Mallard Brood Movements and Wetland Selection in the Canadian Prairie Parklands

By

Garnet Harold Raven

A Thesis Submitted to the
Faculty of Graduate Studies of the University of Manitoba
in Partial Fulfillment of the Requirements
for the degree of

Master of Science

Department of Zoology

January 2004

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES
*****
COPYRIGHT PERMISSION

Mallard Brood Movements and Wetland Selection in the Canadian Prairie Parklands

BY

Garnet Harold Raven

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of

Manitoba in partial fulfillment of the requirement of the degree

Of

MASTER OF SCIENCE

Abstract

Nest success is the most important determinant of population growth in prairie waterfowl, and tremendous resources have been allocated to increasing nest success as part of the North American Waterfowl Management Plan. Although brood survival is also important to mallard (*Anas platyrhynchos*) recruitment rates, knowledge of brood ecology is severely lagging relative to nest success. My study addresses this information gap by exploring mallard brood movements and wetland selection. An increased understanding of mallard brood behaviour will allow landscape management decisions to be more considerate of brood needs, and should lead to greater recruitment.

Data were collected in conjunction with the Prairie Habitat Joint Venture (PHJV) Assessment project from 15 65-km^2 study areas located throughout the Canadian prairie parklands. A total of 308 mallard broods were radio-tracked from hatch until 30-days post-hatch. Models were constructed to predict movement probability (repeated-measures logistic regression) and movement distance (ANCOVA) of broods in relation to brood age, date, and study area. A backwards-elimination procedure was used to simplify models by eliminating non-significant ($P > 0.05$) effects. Models also were constructed to predict wetland selection in relation to wetland permanence, cover type, width of flooded emergent vegetation, brood age, date, dominant vegetation, and percent of seasonal wetlands inundated with water. Information-theoretic techniques were used to select the best fitting models.

Movement probability generally decreased with age, although results varied by hatch date and study area. Later hatched broods moved farther than early hatched broods. Permanence, cover type, the width of flooded emergent vegetation, and the dominant species of vegetation were all important predictors of wetland selection. More permanent wetlands were preferred to ephemeral wetlands, especially in the late brood-rearing season. Semipermanent wetlands dominated by bulrush (*Scirpus* spp.) were preferred, whereas semipermanent wetlands dominated by cattail (*Typha* spp.) were avoided. Seasonal wetlands dominated by sloughgrass (*Beckmannia syzigachne*) were also avoided.

Future management of habitats to enhance duck nest success should also consider brood survival. Based on my results, mallards clearly prefer wetlands with adequate water and flooded emergent cover. These habitat requirements can most easily be met by providing upland nesting habitat in landscapes that already contain an abundance and diversity of natural wetland habitats. Where such wetlands are unprotected and vulnerable to drainage, additional management efforts aimed at wetland protection should be encouraged. Finally, where upland nesting cover and duck populations are abundant, but suitable brood habitat is limiting, restoration or management of more permanent wetlands may be necessary to meet the habitat requirements of ducklings.

Acknowledgements

I gratefully acknowledge the Institute for Wetland and Waterfowl Research, the research arm of Ducks Unlimited Canada, for providing funding for this research. Use of a computer and office space at Ducks Unlimited headquarters was also greatly appreciated. I would like to thank everyone from the Institute at Oak Hammock Marsh for allowing me to feel like part of the group during my research and thesis preparation.

Several people had input on this research in the early planning stages, and I would like to acknowledge Dr. Mike Anderson and Jim Devries for initial ideas. Dave Howerter was instrumental in many facets of the study, from initial planning to data censoring, from GIS data retrieval to statistical analyses, and finally as a committee member. Dave always made time for my questions, even when he was swamped with his own problems. Llwellyn Armstrong helped immensely in statistical analyses, making difficult concepts comprehensive, and I am truly grateful for her insight.

Committee member Dr. Jim Hare was very helpful with any academic questions I had and always made himself available for my inquiries regarding university requirements; this was all disposed with a cheerful and encouraging attitude for which I am thankful. I also thank Dr. Rick Baydack for serving on my committee and making himself available whenever needed.

I am indebted to Dr. Todd Arnold for serving as my principle advisor and guiding me through the graduate experience. Todd's academic and scientific knowledge and experience allowed me to relax and focus on my research. Todd did not allow his move to Minnesota, in the midst of my studies, to affect his superb leadership. He always made

me feel like my research was as important to him as it was to me, and for that I am appreciative.

I would like to give a big thank you to everyone who contributed to the assessment study and specifically to the collection of data used in my thesis. More than 100 assistants worked diligently to collect these data, and I thank them for a job well done.

Thank you to my mother who has always been very supportive of my academic pursuits and gave me the confidence to believe I was capable of anything I chose.

Thank you to my father for instilling in me a love of nature, wildlife and outdoor pursuits that have fueled both my life and career. A better gift could never be given.

Last but not least I would like to thank my best friend and wife, Mary. She encouraged me to follow my heart and gave me her assurances that I had her support in whatever endeavors I wished to pursue. Mary gave me the will to begin, the motivation to continue, and the drive to finish this chapter of our lives. Mary, you are my rock.

Table of Contents

List of Figures

List of Tables

List of Appendices

CHAPTER 1: INTRODUCTION

The Prairie Pothole Region and Waterfowl Production

Abundant small wetlands in the prairie landscape of south-central Canada and the north-central United States were formed from melting ice following the last ice age. This wetland-pocketed landscape is known as the Prairie Pothole Region (PPR), and historically it has been the most important duck breeding area in North America, supporting 50-80% of the continent's surveyed duck population in any given year (Batt et al. 1989). The Canadian prairie parklands comprise the northern section of the PPR, a transitional zone dominated by increasing coverage of aspen trees (*Populus tremuloides*) that separates the (historically) treeless southern prairies from the northern boreal forest.

Historically, the plant communities of the PPR were influenced primarily by wild fires and grazing by bison (*Bison bison*), but these factors ceased to be important following European settlement, leading to invasion by aspen and other woody vegetation. Modern agriculture, however, has had the greatest impact on the prairie landscape since settlement. Cattle have replaced bison on most of the prairies, and many studies show that cattle are detrimental to the native flora, especially around wetlands (Hamilton 1996, Biondini et al. 1999, Knapp et al. 1999). In addition, ranchers often have replaced native plant species with introduced (and often invasive) species such as smooth brome (*Bromus inermis*), crested wheat grass (*Agropyron cristatum*), and alfalfa (*Medicago sativa*). Even more importantly, vast areas of native vegetation have been converted to annual crops, with losses exceeding 80% in many areas of the PPR (Turner et al. 1987). Agriculture also has had a tremendous impact on the wetland community of the PPR; up to 70% of wetlands in prairie Canada have been drained or tilled for crop production (Lands

Directorate 1986, National Wetlands Working Group 1988). Shallow wetlands often are targeted for these operations, resulting in a disproportionate decrease in the number of temporary and seasonal wetlands on the landscape.

The wildlife community of the prairies has changed in concert with the landscape changes and other human influences. Gray wolves (*Canis lupus*) and plains grizzly bears (*Ursus horribilis*), once the dominant predators of the prairies, have been extirpated and replaced by mesocarnivores such as red foxes (*Vulpes vulpes*) and raccoons (*Procyon lotor*), whose smaller size may make them more efficient as waterfowl predators (Sargeant and Raveling 1992). The construction of stock-watering ponds has allowed mink (*Mustela vison*), an efficient predator of ducks and ducklings (Krapu et al. 2000), to colonize areas where insufficient permanent water previously precluded them. Additionally, increasing aspen has resulted in an increased number of perch and nesting sites for avian predators such as great horned owls (*Bubo virginianus*), Swainson's and red-tailed hawks (*Buteo swainsonii* and *B. jamaicensis*), and American crows (*Corvus brachyrhynchos*).

This altered landscape may have rendered duck populations more susceptible to environmental influences. By the mid 1980's a prolonged dry spell on the prairies had exacerbated the effects of a changing landscape, and duck populations declined to levels well below those seen in the previous decade (Canadian Wildlife Service and U.S. Fish & Wildlife Service 1986). Hatching rates and brood survival are important for maintaining duck populations (Johnson et al. 1987, Hoekman et al. 2002), and hence the losses of upland nesting habitats and brood-rearing wetlands to agriculture were believed to be the dominant factors contributing to population decreases in the Canadian parklands (Clark and Nudds 1991, Beauchamp et al. 1996).

In an effort to reverse continental declines in duck populations, the governments of Canada and the United States formed the North American Waterfowl Management Plan (NAWMP) in 1985 (Mexico joined the partnership in 1994). The goals of NAWMP focus on creating landscapes that can support self-sustaining duck populations representative of average population levels recorded during the 1970's.

Numerous government and non-government organizations have formed regional partnerships to accomplish the goals of NAWMP. The largest of these partnerships, or joint ventures, is the Prairie Habitat Joint Venture (PHJV), which focuses on the Canadian PPR (Prairie Habitat Joint Venture 1986). Although Alberta, Saskatchewan, and Manitoba each developed separate plans for addressing waterfowl production problems within their respective provinces, all three provincial plans focused on low nesting success as a result of loss and fragmentation of upland nesting habitat. Upland habitat programs included purchase or lease of annually cultivated cropland and replacing the annual crops with mixtures of perennial grasses and legumes, which were believed to provide more dependable nesting cover for breeding ducks. Financial incentives also were given to landowners to modify their annual cropping practices in ways thought to benefit waterfowl (e.g., no-till and minimum till agriculture, winter versus spring wheat). Habitat programs also targeted existing perennial cover. Such programs included paying producers to delay haying operations until after 15 July, when the majority of nesting ducks have already hatched, or rotating cattle grazing schedules among multiple paddocks to increase nesting cover for waterfowl. These habitat programs were targeted to areas with historically high densities of breeding waterfowl. Ducks Unlimited Canada has been the single largest organization delivering PHJV habitat programs, but numerous other federal, provincial, and non-governmental organizations also have been involved in the PHJV.

