0	0	0.17	0.26	0
Potamogeton crispus	5395	-0.58	0	0.47	0	0	0	0.22	0	0	0	0.27	0	0	0	0	0	0	0	0	0	0	0	-0.68	0
Potamogeton diversifolius	5398	0	0	0.75	0	0	0	0.40	0	0	0	0.73	0.21	0	0	0	0	0	0	0	0	0	0	0	0
Potamogeton foliosus	5404	0	0	0.59	0	0	0	0.52	0	0	0	0.40	0	0	0	0	0	0	0	0	0	0	-1.00	0	0.06
Potamogeton gramineus	5410	0.15	0	-0.41	0	0	0	0	0	0	0	0	0	0.13	-0.73	0	0	0.09	0	0.15	0	0	0	0	0
Potamogeton illinoensis	5413	0.23	0	-0.68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.24	0	0	0.27	0	0
Potamogeton natans	5416	0	0.06	0	0.42	0.13	0	0	0	0.13	0	0	0	0.10	-0.69	0	0.12	0	0.29	0	0	0.08	0.10	0.10	0
Potamogeton nodosus	5419	0	0	0	0	0	0	0	0	0.39	0	0.24	0	0	0	0	0	0	0.13	0	0	0	0	0	0
Potamogeton oakesianus	5420	0	0.83	0	0	0	0	0	0	0	0	0	0	0	0	0.36	0	0	0	0	0	0	0	0	0
Potamogeton pectinatus	5422	0.12	0	0.14	0	0	0	0	0.08	0	0	0	0	0	0.10	0	0	0.13	0	0	0	0	-0.83	0	0
Potamogeton praelongus	5425	0	-0.78	0.18	0	0	0	0.08	0	0	0	0	0.15	0.19	0.12	0	0	-0.78	0	0	0	0	0	0	0
Potamogeton pusillus	5431	0	0.12	0.25	0.67	0.21	0	0	0	0.10	0	0	0.07	0.15	0	0	0.36	0	0.21	0	0	0.18	0.14	0.18	0
Potamogeton richardsonii	5434	-0.62	0	0.17	0	0	0	0.13	0	0	0	-0.91	0	0.23	0.11	0	0.17	-0.93	0.06	0	0	0	-0.88	0	0
Potamogeton robbinsii	5437	-0.62	0	0	0	0	0	0.12	0	0	0	0	0.13	0	0	0	0	0	-0.64	0	0.06	0	0	0	0.17
Potamogeton strictifolius	5440	0	0	0	0	0	0	0	0	0	0	0.82	0	0	0	0	0	0.29	0.23	0.30	0	0	0	0.09	0.21
Potamogeton vaginatus	5443	0	0.79	0.98	0	0	0	0.84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.16	0	0
Potamogeton zosteriformis	5449	-0.66	-0.69	0.35	0	0	0	0.14	0	0.17	0	0.24	0.30	0.20	0.13	0	0.32	-0.66	0.21	0	0	0.09	-0.57	0	0
Ranunculus longirostris	5710	0	0	0.78	0	0	0	0	0	0	0	0.30	0.35	0	0	0	0	0	0	0	0	0	0	0	0
Sagittaria latifolia	6088	0	0	0	0	0.14	0	0.49	0	0	0	0.46	0	0	0	0	0	0	0	0	0	0	0.25	0	0
Sagittaria rigida	6091	0	0.35	0	0.20	0.22	0	0	0	0	0	0.28	0	0	0	0	0	0	0	0	0	0	0.40	0.30	0
Scirpus validus	6304	0.50	0	-0.63	0	0	0	-0.83	0	0	0	0	0	0	0	-0.76	0	0	0	0	0	0.07	0	0	0
Sparganium chlorocarpum	6664	0	0.53	0	0.28	0.26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.63	0.31	0
Spirodela polyrhiza	6730	-1.00	0	0.86	0	0	0	0.25	0	0	0	0.86	0.22	0	0	0	0	0	0	0	0	0	0.17	0	0
Typha latifolia	7078	0	0	0	0	0	0	0.31	0	0	0	0.41	0	0	0	0	0	0	0	0	0	0	0.11	0	0
Utricularia geminiscapa	7114	0	0	0.57	0	0	0	0	0	0.35	0	0	0.30	0.30	0	0	0	0	0.79	0	0	0.64	0	0	0
Utricularia gibba	7117	-1.00	0.66	-0.72	0	0	0	0	0.10	0	0	0	0	0	0	0	0.70	0	0	0	0	0	0	0	0
Utricularia intermedia	7120	0	0.79	0	0	0	0	0	0	0	0	0	0	0	0	0	0.70	0	0	0	0	0	0	0	0
Utricularia vulgaris	7132	-0.96	0.70	-0.93	1.00	0.43	0	-1.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.82	0.34	0
Vallisneria americana	7177	0	-0.63	0	0	0	0	0	0	0.09	0	-0.67	0	0.08	0	0	0	0	0.15	0	0	0	-0.63	0	0.08
Wolffia columbiana	7450	-1.00	0	0.90	0	0	0	0	0	0	0	0.90	0.27	0	0	0	0	0	0	0	0	0	0.16	0	0
SUM ABS. OF COLE'S INDEX**		17.9	14.7	22.6	4.8	4.3	1.5	7.8	2.4	3.6	1.5	11.6	4.8	4.0	4.4	4.3	3.7	5.0	8.7	7.2	1.8	4.7	13.0	5.2	2.0
NO. SPECIES ASSOC. WITH**		27	30	38	9	13	6	19	10	16	4	21	17	17	12	8	7	9	19	18	8	17	27	14	7

