

ES0327

# The Summer Breeding Habitat of Whooping Cranes in Wood Buffalo National Park, Canada

Final Report

by

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prepared for

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## Summary Findings

Through a spatial, multi-scale approach random available habitat was compared with habitat used by whooping cranes on their nesting grounds in Wood Buffalo National Park, Canada. Thirty-two study sites (n=16 nest, n=16 random available) were established in the nesting area in August 1996. Data were gathered via (a) relevés of 300 m<sup>2</sup> (9.8 m radius) which provided detailed site data and served as ground truth for (b) nested circular plots of 25, 50, 100, 200, and 500 m radius in which 21 cover types were mapped onto false color infrared 1:15,840 airphotos.

Noteworthy vascular plant occurrences were: *Scirpus rollandii*, a rare Cordilleran bulrush of marly lakeshores; *Gentiana raupii*, a regionally rare Mackenzie River valley endemic of saline wet meadows; and *Monolepis nuttalliana*, a halophyte rare in the Northwest Territories. The *Scirpus* and *Monolepis* are first occurrences for Wood Buffalo.

Species richness in the wetland communities is fairly low. The relatively high sulphate concentrations may act to limit species diversity.

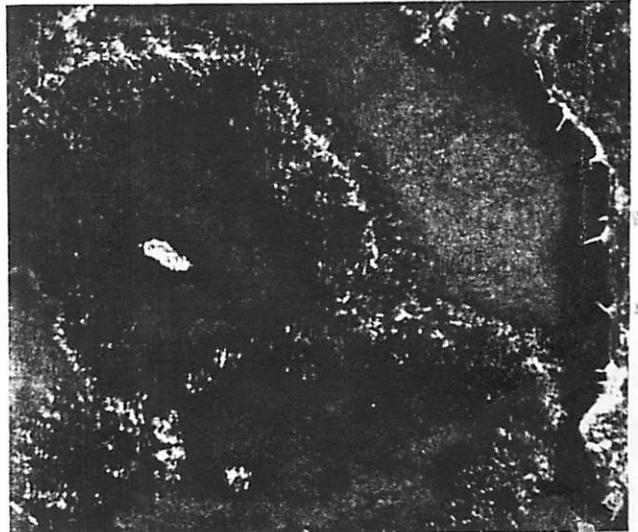
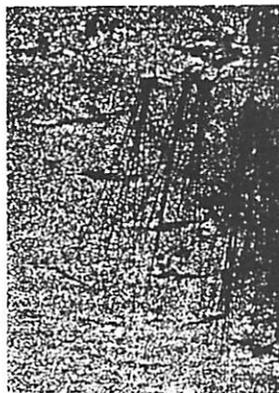
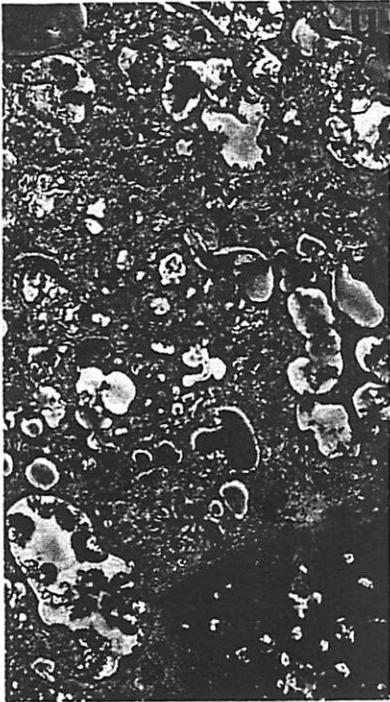
DCA ordination reveals a clear difference between crane nesting habitat (used) and random habitat (available) along axis one. At the scale of 300 m<sup>2</sup>, whooping cranes are choosing their nest habitat rather than nesting at random. Nest sites are bulrush marshes and associated diatom ponds, mixed marshes, and shrub mixed marshes. Non-nest habitats are most commonly shrubby peatlands (i.e., willow/dwarf birch bogs, bog-fens, and fens) and shrub-sedge fens and bog-fens, and less commonly tree mixed marshes and treed peatlands.

Potentially valuable indicators (via DCA) of crane nesting habitat are *Scirpus validus*, benthic diatoms, *Eleocharis palustris*, and *Utricularia minor*, and of non-nest habitat are: *Salix* spp. as a group, *Aulacomnium palustre*, *Salix bebbiana*, *Carex aquatilis*, *Salix myrtilifolia*, *Campylium stellatum*, *Betula glandulosa*, *Polytrichum juniperinum*, and *Picea glauca*.

In decreasing strength of correlation, quantitative ecological parameters correlated with crane nest sites are: distance to nearest concealment cover at 1.5 m ht. (strongest of all correlates), amount of open water, and distance to nearest concealment cover at 0.75 m ht., and those parameters correlated with non-nest habitat are: amount of terrestrial + marsh vegetation, decreased water depth, and distance to nearest water. Cranes "prefer" large concealment distances (i.e., visually open habitat), with large amounts of open water, small amounts of terrestrial vegetation, deeper water, and short distances from the nest site to water.

TWINSPAN classification corroborates the findings of the DCA ordination. There is nearly a complete lack of overlap in the order of samples. At the third TWINSPAN level of division, eight well-defined cover types are recognizable, the first four typical of random, available sites in the crane area, and the latter four typical of sites chosen by whooping cranes: (1)=Willow/dwarf birch and spruce ombrotrophic bogs; (2)=willow/dwarf birch bog-fens with abundant mosses; (3)=willow/dwarf birch/sweet gale strings in marshes, fens, bogs; (4)=willow/dwarf birch bog-fens with abundant water sedge; (5)=shrubby mixed marshes with water sedge and cattail +/- bulrush; (6)= bulrush/cattail mixed marshes with aquatics; (7)= bulrush marshes with diatom ponds; (8)= diatom ponds with bulrushes. Species characteristic of whooping crane nesting habitat occupy the bottom half of the table. The chief plant species indicators of nesting habitat (via TWINSPAN) are *Scirpus validus*, *Typha latifolia*, and *Chara* spp. while that of non-habitat is *Aulacomnium palustre* and to a lesser extent *Salix bebbiana*, *Rubus acaulis*, *Ledum groenlandicum*, and combined *Salix*.

fenestrated



Cluster analysis of plots corroborates the association of bulrush marshes, diatom ponds, and mixed marshes with crane nests and shrub and treed bogs, bog-fens, and fens with random available sites.

Non-parametric MRPP (McCune and Mefford 1995) were used to test the hypothesis of no difference between vegetation types for three group variables: used vs. available sites, burned vs. unburned, and lake bottom color at plot centre. The vegetation composition of nest sites differs from that of random sites, indicative of strong habitat selection. In contrast, there is no detectable difference between burned and unburned vegetation. Lake bottom color is a significant predictor of vegetation composition at the plot scale.

Diatom ponds are a rare form of boreal wetland associated with the nests of whooping cranes. Diatom ponds are found in wetlands in association with bulrush marshes; are shallow (<50 cm deep) and vary in size from 10 to >1000 m in diameter; may evaporate down to diatom muck by late summer; are strongly influenced by dissolution of gypsum; are circumneutral to alkaline and high in sulphates; aquatic macrophytes are few; pond waters are clear; the predominant primary producers are a benthic diatom community that give the ponds a characteristic yellow color (viewed from the air). As the diatom ponds dry they change color from yellow to pink (water table at surface) to cream (dried diatom and sulphate crust). Diatomaceous earth or sedimentary peat underlies the ponds which exist in a dynamic relationship with bulrush marshes, wet meadows, fens, and bogs. In the U.S. wetland classification diatom ponds fit most nearly within the palustrine, unconsolidated bottom, aquatic bed type. In the Canadian wetland classification, the diatom ponds might fit in the marsh/shallow open water complex, with a new distinction at the type level. The strong association between nesting cranes and diatom ponds may be due to a combination of factors such as long sight lines for detection of predators, the association of the ponds with bulrush (their favored nesting material), and use of the ponds for feeding.

Whooping cranes show a preference for the deeper diatom ponds (median pond color = yellow) as nest sites, while at random available shallow ponds that dry out (creme) and point samples with no ponds are more common.

When random available sites are compared to nest sites, significant differences in the suite of ecological parameters are evident. Nest sites are characterized by deeper water, greater distances to concealment at both the 0.75 and 1.5 m heights, greater distance to the nearest tree, lower distances to nearest water, and greater amounts of open water. In contrast, no differences are detectable in any ecological parameter when burned sites are compared to unburned sites.

Historically in Canada, 47% of crane summer occurrences were in the "aspen parkland", 15% in "transitional plains to parkland", 13% in "northern coniferous forest", 8% in "shortgrass plains", 8% in "northern mixed forests", 4% in river deltas, 3% in "transitional (parklands to mixed forest)", and 2% in "tundra". By political jurisdiction, Canadian nest locations were concentrated in southern Saskatchewan (Moose Mountain and Yorkton NW to Battleford and Baliol) and Manitoba (south of Lake Winnipeg west to Oak Lake) and east central Alberta (Wainwright to Witford). By the current national ecoclimatic classification, Canadian nest locations were concentrated in the Grassland Transitional Region (synonymous with the Aspen Parkland zone of various authors), with fewer occurrences to the south (Arid Grassland Region) and to the north (Low and Mid-Boreal Subhumid regions). The location of the present nesting area, in the Mid-Boreal Subhumid region, is peripheral to the core of the former nesting region.

Of particular interest to the current Wood Buffalo breeding population are the District

of Mackenzie records: Ft. Simpson, Ft. Resolution, Ft. Anderson, Rae, Salt River, Big Island (? , Great Slave Lake), Willow River, Hay River, Pine Point, and the Mackenzie Delta (Allen 1952:52), and the northern Alberta records: Ft. Chipewyan, Athabasca River, Paddle River, Lesser Slave Lake, Ft. Vermilion, Steen River, and Old Fort Bay (Lake Athabasca) (Allen 1952:51).

In the United States, the core of the breeding range was in the prairie of four north central states: Iowa, Minnesota, North Dakota, and Iowa. The former/potential natural vegetation of these areas was "bluestem prairie", "wheatgrass-bluestem-needlegrass", "oak-hickory forest", and "northern floodplain forest" (*Populus-Salix-Ulmus*). Two-thirds of the known-breeding was concentrated in northern Iowa.

From Allen's (1952) work, the former nesting habitat of the whooping crane may be surmised: prairie sloughs; small shallow lakes; shallow ponds and open water; willow communities; bulrush marshes; deltas dominated by graminoids, willows, and ponds; mudflats; sandbars; broad and shallow streams; marshes (particularly of bulrush) and mixed marshes of bulrush, cattail, flags, rushes, sawgrass; tussocks. The results of this study agree with Allen (1952) that "muskegs" are non-nest habitat (= organic terrain, e.g., willow/dwarf birch bogs, bog-fens, fens, shrub-sedge fens, treed bogs, etc.). How does the former habitat compare with that of the present?

It is likely that historic and present habitat share the following attributes: small shallow lakes and ponds, willow communities, marshes of bulrush and cattail, mudflats, and perhaps sedges. Conversely, the present nesting habitat is probably atypical or unique (relative to the core of former range) in its diatom ponds, gypsum karst-groundwater discharge hydrogeology, and permafrost. Relative to currently available potential locations for reintroduction, the extent of the disturbance-free area in the present breeding area may be unique. Indeed it would be difficult to find another site in present day North America that is as large and shares most of the attributes of the nesting area in and adjacent to Wood Buffalo National Park.

For the entire period (1938-1995), mean annual growth of the population has been 4.8% (+/-13.6% standard deviation) and mean recruitment 16.7% (+/-9.6%). Up to 1965, annual growth of the population was 4.9% (+/-17.6%) and mean recruitment 20.4% (+/-11.2%). From 1966-1995, annual growth has been 4.7% (+/-8.9%) and mean recruitment 13.2% (+/-6.0%). At an annual growth rate of 4.7%, the Wood Buffalo-Aransas flock presently has a population doubling time of 16-17 years.

Ten-year periodicity in whooping crane population parameters has been verified by Boyce and Miller (1985) and Nedelman et al. (1987). The ARIMA model forecast of future whooping crane numbers produced by Boyce and Miller (1985) for the period 1984-1995 has proven accurate to the present with observed population growth lying within their 95% confidence intervals. The cause of the 10-year periodicity is a topic of immense practical importance to whooping crane recovery. The importance of water to nesting whooping cranes is evident. In northwestern Canada there is a 10-11 year cycle in precipitation that manifests itself in fluctuating levels of discharge and storage of northern rivers and lakes (McNaughton 1991; Kerr and Loewen 1995). In agreement with the crane time series, prominent peaks and troughs in mean annual water levels for Great Slave Lake are observable on an approximate 10-year cycle. Low water levels are evident, e.g., in 1945, 1953, 1959, 1970, and 1981.

A host of factors are involved which modulate or otherwise influence crane population dynamics, such as crane winter nutrition as affected by productivity of blue crabs on the wintering grounds, mortality during migration, etc. However, in light of the strong

relationships between nesting cranes and breeding habitat water conditions, it seems reasonable to suggest that an underlying factor in the 10 year periodicity of crane population dynamics is the 10 year northern hydrological cycle.

From 1966 to 1970, the center of the crane breeding range shifted to the north and west (in 1966 and 1967 some nests may have been missed due to workers' unfamiliarity with the breeding grounds (Kuyt 1981)). Since the early 1970s, the crane population has expanded generally southward. The center of the breeding range, based on 596 reliable nest locations (from 1966-1993) is: 60.24° N, 113.32° W (median: 60.25° N, 113.33° W).

The relatively constant standard error both in latitude and longitude of crane nest locations indicates that both dispersion and infilling are taking place. Whooping crane nest locations are highly contagious at the landscape scale. Such contagion could be due both to habitat selection by breeding birds and to nest site fidelity of the returning pairs (see Kuyt 1981).

At least four temporal scales of dynamism operate in the crane area: (1) Annually, the ponds and wetlands undergo a recharge-drawdown cycle. (2) Surface water and groundwater levels fluctuate on a decadal 10-11 year hydrological cycle (McNaughton 1991), linked to a precipitation cycle (Kerr and Loewen 1995), which is in turn linked to continental and global-scale processes (Holdsworth et al. 1989, among others), and to a 10 year cycle of whooping crane annual recruitment and annual growth rates (Boyce and Miller 1985; Nedelman et al. 1987). (3) Fire, operating on a scale of ~50-250 years, periodically sets back woody encroachment, succession, and peat aggradation, leading to thermokarsting and favoring pond, marsh and fen formation. (4) Peat aggradation operates on a scale of thousands of years.

Aerial observations showed diatom ponds in various stages of progressive succession to bulrush marsh, mixed marshes, and fens (Frontispiece). Retrogressive (peatland to pond) succession is accelerated by fire. Peat stratigraphy clearly shows that retrogressive succession is common there. On a decadal to centennial scale, fire may help to maintain both the diatom ponds, and indirectly, whooping cranes. It would be incorrect, however, to conclude that fire drives this ecosystem and results in the formation of the ponds in general. Rather, groundwater discharge influenced by dissolution of gypsum appears to be the chief process that characterizes this ecosystem.

For 500 m radius plots centered on crane nests, predominant types are Shrub Bog-Marsh (18.5%) and Mixed Marsh (10.4%). Of the 1310 patches analyzed, average patch size was 0.954 ha. Fractal dimensions for the nest plots was (PA method) 1.251 +/- 0.108 or (P(m,L) method), 1.647 +/- 0.119. Landscape diversity ( $H'$ ) = 2.740, dominance (D) = 0.255, evenness = 0.915, scaled dominance = 0.085, combined contagion 50.429, scaled contagion = 0.842, and number of cover types = 20.

For random 500 m radius plots, predominant types are Shrub Featureless Organic Terrain (17.7%) and Shrub Bog-Marsh (9.5%) Of the 1273 patches analyzed, average patch size was 0.981 ha. Fractal dimensions for the random plots was (PA method) 1.283 +/- 0.048, or (P(m,L) method) 1.624 +/- 0.132. Landscape diversity ( $H'$ ) = 2.802, dominance (D) = 0.242, evenness = 0.920, scaled dominance = 0.080, combined contagion = 53.483, scaled contagion = 0.837, and number of cover types = 21.

At the 500 m radius scale, there is no statistical difference in fractal dimensions between nest and random sites by either PA ( $T=-1.606$ ,  $p=0.125$ ) or PmL methods ( $T=1.701$ ,  $p=0.105$ ).

The high landscape diversity is in contrast to the low species diversity of the wetlands. At the 500 m radius scale, landscape structure (as indicated by patch size, fractal dimension,

contagion) and landscape diversity, dominance, and evenness are virtually identical between nest and random locations. Relative to other landscapes in boreal Canada, grain-size is small and perimeter to area ratios are high; there is both a high degree of edge and high spatial diversity.

Two cover types have a significant interaction between plot size and plot type: Bulrush Marshes and Shrub Featureless Organic Terrain (shrub-dominated bogs and fens without ponds, strings, fens, or meadows included in the matrix). Whooping cranes choose *Scirpus validus* habitat out to a radius of 200 m from the nest. In contrast, cranes avoid featureless shrub bogs and fens out to a radius of at least 500 m from the nest. There is weak evidence of habitat selection for other habitat types in aggregate within a 25 m radius of the nest.

## **Monitoring**

Hydrological regime plays an important role in the condition of the wetlands used for nesting and foraging-- although the exact relationship between summer pond depth and annual crane reproduction needs further research. Regional precipitation, groundwater flow, and surface flow are correlated to varying degrees with those within the crane area proper. Water levels in the crane area are affected by groundwater discharge from the Caribou Mountains, local precipitation, and evapotranspiration (McNaughton 1991).

Clearly, the annual monitoring of the crane population its reproduction must continue, and for overriding operational reasons, fire monitoring should also continue. The following assumes that both population and fire monitoring is to continue.

Much climatic and hydrologic monitoring is conducted by other agencies and these provide a potentially useful source of information. Before data such as snowpack in the Caribou Mountain, precipitation at Ft. Smith, and Little Buffalo River stage height can be used for proxy monitoring, research must be conducted to establish the degree of correlation and lag between the available proxy data and the parameters of interest in the crane area (see e.g., a preceding section on crane reproduction and Great Slave Lake mean annual water levels). Once the statistical links and lags are established, a large amount of virtually free proxy data will be available for monitoring habitat water conditions.

The combined results of DCA and TWINSPAN provide a set of species and community indicators which may be used for monitoring (see above).

Once research needs are addressed, data for key climatic/hydrologic indicators should be assembled into a park crane database (both as far back as the record exists, and into the future). Discussion with the appropriate agencies should be held regarding reliability of the data, data gaps, any plans for cessation of data gathering. The goal of the water monitoring would be to assemble and maintain a set of long-term, reliable indices that correlate well with crane area water levels.

The focus of airphoto-based monitoring should be at the community and landscape level. Vegetation communities in the crane nesting area are easy to distinguish with high quality false color infrared photography. I recommend that once every 5 years, a set of airphotos be flown (same scale and type as used in this study). The coverage need not be extensive-- a subset of the area would suffice for monitoring (~20 airphotos)-- but fixed costs and the overall cost/airphoto must be considered. With appropriate technical advice (e.g., US Fish and Wildlife Service), it might be feasible to obtain acceptable vertical airphotos through the use of park contract helicopter or fixed-wing. Weather permitting, each edition of photos should be taken in about mid-July. The framework for the airphoto-based monitoring is

described in detail in the report.

## **Recommendations**

No effects of fire on whooping cranes -- either positive or negative -- are detectable from any of the available data. It is possible that fires may benefit the cranes through favoring graminoid vegetation and ponds over woody and peatland vegetation (although this was not detectable with the data). Due to the potential negative effects of a major fire control operation in the crane area (e.g., nest abandonment, inadvertent helicopter harassment, fire retardant effects on the wetlands, water bombing), it is advisable to classify the area as "modified response".

Under a modified response regime, fire management should consider two factors before undertaking fire suppression in the area: (1) the fire's location in relation to nest locations and known feeding areas; (2) time of the year in relation to crane activities (presence--absence, pre-nesting, nesting, rearing, pre-migration) in order to minimize disturbance, especially during nesting and rearing. Only high altitude flights should be allowed over the area, including those of the fire monitoring program. No medium class helicopters should be allowed over or in the crane area at any time when cranes are present.

The crane population is healthy and growing. The nesting habitat is healthy. No manipulation or intervention is required in either case. Support for establishing two new wild population of whooping cranes should, however, be maintained. High priority protection of the cranes and their habitat should continue. Parks Canada opposition to construction of any communications towers within the breeding range and the migration path of the cranes should continue.

A long-term scientifically credible monitoring and research program should be established. The basic elements are already in place: population, water, and fire monitoring, and the habitat monitoring suggestions above. The next step in the habitat study should be to document the summer diet of the whooping crane and relate that diet to the habitat findings of this work.

## **Introduction**

Whooping Cranes (*Grus americana*) are an endangered species in the United States (WCRT 1994a), and are protected in Canada under federal, provincial, and territorial legislation (WCRT 1994b). As of December 1995, there were three wild populations: a declining Rocky Mountain flock of 3 birds; a Florida non-migratory flock of 58 birds established in 1993 from captive-reared birds, and a self-sustaining migratory population of 158 birds that breeds in Wood Buffalo National Park and winters on the Texas Coast (WCRT 1994a,b; B. Johns, pers. comm. 1996). Historic population declines have been attributed to habitat destruction, shooting, and human displacement (WCRT 1994a).

A primary objective of the recovery plan for Whooping Cranes is to establish two additional self-sustaining wild populations, each with a minimum of 25 breeding pairs, by the year 2020 (WCRT 1994a,b). Towards that end, the plan outlines a list of goals. Many of the goals point to a need to better understand the breeding habitat of cranes, such as: locate and describe breeding habitat; determine availability of suitable habitat for breeding, staging, migrating, and other essential uses; integrate habitat mapping with historical nesting patterns using GIS; determine factors affecting habitat quality; identify key habitat areas required to

attain recovery goal.

This study was undertaken to further understanding of whooping crane breeding habitat through a spatial multi-scale approach. Ecologists search for appropriate spatial and temporal scales to elucidate pattern and process in natural systems (Baker et al. 1995). Choice of the wrong scale can lead to erroneous conclusions or to the inability to reach any conclusions. Characterizing whooping crane nesting habitat is a question of scale. Do nesting cranes choose habitat that is different from a random sample? If so, what characteristics best typify whooping crane breeding habitat?

Scale and pattern are related. Greater sandhill crane (*Grus canadensis tabida*) nests in the Seney NWR in Michigan are randomly distributed on the landscape (Baker et al. 1995). Are whooping crane nests random on the landscape? Such a question is central to understanding the relationship between crane population changes, habitat availability, and total potential crane populations in the future. As crane numbers have increased over the past decades, has the pattern of nesting been random or clumped; has there been infilling, or radiation from foci along identifiable vectors?

Spatial analyses of greater sandhill crane nesting habitat have recently been completed by Baker et al. (1995). The authors avoided the pitfalls of single-scale comparisons of resource use and availability through the use of five spatial scales of nested circular plots centered on randomly chosen sandhill crane nests (used habitat) compared with nested circles centered on purely random points (available habitat). They found that greater sandhill cranes chose nest sites in or near seasonally flooded emergent (non-woody) wetlands and avoided forested uplands; they found no habitat selection beyond 200 m from the nest.

The objectives of this study are (1) to evaluate nesting habitat use; (2) to compare habitat characteristics of nesting ponds with potential nesting areas within the study area; (3) to determine, if technically feasible with existing data, the role of fire in crane nesting habitat; (4) to define key ecological criteria which may be used to identify potential whooping crane nesting habitat; (5) to establish a conceptual framework for long-term monitoring of key ecological components in the study area.

Comparison of landscape cover types, plant species, fire occurrence, and spatial and landscape-structural attributes (e.g. false color of water bodies, distance to nearest pond or tree, fractal dimension) are made between used and random available habitat. Other aspects of the study examine pond water levels as they relate both to crane reproduction and to regional-scale climatic forcing, and spatial and temporal patterns of crane nesting. The findings of this work should assist in the search for appropriate breeding habitat in which to establish new wild populations of Whooping Cranes.