The PHJV Assessment Project

To quantify the effectiveness of PHJV habitat programs, Ducks Unlimited Canada initiated a large-scale research project known as the Prairie Habitat Joint Venture Assessment in 1993 (Anderson et al. 1995). The PHJV Assessment focused on duck nesting patterns because low nesting success was thought to be the most important factor limiting dabbling duck production in the PPR (e.g., Cowardin and Johnson 1979, Cowardin et al. 1985). However, knowledge concerning brood ecology was severely lacking during the planning stages of the PHJV Assessment. In fact, the mallard (*Anas platyrynchos*) productivity model (Johnson et al. 1987, Cowardin et al. 1988) used to plan for delivery of PHJV habitat programs modeled duckling survival as a constant because reliable predictors of duckling survival were lacking. However, Ducks Unlimited biologists involved in Assessment planning recognized this information gap and consequently designed their study to collect brood survival data in addition to nesting information. Subsequent research has shown that duckling survival trails only nesting success and breeding female survival in affecting the annual population dynamics of prairie mallards (Hoekman et al. 2002).

The PHJV Assessment study monitored 3,618 radiomarked mallard females on 27 Assessment sites between 1993 and 2000 (typically 135-137 females per site). I was involved in the Assessment study as a Research Technician in 1997, a Research Crew

Leader in 1998 and 1999, and a Research Site Leader in 2000. Sites typically encompassed 25 legal sections (65.1 – 68.0 km^2, except one site was 55.4 km^2 and another was 80.4 km^2) and were studied for a single year. Radio-marked females were captured prior to the nesting season and were monitored daily through most of the brood-rearing period (typically until ducklings reached 30 days of age). Included with these radiotracking histories were data on duckling survival, brood movements, and wetland habitat characteristics. The extensive temporal and spatial nature of these data allowed for an unprecedented opportunity to analyze mallard brood movements and wetland habitat selection.

Mallard Brood Ecology

Mallard brood movement patterns evolved over thousands of generations in a prairie landscape that has only recently been affected by modern agricultural activities. Since settlement by immigrants began, roughly a century ago, many wetlands have been drained and native upland vegetation has been cultivated and converted to annual croplands. Understanding the factors influencing brood movements in this altered landscape is critical to ongoing waterfowl management efforts.

Overland movements by mallard broods are more frequent when the ducklings are young (Talent et al. 1982). Mortality also appears to be higher during this time (Ball et al. 1975, Talent et al. 1983, Orthmeyer and Ball 1990, Rotella and Ratti 1992a), suggesting a possible relationship between movements and survival. Discovering what factors affect the frequency or distance of movements may help explain the relationship between movements and survival.

Habitat use and availability can also influence duckling survival (Rotella and Ratti 1992a). Mallard broods do not always select the wetland nearest their nesting location (Dzubin and Gollop 1972, Cowardin et al. 1985), and they move frequently even though their previous wetland still retains water (Talent et al. 1982, Rotella and Ratti 1992b), indicating that some sort of habitat selection process is involved. It is assumed that organisms will select habitats that maximize their fitness, although tests of this assumption are rare (Clark and Shutler 1999, Morris and Davidson 2000). Understanding the selection processes that mallards use when selecting brood habitat would allow managers to make better informed decisions concerning protection or enhancement of wetland and associated upland habitats, thereby improving brood survival and overall population recruitment.

Previous studies of habitat selection by mallard broods may provide some clues as to what factors are important in the selection process. The amount or species composition of emergent vegetation may help explain patterns of brood use (Berg 1956, Lokemoen 1973, Mack and Flake 1980, Talent et al. 1982). The dominant vegetation of a wetland is related to permanence (i.e., hydroperiod, or typical depth and duration of flooding; Steward and Kantrud 1971, Grosshans 2001). However, there has been disagreement about how wetland permanence affects wetland selection by broods, with both seasonal (Talent et al. 1982, Duebbert and Frank 1984) and more permanent wetlands (Stoudt 1971) being identified as most important. The dominant vegetation of a wetland may help clarify why this discrepancy exists. Stoudt (1971) indicated that open water also may be important to wetland selection by broods, and hence habitat quality might vary according to wetland cover type (Stewart and Kantrud 1971), which describes different patterns of juxtaposition between emergent cover and open water.

In summary, the principle objective of my study was to determine key factors influencing resource-use decisions by mallard broods, which in turn are likely to influence duckling survival. Brood survival is a very important vital rate affecting rate of population change in mallards (Hoekman et al. 2002), but it is one of the least studied components of the mallard's life cycle. Despite its importance, knowledge of brood behaviour is difficult to obtain because mallard hens accompanied by ducklings are very secretive and, thus, are difficult to observe by conventional means. By increasing our understanding of brood decisions pertaining to movements and habitat selection, future landscape management can be more considerate of the habitat needs of mallards (and other related duck species) during the brood-rearing period.

Thesis Organization

The PHJV Assessment project comprised 27 different study sites between 1993 and 2000 (2 – 4 sites per year). However, only the 15 study areas completed between 1993 and 1997 were included in this study, as it was hoped to associate these analyses with concurrent analyses of brood and duckling survival being conducted by another investigator (D. Howerter, unpubl. data). Although it would have been interesting and informative to correlate patterns of movement and habitat selection with subsequent survival, such analyses could not be included in my thesis because they are included within another investigation.

Chapter 2 of my thesis deals with movement patterns exhibited by mallard broods on 15 PHJV Assessment sites located throughout the Canadian prairie parklands, whereas

Chapter 3 investigates the wetland selection process exhibited by these same broods. Finally, Chapter 4 summarizes my most important findings and provides key management recommendations.

Chapters 2 and 3 were each written as stand alone manuscripts in anticipation of submission to scientific journals. Chapter 2 is intended for the Canadian Journal of Zoology and utilizes a more traditional statistical format that involves model fitting via formal hypothesis testing, whereas Chapter 3 is intended for The Journal of Wildlife Management and utilizes a newer model-fitting approach that involves information theory (Anderson and Burnham 2002). Although this results in some methodological inconsistencies between chapters, it provided me with the opportunity to utilize and gain familiarity with both of these commonly used statistical methods. Despite the different statistical approaches to model fitting, there was complete overlap in study areas and methods of data collection, and hence there is some overlap and repetition between these two chapters, most notably in the methods sections.

CHAPTER 2: MALLARD BROOD MOVEMENTS IN THE CANADIAN PRAIRIE PARKLANDS

Introduction

Brood survival is one of the most important determinants of population growth in mallards (Cowardin and Johnson 1979, Hoekman et al. 2002). But to manage a landscape for increased brood survival, waterfowl managers must first understand the survival strategies employed by broods. The prairie parkland region of Canada has been highly modified by agriculture (Turner et al. 1987), with up to 70% of wetlands having been drained since European settlement (Lands Directorate 1986, National Wetlands Working Group 1988). Understanding how altered landscapes influence brood movement patterns and distinguishing important factors influencing these movements is important for waterfowl management within this highly modified landscape.

The majority of duckling mortality occurs during the first two weeks post-hatch (Ball et al. 1975, Talent et al. 1983, Orthmeyer and Ball 1990, Rotella and Ratti 1992a). This also is the period when most overland movement occurs (Talent et al. 1982), but it is not clear whether this is cause or effect. Movements may be a response to duckling losses (i.e., as females attempt to move their offspring to safer habitats), or alternatively, losses may occur as a result of movements (e.g., loss and separation of young ducklings, or predation during overland movements; Talent et al. 1983, Rotella and Ratti 1992a). Talent et al. (1983) found that little mortality occurred during overland moves, whereas others observed that movement distance and survival were negatively correlated (Ball et al. 1975, Rotella and Ratti 1992b). Exploring factors affecting frequency and distance of moves by mallard broods may clarify how survival is related to interwetland movements.

Several studies have found that mallard broods hatched early in the season have a greater chance of survival than late-hatched broods (Orthmeyer and Ball 1990, Rotella and Ratti 1992a, Sayler and Willms 1997, Krapu et al. 2000; but see Mauser et al. 1994a). This might occur because late-hatched broods have to move farther or more frequently because wetlands are more likely to become dry later in the season. Knowledge of how brood movements change as the season progresses may increase our understanding of these seasonal patterns in survival.

A brood's location may represent a tradeoff between safety (from predators and the elements) and food resources. If the wetland a brood currently occupies does not meet its needs and a more suitable alternative is available, then a movement may be warranted. Longer moves presumably increase the risk of predation while traveling overland (Ball et al. 1975, Rotella and Ratti 1992a), but longer moves are likely to be beneficial because they increase the number of available wetlands. If more wetlands are available, broods will have a greater selection of ponds from which to chose, hence wetlands with better brood-rearing habitat should be available. Perhaps there is a distance at which the risks incurred during a move outweigh the benefits a move typically can provide. This distance may vary according to brood age or date.

Ball et al. (1975) and Rotella and Ratti (1992b) reported a negative correlation between number of surviving ducklings and distance of overland travel, thus hinting that overland moves by ducklings were costly. However, Dzus and Clark (1997) found no correlation between length of first move and duckling mortality, or between total distance traveled over the first 14 days post-hatch and duckling mortality. Likewise, Talent et al. (1983) found that few ducklings and no entire broods were lost during overland moves.

This lack of agreement on cost of overland moves by broods suggests that other factors may be important. Duckling mortality during overland moves may be a function of vegetation and terrain (Talent et al. 1983, Rotella and Ratti 1992a). If vegetation density can help protect ducklings from the elements or predators, then it also may affect brood movements. Time of season affects density and concealment of upland vegetation and consequently may affect seasonal strategies of brood movements.

Characteristics or distribution of local wetlands may influence the frequency and distance of moves. Rotella and Ratti (1992b) found that distance of first moves increased in areas of lower wetland density. Regional moisture levels have been indexed as the percentage of seasonal wetlands holding water (Krapu et al. 2000), and this index has been shown to be positively correlated with brood survival (Rotella and Ratti 1992a, Krapu et al. 2000). Seasonal wetlands show the most variation in abundance and therefore are thought to be the best indicators of local moisture levels (Krapu et al. 1997). However, semipermanent wetlands are more likely to retain water during the brood-rearing period and may be better indicators of brood habitat (Stoudt 1971).

