Habitat selection by sympatric black ducks and mallards in Abitibi, Quebec.

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Suggested Short Title:

Habitat selection by black ducks and mallards.

A la Terre du Milieu,
A la Rivière aux Biscuits,
Et à la Vie qui y demeure...

A la Mémoire de vous deux,
A cher Papa et chère Lucie,
Et aux vivants qui demeurent...

ABSTRACT

Habitat use by sympatric black ducks (Anas rubripes) and mallards (A platyrhynchos) was studied in Abitibi, Quebec during May-August 1988 and 1989.

Black duck broods preferred emergent and shrub-rich areas in both years. Mallard broods' habitat use differed from 1988 to 1989 (from emergent to shrub-emergent areas) when average water levels were higher. Diversity of habitats seems more important to rearing black ducks than to mallards. Rearing mallards seem to modify their use of habitats according to changing habitat availability. Daily survival rates differed only slightly between "species".

Telemetry was used to study wetland use by six mallard and three black duck non-breeding females. Swamps were preferred whereas ericaceous shrub wetlands were avoided by both "species". Beaver (Castor canadensis) ponds were extensively used during the moulting period. Home ranges averaged 302.7 ha for black ducks and 201.2 ha for mallards.

ABREGE

L'utilisation des habitats par les canards noirs (<u>Anas rubripes</u>) et colverts (<u>A</u>. <u>platyrhynchos</u>) vivant en sympatrie fut étudiée en Abitibi, Québec, de mai à août 1988 et 1989.

La deuxième année fut caractérisée par un niveau d'eau moyen plus élevé. Les couvées noirs ont préférés les marais à plantes émergentes et les marécages arbustifs en 1988 et en 1989. Les habitats préférés par les couveés colverts ont différés de 1988 à 1989 (des marais à plantes émergentes aux marécages arbustifs). La diversité des habitats semble plus importante pour les couvées de canards noirs que colverts. Les couvées de colverts semble modifier leur utilisation des habitats selon les changements de disponibilité. Le taux de survie des canetons des deux "espèces" n'ont que très peu différé.

Les terres humides utilisées par six femelles colverts et trois femelles noirs non-reproductives furent étudiées par télémétrie. Les deux "espèces" ont préférés les marécages alors que les tourbières furent évités. Les terres humides modifiées par les castors (<u>Castor</u> <u>canadensis</u>) furent grandement utilisées surtout en période de mue. Les aires d'activités des canards noirs s'étendaient sur 302.7 ha en moyenne, les aires des colverts, sur 201.2 ha.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

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PREFACE

The decline in black duck numbers in North-America has been described as "An evolutionary biologist's dream; a waterfowl manager's nightmare" (Ankney, in press). Possible causes of the decline include overhunting, deforestation, competitive exclusion and genetic swamping by the mallard (Rusch et al. 1989). Although mallard competition for habitats is regarded as one of the most serious causes, it is, to date, the least studied hypothesis. No extensive analysis exists of the relative habitat preferences of mallards and black ducks on shared breeding areas.

The thesis examined habitat selection by breeding sympatric mallards and black ducks.

The thesis is divided into two papers to be published separately. First, micro-habitat preferences of mallards and black ducks were examined during the brood-rearing period. Usage of vegetation form groups within wetlands (termed "microhabitats") were noted from the movements of unmarked brood-rearing females. The study also compared survival rates of sympatric black duck and mallard ducklings. Habitat selection by the populations of black ducks and mallards in the Abitibi region of Quebec has never been studied.

The second study investigates macro-habitat preferences of sympatric radio-tagged mallard and black duck females. Most females were non-breeding and could fly to and use an important range of wetlands. The study also compared home range overlaps and size for sympatric mallard and black duck females. In this paper I applied different methods of estimating home range areas and of measuring habitat selection, and compared their results.

Capture and transmitter installation caused paired females to abandon their nests and brood-rearing females to abandon all ducklings. Hence, wetland selection by radio-tagged breeding individuals could not be measured.

The following is included in accordance with the regulations of the McGill Faculty of Graduate Studies:

"The candidate has the option, subject to the approval of the Department, of including as part of the thesis the text, or duplicated published text (see below), of an original paper, or papers. In the case the thesis must still conform to all other requirements explained in Guidelines Concerning Thesis Preparation. Additional material (procedural and design data as well as descriptions of equipment) must be provided in sufficient detail (e.g., in appendices) to allow a clear and precise judgement to be made of the importance and originality of the research reported. The thesis should be more than a mere collection of manuscripts published or to be published. It must contain a general abstract, a full introduction and literature review and a final overall conclusion. Connecting texts, which provide logical bridges between different manuscripts are usually desirable in the interests of cohesion.

It is acceptable for theses to include as chapters authentic copies of papers already published, provided these are duplicated clearly on regulation thesis stationary and bound as an integral part of the thesis. Photographs or other materials, which do not duplicate well must be included in their original form. In such instances, connecting texts are mandatory and supplementary explanatory material is almost always necessary.

The inclusion of manuscripts co-authored by the candidate and others is acceptable but the candidate is required to make an explicit statement on who contributed to such work and to what extent (see below), and supervisors must attest to the accuracy of the claims, e.g., before the Oral Committee. Because the task of the Examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear. Candidates following this option must inform the Department before it submits the thesis for review".

Section I will be submitted to "The Auk" under the title: "Habitat use by brood-rearing sympatric black ducks and mallards". A shortened version of section II will be submitted to "The Journal of Wildlife Management" under the title: "Wetland use and home range of radio-tagged sympatric black ducks and mallards".

Authorship will go to the candidate, Suzanne Carrière, co-authorship to Roger D. Titman, supervisor of the thesis. Dr. Rodger D. Titman contributed to the formulation of the thesis' objective and hypotheses, the initial elaboration of the methodology, the provision of funds and literature, and revised all drafts. The candidate contributed to the above mentioned tasks. The final elaboration of the methodology, the collection of data, their analysis and interpretation, and the writing of all drafts were performed by the candidate.

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LITERATURE REVIEW

The status of the American black duck (*Anas rubripes* Brewster) populations has received considerable attention after a large decline in numbers was registered in the late 1950s and early 1960s (Rogers and Patterson 1984). An apparent long-term decline of black duck numbers has since been monitored in the Atlantic and Mississippi flyways and the species is now of priority concern in the North American Waterfowl Management Plan (Rusch et al. 1989). Yet, the volume of papers directly related to black duck biology, ecology, evolution, distribution and management in the waterfowl literature is small compared to the amount of papers published on the closely related common mallard (*A. platyrhynchos* L.) (Johnsgard 1961, Avise et al. 1990). Concomitant to the decline in black duck numbers, the distribution of mallards has increased to the East (e.g., Collins 1974, Johnsgard and DiSilvestro 1976, Dennis et al. 1984), and the breeding and wintering areas of black ducks and mallards now largely overlap.

The present literature review is divided into three sections. The first section presents reviews on the black duck population status and decline. Consequently, it also presents the debate concerning the probable causes of the continental decline in black duck numbers. It emphasizes papers pertaining to the effects of the mallards' increased distribution on black duck populations.

The second section briefly covers the theoretical aspects of habitat selection and its consequences on competition, or vice versa. Habitat selection theory may form a promising background for the formulation of future hypotheses on black duck and mallard competition for habitats.

The last section attempts to summarize what is known of black duck and mallard breeding habitat preferences in the different parts of their range and to compare their reproductive success.

Black Duck Decline and the Mallard

In early papers related to black duck decline, Johnsgard (1961,1967) already associated it with an increased sympatry in mallard and black duck distributions. However, Johnsgard did not treat them as effect and cause. Both were effects of a suggested common cause: deforestation and changes in land use (Johnsgard 1961), which favored mallards over black ducks. Hybridization (or swamping through hybridization) could not singly account for the black ducks decreasing numbers, as hybridization rates were sufficiently low (Johnsgard 1967). Hence, deforestation and changes in habitat use worked at two levels; they caused increased sympatry between black ducks and mallards, which in turn led to increased hybridization, and they directly caused black duck numbers to decline through lower reproductive success and lower survival. Interspecific competition was not directly cited as a cause.

Later, Heusmann (1974) derived similar conclusions, but stated that the release of game-farm stock also helped to explain the increasing numbers of mallards in the East.

Following a first symposium on black duck management and research (Barske 1968), overhunting was estimated to be an important cause of black duck decline and a moratorium on black duck hunting was suggested (Addy and Martinson 1968). By 1982, hunting was cited as the primary cause (Grandy 1983), and "the depth of disagreement on this point came into the open ... when the Humane Society of the U.S. intervened in Federal court in an attempt to force the U.S. Fish and Wildlife Service to prohibit black duck hunting in the United States" (Rogers and Patterson 1984). The 1982-83 black duck season nonetheless opened (Feierabend 1984). The overhunting hypothesis has been challenged many times (Anderson and Burnham 1976, Rogers and Patterson 1984, Ankney et al. 1987, Nichols et al. 1987, Rusch et al. 1989). However, since recent harvest reductions, black duck breeding pair surveys have indicated from 14-18% increases in pairs in the Maritimes and Quebec (J.R. Longcore, pers. com.).

A number of other factors were listed for investigation as possible causes of the decline: lead shot poisoning, contamination of habitats by acid rain and insecticides for gypsy moth and spruce budworm control, predation of breeding females and human disturbance (Feierabend 1984). Rusch et al. (1989) have reviewed available data on their possible effects on the black duck and found them mostly non-conclusive.

Hybridization, habitat loss, interspecific competition hypotheses and the overhunting hypothesis in particular were generally tested on data from the winter surveys, the breeding bird survey and the Christmas Bird Count (Krementz et al. 1987, Nichols et al. 1987, Ankney et al. 1987, 1989; Conroy et al. 1989, Rusch et al. 1989). Much of the debate on the possible causes of the decline lay in the inherent biases of these surveys and counts, and whether they permit a critical test of the different hypotheses. Many suggested that more field and enclosure experiments were (and are still) needed to test them (Anderson et al. 1987, Conroy et al. 1989, Rusch et al. 1989).

For example, Brodsky and Weatherhead (1984) found that mallard drakes were more successful than black ducks in obtaining a mate when courting female black ducks. Brodsky et al. (1988, 1989) studied captive mallards and black ducks and found that (1) mallard drakes usually dominated black duck drakes, (2) female mallards and black ducks usually associated with the dominant male, and (3) males and females mostly associated with the species they were raised with. Referring to these results, Rusch et al. (1989) concluded that "it may be impossible to halt the decline of the black duck populations that are sympatric with mallards".

Complementing experiments and traditional survey and harvest data, surveys of breeding ducks in the boreal region (a region not usually studied) were undertaken (Kaczynski and Chamberlain 1968, Boyd 1984, Bordage 1988a, 1988b). Their results suggest that breeding black ducks may not be especially scarce compared to other ducks in North America (Rusch et al. 1989): black ducks seem to have decreased less than presumed from winter counts and to have increased in the eastern part of Canada. Most interesting were the increasing mallard numbers in regions of largely black duck dominance in the boreal forest (Bordage 1988b, Rusch et al. 1989).

A similar rapid spreading of mallard and hybrids was observed in New Zealand (Gillespie 1985), representing a potential threat to the conservation of pure grey ducks (A. superciliosa). Habitat reduction followed by introgression are cited as probable causes of the grey duck population decline (Gillespie 1985).

Habitat selection by allopatric mallards and black ducks has been studied (see below in this literature review). However, black duck habitat preferences are comparatively less understood than those of mallards, especially in the breeding period. A model of habitat use was developed only recently for black ducks (Deifenbach and Owen 1989), whereas models referring to the mallard were available ten years ago (Walters et al. 1974, Anderson 1975, Brown et al. 1976, Cowardin and Johnson 1979).

The extreme wariness of black ducks and the cover potential and inaccessibility of the boreal forest has deterred many studies. For example, little is known of the effect of modern logging and large-scale hydroelectric development on the population of breeding black ducks in central and northern Quebec (Rusch et al. 1989). Furthermore, no extensive analysis exists of the relative habitat preferences of mallards and black ducks on shared breeding areas.

Studies testing the competitive exclusion hypothesis are lacking. Competition can be very difficult to detect in nature (Schoener 1983). Ducks were termed "appropriate" to test competition hypotheses, being generally higher-trophic level consumers and subject to low predation in the breeding period (Nudds 1983). However, one must generally relies on measures of ecological overlap (e.g., Nudds 1983) to detect competition, despite their much debated suitability (Schoener 1983, Rosenzweig 1985).

Determining whether habitat preferences overlap may cast some light on the possible competitive exclusion of black ducks by mallards.

Habitat Selection and Competition

The theoretical aspects of habitat selection were reviewed by Rosenzweig in 1985. One of the first points discussed by Rosenzweig (1981, 1985) concerns the precise definition of widely used terms in habitat selection studies: generalists, opportunists, specialists and selector. He formed two groups of terms; one describing behaviors, the other describing abilities (i.e., reflecting fitness).

Opportunist thus means an individual using habitats in their encountered proportions (behavior). A generalist is able to use all habitats equally well (i.e., its fitness in one habitat precisely equals its fitness in another), but does not necessarily use them proportionally (i.e., is not necessarily an opportunist).

Selector means an individual selecting habitats in proportions different from those it encounters. A specialist is more "adept at using some subset of patches" (Rosenzweig 1985) but may still behave in an opportunistic way (being therefore an opportunistic specialist). Rosenzweig (1985) noted that "it is even possible that an individual will choose to avoid using the habitats for which it is specialized".

He also pointed out that habitat selection theory is clearly a branch of optimal foraging theory. From simpler models assuming fixed, cost-free environment with a given (usually two patches) habitat structure, theorists developed models involving searching costs and density-dependent habitat choices. These models either assume that resources per capita decline as population density increases (i.e., that fitness is a function of density in each habitat type (Fretwell and Lucas 1970)) or that searching for habitat patches is costly (Charnov 1976, Rosenzweig 1981) or both (Rosenzweig 1981, Holt 1985).

Fretwell and Lucas' (1970 and in Rosenzweig 1985) model resulted in an interesting conclusion for researchers studying habitat selection in the field. They predicted that species must abandon habitat selection and become more opportunistic as their population density rises. Opportunism will arise when density is so high that the specialist's fitness is the same in all habitat types. Rosenzweig (1981) added that if selection has a cost, opportunism should be preferred even before density is high enough to equalize fitness in different patches.

Thus, habitat selection studies, where one wants to compare the utility of habitats, may be best performed when or where a species is rare. If two species are involved, this advice is reinforced. The theory of density-dependent habitat selection has been successfully tested for two pairs of bird species and other animals (see Rosenzweig 1985).