## Study Area

### Climate

The area is located in the Subhumid Mid-boreal ecoclimatic region in which summers are warm and moist; winters are very cold and snowy; July is the warmest and wettest month; and frost-free period is 80-120 days (Ecoregions Working Group 1989). Climatic normals (1961-90) for Ft. Smith airport, located about 50 km east of the study area core are: mean daily temperature -3.0 C, July mean temperature 16.3 C, degree-days above 5C = 1162; annual precipitation is 352.9 mm; 14 thunderstorms per year; the land is usually snow-free by

early to mid-May and snow-covered by mid-October (Environment Canada 1993).

### **Physiography and Terrain**

Regionally, the area is part of the Great Slave Plain physiographic division (Geological Survey Canada 1970), typified by till plains, sandplains, and carbonate deposits over karst (Airphoto Analysis Associates 1979).

Bedrock is the Middle Devonian Nyarling Formation gypsum karst and minor limestone. Topography is level to depressional (Airphoto Analysis Associates 1979). Most of the area is affected by calcium sulphate groundwater discharge, part of a groundwater flow system originating in the Caribou Hills to the southwest (McNaughton 1991). The chemistry of springs and ponds is strongly influenced by the dissolution of gypsum; dominant ions in the water samples are: sulphate, calcium, bicarbonate, and magnesium, with lesser amounts of sodium, potassium, and chloride; ponds are circumneutral to alkaline (pH usually between 7.2 and 8.7; McNaughton 1991). Novakowski (1966) noted that ponds used by whooping cranes for feeding and nesting ranged in pH from 7.6 to 8.3, while that in adjacent unused ponds ranged from 7.2 to 7.3. In the core of the area, ~50% of the landscape is covered by ponds (Airphoto Analysis Associates 1979).

Most of the surficial deposits are organic terrain (>80%), particularly in the core of the nesting area. Subdued rises of unoriented and fluted loamy tills dot the area (Airphoto Analysis Associates 1979). Permafrost underlies much of the area (~30% according to Airphoto Analysis Associates 1979), particularly the palsa and peat plateau landforms. Permafrost degradation is common. Thermokarsting of ground ice, e.g., after fire, may be an important process leading to landscape diversity and to the formation of diatom ponds in former peatlands. Due to recent fires, most palsas and peat plateaus in the study area lack the typical light-toned *Cladonia*-dominated surface; they are brownish due to shrub and moss dominance.

### **Soils**

Bog and fen peats are typically mesic in texture (Om); floating mats are fibric near the surface and become mesic with depth (Of to Om); diatom ooze deposits are humic (Oh) since its predominant constituents are diatoms, blue green algae, and bacteria, with only minor amounts of *Chara* and macrophytes such as *Utricularia*.

Predominant soils in the study area (nomenclature after Canada Soil Survey Committee 1978; observations from fieldwork) are as follows. The soils of floating mats (*Scirpus*, *Typha*, with or without *Carex aquatilis* and brown mosses) are typically Hydric Mesisols and Hydric Fibrisols. In fens and some marshes, Typic Mesisols predominate. Deep marl deposits form Typic Humisols. Some fen and bog profiles lack permafrost within 1.2 m of the surface and are classified as Typic Fibrisols. Lenses of frozen material are common. In the higher, drier portions of the organic terrain, the typical soils are Mesic Organic Cryosols and Fibric Organic Cryosols. On mineral terrain, Rego Gleysols and Eutric Brunisols predominate ((Airphoto Analysis Associates 1979). Drainage is very poor to poor on the organic terrain and imperfect to moderately-well on the mineral terrain.

### **Vegetation**

A mosaic of diatom ponds, bulrush marshes, mixed marshes, shrub marshes, water sedge wet meadows and fens, bog-fens, and bogs dominate the wetland complex. Fen and bog types may be either shrub-dominated (dwarf birch, *S. athabascensis*, *S. candida*, *S.*

*myrtilifolia*, *S. planifolia*, other willows, sweet gale, and Ladrador tea), or tree-dominated (white spruce, black spruce, larch, and Alaska birch). The thicker peat landforms are typically palsas and peat plateaus in which thermokarst ponds are common. Upland forests are typified by closed to open canopy of white spruce, jack pine, and aspen.

## **Fauna**

A useful annotated list of invertebrates (37 taxa), fishes (fathead minnow, finescale dace, northern pearl dace, brook stickleback), amphibians (wood frog, striped chorus frog), birds (115 species), and mammals (10 species) observed in the nesting area in 1955 appears in Allen (1956). Kuyt (1991) documented a communal overwintering site of the canadian toad in the area. Novakowski (1966) collected many of the same invertebrates documented by Allen (1956). Allen observed 26 bird species at the crane nesting ponds, including confirmed breeding of arctic loon, lesser yellowlegs, mew gull, and yellow-rumped warbler. On a 27 May 1955 canoe trip down the Little Buffalo River, Allen observed 971 birds of 53 species, the commonest were: spotted sandpiper, american goldeneye, american widgeon, green-winged teal, and mallard. Common large mammals are wolf, black bear, and moose. Other mammals observed occasionally are lynx, least chipmunk, red squirrel, beaver, snowshoe hare, caribou, and wood bison. Most mammals and birds appear to concentrate their activities along the streams that drain the area, rather than in the organic terrain. The apparent absence of muskrats, in spite of the abundance of marshes, is interesting. It is likely that winter water levels are insufficient for overwintering muskrats as they require sufficient water depths to prevent freezing to bottom (Boutin and Birkenholz 1987). Recent stable isotope studies indicate that nesting Whooping Cranes feed at about the same trophic level as Peregrine Falcons and that fish may form a dominant part of their diet (J. Duxbury and G. Holroyd, pers. comm. 1996).

## **Methods**

### **Pre-Field**

As a means to plan for the fieldwork, on the 28 and 29 May 1996 I accompanied the Canadian Wildlife Service--Wood Buffalo National Park--US Fish and Wildlife Service team during the spring egg pick-up flights. At that time habitat pre-typing was done.

Study sites were stratified into available (n=16) and used sites. The used (i.e., 1996 nest) sites were chosen by random numbers from the list of 41 nests (4 randomly chosen nests had to be rejected due to lack of airphoto coverage). Choice of available sites was more complex for two reasons: (1) sample points which fell within closed crown forests and open water of lakes were ignored because cranes do not use such areas for nesting; (2) colour infrared airphotos exist for only a subset of the crane area. The area covered by false-color infrared airphotos (scale 15,840, July 1993) was divided into 891 one km<sup>2</sup> cells on 1,50,000 topographic maps. Each cell was sub-divided into 100 one ha blocks (00-99). A five digit random number was used to place a random point-- the first three digits specified the cell number and the last two digits the block number. Plotted points were then transferred to airphotos. If the random point was not within closed crown forest or in open water of a lake, it was accepted.

## Field

Fieldwork was conducted from 12-15 August 1996. Travel to and from the whooping crane was via helicopter. Available study sites were located on the ground via pinpoints on airphotos and UTM coordinates taken from topographic maps. Nest sites were located with the assistance of Brian Johns (Canadian Wildlife Service, whooping crane biologist).

## Stand-Level Cover Types

Fieldwork centered on gathering data for the stand-level analyses and on ground truth for the landscape studies. Effort was made to use the same cover designations at both levels, but differences in scale and pattern required some divergence. In addition, field cover types were used more as a convenience for field descriptions as the actual stand-level cover types was defined later via ordination and classification.

Pure field types were: Bulrush Marsh (see SV code under Landscape-Level Cover Types, below); Cattail Marsh (MM); Sedge Meadow (CA); Mixed Marsh (*Scirpus* +/- *Typha* +/- *Carex aquatilis*; MM); Willow/Dwarf Birch Treeless Organic Terrain (as strings (TOTS) and as featureless shrub and shrub-sedge communities (TOTF)); Spruce-Larch Treed Organic Terrain (as strings (OTS) and as featureless bogs and fens (OTF)); Open Water (B,T,P below); Algal Muck (C). Mosaic types used were: Treeless Bog-Fen (TBF), Treed Bog-Fen (BF), Shrubby Mixed and Bog-Marsh (TBM), and Treed Mixed and Bog-Marsh (BM). Nomenclature is in general congruent with National Wetlands Working Group (1988). The mosaic bog-marsh types have no good synonyms, a fact due perhaps to both the unusual nature of these transitional marsh to peatland communities and to differences in spatial scale.

## Field Sampling

At each site a 300 m<sup>2</sup> circular (9.8 m radius) releve was established. The following data were gathered to supplement each releve: habitat type at plot centre; habitat type was estimated to 10% cover for the NE, SE, SW, and NW quadrants (e.g., 90% string bog, 10% open water); an accurate GPS location based on 5-10 minutes of point averaging; pond bottom color at plot centre (none, creme, pink, brown, yellow); if pond present in plot, its substrate composition, origin, and texture was noted; both the pond (if present) and a representative location were augered to 1.2 m depth along which the type and thickness of strata (peat, diatom ooze, and till) were noted; four water depths/depths to water table were taken @N, S, E, W, one meter from plot centre; along sight lines at heights of 0.75 m and 1.5 m, the distance to concealment (total obscuration) was measured; evidence of fire was sought, and if found 3 basal clippings of regeneration were made in order to date the fire; ground and aerial photos; use of area by cranes and other animals; and general notes.

The focus of each releve was an enumeration of all plant species present and their percent cover (trace, 1,2,3,4,5,10, 15, 20...%). Algae were a special case in that their percent cover was noted as a group, either submerged or as drying pond bottoms.

## Analytical Ordination and Classification

In order to de-emphasize the influence of rare species, the ordination and classification of the releve data was limited to species that occurred  $\geq 5$  times in the 32 plots, with four exceptions of species with high indicator value: *Drepanocladus uncinatus* (n=4), *Polytrichum juniperinum* (n=4), *Potamogeton pectinatus* (n=4), and *Carex atherodes* (n=3, but dominant

when present). A total of 46 species was analyzed. Ordination and classification employed PC-Ord (McCune and Mefford 1995). Scientific and common names for vascular plants follow Porsild and Cody (1980) with one exception: *Betula neoalaskana* (= *B. papyrifera* var. *neoalaskana*). Scientific and common names for mosses and lichens follow Vitt et al. (1988), and those for diatoms follow Germain (1981), Schoeman and Archibald (1976), and Patrick and Reimer (1966, 1975).

### **Benthic Algal Communities**

To characterize the pond bottom algal communities, two samples (one preserved in iodine and one unpreserved) were taken from a pink-bottom and a two from a yellow-brown bottom pond. The pink bottom sample was a from typical drying isolated pond (yellow bottom when containing water); the yellow-brown bottom sample was from nest pond 96-38, connected to a nearby stream. The samples were sent to Dr. Gordon Goldsborough of the University of Manitoba who performed the labwork and identified the specimens. A small quantity of each sample was washed several times in distilled water to remove the preservative, if present, followed by centrifugation to collect the algae. Samples were digested overnight in 30% hydrogen peroxide to reduce the amount of organic matter, followed by overnight in 1 normal hydrochloric acid to remove carbonates (very little was encountered). Samples were then place in distilled water, an aliquot of which was transferred to a coverslip, dried, then combusted at 600°C to remove all remaining organic matter. Coverslips were bonded permanently to slides using Naphrax diatom medium and examined at 1000X under oil immersion. Since diatom frustules do not degrade readily at low temperature (the samples were stored at 4°C), the unpreserved specimens were examined.

### **Mapping and Spatial Analyses**

Prior to mapping the cover types, the following parameters were assessed: dominant color of ponds within five nested plots of radii (25, 50 100, 200, 500 m, corresponding to areas of 0.2, 0.8, 3.1, 12.6, and 78.5 ha); distance to nearest tree from plot center, distance to nearest water. On clear acetates overlain on the airphotos, cover types were mapped for each of the 32 plots. In order to prevent mapping bias between random and nest sites, plots were mapped alternately in succession (random, nest, random, nest...). At the end of the first iteration, all early plots were scrutinized polygon by polygon, while all later plots were checked for errors also. Two types of errors were sought: mislabelling of polygons with incorrect cover types, and bias in spatial scale (i.e., a change in minimum polygon size independent of a change in landscape grain).

Spatial analyses took two forms: a test of crane habitat selection at (nest vs. random sites) over five spatial scales, and analyses of landscape structure and diversity.

In order to test for habitat selection, for each of the 32 plots, cover type polygons, plot centers, and additional control points, were digitized into a SPANS GIS database. The percent landscape composition was determined at five spatial scales for 21 cover types. Through the MGLH/MANOVA repeated measures/Test procedure in Systat (Wilkinson et al. 1992), Multiple ANOVA and univariate F tests were run to determine if there were evidence of habitat selection by whooping cranes and at what spatial scale. As an independent test of spatial scale of habitat selection, multiresponse permutation procedures (MRPP, Euclidean distance) were run. Rather than examine each cover type individually, in the MRPP each habitat cover type was treated as a "species" within a landscape releve (i.e., all cover types were considered in aggregate).

In order to determine landscape structure and diversity, plot cover raster files were imported into the RM Spatial Analysis package (supplied courtesy of C. Flather, USDA Forest Service). A comparison was then made of landscape diversity, dominance, areal cover, patches, and fractal measures for random vs. nest sites. The landscape-level cover types used are presented below, along with their airphoto characteristics.

### Landscape-Level Cover Types

Twenty-one cover types were used in the landscape-level mapping: 15 "pure" and 6 mosaic types. The typical lower limit for delimitation of a polygon was 0.1 ha (2 by 2 mm on airphoto). In many cases shrub and tree strings, flarks, open water in marshes, and diatom ponds were too narrow for mapping as pure types and were included under one of the mosaic types. The mosaic types (TBF, BF, TBM, BM, TOTX, OTX) are for fine-grained areas where pure types are unmappable; they are intermediate in photo characters. The break between treeless organic terrain (TOT) and treed organic terrain (OT) is >10% cover trees of >5-6 m tall = OT; if cover or height is lower, it is TOT. The following types were recognized; their airphoto characteristics are given.

### Pure Types

#### Graminoid

- MM = mixed marsh; blotchy, irregular pattern, with sometimes dark patches of water; colour and graininess variable: from yellow to light pink, grainless (*Carex aquatilis* dominance) to olive, slightly grainy (*Scirpus validus*) to pinkish tan and slightly grainy (*Typha latifolia* and *Carex aquatilis*), to pure tan or blue-green (depends on relative amounts of overwintered vs. fresh cattail stems) and very grainy and patchy (*Typha*).
- SV = *Scirpus validus*; olive, arcuate patterns, typically within well-defined drainage basins; very fine grain, incl. greenish to turquoise very small patches of water.
- CA = *Carex aquatilis* (wet meadow to fen flarks); yellow to pink, grainless, featureless; may include small amounts of *Carex atherodes*, *Calamagrostis inexpansa*, *C. neglecta*.

#### Open Water

- B = greenish to greenish black to black open water; usually deeper than other colours, often connected to flowing water and to mixed marshes.
- T = turquoise open water
- P = powder blue open water
- C = creme "open water" (i.e., algal surface drying with a whitish desiccation crust).

#### Upland Forests

- UF = upland forests of white spruce, aspen, jack pine, paper birch, with lesser amounts of black spruce and larch; a minor type on till-cored upland rises
- BUF = recently-burned upland forests dominated by shrubs and small trees

#### Shrub Organic Terrain

- TOTS = shrub strings; medium to bright pink, grainy, puffy if tall canopies present, no shadows; string pattern.
- TOTF = shrub featureless (= shrub fen, shrub bog); pink to dull red, grainy; no strings, shadows, flarks, meadows or diatom ponds.

## Treed Organic Terrain

OTS = tree strings; matrix medium pink to red (*Ledum*, *Betula neoalaskana*, etc.); olive is spruce and larch; tree shadows.

OTF = featureless treed bogs, fens; same as OTS, but no strings.

## Peat Plateaus

BPP = burned peat plateau; pure olive with whitish pond inclusions (thermokarst ponds); domed to mounded, irregular surface; grainy, sometimes with a few trees.

PP = peat plateau; dull brownish red, domed or mounded irregular surface; usually with small trees.

## Mosaic Types

### String Fens and Bog-Fens

TBF = TOTS/CA (shrub string/*Carex* fen flark mosaic); incl. TOTF/CA

BF = OTS/CA (tree string/*Carex* fen flark mosaic); incl. OTF/CA

### Shrub/Marsh and Tree/Marsh Complexes

TBM = TOTS/MM (shrub string/mixed marsh mosaic); incl. TOTF/MM

BM = OTS/MM (treed string/mixed marsh mosaic); incl. OTF/MM

### Shrub/Pond and Tree/Pond Complexes

TOTX = Shrubs with ponds; typically shrub strings around ponds that are too small to map individually.

OTX = Trees with ponds, as in TOTX.

## Spatial Scale of Resolution

Resolution of the ground truth field data is the 300 m<sup>2</sup> releve (0.03 ha). Resolution of the airphoto data is the minimum polygon size of ~1000m<sup>2</sup> (0.1 ha).

## Results

The statistical normality of ecological parameters was determined by the Lilliefors test. Pond bottom color at plot centre, dominant pond bottom color at plot sizes of 25, 50, 100, 200, and 500 m radius, water depth, substrate type, distance to nearest tree, distance to nearest water, utm easting, open water %, and terrestrial+marsh % were all non-normal at alpha=0.05. Distance to concealment at 0.75 m (p=0.07), distance to concealment at 1.5 m (p=0.26), burn age (p=0.44), utm north (p=0.18) were normally-distributed, as were whooping crane annual recruitment (p=0.91), annual growth rate (p=0.26), and mean annual water level of Great Slave Lake (p=0.21).

## General Observations

Noteworthy vascular plant occurrences were: (a) *Scirpus rollandii*, a rare Cordilleran bulrush of marly lakeshores (Porsild and Cody 1980); (b) *Gentiana raupii*, a regionally rare Mackenzie River valley endemic of saline wet meadows (Porsild and Cody 1980); (c) *Monolepis nuttalliana*, a halophyte rare in the Northwest Territories (Porsild and Cody 1980). Neither the *Scirpus* nor the *Monolepis* are listed by Cody (1995), and are thus first

occurrences for Wood Buffalo. See Appendix 1 for a list of bryophytes and lichens identified from the crane area.

Species richness in the wetland communities is fairly low. For example, fairly common marsh species such as *Acorus calamus*, *Alisma triviale*, *Calla palustris*, *Sagittaria cuneata*, and *Sparganium eurycarpum* were not observed in the fieldwork. In the crane area, the pH of surface waters is high, usually in the 7.2 to 8.7 range (McNaughton 1991). Typically, high pH communities tend toward high species diversity (e.g., Vitt et al. 1988; Robinson et al. 1989; Timoney et al. 1993). However, physiological and soil factors correlated with high pH probably influence communities more than the simple concentration of hydrogen ions, such as effects on solubility of elements, competition, toxicity, and soil structure (Oosting 1956; Salisbury and Ross 1978). The water chemistry in the crane area is strongly influenced by dissolution of gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ), rather than of carbonate rocks. The relatively high sulphate concentrations may act to limit species diversity. Communities on gypsum terrain tend to have distinctive floras, faunas, and community nutrient relationships (Whittaker 1975).

## Ordination and Classification of Whooping Crane Nesting Area study sites

### Detrended Correspondence Analysis (DCA)

The DCA plot ordination (Figure 1) reveals a clear difference between crane nesting habitat (used) and random habitat (available) along axis one. Sites used by cranes occupy the left side of the ordination and random available sites the middle and right of the ordination. At the detailed plot scale ( $300 \text{ m}^2$ ), whooping cranes are choosing their nest habitat rather than nesting at random. Nest sites are bulrush marshes and associated diatom ponds, mixed marshes, and shrub mixed marshes. Non-nest habitats are most commonly shrubby organic terrain (i.e., willow/dwarf birch bogs, bog-fens, and fens) and shrub-sedge fens and bog-fens, and less commonly tree mixed marshes and treed organic terrain.

As axis 1 accounts for 44% of the variation in plant species occurrence and abundance (Table 1), those species correlated with axis 1 are potentially valuable indicators of crane nesting habitat (Table 2). In decreasing strength of correlation, species negatively correlated with axis 1 (i.e., with crane nest sites) are: *Scirpus validus*, algae (benthic diatom and blue-green algal communities), *Eleocharis palustris*, and *Utricularia minor*, and those positively correlated with axis 1 (indicators of non-nest habitat), are: *Salix* spp. as a group, *Aulacomnium palustre*, *Salix bebbiana*, *Carex aquatilis*, *Salix myrtilifolia*, *Campylium stellatum*, *Betula glandulosa*, *Polytrichum juniperinum*, and *Picea glauca*. For graphic comparison, the relative abundance of 12 indicator species is overlain on the plot ordination (Figure 2).

In decreasing strength of correlation, quantitative ecological parameters (Table 3) negatively correlated with axis 1 (i.e., with crane nest sites) are: distance to nearest concealment cover at 1.5 m ht. (strongest of all correlates), amount of open water, and distance to nearest concealment cover at 0.75 m ht., and those parameters positively correlated with axis 1 (indicators of non-nest habitat) are: amount of terrestrial + marsh vegetation, water depth, and distance to nearest water. Cranes "prefer" large concealment distances (i.e., visually open habitat), with large amounts of open water, small amounts of

terrestrial vegetation, deeper water, and short distances from the nest site to water. Vectors of significant parameters are overlain on the plot ordination (Figure 3).

The DCA species ordination (Figure 4) reveals a similarly clear division of communities. Minerotrophic wetland and pond species occupy the left of the ordination, mixed marsh and rich fen species the left center, poor fen, wet meadow, and bog-fen species occupy the right center, and bog species the ordination right. Those "species" that are ecologically dissimilar from others, and may form monospecific stands, clones, or thickets occupy isolated positions, such as the benthic algae community, *Scirpus validus*, *Carex atherodes*, *Cladonia* spp., and *Salix bebbiana*. Conversely, closely-related assemblages are clustered, e.g., *Ledum groenlandicum*, *Tomenthypnum nitens*, *Drepanocladus uncinatus*, and *Aulacomnium palustre*, characteristic of the drier peats.

## TWINSpan

The TWINSpan classification (Table 4 and Appendix 2) corroborates the findings of the DCA ordination. There is nearly a complete lack of overlap in the order of samples, with random sites occupying the left side and used nest sites the right side of the table. The exceptions are instructive. Site N11 is located in a bulrush/diatom pond surrounded by dwarf birch-Labrador tea-sweet gale strings (post-fire). N16 is a diverse post-fire shrubby mixed marsh dominated by bulrush, cattail, *Salix planifolia*, *Drepanocladus revolvens*, *Campyllum stellatum* and Alaska birch in an area of low strings. N23 is also a diverse post-fire shrubby mixed marsh, co-dominated by cattail, water sedge, duckweed, and bladderwort, with *Salix planifolia* and Alaska birch. Site R29 is yet another diverse, post-fire shrubby mixed marsh co-dominated by water sedge, cattail, bulrush, dwarf birch, and larch with *Salix planifolia* and *S. athabascensis*. Site R19 is a bulrush shrubby marsh with water sedge, dwarf birch, and sweet gale with no sign of former fire. Site R24 is an unusual post-fire shrubby mixed marsh dominated by *Myriophyllum verticillatum* with *Calliergon giganteum*, cattail, water sedge, dwarf birch, and *Drepanocladus revolvens*. Thus all six sites are mosaics of graminoid and woody vegetation and ponds. Five of six sites were burned within the past 15 years and are thus compositionally variable. The degree of overlap between the nest and random available sites is consistent with random sampling in that some random sites will, by chance, be equivalent to sites chosen by cranes.

At the third TWINSpan level of division, eight well-defined cover types are recognizable, the first four typical of random, available sites in the crane area, and the latter four typical of sites chosen by whooping cranes: (1)=Willow/dwarf birch and spruce ombrotrophic bogs; (2)=willow/dwarf birch bog-fens with abundant mosses; (3)=willow/dwarf birch/sweet gale strings in marshes, fens, bogs; (4)=willow/dwarf birch bog-fens with abundant water sedge; (5)=shrubby mixed marshes with water sedge and cattail +/- bulrush; (6)= bulrush/cattail mixed marshes with aquatics; (7)= bulrush marshes with diatom ponds; (8)= diatom ponds with bulrushes. Species characteristic of whooping crane nesting habitat occupy the bottom half of the table. The chief plant species indicators of nesting habitat are *Scirpus validus*, *Typha latifolia*, and *Chara* spp. while that of non-habitat is *Aulacomnium palustre* and to a lesser extent *Salix bebbiana*, *Rubus acaulis*, *Ledum groenlandicum*, and combined *Salix*.