Based on my review of the literature, I predicted that brood age would be an important predictor of movement frequency, with younger broods moving more often than older broods. Also, I believed that broods hatched later in the season would have a lower probability of moving due to decreasing wetland availability caused by drying wetlands late in the season. However, due to decreasing wetland densities and increased upland cover, I expected moves to be longer as the season progressed and as ducklings aged. Using similar logic, I predicted that later hatched broods would move farther from the nest than early hatched broods.

Methods

Study Areas

The Prairie Habitat Joint Venture (PHJV) Assessment Project is described in Chapter 1. Study areas used in this analysis included 15 PHJV Assessment study sites sampled from 1993 through 1997. These included two sites in 1993 (Punnichy, SK; and Hamiota, MB), three sites each in 1994 (Erskine, AB; Davis, SK; and Belmont, MB), 1995 (Shoal Lake; MB, Kutawa, SK; and Camp Lake, AB), and 1996 (Pine Lake, AB; Parkside, SK; and Baldur, MB), and four sites in 1997 (Willowbrook SK; Mixburn, AB; Elnora, AB; and Allan Hills West, SK) (Figure 2.1).

Data Collection

Approximately 135 pre-laying female mallards were decoy trapped (Sharp and Lokemoen 1987, Ringelman 1990, Paquette et al. 1997) at each Assessment Site (only 111 at Hamiota, 123 at Punnichy, 127 at Kutawa). Each hen was weighed, measured, and banded and received an implanted 22g radio-transmitter intra-abdominally (Olsen et al. 1992, Rotella et al. 1993, Paquette et al. 1997). Anchored backpack radio attachments were used on several hens at Camp Lake, Erskine, Hamiota, Kutawa, and Shoal Lake, but any effects on brood behaviour caused by these alternative transmitters are presumed to be slight (Paquette et al. 1997). Radioed hens were intensively tracked throughout the breeding season to document their nesting histories (see Paquette et al. 1997, Hoekman et al. 2002 for additional detail). Any females that hatched their nests were eligible to become part of this study.

Nests of non-radioed mallards also were found through nest searches conducted using ATV-towed cable-chain drags, hand-held rope drags, or beat-outs (Higgins et al.

Figure 2.1. Locations of the 15 PHJV Assessment study sites used to evaluate mallard brood movement patterns in the Canadian prairie parklands.

1977, Klett et al. 1986, Paquette et al. 1997). Small, portable fences often were erected around these nests to reduce the risks of mammalian predation (Sargeant et al. 1974). These hens were trapped at approximately 20 days of incubation using mist nets (Bacon and Evrard 1989), purse traps (modified from Coulter 1958), automatic nest traps (Weller 1957), and walk-in traps (Dietz 1994). These hens also were weighed, measured and banded, but were fitted with an 8 g anchored backpack transmitter (Mauser and Jarvis 1991, Paquette et al. 1997). All research procedures were approved by the University of Saskatchewan's Protocol Review Committee on Animal Care and Supply (Protocol number 920007).

Each nesting hen was radio-tracked daily until hatch, at which time the nest was visited to determine the number of ducklings that had hatched. At least one radio location per day was collected during brood rearing, unless a movement between wetlands had occurred since the previous location, in which case two daily locations were collected. Counts of surviving ducklings were obtained as soon after hatch as possible, and every week thereafter until ducklings were 30 days old. Brood counts were conducted from a distant vantage point without disturbing the brood.

Telemetry locations were collected using a truck-mounted null array system (Paquette et al. 1997). The wetland being used by the brood was determined through triangulation from known locations. If telemetry error polygons encompassed more than one wetland, the actual wetland was verified by approaching and triangulating with a handheld antenna.

In July or August aerial photographs of each study site were taken at a scale of 1:5000. Stereo pairs of photos were used to delineate and digitize habitat maps for each study site. Each site's digitized map was then imported into SPANS geographical information system (GIS; PCI Geomatics, Richmond Hills, Ontario, Canada) where a wetlands data layer was constructed. Each wetland was uniquely numbered to allow merging with the brood tracking data in SPANS. Universal Transverse Mercator (UTM) locations were given to each wetland and each brood location. If the wetland was less than 5 hectares (ha), the brood was assigned to the centroid of the pond. But if the wetland was larger than 5 ha, a more accurate brood location was used when available. The resulting dataset included a brood hen's geographic location at specific times for each day the hen was tracked.

The data were censored to include only broods that were tracked for at least 29 days after leaving the nest. The exact time of hatch was unknown, but ducklings usually leave the nest one day after hatch (Weller 1964). Therefore brood hens were usually tracked until their ducklings were 30 days old. Locations of brood hens more than 30 days post-hatch were removed from analysis because hens spend increasing amounts of time away from their broods (Talent et al. 1983), and hence their locations are not necessarily indicative of the location of their broods. To remove bias caused by tracking hens that had lost their broods, only hens that had ≥ 1 duckling survive to 30 days of age were included in the analysis.

Following these censoring decisions, 308 broods remained for analysis from the 15 study sites. Straight-line movement distances for these broods were calculated using UTM locations and the Pythagorean formula. I disregarded movements of more than 300 m, where the hen returned to the initial wetland the following day. Mallard hens are known to leave their broods for short periods of time each day (Rotella and Ratti 1992b, Pietz and Buhl 1999), and I believed these longer round-trip moves were of the hen and not the brood. A brood's first move was calculated using the UTM locations of the nest and the first brood wetland. I also measured the straight-line distance from the nest to the brood's final location at 30 days post hatch and calculated the accumulated distance of all moves made by a brood between hatch and 30 days post hatch.

Data Analysis

Movement Probability

A repeated-measures logistic regression analysis (PROC GENMOD; SAS Institute 1996) was used for modeling the probability of movement as a function of brood age, hatch date, study area, and all second-order interactions. A backwards-elimination procedure was used to simplify this initial model. I deleted non-significant ($P > 0.05$) variables, beginning with the highest P-value, until all remaining variables were either significant or included within a significant interaction, provided that the overall model was also significant at $P < 0.05$.

Movement Distance

I first attempted to model all brood movements in aggregate. Distances were $\log_e$-transformed to help normalize the responses. An analysis of covariance (ANCOVA) with individual broods treated as random effects was used to model movement distance as a function of brood age, hatch date, study area, and all second-order interactions among these variables. I also included brood-age^2 and hatch-date^2 in the model in case relationships with these variables were curvilinear (Anderson and Burnham 2002). An ANCOVA is appropriate when both categorical (i.e., study area) and continuous (i.e, brood age and hatch date) variables are included in the modeling process. Using a mixed model, with individual broods treated as random effects, accounted for the non-independent nature of multiple movements by the same brood. A backwards-elimination procedure similar to that described for movement probability was used to simplify this model.

A similar procedure was used to model: 1) first move distance of broods, 2) the straight-line distance from nest to day 30 location, and 3) the accumulated distance of all moves made by each brood between hatch and 30 days of age. Brood age was not a covariate in these models and individual broods were not treated as random effects because only one distance was included for each brood, but otherwise the modeling procedure was identical to that described for aggregate moves. All distance analyses were performed using PROC MIXED (SAS Institute 1996).

Results

A priori analyses:

My data included 308 individual broods that made a total of 2,345 interwetland movements from hatch through 30 days of age. The mean movement distance was 341 m (SD = 340: minimum = 9 and maximum = 5,543 m). Over 95% of brood movements were less than 1 km.

The daily probability of brood movements was a complex function of study area, brood age, brood age squared, Julian hatch date (e.g., 1 July = 182), a brood age by hatch date interaction, and a brood age by study area interaction (Table 2.1). The effect of brood age on movement probability varied among study areas (Figure 2.2), but almost all study sites showed pronounced declines in movement probability as broods became

Table 2.1. Factors affecting daily movement probabilities of 308 mallard broods on 15 study areas in the Canadian prairie parklands. Non-significant ($P > 0.05$) factors were deleted from the final model unless they were contained within a significant interaction effect. Predictive equations from the final model are plotted in Figure 2.2.

Factor[a]	**df**	χ^2	**P**
Brood Age	1	0.26	0.61[b]
Brood Age ^{2}	1	39.69	< 0.0001
Hatch Date	1	1.53	0.22[b]
Hatch Date ^{2}	1	0.06	0.81
Study Area	14	34.61	0.0017
Brood Age * Hatch Date	1	14.47	0.0001
Brood Age * Study Area	14	28.05	0.014
Hatch Date * Study Area	14	17.38	0.24

[a] Factors listed in bold type were part of the final model.

[b] Although these two variables were not significant, they were contained within significant higher-order interactions and were therefore retained in the final model.

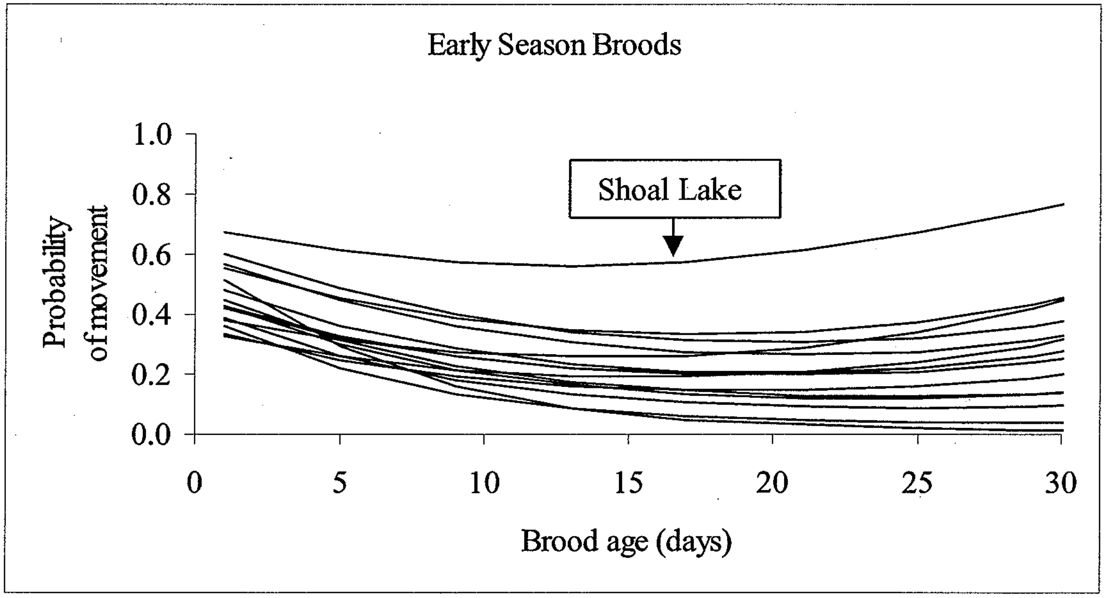
older. The Shoal Lake study site was an obvious exception to this pattern, and this site contributed substantially to the age by study area interaction. The relationship between brood age and movement probability was strongly quadratic, with the probability of movement decreasing rapidly with brood age during the first 2 weeks of brood rearing, but flattening out during the following 2 weeks (Figure 2.2). There was also a pronounced age by hatch date interaction, with age exhibiting a much stronger effect on movement probability as the brood-rearing season progressed (Figure 2.2).