Since Lawlor and Maynard Smith's (1976) theoretical work and the development of "isoleg"[1] analysis (Rosenzweig 1981),

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[1] From the Greek <u>iso</u>-, same: <u>lego</u>, to choose. Isoline defining a boundary of habitat choices in state-space (n dimensions graph, in which each dimension is the density of a species). "An isoleg is a set of points in this space such that (a) at every point the optimal foraging strategy of the individuals of one species is to ignore completely the opportunity to use a unique set of habitat types, and (b) from

the relationship between habitat selection and competition has been explored (Pimm and Rosenzweig 1981, Rosenzweig 1981).

The theoretical study of density-dependent habitat selection and interspecific competition is based on a two-species hypothetical system similar to the system modelled by Lotka-Volterra equations. The zero isoclines of these equations are usually plotted on a graph where each axis represents the density of a species (see Slobodkin in Rosenzweig 1981).

Rosenzweig (1981) and Pimm (Pimm and Rosenzweig 1981) then drew isolegs for different systems (e.g., with two species whose habitat preferences were distinct or shared), and "tracked" the isocline of each species across the two isolegs.

In doing so, they willingly assumed that two species with greater habitat utilization overlap have higher competitive alphas [2] than a similar pair, which selects less similar habitat types (Rosenzweig 1981). The debate on the relationship of competition and ecological overlap is a never-ending one (Schoener 1983). The study of habitat selection and of ecological overlap (where the resource is habitat) converge here, both leading to the study of competition dynamics.

Studying the isoleg systems dynamically brought interesting results. Rosenzweig (1981, 1985) showed that

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every point, an infinitesimal increase (or decrease) in density... results in a change in optimal foraging strategy such that a particular additional habitat type ought to be used...") (Rosenzweig 1981).

[2] The interactive effect of species *j* on species *i* where

$$\alpha_{ij} = (\partial \ln \overline{W}_i / \partial N_j) / (\partial \ln \overline{W}_i / \partial N_i) .$$

N_i is the density of *i* and ln W_i is its per capita rate of increase (Rosenzweig 1981).

coexistence is likely to occur when densities are such that there is no overlap in habitat use. Although competition is an intrinsic part of the system, being one of the formative forces, the competitive alpha will equal zero and no ecological overlap will be measured (Rosenzweig 1981, 1985).

This ambiguity certainly troubles the theoretician, but it translates to a fearful problem when viewed by a field ecologist. The problem of how to define competition leads to the problem of how to measure it. Pimm and Rosenzweig (1981) suggested that a definition of competition has four aspects.

The first is the slope of the isocline at equilibrium or the so-called competitive alpha. The second is the effect of a species on its competitor when the competitor invades the species' preferred patch (ability of a species to "protect" a patch). A third is the equilibrial increase in density of a species when the competitor is removed. The last is the overlap in resource use between species.

Pimm and Rosenzweig (1981) noted that each aspect, taken alone can form a definition of competition and can be measured. However, they are contradictory. The first two and the last two definitions will give correlated answers for a particular system, but each pair of answers will tend to be inversely correlated (Pimm and Rosenzweig 1981).

A measure of ecological overlap is only one way of estimating the degree of competition between two species. Habitat overlap analysis is only one way of estimating ecological overlap.

One must then be aware of when and where large overlap is likely to mean strong competition or vice versa. Knowing some aspects of the studied system can help the interpretation of results of habitat overlap studies in terms of interspecific competition. Summing from above, these aspects can be:

(1) The density of both species in the study area compared to their density elsewhere. Species tend to abandon

habitat selection and become more opportunistic as their density rises and this is independent of the other species' status.

(2) The preference of each species when the other is absent. If two allopatric species share habitat preferences but they select different habitats when in sympatry, competition is likely to be present in the sympatric system.

(3) The evolutionary recentness of the sympatry. If the sympatry is evolutionarily old and no habitat overlap is detected, natural selection is likely to have produced competitive coexistence through habitat selection. Hence competition may be present as a formative force of the system but may not be detected.

Finally, empirical and theoretical competition studies (Schoener 1974, 1983) suggest that one more aspect must be known:

(4) The scale of habitat selection in the studied system. Macrohabitat overlap is usually inversely related to experimentally demonstrated competition (Schoener 1983), micro-habitat overlap being directly related. In measuring overlap, one assumes that individuals of both species can select habitat types according to their proportions in the system. This assumption is more likely to be violated if habitat types are macrohabitats (Schoener 1983). Habitats may merely be the "arenas of competition rather than categories of resources" (Schoener 1983).

Breeding Mallard and Black Duck Habitat Selection

A habitat can be defined as "...a spatially continuous vegetation type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types" (Hutto 1985, p.456). Under this definition, micro-habitats are locations within habitat types (e.g., feeding heights in a forest) and macrohabitats are synonymous to habitat types. Micro-habitat choices are usually based on the individual's own previous experience and on exploration (Hutto 1985, p.457). Macrohabitats are generally used as a geographical or historical consequence of the inopportunity to discover other areas and also as a consequence of innate instructions passed on by successful ancestors (Hutto 1985).

These mechanisms are not mutually exclusive. New macrohabitats may be explored by migrating bird species, whereas it is the propensity to explore, which is innate (e.g., wintering black ducks and mallards; Diefenbach et al. 1988). Boundaries between habitats can be difficult to define and at the smallest scale (micro-habitats): the resource may be best qualified as a continuum of patch qualities.

Wetland types are usually considered habitat types per se (Cowardin et al. 1979, Jacques and Hamel 1982, Canada/Ontario Steering Committee 1984) although the scale of investigation is rarely clearly stated in waterfowl habitat studies. Habitat types can be vegetation forms (e.g., Courcelles and Bédard 1979), wetland types (e.g., Ringelman et al. 1982), wetland complexes (e.g., Gilmer et al. 1975) and landscape forms (e.g., Bellrose 1979). This list clearly goes from micro-habitats to macrohabitats but the division between these two scales is less than clear. This division may be simply impossible to draw to everyone's satisfaction, hence habitat is redefined in every study and the question of scale is at best only implied.

Morris (1983) gives precise definitions, mainly useful in multivariate analysis studies. Macrohabitats are defined as " distinguishable units whose minimum area corresponds to that within which an average individual performs all of its biological functions (home range) during a typical activity cycle" (Morris 1983). He quantifies micro-habitats by "physical/chemical variables that influence the allocation of time and energy by an individual within its home range".

I considered vegetation forms (Canada/Ontario Steering Committee 1984) to be micro-habitats and wetland types to be macrohabitats (or habitats per se). Within both groups categories can be formed, which are physiognomically distinct but the wetland types also can be spatially distinct whereas vegetation forms within wetland always intersperse. These also follow Morris' (1983) definitions, although waterfowl average minimum home ranges may include more than one wetland complex (see Mallard and Black Duck Home Ranges).

Habitat Selection by Mallards.---

Habitat preferences by breeding mallards were extensively studied in the prairie pothole region[3]. About 60% of the North American mallards breed in this region (Bellrose 1979).

The mallard is recognized as a highly adaptable species and is considered a generalist at several habitat scales (Gilmer et al. 1975, Bellrose 1979, Rogers and Patterson 1984, for wintering habitats: Deifenbach et al. 1988). Within the prairie pothole region, studies of wetland use tend to demonstrate an opportunistic behavior by breeding mallards.

No difference in the use of wetland types was reported for mallards breeding in the prairie potholes of south-central Dakota (Dwyer et al. (1979) and in the aspen parkland of Saskatchewan (Mulhern et al. 1985).

Broods showed a preference for larger and seasonal wetlands with vegetative cover only in years with low brood density and high wetland availability, otherwise they used wetlands in proportion to their availability (Talent et al. 1982, Mulhern et al. 1985).

This may be consistent with the habitat selection hypothesis that birds become opportunists when population densities are high (Fretwell and Lucas 1970, Fretwell 1972). Breeding mallard and other dabbling duck densities are known

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[3] In its traditional definition described by Bellrose (1979), including all vegetative prairie associations (mixed, shortgrass and tallgrass) and the parklands.

to be higher in the prairie pothole region than in any other region in North America (Bellrose 1979, Wishart et al. 1983). Opportunism in the use of wetland types thus may be expected, particularly during drier, low pond density years in this part of the mallard distribution. Mallards appear to be the least tolerant to crowding when compared to other prairie ducks (Bellrose 1979).

Ball and Nudds (1989) suggested that the density-dependence may be examined for mallards by correlating population density with the degree of habitat selectivity found across various studies.

Monda and Ratti (1988) commented on the inappropriateness of stereotypic classification of a species as generalists or specialists. They noted that mallards functioned as ecological specialists at their study area in Eastern Washington, although mallards were usually classified as generalists (Monda and Ratti 1988). Independently of their proclaimed ability to use all available types of habitat, mallards seem to become "picky" (Rosenzweig 1981) in several regions at several habitat scales.

Mallards will typically show preference for emergent vegetation (Poysa 1983) and areas with a high vegetation-water interspersion index (Kaminski and Prince 1984). Ball and Nudds (1989) manipulated marsh openings and concluded that mallards select the size of openings in emergent vegetation and that the abundance of aquatic macroinvertebrates is finally used to decide where to feed.

Isolation from other pairs, availability of macro-invertebrates and proximity of good nesting cover appear important factors in wetland selection by breeding mallard pairs (Gilmer et al. 1975, Krapu 1979, Godin and Joyner 1981, Kaminsky and Prince 1981, Krapu et al. 1984, Ball and Nudds 1989).

Hens with broods also generally use emergent vegetation for escape cover (instead of diving), and as feeding areas

(Stoudt 1971, Mack and Flake 1980, Monda and Ratti 1988). Godin and Joyner (1981) noted that mallard broods studied in Southern Ontario were attracted to large emergent ponds (> 1 ha), which provide some surface cover for escape. Brood-rearing mallards (and black ducks) preferred man-made (mostly sewage) ponds with 30% or more of the surface covered by emergents and with a high shoreline irregularity index (>1.5) (Bélanger and Couture 1988).

Because of this general association with emergent vegetation and the fact that marsh habitat is dominant over its North-American breeding range, the mallard was considered as a possible forest habitat selector only recently.

Bellrose (1979) studied waterfowl species distribution and habitats in North America at the scale of landscape forms. He found that "wetlands with some wooded vegetation influence mallards more than other (prairie) dabblers" (Bellrose 1979). Mallard percentage distribution ranked highest in closed taiga, subarctic deltas, prairie parkland, Great Lakes forest and intermountain valleys. Considering this, it seems contradictory that mallards are the most abundant of the dabbling ducks in shortgrass prairies (Bellrose 1979; Table 3).

Mallard pairs successfully breed in forested regions (Cowardin et al. 1967, Gilmer et al. 1975, Kirby and Riechman 1985). Moreover, there is evidence that pairs may actively select wetlands with some forested sections (Dwyer 1970, Bellrose 1979, Kirby and Riechman 1985) and that females with broods will select shrub cover when available (Dwyer 1970, Gilmer et al. 1975).

In the prairie pothole region, Dwyer (1970) found that nonagricultural land potholes surrounded by forest were preferred by mallard pairs and broods.

In conclusion, the mallard overwhelms all other dabblers in the prairie pothole region, especially in the parklands (Bellrose 1979). It forms the majority of dabblers in all forested north-western regions except Alaska (Bellrose 1979, Table 3). In the closed taiga of Ontario and Quebec, mallard pairs are estimated to be only 10% less abundant than the black ducks (Bellrose 1979).

Breeding successfully in agricultural, forested, southern and northern habitats, the mallard differs from the black duck, which occupies one of the most homogeneous breeding ranges in North America (Bellrose 1979).

Habitat Selection by Black Ducks.---

The major part of the breeding domain of the black duck is the Eastern boreal forest (Bellrose 1979, Bordage 1988a,b). This large homogeneous landscape bears low densities of dabbling ducks, but almost the entire population of breeding black ducks (Bellrose 1979).

A third (200 000 pairs) of the Continental population and half of the Canadian population was estimated to breed in Quebec on 1 250 000 km ^{2} of boreal forest (Reed in Bordage 1988b).

In the coastal section of their range, black ducks use streams, and tidal, shallow salt marshes (Reed 1970, Seymour 1978, Seymour and Titman 1984). Black duck also breed on wetlands surrounded by hardwood, mixed forest and cultivated fields, in the southern section of their breeding range (Stotts and Davies 1960, Laperle 1974, Courcelles and Bédard 1979, Ringelman et al. 1982, Ringelman and Longcore 1982a). At the landscape scale, the black duck generally uses forested habitat.

In 1985, the Canadian Wildlife Service initiated a monitoring program of breeding pairs in an area of 100 000 km^2 centred north of the Gouin Reservoir, Quebec (Bordage 1988a,b). This study area encloses a large section of closed taiga (73%) with mixed forests (27%) at its southern limit. Aerial surveys provided an estimate of 10 500-15 000 breeding pairs (Bordage 1988a,b).

Half of the observed pairs used small lakes (smaller than 10 ha), which accounted for only 7.1% of the total surface water in the study area. Black duck pairs (19.6 % of observed pairs) also used streams more than expected from the small water surface they provided (2.8%). Rivers, bogs and large lakes (10-100 ha) were used according to their availability. Black duck pairs avoided very large lakes (>1 km^2) (Bordage 1988a).

Cover and isolation provided by streams and small water bodies seem to be important factors in wetland selection by black duck pairs breeding in the boreal forest. Bogs also provide some cover and isolation but seem less clearly selected by black ducks. Ombrotrophic peatlands enclose wetlands poor in macroinvertebrates (Ringelman et al. 1982), which are important food for nesting black ducks (Reinecke and Owen 1980).

Ringelman et al. (1982) reported similar avoidance of ericaceous shrub-rich areas by black ducks. Black duck pairs breeding in Maine preferred herbaceous emergent wetlands and deciduous swamps and thickets over organic bottom, evergreen forested and evergreen shrub-rich wetlands. Black ducks also frequently used streams and small pools formed of accumulated water or snowmelt in wooded and meadow habitat. Ringelman et al. (1982) suggested that black duck pairs select for good cover and food, mostly provided by flooded deciduous timber, alder and willow, and by herbaceous wetlands.

Active beaver (Castor canadensis) ponds seem essential to black duck rearing broods in the large inland section of their range (Renouf 1972). Active beaver ponds shelter a higher density of broods than inactive ones, providing more abundant cover and more stable water levels (Renouf 1972).