While the wetland types recognized in this study are in general congruent with those of National Wetlands Working Group (1988), differences in scale, characteristics of both prairie and boreal wetland zones, and the unique nature of the nesting area has necessitated

some divergence. In general the following synonyms apply: (1) shrub bog and treed bog; (2) shrub bog-fen; (3) bog or fen string; (4) shrub bog-fen and wet meadow; (5) tall shrub shallow marsh and meadow marsh; (6) tall rush deep marsh and deep shore marsh; (7) and (8) no equivalent.

The utility of determining *Salix* to species is shown by the varied positions of the commoner willows in the table: *Salix bebbiana* and *S. myrtilifolia* typical of non-habitat, *S. athabascensis*, *S. candida*, and *S. pedicellaris* of little indicator value, and *S. planifolia* typical of mixed and cattail marshes. The ordination position of *Salix bebbiana* is somewhat surprising. Of the boreal willows, Bebb's willow typically occupies the most "upland" of sites, yet in the crane area it is common on the organic terrain. Its commonness is perhaps related to the prevalence of recently-burned areas, as Bebb's willow sprouts prolifically after fire. In all, ten species of willows were identified from the crane area. Only those willows occurring in five or more sites were included in the ordination/classification. The other willows are *S. brachyphylla*, *S. maccalliana*, *S. padophylla*, and *S. serissima*.

### Cluster Analysis

Unlike TWINSpan, which performs poorly when more than one ecological gradient is present, cluster analysis can be used to classify data responding to any number of ecological gradients (McCune and Mefford 1995). While the results of the TWINSpan analysis evince a clear gradient from marshes to bogs, a cluster analysis was performed to determine if a similar interpretation would be valid.

Cluster analysis of plots (Figure 5) corroborates the association of bulrush marshes, diatom ponds, and mixed marshes with crane nests and shrub and treed bogs, bog-fens, and fens with random available sites. Nest sites are concentrated in the top half of the cluster dendrogram and random sites the lower half. In between, shrubby bog marshes predominate, along with "hybrid" relevés in which the plot boundaries encompassed distinct communities such as diatom ponds with intervening organic terrain (typically bog) strings. Again, the degree of overlap in vegetation similarity between random and nest sites is consistent with random expectations.

### Multi-Response Permutation Procedures (MRPP, Euclidean Distance)

Non-parametric MRPP (McCune and Mefford 1995) were used to test the hypothesis of no difference between vegetation types for three group variables: used vs. available sites, burned vs. unburned, and lake bottom color at plot centre.

The vegetation composition of nest sites differs from that of random sites ( $T=-8.34$ ,  $p=0.00002$ ), indicative of strong habitat selection. See the DCA, TWINSpan, and Cluster Analysis sections above for details.

In contrast, there is no detectable difference between burned and unburned vegetation ( $T=-0.29$ ,  $p=0.30481$ ). Such a result is understandable in that many communities in the whooping crane nesting area are early successional edaphic types. Thus, after fire resets succession, the resultant community is little younger than the surrounding unburned types. Secondly, the stochastic nature of early succession following fire results in large compositional variation within the burn group. While fire appears to exert no detectable effect on the predominantly early successional wetland vegetation, the question remains "does fire exert an influence on crane nest selection?" Of the 32 study sites, there were 4 random unburned, 6 nest unburned, 12 random burned, and 10 nest burned. There is no detectable difference in frequency of nest vs. random sites in the burned and unburned categories

(Mann-Whitney U 144.0,  $p=0.564$ ). Fire appears to exert no detectable effect on crane nest selection. Nor has direct mortality to whooping eggs, chicks, or adults as a result of fire been observed to date (WCRT 1994a).

Lake bottom color is a significant predictor of vegetation composition at the plot scale ( $T=-1.92$ ,  $p=0.04209$ ). In general, yellow-bottomed ponds are associated with the bulrush and bulrush/diatom communities, no ponds or creme ponds (muck flats) are associated with the shrub and treed bogs and fens, and a wide variety of pond bottom colours is typical of the intermediate nature of mixed and shrubby marshes. The topic of lake colors and crane nesting is explored below.

## **The Diatom Ponds Environment**

The area is located in a region of groundwater discharge with its source in the Caribou Hills (~ 80 km to the southwest). Precipitation falling on the uplands infiltrates through underlying Devonian aquifers then radiates northeast into the crane area (McNaughton 1991). Most of the ponds are groundwater-fed, hydrologically-isolated from the streams that course through the area. Annual water levels fluctuate strongly, with maxima after snowmelt in spring and minima in late summer. In an average year, more than half the ponds drawdown to muck surfaces by late summer.

The predominant bedrock is gypsum karst ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ), and its dissolution is responsible for the alkaline character of the surface water. The four major ion species vary widely in concentration (data from McNaughton 1991) with medians (ppm) of: sulphate ~1700, calcium ~500, bicarbonate ~ 350, and magnesium ~150; lesser ions include chloride ~55, sodium ~47, and potassium ~5.5 ppm. Most conductivity values are in the 0.5-3.0 mS/cm range; pHs range from 7.2-8.7 ( $n=95$ , with 2 outliers of  $\text{pH}>9$ ). For the most part, the water column is transparent (Allen (1956) found the water column to be nearly devoid of plankton). At 10 of the 32 study sites, a mineral layer was encountered within 1.2 m of the surface: usually a gleyed silty clay glacial till. At all other sites, organic deposits were deeper than 1.2 m.

## **Pond Bottom Material**

Earlier studies in the crane area (e.g., Allen 1956; Novakowski 1966; McNaughton 1991), referred to the pond bottoms as "marl". Marl is variously defined as: (1) "A mixture of calcium carbonate and clay" (Longwell et al. 1969); (2) "Calcium carbonate compounds deposited by algal physiology or by other organisms; concretions that precipitate from hard water, mixed with clay..." (Prescott 1978); (3) "Soft and unconsolidated calcium carbonate, mostly mixed with varying amounts of clay or other impurities...calcareous deposits in lake bottoms and organic terrain in which the percentage of calcium carbonate may range from 90 to less than 30%." (Mollard 1982). Sedimentary peat (>17% organic carbon) and diatomaceous earth (<17% organic carbon) are formed in water bodies and are composed of mainly algae and diatoms with some aquatic plants and bacteria (Tarnocai and Schuppili 1987).

Allen (1952) quoted a letter from a Dr. Lackey (Univ. of Florida) who analyzed some of the material: "The protein content of the mud is far higher than I would ever expect and I would judge it to be due to bacteria, blue-green algae, and diatoms. It is certainly significant..." Allen (1956) reported that fat composed 9.2%, nitrogen 3.4%, and protein 2.5% of the dry weight. Novakowski (1966) presented data from 16 sites with a mean ash content

of 85.4% +/- 9.6% sd, and by inference volatile solids of ~14.6%, and organic carbon of ~7.3%. He noted that "The species composition of the marl is mostly diatoms..."

As the material is not composed primarily of calcium carbonate and clay, it is not marl. Three sedimentary peat deposits from the boreal Northwest Territories reported in Tarnocai and Schuppli (1987) had an ash content of 31-74% (by inference, ~26-69% volatile solids, and ~13-35% organic carbon. The available data (Allen 1956; Novakowski 1966) indicate that organic carbon content may range widely, but in general the material has a low organic carbon content and thus might be classed as diatomaceous earth. The material varies widely in color from blue-gray to beige to olive to dark olive brown, is jelly-like and soft, non-fibrous, and is composed of granular aggregates that are most prominent after the material is dry. Gypsum salts may bind the diatoms and other algae into the aggregates. Most of the taxa present in the pond bottoms are benthic forms (see next section).

### **Algal Community Composition**

Allen (1956) reported the cyanobacteria *Gomphosphaerium*, *Aphanocapsa*, and *Chroococcus*, the green algae *Chlorella* and *Cosmarium*, and the bacterium *Sphaerotilus* from the diatom ponds. In samples collected, the benthic community was composed of <10% cyanobacteria and >90% diatoms. The samples were analyzed for their predominant diatom taxa (Tables 5, 6). The lists are not exhaustive but they are likely representative of the common and dominant taxa. The specimen from the yellow-brown bottom (connected to a stream) contained many more diatoms and a greater richness of taxa than found in the pink bottom (isolated pond) sample. There was some overlap in composition between the two samples, particularly with respect to the dominants. Overall, >= 23 diatom taxa were identified. Chrysophyte scales and cysts (unidentifiable) were also common in the samples. As the size of the sample is small, little ecological significance should be attached at present to the differences between the samples.

Most of the taxa are benthic. Quite a few have stalks or mucilage pads (e.g., *Cymbella* spp.) by which they hold themselves to the substrate. However, the yellow-brown bottom specimen contains a few typically planktonic taxa (e.g., *Fragilaria crotonensis*, *Tabellaria fenestrata*). These species might have been living in the benthos or they may have "rained" down from the plankton.

The occurrence of *Rhopalodia gibba* and *Epithemia* spp. is interesting, as these taxa may contain endosymbiotic cyanobacteria that provide them with inorganic nitrogen (Floener and Bothe 1980; Bahls and Weber 1988; DeYoe et al. 1992). These taxa may be indicative of low nitrogen conditions under which their ability to fix nitrogen gives them a competitive advantage. Many of the taxa tend to occur under high conductivity, alkaline conditions, and are considered calciphilic (e.g., *Amphipleura pellucida*, *Rhopalodia gibba*, *Mastogloia smithii*, *Epithemia* spp.). The diatom profile is characteristic of an alkaline environment, perhaps one low in inorganic nutrients.

### **Wetland Classification of the Ponds**

The diatom ponds appear to represent a heretofore undescribed pond/wetland community. From the above, the diatoms ponds may be viewed as spring-fed, intermittent to shallow, hardwater, alkaline wetlands of the "bicarbonate - sulphate with calcium and magnesium" type (National Wetlands Working Group 1988). The benthic deposits appear to be a mixture of diatom and blue-green algae remains and gypsum minerals. Worldwide, ancient deposits of consolidated diatoms (diatomites) are relatively common, but modern day

diatomaceous earth deposits are not (W. Last, pers. comm. 1996). As a boreal or prairie wetland type, they are undescribed, and are apparently rare.

It seems that the diatom ponds may be unique in both the American and Canadian wetland classification systems. In any case, the diatom wetlands do not fit neatly in either system. In the U.S. wetland system, the ponds may fit under the palustrine system, unconsolidated bottom class; aquatic bed subclass with a new distinctive description based on "dominance", "water chemistry" or other attributes (a dominance type "algal" exists, but not specifically for diatoms). Chemical modifiers are based on salinity or pH.

In the Canadian wetland system, the diatom ponds might fit in the Marsh/Shallow open water complex, with a new distinctive description at the Type level.

### **Geographic Distribution**

The geographic distribution of diatom ponds remains undocumented. Timoney (field observ. from aircraft) has observed yellow-bottomed ponds sporadically elsewhere in Wood Buffalo National Park. S.C. Zoltai (field observ.) has observed yellow-bottomed pools in tundra near Churchill, Manitoba, as has G. Goldsborough (unpub. data) who found that the benthos there contained cyanobacteria but no diatoms. C. Tarnocai (pers. comm. 1997) has observed shallow pools in bogs along the west coast of British Columbia in which diatoms flourish and form a sedimentary peat; he has also observed reddish-coloured shallow lakes, some of which dried out during the summer, along the highway between Rae and Fort Providence, Northwest Territories.

Turquoise (true color) lakes, incidentally, appear to be a related community: some larger lakes in the whooping crane nesting area, elsewhere in Wood Buffalo National Park, and north of Yellowknife, Northwest Territories (e.g., Gordon Lake) are a brilliant turquoise. Bottom samples were collected from Pine Lake, WBNP, a spring-fed, oligotrophic, clear water lake in gypsum karst terrain about 60 km south of Ft. Smith, Northwest Territories. Turquoise portions of the lake support a benthic crust ~4 mm thick, leathery in texture, composed of cyanobacteria, diatoms, and mineral grains. The color of these turquoise lakes is evidently due to phycocyanin. Cyanobacteria of the Pine Lake benthos include *Anabaena*, *Rivularia*, *Spirulina*, and diatoms species include (\* genera also found in the diatom ponds of the whooping crane area) *Amphora*\*, *Cocconeis*, *Cymbella*\*, *Epithemia*\*, *Gomphonema*\*, *Hantzschia*, *Mastogloia*\*, *Navicula*\*, *Nitzschia*\*, *Rhopalodia*\*, and *Stephanodiscus* (unpub. data).

### **The Association between Diatom Ponds and Nesting Whooping Cranes**

The strong positive association between nesting cranes and diatom ponds may be due to a combination of factors such as (a) long sight lines for detection of predators (nesting whooping cranes "prefer" large concealment distances (i.e., visually open habitat), with large amounts of open water, small amounts of terrestrial vegetation, deeper water, and short distances from the nest site to water (see also Armbruster 1990)); (b) the association of the ponds with bulrush, their favored nesting material (WCRT 1994a,b); and (c) use of the ponds for feeding.

Practical difficulties have hampered the elucidation of the summer diet of cranes, such as unavailability of stomach contents and prevention of research-related disturbance to the nesting birds. Previous workers have documented a list of possible direct or indirect food

items (Allen 1956; Novakowski 1966), including snails, crustaceans, large insect larvae, frogs, rodents, small birds, fishes, and berries. Through the use of stable isotopes and collection of crane scats, Duxbury and Holroyd (unpub. data) have shown that whooping cranes are omnivorous on their breeding grounds, but consume more animals than plants; the stable isotope ratios of their scats may indicate a preference for fish; they appear to feed at the same trophic level as peregrine falcons.

As a possible base for the aquatic food chain, the benthic algal community deserves attention (e.g., Hecky and Hesslein 1995; Neill and Cornwell 1992). Sullivan and Moncreiff (1990) found that the base of the food chain for a salt marsh's invertebrates and fishes was the benthic and planktonic algae with only minor contributions from vascular plants. The structure of the breeding ground food web deserves future attention.

## **Crane Nesting and other Ecological Parameters at the Plot-Level**

### **Lake Bottom Colors**

Both on the landscape and on false-color aerial photographs, there is wide variation in the color of lake and pond bottoms in the whooping crane area. For the most part, the water column is transparent and its perceived color is due to reflection from the bottom. True colors range from (1) brown and black (usually in deep marshes, in lakes and ponds connected to streams, and in streams; the dark colors are primarily fine detrital matter); (2) yellow (the typical color of diatom pond bottoms); (3) pink (recently exposed algal communities undergoing subaerial desiccation); (4) creme (algal communities that have dried sufficiently for a light-toned sulphate ("salt crust") layer to coat the surface); (5) no water bodies. False colors range from (1) greenish to black; (2) turquoise; (3) powder blue; (4) creme; (5) none. Ground truth comparisons showed that true color 1 = false color 1, 2=2, etc. In general the deepest waters are brown to black (false color = greenish to black), followed by yellow (turquoise), pink (powder blue), creme (creme), and none. The only overlap or confusion is in pale greenish-hued areas which ground truth showed were sometimes shallower than turquoise areas. Secondly, in some areas pond colors varied so widely as to make classification into one dominant color difficult. Notwithstanding the difficulties of classification, it appears that whooping cranes show a preference ( $p=0.011$ ) for the deeper diatom ponds (median pond color = yellow) as nest sites (Table 7), while at random available shallow ponds that dry out (creme) and point samples with no ponds are more common (median pond color = creme). The relationship appears to be specific to the nest point as the statistics indicate only a weak preference for the deeper waters (as indicated by greenish to black and turquoise) out to a radius of about 100 m, beyond which no differences in random/nest dominant lake colors is apparent.

### **Relationships between quantitative ecological parameters**

When random available sites are compared to nest sites, significant differences in the suite of ecological parameters are evident (Table 8). Nest sites are characterized by deeper water (7 cm deep vs. 13.5 cm to water table, sampled in mid-August), greater distances to concealment at both the 0.75 (3.3 vs. 1.4 m) and 1.5 m heights (16.4 vs. 3.5 m), greater distance to the nearest tree (55.4 vs. 15.8 m), lower distances to nearest water (4.0 vs. 27.7 m), greater amounts of open water (5 vs. 0%, sampled in mid-August), and lower amounts of terrestrial + marsh vegetation (79.0 vs. 96.5%). For whooping crane migration habitat,

Armbruster (1990) concluded that horizontal visibility distance at 1 m ht must exceed 20 m, and optimum water depth should be  $\leq 30$  cm.

In contrast, no differences are detectable in any ecological parameter when burned sites are compared to unburned sites.

## **A Comparison of Nesting Habitat in Wood Buffalo with that of Former Nesting Habitat in North America**

The breeding range of the whooping crane has varied over time, perhaps reaching its greatest extent during the Pleistocene (Allen 1952). In an exhaustive review of the whooping crane, Allen (1952) documented all the known breeding, wintering, and migrating occurrences for the species from the Pleistocene to 1948. For historic times, a pre-1870 peak population of 1,300 to 1,400 birds has been estimated, at which time the range of the whooping crane extended from the Arctic Coast (Anderson River) south to central Mexico, west to Utah, and east New Jersey and South Carolina (Allen 1952). Human activities such as settlements, wetland drainage, agriculture, and hunting precipitated an approximate 97% decline in the crane population and a concomitant range shrinkage (most rapid between 1865 and 1899) (Allen 1952, WCRT 1994a,b). For the purposes of comparison with the present, the cranes' breeding range for the period 1748-1922 is useful. Then, and now, the whooping crane was a bird of the interior grassland biome of the Great Plains.

### **Former Canadian Summer Range and Associated Vegetation Zonation**

In Canada, 47% of crane summer occurrences were in the "aspen parkland", 15% in "transitional plains to parkland", 13% in "northern coniferous forest", 8% in "shortgrass plains", 8% in "northern mixed forests", 4% in river deltas, 3% in "transitional (parklands to mixed forest)", and 2% in "tundra" (Allen 1952). By political jurisdiction, Canadian nest locations were concentrated in southern Saskatchewan (Moose Mountain and Yorkton NW to Battleford and Balfour) and Manitoba (south of Lake Winnipeg west to Oak Lake) and east central Alberta (Wainwright to Witford). By a current national ecoclimatic classification (Ecoregions Working Group 1989), Canadian nest locations were concentrated in the Grassland Transitional Region (synonymous with the Aspen Parkland zone of various authors), with fewer occurrences to the south (Arid Grassland Region) and to the north (Low and Mid-Boreal Subhumid regions). The location of the present nesting area, in the Mid-Boreal Subhumid region, is peripheral to the core of the former nesting area.

Of particular interest to the current Wood Buffalo breeding population are the District of Mackenzie records: Ft. Simpson, Ft. Resolution, Ft. Anderson, Rae, Salt River, Big Island (?), Great Slave Lake, Willow River, Hay River, Pine Point, and the Mackenzie Delta (Allen 1952:52), and the northern Alberta records: Ft. Chipewyan, Athabasca River, Paddle River, Lesser Slave Lake, Ft. Vermilion, Steen River, and Old Fort Bay (Lake Athabasca) (Allen 1952:51). While the above records are reliable, some may be from non-breeding summer wanderers rather than nesting birds.

Two migratory locations are also of interest to Wood Buffalo management. E.T. Seton (in Bent 1926:229) noted that "Belalise (the Indian guide) says that every year a few come to Fort Chipewyan, then go north with the waveys to breed. In the fall, they come back for a month and linger on the great marshes about Fort Chipewyan." Residents of the Ft. Vermilion area occasionally observe birds in spring and fall: "...during the 1940's, groups of 4-6 were often seen in the stubble fields... 40 km southwest of Fort Vermilion. The birds

would stay a few days, then disappear... in the spring of 1981...several on a mudflat 1 km downstream of Fort Vermilion on the Peace River... Whooping Cranes in his field 16 km north of Fort Vermilion... in the fall of 1973 near the junction of the Wabesca and Peace Rivers, 40 km downstream of Fort Vermilion, he saw two adult and two young fly low overhead." (Gainer 1986).

### **Former American Summer Range and Associated Vegetation Zonation**

In the United States, the core of the breeding range was in the prairie of four north central states: Iowa, Minnesota, North Dakota, and Iowa (Allen 1952). The former/potential natural vegetation (after Küchler 1975) of these areas was "bluestem prairie", "wheatgrass-bluestem-needlegrass", "oak-hickory forest", and "northern floodplain forest" (*Populus-Salix-Ulmus*). Two-thirds of the known-breeding was concentrated in northern Iowa.

### **Former Nesting Habitat**

Allen's (1952) documentation of the former range and occurrences of the whooping crane was a herculean task. His efforts to document former habitat were frustrated both by lack of available data and by human-induced changes: "Many of these areas disappear from view, swallowed up by the progress of drainage and agriculture...the 'improvements' wrought by man, have so altered the face of the earth in many instances that today we gain but a poor conception of the original character of the region by first-hand observation" (Allen 1952:18, 21).

From's Allen's (1952) work, the following nesting habitat observations may be gleaned: (1) "probably the sloughs and shallow lakes of one of the willow communities"; (2) "Manitoba Lowlands... an area of many small lakes, open as well as treed muskegs, grassy depressions between former beach ridges, bulrush marshes and patches of mixed forest"; (3) "... great marshes about the mouth of the Red River"; (4) "...near Ft. Chipewyan... the broad delta of the (Peace-) Athabaska may well have been a nesting site"; (5) "No nests were reported from muskeg and mixed forest except the doubtful one from the 'bush,'""; (6) "There were tall stands of cattail and other nesting birds included mallards, shovellers, teal, rails, coots, bitterns, yellow-headed blackbirds and marsh wrens. All of these are characteristic birds in the willow communities... within aspen parkland"; (7) "... the terrain was generally open, gently rolling prairie, with many shallow ponds, marshes and mudflats. At the heads of the draws there were patches of heavier growth and straggling timber grew along the banks of the smaller streams. The larger streams were often broad and shallow, with shifting sandbars and frequent mudflats"; (8) "... a great, flat prairie interspersed with marshes and small lakes"; (9) "Pond and shallow water, overgrown with rushes stretched for miles with occasional tracts of tussocks."

Later, Allen added the following American habitat notes (1956:33) (1) "An open site in a 'burnt slough,' near water 8" to 10" in depth"; (2) "In a 'swale of flags and rushes'"; (3) "In the center of an immense marsh, 1 mile from higher ground"; (4) "In open water, 1 1/2 ft. depth nearby, set in a large marsh of 'rushes and sawgrass'; and Canadian habitat notes: (5) "In a damp, swampy part of the prairie"; (6) "An open site, 30 ft. in diameter, in one end of a 3000 acre marsh, 3 miles by 1 to 2 miles in extent. Water depth averaged 'knee deep' and was heavily grown with uncut grass"; (7) "In a 'heavy marsh' of rushes and sedges with water depth of two feet". In the above, "tussocks" may be sedge wet meadows; "rushes" may be *Scirpus* and/or *Eleocharis*, "flags" may be *Iris*, and sawgrass may be some kind of *Carex* with scabrous leaves, or perhaps *Cladium mariscoides* (Muhl.) Torr. (twig-rush, a Cyperaceae

of swamps and marshes, a congeneric of *Cladium jamaicense* Crantz, the true saw-grass of the Everglades, etc.(Fernald 1970)).

From the above, the former nesting habitat of the whooping crane may be surmised: prairie sloughs; small shallow lakes; shallow ponds and open water; willow communities; bulrush marshes; deltas dominated by graminoids, willows, and ponds; mudflats; sandbars; broad and shallow streams; marshes (particularly of bulrush) and mixed marshes of bulrush, cattail, flags, rushes, sawgrass; tussocks. As Allen (1952) found, "muskegs" are non-nest habitat (= organic terrain, e.g., willow/dwarf birch bogs, bog-fens, fens, shrub-sedge fens, treed bogs, etc.). How does the former habitat compare with that of the present?

It is difficult to compare general historic accounts with a specific present account. It is likely that historic and present habitat share the following attributes: small shallow lakes and ponds, willow communities, marshes of bulrush and cattail; mudflats (in the broad sense), and perhaps tussocks (i.e., sedges). Conversely, the present nesting habitat is probably atypical or unique (relative to the core of former range) in its diatom ponds, gypsum karst-groundwater discharge hydrogeology, and permafrost. Relative to currently available potential locations for reintroduction, the extent of the disturbance-free area in the present breeding area may be unique. Indeed it would be difficult to find another site in present day North America that is as large and shares most of the attributes of the nesting area in and adjacent to Wood Buffalo National Park.