Mean movement distance was a function of study area, brood age, hatch date, and a study-area by brood-age interaction (Table 2.2). The effect of brood age on mean movement distance varied by study area, but most of this effect seemed to occur at only one study area, Camp Lake (Figure 2.3). Hatch date was positively correlated with movement distance, with later hatched broods making longer movements than early hatched broods.

First move distances averaged 353 m (SD = 388). The maximum first move was 2,354 m, but 95% of moves were less than 1 km. First move distance was positively correlated with hatch date (Table 2.3; $\log_e$(first move distance) = 3.8533 + 0.009291 * Hatch Date; $R^2 = 0.03$), but no other variables were significant (Table 2.3).

The straight-line distance between the nest and a brood's location at 30 days post-hatch averaged 760 m (SD = 612). The maximum 30-day distance was 3,718 m, but over 95% of the distances were < 2 km. The straight-line distance traveled from the nest to a brood's location 30 days post-hatch was a positive function of hatch date (Log_e(30-day distance) = 4.9339 + 0.007914 * Hatch Date; $R^2 = 0.02$), but no other variable affected this relationship (Table 2.4).

Figure 2.2. Study-area specific response of predicted probability of movement as a function of age for early hatched mallard broods (top) and late hatched mallard broods (bottom) in the Canadian prairie parklands. Early hatched broods are represented by a Julian hatch date of 150 (30 May). Late hatched broods are represented by a Julian hatch date of 190 (9 July). Shoal Lake, MB differed markedly from all other study areas and is individually labeled in each figure.



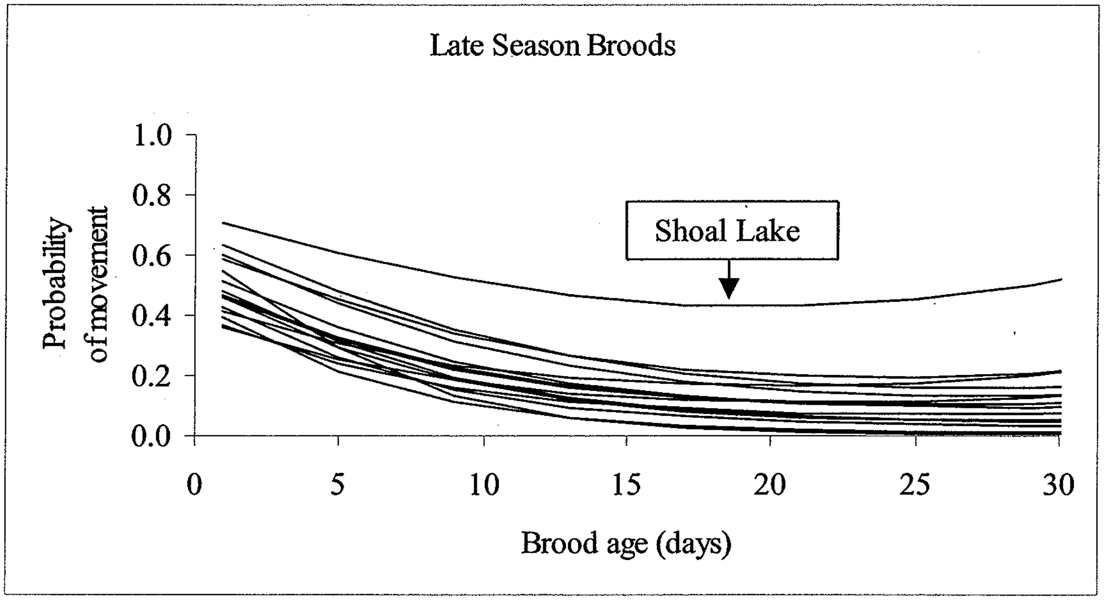


Table 2.2. Factors affecting mean interwetland movement distances (N = 2,345) of 308 mallard broods on 15 study areas in the Canadian prairie parklands. Non-significant ($P > 0.05$) factors were deleted from the final model unless they were contained within a significant interaction effect. Predictive equations from the final model are plotted in Figure 2.3.

Factor[a]	**df**	**F**	**P**
Brood Age	1	2.33	0.13[b]
Brood Age ^{2}	1	0.91	0.34
Hatch Date	1	4.28	0.04
Hatch Date ^{2}	1	0.52	0.47
Study Area	14	1.82	0.03
Brood Age * Hatch Date	1	1.38	0.24
Brood Age * Study Area	14	2.39	0.003
Hatch Date * Study Area	14	1.50	0.11

[a] Factors listed in bold type were part of the final model.

[b] Although this variable was not significant, it was contained within significant higher-order interaction.

Figure 2.3. Predicted movement distance by mallard broods as a function of age. Each plotted line represents a different study area (Camp Lake, AB was the most atypical site and is individually labeled).

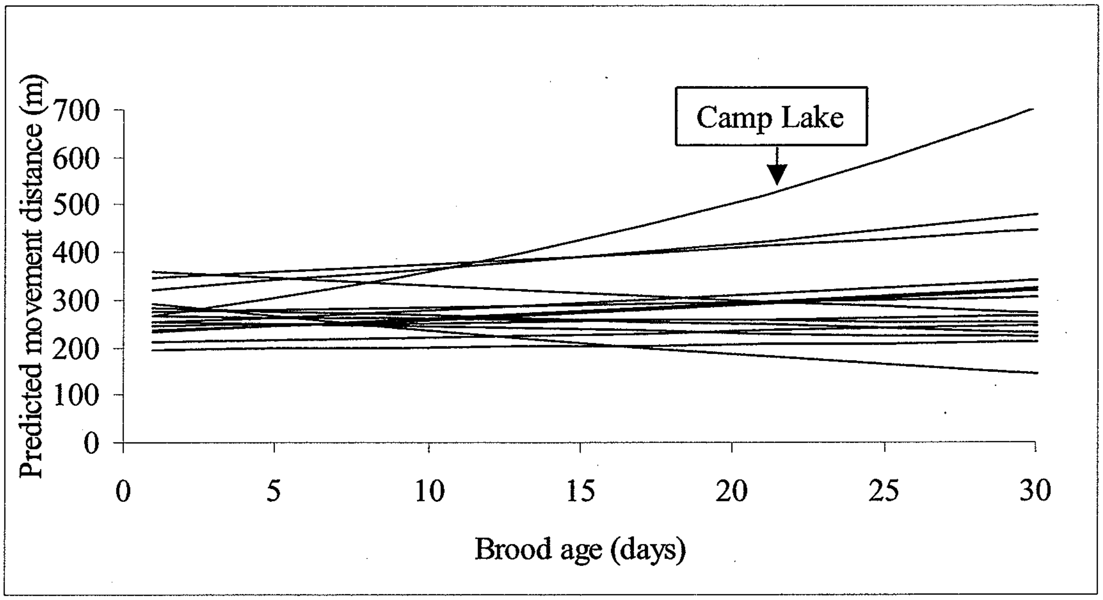


Table 2.3. Factors affecting nest to first wetland movement distances of 308 mallard broods on 15 study areas in the Canadian prairie parklands. Non-significant ($P > 0.05$) factors were deleted from the final model unless they were contained within a significant interaction effect.

Factor[a]	**df**	**F**	**P**
Hatch Date	1	9.63	0.002
Hatch Date ^{2}	1	0.47	0.49
Study Area	14	1.71	0.054
Hatch Date * Study Area	14	1.30	0.20

[a] Factors listed in bold type were part of the final model.

Table 2.4. Factors influencing straight-line distance from the nest to brood location at 30 days post-hatch for mallard broods in the Canadian prairie parklands. Non-significant ($P > 0.05$) factors were deleted from the final model unless they were contained within a significant interaction effect.

Factor[a]	**df**	**F**	**P**
Hatch Date	1	7.43	0.007
Hatch Date ^{2}	1	0.00	0.95
Study Area	14	1.27	0.22
Hatch Date * Study Area	14	0.97	0.49

[a] Factors listed in bold type were part of the final model.

The accumulated distance of moves made by broods from their nest to their 30-day location averaged 2,478 m (SD = 2,300). The maximum 30-day accumulated distance was 16,930 m, but over 95% of the accumulated distances were less than 6 km. The accumulated distance of moves made by broods from their nest to their 30-day location was unaffected by hatch date, but differed among study areas (Table 2.5).

Post-hoc analyses:

Study area was an important variable predicting daily probability of moving (Figure 2.2) as well as distance moved by mallard broods (Figure 2.3). However, study area was a categorical variable that required 14 degrees of freedom to model (i.e, with k = 15 study areas). Hence, I was interested in trying to identify site-specific covariates that could more efficiently explain among study area variation (i.e., with 1 rather than 14 d.f.). Moreover, such site-specific covariates could help identify the underlying causative factors that contributed to among-site variation in brood movements, and thus further our understanding of brood ecology.

Wetland density has been found to affect movement distances of mallard broods (Rotella and Ratti 1992b), and Krapu et al. (2000) found that the percent of seasonal wetlands holding water was an important predictor of brood survival, so I speculated that these two variables may be useful covariates to describe among study-area variation in movement probability and movement distance. Wetlands on each study area were visited in late summer to determine whether each wetland was dry or inundated. I calculated the percentage of seasonal wetlands and the percentage of semipermanent wetlands that were inundated to characterize the relative wetness of each study site (Stewart and Kantrud 1971). I also calculated the average number of seasonal wetlands and semipermanent

Table 2.5. Factors affecting accumulated distance traveled from the nest to brood location at 30 days post-hatch for mallard broods in the Canadian prairie parklands. Non-significant ($P > 0.05$) factors were deleted from the final model unless they were contained within a significant interaction effect.