In the hardwood-spruce forest of Maine, most ponds selected by black duck females rearing broods contained active beaver colonies (Ringelman and Longcore 1982a). Beaver ponds were large wetlands containing flooded alder, willow, and herbaceous vegetation. Ringelman and Longcore (1982a) noted that alder-shrub communities with herbaceous understory provide food-rich habitats because of symbiotic nitrogen fixation in alder root nodules (Tilton and Bernard in Ringelman and Longcore 1982a). Brood-rearing black ducks, similarly to breeding pairs, avoided ericaceous shrub areas. They also avoided areas growing submerged plants only, and open water (Ringelman and Longcore 1982a).

Brood-rearing black ducks on the Maritime coast seem to prefer streams rather than saltwater and freshwater marshes (Seymour 1984). Broods could disperse along streams and be less vulnerable to predation and possible competition from other broods. However, Seymour (1984) noted that a shortage of food may force brood-rearing females to move into estuaries.

Studies of habitat selection by sympatric breeding black ducks and mallards are rare and mostly have been performed in the south-western section of the black duck breeding range.

Barclay (1970) studied breeding mallard (81% of the studied population) and black duck pairs which shared a large diked marsh in Ohio. He noted that black ducks mostly used wooded areas, where many dikes were covered by brush and trees. Conversely, activity centers of mallards possessed many similarities with potholes (Barclay 1970). A high degree of interaction on the study site suggested that black ducks and mallards were competing for habitat and nest sites, with mallards dominating the interaction (Barclay 1970).

Courcelles and Bédard (1979) studied black duck, mallard, and other dabbler selection of micro-habitats, mostly during their moulting stage, on a marsh in Southwestern Quebec. All dabbling species similarly preferred an area of broken cattails interspersed with open water rich in free-floating and submerged plants situated near shore (Courcelles and Bédard 1979).

Black ducks also share man-made ponds with mallards and other dabbling ducks to rear their broods. For example, sewage ponds which contain >30% emergent vegetation and a high index of shoreline irregularity were used (Bélanger and Couture 1988).

The western section of the black duck's breeding range is composed mainly of the Great Lakes mixed forest (Bellrose 1979). This region and the Upper St. Lawrence River are shared by breeding black ducks, mallards and other dabbling species. Bellrose (1979) noted that where the ratio of precipitation:evaporation is highest (i.e., in swampy boreal forest), the black duck appears to be most able to compete with the advance of the mallard. Moreover, the regions of increasing mallards are characterized by higher agricultural development than the rest of the black duck's breeding range.

Mallard and Black Duck Home Ranges.---

Home range was first defined by mammalogists as: "that area, traversed by the individual in its normal activities of food gathering, mating ..." (Burt 1943, Hayne 1949). Territory was defined as " the protected part of the home range" (Burt 1943).

The home range concept was later extended to birds in general (Odum and Kuenzler 1955) and waterfowl in particular (Dzubin 1955, Sowls in Gilmer et al. 1975). Waterfowl home ranges usually refer to the areas occupied during the prelaying, nesting, brood-rearing and moulting periods on the breeding grounds (Dzubin 1955).

Several methods of estimating home ranges exist which derive as many shapes: the minimum polygon, the smallest convex polygon, the circle based on mean location radius and the 95% confidence ellipse (Hayne 1949, Jennrich and Turner 1969). Newer harmonic mean (Dixon and Chapman 1980) and Fourrier transformation (Anderson 1982) procedures do not result in predetermined shapes. They more closely follow the original definition of home range, permitting the location of points of greatest activity (Dixon and Chapman 1980). However, they require access to computer programs. The simpler convex polygon procedure is generally used in waterfowl field studies.

Dwyer et al. (1979) estimated mallard home ranges comprised 468 ha in the prairie pothole region, based on six radio-tagged breeding females. In forested Minnesota, Gilmer et al. (1975) found an average home range size of only 210 ha for 12 female mallards. Male home range size averaged 240 ha. Dwyer et al. (1979) hypothesized that the differences in home range size of forest-dwelling and prairie mallards reflects major differences in type and distribution of water areas. Larger home ranges were adaptive to unpredictable wetland quality and water condition of the semiarid sections of the prairies.

Kirby and Riechman (1985) studied mallard home range size in Minnesota where a population used larger wetlands than studied by Gilmer et al. (1975). Average home range size was 540 ha (40-1440 ha) for eight females and 620 ha (70-1140 ha) for five male mallards. Individual home ranges also varied greatly. Kirby and Riechman (1985) thus suggested that within forested regions, home range sizes vary according to habitat type, distribution and population density, as home range sizes usually vary between prairies and forested regions.

Ringelman et al. (1982) reported that the size of home ranges occupied by breeding black ducks in Maine varied among individuals but not between reproductive stages. Home ranges averaged 109 ha for incubating females (10) and 130 ha for prelaying and laying females (7). Home ranges of breeding males (7) averaged 231 ha. Breeding black ducks seemed to occupy smaller average home ranges than mallards breeding in forested regions.

Home ranges of both mallards and black ducks have a tendency toward linearity (Gilmer et al. 1975, Dwyer et al. 1979, Ringelman and Longcore 1982a, Kirby and Riechmann 1985).

Home range size and shape of sympatric mallards and black ducks have never been reported. Barclay (1970) studied activitiy centers for sympatric mallards but not for black ducks. The centers were relatively small (average 0.61 ha), possess high shoreline index values (average 3.55) and were sparsely vegetated. Black duck activity centers were much less detectable, being in or near wooded areas (Barclay 1970).

Nesting Success.---

Dzubin and Gollop (1972; Appendix E) obtained an average mallard nesting success of 33.8% (7-57%) from studies done prior to 1960 in the pothole region of the Dakotas and southern Canada. Dzubin and Gollop (1972) also reported higher nesting success (67%) in grassland habitat than in parkland (36%) during a 1952-58 study performed in the Canadian pothole region. Mallard nest success averaged 47% (13-85%) in nine studies (Weller in Johnsgard 1975).

Island-nesting mallards generally have higher nest success (>55%) than upland-nesting mallards (Dzubin and Gollop 1972, Laperle 1974, Duebbert et al. 1983).

In a forested region, Cowardin et al. (1967) reported higher success (86%) for mallards and black ducks nesting in stumps than for individuals nesting on the ground (65%).

In Chesapeake Bay, Maryland, Stotts and Davis (1960) estimated black duck nest success to be 38%. In the St. Lawrence estuary, mainland-nesting black ducks showed a nest success of 28%, those using a large island 44%, and those using other islands 52% (Reed 1975).

On St. Lawrence River islands, similar success rates were estimated for sympatric black ducks (54%) and mallards (59%) (Laperle 1974). However, black duck annual success rates varied greatly compared to mallards. This suggested that mallards were less affected by annual water fluctuations than were black ducks (Laperle 1974).

Most studies yield nesting success estimates based on the proportion of nests that succeeded of the total nests found. This index is prone to overestimate success because nests found in a late stage are more likely to succeed than those found earlier (Johnson 1979, Klett et al. 1986). Mayfield (1961,1975) developed a technique, which forms a basis for the comparison of nest success. The estimate compiles only the information recorded during the period a nest was under observation (Mayfield 1975). Miller and Johnson (1978, Johnson 1979) modified the Mayfield (1961,1975) technique for waterfowl, recognizing that there is generally a long period between observations.

Using the modified Mayfield method (1961,1975, Johnson 1979), Lokemoen et al. (1989) estimated lower mallard nesting success (11%) than average success previously recorded in North Dakota.

Using the unmodified Mayfield (1961) method, Reed (1975) estimated a daily rate of nest loss of 7% for estuary nesting black ducks. From this daily rate, Mayfield nest success can be estimated as $(1-0.07)^h$ where h is the mean age of clutches at hatching (26 days) (Klett et al. 1986). This nest success (15%) is lower than the lowest success rate (28% for mainland-nesting individuals) estimated using the older method (Reed 1975).

Duckling Survival Rate.---

In the prairie pothole region, Dzubin and Gollop (1972; Appendix C) compiled an average survival rate of mallard ducklings from class Ia (1-6 days) (Gollop and Marshall 1954) to flight stage of 64% (41-89%), from studies done prior to 1960.

Stotts and Davis (1960) measured low (9.2%) mortality of ducklings from hatching to flying age, for black ducks of the Chesapeake Bay, Maryland.

Total-brood losses are generally high and failure to record them overestimates survival rates (Ringelman and Longcore 1982b). Studies on marked or radio-tagged brood-rearing females permit the estimation of total brood mortality. This type of mortality is still difficult to estimate if females or broods are not individually marked (Dzubin and Gollop 1972, Ringelman and Longcore 1982b).

The following studies considered total-brood mortality: Dzubin and Gollop (1972) estimated lower survival rate in grassland (early: 56%, late hatching: 61%) than in parkland (early: 71%, late hatching: 86%); Sorensen (1978) obtained 56% mortality (survival: 44%) from class Ia to late class III in the parklands of Alberta; Talent et al. (1983) measured a survival rate of 35% in the prairie pothole region; Mallard rearing success averaged 44% in forested Minnesota (Ball et al. 1975).

Wright (1954 in Ringelman and Longcore 1982b) reported 79% duckling survival rate by black ducks. In the St. Lawrence estuary, Reed (1975) estimated that 34% of black duck young that hatched, reached flight age, and about 55% of all broods produced at least one fledged young.

Ringelman (in Ringelman and Longcore 1982b) modified the Mayfield (1961,1975) method for application to duckling survival. This method assumes independence among the fate of individual ducklings but this assumption may not always be valid (Reed 1970). However, Ringelman and Longcore (1982b) suggested that duckling survival was independent among brood members, at least for their data.

The Mayfield method applied to duckling survival offers less biased estimates than average late class III (44-60 days old) minus class Ia (1-6 days old) rates. It weights estimates for the different exposure experienced by each brood (Ringelman and Longcore 1982b).

Survival rates vary substantially over time or age for duck broods (Reed 1970, Ringelman and Longcore 1982b, Orthmeyer and Ball 1990). Hence, many authors suggest that rates be partitioned into intervals of more stable rates (Johnson 1979, Bart and Robson 1982, Heisey and Fuller 1985), usually corresponding with the age classes described by Gollop and Marshall (1954).

In Montana, using the Mayfield method, Orthmeyer and Ball (1990) measured an interval survival rate of 47% for mallard ducklings 1-18 days old. They measured a rate of 89% for the interval 19-45 days and 95% for the interval 46-60 days. Multiplying interval rates gives an overall survival to fledging of 39.5%. Total brood loss accounted for 60% of all duckling losses.

Using recapture versus return rate data, Lokemoen et al. (1989) estimated 68% survival of mallard ducklings reared in the prairie pothole region of North Dakota.

In Maine, Ringelman and Longcore (1982b) found black duck survival to be 61% for the Ia-IIa interval (1-24 days old), and 70% for the IIb-III interval (25-60 days old). Overall survival rate averaged 42%. About 81% of all broods fledged at least one young (Ringelman and Longcore (1982b). Reed (1970) reported 34% duckling survival for estuary black ducks, total-brood mortality included.

For both mallards and black ducks, survival rates tend to increase as ducklings age (Ringelman and Longcore 1982b, Orthmeyer and Ball 1990). Orthmeyer and Ball (1990) also found that 90% of total mallard brood loss occurred early after hatching (first 14 days).

Conclusions

Competitive exclusion by mallards is believed to be an important cause of the black duck decline. However, studies testing this hypothesis are lacking. Measures of habitat preference overlap may cast some light on the possible competition for habitats between breeding black ducks and mallards.

Black duck habitat preferences are comparatively less studied than those of mallards, especially in the breeding period. No extensive analysis exists of the relative habitat preferences of mallards and black ducks on shared breeding grounds.

Studies of allopatric mallards and black ducks tend to demonstrate some overlap in habitat preferences. The mallard is recognized as a highly adaptable species. Mallard habitat use is largely influenced by habitat availability in its extensive breeding range. It typically shows preference for emergent vegetation and successfully breeds in forested areas. The majority of black ducks breed in the boreal forest on small lakes, streams and beaver ponds.

Home range size and reproductive success of black ducks and mallards are to some extent influenced by the available habitat. However, when measured using recent methods, the rerpoductive success of allopatric black ducks and mallards show some similarities (nesting success; BD:15%, M:11%, duckling survival; BD:34-42%, M:39-44%). Measures of the reproductive success of sympatric black ducks and mallards are rare. Such measures are needed to help our interpretation of results of habitat studies in terms of interspecific competition.

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Section I: Habitat use by brood-rearing sympatric mallards and black ducks.

ABSTRACT

Micro-habitat use by brood-rearing mallards (Anas platyrhynchos) and black ducks (A. rubripes Brewster) in sympatry was studied in Abitibi, Quebec in 1988 and 1989. Water levels increased from 1988 to 1989 (0.5 m higher in 1989) and the ratio of broods of black ducks to mallards observed changed from 1:2.8 to 1:1.35. Black duck broods preferred thicket and emergent areas in 1988, while mallards used emergent areas almost exclusively. In 1989, they both used vegetation groups according to their availability. Micro-habitat use by mallard broods changed from 1988 to 1989 (from emergents to more available flooded shrub areas with emergents). However, micro-habitat use by black duck broods did not change from 1988 to 1989. Flooded thickets were used by the black duck even in 1988, when availability was low.

Diversity of vegetation groups seems to be more important to rearing black ducks than to mallards. Rearing mallards seem to modify their use of habitats according to changing habitat availability. Daily survival rates of black duck (0.9763) and mallard (0.9820) ducklings slightly differed (0.05>P>0.02).

INTRODUCTION

Following a decline in numbers since the late 1950's, the status of the American black duck (Anas rubripes) has been a matter of increasing concern to wildlife managers. Simultaneously, the distribution of the mallard (A. platyrhynchos) has increased eastward so that breeding and wintering areas of black ducks and mallards now largely overlap (Johnsgard 1961, 1967; Rogers and Patterson 1984).

Studies that investigate interspecific competition for habitats between mallards and black ducks in shared breeding areas are needed to help us understand how increased interaction with mallards has affected black duck populations.

The mallard is recognized as a highly adaptable species and is considered a generalist at several scales of habitat selection (Gilmer et al. 1975, Bellrose 1979, Rogers and Patterson 1984). In the prairie pothole region (where an estimated 60% of the North-American population breed (Bellrose 1979)), mallards tend to behave opportunistically, especially in years of high brood density and low wetland availability (Talent et al. 1982, Mulhern et al. 1985).