* Experiment wise significance at chi-square p<0.05
** Columns will not add to these totals because of deleted species

Appendix B (continued)

Species no.	5386	5395	5398	5404	5410	5413	5416	5419	5420	5422	5425	5431	5434	5437	5440	5443	5449	5710	6088	6091	6304	6664	6730	7078	7114	7117	7120	7132	7177	7450
5263																														
5383																														
5386	1																													
5395	0	1																												
5398	0	0	1																											
5404	0	0.55	0	1																										
5410	0	0	0	0	1																									
5413	0	0	0	0	0	1																								
5416	0	0	0	0	0	0	1																							
5419	0	0	0.14	0	0	0	0	1																						
5420	0	0	0	0	0	0	0	0	1																					
5422	0	0	0	0	0	0.11	0	0	0	1																				
5425	0	-0.93	0	0	0	0	0	0	0	-0.72	1																			
5431	0	0	0	0	0	0.19	0	0	0	0	0	1																		
5434	0.24	0	0	0	0	0	0	0	0	0	0.07	0	1																	
5437	0	-0.88	0	0	0	0	0	0	0	-0.87	0	0	0.06	1																
5440	0	0	0	0	0	0.26	0.19	0	0	0	0	0	0	0	1															
5443	0	0.97	0	0.95	0	0	0	0	0	0	0	0	0	0	0	1														
5449	0	0	0.35	0	0	0	0.20	0	0	0	0.16	0	0.13	0	0	0.35	1													
5710	0	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0.42	1												
6088	0	0.49	0	0.47	0	0	0	0	0	0	0	0	0	0	0	0	0.45	0	1											
6091	0.14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1										
6304	0	0	0	0	0	0	0	0	0	-0.89	0	0	-0.86	0	0	-0.73	0	0	0	0	1									
6664	0	0	0	0	0	0.36	0	0	0	0	0	0.51	0	0	0	0	0	0	0	0	0	1								
6730	0	0	0.55	0	0	0	0	0.12	0	0	0	0	0	0	0	0.26	0.32	0	0	0	0	0	1							
7078	0	0.32	0	0.33	0	0	0	0	0	0	0	0	0	0	0.44	0	0	0.51	0.14	0.13	0	0	0	1						
7114	0	0	0	0	0	0	0	0	0	0	0.24	0.60	0.23	0	0	0	0	0	0	0	0	0	0	0	1					
7117	0	0	0	0	0	0	0	0	0.73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1				
7120	0	0	0	0	0	0	0	0	0.68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.89	1			
7132	0	0	0	0	0	0	0	0	0	0	0	0.35	0	0	0	0	0	0	-0.91	0	0	0	0	0	0	0	0	1		
7177	0.37	-0.62	0	0	0.16	0	-0.67	0.33	0	0	0	0	0.13	0.08	0	0	0	0.38	0	0.58	0	0	0	0	0	0	0	0	1	
7450	0	0	0.76	0	0	0	0	0.17	0	0	0.25	0	0	0	0	0.29	0.25	0	0	-0.67	0	0	0	0.64	0	0	0	0	0	1
	1.8	7.7	4.4	4.9	2.1	1.8	4.2	1.5	2.8	3.6	6.0	4.4	5.1	5.2	1.6	6.0	8.5	2.7	3.3	2.6	6.7	3.7	5.5	3.1	4.4	5.1	3.1	8.6	5.9	5.6
	8	13	11	9	8	6	18	7	5	10	15	17	16	13	7	9	24	7	8	11	13	10	13	10	11	9	5	13	16	11

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