Factor[a]	**df**	**F**	**P**
Hatch Date	1	1.13	0.29
Hatch Date ^{2}	1	0.04	0.84
Study Area	14	2.80	0.0006
Hatch Date * Study Area	14	1.10	0.36

[a] Factors listed in bold type were part of the final model.

wetlands per square kilometer (both wet and dry) for each study area. For analysis I utilized all four variables to try to determine which wetland variable was the best predictor of mallard brood movements.

Of the four post-hoc covariates I considered, the percentage of semipermanent wetlands inundated with water was the best predictor for both the probability of a brood movement and the average distance of brood movements. The relationship between the probability of a brood movement and the percentage of semipermanent wetlands inundated with water varied with brood age. The percentage of inundated semipermanent wetlands did not greatly affect the probability of a young brood making a move, but as broods aged their movement probability became increasingly dependent on the percentage of semipermanent wetlands inundated with water; however, this trend was not as strong in the latter part of the season (Figure 2.4).

The relationship between brood movement distance and the percentage of semipermanent wetlands inundated with water also varied with brood age. Again, the moisture indicator had little effect on movement distance among young broods, but older broods moved farther as the percentage of inundated semipermanent wetlands decreased (Figure 2.5).

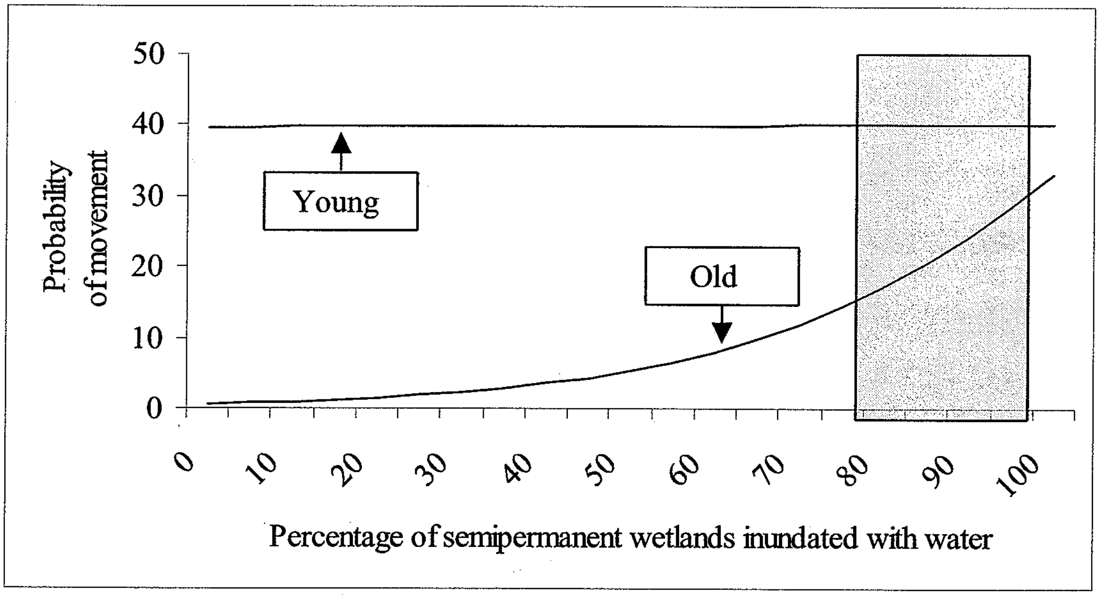
Discussion

Movement Probabilities:

Other studies found that younger broods moved more often than older broods (Talent et al. 1982, Rotella and Ratti 1992b, Dzus and Clark 1997). In this study there was considerable among-study-area variation in how brood age affected movement probability, but younger broods almost always moved more often than older broods,

Figure 2.4. Predicted daily probability of movement for young (3 days old) and old (30 days old) mallard broods as the percentage of semipermanent wetlands inundated with water changes. A) Julian Hatch Date = 150. B) Julian Hatch Date = 190. The shaded region represents the observed range of the covariate over 15 study areas.

A)



B)

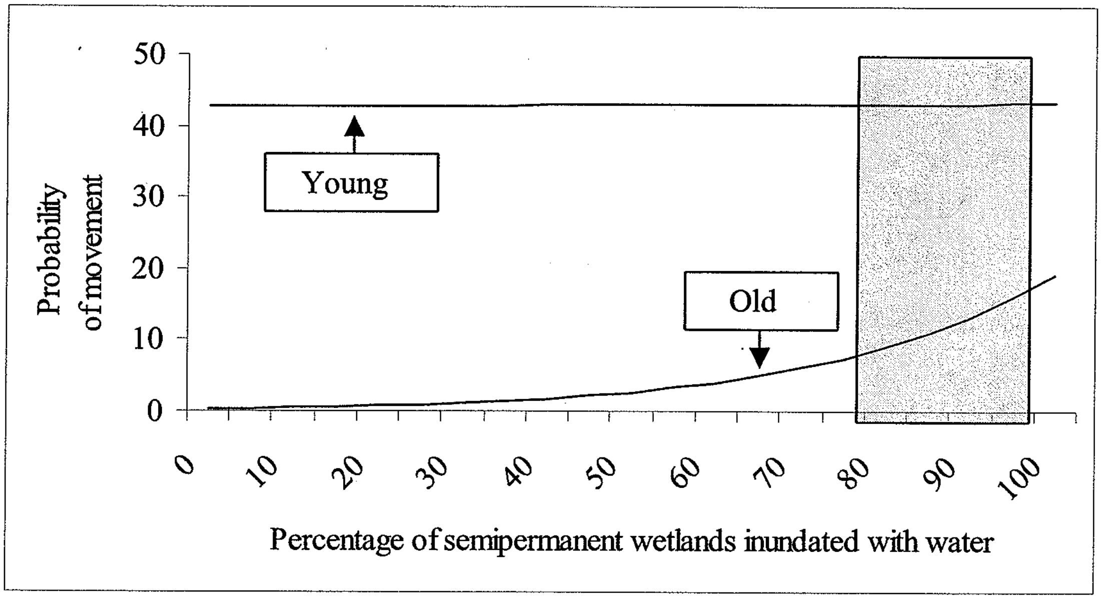
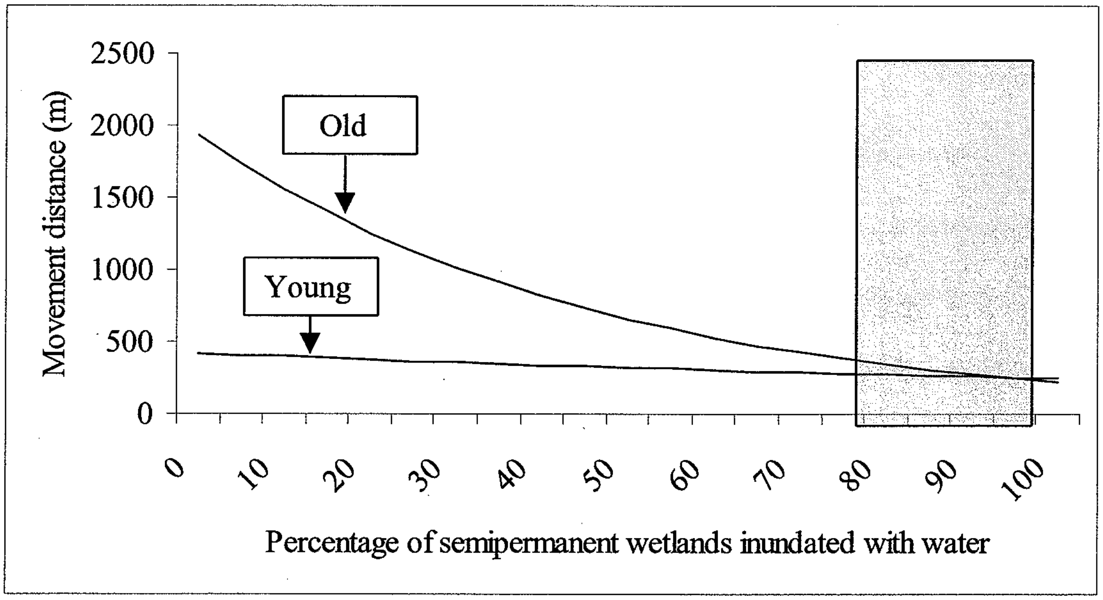


Figure 2.5. Predicted movement distance of young (3 days old) and old (30 days old) mallard broods as a function of semipermanent wetland inundation on the local study area. The shaded region represents the observed range of the covariate over 15 study areas.



especially later in the brood-rearing season (Figure 2.2). Young broods usually made several moves while searching for a suitable wetland, but once one was found they tended to remain there for an extended period. Post-hoc analysis showed that much of the among-study-area variation in movement probability could be explained by the percentage of semipermanent wetlands containing water, especially among older broods.

The Shoal Lake site was an obvious outlier with respect to much higher probability of brood movements (Figure 2.2). Among study areas, Shoal Lake was average in regards to wetland density, but it had one of the greatest percentages of wetlands inundated with water (Appendix 1).

Movement Distances:

Hatch date was the most important predictor of variation in movement distances among mallard broods. Later-hatching broods had longer average moves (Table 2.2), first moves (Table 2.3), and straight-line distances from their nest to their 30-day location (Table 2.4). This variation may be related to anthropogenic changes that occurred during the interval between first and last hatching broods (earliest hatch date = 18 May, latest hatch date = 9 August). During the early brood-rearing season crops are typically short and sparse and broods making overland movements may be especially susceptible to predation and the elements. Later in the season, as upland vegetation becomes taller and denser, upland moves by broods may pose less risk. Early in the brood-rearing season a brood may be better served by moving to several nearby wetlands en route to a desired wetland, whereas later in the season it may be better to make one substantial movement to reach the desired destination.