Mallards successfully breed in forested regions (Bellrose 1979), selecting overhanging brush and emergent vegetation areas (Cowardin et al. 1967, Gilmer et al. 1975, Kirby et al. 1985). Mallard broods will typically show preference for emergent vegetation (Mack and Flake 1980, Godin and Joyner 1981, Bélanger and Couture 1988, Monda and Ratti 1988), using it as escape cover (Stoudt 1971). Dwyer (1970) found that potholes surrounded by some forest areas were preferred by mallard pairs and broods. Bellrose (1979) noted that mallards are the prairie dabblers most influenced by wetlands with some wooded vegetation.

Black ducks breed mostly in closed eastern taiga (Bellrose 1979, Bordage 1988). They also breed on wetlands surrounded by mixed-hardwood forest and cultivated areas (Stotts and Davies 1960, Bellrose 1979, Courcelles and Bédard 1979, Ringelman and Longcore 1982a), and in estuaries (Reed 1970, Seymour 1984). Brood-rearing black ducks typically use streams (Seymour 1984, Bordage 1988) and flooded thicket areas with emergent vegetation, i.e., ponds created by beavers (_Castor canadensis_) (Renouf 1972, Ringelman and Longcore 1982a).

Little is known of the relative preferences of brood-rearing mallards and black ducks on shared breeding grounds (Courcelles and Bédard 1979, Bélanger and Couture 1988). Management of potential habitat preferred by black ducks may prove to be an efficient way to maintain their populations in present overlapping regions.

The objective of this study was thus to examine brood-rearing habitat preferences and duckling survival rates of mallards and black ducks on shared breeding grounds.

Assuming that females choose habitats similar to the ones where they were reared, it can be suggested that mallard and black duck hens with broods should select different (emergents vs flooded thickets) habitats when available.

I thus predicted that hens with broods will use some micro-habitats more than predicted by their availability and that black duck and mallard use will differ. If preferred micro-habitats were present on the shared rearing wetlands of the Harricana River, Quebec, black duck and mallard duckling survival rates should be similar. Hence, I also predicted that black duck and mallard duckling daily survival rates will be similar across habitats.

STUDY AREA AND METHODS

This study was conducted on an upper section of the Harricana River and on the Laine tributary, 20 km northwest of Val d'Or (48° 03'N, 77° 47'W), Quebec. This region lies on clay belts of the Precambrian Shield (Marie-Victorin 1964, Remick 1969). Agriculture, forest and mining industries have reduced the extent of the original boreal forest relatively recently (Dutilly and Lepage 1951, Innes 1960, Ministère de l'Énergie et des Ressources 1985).

The Harricana River is 45-75 m wide and forms riverine wetlands, which extend 300 m on average (maximum 910 m) on both sides of the river. The Laine river is 30 m wide with wetlands extending 160 m on both sides. River canals are 3-5 m deep (D. Nadeau, pers. comm.) with banks levelling quickly to form shallow basins that are permanently flooded. Palustrine wetlands and ponds modified by beaver were present. Aspen (Populus tremuloides) and birch (Betula papyrifera) dominated in upland areas surrounding wetlands. Mixed stands of hardwoods and conifers (Picea spp., Abies balsamea), old and cultivated fields (Poa spp.) and burned (1984) conifer sites were also present.

I selected four wetlands, representing the diversity of micro-habitats present in the study area, for detailed observations of unmarked broods. The shrub-rich marsh (Fig. 1.1, A) and the low-shrub fen (Fig. 1.1, C) were flooded plains of the Harricana River. Maximum of 14 ha of the marsh were visible from a tree tower 18 m high. The fen was observed from a camouflaged platform on a boat and 13 ha were visible. The low-shrub marsh (Fig. 1.1, B) was on a section of the Laine River where 21 ha were visible from a 15-m tree tower. The palustrine wetland (Fig. 1.1, D) was formed by a narrow-leaved emergent marsh with a deciduous-swamp section modified by beavers. A 7-m metal tower permitted the observation of 16 ha of this wetland.

I classified micro-habitat type into six vegetation form groups[4]: swamp-tall-shrub (swts), low-shrub (ls), patchy narrow-emergent (nep), robust-leafed emergent (re), narrow-leafed emergent (ne) and floating-submerged plant (fsu) (Canada/Ontario Steering Committee on Wetland Evaluation 1984).

Micro-habitat usage, position and activity of black duck and mallard broods were noted at five minute intervals from towers in the four selected wetlands. I assumed that each observation was independent since broods were capable of crossing the entire observed wetland at least once in five minutes. Habitat usage was defined by the vegetation form group in which the ducks were observed. Positions were recorded on 1:2700 maps to a resolution of 0.125 ha. Maps were on scale enlargements of 1:15 000 aerial photographs. Activities were classified as feeding, swimming, preening and sleeping. The activity performed by the majority of ducklings in the observed brood was recorded.

Two observers surveyed one wetland each for 3-4 hrs per day from late May through July during 1988 and 1989. Visits were scheduled within three daytime periods, i.e., morning (sunrise-1030), mid-day (1035-1600) and evening (1605-sunset), corresponding to periods of different waterfowl activity (Ringelman and Flake 1980). In 1988, ducks were more active in the morning and evening periods (see Longcore and Ringelman 1980). Therefore, in 1989 I doubled the morning and evening visits, attempting to increase the number of broods observed.

Water fluctuations were recorded by regularly marking the river water level on a bridge support and noting the changes from the highest level observed.

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[4] Plant species names associated with each groups are given in Appendix 1.

river water level on a bridge support and noting the changes from the highest level observed.

The hypothesis that mallard and black duck rearing habitat use and availability differed significantly was tested with a z statistic (Neu et al. 1974). The availability of each micro-habitat was defined as the total surface area of each group within the 4 wetlands observed. I defined use as the number of observations of mallard and black duck broods within each vegetation form group. The availability of habitats changed between rearing seasons, hence the test was performed separately for 1988 and 1989.

The hypothesis that mallard and black duck broods had significantly different habitat preferences was tested with a Chi-square statistic. The difference in the proportion of use by mallards and black ducks was tested for each micro-habitat using 2X2 G statistics (Sokal and Rohlf 1981:737-738).

Hens and broods could swim through an area to reach and select habitats for different activities. Habitat used during swimming may not represent habitat actively selected by hens. Therefore, all habitat analyses were performed for feeding, preening and sleeping activities only. If I observed the majority of ducklings in a brood feeding while swimming, the observation was noted as feeding.

I used the Mayfield (1961, 1975, Johnson 1979, Ringelman and Longcore 1982b) method to estimate duckling survival. Individual broods were identified through a combination of records indicating "species", age class (Gollop and Marshall 1954) and number of ducklings. Only broods sighted at least twice were used to calculate the survival rates. Mortality was assumed when brood size had decreased in subsequent observations.

RESULTS

Observations of unmarked birds on the four selected wetlands (Fig. 1.1) permitted to estimate a ratio of mallard and black duck broods in the study area. I assumed that these wetlands were representative of the entire study site. In 1988, a ratio of 0.62 black duck to one mallard broods was observed (total 26 different broods, not different from 1:1; $Z = 0.98$, $P = 0.16$) and in 1989, a ratio of 0.78:1 was estimated (total 25 broods, not different from 1:1; $Z = 0.40$, $P = 0.34$). For 1988 and 1989 combined, the proportion of mallard to black duck broods did not differ in the four observed wetlands ($X^2 = 4.23$, $df = 3$, $P > 0.1$).

Annual differences in micro-habitat (i.e., vegetation form group) availability resulted from differences in water depth between 1988 and 1989 (Fig. 1.2). Water was 0.3-0.8 m higher from early May to August 1989 than in 1988. Narrow-leafed emergents were not visible until late June 1989. For this reason, I divided the 1989 data into two periods: (1) before and (2) after plant emergence, and performed separated habitat analyses. The dividing date was arbitrarily defined as 25 June, in the last week of June.

When the first broods appeared in early June 1988, narrow-leafed emergents formed already relatively dense patches. In 1989, emergent plants were not available to early broods. However, areas of flooded deciduous forest, fields and thicket swamps (which were never flooded in 1988) were available to early broods until mid-June in 1989.

Observations of brood movements on the four wetlands were analyzed only for vegetation form group preferences for feeding, preening and sleeping activities. In 1988, both black duck and mallard broods used rearing micro-habitats more than predicted by their availability (X^2, $P<0.005$). Black duck hens selected narrow-leafed emergent areas whereas robust-leafed emergents were avoided. Swamp and shrub-rich areas were used as predicted by their availability (Table 1.1). However, use of these areas may have been underestimated because of their high cover potential. In 1988, brood-rearing mallards preferred narrow-leafed emergent and floating-submerged plant areas and avoided all other micro-habitats (Table 1.1).

Black duck and mallard habitat use differed significantly in 1988 (X^2, $P<0.005$). Black duck broods used more swamp, shrub-rich and patchy narrow-leafed emergent areas than mallards (2X2 G tests, $P<0.001$). Mallards were found more often in robust and narrow-leafed emergents ($P<0.01$).

In 1989, before plant emergence, both black duck and mallard broods preferred low-shrub areas while avoiding swamps and shallow water areas (Table 1.2). Again, I suspect that use of swamp and shrub-rich sections may have been underestimated. After emergents appeared, mallard and black duck broods used all micro-habitat types in proportion to their availability (Table 1.3). Consequently, I did not perform the Neu et al. (1974) test. Overall micro-habitat use by mallards and black ducks did not differ in 1989 ($X^2 = 4.92$, $0.5>P>0.25$).

I calculated lower daily survival rates for black duck and mallard ducklings in 1988 than in 1989 (Table 1.4). Within a single year, mallard and black duck estimates did not differ. However, slightly higher ($0.05>P>0.01$) daily survival rates for combined years were recorded for mallards (0.9820) than for black ducks (0.09763).

DISCUSSION

Habitat Selection

In 1988, both mallard and black duck broods made extensive use of narrow-leafed emergent areas. However, in 1989, herbaceous plants were not available or rare until late June and large patches of ericaceous shrub (forming 33% of vegetated wetland) were used extensively by mallard and black duck broods. Near the time of plant emergence, herbaceous vegetation was available only in shrub areas where shallow waters permitted their growth. Consequently, flooded ericaceous shrub sections of wetlands were used when emergents were less available, providing food and some cover.

Many authors stress the importance of herbaceous plants as vegetation supporting high biomass of aquatic invertebrates and providing escape cover (Courcelles and Bédard 1979, Krapu 1979, Reinecke and Owen 1980, Poysa 1983, Kaminski and Prince 1984). Mallard broods typically show preference for emergent vegetation (Stoudt 1971, Mack and Flake 1980, Godin and Joyner 1981) and for high emergent-water interspersion (Ball and Nudds 1988). Swamps and flooded tall shrubs, which provide cover from bad weather and predators also are important to waterfowl (Dwyer 1970, Ringelman and Longcore 1982a, Kirby et al. 1985). Ringelman and Longcore (1982a) noted that alder-shrub communities with herbaceous understorey may form food-rich habitats for broods. These communities develop macroinvertebrate-rich waters because of symbiotic nitrogen fixation in alder root nodules (Tilton and Bernard 1975, Ringelman and Longcore 1982a). However, ericaceous shrubs offer little food and shelter and seem relatively avoided by black ducks and mallards (Courcelles and Bédard 1979, Ringelman and Longcore 1982a, Ringelman et al. 1982, Bordage 1988).

In 1989, after plant emergence, mallard and black duck broods used vegetation forms in proportion to their availability. This however, must be interpreted cautiously. Use of low visibility sections such as swamps may have been underestimated, causing apparent opportunism. Opportunistic behavior by black ducks was never reported and for mallards, only in the prairie pothole region (pairs: Dwyer et al. 1979, Mulhern et al. 1985, broods: Talent et al. 1982). In theory, opportunism is expected when population densities are high or available wetlands rare (Fretwell and Lucas 1970, Ball and Nudds 1988), and dabbler densities are known to be higher in the prairie pothole region than in any other region in North America (Bellrose 1979, Wishart et al. 1983).

The water level changes between 1988 and 1989 allowed the identification of some differences in micro-habitat use by rearing mallards and black ducks. During low water levels in 1988, mallard broods were rarely observed in swamp and shrub areas whereas black ducks used them as well as narrow-leafed emergent areas (Tables 1.1). Overall, in 1989, mallards transferred the majority of their activities to swamp and shrub-rich areas thus using micro-habitats similar to ones used by black duck broods. Black duck changes in habitat use between the two years were less detectable. They used shrub areas even during periods of low availability suggesting that cover may be more essential to rearing black duck hens than to mallards.

Differences in frequency of mallard and black duck brood observations also suggest a relative preference for cover by black ducks compared to mallards. The four wetlands were used by similar numbers of mallard and black duck broods but the ratio of black duck:mallard observations differed. In 1988, for each black duck observation, 2.80 mallard observations were noted, a ratio significantly smaller than the ratio of black duck: mallard broods (1:1.6) present that year (P = 0.03). In 1989, when mallards and black ducks used similar habitat types, this ratio became 1:1.35 before plants emerged (not different from 1 BD: 1.33 M present, P = 0.49) and 1:1.50 after plant emergence (not different from 1 BD: 1.25 M present, P = 0.22).

In general, diversity of micro-habitats seems important to rearing black ducks. Mallard hens seemed to prefer narrow-leafed emergent and floating plant micro-habitats. They also seem to modify their use of habitats according to changing habitat availability.

Duckling Survival

High water levels in 1989 were not catastrophic. No data exist concerning the Harricana River water levels before summer 1988 but high river flow variations and average measures of spring rain and snowfall suggest that water levels similar to 1989 are not exceptional (Ministère des Richesses Naturelles 1969, Atmospheric Environment Service 1980). Both black duck and mallard duckling daily survival rates increased that year ($P<0.001$). This may be explained by an increase in micro-habitat diversity in 1989; more wetland areas covered by vegetation were available (1988: 33.1 ha, 1989: 46.6 ha). Even before plant emergence in 1989, 33.3 ha of wetland were covered by vegetation, mostly tall and small shrubs.

The daily survival rate for black ducks over the two years combined was slightly lower than the mallard daily rate ($0.05>P>0.01$). This translates into 24% (0.9763^{60}) probability of a black duck duckling surviving the 60-day rearing period and a probability of 34% for a mallard duckling. The small sample sizes (BD:8, M:9) involved in estimating survival preclude further discussion regarding a difference between black duck and mallard survival rates on my study site.

Furthermore, survival vary substantially over the rearing period for duck broods (Ringelman and Longcore 1982). Several authors suggest that survival rates be partitioned into intervals of more stable rates (Johnson 1979, Bart and Robson 1982, Heisey and Fuller 1985). However, small sample sizes of classes IIb and IIc (26-43 days old) prevented this partitioning.