## **Is the Whooping Crane Population Modulated by the Northern Hydrological Cycle?**

Whooping crane annual recruitment and annual growth rates (Figure 6) show pronounced peaks and troughs on an approximate 10 year cycle (Boyce and Miller 1985; Nedelman et al. 1987). For example, poor production years occurred in 1941, 1952, 1962, 1972, 1981, and 1991. High frequency flutter (annual variation) in both recruitment and annual growth rate are evident in the early years (up to the mid-1960s), after which both annual variation declines and 10-year periodicity becomes more evident. For the entire period (1938-1995), mean annual growth of the population has been 4.8% (+/-13.6% standard deviation) and mean recruitment 16.7% (+/-9.6%). Up to 1965, annual growth of the population was 4.9% (+/-17.6%) and mean recruitment 20.4% (+/-11.2%). From 1966-1995, annual growth has been 4.7% (+/-8.9%) and mean recruitment 13.2% (+/-6.0%). Mirande et al. (1992) estimated a 3.6% risk of extinction (as of 1990), and a potential total population of 500 birds by the year 2018. At an annual growth rate of 4.7%, the Wood Buffalo-Aransas flock presently has a population doubling time of 16-17 years.

While it is most likely that the early high frequency variation in crane recruitment and annual growth rate was simply the result of the inherent variability of a small sample size (total flock was only 16-44 birds from 1938-1965). Egg collection, which began in 1967 (Kuyt 1981), may have played a complex role in post-1966 population dynamics. While egg collection might be assumed to lower overall growth rates, the method of collection may have acted to dampen population variation in that (1) the possibility of raising two young was removed (thereby damping potential production) and (2) birds with nests in which the egg or both eggs were non-viable were assisted through researchers' switching a non-viable egg with a viable egg collected from another nest (thereby raising potential production).

Ten-year periodicity in whooping crane population parameters has been verified by

Boyce and Miller (1985) and Nedelman et al. (1987). The ARIMA model forecast of future whooping crane numbers produced by Boyce and Miller (1985) for the period 1984-1995 has proven accurate with observed population growth lying within their 95% confidence intervals. The cause of the 10-year periodicity is a topic of immense practical importance to whooping crane recovery. Until recently the widespread 10-year population cycles of boreal animals such as snowshoe hares (Keith 1963) were without plausible explanations. Sinclair et al. (1993) have found that phases of the snowshoe hare cycles across northern Canada appear to be entrained by periods of high amplitude in solar activity, and drift apart during periods of low solar activity. Similarly, flooding of the Peace-Athabasca Delta and muskrat population fluctuations there have been shown to correlate with changes in solar activity which may act to modulate the muskrat cycle through a climatic link acting through temperature, precipitation, and likelihood of ice-jams (Timoney et al. 1997). Increasing solar activity has been associated with lower winter temperatures north of latitude 45 N (Haigh 1994) and intensified Hadley circulation and northward displacement of storm tracks (Kerr 1995).

The importance of water to nesting whooping cranes is evident (see above section and Table 8). In northwestern Canada there is a 10-11 year cycle in precipitation that manifests itself in fluctuating levels of discharge and storage of northern rivers and lakes (McNaughton 1991; Kerr and Loewen 1995). Net snow accumulation on Mt. Logan is modulated in part by the interaction between sunspot cycles and the El Niño-Southern Oscillation which influence precipitation and temperature over broad regions (Holdsworth et al. 1989; Kane and Teixeira 1990; van Loon and Labitzke 1994). While it would be ideal to explore the relationship between crane populations and water levels in the nesting area, there are no long-term water data for the crane nesting area. Mean annual water levels for Great Slave Lake (Figure 7) provide an acceptable surrogate as the data span a similar time window (1939-1992) and the great size of the watershed tends to dampen local and high frequency variation in precipitation. As with the crane time series, prominent peaks and troughs are observable on an approximate 10-year cycle. Low water levels are evident, e.g., in 1945, 1953, 1959, 1970, and 1981.

While an analysis of the Great Slave Lake and crane population time series is beyond the scope of this study, correlations were explored to point the direction for further research. Crane annual recruitment, its three year running mean, annual growth rate, and its three year running mean, were correlated with Great Slave Lake water levels (unaveraged and three year running mean), unaveraged Great Slave Lake water levels lagged one and two years behind, and unaveraged Great Slave Lake water levels advanced one and two years after the crane data. Pearson correlations were run on the coincident full data set (1939-1992), the portion up to 1965, and the portion from 1966-1992. No significant correlations were detected for the full data set, nor for the period prior to 1966. For the period 1966-1992, unaveraged GSL water levels correlated with smoothed crane recruitment ( $r=0.42$ ,  $p=0.03$ ); smoothed GSL water levels correlated with smoothed annual population growth rate ( $r=0.38$ ,  $p=0.05$ ), recruitment ( $r=0.38$ ,  $p=0.05$ ), and smoothed recruitment ( $r=0.48$ ,  $p=0.01$ ); and GSL water levels in the year prior to crane nesting correlated with smoothed annual growth rate ( $r=0.37$ ,  $p=0.05$ ), recruitment ( $r=0.40$ ,  $p=0.03$ ), and smoothed recruitment ( $r=0.43$ ,  $p=0.02$ ).

To what extent do inter-annual fluctuations in whooping crane nesting pond water levels correlate with water levels on Great Slave Lake and also with crane reproduction? Mean pond depths for the period 1976-1994 (after Deonarain 1995) were correlated with unaveraged GSL mean annual water levels ( $r=0.526$ ,  $p=0.03$ ,  $n=17$ ), yet not correlated significantly with smoothed, lagged, or advanced GSL annual water levels. Annual crane

reproduction parameters were all correlated with annual average pond depths in the crane area: population annual growth ( $r=0.717$ ,  $p=0.001$ ,  $n=19$ ), smoothed annual growth ( $r=0.748$ ,  $p<0.001$ ,  $n=19$ ), recruitment ( $r=0.723$ ,  $p<0.001$ ,  $n=19$ ), and smoothed recruitment ( $r=0.677$ ,  $p=0.001$ ,  $n=19$ ).

For an inter-nest comparison, a small dataset was analyzed (spanning the years 1990-1993) for water levels (at time of egg pickup) at individual crane nests, # of chicks censused at that nest at two dates later in summer, and # of chicks from that nest censused at year end at Aransas. There are many missing observations, the water level data span only four years during which there were no major drawdowns or high water events, the data are limited to nest sites (therefore the data are not indicative of a wetland water gradient as it relates to nesting), and the assumption that water levels at time of egg pickup (late May) are relevant to mid and late summer is untested. With these reservations in mind, there were no significant differences in nest pond depths grouped by number of surviving chicks (0 or 1) (for first summer date  $p=0.41$ ,  $n=82$ ; second summer date  $p=0.53$ ,  $n=66$ , and Aransas  $p=0.53$ ,  $n=66$ , Mann-Whitney U tests). Median nest pond depths for those with zero chicks was 15.5 cm, 17.5 cm, and 17.5 cm for the early summer, later summer, and Aransas survival dates. Median nest pond depths for those with one chick was 17.3 cm, 17.7 cm, and 17.7 cm for the early summer, later summer, and Aransas survival dates. As more data are gathered, particularly in low water and high water years, the relationship between pond depths at the nest site and chick production may be elucidated.

Clearly, other factors must be involved which modulate or otherwise influence crane population dynamics, such as crane winter nutrition as affected by productivity of blue crabs on the wintering grounds, mortality during migration, etc. However, in light of the strong relationships between nesting cranes and breeding habitat water conditions, it seems reasonable to suggest that an underlying factor in the 10 year periodicity of crane population dynamics is the 10 year northern hydrological cycle.

## **Nest Spatial Patterns of an Expanding Whooping Crane Population, 1966-1993**

Over the period 1966 to 1993, the population of the wild whooping cranes grew from 43 to 143 birds. Of interest to whooping crane restoration is the question of eventual population limitation through occupancy of all available habitat. Is there evidence that cranes are saturating their habitat, or might population growth continue unchecked for decades to come?

In a growing population characterized by dispersion to new locations, the standard error of geographic locations would tend to rise over time. In a population characterized by infilling, the standard error in locations would tend to fall over time. If both dispersion to new locations and infilling were taking place, standard errors would tend to remain constant. Latitudes and longitudes of crane nest locations  $\pm$  one standard error (Figures 8, 9) indicate spatial changes in the crane nests. From 1966 to 1970, the center of the crane breeding range shifted to the north and west (in 1966 and 1967 some nests may have been missed due to workers' unfamiliarity with the breeding grounds (Kuyt 1981)). Since the early 1970s, the crane population has expanded generally southward (Figure 8). The center of the breeding range, based on 596 reliable nest locations (from 1966-1993) is:  $60.24^\circ$  N,  $113.32^\circ$  W (median:  $60.25^\circ$  N,  $113.33^\circ$  W).

The relatively constant standard error both in latitude and longitude indicates that both

dispersion and infilling are taking place. Large error bars highlight years in which dispersion to new areas took place, such as in 1971 to the Nyarling, in 1977 to Alberta, and in 1982 to the Lobstick area). The dispersion and infilling of the whooping crane population is detailed in Figure 10. Most of the population growth is due to infilling in the Sass and Klewi areas. Since both infilling and dispersion continue, and observations indicate seemingly suitable unoccupied range, there is no reason to conclude that whooping cranes will be limited by available habitat in the near future.

Is the distribution of crane nests randomly distributed across the landscape? In contrast to sandhill cranes at Seney NWR, in any given year (Figure 10), and for the entire record (Figure 11), it is clear that whooping crane nest locations are highly contagious at the landscape scale. Such contagion could be due both to habitat selection by breeding birds and to nest site fidelity of the returning pairs (see Kuyt 1981).

## Landscape Dynamics

At least four temporal scales of dynamism operate in the crane area: (1) Annually, the ponds and wetlands undergo a recharge-drawdown cycle. (2) Surface water and groundwater levels fluctuate on a decadal 10-11 year hydrological cycle (McNaughton 1991), linked to a precipitation cycle (Kerr and Loewen 1995), which is in turn linked to continental and global-scale processes (Holdsworth et al. 1989, among others), and to a 10 year cycle of whooping crane annual recruitment and annual growth rates (Boyce and Miller 1985; Nedelman et al. 1987). (3) Fire, operating on a scale of ~50-250 years, periodically sets back woody encroachment, succession, and peat aggradation, leading to thermokarsting and favoring pond, marsh and fen formation. (4) Peat aggradation operates on a scale of thousands of years.

Sixty-one ages were collected to date post-fire regeneration, typically from dwarf birch (*Betula glandulosa*), with some willow (*Salix*), Alaska birch (*Betula neoalaskana*), and river alder (*Alnus incana*). Surprisingly, ages varied significantly, indicating that either post-fire regeneration did not follow immediately after the major 1981 fire (most likely), or that other fires have occurred in the area more recently. For random nest sites, the oldest basal ages by site were: 9, 17, 16, 14, 23, 11, 14, 15, 8, and 16 (median 14.5 years). For random available sites, the oldest basal ages by site were: 12, 15, 11, 10, 13, 12, 16, 16, 14, 10, 13, and 9 (median 12.5 years). Since only 2-3 samples were collected per burned site, it is likely that the oldest regeneration may have been missed in some cases. The ages may be interpreted safely as the minimum number of years since fire.

Soil augering at plot centre and aerial observations indicated long-term landscape changes, both pond and marsh to peatland (peat aggradation) and peatland to pond and marsh (peat degradation) succession. At 10 of 32 sites a mineral layer was encountered (within 1.2 m of surface) below the organic deposits, usually a gleyed silty clay glacial till. At all other sites, organic deposits were deeper than 1.2 m. Commonly, loose fibric floating mats or mesic peats lay directly above diatom deposits. The latter pattern indicates a pond to peatland succession. Also common were (a) deep deposits of diatoms, indicative of long-term open pond conditions; and (b) an admixture of diatom deposits and marsh peat, indicative of bulrushes within a diatom pond. At other sites, diatom deposits overlie fen, marsh and bog peats, indicative of a peatland or marsh being replaced by a diatom pond.

Aerial observations showed diatom ponds in various stages of progressive succession to bulrush marsh, mixed marshes, and fens (Frontispiece). Retrogressive (peatland to pond) succession is accelerated by fire. Peat stratigraphy clearly shows that retrogressive succession

is common there. On a decadal to centennial scale, fire may help to maintain both the diatom ponds, and indirectly, whooping cranes. It would be incorrect, however, to conclude that fire drives this ecosystem and results in the formation of the ponds in general. Rather, groundwater discharge influenced by dissolution of gypsum appears to be the chief process that characterizes this ecosystem.

In Canadian boreal wetlands, development is toward treed bogs, with an average rate of fen and bog peat accumulation of about 4-8 cm / 100 years (National Wetlands Working Group 1988). Rates of sedimentary peat accumulation vary widely across Canada from 0.2-9 cm / 100 years (Tarnocai and Schuppli 1987) (no data from the Northwest Territories). Most of the organic deposits of the crane nesting area exceed 1 m depth. As accumulation rates vary, and there are no data for transitional marsh-fen peats (a major constituent of the organic profiles), there is presently no way to surmise the age of the deposits.

### **Landscape Composition, Diversity and Fractal Dimension**

For 500 m radius plots centered on crane nests (Table 9), predominant types are Shrub Bog-Marsh (18.5%) and Mixed Marsh (10.4%); taken together, open water diatom ponds occupy 22.6% of the landscape (Cream + Powder Blue + Turquoise + Greenish to Black Ponds). Bulrush Marshes occupy 4.5%, and Shrub Featureless Organic Terrain 6.6%, respectively. Of the 1310 patches analyzed, average patch size was 0.954 ha. The smallest patches were Greenish to Black Ponds and Bulrush Marshes and the largest patches Peat Plateaus and Shrub Bog-Marshes. In general, patch size is small relative to typical boreal vegetation patches, indicative of high spatial diversity. Overall fractal dimensions for the nest plots was (PA method) 1.251 +/- 0.108 or by P(m,L) method, 1.647 +/- 0.119. Landscape diversity ( $H'$ ) = 2.740, dominance (D) = 0.255, evenness = 0.915, scaled dominance = 0.085, combined contagion 50.429, scaled contagion = 0.842, and number of cover types = 20.

For random 500 m radius plots (Table 10), predominant types are Shrub Featureless Organic Terrain (17.7%) and Shrub Bog-Marsh (9.5%); taken together, open water diatom ponds occupy 20.5% of the landscape. Bulrush Marshes occupy 2.9%. Of the 1273 patches analyzed, average patch size was 0.981 ha. The smallest patches were Bulrush Marshes and Shrub Organic Terrain Strings, and the largest patches were Upland Forest, Treed Organic Terrain in a Diatom Pond matrix (OTX), and Peat Plateaus. Patch size is small relative to typical boreal vegetation patches. Overall fractal dimensions for the random plots was (PA method) 1.283 +/- 0.048, or by P(m,L) method, 1.624 +/- 0.132. Landscape diversity ( $H'$ ) = 2.802, dominance (D) = 0.242, evenness = 0.920, scaled dominance = 0.080, combined contagion = 53.483, scaled contagion = 0.837, and number of cover types = 21. At the 500 m radius scale, there is no statistical difference in fractal dimensions between nest and random sites by either PA ( $T=-1.606$ ,  $p=0.125$ ) or PmL methods ( $T=1.701$ ,  $p=0.105$ ).

The most complex-shaped communities (Tables 9, 10) in the crane area are shrub strings, mixed marshes, treed strings, and both tree and shrub featureless organic terrain, and the simplest-shaped communities are burned and unburned peat plateaus and diatoms ponds.

It is difficult to put landscape diversity and fractal measures into a context with other studies, as they are both rarely measured, especially in a boreal ecosystem. In general, patch size is small and landscape diversity is high for a boreal environment where patch sizes may measure many ha and only a few cover types may dominant hundreds of km<sup>2</sup>. For the subarctic treeline of Northwestern Canada, Timoney et al. (1993) found median patch sizes of tree and tundra vegetation of 36 ha and 13 ha, respectively. Walker (1995) calculated PA

fractals of ~1.3 for three cover types in Riding Mtn. National Park. Krummel et al. 1987 found a domain break at a patch area of 150-183 acres (~ quarter section)-- smaller patches (affected by agriculture) had a fractal dimension (P-A method) of 1.15 to 1.25, larger patches (with +/- natural boundaries) had a fractal dimension of ~1.4). In general, the crane area appears to be characterized by high P(m,L) fractal values (>1.6), indicative of widely-dispersed (non-isolated, non-contagious) communities. As GIS-based landscape analyses become more common in the future it will be possible to place the landscape measures of the crane area into a more informative context.

At the 500 m radius scale, landscape structure (as indicated by patch size, fractal dimension, contagion) and landscape diversity, dominance, and evenness are virtually identical when nest and random plots are compared (Table 11).

The question of habitat composition and selection as it relates to random and nest plots is next explored.

### **Habitat Selection at Five Spatial Scales**

Analysis of the percent landscape composition at five spatial scales for 21 cover types (Table 12), permits a basic question to be explored: are there any habitat types that are either selected or avoided by nesting whooping cranes, and at what spatial scale does this interaction occur? Multivariate ANOVA tests (Table 13) indicated that only two cover types have a significant interaction between plot size and plot type: Bulrush Marshes and Shrub Featureless Organic Terrain (shrub-dominated bogs and fens without ponds, strings, fens, or meadows included in the matrix). The spatial scale of habitat selection for these cover types on whooping crane habitat selection was then examined via univariate F tests (Table 14, Figure 12). Whooping cranes choose *Scirpus validus* habitat out to a radius of 200 m from the nest. In contrast, cranes avoid featureless shrub bogs and fens out to a radius of at least 500 m from the nest.

As an independent test of spatial scale of habitat selection, multiresponse permutation procedures (MRPP, Euclidean distance) were run (Table 15). Rather than examine each cover type individually (as in Tables 13, 14), in the MRPP each habitat cover type was treated as a "species" within a landscape releve. When all cover types are considered in aggregate, whooping crane nesting habitat selection is evident out to at least 500 m from the nest. To account for the influence of Bulrush Marshes and Shrub Featureless Organic Terrain on habitat selection, MRPP was run again with these two types excluded. There is weak evidence of habitat selection at the 25 m radius scale ( $p=0.056$ ), and no other evidence of habitat selection at other scales. The clear conclusion is that whooping cranes strongly select for Bulrush Marshes (up to 200 m from the nest), strongly avoid Shrub Featureless Organic Terrain (up to 500 m from the nest), and may select (weakly) for other habitat types in aggregate within a 25 m radius of the nest.

### **The Scale Context in Crane Habitat Selection**

The nested design of this study employed two different types of data: (1) detailed plot descriptions based on ground studies, and (2) habitat mapping on 1:15,840 scale airphotos. The spatial grain-size of the ground studies was a 0.03 ha plot (9.8 m radius), whereas that for the airphoto-based habitat analyses was a 0.1 ha polygon and a plot size of 0.2 ha (25 m radius). Within each ground plot, numerous measurements and estimates were made (see

Field Methods) while the fundamental measurement in the habitat analysis was a cover type polygon, and therefore the difference in information resolution of the two types of data is greater than the difference in spatial resolution alone. Baker et al (1995) found that a 0.1 ha grain-size, while small relative to an entire wetland, may in some cases be too large to describe the vegetation around a nest.

Landscape transitions (i.e., habitat boundaries) tend to be sharp rather than clinal in the crane area. Such sharp transitions (<10 m "ecotone") are likely the outcome of discontinuities in water and peat accumulation. The grain-size of the landscape spatial pattern varies widely, but in the core of the crane area it is fine-grained. Depending on the habitat classification used, polygons for pure cover types may be smaller than 0.1 ha, and therefore it was necessary to use mosaic types in many cases. Relative to other landscapes in boreal Canada, grain-size is small and perimeter to area ratios are high; there is both a high degree of edge and high spatial diversity. Perhaps the abundance of habitat edges and the spatial diversity are important to the cranes. It is not possible to test that assertion at present because the entire area for which there are airphotos is typified by high edge and spatial diversity.

While indicators of crane nesting habitat necessarily differ between the detailed field data and the habitat mapping data, it is important to realize that the data are speaking at different scales of resolution. Differences in results may be viewed as complementary rather than contradictory. For example, at the mapping scale, only Bulrush Marshes and Shrub Featureless Organic Terrain were the only habitat types showing crane selection or avoidance. In contrast, at the detailed field scale, many indicators may be identified, e.g., various vegetation types, plant species, structural indicators such as distance to woody concealment, water depth, and distance to nearest water; and pond bottom color. The strength of the field studies is their power to detect differences between random and nesting habitat; their weakness is their limited spatial scale.

Thus when searching for new areas in which to introduce whooping cranes it is essential to be sensitive to scale of resolution. The findings of this study, to be useful to reintroduction efforts, must be applied at the appropriate scales. Hopefully, in the search for new breeding areas, a multiple-scale approach will be taken.

## **Long-Term Monitoring of Cranes and the Nesting Area: A Conceptual Framework**

### **General Considerations**

It is difficult to envision an expansion of operational costs to Wood Buffalo during this period of cutbacks and low funding. Unless new funding can be found to support an expansion of the current crane-related operations, only the most fiscally modest recommendations have potential for implementation. Therefore, the approach I have taken is a compromise between ecology and economy.

Hydrological regime plays an important role in the condition of the wetlands used for nesting and foraging-- although the exact relationship between summer pond depth and annual crane reproduction needs further research. Regional precipitation, groundwater flow, and surface flow are correlated to varying degrees with those within the crane area proper. Water levels in the crane area are affected by groundwater discharge from the Caribou Mountains,

local precipitation, and evapotranspiration (McNaughton 1991).

Clearly, the annual monitoring of the crane population its reproduction must continue, and for overriding operational reasons, fire monitoring should also continue. The following assumes that both population and fire monitoring is to continue.

### **Research Needs**

Much climatic and hydrologic monitoring is conducted by other agencies and these provide a potentially useful source of information. Before data such as snowpack in the Caribou Mountain, precipitation at Ft. Smith, and Little Buffalo River stage height can be used for proxy monitoring, research must be conducted to establish the degree of correlation and lag between the available proxy data and the parameters of interest in the crane area (see e.g., a preceding section on crane reproduction and Great Slave Lake mean annual water levels). For example, what is the correlation between stage height of the Sass and Klewi Rivers (where they cross Highway 5) and hydrological data collected by other agencies (such as Ft. Smith precipitation)? Once the statistical links and lags are established, a large amount of virtually free proxy data will be available for monitoring habitat water conditions.

### **Species and Community Level Indices**

The combined results of DCA and TWINSPAN provide a set of species and community indicators. Plant taxa indicators of nesting habitat are algae (benthic diatom and blue-green algal communities), *Chara* spp., *Eleocharis palustris*, *Scirpus validus*, *Typha latifolia*, and *Utricularia minor*. Plant taxa indicators of non-habitat are: *Aulacomnium palustre*, *Betula glandulosa*, *Campylium stellatum*, *Carex aquatilis*, *Ledum groenlandicum*, *Picea glauca*, *Polytrichum juniperinum*, *Rubus acaulis*, *Salix bebbiana*, *Salix myrtilifolia*, and combined *Salix*.

At the community level, indicators of nesting habitat are: shrubby mixed marshes with water sedge and cattail +/- bulrush; bulrush/cattail mixed marshes with aquatics; bulrush marshes with diatom ponds; and diatom ponds with bulrushes. Vegetation typical of random available habitat are: willow/dwarf birch and spruce ombrotrophic bogs; willow/dwarf birch bog-fens with abundant mosses; willow/dwarf birch/sweet gale strings in marshes, fens, bogs; willow/dwarf birch bog-fens with abundant water sedge.

### **Water Monitoring**

Once research needs are addressed (see above), data for key climatic/hydrologic indicators should be assembled into a park crane database (both as far back as the record exists, and into the future). Discussion with the appropriate agencies (e.g., Water Survey of Canada, Environment Canada, Canadian Wildlife Service) should be held regarding reliability of the data, data gaps, any plans for cessation of data gathering. The goal of the water monitoring would be to assemble and maintain a set of long-term, reliable indices that correlate well with crane area water levels.

### **Airphoto-based Monitoring**

Monitoring at the species level is time consuming, can be taxonomically difficult, and is prone to year-to-year variations (high frequency noise). It is not appropriate to a situation of limited personnel and funding. The focus of monitoring should be at the community and landscape level. Vegetation communities in the crane nesting area are easy to distinguish

with high quality false color infrared photography (see Methods: Landscape-Level Cover Types).