Nest-site selection may be another factor affecting seasonal variation in distance of first moves. Typically, mallard hens will nest near wetlands early in the season, as this is where some of the best nesting cover is found. As the season progresses, upland vegetation grows and provides better nesting cover throughout the entire landscape. Consequently, late-season broods often hatch farther from wetlands than early season broods (Howerter 2003), and their resultant first move will necessarily be longer.

Wetland availability was probably the most important factor causing broods to make longer moves later in the brood-rearing season. Typically, temporary and seasonal wetlands dry up during the summer, resulting in fewer habitat choices for late-hatching broods (during severe droughts, semipermanent wetlands also dry up). A decreasing density of available wetlands would increase the likelihood of longer moves late in the brood-rearing season. Indeed, post-hoc analysis showed that a large component of among study area variation in movement distances resulted from a negative correlation between movement distances and the percentage of semipermanent wetlands containing water (Figure 2.5). If moisture can explain study area variation in movement distance, then it is reasonable to believe it could also affect seasonal movement patterns. However, I could not test this directly because I did not have within-season data on wetland availability.

Brood age was not an important predictor of movement distance except when combined with study area (Figure 2.3). However, this interaction seemed to be almost entirely due to a positive correlation between age and distance moved at the Camp Lake study site. Unique wetland attributes at Camp Lake may have contributed to this pattern; although Camp Lake had one of the highest wetland densities, it was among the lowest in percentage of wetlands inundated with water (Appendix 1). Indeed, post-hoc analysis showed that the percentage of semipermanent wetlands inundated with water could explain some of the among study-area variation in movement distances among older broods. Young broods were relatively unaffected by moisture levels, but older broods moved farther as the percentage of semipermanent wetlands inundated with water decreased (Figure 2.5).

Similar to Rotella and Ratti (1992b), who found no relationship between wetland density and distance moved or number of moves made by mallard broods, I found that wetland density explained little of the among-study-area variation in movement distance. However, wetland density for this study was measured from airphotos and all delineated wetlands were included in count totals, regardless of whether they contained water. For this reason, I believe the percentage of wetlands containing water was a superior wetland covariate for predicting study area variation in movement patterns.

Several previous studies have shown that seasonal wetlands are most important to broods (Talent et al. 1982, Mauser et al. 1994b, Krapu et al. 2000). However, my post-hoc analyses showed that semipermanent wetlands were a superior predictor of among study-area variation in movement patterns of mallard broods. However, wetland classification for my study was conducted in late July and August, when many seasonal wetlands typically were dry. Perhaps if wetland inundation data had been collected earlier during the peak brood-rearing period, seasonal wetlands might have been a better predictor of brood movements. Also, wetland inundation data were measured coarsely as either wet (any amount of water) or dry. Future studies should consider recording more specific inundation levels during wetland classification (e.g., dry, ¼, ½, ¾, or fully flooded). Simply because a wetland is wet does not mean it contains sufficient water to be suitable as brood habitat. The factors that influence whether or not a particular wetland is appropriate brood habitat for mallards are the subject of the next chapter.

CHAPTER 3: WETLAND SELECTION BY MALLARD BROODS IN THE CANADIAN PRAIRIE PARKLANDS

Duckling survival is the third most important component of population change in mallards, trailing only nesting success and female survival during the breeding season (Cowardin and Johnson 1979, Hoekman et al. 2002). Habitat use and availability are believed to strongly affect duckling survival during the brood-rearing period (Rotella and Ratti 1992a), hence a better understanding of habitat selection by mallard broods should aid management efforts to increase mallard populations.

Many factors are currently known to affect wetland use by broods. Several studies have found that brood use was positively correlated with the amount of emergent vegetation in a wetland (Berg 1956, Lokemoen 1973, Mack and Flake 1980). Wetland permanence (Stewart and Kantrud 1971) also impacts brood use. Stoudt (1971) found that broods selected semipermanent and permanent wetlands in the Canadian parklands, whereas Duebbert and Frank (1984) and Talent et al. (1982) suggested that seasonal wetlands were preferred in North Dakota. Duckling age can also play a part in habitat selection; Berg (1956) and Keith (1961) believed broods moved to larger, more permanent wetlands as they matured. Still other studies found annual variation in habitat use (Talent et al. 1982, Mulhern et al. 1985, Rotella and Ratti 1992b), with broods using more permanent wetlands during drier years.

If annual variation in habitat conditions can affect wetland selection, then seasonal variation might have a similar effect. Wetland availability can decrease dramatically from early to late summer due to evapotranspiration (Stewart and Kantrud

1971), and what may appear as older broods using more permanent wetlands may instead be a temporal response to seasonally declining wetland availability.

Several studies have found that the amount of emergent vegetation affected brood use of wetlands (Lokemoen 1973, Mack and Flake 1980), but the effects of different cover types (sensu Stewart and Kantrud 1971) have not been considered. Stoudt (1971) found that wetlands with <50% of the surface area covered with emergent vegetation were preferred over more densely vegetated wetlands, whereas Talent et al. (1982) found that seasonal wetlands selected by mallard broods contained a central expanse of open water with emergent cover around the edges. It thus appears that mallard ducklings may prefer a mixture of open water plus protective emergent cover, but this aspect of wetland selection has not been adequately addressed.

Little quantitative research has been done to relate wetland selection by broods to dominant species of emergent vegetation. In a wet year, Talent et al. (1982) found that mallard broods preferred seasonal wetlands dominated by whitetop rivergrass *(Scolochloa festucacea)*, but avoided other seasonal wetlands. Both permanency class and emergent vegetation can be important to wetland selection by broods (Rotella and Ratti 1992b, Talent et al. 1982), but because dominant vegetation is confounded with permanency (Stewart and Kantrud 1971), it is difficult to quantify the relative influence of each factor.

Historically, many studies have relied on visual observations to determine habitat use (Berg 1956, Evans and Black 1956, Keith 1961, Stoudt 1971, Lokemoen 1973, Mack and Flake 1980, Mulhern et al. 1985) but these studies should be viewed skeptically because brood sightability can vary tremendously among different habitat types (Talent et al. 1982, Giudice 2001). Moreover, most habitat selection studies have examined one habitat attribute at a time, ignoring the often confounding and correlated interrelationships among variables. Such biases were removed in my study, because wetland use was determined unambiguously using radio telemetry, and multiple habitat attributes were examined simultaneously using multivariate analysis.

My study attempts to answer many of the unanswered questions relating to wetland selection by mallard broods in the Canadian prairie parklands. I predicted that the amount of emergent vegetation would be positively correlated with wetland selection, and I also believed that season and brood age would affect this correlation, with emergent vegetation being more important to young broods and early during the brood-rearing season. I also predicted that wetland permanency and cover type would be important predictors of wetland selection by mallard broods, with semipermanent wetlands being selected more than seasonal wetlands (especially late in the season), and heavily vegetated wetlands being more important (especially for young broods). Since wetland availability differed markedly across the study sites and presumably declined seasonally, I further believed that calendar date or a local moisture indicator would be an important modifier affecting wetland permanency selection. Finally, I predicted that dominant vegetation species would be important in wetland selection by mallard broods.

Study Areas

The Prairie Habitat Joint Venture (PHJV) Assessment Project is described in Chapter 1. Study areas used in this analysis (n=15) included two study sites in 1993 (Punnichy, SK; and Hamiota, MB), three sites each in 1994 (Erskine, AB; Davis, SK; and Belmont, MB), 1995 (Shoal Lake, MB; Kutawa, SK; and Camp Lake, AB), and 1996

(Pine Lake, AB; Parkside, SK; and Baldur, MB), and four sites in 1997 (Willowbrook SK; Mixburn, AB; Elnora, AB; and Allan Hills West, SK) (see Figure 2.1).

Methods

Telemetry Data

From 111 to 137 pre-laying female mallards were decoy-trapped (Sharp and Lokemoen 1987, Ringelman 1990) at each Assessment Site. Each hen was weighed, measured, banded, and radiomarked with a 22g intra-abdominal transmitter (Olsen et al. 1992, Rotella et al. 1993, Paquette et al. 1997). Radiomarked hens were intensively tracked throughout the breeding season to document their nesting histories.

Nests of non-radioed mallards also were found using a variety of methods, including ATV-towed cable-chain nest drags, hand-held rope drags, and walking through the vegetation while striking it with a willow switch (Higgins et al. 1977, Klett et al. 1986, Paquette et al. 1997). Small portable fences were placed around a sample of these nests to increase the likelihood of hatching (Sargeant et al. 1974). Nesting females were trapped at approximately 20 days of incubation using mist nets (Bacon and Evrard 1989), purse traps (modified from Coulter 1958), drop-door nest traps (Weller 1957), or walk-in traps (Dietz 1994). Nest trapped hens also were weighed, measured, and banded, but were fitted with an 8 g anchored-backpack transmitter (Mauser and Jarvis 1991, Paquette et al. 1997). All research procedures were approved by the University of Saskatchewan's Protocol Review Committee on Animal Care and Supply (Protocol number 920007).

Each nesting hen was radiotracked daily until her nest either failed or hatched; all hatched nests were eligible to become part of my study. At least one radio-location per day was collected during brood rearing, unless a movement between ponds had occurred since the previous location, in which case 2 radio-locations were collected.

Telemetry locations were collected using a truck-mounted null array system (Paquette et al. 1997). The pond being used by the brood was determined through triangulation from known locations. If telemetry error polygons encompassed more than one wetland, the actual wetland was verified by approaching and triangulating with a handheld antenna.

Wetland Classification

Every wetland basin that contained water at some point during the waterfowl-breeding season was visited and classified, primarily between late July and mid-August. Wetland attributes collected during classification included permanency, cover type (Stewart and Kantrud 1971), dominant species of emergent vegetation, average width of flooded emergent vegetation, and whether or not the basin contained water at classification time.