In general, survival of black duck ducklings, from hatching to fledging, vary from 34% (Reed 1975) to 42% (Ringelman and Longcore 1982b). When total-brood losses were not considered, higher rates were estimated (79% :Wright 1954, 91% :Stotts and Davis 1960). In this study, broods were unmarked and total-brood mortality could not be measured, overestimating survival (Ringelman and Longcore 1982b). Considering this, the estimate of black duck rearing success (24%) was lower than expected from other studies (Reed 1975, Ringelman and Longcore 1982b).

Mallard rearing success (34%) was also lower than rates measured in forest-dwelling mallard studies where total-brood mortality was considered (44%:Alberta parklands in Sorensen 1978, 44%:forested Minnesota in Ball et al. 1975, 40%:Montana in Orthmeyer and Ball 1990). In Manitoba parkland, Dzubin and Gollop (1972) measured mallard duckling survival as high as 86%. In the prairie pothole region, Talent et al. (1983) estimated a duckling survival rate of 35% for mallards.

Habitat analysis and survival measures suggest that brood-rearing mallards are able to use different vegetation groups (i.e., emergents and shrubs) equally well. Consequently, the array of micro-habitats used by mallards greatly overlap those most used by black duck hens, at least in the Harricana River wetlands. There is potentiality for competition between mallard and black duck broods for emergent areas, and for shrub-rich sections when emergent areas are rare. However, this assumes that: (1) the use by a brood of one area (i.e., of its resources) deprives other broods of it and (2) that restricted use of these resources can decrease brood survival and hence reproductive success ("consumptive" competition, Schoener 1983: p.258). On my study site, no aggression or avoidance between broods suggested "encounter" (Schoener 1983) competition between mallards and black ducks.

Measures of resource overlap have been used to define competition, although with restrictions: is habitat overlap inversely or directly related to competition? (Pimm and Rosenzweig 1981, Schoener 1983, Rosenzweig 1985). Macrohabitat overlap was shown to be usually inversely related to experimentally demonstrated competition, whereas micro-habitat overlap is usually directly related (Schoener 1983). Micro-habitats are more likely to be resources for which individuals compete, not simply "arenas of competition" (Schoener 1983). Micro-habitats need not be resources per se, resource abundance may simply be related to some habitat characteristic measured. Moreover, if the sympatry is evolutionarily recent, such as for black ducks and mallards in northwestern Quebec (L. Belisle, pers. comm., Bordage 1988), and a micro-habitat preference overlap is detected, interspecific competition is more likely to be present (Rosenzweig 1985).

Studies on ecological overlap and reproductive success on the shared breeding grounds throughout Northeastern America may cast more light on the possible competitive exclusion of black ducks by mallards. Special attention may be given to very recent overlapping breeding areas such as in northern Quebec (Bordage 1988, Rusch et al. 1989) where little is known of the effect of habitat changes on the population of breeding black ducks (Rusch et al. 1989).

Management Implications

Management of shrub-rich habitat with little emergents will probably fail to favour black duck broods over mallards. Conversely, management of emergent marshes with no flooded thicket section will favour mallards in rearing areas shared by black ducks. A high level of diversity of available microhabitats seems essential to rearing black ducks.

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Table 1.1. Micro-habitat availability and use by brood-rearing black ducks and mallards during feeding, sleeping and preening, in four wetlands of the Harricana River, Quebec, June-August 1988.

Habitat type[1]	Available area (ha)	Expected use[2]	Observed use(prop.)	Use Avail[3]
Black ducks				
swtsls	10.8	18.3	13 (0.23)	0
nep	7.2	12.2	7 (0.12)	0
re	3.4	5.7	1 (0.02)	-
ne	8.3	14.0	25 (0.44)	+
fsu	3.4	5.8	10 (0.18)	0
Total	33.1	56		
Mallards				
swtsls	10.8	50.3	1 (0.01)	-
nep	7.2	33.6	1 (0.01)	-
re	3.4	15.6	7 (0.04)	-
ne	8.3	38.5	97 (0.63)	+
fsu	3.4	16	48 (0.31)	+
Total	33.1	154		

BD: X^2 = 237.56, df = 4, p<0.005, M: X^2 = 19.24, df = 4, p<0.005

[1] Open water excluded. swtsls = swamp, tall and low shrub, nep = patchy emergent, re = robust-leafed emergent, ne = narrow-leafed emergent, fsu = floating and submerged plant

[2] Expected use = (Avail. area / Total area) x Total obs. use

[3] 0 if 95% CI of observed use overlaps with expected use (usage = availability), + if habitat used more than predicted by its availability, - if used less.

Table 1.2. Micro-habitat availability and use by brood-rearing black ducks and mallards during feeding, sleeping and preening, in four wetlands of Harricana River, Quebec, before plant emergence in June 1989.

Habitat type[1]	Available area (ha)	Expected use[2]	Observed use(prop.)	Use: Avail.[3]
Black ducks				
swts	15.9	17.2	10 (0.18)	-
ls	17.4	18.7	43 (0.75)	+
nep-re-ne	19.5	21 0	4 (0 07)	-
Total	52.8	57		
Mallards				
swts	15.9	23.2	9 (0.12)	-
ls	17 4	25.3	67 (0.87)	+
nep-re-ne	19.5	28.4	1 (0.01)	-
Total	52.8	77		

BD. $X^2 = 48.72$, df = 2, $p<0.005$. M: $X^2 = 103.8$, df = 2, $p<0.005$.

[1,2,3] refer to Table 1.1

Table 1.3. Micro-habitat availability and use by brood-rearing mallards during feeding, sleeping and preening, in four wetlands of Harricana river, Quebec, after plant emergence, June-August 1989.

Habitat type[1]	Available area (ha)	Expected use[2]	Observed use(prop)
Black ducks			
swts	7 6	6.2	10 (0.27)
ls	16.3	13.3	5 (0.13)
nep	7.6	6.2	8 (0.21)
rene	12.0	9.8	13 (0.34)
fsu	3.1	2.5	2 (0.05)
Total	46 6	38	
Mallards			
swts	7 6	9.4	9 (0.16)
ls	16.3	19.9	22 (0.38)
nep	7 6	9.3	12 (0.21)
rene	12.0	14.6	13 (0.23)
fsu	3.1	3.8	1 (0.02)
Total	46 6	57	

BD: $X^2 = 9.13$, df = 4, $0.1>p>0.05$, M: X^2 after emerg. = 3.25, df = 4, $0\ 75>p>0\ 5$, hence Neu et al. tests were not performed

[1,2,3] refer to table 1.1.

Table 1.4. Daily survival rates (s) of black duck and mallard ducklings on four wetlands of the Harricana River, Quebec, June-July 1988 and 1989.

Year	No. diff. broods[1]	No. brood sighted	Av. time between sighted	Total exposure (duckling-(days)	Total losses days)	s
Black duck						
1988	4	11	6.4 (1-14)	250	9	0.9640 a
1989	4	12	4 0 (1-7)	215	2	0.9907 b
Combined years				465	11	0.9763 c
Mallard						
1988	5	10	10.0 (1-16)	303.5	8	0.9736 a
1989	4	14	5.6 (1-28)	363 5	4	0.9890 b
Combined years				667	12	0.9820 d

Values with same letter do not differ significantly (t tests, a-b· $P<0.001$, c-d: $0.05>P>0.01$)

[1] Only broods sighted twice were included to satisfy the Mayfield method requirements (Johnson 1979). Total number of different broods on the four wetlands, in 1988 BD· 10, M· 16, in 1989 BD: 11, M: 14

Average class-I brood sizes were, in 1988, 8.0 black ducks (n=8) and 7 4 mallards (n=5), in 1989, 8.0 black ducks (n=7) and 6.7 mallards (n=7). Average class-III brood sizes were, in 1988, 4 3 black ducks (n=7) and 5.8 mallards (n=11); in 1989, 4.2 black ducks (n=4) and 7.0 mallards (n=3). These averages are from all broods observed on the study area (Fig. 1.1).

Figure 1.1. Location of the four observed wetlands on the Harricana and Laine Rivers, Quebec. A. shrub-rich marsh (14 ha) B. low-shrub marsh (21 ha) C. low-shrub fen (13 ha) D. narrow-leaved emergent marsh and deciduous swamp (16 ha). A,B,C are riverine wetlands, D is a palustrine wetland.

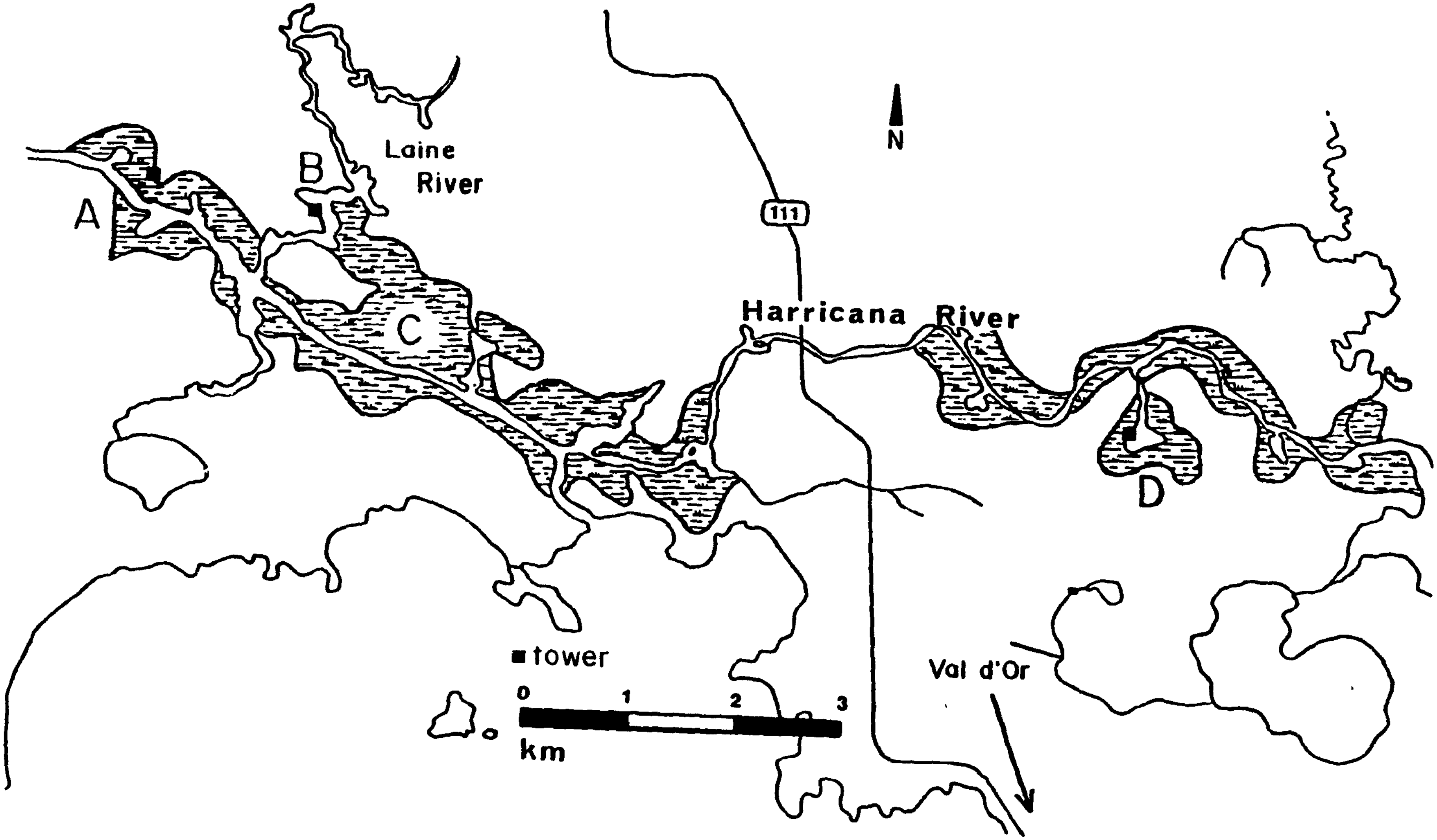
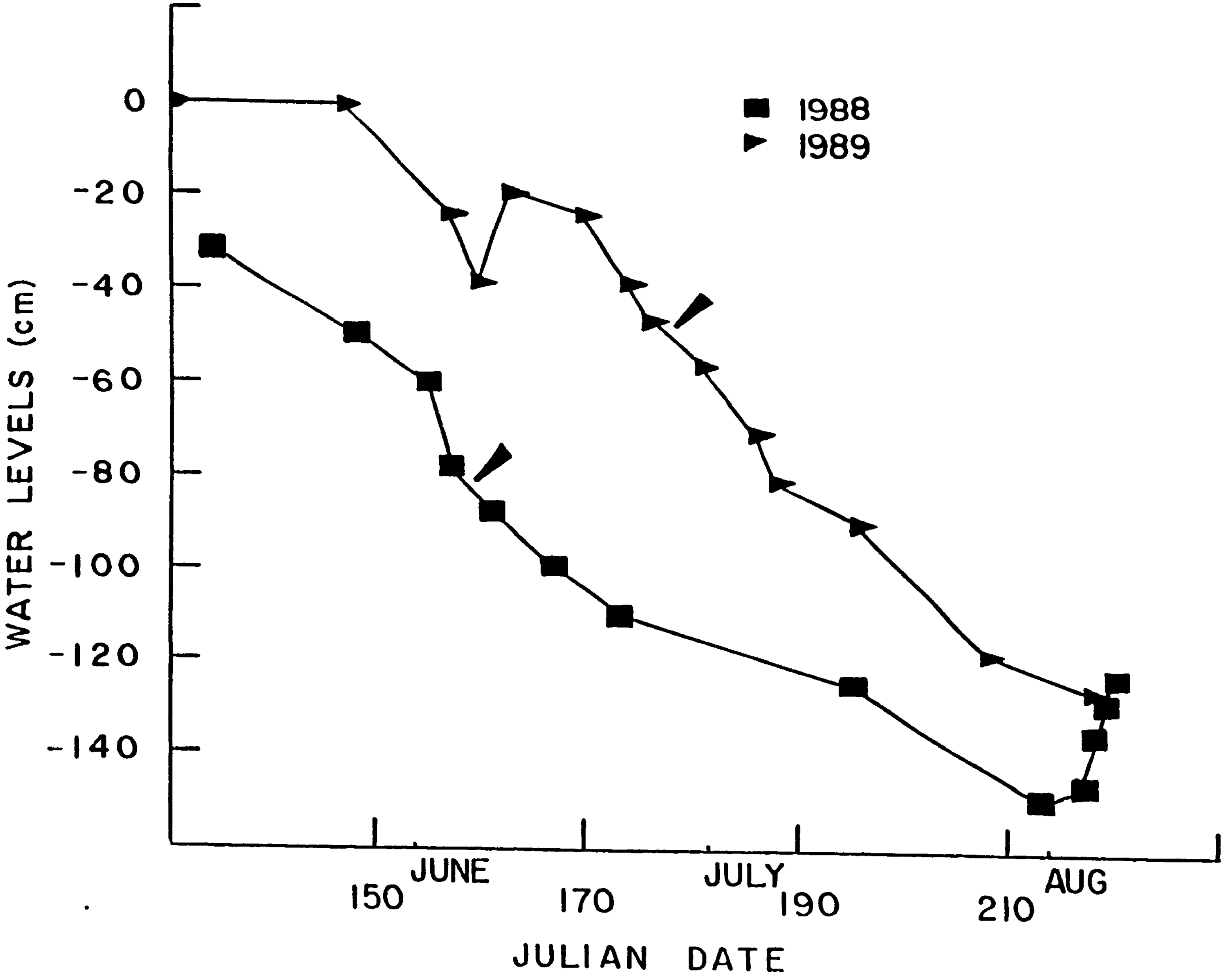

Laine
River
B
A
111
N
C
Harricana River
D
tower
0
1
2
3
km
Val d'Or

Figure 1.2. Water level fluctuations of the Harricana River, Quebec from 9 May to 7 August 1988 and 1989. Arrows indicate starting date of plant emergence above the water line.