**Airphotos.** I recommend that once every 5 years, a set of airphotos be flown (same scale and type as used in this study). The coverage need not be extensive-- a subset of the area would suffice for monitoring (~20 airphotos)-- but fixed costs and the overall cost/airphoto must be considered. With appropriate technical advice (e.g., US Fish and Wildlife Service), it might be feasible to obtain acceptable vertical airphotos through the use of park contract helicopter or fixed-wing. Weather permitting, each edition of photos should be taken in about mid-July.

**Framework.** Ten areas for monitoring should be chosen; I recommend that each area be a circular plot of one km diameter, inside of which percent community cover should be estimated by cover type. For both efficiency, ground truth, and to maximize the length of the record, the ten chosen should be from the 32 plots analyzed for this study. Each plot should be mapped into community type polygons. At the same time, distance to the nearest tree and to nearest water from plot centre, and cover of open water should be assessed. Due to the relationship between water depth and the false color of water bodies, a good index of water conditions in each plot will be available through assessing the percent cover of water bodies by pond color (as done in this study). Percent cover by community for each plot could be estimated by one of three methods: (1) visually (fast, inexpensive, least accurate); (2) dot grid (moderately fast, inexpensive, and accurate); or (3) digitizing into a GIS (slowest, most expensive, most accurate). If the latter option is chosen, landscape structural attributes could be assessed, such as total length of shoreline by pond type, type perimeter:area ratios, type fractal dimension. By resampling identical plots, trends in hydrological regime and succession would be evident. These data and trends could be linked to the crane population, fire, and water monitoring. Much remains to be learned regarding the dynamics of cranes, climate, and their habitat.

## **Recommendations**

No effects of fire on whooping cranes -- either positive or negative -- are detectable from any of the available data. It is possible that fires may benefit the cranes through favoring graminoid vegetation and ponds over woody and peatland vegetation (although this was not detectable with the data). Due to the potential negative effects of a major fire control operation in the crane area (e.g., nest abandonment, inadvertent helicopter harassment, fire retardant effects on the wetlands, water bombing), it is advisable to classify the area as "modified response".

Under a modified response regime, fire management should consider two factors before taking fire suppression action in the area: (1) the fire's location in relation to nest locations and known feeding areas; (2) time of the year in relation to crane activities (presence--absence, pre-nesting, nesting, rearing, pre-migration) in order to minimize disturbance, especially during nesting and rearing. Only high altitude flights should be allowed over the area, including those of the fire monitoring program. No medium class helicopters should be allowed over or in the crane area at any time when cranes are present.

The crane population is healthy and growing. The nesting habitat is healthy. No manipulation or intervention is required in either case. Support for establishing two new wild

population of whooping cranes should, however, be maintained. High priority protection of the cranes and their habitat should continue. Parks Canada opposition to construction of any communications towers within the breeding range and the migration path of the cranes should continue.

A long-term scientifically credible monitoring and research program should be established. The basic elements are already in place: population, water, and fire monitoring, and the habitat monitoring suggestions above. The next step in the habitat study should be to document the summer diet of the whooping crane and relate that diet to the habitat findings of this work.

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## List of Figures

Frontispiece. The whooping crane nesting area landscape. (a) Whooping crane on nest (upper right) on *Scirpus validus* - *Carex aquatilis* bands within a yellow diatom pond (28 May

1996); note lack of shrub cover; area was burned, probably in 1981; (b) whooping crane tracks on shore of cream-toned diatom pond (12 Aug 1996); (c) typical landscape in northern, drier, part of crane area: ponds succeeding to *Carex aquatilis* marshes within a shrub string matrix; ponds are typically too dry for nesting cranes (12 Aug 1996); (d) whooping crane nest in light-toned *Scirpus* - *Carex* - *Typha* mixed marsh before green-up (bird off nest), associated with deep water pools (black), surrounded by typical yellow diatom ponds (28 May 1996); (e) mosaic of shallow ponds of varying depths, *Scirpus* beds, burn-origin *Salix* - *Betula glandulosa* / *Ledum* dry bogs, and remnant unburned white spruce (13 Aug 1996); (f,g,h) false color infrared images, scale 1 cm = 158 m, July 1993, reproduced courtesy of Wood Buffalo National Park; (f) turquoise (true color yellow), powder blue (pink), and greenish (brownish) ponds; *Carex aquatilis* wet meadow in photo center is an infilling pond complex; stippled pink is treed organic terrain; photo SK-3-16; (g) large mixed marsh complex (olive), powder blue ponds, black ponds connected to streams; pink tones are shrubby mixed marshes; dark stippling is treed organic strings; photo SK-3-14; (h) recently-burned landscape (probably 1981) with typical brownish-olive peat plateau and associated thermokarst ponds; turquoise, powder blue, and cream ponds, olive *Scirpus* beds associated with diatom ponds; grainy pink is shrub - sedge bogs and fens; photo SK-9A-5.

Figure 1. DCA plot ordination. Vegetation class symbols are: ● Bulrush Marshes and Diatom Ponds; ▲ Mixed Marshes; ▼ Shrub Mixed Marshes; ◆ Treed Mixed Marshes; ◀ Shrub - Sedge Fens and Bog-Fens; ▶ Shrubby Organic Terrain; ■ Treed Organic Terrain.

Figure 2. Overlays of percent cover values of 12 indicator species on the DCA plot ordination; (a) diatoms and blue-green algae, (b) *Aulacomnium palustre*, (c) *Betula glandulosa*, (d) *Campylium stellatum*, (e) *Carex aquatilis*, (f) *Eleocharis palustris*, (g) *Picea glauca*, (h) *Salix bebbiana*, (i) *S. myrtilifolia*, (j) all willow species, (k) *Scirpus validus*, (l) *Typha latifolia*.

Figure 3. Vectors of significant quantitative ecological parameters ( $R^2$  cutoff 0.16) overlain on the DCA plot ordination. Numbers 1-16 are nest sites, 17-32 are random available sites. Length of the vector is proportional to strength of correlation. Dis1.5 and Dis.75 are distance to nearest concealment at 1.5 and 0.75 m above ground; Openwa is percent cover of open water; Terrma is percent cover of terrestrial vegetation + marsh; Nearwa is distance to nearest water; Waterd is water depth.

Figure 4. DCA species ordination. Species codes use first four letters of genus and first two letters of species, with exceptions: 'Algae' = diatoms and blue-green algae; 'Salixa' = combined cover of all willow species.

Figure 5. Cluster analysis of plots based on species abundance (method: 2W/(A+B), centroid; percent chaining = 9.26). Type codes: BM = treed marsh complex; MM = mixed marsh; OT = spruce-larch organic terrain; SV = bulrush marsh; SVDi = bulrush marsh/diatom pond complex; TBF = shrubby bog-fen complex with water sedge; TBM = shrub marsh complex; TOT = willow-dwarf birch organic terrain; TOTX = shrub organic terrain strings in pond complex.

Figure 6. Whooping crane annual recruitment [= # young / #adults] and annual population growth rate [= total flock<sub>(year x)</sub> - total flock<sub>(year x-1)</sub>/total flock<sub>(year x-1)</sub>, 1938-1995]. Year-end census raw data courtesy of B. Johns, Canadian Wildlife Service.

Figure 7. Great Slave Lake mean annual water level (m), 1939-1992. Data from Kerr and Loewen (1995).

Figure 8. Latitude of crane nests: mean +/- one standard error, 1966-93.

Figure 9. Longitude of crane nests: mean +/- one standard error, 1966-93.

Figure 10. Crane nest locations by year, 1966-1993; ellipse is the 95% confidence interval of the bivariate centroid.

Figure 11. All crane nest locations, 1966-1993 (n=596). Graph is ~77 km by 77 km.

Figure 12. Box and whisker plots of Bulrush Marsh cover (SV, top) and Shrub Featureless Organic Terrain cover (TOTF, bottom) by plot type for five plot sizes. Top and bottom of box is the 75th and 25th percentiles; center line is the median; top and bottom whiskers mark the maximum and minimum values, unless there are outliers; in that case, a whisker marks the maximum or minimum exclusive of outliers; asterisks lie beyond >1.5 times, and open circles >3 times, the interquartile range plus the 75th percentile.

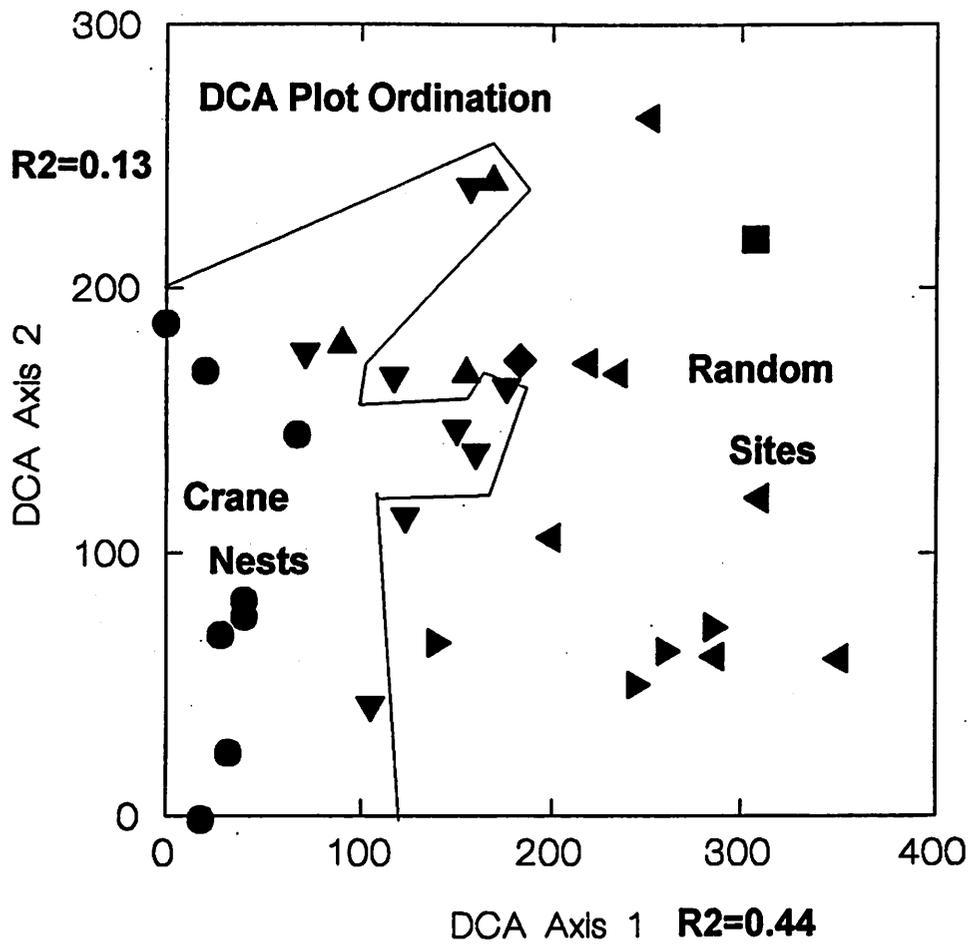
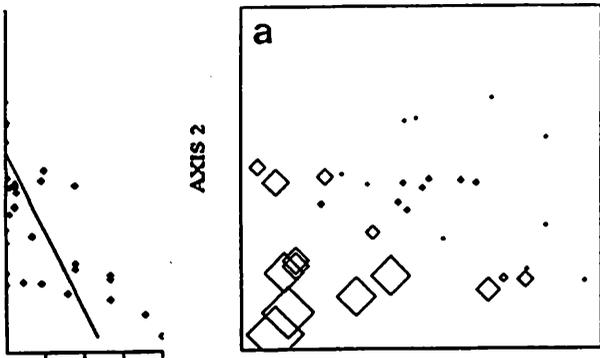


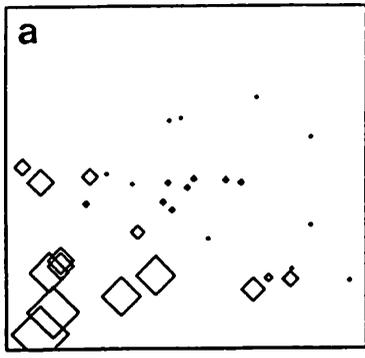
Figure 1. DCA plot ordination. Vegetation class symbols are: ● Bulrush Marshes and Diatom Ponds; ▲ Mixed Marshes; ▼ Shrub Mixed Marshes; ◆ Treed Mixed Marshes; ◀ Shrub - Sedge Fens and Bog-Fens; ▶ Shrubby Organic Terrain; ■ Treed Organic Terrain.



Algae

CORRELATIONS

Axis	r	tau
1	-.595	-.494
2	-.667	-.481
3	.831	.184



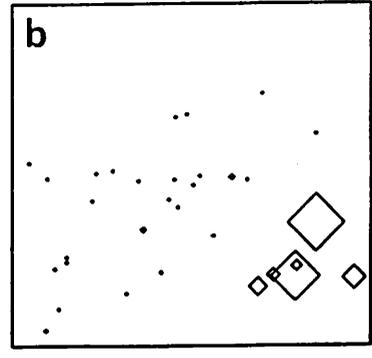
AXIS 1



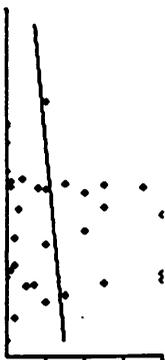
Aulapa

CORRELATIONS

Axis	r	tau
1	.561	.517
2	-.273	-.263
3	.832	.875



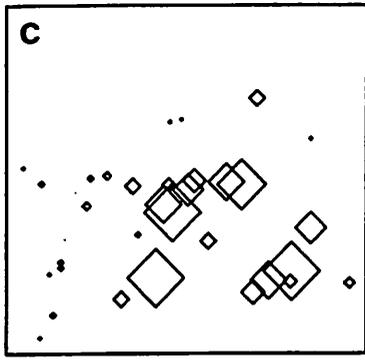
AXIS 1



Betugi

CORRELATIONS

Axis	r	tau
1	.442	.488
2	-.114	-.129
3	-.188	-.112



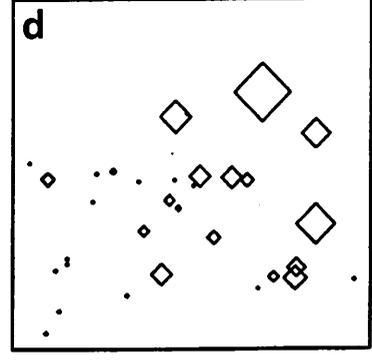
AXIS 1



Campst

CORRELATIONS

Axis	r	tau
1	.521	.482
2	.482	.217
3	-.484	-.316



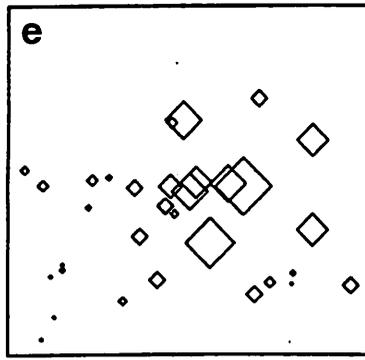
AXIS 1



Careaq

CORRELATIONS

Axis	r	tau
1	.457	.435
2	.391	.317
3	.145	-.882



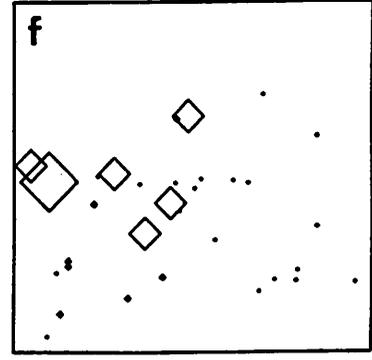
AXIS 1



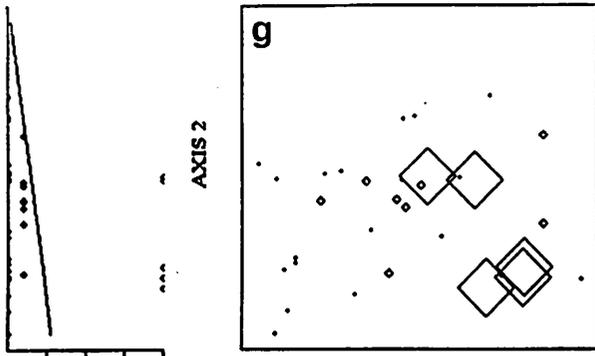
Eleopa

CORRELATIONS

Axis	r	tau
1	-.385	-.451
2	.279	.126
3	-.835	-.884

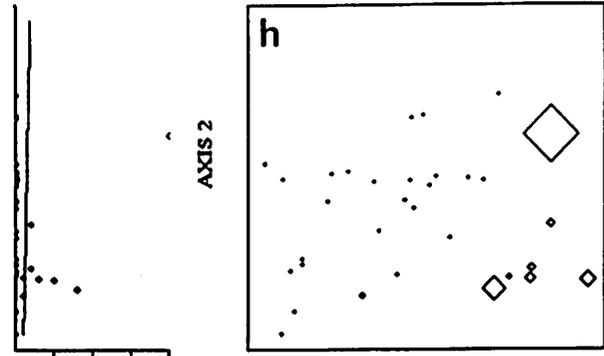
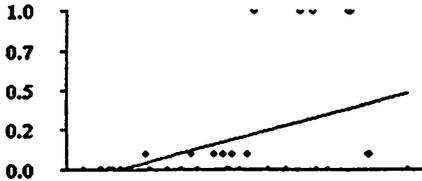


AXIS 1



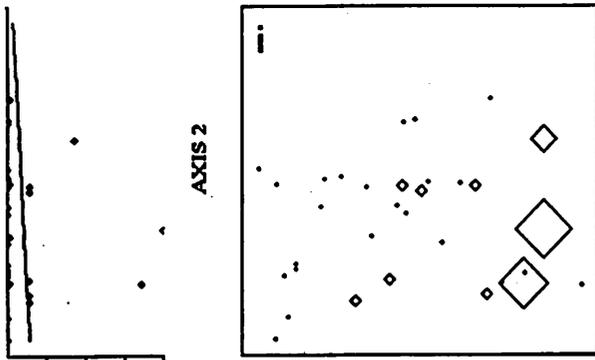
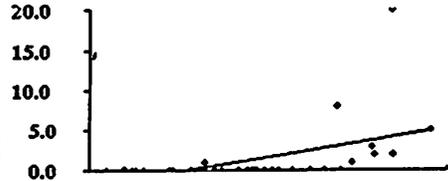
Picegl

**CORRELATIONS**  
 Axis r tau  
 1 .428 .374  
 2 -.142 -.856  
 3 -.856 -.824



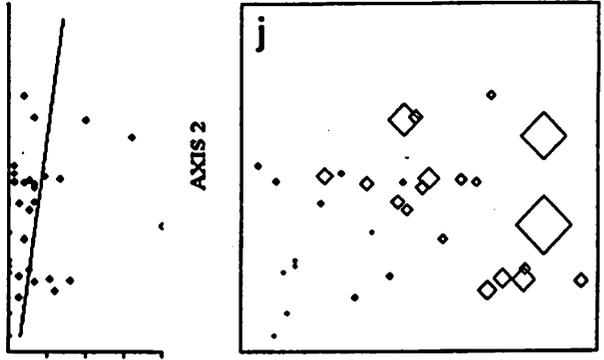
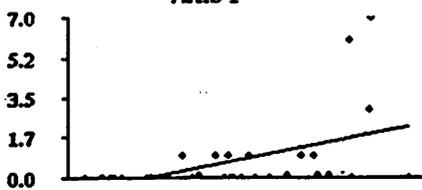
Salibe

**CORRELATIONS**  
 Axis r tau  
 1 .487 .437  
 2 .844 -.281  
 3 .155 .148



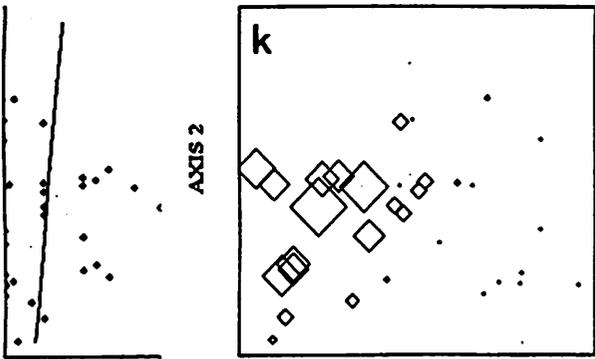
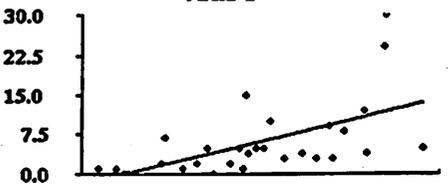
Salimy

**CORRELATIONS**  
 Axis r tau  
 1 .482 .433  
 2 -.886 -.877  
 3 .861 .877



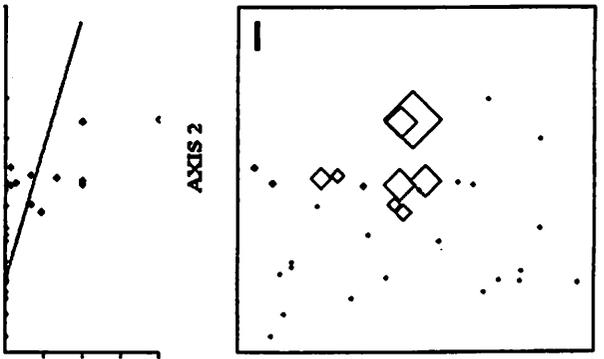
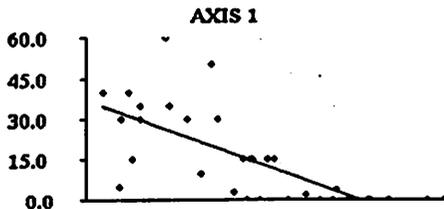
Salixa