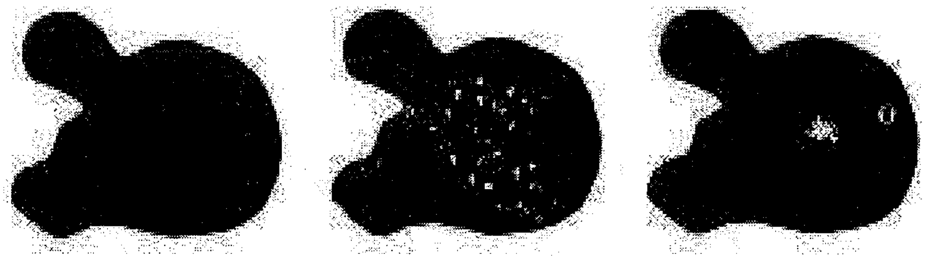
Wetlands were divided into 7 permanency groups based on dominant emergent vegetation (Stewart and Kantrud 1971). Ephemeral ponds were dominated by low prairie grasses and usually held water for only a brief period in early spring; they usually were dry before the first brood hatched. Temporary ponds were dominated by fine sedges and forbs and typically became dry early in the breeding season. Seasonal ponds were dominated by coarse emergent sedges or grasses and usually held water for some or all of the brood-rearing season, depending on moisture levels in the area. Semipermanent ponds were dominated by cattails (*Typha* spp.) or bulrushes (*Scirpus* spp.) and usually held water throughout the brood rearing season, but may have became dry in very dry areas. Permanent ponds were dominated by submerged aquatic plants and held water throughout the brood rearing season. Alkali ponds were relatively permanent, but supported vegetation characteristic of high salinity levels (e.g., alkali bulrush, *Scirpus maritmus*). Finally, tillage ponds occurred in cropped land and had basins that had been completely tilled. Most tillage ponds were originally ephemeral, temporary, or seasonal wetlands, but could not be recognized as such because their identifying vegetation had been eliminated through tillage.

Five wetland cover types were recognized for this study (Steward and Kantrud 1971; Figure 3.1). Cover type 1 wetlands had a continuous stand of emergent vegetation with open water areas (or bare soil if the basin was dry) covering less than 5% of the central wetland basin. Cover type 2 wetlands had scattered patches of emergent cover located throughout the wetland, with open water (or bare soil) covering from 5 to 95% of the basin area. Cover type 3 wetlands contained a central expanse of open water (or bare soil) averaging 5 – 95% of the basin area and were ringed by a peripheral band of emergent cover averaging ≥ 2 m in width. Cover type 4 wetlands had > 95% coverage of open water and/or had bands of emergent cover averaging < 2 m in width. Finally, tillage ponds were unvegetated and were considered cover type 0.

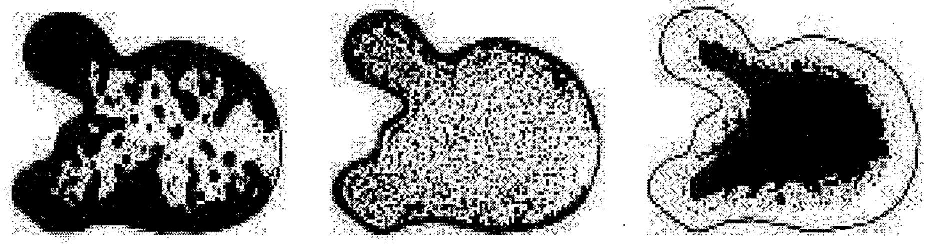
The dominant species (or sometimes genus) of emergent vegetation was recorded for all seasonal and semipermanent wetlands. Dominant species comprised > 50% of the emergent vegetation in the basin.

The average width of flooded emergent vegetation was also recorded for all wetlands containing water. If the wetland was cover type 1, then the average radius of the wetland's flooded vegetation was used.

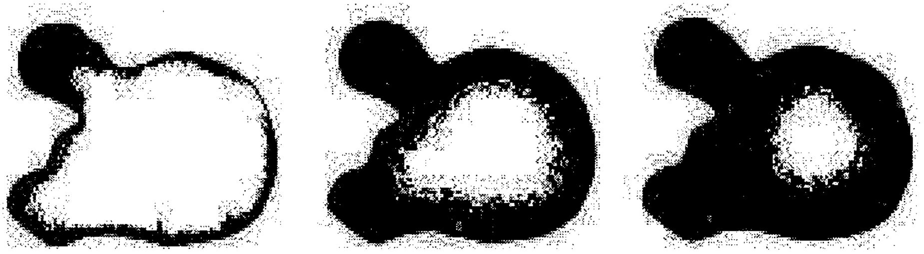
Figure 3.1. Basic cover types of wetlands. White areas indicate open water or bare soil; shaded areas indicate emergent vegetation (taken from Stewart and Kantrud 1971). Cover type 0 wetlands are not shown and are considered to be tillage ponds for the purpose of this study.



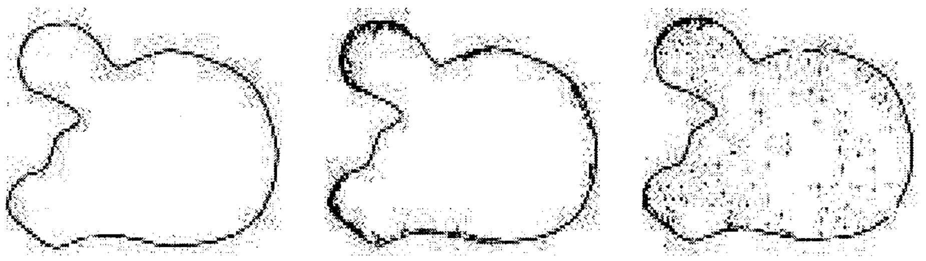
Cover Type 1



Cover Type 2



Cover Type 3



Cover Type 4

Spatial Summarization of Data

Each study site was flown and photographed using 1:5000 black and white stereoscopic photos. Photos were used to delineate and digitize habitat maps for each study site. Each site's digitized map then was imported into SPANS geographical information system (GIS; PCI Geomatics, Richmond Hills, Ontario, Canada) where a wetlands data layer was constructed. Each distinct wetland basin was numbered in this layer in order to merge brood tracking data with each wetland's geographic location in SPANS. Universal Transverse Mercator (UTM) locations were given to each brood wetland. If a wetland was < 5 hectares (ha) the centroid UTM location was used, but for wetlands > 5 ha, a more accurate UTM was used if available. This resulted in a dataset that included a brood hen's geographic location at each specific time she was radio-tracked, along with related wetland habitat data for each location.

The data were censored to include only broods that were tracked for ≥ 29 days after leaving the nest. The exact time of hatch was unknown, but ducklings usually leave the nest 1 day after hatch (Weller 1964), thus most brood hens would have been tracked until their ducklings were 30 days old. Locations of brood hens more than 30 days after hatch were removed from analysis because hens spend an increasing amount of time away from their broods (Talent et al. 1983), and hence their locations may not have been indicative of the location of their broods. To remove bias caused by tracking hens that had lost their entire brood, only hens that had ≥ 1 duckling survive to 30 days of age were included in the analysis.

Following these censoring decisions, 308 broods remained for analysis. Straight-line movement distances were calculated using UTM locations and the Pythagorean formula ($\partial = \sqrt{[(X_1-X_2)^2+(Y_1-Y_2)^2]}$). Movements of more than 300 m, after which the hen returned to the initial wetland the following day, were disregarded. Mallard hens are known to regularly leave their broods in order to feed or explore (Rotella and Ratti 1992b, Pietz and Buhl 1999), and these longer round-trip moves probably represented moves by the hen unaccompanied by the brood.

A brood hen's first move was calculated using the UTM locations of her nest and the first brood pond (Chapter 2). I found that 80% of first moves were < 500 m. Consequently, I used SPANS software to establish a fixed radius of 500 m around each brood hen's nest and subsequent locations to determine habitat availability for each move (Figure 3.2). If at least part of the selected wetland was not included within this 500 m radius circle, then the observation was discarded. All remaining wetland polygons within the 500 m radius of a brood's location were deemed to represent available but unused wetlands. Attributes included with the available wetlands were wetland permanency class, cover type, dominant emergent vegetation, width of flooded emergent vegetation, and whether or not the pond was dry.

The data now comprised a "choice set" (Cooper and Millspaugh 1999; Figure 3.3) of used and unused wetlands that could be examined for evidence of non-random wetland selection.

Statistical Analysis

Habitat preferences were examined using a multinomial logit form of a discrete choice model (Cooper and Millspaugh 1999, Manly et al. 2002:150). Primary predictors used to model wetland selection were wetland permanency (PERM), wetland cover type (COVER), and the width of flooded emergent vegetation (WIDTH) (Table 3.1). I also

Figure 3.2. The method used to define the choice set for an individual brood hen at each of her locations throughout the brood rearing period. Point A marks the location of her nest. The boundary of the choice set for her first wetland selection is defined by a circle, centered at point A with a radius of 500 m. Point B marks the location of her first chosen wetland post-hatch. Points C through E represent subsequent chosen wetlands throughout the brood rearing stage.

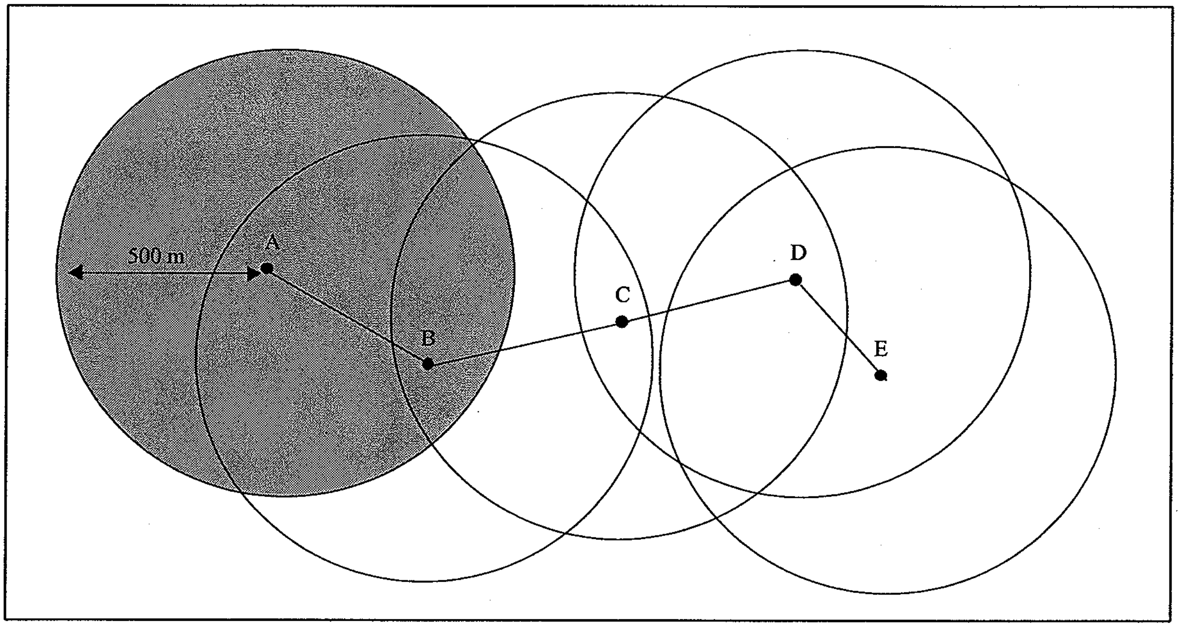


Figure 3.3. An example of a simplified choice set where the polygons are the available wetlands for the hen, from her location at point A.