WATER LEVELS (cm)
0
-20
-40
-60
-80
-100
-120
-140
JULIAN DATE
150
170
190
210
JUNE
JULY
AUG
■ 1988
▶ 1989

Connecting statement

In the first section, unmarked brood-rearing black ducks and mallards were studied. I analyzed their use of habitats within wetlands. In the following section, I studied wetland selection by radio-tagged non-breeding females and studied their home ranges. Wetland selection and home range characteristics of one breeding mallard female also were analysied.

Section II: Wetland use and home range of radio-tagged sympatric black ducks and mallards.

ABSTRACT

Telemetry techniques were used to study wetland use and home range of three non-breeding black duck (*Anas rubripes* Brewster) and six non-breeding mallard (*A. platyrhynchos* L.) hens in Abitibi, Quebec during the 1988 and 1989 breeding seasons. Thicket wetlands and swamps were selected, and ericaceous shrub wetlands avoided by both black ducks and mallards. During the moulting period, beaver (*Castor canadensis*) ponds were used extensively by all females. Mean home range area was 302.7 ha for black ducks and 201.2 ha for mallards, with high (>3.0) linearity indices.

INTRODUCTION

Since the 1950s, black duck (*Anas rubripes* Brewster) numbers have decreased to a point that this species is now identified as one of international concern by the North American Waterfowl Management Plan (Rusch et al. 1989). Besides recent harvest reductions, which seem to produce encouraging population response (J.R. Longcore, pers. comm.), habitat management is among the tools suggested to reverse the downward trend (Ankney et al. 1987, Rusch et al. 1989, Kehoe, in press). However, an understanding of the habitat preferences of black ducks has been limited by different factors. Quantifying habitat selection is complicated by the low densities of black duck populations on their breeding grounds (Bellrose 1979, Ringelman et al. 1982, Wishart et al. 1983), by thier extreme wariness, and by the cover potential of the inland forested breeding habitat (Ringelman et al. 1982).

Coincident with the decline of black ducks, mallard (*A. platyrhynchos* L.) numbers have increased in the east (Collins 1974, Johnsgard and DiSilvestro 1976, Dennis et al. 1984, Rusch et al. 1989) such that the breeding and wintering areas of the two closely related species (Johnsgard 1961, Avise et al. 1990) now overlap. Some studies have been done on the breeding biology of black ducks and mallards where they coexist (Cowardin et al. 1967, Coulter and Miller 1968, Barclay 1970, Laperle 1974, Courcelles and Bédard 1979). However, to my knowledge no analysis exits of the patterns of use of different wetland types by sympatric mallards and black ducks. We must gain a better understanding of the possible competition for habitat between mallards and black ducks on their shared breeding grounds.

The objective of this study was to examine wetland preference, as well as home range size and overlap for sympatric breeding mallards and black ducks.

In the prairie pothole region, mallards use more open wetland habitat than do black ducks in the forested habitat, which covers most of their breeding range (Stotts and Davies 1960, Renouf 1972, Gilmer et al. 1975, Dwyer et al. 1979, Ringelman et al. 1982, Talent et al. 1982). Mallards typically show preference for emergent vegetation (Poysa 1983, Kaminski and Prince 1984) but may as well use forested and shrub-rich wetlands (Dwyer 1970, Gilmer et al. 1975, Bellrose 1979, Kirby et al. 1985). Black ducks typically use small lakes, streams, swamps and beaver-modified wetlands (Stotts and Davies 1960, Reed 1970, Renouf 1972, Ringelman et al. 1982, Seymour 1984, Bordage 1988).

I hypothesized that mallards and black ducks would select different habitats on the breeding grounds of the Harricana River, Quebec. I predicted that mallards and black ducks would actively select habitats and that the rank ordering of their preferred habitats would differ.

Waterfowl population densities are typically low in boreal regions (Bellrose 1979, Ringelman et al. 1982, Boyd 1984). At low population densities, home range sizes of waterfowl are believed to be primarily affected by the predictability of the environment and the distribution or availability of preferred habitats : predictable, widely distributed wetlands permitting small home ranges (Dwyer et al. 1979, Ringelman et al. 1982, Kirby et al. 1985). I hypothesized that mallards and black ducks on shared breeding grounds would have similar home range sizes if the different preferred habitats are equally available on the study site.

STUDY AREA

The study area was 20 km northwest of Val d'Or, Quebec. It included a section (45-75 m wide, flowing west) of the Harricana River and the Laine tributary (30 m wide, flowing south). Pure stands of hardwoods (*Populus tremuloides*, *Betula* spp.) and conifers (*Picea* spp. *Abies balsamea*) with small sections of mixed forest occupied 60% of upland areas. Old and cultivated (*Poa* spp.) fields covered the remaining levelled sites. Lowlands were dominated by poplar, birches, willows (*Salix* spp.) and alders (*Alnus* spp.), with tamarack (*Larix laricina*) in more acidic sections. Bogs and fens were typified by ericaceous shrub species (*Chamaedaphne calyculata*, *Kalmia polifolia*, *Myrica gale*, *Andromeda glancophylla*) and meadow-sweet (*Spiraea latifolia*). Marshes were mostly covered by spike-rushes (*Eleocharis* spp.), sweet-flag (*Acorus calamus*), sedges (*Carex* spp.), rushes (*Juncus* spp.) and members of the Gramineae family on drier sites. Typical floating bur-reeds (*Sparganium fluctuans*), pond-lily (*Nuphar variegatum*) and amphibious knot-weed (*Polygonum amphibium*). Cattails (*Typha* spp.) were present only on a marginal basis. Ten wetlands (in total 120 ha) were modified by beaver (*Castor canadensis*).

Wetlands (excluding lakes and rivers) covered about 20% (530 ha) of the study area. I classified wetlands into four types according to the Canada/Ontario Steering Committee on Wetland Evaluation (1984). Bogs and fens were grouped in one type, forming 44% of wetland habitats. Marshes, flooded thickets and swamps made up 28%, 21% and 7% of total wetland area respectively. More details on the study area were presented in Section I.

METHODS

Data on macrohabitat selection were obtained by following radio-tagged birds from May through July in 1988 and 1989. Birds were captured in decoy traps (Sharp and Lokemoen 1987) during spring. Captured birds were fitted with back-mounted radio transmitters weighing approximately 35 g (Dwyer 1970). Each bird was located 1-3 times per day from mobile vehicles or a fixed mast using conventional telemetry techniques (Ringelman et al. 1982). Locations were noted on topographical maps (1:50 000) in Universal Transverse Mercator units to the nearest 200 m. When birds were absent for more than 2 days, I searched the territory within 20 km of the study area from a Cessna 180 with externally attached antennae. I attempted to obtain a sight recording for each bird at least once a week to determine its status (paired, nesting, rearing or moulting).

Home ranges were estimated (McPAAL program, Stuwe and Blohowiak, pers. comm.) using the smallest convex polygon method (Odum and Kuenzler 1955, Jennrich and Turner 1969), the 95% ellipse method (Jennrich and Turner 1969) and the harmonic mean method (Dixon and Chapman 1980). An index of linearity (Ables 1969) was estimated for all convex polygon home ranges, by dividing the maximum length by the maximum width measured at 90 ° to the length. Centers of activity were located based on the harmonic mean method, at the grid points of the minimum reciprocal mean distance deviation (Dixon and Chapman 1980)[5]. I calculated distances between activity centers if more than one center was found in the home range. I defined home ranges by forming activity isolines (Dixon and Chapman 1980) which contained (to the nearest 500 m) at least 95% of

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[5] See Basic programs HOMERANG and DATACESS in Appendix 2.

all locations for each radio-tagged bird. Areas of intensive activity were defined by 500-m isolines. Differences in black duck and mallard home range sizes and linearities were tested using the Mann-Whitney U test (Sokal and Rohlf 1981).

The Johnson (1980, Frank and Lopas 1985) and Friedman (in Alldredge and Ratti 1986) methods were used to test the null hypothesis that use and availability of each wetland type were equal. These methods provide an ordering of habitats from least to most preferred and permit the exclusion of less used habitat types without significantly altering the selection pattern (Alldredge and Ratti 1986). The Neu method (Neu et al. 1974) was used when a small sample of birds (i.e., no. of birds < no. of habitats) prevented analysis using the Johnson (1980) method.

Use was defined as the number of telemetry locations for each bird on each wetland type. Habitat availability was defined as the total surface area of each type within the circular area available to each bird (Hayne 1949, Ringelman et al. 1982). The centre of these areas was the arithmetic mean (mean x by mean y coordinates) of the different telemetry locations and their radius was the distance from this centre to the farthest location. These available circular areas do not define home ranges per se. They delineated areas larger than the home range hence decreasing biases because home ranges are the outcome of some habitat selection. They permit the inclusion of wetlands not used by ducks but potentially available because ducks did fly to wetlands situated at a similar distance (Ringelman et al. 1982).

RESULTS

Six female mallards and three female black ducks provided data for wetland selection analysis. Telemetry locations noted during moulting periods were excluded from the habitat analysis as non-independent data (Alldredge and Ratti 1986), because moulting birds could not fly and freely select wetlands. One radio-tagged female mallard made two nest attempts in 1989. Habitat selection by this mallard was analyzed separately for the reproductive stages and the post-breeding stage. All other birds failed to breed after being fitted with the transmitter. One radio-tagged female mallard paired with a radio-tagged male mallard until 15 June 1989, but nesting was never initiated.

Habitat Selection

Mallards used wetland types more than expected by their availability ($P < 0.005$ in Table 2.1). The Johnson method produced, for mallards, the following rank ordering of wetland types from most to least preferred (left to right):

Thicket Swamp Fen Marsh

Habitat types underscored by the same line were not used differently according to the Waller-Duncan procedure (Johnson 1980). The Friedman method produced an ordering of habitat types similar to the one obtained by the Johnson method:

Thicket Swamp Fen-Marsh

The same rank was obtained for the fen and marsh types.

Habitat selection by one female mallard during laying and incubation until first nesting failure (5 May - 18 May 1989, 14 locations) was analyzed using the Neu et al. (1974) method. All habitat types were used in proportion to their availability. The test could not detect any preferences or avoidances ($X^2 = 7.34$, $P > 0.05$).

Selection by black ducks was analyzed using the Friedman (Alldredge and Ratti 1986) and the Neu et al. (1974) tests. The Johnson method was not used because it requires that the number of habitats tested be equal to or smaller than the number of bird observations. Our data did not satisfy this: four habitat types were analyzed for selection by three hens. According to the Friedman method, black ducks (Table 2.2) used all wetland types according to thier availability ($P = 0.727$). However, a preference for swamps and an avoidance of fens was detected after use and availability for all black ducks were combined and the Neu et al. (1974) method was used ($P < 0.005$).

All females for which the moulting period was known (2 mallards and 2 black ducks) used shrub-rich marshes modified by beavers as moulting areas.

Home Ranges

The sizes of the home ranges occupied by female black ducks and mallards did not differ (Mann-Whitney, $P > 0.10$), and this is independent of the method used to estimate areas (Tables 2.3, 2.4). In general, the 95% ellipse and the harmonic mean methods estimated similar home range areas and the convex polygon method yielded the smallest estimates (Friedman rank test, $P < 0.005$). Areas of home ranges greatly differed among individual mallards (Table 2.3). The two smallest home ranges were typified by only one center of activity (Table 2.4: Mb-88, Mc-89), i.e., point of greatest activity (Dixon and Chapman 1980). Both centers were located in palustrine wetland rich in tall-shrubs (thicket type). One black duck home range had only one center of activity situated in low-shrub fen but still occupied an area similar to birds having multiple activity centers (Table 2.4: Ba-88).

Four of the six female mallards used the same palustrine marsh (with a section created by beaver) as their intensive activity range and their entire home ranges largely overlapped (Fig. 2.1). Other female mallards intensively used a palustrine thicket wetland (Fig. 2.1: Mb-88) and a treed low-shrub fen (Fig. 2.1: Md-89). The wetland types that dominated in intensive activity ranges of black ducks were diversified (Fig. 2.2). One female (Fig. 2.2: Ba-88) intensively used a riverine low-shrub fen and the two others (Fig. 2.2: Bb-89, Bc-89) used a marsh and a thicket wetland, both with sections modified by beaver.

High linearity indices (Table 2.3) and a tendency toward double activity centers (Tables 2.4) dominated both mallard and black duck home ranges. Birds used one area until late June to mid-July then moved to a second area. Wetlands located between these two centers were rarely used. This suggests that linear home ranges were created by the sequential use of two selected wetland complexes. Riverine wetlands may favor linear home ranges parallel to the river. However, on this study site, the second wetlands used were generally dominated by different habitat types from the first and situated on different drainage. All linear home ranges had their long axis north-south, one extremity located near the Harricana River, the other on lacustrine wetlands. The average width of the convex polygon home ranges was 864.3 m (100-1750 m) for mallard hens and 1166.6 m (700-1600 m) for black ducks.