**CORRELATIONS**  
 Axis r tau  
 1 .618 .568  
 2 .238 .188  
 3 -.855 -.829



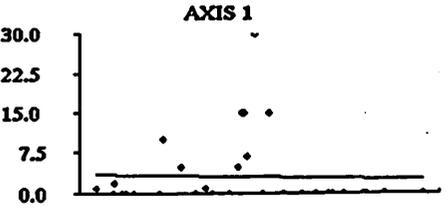
Scirva

**CORRELATIONS**  
 Axis r tau  
 1 -.718 -.624  
 2 .117 .114  
 3 -.333 -.298



Typha

**CORRELATIONS**  
 Axis r tau  
 1 -.848 -.159  
 2 .511 .481  
 3 .354 -.813



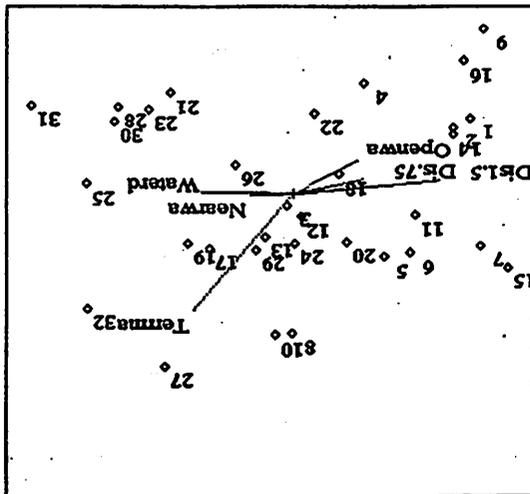
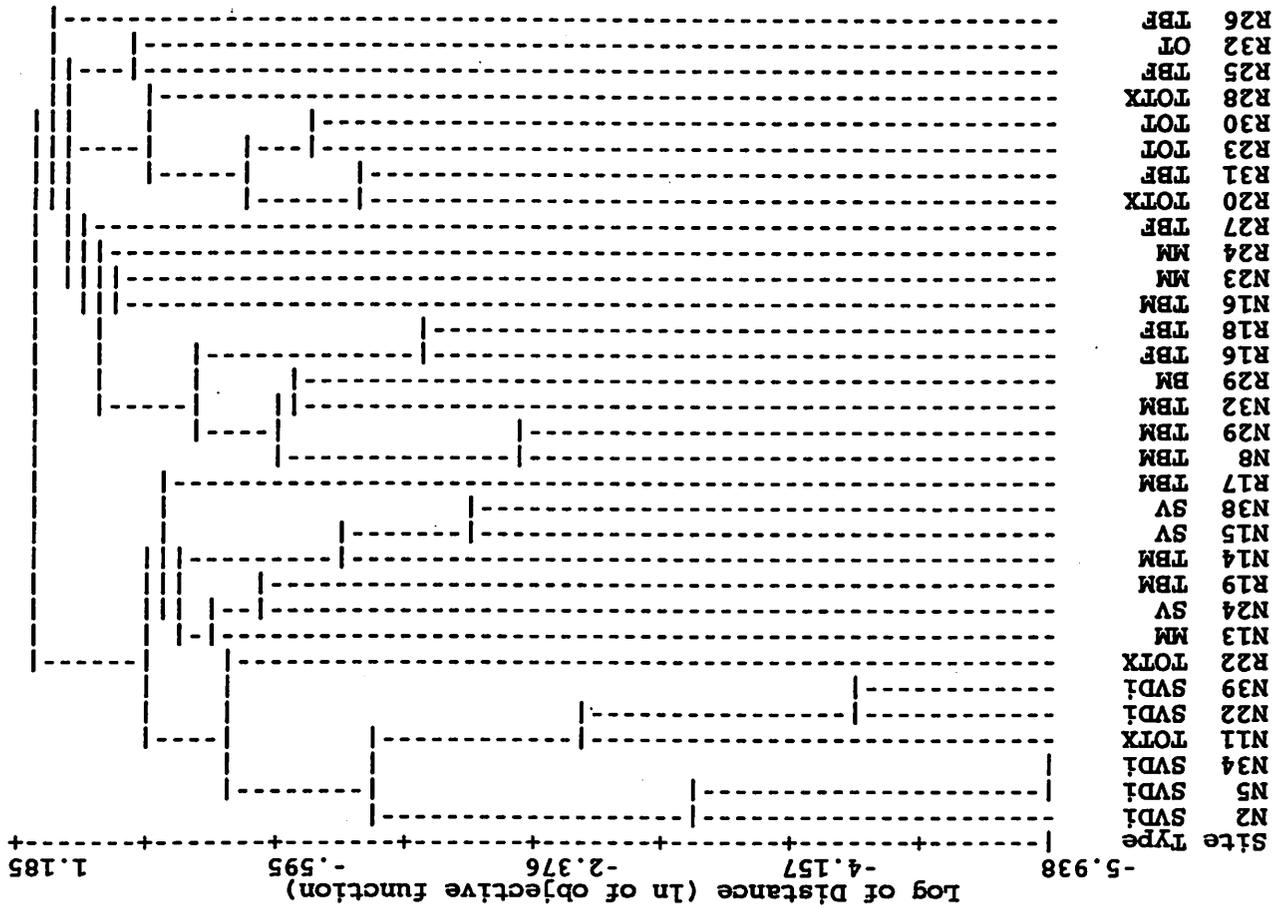
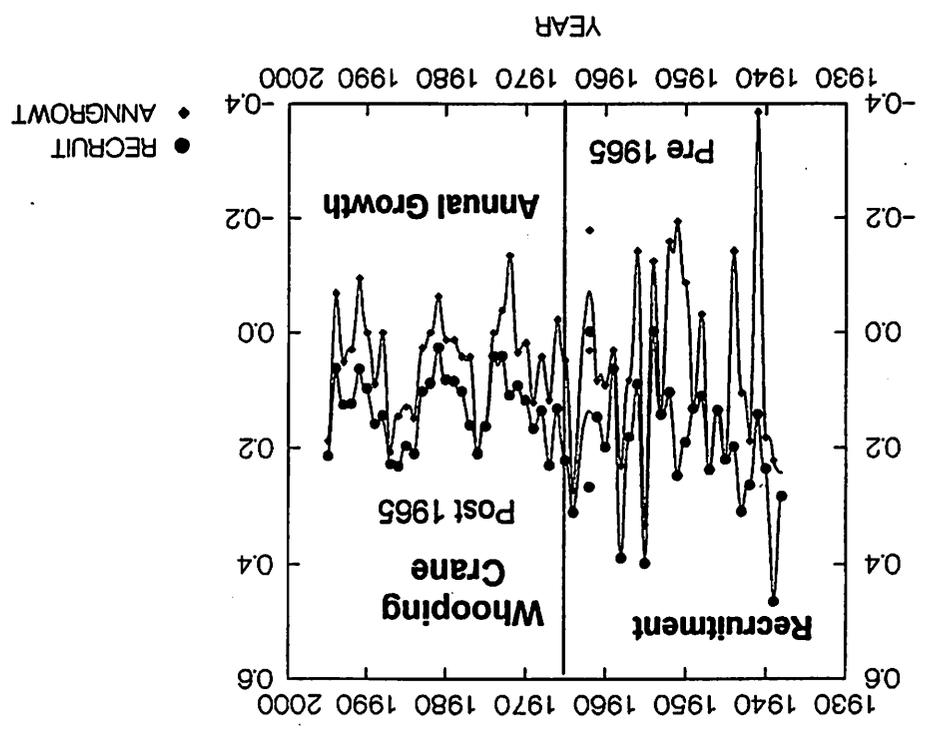
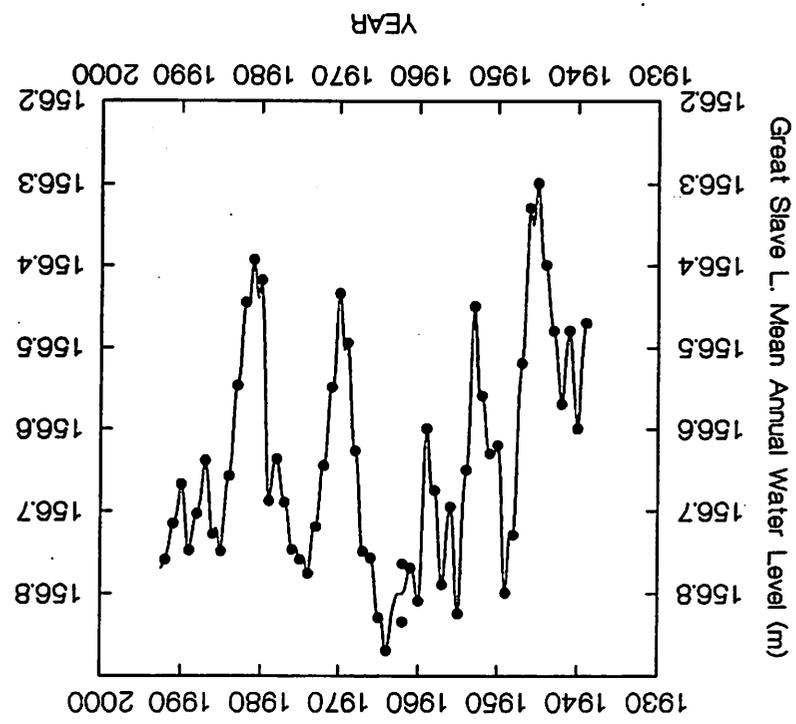




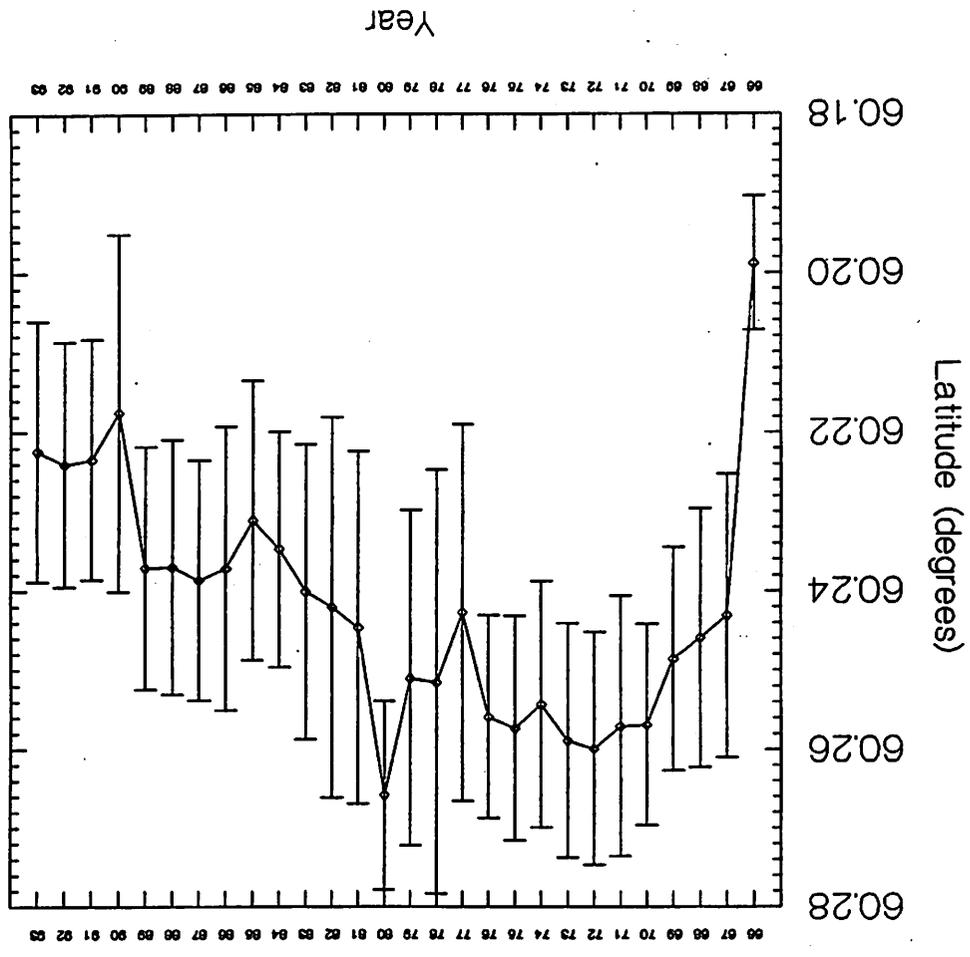
Figure 5. Cluster analysis of plots based on species abundance (method:  $2W/(A+B)$ , centroid, percent chaining = 9.26). Type codes: BM = reed marsh complex; MM = mixed marsh; OT = spruce-larch organic terrain; SV = bulrush marsh; SVDI = bulrush marsh/diatom pond complex; TBF = shrubby bog-ten complex with water sedge; TBM = shrub marsh complex; TOT = willow-dwarf birch organic terrain; TOTX = shrub organic terrain strings in pond complex.

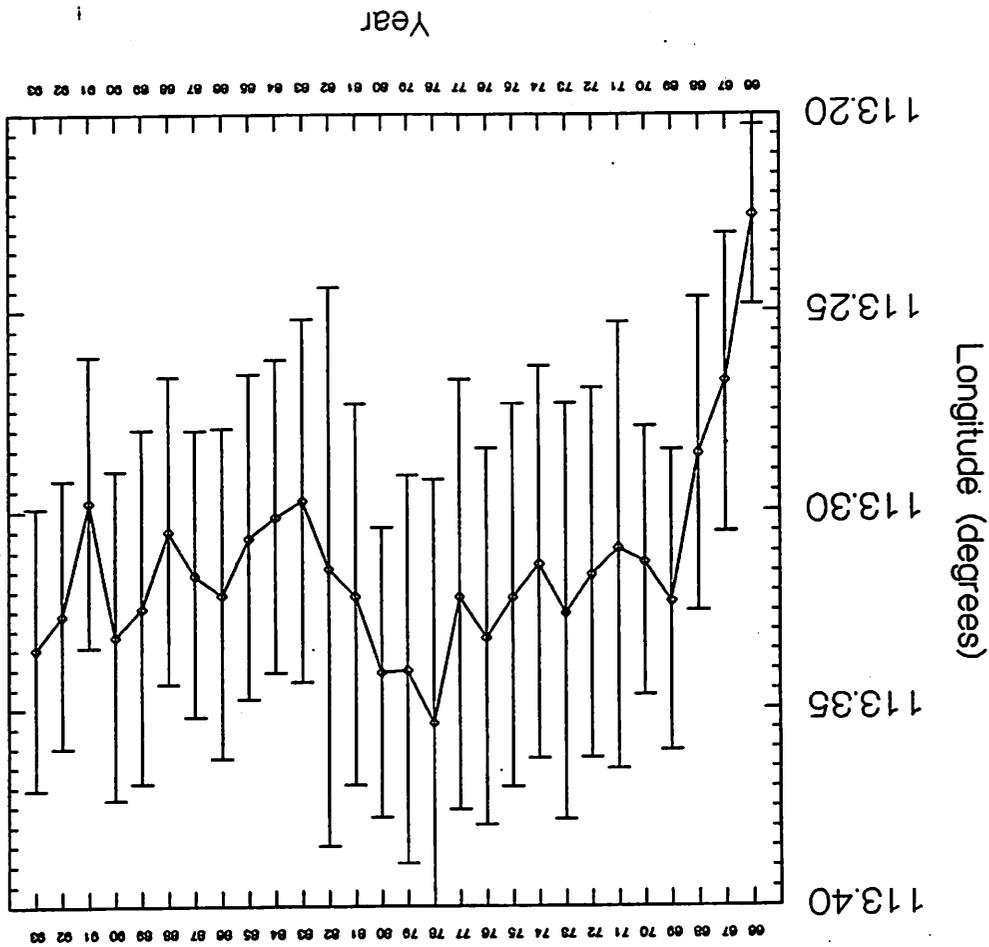


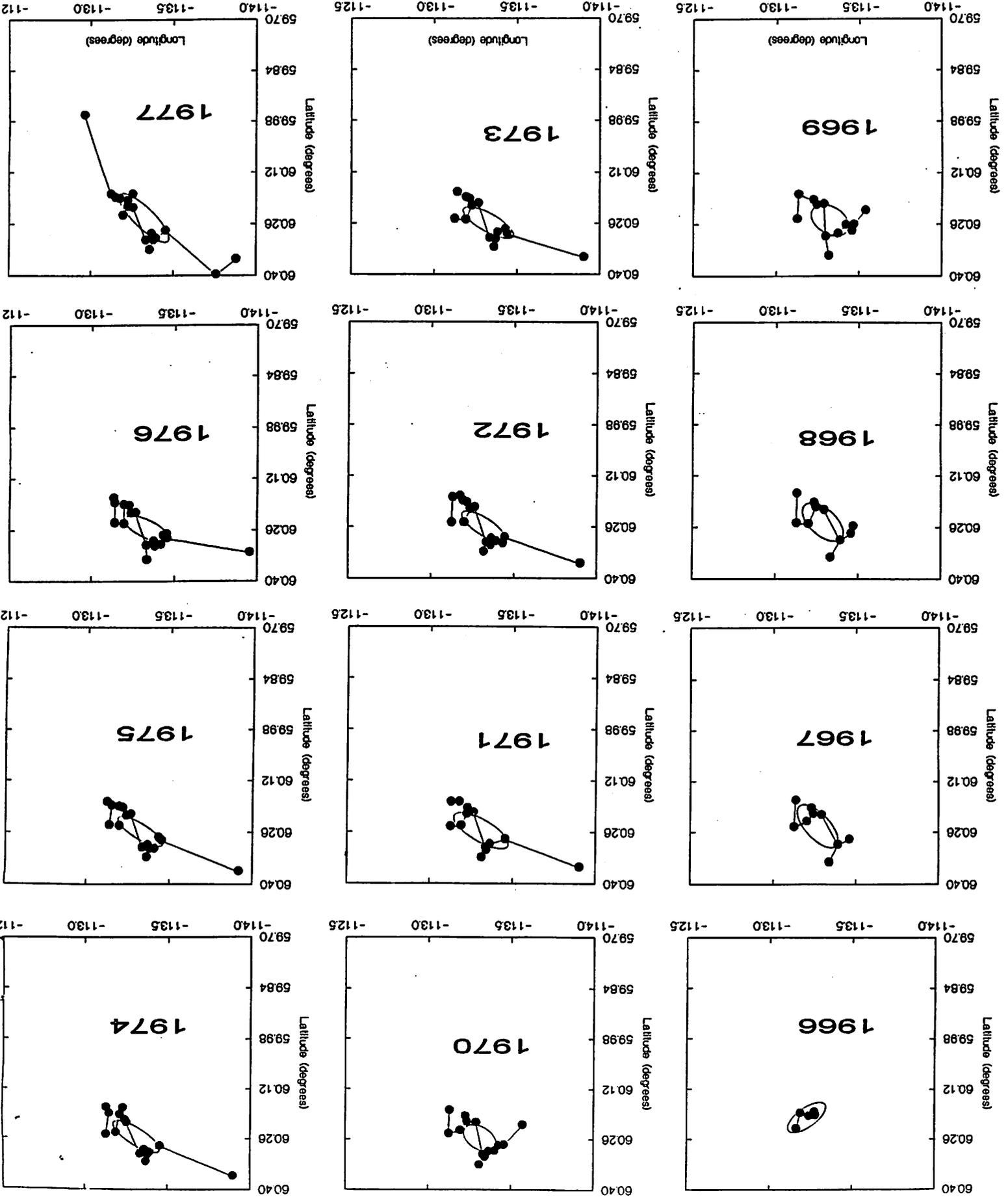


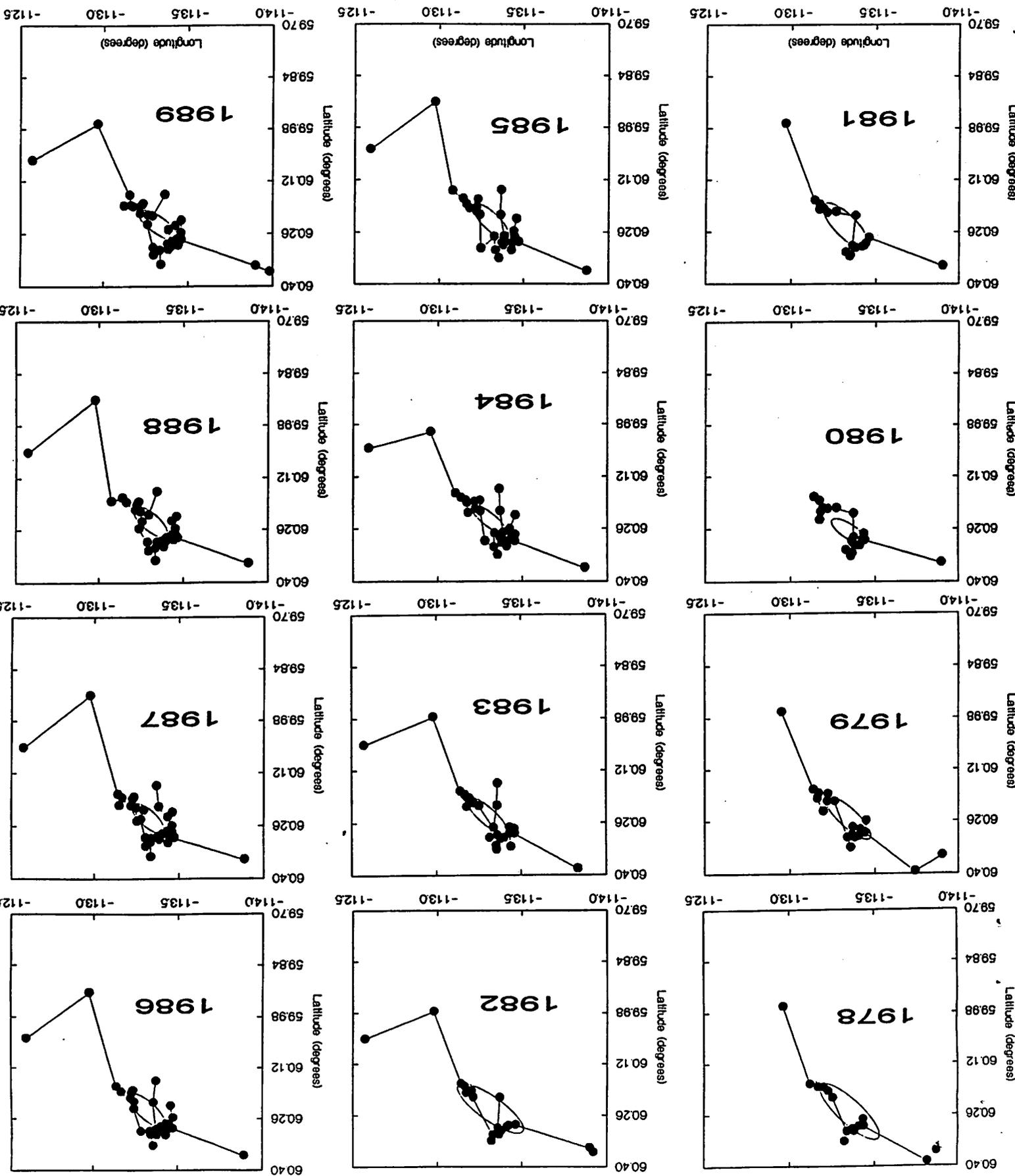


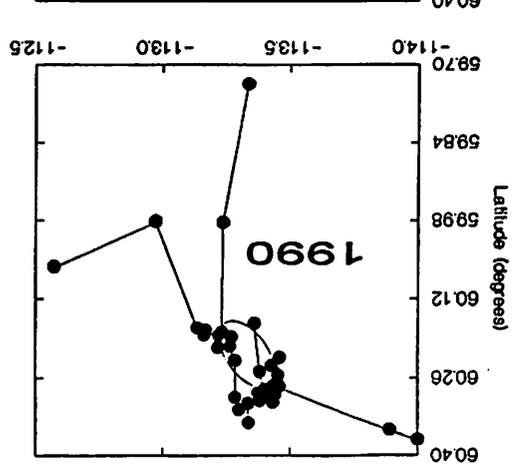
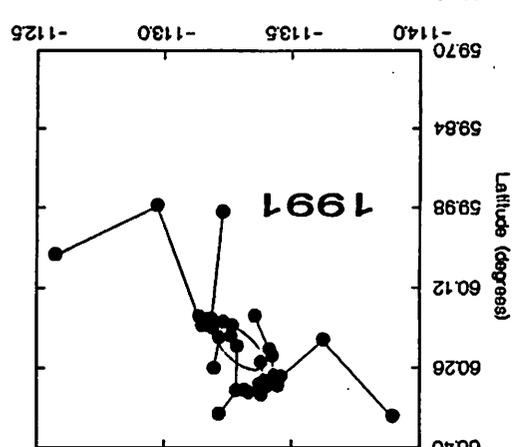
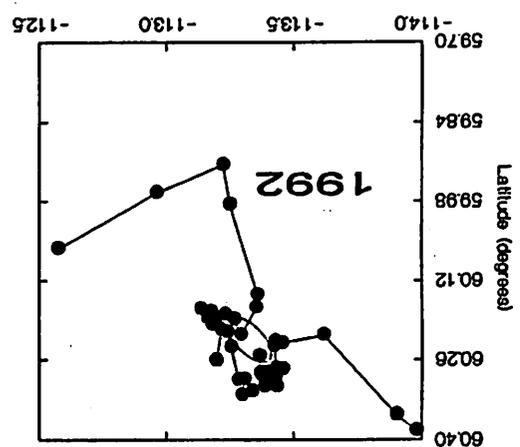
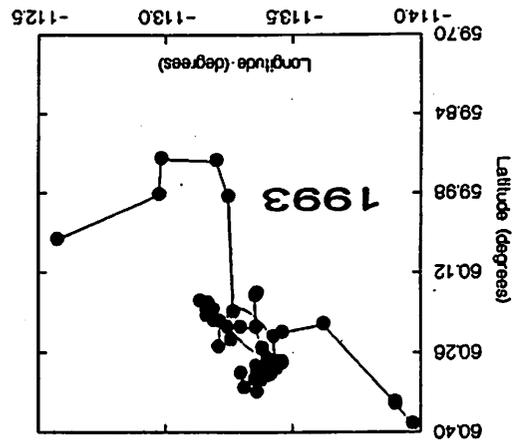
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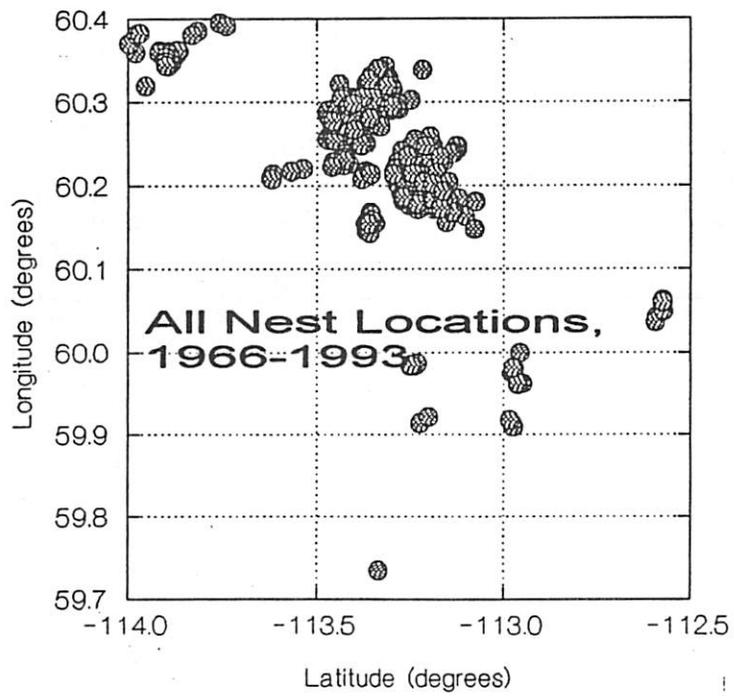
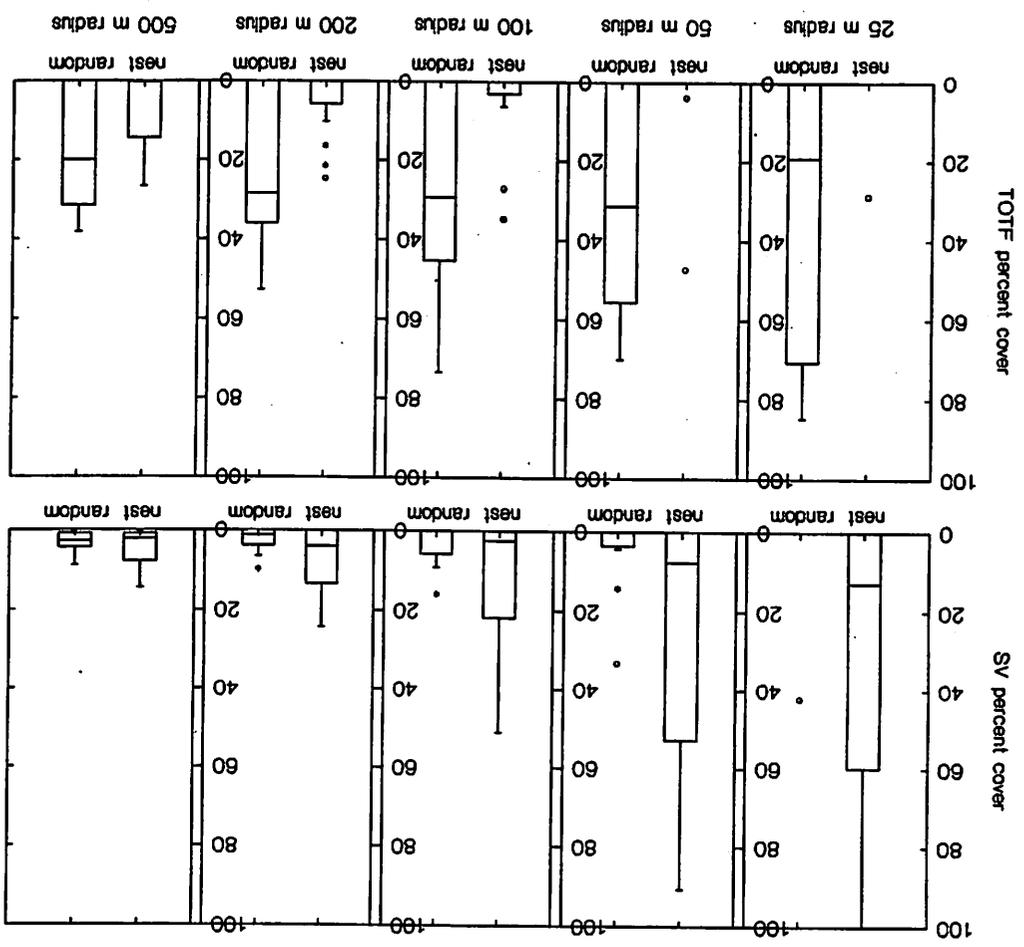