Nesting Attempts

One female mallard (Ma) was radio-tagged on 16 June 1988 while rearing four ducklings of age class Ic (13-18 days old:

Gollop and Marshall 1954) and was relocated on 13 May 1989 within 500 m of her last location 8 August 1988. This hen demonstrated fidelity to the home range, using the same wetlands in both years. None of her ducklings fledged in 1988. In 1989, she attempted to nest twice (2nd successful) within 2 ha of treed-bog habitat and lost eight ducklings on the nearest wetland (bog 250 m east) two days after hatching (27 June). Incubation of the first nest started on 13 May 1989 with nine eggs and ten eggs were incubated in the second nest beginning 28 May 1989.

Nests (2 by radio-tagged, 1 by unmarked mallards) were situated under black spruce (height 5-6 m) in forested peatland habitat. Construction material was black spruce, tamarack and leafless twigs of ericaceous shrubs and moss (Sphagnum spp.). The nests were at 61 m, 45 m, and 18 m from open water.

The convex polygon home range occupied by the radio-tagged mallard during the prelaying period was 111 ha, 65 ha were used during the laying period and 30 ha during incubation. After loss of ducklings (post-breeding), the hen changed her center of activity from a bog and forested streams to a beaver-modified marsh and used a 25-ha home range, presumably while moulting. Home ranges estimated using the harmonic mean method and the 95%-ellipse method tended to increase from laying to incubation period and were larger than convex polygons (Table 2.5). Linearity indices (Table 2.6) are comparable to those obtained for home ranges of non-breeding birds (Table 2.3).

DISCUSSION

Habitat Selection

Habitat selection analyses suggest similar preferences for thicket wetlands and swamps and avoidance of ericaceous shrub wetlands by both mallards and black ducks.

Habitat preferences by these non-breeding ducks were generally consistent with preferences reported for allopatric breeding mallard and black duck pairs. Other studies have reported avoidance of ericaceous shrubs by black ducks (Ringelman et al. 1982). Preference for thicket wetlands and swamps were reported for black ducks and for forest-dwelling mallards (Gilmer et al. 1975, Kirby et al. 1985). Dwyer (1970) found that nonagricultural land potholes surrounded by forest were preferred by mallard pairs and broods.

Wetlands were used according to their availability by mallards breeding in the prairie potholes of south-central Dakota (Dwyer et al. 1979) and aspen parklands of Saskatchewan (Mulhern et al. 1985). This is consistent with the habitat selection hypothesis that birds may become opportunists when population densities are high (Fretwell and Lucas 1970, Fretwell 1972). Breeding mallard densities are higher in the prairies than in the forested regions (Bellrose 1979, Wishart et al. 1983). No studies reported opportunistic wetland use by breeding black ducks.

Almost all thicket wetlands and swamps present in mid and late July were associated with active beaver ponds. These areas seem important to both mallards and black ducks during the moulting period when water levels are lowest in July. Beaver-created swamps and thicket wetlands possess the seclusion and cover potentials required by flightless birds (Renouf 1972, Fredrickson and Drobney 1979, McCall, in press).

Alldredge and Ratti (1986) studied the performance of different statistical methods for analysing habitat selection, using simulated conditions (4 habitats and 10 animals). Type II errors for all methods were particularly high and variable (5.6-98.7 %) for the primary tests of significance (Johnson F, Friedman X_r, Neu X^2). Not surprisingly, different patterns of habitat selection thus frequently appear as the different statistical techniques are used (Alldredge and Ratti 1986). Because of large Type II error rates, the null hypothesis is rejected only if differences in use and availability are exceptionally large.

White and Garrott (1986) demonstrated that the power of the test by Neu et al. (1974) to detect habitat selection decreases as habitat complexity (i.e., smaller scale) increases and as triangulation precision and sampling effort decrease. This telemetry study uses wetlands as habitats, which represents relatively low habitat complexity. The minimum area of habitat available was larger than the telemetric resolution. However, the number of telemetry locations was small, especially for black ducks. For selection to be detected by the test of Neu et al. (1974) or any other tests (White and Garrott 1986), black ducks and mallards must strongly select wetland types.

Confidence in the accuracy of habitat use patterns increases when different methods yield similar results such as for the mallard habitat preferences. The Neu et al. (1974) method seems to perform better than others when the numbers of animals and habitats are small (Alldredge and Ratti 1986). Hence, habitat selection measured by this method may be regarded as more accurate for the black duck.

Home Ranges

Black duck home ranges were approximately 100 ha larger than that of mallards, independent of the method used to estimate areas. However, this was not statistically different because of large variances between individuals and small sample sizes. Home ranges of all birds were monitored during approximately the same period (May-August) in 1988 and 1989. Variances in home range sizes, especially for mallards, cannot be explained by discrepancies in monitoring time spans alone. Smaller home ranges can best be explained by the presence of only one activity center and the fact that the female did not move to a different wetland before moulting.

The average convex polygon home range of female mallards (201 ha) is similar to home ranges (210 ha) reported for breeding forest-dwelling mallards by Gilmer et al. (1975), although home ranges greater than 300 ha were measured in the present study. Kirby et al. (1985) estimated larger and more variable home ranges (540 ha, ranging 40-1446) for mallards breeding in forested habitat. In prairie habitat, home range size averages 468 ha (Dwyer et al. 1979).

I estimated seemingly larger convex polygon ranges for non-breeding black ducks (303 ha) than Ringelman et al. (1982) reported for breeding females (210 ha).

Home range sizes seem greatly influenced by availability of habitats. Larger home ranges occurred when females travelled to another center of activity situated in thicket wetlands in late summer. Smaller home ranges occurred when the female stayed near the same activity center where swamp or thicket wetland was available. The variability in size decreases if home ranges are classified according the number of activity areas (Table 2.3). This large variability because of differential availability of habitats in or near individual home ranges may prevent the detection of size differences between reproductive stages (as in Gilmer et al. 1975, Dwyer et al. 1979), especially as few radio-tagged individuals are usually studied (Ringelman et al. 1982, Kirby et al. 1985).

Management Implications

On the wetland scale, non-breeding black duck and mallard females apparently share a preference for thicket wetlands, especially during the moulting period. Such wetlands are frequently created by active beaver colonies (Renouf 1972, Ringelman et al. 1982, McCall, in press). This further emphasizes their importance to waterfowl during annual periods of low water levels or during dry seasons. Managing more thicket wetlands in shared breeding areas may not favour black ducks over mallards. However, information is needed on the wetland preferences of sympatric nesting black ducks and mallards on several shared breeding grounds.

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Table 2.1. Wetland selection by female mallards radio-tagged on the Harricana River, Quebec, May-August 1988-89.[1]

	Ranks of the diff in use and availability			
Bird-year	Marsh	Fen	Thicket	Swamp
Ma-88[2]	2	4	1	3
Mb-88	3	4	2	1
Ma-89[3]	4	2	1	3
Mc-89	4	3	1	2
Md-89	3	4	1	2
Me-89	4	3	2	1
Totals	20	20	8	12

[1] Rank 1 denotes the highest use availability ratio. Total number of telemetry locations analyzed = 158 Locations noted during the moulting period were excluded from the analyses as non-independent data (Alldredge and Ratti 1986) Thickets and swamps were selected (Friedman $X^2 = 45\ 96$, $P < 0.005$, Johnson $F = 221\ 0$, df = 3 and 3, $P < 0\ 001$).

[2] Mallard "a", season of observation "1988"

[3] Includes locations noted before the laying period of the 1st nesting attempt and after the 2nd nesting attempt (27 April-4 May and 27 June-12 July 1989)

Table 2.2. Wetland use by female black ducks radio-tagged on the Harricana River, Quebec, May-August 1988-89. *

	Ranks of the diff in usage and availability			
Bird-year	Marsh	Fen	Thicket	Swamp
Ba-88	3	1	4	2
Bb-89	2	4	3	1
Bc-89	3	4	1	2
Totals	8	9	8	5

* Rank 1 denotes the highest use:availability ratio. Total number of telemetry locations analyzed = 84 Locations noted during the moulting period were excluded from the analysis as non-independent data (Alldredge and Ratti 1986) According to the Friedman test (Alldredge and Ratti 1986), black ducks used wetland types according to their availability ($X^2 = 1.8$, $P = 0.727$), but preferred swamps ($P < 0.005$) according to Neu et al (1974) test Data did not satisfy the requirement of the Johnson (1980) method: number of birds > number of habitats

Table 2.3. Characteristics of smallest convex polygon and 95% ellipse home range estimates for six female mallards and three female black ducks radio-tagged on the Harricana River, Quebec, May-August 1988-89.[1]

Bird-year	Convex polygon		95% ellipse area (ha)
	Area (ha)	Linearity[2]	
Mallard			
Ma-88	302	2.6	839
Mb-88	3	6.0	10
Ma-89[3]	298	3.0	642
Mc-89	11	2.8	42
Md-89	372	6.0	1340
Me-89	318	1.6	584
Means	201.2	3.67	576.2
Black duck			
Ba-88	116	4.2	209
Bb-89	339	3.8	659
Bc-89	453	2.2	1221
Means	302.7	3.4	696.3

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[1] Black duck and mallard home range areas and linearity were not significantly different (Mann-Whitney U-test, $P > 0.10$)

[2] Index computed as maximum length divided by maximum width

[3] Home range for all reproductive stages combined.

Table 2.4. Characteristics of harmonic mean home ranges for six female mallards and three female black ducks radio-tagged on the Harricana River, Quebec, May-August 1988-89.[1]

	Area (ha)		Dist. bet activity
Bird-year	home range	IA range	centers[2] (m)
Mallard			
Ma-88	885	37	2550
Mb-88	90	90	
Ma-89[3]	621	14	1600
Mc-89	299	79	
Md-89	417	50	4800
Me-89	266	37	2500
Means	429.7	51.2	2862.5 [4]
Black duck			
Ba-88[2]	309	64	
Bb-89	541	41	2600
Bc-89	730	23	2416 7 [5]
Means	526.7	42.7	2508 3 [4]

[1] Home ranges are defined by the isoline (to the nearest 500 m) containing at least 95% of locations. The 500-m isolines define intensive activity (IA) ranges Difference between mallard and black duck harmonic home range areas were not significant (Mann-Whitney U-test, P > 0.01)

[2] When the range has only one activity center, no value is given

[3] Home range during all reproductive stages combined

[4] Mallard n = 4, black duck n = 2

[5] Mean distance between three activity centers, (3200, 2550, 1500 m)

Table 2.5. Characteristics of home ranges of a radio-tagged female mallard[1] during prelaying, laying, incubating and post-breeding periods in 1989 on the Harricana River, Quebec.

Reproductive stage	Areas (ha) HMH[2] range	 95% ellipse	 Convex Polygon	Convex Polygon linearity[3]
Prelaying	298	531	111	2 0
Laying	121	334	65	1 2
Incubation	144	601	30	3 8
Post-breeding	100	94	25	2.5

[1] Bird Ma-89.

[2] Harmonic mean home (HMH) ranges are defined by the isoline (to the nearest 500 m) containing at least 95% of locations.

[3] Computed as maximum length divided by maximum width

Figure 2.1. Harmonic mean home ranges of five non-breeding and one breeding (Ma-89) female mallards northwest of Val d'Or, Quebec. Centers of activity are indicated by solid dots. Dashed lines define the home ranges; solid lines show intensive activity ranges.

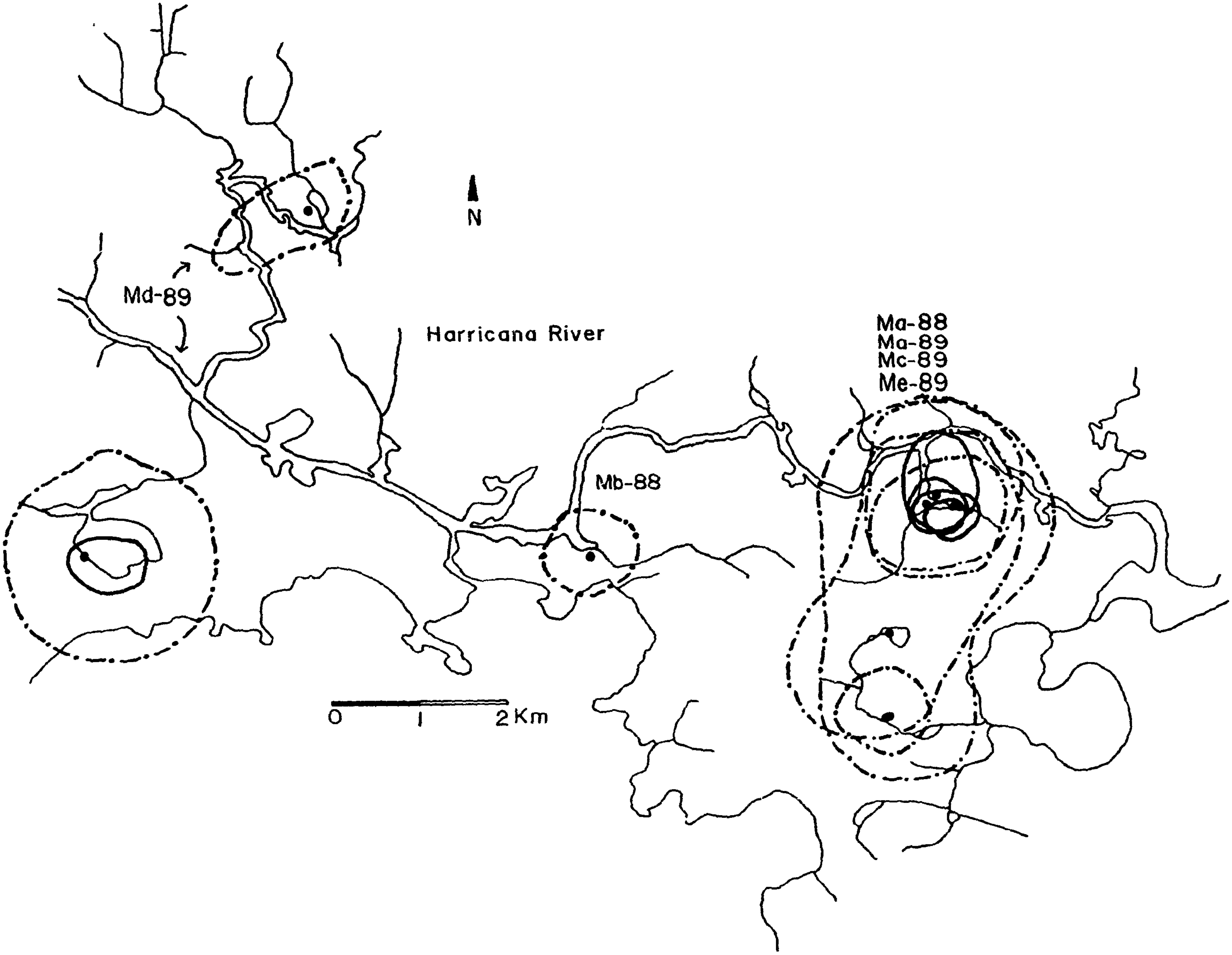
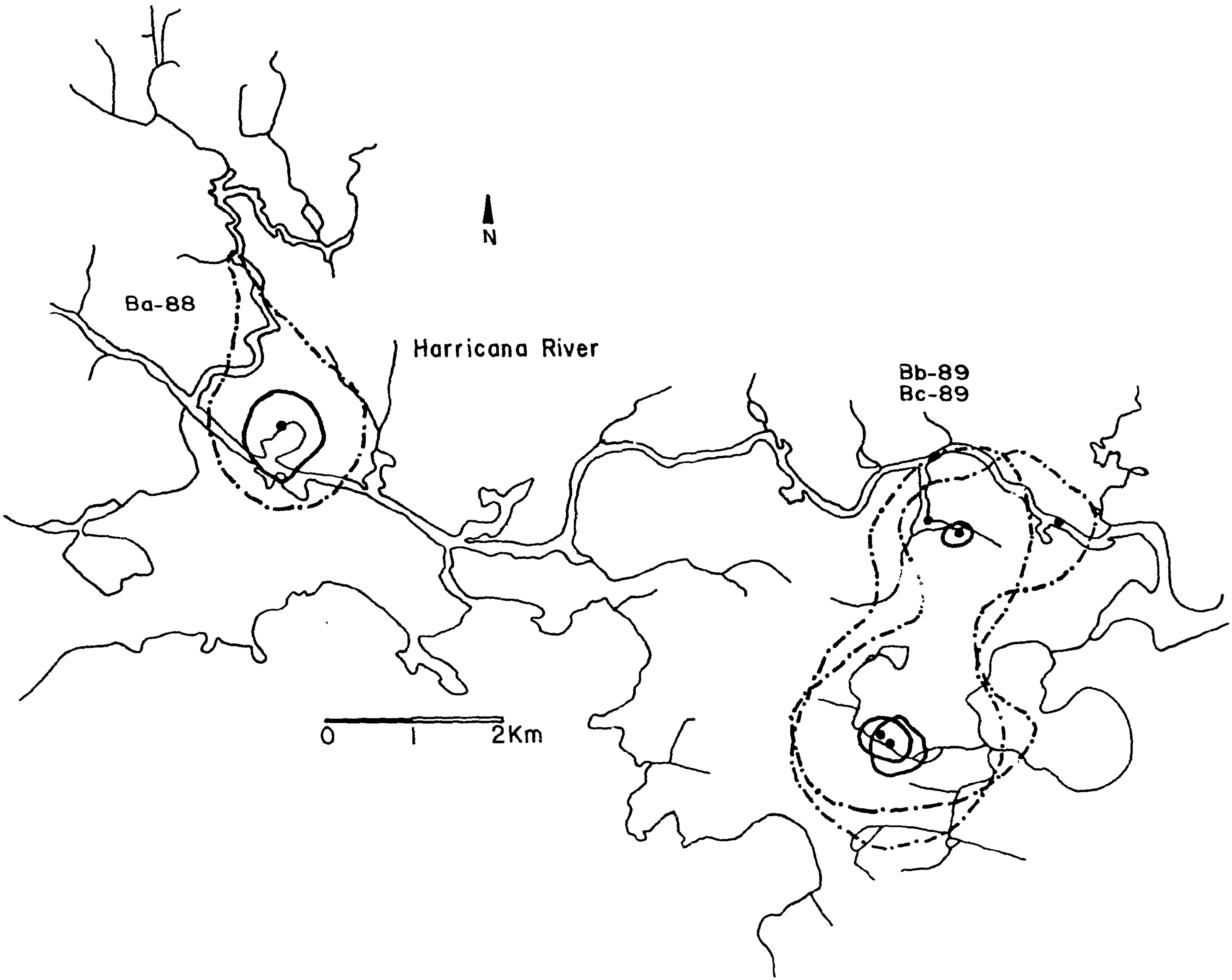

N
Md-89
Harricana River
Ma-88
Ma-89
Mc-89
Me-89
Mb-88
0
1
2 Km

Figure 2.2. Harmonic mean home ranges of three non-breeding female black ducks northwest of Val d'Or, Quebec. Centers of activity are indicated by solid dots. Dashed lines define the home ranges; solid lines show intensive activity ranges.


N
Ba-88
Harricana River
Bb-89
Bc-89
0
1
2Km

GENERAL CONCLUSIONS

At the micro-habitat scale, sympatric black duck and mallard hens with broods similarly prefer narrow-emergent areas. However, black duck broods may require more diversified habitats than mallards. Black ducks used shrub-rich areas even at very low availability. Rearing mallards seem to modify their use of habitats according to changing habitat availability.

At the wetland scale, sympatric non-breeding females of both "species" preferred swamps and thicket wetlands to fens and marshes. Ponds created by beavers are particularly important during the moulting period when water levels are low. Home ranges of six of nine females overlapped extensively.

APPENDICES

Appendix 1. Plant species by vegetation form group. Classification follows Canada/Ontario steering committee on wetland evaluation (1984) except where noted. Taxonomy follows Marie-Victorin (1964).

Vegetation form group Common name	Species name
Swamp trees	
Balsam fir	*Abies balsamea* (L.) Mill.
Birch	*Betula papyrifera* Marsh.
Poplar	*Populus tremuloides* Michx.
Spruce black	*Picea mariana* (Mill.) BSP.
Tamarack	*Larix laricina* (Du Roi) K. Koch.
Tall shrubs	
Alder	*Alnus* spp.
Dwarf-birch	*Betula pumila* L.
Red-osier dogwood	*Cornus stolonifera* Michx.
Willow	*Salix* spp.
Low-shrubs	
Bog rosemary	*Andromeda glaucophylla* Link.
Leatherleaf	*Chameadaphne calyculata* (L.) Moench
Spiraea	*Spiraea latifolia* (Ait.) Borkh.
Sheep Laurel	*Kalmia augustifolia* L.
Swamp Laurel	*K. polifolia* Wang.
Sweet gale	*Myrica Gale* L.
Patchy narrow-leafed emergents [6]	
Black-girded wool-rush	*Scirpus atrocinctus* Fernald
Bulrush	*Scirpus* spp.
Common rush	*Juncus effucus* L.
Sedges	*Carex* spp.
Water parsnip	*Sium suave* Watt.
Grasses etc.	*Zizania* spp., other mem. of Gramineae fam.
Narrow-leafed emergents	
Horsetail	*Equisetum* spp.
Spike-rush	*Eliocharis* spp.

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[6] Sub-group of narrow-leafed emergents, generally growing in drier sites and taller (1-2 m) than other narrow-leafed emergents.

Vegetation form group Common name	Species name
Robust-leaved emergents	
Larger blue-flag	*Iris versicolor* L.
Sweet-flag [7]	*Acorus Calamus* L.
Floating-submerged plants [8]	
Amphibious knot-weed	*Polygonum amphibium* L.
Broad-leaved arrow-leaf	*Sagittaria latifolia* Willd.
Bur-reed floating	*Sparganium fluctuans* (Morong) B.L. Robinson
Bur-reed narrow-leafed	*S. augustifolium* Michx.
Emerged pondweed	*Potamogeton epihydrus* Raf.
Variegated pond-lily	*Nuphar variegatum* Engelm.
Water-weed	*Elodea* spp.

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[7] Not classified in Canada/Ontario wetland evaluation (1984).

[8] Including short (less than 0.3 m above water line) broad-leafed emergents.

Appendix 2. Description of HOMERANG and DATACESS programs calculating mean distance deviation (MDD) values for harmonic mean home ranges.

HOMERANG is a short interactive program written in BASIC. This program calculates the mean distance deviation (Dixon and Chapman 1980) for each dot on an arbitrary grid. Telemetry locations are entered in X and Y format (usually UTM units), using the program function 1 (Create data file).

Data are saved separately for each animal and can be reviewed using DATACESS or analyzed again using HOMERANG function 2 (Choose data file).

The program is run using function 3 (Run program) and can be ended only at the menu call (function 4) or after it has been successfully run. It will print all deviation values, hence the printer must be ready before function 3 is called.

Functions:

(1) Create data file (coded in lines 105-210).

It first asks for a new filename (usually the radio frequency of the animal). The rame must be entered "filename.ext". It will overwrite any other file which already possesses that name. Second, the program asks for a 3-digit code number which will be needed for each X-Y locations (eg. 001). It then asks for the X coordinate of location 1 and its Y coordinate. The location code number, the X and Y are requested until 0 is entered as the X, then the menu is returned. Errors in location coordinates may be corrected by re-entering code numbers, X, and Y values.

(2) Choose data file (coded in lines 305-360).

This function is called if an already created data file must be used to run the program. If function 2 is called, function 1 must not be called and vice versa. The filename must be entered as "filename.ext".

Function 1 and 2 open a data file. The program will not run if no data file is opened and an error message will appear. The data file will be closed automatically before printing output.

(3) Run program (coded in lines 410-850).

An imaginary grid is created over all telemetry locations. The grid limits are first asked. The western limit is a positive value smaller than the smallest X coordinate in the data file. The southern limit is a positive value smaller than the smallest Y coordinate in the data file, etc. For example, if the smallest X = 110, the west limit = 100. All limits must entered using the same grid system as the coordinates (i.e., UTM).

The program then asks for the total number of locations measured for the animal. This is an opportunity to subsample n locations from the first to last-n locations, and to test the program with few calculations.

The grid reference precision sets the number of grid dots for which a MDD is calculated. One, 2, 5, and 10 are step values; the greater the value, the larger is the step to the nest dot and the smaller is the precision (and calculation time).

The program then calculates the series of MDD and cannot be stopped unless the computer is rebooted. It may take several minutes.

If the desired results are the positions of activity centers only, the program may be best run first at low precision and using a large grid. The map resulting is drawn, and the program is rerun using a smaller grid around the activity center (areas of dots with highest MDD) and set at the highest precision.

On the output, three columns are formed. The first two columns are the X and Y values of each dot on the arbitrary grid (East-West = X values, South-North = Y values). The third column is the MDD for each dot. The harmonic mean home range can then be mapped following Dixon and Chapman's (1980) instructions.

PROGRAM HOMERANG

```
10 print: print"FUNCTIONS": print
11 o$= "n"
15 rem ask functions to be performed
20 print 1,"CREATE DATA FILE"
30 print 2,"CHOOSE DATA FILE"
40 print 3,"RUN PROGRAM"
50 print: print: input "FUNCTION";function
60 if(function<1) or (function>4) then goto 70 else goto 80
70 print "BAD FUNCTION NUMBER": goto 10
80 on function goto 105,305,410,90
90 end
105 if o$= "Y" then print"FILE ALREADY OPEN": goto 20
110 rem create a new data file
115 input"ENTER NEW DATA FILE NAME";filename$
120 open"R",#1,filename$,8
130 field#1,4 as a$,4 as b$
140 input"3-DIGIT CODE";code%
150 input"VERTICAL UTM";x%:if x%=0 then goto 210
160 input"HORIZONTAL UTM";y%:print
170 lset a$=mki$(x%): rem convert to string
180 lset b$=mki$(y%): rem and save in file
190 put#1,code%
200 goto 140
210 o$= "Y";goto 20
305 if o$= "Y" then print"FILE ALREADY OPEN":goto 20
```

```
310 rem open an already created file
320 print:input"ENTER FILE NAME (USING "s)";filename$
330 print: o$= "y"
340 open"r",#1,filename$,8
350 field#1,4 as A$,4 as b$
355 print"FILE",filename$,"NOW OPEN"
360 goto 20
410 input"WEST LIMIT";west%
420 inpu"EAST LIMIT";east%
425 input"SOUTH LIMIT";south%
430 input"NORTH LIMIT";north%
450 input"TOTAL NUMBER OF LOCATIONS ON THAT BIRD";p%
460 print:print"GRID REFERENCE PRECISION"
470 input"ENTER INTEGER 1,2,5,10";z%
510 rem calculates maximum grid length
520 maxrv%=east%-west%: maxrh%=north%-south%
530 rem dimensions of array variables
540 dim x(maxrv%,p%): dim y(maxrh%,p%)
550 dim r(p%): dim mo(maxrv%,maxrh%)
600 rem calculates x and y
610 for gv%=west% to east% step z%
615 rgv%=gv%-west%
620 for gh%=south% to north% step z%
625 rgh%=gh%-south%
630 for code%=1 to p%
640 get#1,code%
650 x(rgv%,code%)=abs(cvi(a$)-gv%)
660 y(rgh%code%)=abs(cvi(b$)-gh%)
670 next code%
680 next gh%
690 next gv%
700 calculates r and mean distance deviation
720 for gv%=west% to east% step z%
```

```
725 rgv%=gv%-west%
730 for gh%=south% to north% step z%
735 rgh%=gh%-south%
737 invr=0
740 for code%=1 to p%
745 rem Pithagore theorem
750 ifx(rgv%,code%)=0 and y(rgh%,code%)=0 then r(code%)=0
else r(code%)=sqr(x(rgv%,code%)^2+y(rgh%,code%)^2)
755 if r(code%)<1 then r(code%)=r(code%)+1
800 invr=invr+(1/r(code%))
810 next code%
820 mo(rgv%,rgh%)=1/((1/p%)*invr)
830 next gh%
840 next gv%
850 close#1:o$= "N"
910 rem output of mean distance deviation per grid point
920 lprint:lprint"OUTPUT":lprint
930 lprint"UTM GIVEN AS ON MAP"
940 lprint"WEST-EAST","SOUTH-NORTH","DEVIATION"
950 for gh%=south% to north% step z%
960 rgh%=gh%-south%
970 for gv%=west% to east% step z%
980 rgv%=gv%-west%
990 lprint gv%,gh%,mo(rgv%,rgh%)
991 next gv%
992 next gh%
995 goto 90
```

PROGRAM DATACESS

```
5 input"DATA FILE TO ACCESS"; filename$
6 input "NUMBER OF LOCATIONS TO RETREIVE";p%
10 open"r",#1,filename$,8
20 field#1,4 as a$,4 as b$
```

```
25 lprint"CODE","VERT. UTM","HORI. UTM"
30 for code%=1 to p%
40 get#1,code%
50 lprint code%,cvi(a$),cvi(b$)
70 next code%
80 end
```

LITERATURE CITED

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.