Fig. 11



## List of Tables

Table 1. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space.\*

Table 2. Pearson and Kendall correlations of species with the DCA ordination axes in species space. Critical values for Kendall's tau at 45 df: 0.349 @p=0.05, 0.449@p=0.01.

Table 3. Pearson and Kendall correlations of quantitative ecological parameters with the ordination axes in species space.

Table 4. TWINSpan classification of whooping crane plots and species. Species and habitat Interpretations generally use TWINSpan groups split at the third level (111 vs. 110, etc.). 'R' sites are random, 'N' sites are whooping crane nest sites. Habitat interpretation groups (base of table): 1=Willow/dwarf birch and spruce ombrotrophic bogs; 2=willow/dwarf birch bog-fens with abundant mosses; 3=willow/dwarf birch/sweet gale strings in marshes, fens, bogs; 4=willow/dwarf birch bog-fens with abundant water sedge; 5=shrubby mixed marshes with water sedge and cattail +/- bulrush; 6= bulrush/cattail mixed marshes with aquatics; 7= bulrush marshes with diatom ponds; 8= diatom ponds with bulrushes.

Table 5. Diatoms of a pink bottomed (isolated) pond (identified by G. Goldsborough).

Table 6. Diatoms of a yellow-brown bottomed pond, connected to a stream (identified by G. Goldsborough).

Table 7. Frequencies of pond bottom colors of random and nest sites at the plot and landscape levels. The Mann-Whitney U statistic tests for a difference in lake colors grouped by random vs. nest sites.

Table 8. Relationships between quantitative ecological parameters for random (n=16) vs. used sites (n=16, table top) and those for unburned (10) vs. burned sites (n=22, table bottom).

Table 9. Landscape composition and fractal dimensions of the 500 m radius plots centered on whooping crane nests by cover type. Total pixels (5 X 5 m) = 500014, total patches = 1310.

Table 10. Landscape composition and fractal dimensions of the 500 m radius random available plots by cover type. Total pixels (5 X 5 m) = 499593, total patches = 1273.

Table 11. Landscape summary statistics by 500 m radius plot type.

Table 12. Cover type percent means, medians, and SE by plot type (nests, random) and plot size. Cover types: Cream Pond = C, Powder Blue Pond = P, Turquoise Pond = T, Greenish to Black Pond = B, Bulrush Marsh = SV, Mixed Marsh = MM, Water Sedge = CA, Shrub organic terrain featureless = TOTF, Treed organic terrain featureless = OTF, Shrub Strings = TOTS, Treed Strings = OTS, Shrub Bog-Fen = TBF, Treed Bog-Fen = BF, Shrub Bog-Marsh = TBM, Treed Bog-Marsh = BM, Shrub OT with Ponds = TOTX, Treed OT with Ponds =

OTX, Peat Plateau = PP, Burned Peat Plateau = BPP, Upland Forest = UF, Burned Upland Forest = BUF. The number following the cover type refers to plot size (1=25, 2=50, 3=100, 4=200, and 5=500 m radii).

Table 13. ANOVA tests for cover type interactions between plot size and nests vs. random locations (plotype). G-G P is the Greenhouse-Geisser epsilon corrected p, and H-F is the Huynh-Feldt epsilon corrected p. Cover types with a G-G or H-F  $p < 0.05$  for the interaction between plotsize and plotype are shown in bold.

Table 14. Univariate F tests of spatial scale of habitat selection by nesting whooping cranes, for (a) Bulrush Marshes, and (b) Shrub Featureless Organic Terrain.

Table 15. Multi-response permutation procedure tests of spatial scale of habitat selection by nesting whooping cranes for (a) all cover types on the landscape, and (b) all cover types except Bulrush Marshes (SV) and Shrub Featureless Organic Terrain (TOTF).

Table 1. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space\*

R SQUARED		
AXIS	INCREMENT	CUMULATIVE
1	.440	.440
2	.129	.568
3	.061	.630

\* Number of entities = 32, number of entity pairs used in correlation = 496; Distance measure for original distance =  $1-2W/A+B$

Table 2. Pearson and Kendall correlations of species with the DCA ordination axes in species space. Critical values for Kendall's tau at 31 df: 0.349 @p=0.05, 0.449@p=0.01. \*-signif. @ p=0.05, \*\*=signif. @ p=0.01.

Species	AXIS: 1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Algae	-.595	.354	-.494**	-.667	.445	-.401*	.031	.001	.104
Andrpo	-.022	.000	.204	-.062	.004	-.241	-.001	.000	.075
Astebo	-.252	.064	-.213	-.036	.001	-.056	.023	.001	-.034
Aulapa	.561	.315	.517**	-.273	.075	-.263	.032	.001	.075
Betugl	.442	.195	.400*	-.114	.013	-.129	-.188	.035	-.112
Betune	.063	.004	.073	.328	.108	.311	.054	.003	.131
Bryups	.247	.061	.064	-.018	.000	.044	-.195	.038	-.183
Calain	.459	.211	.337	-.296	.088	-.200	.172	.030	.166
Calane	.380	.145	.235	.346	.120	.029	-.013	.000	.023
Callgi	-.061	.004	-.220	.130	.017	.238	.356	.126	.244
Campst	.521	.271	.402*	.402	.162	.217	-.404	.163	-.316
Careat	.249	.062	.227	.397	.158	.284	-.366	.134	-.284
Careaq	.457	.209	.435*	.391	.153	.317	.145	.021	-.002
Chara	-.403	.162	-.335	.230	.053	.318	-.143	.020	-.173
Cicuta	-.032	.001	.007	.432	.187	.360*	.320	.102	.137
Cladsp	.429	.184	.303	-.249	.062	-.241	.200	.040	.041
Drepad	.116	.013	.117	.069	.005	.097	-.392	.154	-.296
Drepre	-.060	.004	-.221	.222	.049	.112	.327	.107	.048
Drepun	.334	.111	.314	-.130	.017	-.074	-.115	.013	-.008
Eleopa	-.385	.148	-.451**	.279	.078	.126	-.035	.001	-.084
Galitr	-.014	.000	-.210	.053	.003	.304	.097	.009	.164
Larila	.272	.074	.208	-.053	.003	-.030	-.357	.128	-.190
Ledugr	.528	.279	.217	-.445	.198	-.372*	.171	.029	.132
Myriga	.179	.032	.128	-.250	.062	-.199	-.064	.004	-.097
Myrios	-.006	.000	-.158	.108	.012	.174	.635	.403	.226
Picegl	.428	.183	.374*	-.142	.020	-.056	-.056	.003	-.024
Picema	.012	.000	.038	-.234	.055	-.305	-.059	.003	.068
Polyju	.407	.166	.397*	-.331	.110	-.207	.265	.070	.364*
Potape	-.382	.146	-.337	.201	.040	.212	-.097	.009	-.004
Potepa	.033	.001	-.018	.277	.077	.408*	.208	.043	-.074
Rubuac	.224	.050	.179	-.151	.023	-.113	-.044	.002	-.129
Saliat	.354	.125	.275	-.050	.002	-.032	-.179	.032	-.119
Salibe	.487	.237	.437*	.044	.002	-.281	.155	.024	.148
Salica	.077	.006	.091	.375	.140	.346	-.321	.103	-.258
Salimy	.482	.233	.433*	-.086	.007	-.077	.061	.004	.077
Salipe	.098	.010	.079	.224	.050	.087	.006	.000	.102
Salipl	-.065	.004	-.109	.440	.194	.334	-.082	.007	-.008
Salixa	.610	.372	.568**	.230	.053	.188	-.095	.009	-.029
Scirva	-.718	.516	-.624**	.117	.014	.114	-.333	.111	-.290
Scorsc	-.030	.001	-.204	-.021	.000	.027	.212	.045	.064
Stelcr	-.051	.003	-.045	.015	.000	.024	.010	.000	.115
Tomeni	.321	.103	.261	-.225	.051	-.091	-.065	.004	-.072
Trigma	-.087	.008	.014	.009	.000	-.199	.107	.011	.101
Typhla	-.040	.002	-.159	.511	.261	.481**	.354	.125	-.013
Utrimi	-.374	.140	-.423*	.258	.067	.259	-.049	.002	.023
Vaccvi	.397	.158	.235	-.427	.182	-.353*	-.026	.001	.031

Table 3. Pearson and Kendall correlations of quantitative ecological parameters with the DCA ordination axes in species space. Critical values for Kendall's tau at 31 df: 0.349 @p=0.05, 0.449@p=0.01. \*-signif. @ p=0.05, \*\*=signif. @ p=0.01.

AXIS:	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
<u>Parameter</u>									
Water depth#	.564	.318	.391*	-.055	.003	-.257	.009	.000	.016
Distance @0.75	-.493	.243	-.393*	-.232	.054	-.071	.137	.019	.136
Distance @1.50	-.714	.510	-.530**	-.217	.047	-.044	.175	.031	.174
Nearest tree	-.189	.036	-.232	-.218	.048	-.199	.266	.071	.265
Nearest water	.384	.147	.390*	.076	.006	.183	.140	.019	.019
Burn age	.272	.074	.185	-.020	.000	-.065	.171	.029	.103
Open water%	-.475	.226	-.411*	-.359	.129	-.107	-.050	.003	.070
Terrest.+marsh%*	.593	.352	.494**	.667	.445	.401*	-.034	.001	-.104

# water depths are negative-- thus 10 cm of standing water = -10; the + correlation with axis 1 indicates that greatest water depths are on left side of ordination

\* terrestrial + marsh vegetation is a coarse filter used to compare this class with open water; grouping terrestrial with marsh vegetation, however, obscures important ecological differences; a more accurate comparison of cover classes in regard to nest vs. random sites is made in the landscape/GIS portion of the paper



Salix candida	----22--23442422254442---3322---	0101	Willow in wet meadow, fen, and marsh mosaics
Scorpidium scorpioides	-----38-----225---74--2----	01001	
Salix all spp.	545757642444446565455354333222--	01001	
Carex aquatilis	64675724677866577646765443532---	01001	
Bryum pseudotriquetrum	-2--45--22-----32322-2--24---2-	01001	
Salix pedicellaris	--23-----3--3--2-----	01000	
Scirpus validus	-----67-4-446-68666-7987777685	001	Bulrush marshes
Potentilla palustris	--2-----32--233224-22-22222----	001	
Eleocharis palustris	-----23---2-23---3---2334222--	001	
Drepanocladus revolvens	-----254-35-5--35656232342-22-	001	
Myriophyllum spicatum	-----22-83---2-----	0001	Assemblage characteristic of mixed marshes
Cicuta spp.	-----222-2--22-----	0001	
Betula neoalaskana	3--2-----445-54--2---2-----	0001	
Stellaria crassifolia	-----2-----23-4-2-----3-	000011	Cattail marshes, willow/cattail marshes**
Typha latifolia	-----676355266-3542----	000010	
Salix planifolia	-----2-----655-2--2533----2--	000010	
Galium trifidum	-----2--42-2--222-----	000010	
Calliargon giganteum	-----2--87-77-22----2-	000010	
Utricularia minor	-----4---22-436242-2--	00000	Pond aquatics associated with marshes
Potamogeton pectinatus	-----2-24-3-----	00000	
Chara spp.	-----4-----44-647582----	00000	

Plot Groups

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00000001111111000000000000011111  
00001110001111000000001111100011

Habitat  
Interpretation  
Groups  
111122233344445555555666677788

Notes: \* Calamagrostis neglecta and C. inexpansa are more characteristic of bog margins, wetter spots, and salt-affected situations.  
\*\*Stellaria crassifolia is +/- restricted to whooping crane nest mounds.

Table 5. Diatoms of a pink bottomed (isolated) pond (identified by G. Goldsborough).

<i>Amphora ovalis</i>	<i>Navicula cryptocephala</i>
<i>Cymbella cistula</i>	<i>Navicula oblonga</i>
<i>Cymbella minuta</i> (abundant)	<i>Nitzschia amphibia</i>
<i>Epithemia turgida</i>	<i>Nitzschia palea</i> (abundant)
<i>Mastogloia smithii</i> (abundant)	<i>Pinnularia</i> sp. (hilseana?)
<i>Navicula accommoda</i>	

Table 6. Diatoms of a yellow-brown bottomed pond, connected to a stream (identified by G. Goldsborough).

<i>Amphipleura pellucida</i> (abundant)	<i>Navicula accommoda</i>
<i>Amphora</i> sp. (ovalis?)	<i>Navicula cryptocephala</i> (abundant)
<i>Cymbella angustata</i> (abundant)	<i>Navicula cuspidata</i> (abundant)
<i>Cymbella cistula</i> (abundant)	<i>Navicula oblonga</i>
<i>Cymbella minuta</i>	<i>Navicula peregrina</i>
<i>Cymbella pusilla</i> (abundant)	<i>Nitzschia</i> sp.
<i>Diatoma tenue</i>	<i>Nitzschia amphibia</i> (very abundant)
<i>Epithemia sorex</i> (abundant)	<i>Nitzschia palea</i>
<i>Epithemia turgida</i> (abundant)	<i>Rhopalodia gibba</i>
<i>Fragilaria crotonensis</i>	<i>Synedra fasciculata</i>
<i>Gomphonema acuminatum</i>	<i>Tabellaria fenestrata</i>
<i>Mastogloia smithii</i>	

Table 7. Frequencies of pond bottom colors of random and nest sites at the plot and landscape levels. The Mann-Whitney U statistic tests for a difference in lake colors grouped by random vs. nest sites.

Plot Level True Color	Color at Plot Centre		Landscape Level, False Colours	Dominant Color in 25 m radius		Dominant Color in 50 m radius		Dominant Color in 100 m radius		Dominant Color in 200 m radius		Dominant Color in 500 m radius	
	Random	Nest		Color	Random	Nest	Random	Nest	Random	Nest	Random	Nest	Random
Brown	0	1	Greenish to Black	4	5	4	8	4	8	4	4	2	5
Yellow	3	8	Turquoise	2	3	1	3	3	4	4	7	5	5
Pink	0	2	Powder Blue	4	3	4	2	4	2	6	3	7	3
Creme	7	3	Creme	1	1	3	2	4	2	2	2	2	3
None	6	2	None	5	4	4	1	1	0	0	0	0	0
M-W U Statistic.	192.5			142.5		177.5		174.0		143.0		152.0	
p value	0.011			0.317		0.053		0.071		0.556		0.884	

Table 8. Relationships between quantitative ecological parameters for random (n=16) vs. used sites (n=16, table top) and those for unburned (10) vs. burned sites (n=22, table bottom).\*

Parameter/ Statistic	Water Depth (cm)		Concealment @ 0.75 (m)		Concealment @1.5 (m)		Nearest Tree (m)		Nearest Water (m)		Open Water (%)		Terrestrial + Marsh (%)	
	Random	Nest	Random	Nest	Random	Nest	Random	Nest	Random	Nest	Random	Nest	Random	Nest
Median	13.5	-7	1.4	3.3	3.5	16.4	15.8	55.4	27.7	4.0	0.0	5.0	96.5	79.0
M-W U Statistic	233.0		24.0		35.5		68.0		185.0		75.5		190.5	
p value	0.000		0.000		0.000		0.023		0.030		0.039		0.017	
	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned
Median	9.5	1.0	1.8	2.1	14.3	10.7	35.6	51.5	6.4	11.9	5.0	1.0	87.5	95.0
M-W U Statistic	118.5		110.0		132.0		81.5		86.0		134.5		79.5	
p value	0.729		1.000		0.371		0.245		0.324		0.300		0.210	

\* negative water depths indicate standing water, positive values indicate depth to water table

Table 9. Landscape composition and fractal dimensions of the 500 m radius plots centered on whooping crane nests by cover type. Total pixels (5 X 5 m) = 500014, total patches = 1310.

Cover Type	Cover	# Patches	Aver. Size (ha)	PA Fractal Mean.	P(m,L) Fractal Mean
Cream Pond	0.0357	68	0.655	1.303	1.665
Powder Blue Pond	0.0741	138	0.671	1.247	1.643
Turquoise Pond	0.0743	158	0.588	1.240	1.619
Burned Peat Plateau	0.0030	4	0.928	0.886	1.755
Bulrush Marsh	0.0454	139	0.409	1.245	1.470
Greenish to Black Pond	0.0422	138	0.382	1.235	1.447
Treed OT with Ponds	0.0357	41	1.089	1.303	1.567
Treed OT, featureless	0.0499	41	1.520	1.321	1.673
Mixed Marsh	0.1036	102	1.269	1.284	1.706
Shrub OT with Ponds	0.0647	110	0.735	1.274	1.591
Shrub OT, featureless	0.0661	53	1.559	1.303	1.642
Treed Bog-Fen	0.0176	13	1.696	1.232	1.734
Water Sedge	0.0291	33	1.103	1.262	1.681
Shrub Bog-Marsh	0.1847	95	2.430	1.308	1.735
Shrub Bog-Fen	0.0463	35	1.653	1.288	1.694
Treed Bog-Marsh	0.0411	36	1.426	1.220	1.713
Treed Strings	0.0379	64	0.741	1.329	1.513
Peat Plateau	0.0171	4	5.358	1.071	1.906
Shrub Strings	0.0139	28	0.621	1.421	1.427
Upland Forest	0.0176	10	2.206	1.254	1.761

Table 10. Landscape composition and fractal dimensions of the 500 m radius random available plots by cover type: Total pixels (5 X 5 m) = 499593, total patches = 1273.

Cover Type	Cover	# Patches	Aver. Size (ha)	PA Fractal Mean	P(m,L) Fractal Mean
Cream Pond	0.0445	116	0.479	1.290	1.591
Powder Blue Pond	0.0537	134	0.501	1.237	1.559
Turquoise Pond	0.0710	140	0.634	1.239	1.636
Burned Peat Plateau	0.0341	26	1.639	1.209	1.774
Bulrush Marsh	0.0290	113	0.321	1.256	1.411
Greenish to Black Pond	0.0362	97	0.467	1.263	1.443
Treed OT with Ponds	0.0366	22	2.075	1.296	1.734
Treed OT, featureless	0.0613	58	1.320	1.314	1.646
Mixed Marsh	0.0489	45	1.358	1.384	1.656
Shrub OT with Ponds	0.0667	71	1.173	1.265	1.672
Shrub OT, featureless	0.1769	114	1.938	1.347	1.715
Treed Bog-Fen	0.0268	19	1.759	1.361	1.674
Water Sedge	0.0390	58	0.840	1.245	1.631
Shrub Bog-Marsh	0.0948	84	1.410	1.264	1.707
Shrub Bog-Fen	0.0681	60	1.417	1.243	1.663
Treed Bog-Marsh	0.0220	22	1.249	1.244	1.622
Treed Strings	0.0155	36	0.537	1.320	1.394
Peat Plateau	0.0097	6	2.015	1.290	1.667
Shrub Strings	0.0065	24	0.339	1.345	1.318
Upland Forest	0.0452	19	2.969	1.296	1.780
Burned Upland Forest	0.0135	9	1.869	1.231	1.809

Table 11. Landscape summary statistics by 500 m radius plot type.

	Diversity (H')	Dominance (D)	Scaled Dominance (D)	Combined Contagion	Scaled Contagion	Commun. Richness (n)	Mean Patch (ha)	PA Fractal +/- s.d.	P(m,L) Fractal +/- s.d.
Nest Plots	2.740	0.255	0.085	50.429	0.842	20	0.954	1.251 +/- 0.108	1.647 +/- 0.119
Random Plots	2.802	0.242	0.080	53.483	0.837	21	0.981	1.283 +/- 0.048	1.624 +/- 0.132

Table 12. Cover type percent means, medians, and SE by plot type (nests, random) and plot size. Cover types: Cream Pond = C, Powder Blue Pond = P, Turquoise Pond = T, Greenish to Black Pond = B, Bulrush Marsh = SV, Mixed Marsh = MM, Water Sedge = CA, Shrub organic terrain featureless = TOTF, Treed organic terrain featureless = OTF, Shrub Strings = TOTS, Treed Strings = OTS, Shrub Bog-Fen = TBF, Treed Bog-Fen = BF, Shrub Bog-Marsh = TBM, Treed Bog-Marsh = BM, Shrub OT with Ponds = TOTX, Treed OT with Ponds = OTX, Peat Plateau = PP, Burned Peat Plateau = BPP, Upland Forest = UF, Burned Upland Forest = BUF. The number following the cover type refers to plot size (1=25, 2=50, 3=100, 4=200, and 5=500 m radii).

NEST SITES

	B1	B2	B3	B4	B5
MEAN	5.476	5.337	4.851	4.368	4.219
STD. ERROR	3.777	3.100	2.216	1.090	0.739
MEDIAN	0.000	0.000	0.000	2.800	3.845
	BF1	BF2	BF3	BF4	BF5
MEAN	0.000	0.000	0.000	0.135	1.773
STD. ERROR	0.000	0.000	0.000	0.135	1.112
MEDIAN	0.000	0.000	0.000	0.000	0.000
	BM1	BM2	BM3	BM4	BM5
MEAN	0.709	3.044	5.097	4.122	4.115
STD.ERROR	0.709	2.009	3.172	2.356	1.510
MEDIAN	0.000	0.000	0.000	0.000	0.310
	BPP1	BPP2	BPP3	BPP4	BPP5
MEAN	0.000	0.000	0.000	0.000	0.299
STD.ERROR	0.000	0.000	0.000	0.000	0.244
MEDIAN	0.000	0.000	0.000	0.000	0.000
	BUF1	BUF2	BUF3	BUF4	BUF5
MEAN	0.000	0.000	0.000	0.000	0.000
STD.ERROR	0.000	0.000	0.000	0.000	0.000
MEDIAN	0.000	0.000	0.000	0.000	0.000
	C1	C2	C3	C4	C5
MEAN	2.835	4.799	6.036	5.517	3.571
STD.ERROR	2.636	3.320	4.126	3.721	1.614
MEDIAN	0.000	0.000	0.000	0.000	0.570
	CA1	CA2	CA3	CA4	CA5
MEAN	0.000	3.474	4.994	2.700	2.915
STD.ERROR	0.000	2.406	3.352	1.497	1.355
MEDIAN	0.000	0.000	0.000	0.000	1.045
	MM1	MM2	MM3	MM4	MM5
MEAN	10.696	11.408	12.175	13.067	10.358

STD.ERROR	6.623	5.999	5.084	3.483	2.388
MEDIAN	0.000	0.000	0.000	6.985	12.015
	OTF1	OTF2	OTF3	OTF4	OTF5
MEAN	0.516	1.182	3.879	4.230	4.982
STD.ERROR	0.516	1.182	2.450	2.054	2.571
MEDIAN	0.000	0.000	0.000	0.000	1.840
	OTS1	OTS2	OTS3	OTS4	OTS5
MEAN	0.000	1.218	1.790	2.868	3.784
STD.ERROR	0.000	0.711	0.944	0.982	1.275
MEDIAN	0.000	0.000	0.000	1.955	1.465
	OTX1	OTX2	OTX3	OTX4	OTX5
MEAN	0.966	2.131	2.906	2.904	3.584
STD.ERROR	0.738	1.472	1.381	1.397	1.227
MEDIAN	0.000	0.000	0.000	0.000	2.110
	P1	P2	P3	P4	P5
MEAN	12.113	8.256	5.040	6.523	7.388
STD.ERROR	6.897	4.794	3.059	3.299	1.866
MEDIAN	0.000	0.000	0.000	1.860	4.815
	PP1	PP2	PP3	PP4	PP5
MEAN	0.000	0.000	0.676	0.529	1.708
STD.ERROR	0.000	0.000	0.676	0.369	1.152
MEDIAN	0.000	0.000	0.000	0.000	0.000
	SV1	SV2	SV3	SV4	SV5
MEAN	33.699	24.301	12.281	7.059	4.539
STD.ERROR	10.025	7.743	4.212	2.049	1.299
MEDIAN	12.885	7.735	2.515	4.060	2.230
	T1	T2	T3	T4	T5
MEAN	2.964	4.351	6.823	7.599	7.439
STD.ERROR	2.964	4.072	4.822	3.606	2.118
MEDIAN	0.000	0.000	0.000	0.365	4.245
	TBF1	TBF2	TBF3	TBF4	TBF5
MEAN	4.704	4.692	3.827	5.669	4.649
STD.ERROR	4.704	4.692	3.104	3.140	1.853
MEDIAN	0.000	0.000	0.000	0.000	1.545
	TBM1	TBM2	TBM3	TBM4	TBM5
MEAN	23.518	20.504	19.800	20.688	18.448
STD.ERROR	10.276	8.432	6.520	4.913	3.118
MEDIAN	0.000	0.000	4.415	18.500	22.465

	TOTF1	TOTF2	TOTF3	TOTF4	TOTF5
MEAN	1.804	3.206	4.680	4.643	6.611
STD.ERROR	1.804	2.949	2.635	2.149	2.595
MEDIAN	0.000	0.000	0.000	0.000	0.110

	TOTS1	TOTS2	TOTS3	TOTS4	TOTS5
MEAN	0.000	0.716	0.985	1.236	1.384
STD.ERROR	0.000	0.661	0.688	0.927	0.664
MEDIAN	0.000	0.000	0.000	0.000	0.000

	TOTX1	TOTX2	TOTX3	TOTX4	TOTX5
MEAN	0.000	1.379	4.004	5.731	6.485
STD.ERROR	0.000	1.025	2.156	2.423	1.584
MEDIAN	0.000	0.000	0.000	1.955	5.095

	UF1	UF2	UF3	UF4	UF5
MEAN	0.000	0.000	0.157	0.413	1.751
STD.ERROR	0.000	0.000	0.157	0.413	1.751
MEDIAN	0.000	0.000	0.000	0.000	0.000

#### RANDOM SITES

	B1	B2	B3	B4	B5
MEAN	0.258	1.039	1.585	2.377	3.614
STD. ERROR	0.258	0.965	0.902	0.717	0.956
MEDIAN	0.000	0.000	0.000	0.970	3.160

	BF1	BF2	BF3	BF4	BF5
MEAN	0.451	1.451	2.133	2.056	2.689
STD. ERROR	0.451	1.166	1.386	1.110	0.990
MEDIAN	0.000	0.000	0.000	0.000	0.265

	BM1	BM2	BM3	BM4	BM5
MEAN	6.959	5.963	3.223	2.454	2.206
STD. ERROR	6.064	4.274	2.208	1.226	0.797
MEDIAN	0.000	0.000	0.000	0.000	0.765

	BPP1	BPP2	BPP3	BPP4	BPP5
MEAN	2.449	3.169	3.794	3.479	3.429
STD. ERROR	2.449	2.446	2.732	1.951	1.691
MEDIAN	0.000	0.000	0.000	0.000	0.160

	BUF1	BUF2	BUF3	BUF4	BUF5
MEAN	2.319	2.436	1.814	1.357	1.336
STD. ERROR	2.319	2.436	1.814	1.357	0.921
MEDIAN	0.000	0.000	0.000	0.000	0.000

	C1	C2	C3	C4	C5
MEAN	2.255	3.295	2.828	5.076	4.474
STD. ERROR	1.736	2.261	1.895	2.571	2.063
MEDIAN	0.000	0.000	0.000	0.000	1.720
	CA1	CA2	CA3	CA4	CA5
MEAN	7.023	4.244	2.466	3.378	3.901
STD. ERROR	4.803	2.921	1.651	1.283	1.374
MEDIAN	0.000	0.000	0.000	0.595	1.330
	MM1	MM2	MM3	MM4	MM5
MEAN	7.410	8.739	9.254	7.994	4.873
STD. ERROR	4.837	4.140	3.561	2.719	1.708
MEDIAN	0.000	0.000	0.000	1.370	1.935
	OTF1	OTF2	OTF3	OTF4	OTF5
MEAN	0.644	1.684	2.413	2.496	6.109
STD. ERROR	0.644	1.263	1.342	1.122	1.558
MEDIAN	0.000	0.000	0.000	0.000	4.005
	OTS1	OTS2	OTS3	OTS4	OTS5
MEAN	0.000	0.967	1.514	1.506	1.554
STD. ERROR	0.000	0.967	1.382	0.999	0.435
MEDIAN	0.000	0.000	0.000	0.000	0.690
	OTX1	OTX2	OTX3	OTX4	OTX5
MEAN	7.796	6.071	5.327	4.339	3.644
STD. ERROR	5.603	4.458	4.289	2.924	1.885
MEDIAN	0.000	0.000	0.000	0.000	0.000
	P1	P2	P3	P4	P5
MEAN	2.062	4.889	6.269	4.202	5.372
STD. ERROR	1.458	2.869	2.683	1.571	1.056
MEDIAN	0.000	0.000	0.000	0.340	4.540
	PP1	PP2	PP3	PP4	PP5
MEAN	0.000	0.000	0.091	0.433	0.970
STD. ERROR	0.000	0.000	0.091	0.429	0.542
MEDIAN	0.000	0.000	0.000	0.000	0.000
	SV1	SV2	SV3	SV4	SV5
MEAN	5.284	3.671	3.213	2.322	2.903
STD. ERROR	3.609	2.171	1.195	0.701	0.582
MEDIAN	0.000	0.000	0.000	1.240	2.920
	T1	T2	T3	T4	T5
MEAN	4.961	5.391	6.640	6.772	7.087

STD. ERROR	4.099	4.529	4.085	3.220	2.192
MEDIAN	0.000	0.000	0.000	0.310	3.840
	TBF1	TBF2	TBF3	TBF4	TBF5
MEAN	9.343	7.863	6.293	7.317	6.821
STD. ERROR	6.175	4.701	3.277	2.397	1.991
MEDIAN	0.000	0.000	0.000	0.020	2.600
	TBM1	TBM2	TBM3	TBM4	TBM5
MEAN	0.000	0.681	3.946	9.112	9.473
STD. ERROR	0.000	0.608	1.389	2.448	2.176
MEDIAN	0.000	0.000	1.830	7.325	8.565
	TOTF1	TOTF2	TOTF3	TOTF4	TOTF5
MEAN	32.732	29.620	26.404	22.081	17.718
STD. ERROR	8.833	6.879	6.157	4.556	3.665
MEDIAN	19.070	31.375	29.285	28.450	20.035
	TOTS1	TOTS2	TOTS3	TOTS4	TOTS5
MEAN	1.611	2.274	1.361	0.420	0.656
STD. ERROR	1.611	2.274	1.361	0.383	0.293
MEDIAN	0.000	0.000	0.000	0.000	0.000
	TOTX1	TOTX2	TOTX3	TOTX4	TOTX5
MEAN	6.443	6.554	8.306	8.144	6.669
STD. ERROR	4.352	4.009	4.614	3.237	1.939
MEDIAN	0.000	0.000	0.000	0.115	2.500
	UF1	UF2	UF3	UF4	UF5
MEAN	0.000	0.000	1.129	2.686	4.498
STD. ERROR	0.000	0.000	0.844	1.335	2.308
MEDIAN	0.000	0.000	0.000	0.000	0.000

Table 13. Multivariate ANOVA tests for cover type interactions between plot size and nests vs. random locations. G-G P is the Greenhouse-Geisser epsilon corrected p, and H-F is the Huynh-Feldt epsilon corrected p. Cover types with a G-G or H-F  $p < 0.05$  for the interaction between plotsize and plotype are shown in bold.

	F Statistic	P	G-G P	H-F P
C	1.053	0.383	0.356	0.361
P	2.329	0.060	0.117	0.112
T	0.215	0.930	0.766	0.785
BPP	0.218	0.928	0.779	0.799
SV	6.107	0.000	<b>0.015</b>	<b>0.013</b>
B	0.831	0.508	0.414	0.422
OTX	1.849	0.124	0.180	0.179
OTF	0.633	0.640	0.533	0.548
MM	0.135	0.969	0.812	0.828
TOTX	1.200	0.315	0.311	0.313
TOTF	5.010	0.001	<b>0.014</b>	<b>0.012</b>
BF	0.652	0.627	0.532	0.548
CA	2.134	0.081	0.130	0.125
TBM	2.254	0.067	0.132	0.129
TBF	0.182	0.947	0.723	0.736
BM	1.715	0.151	0.196	0.194
OTS	0.705	0.590	0.549	0.569
PP	0.267	0.898	0.773	0.796
TOTS	1.281	0.281	0.276	0.278
UF	0.827	0.511	0.449	0.460
BUF	0.375	0.826	0.562	0.571

Table 14. Univariate F tests of spatial scale of habitat selection by nesting whooping cranes, for (a) Bulrush Marshes, and (b) Shrub Featureless Organic Terrain.

(a)	SV1	SV2	SV3	SV4	SV5
F Statistic	7.112	6.582	4.291	4.786	1.323
P	0.012	0.016	0.047	0.037	0.259
(b)	TOTF1	TOTF2	TOTF3	TOTF4	TOTF5
F Statistic	11.768	12.456	10.522	11.985	6.117
P	0.002	0.001	0.003	0.002	0.019

Table 15. Multiresponse permutation procedure tests of spatial scale of habitat selection by nesting whooping cranes for (a) all cover types on the landscape, and (b) all cover types except Bulrush Marshes (SV) and Shrub Featureless Organic Terrain (TOTF).

(a)	25 m	50 m	100 m	200 m	500 m
T Statistic	-6.095	-5.203	-3.871	-3.314	-2.456135
P	0.000095	0.000307	0.002802	0.009339	0.027907
(b)	25 m minus SV,TOTF	50 m minus SV,TOTF	100 m minus SV,TOTF	200 m minus SV,TOTF	500 m minus SV,TOTF
T Statistic	-1.794	-0.670	-0.664	-0.581	-1.384
P	0.056071	0.226923	0.230342	0.235375	0.094826

**Appendix 1.** Bryophytes and lichens collected in the Whooping Crane Nesting Area, sorted by site number. Species codes use the first four letters of the genus and the first three letters of species. 'xxx' indicates a continuation of the line above. Blank in the Species column signifies a general note. Numbers in the Notes column are cover percents. Collections and identifications are by Anne Robinson.

Site-No.	Species	Notes
N05		Bryupse, Dreprev, Campste, Scorsco, Aulapal, Tomenit, Callgig;
N05	xxx	nearby: Drepunc
N08-01	Drepadu	
N08-02	Ambler	
N08-03	Plagell	with Callgig 40, Scorsco, Campste 1, Bryupse 1, Dreprev 5
N08-04	Platjun	
N11-01	Liverwort	with Bryupse, Dreprev, and Campste at edge; Aulapal in shrubs
N11-02	Hypnaceae	
N13-01	Bryupse	
N13-02	Aulapal, Tomenit, Ptilpul, Callgig	
N13-02	Bracsal	also: Peltaph, Cladgra, Cladcom, Hylospl, Sphafus, Cladmit,
N14		covers: Callgig 20, Dreprev, Campste, Bryupse
N15-01	Bracsal	with Drepunc and Bryum sp. on strings; Dreprev 2, Bryupse 2,
N15-01	xxx	and Campste 3 in Scirval
N16-01	Dreprev	
N16-02	Campste	with Drepadu, Bryupse, and Luna moth caterpillar
N23-01	Pohlsp.	
N23-02	Drepadu	with Campste, Dreprev, Bryupse, Callgig
N23-03	Cratcom	
N23-04	Bryupse	
N23-05	Rhizmag	
N24-02	Bryupse	no -01, with Scorsco 30, Dreprev 2, Campste 1
N29		Bryupse, Brac; covers: Scorsco 5, Dreprev 10, Callgig 20, Campste 2,
N32-01	Leptpyr	no -02
N32-03	Cratcom	with Campste, Bryupse
N34		on strings: Ptilpul, Hylospl, Pleusch, Cladmit, Cladran, Cladcor
N34-01	Campste	with Scorsco just into marl
N34-02	Bryupse	pond edge
N34-03	Liverwort	pond edge
N38-01	Dreprev	with Scorsco, Callgig
N39-01	Campste	no -02, all Campste
R16-01	Campste	with Bracsal
R16-02	Drepadu	with Aulapal, Leptpyr
R16-03	Hypnpra	
R17-01	Dreprev	high on mound; 5% cover
R17-01	Scorsco	dead; at mound base
R17-01	Cladmit	mound top
R17-01	Campste	mound side; 2% cover
R17-01	Aulapal	mound top; 1% cover
R17-01	Bryupse	high on mound
R18-01	Bracsal	hummock bottom
R18-02	Bryum sp.	
R18-04	Campste	no R18-03
R18-05	Dreprev	with Cerapur, Leptpyr

R19		just above water: Callgig; in water: Scorsco
R19		mound species: Campste, Dreprev, Bryupse; at shrub bases:
R19		Tomenit
R19-01, 02		small unidentifiable pleurocarps
R19-03	Drepadu	
R20-01	Myliano	
R20-02	Bryum sp.	
R20-03		thalloid liverworts
R20-04	Sphafus	with Peltcan, Cladfim, Polyjun, Aulapal, Leptpyr, Cladgra
R20-05	Pohnut	
R20-06	Cladbot	
R20-07	Cladsul	
R20-08	Cladbel	cf. bellidiflora
R20-09	Cladecm	
R22	Bryum	cf. R17
R22-01	Dreprev	
R22-02	Scortur	
R22-03	Campste	with Scorsco
R22-04	Bracsal	
R22-05	Drepunc	
R22-06	Drepadu	
R23-01	Cladsulph	with Cladfim, Cladbot, Cladgra, Cerapur
R23-02	Cladcom	
R23-03	Myliano xxx	with Peltaph, Pleusch, Pohnut, Cerapur, Aulapal, Hylospl, Cladmul, Cladran, Cladmit, Tomenit, Cladchlo
R24-01	Drepadu	
R24-03	Campste	
R24-04	Bryupse	
R24-05	Callgig	
R24-06	Bryum	
R25-01	Camphis	
R25-02	Leptpyr	
R25-03	Liverwort	
R25-04	Bryupse	with Aulapal, Meesuli, Peltaph
R25-05	Drepunc	with Tomenit, Campste
R25-06	Campste xxx	covers: Campste 10, Drepunc 15, Aulapal 25, Bryum 5, Tomenit 5
R26		covers: Scorsco 50, Campste 1, Dreprev 2, Bryupse +, Aulapal +
R27	Drepadu	on string
R27-01	Bryum	cf. R18
R27-02	Campste	
R27-03	Callstr	?; one strand;
R27-04	Drepadu	with Bryum sp.
R27-05	Pleusch	
R28-01	Camppol	
R28-01-10		with Tomenit, Aulapal, Leptpyr, Peltaph
R28-02	Marcpol	
R28-03	Campste	
R28-04	Drepunc	
R28-05	Peltcan	
R28-06	Cephalozia	

R28-07	Liverwort?	
R28-08	Bryum sp.	
R28-09	Bracsp.	
R28-10	Polyjun	
R28-10	Cladfim	
R28-10	Platjun	
R28-11	Campste	
R28-12	Camphis	
R28-13	Cladgra	R28-10-13 with Lophozia, Cerapur, Mylia anomala
R29-01	Platjun	"little green pleuros" of shrub string
R29-02	Bracsp.	"little green pleuros" of shrub string; no R29-03
R29-04	Plagell	with Cratcom 2, Campste 5, Bryupse 1
R29-05		"little green pleuros"
R29-06	Cratcom	
R29-07	Liverworts	Liverwort complex
R29-08	Liverworts	
R29-09	Campste	with Bryupse
R30-01	Meesuli	
R30-02	Campste	
R30-03	Liverworts	
R30-04	Rhizand	no R30-05
R30-06	Distichium	no R30-07
R30-08	Liverworts	with Aulapal, Peltpol, Cladmul, Cladmit, Pleusch, Leptbry,
R30-08	xxx	Bryupse,
R30-09	Cladsul	Cladbac, and Drepadu
R30-10	Cladcor	
R30-11	Cladgra	
R30-12	Campste	
R30-13	Bleptri	
R30-14	Cladcoc	
R31-01	Myliano	
R31-02		thalloid liverwort
R31-03	Cladsul	with Peltpal, Cladmul, Cladmit, Cladcor, Peltaph, Polyjun 10,
R31-04	Sphasp.	Cladfim, Cerapur, Sphafus, Aulapal 10, Cladgra,
	xxx	Cladssp complex 15
R31-05	Pohlmut	
R31-06	Cladcen	
R31-07	Cladconi	
R31-08	Cladcrista	
R32	Bracsal	
R32	Camppol	
R32-01	Campste	with Bryum, Marcpol, Tomenit, Aulapal
R32-02	Bractur	
R32-03	Bryum	with Leptpyr, Cerapur, Peltpal, Polyjun

**Appendix 2.** Two-way Indicator Species Analysis (TWINSPAN) Crane classification Specifications: number of samples 32; number of species 46; length of raw data array 1160 non-zero items. Pseudospecies cut levels (%): 0, .1, 1, 2, 5, 10, 20, 40, 60. Options: minimum group size for division = 5; maximum number of indicators per division = 5; maximum number of species in final table = 46; maximum level of divisions = 6. Length of data array after defining pseudospecies: 2228; total number of species and pseudospecies 269; number of species 46. The following is the classification of samples and species, edited for length.

### Samples

DIVISION 1 (N= 32), i.e. group \*; Eigenvalue: .352 at iteration 1  
INDICATORS and their signs: Typhla 1(+), Scirva 5(+), Aulapa 1(-)  
ITEMS IN NEGATIVE GROUP 2 (N= 14), i.e. group \*0: N11, R16, R17, R18, R20, R22, R23, R25, R26, R27, R28, R30, R31, R32  
ITEMS IN POSITIVE GROUP 3 (N= 18), i.e. group \*1: N2, N5, N8, N13, N14, N15, N16, N22, N23, N24, N29, N32, N34, N38, N39, R19, R24, R29  
DIVISION 2 (N= 14), i.e. group \*0; Eigenvalue: .303 at iteration 2  
INDICATORS and their signs: Salibe 1(-) Aulapa 4(-) Salixa 5(-)  
ITEMS IN NEGATIVE GROUP 4 (N= 7), i.e. group \*00: R20, R23, R25, R28, R30, R31, R32  
ITEMS IN POSITIVE GROUP 5 (N= 7), i.e. group \*01: N11, R16, R17, R18, R22, R26, R27  
DIVISION 3 (N= 18), i.e. group \*1; Eigenvalue: .266 at iteration 2  
INDICATORS and their signs: Salixa 3(-)  
ITEMS IN NEGATIVE GROUP 6 (N= 13), i.e. group \*10: N8, N13, N14, N15, N16, N23, N24, N29, N32, N38, R19, R24, R29  
ITEMS IN POSITIVE GROUP 7 (N= 5), i.e. group \*11: N2, N5, N22, N34, N39  
DIVISION 4 (N= 7), i.e. group \*00; Eigenvalue: .295 at iteration 2  
INDICATORS and their signs: Rubuac 1(+)  
ITEMS IN NEGATIVE GROUP 8 (N= 4), i.e. group \*000: R20, R30, R31, R32  
ITEMS IN POSITIVE GROUP 9 (N= 3), i.e. group \*001: R23, R25, R28  
DIVISION 5 (N= 7), i.e. group \*01; Eigenvalue: .281 at iteration 1  
INDICATORS and their signs: Ledugr 3(-)  
ITEMS IN NEGATIVE GROUP 10 (N= 3), i.e. group \*010: N11, R17, R26  
ITEMS IN POSITIVE GROUP 11 (N= 4), i.e. group \*011: R16, R18, R22, R27  
DIVISION 6 (N= 13), i.e. group \*10; Eigenvalue: .226 at iteration 2  
INDICATORS and their signs: Scirva 7(+), Chara 5(+), Betugl 5(-)  
ITEMS IN NEGATIVE GROUP 12 (N= 8), i.e. group \*100: N8, N16, N23, N29, N32, R19, R24, R29  
ITEMS IN POSITIVE GROUP 13 (N= 5), i.e. group \*101: N13, N14, N15, N24, N38  
DIVISION 7 (N= 5), i.e. group \*11; Eigenvalue: .412 at iteration 1  
INDICATORS and their signs: Betugl 1(-)  
ITEMS IN NEGATIVE GROUP 14 (N= 3), i.e. group \*110: N5, N34, N39  
ITEMS IN POSITIVE GROUP 15 (N= 2), i.e. group \*111: N2, N22  
DIVISION 12 (N= 8), i.e. group \*100; Eigenvalue: .261 at iteration 2  
INDICATORS and their signs: Salipl 3(-)  
ITEMS IN NEGATIVE GROUP 24 (N= 3), i.e. group \*1000: N16, N23, R29  
ITEMS IN POSITIVE GROUP 25 (N= 5), i.e. group \*1001: N8, N29, N32, R19, R24  
DIVISION 13 (N= 5), i.e. group \*101; Eigenvalue: .305 at iteration 1  
INDICATORS and their signs: Astebo 1(+)  
ITEMS IN NEGATIVE GROUP 26 (N= 3), i.e. group \*1010: N14, N24, N38  
ITEMS IN POSITIVE GROUP 27 (N= 2), i.e. group \*1011: N13, N15  
DIVISION 25 (N= 5), i.e. group \*1001; Eigenvalue: .319 at iteration 1  
INDICATORS and their signs: Algae 1(+)