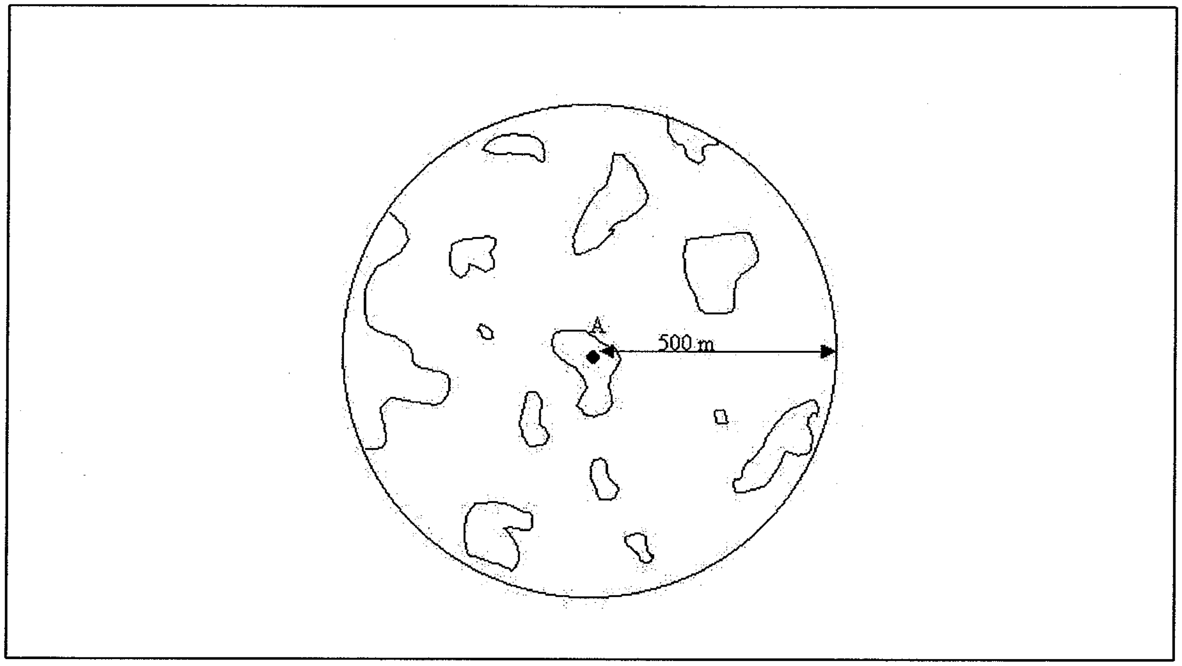


Table 3.1. Covariates and abbreviations used in modeling wetland selection by mallard broods in the Canadian prairie parklands.

Covariate	Abbreviation
Wetland Permanency	PERM
Ephemeral wetland	PERM(I)
Temporary wetland	PERM(II)
Seasonal wetland	PERM(III)
Semipermanent wetland	PERM(IV)
Permanent wetland	PERM(V)
Alkali wetland	PERM(VI)
Tillage wetland	PERM(VII)
Wetland Cover Type	COVER
0 (tillage wetland)	COVER(0)
1 (closed stand of emergent vegetation)	COVER(1)
2 (mixed stand of emergent vegetation and open water)	COVER(2)
3 (central expanse of open water)	COVER(3)
4 (dominated by open water)	COVER(4)
Wetland Vegetation[a]	VEG
Bechmannina syzigachne (sloughgrass)	BESY
Scolochloa festucacea (whitetop rivergrass)	SCFE
Glyceria grandis (tall manna grass)	GLGR
Carex atherodes (slough sedge)	CAAT
Scirpus spp. (bulrush)	SCSP

Typha spp. (cattail)	TYSP
Other[b]	Other
Width of flooded emergent vegetation	WIDTH
Age (days from hatch)	AGE
Date (Julian date)	DATE
Percent of seasonal wetlands holding water	%WET-III

[a] Vegetation species BESY, SCFE, GLGR and CAAT interact with seasonal wetlands and TYSP, SCSP, CAAT and SCFE interact with semipermanent wetlands in the model building process.

[b] Other = Combined dominant vegetation species that are represented in < 5% of wetlands for the respective permanency.

wanted to consider dominant species of vegetation (VEG), but this variable is very dependent on wetland permanency (Stewart and Kantrud 1971), especially among seasonal and semipermanent wetlands (i.e., cattail is an identifying feature of semipermanent wetlands). Therefore, I set up a permanency by dominant vegetation interaction for seasonal and semipermanent wetlands. For seasonal wetlands, the interacting vegetations were sloughgrass (*Beckmannia syzigachne*), whitetop rivergrass (*Scolochloa festucacea*), tall manna grass (*Glyceria grandis*), slough sedge (*Carex atherodes*), and "other". For semipermanent wetlands, the interacting vegetations were bulrush (*Scirpus* spp.), cattail (*Typha* spp.), slough sedge, whitetop rivergrass, and "other".

Ambient moisture conditions on a given study site could influence how wetland permanency affects habitat selection by broods. Obviously, dry wetlands are not available for selection by broods. Unfortunately, wetland classification for the study sites was usually completed in late July and August, about 2 months after the start of brood rearing. Therefore, many wetlands that were classified as dry may have been available to broods earlier in the season. Consequently, removing all dry wetlands from analysis would not be prudent. Nevertheless, closer inspection showed that many dry wetlands were classified as ephemeral, temporary, or tillage ponds. Through field knowledge I knew that these wetlands almost always became dry early in the breeding season, before most broods are hatched. Therefore, any selection against these wetlands would be meaningless, since they were actually unavailable to broods. I therefore removed all dry ephemeral, temporary, and tillage wetlands from analysis. However, many seasonal and semipermanent wetlands that were dry during classification may have retained water during some portion of the brood-rearing period and these wetlands should not be deleted. The percentage of seasonal wetlands holding water (%WET-III) is typically a good indication of local moisture (Krapu et al. 2000) and I used this variable as a proxy for local wetland conditions. By including an interaction between wetland permanency and local wetland conditions (i.e., PERM * %WET-III), I was able to account for dry (primarily seasonal) wetlands that were not actually available to broods.

Duckling age (AGE) also may be important in the wetland selection process, but age can not be a primary predictor because it does not have the potential to change with each selection. By considering age as a categorical variable; i.e., by contrasting young (≤ 15 days old) versus old (> 15 days old) broods, important age interactions could nevertheless be examined. Since age could not always change between selections, its effect on wetland selection could only be considered interactively with 1 of the primary predictors. For the same reasons, date (DATE) was used as a categorical variable in the modeling process, but only as an interaction with primary predictors. Selections made on or before 30 June (i.e., the approximate midpoint of brood rearing) were considered early, whereas selections made after 30 June were considered late.

Once the potential covariates were identified, it was important to consider how best to incorporate them in the discrete choice model. Models were estimated using the discrete choice modeling program in SAS (PROC PHREG; SAS Institute 1996), which requires all categorical variables to be identified and compared to a common baseline within that category. For example, if there are 5 cover types (0-4), then 1 cover type must be identified as the baseline so the remaining 4 cover types can be evaluated in relation to this common baseline. The category that is chosen as the baseline does not affect the resulting parameter estimates or the ultimate probability of selection for each category.

From this point I conducted a systematic *a priori* procedure to evaluate and select models. Each primary predictor was run as a single variable discrete choice model. Next, each variable was systematically added to each other variable and the resulting bivariate models were evaluated. Additional variables were added when all possible arrangements with fewer variables had been exhausted, and then these multivariate models were evaluated. Age and date were only added to models as interactions with permanency, cover type, and flooded emergent width. Dominant wetland vegetation and the percentage of seasonal wetlands containing water were only included in models as interactions with permanency. If an interaction with a primary predictor was included in a model, then the accompanying primary predictor also was included.

Specifying one category for age or date interactions with permanency and cover type kept the numbers of parameters manageable and reduced model complexity. But knowing which category would best illustrate an interaction for wetland selection required some *a priori* knowledge of the system. Seasonal and semipermanent wetlands were the most plentiful in the data, and their selection was most in question in the literature. Consequently, permanency interactions with age and date were structured to evaluate the selection of seasonal versus semipermanent wetlands. Similarly, I structured age and date interactions with cover type to contrast cover type 1 and 3 wetlands. These cover types are the most abundant, but have distinctly different configurations (Figure 3.1). Other models, using all categories of permanency or cover types, were considered after important age and date interactions had been discovered. This procedure was conducted to ensure that non-specific but potentially important interactions were not missed.

Using only primary predictors resulted in 7 *a priori* models. Systematically adding permanency interactions for percentage of seasonal wetlands containing water, dominant vegetation, date, and age, as well as cover type and flooded emergent vegetation interactions for date and age, resulted in 155 *a priori* models. Three additional models were derived from these models, for a total of 158 models.

Support for potential models was evaluated using Akaike's Information Criteria (AIC) (Akaike 1973 as cited in Anderson and Burnham 2002). AIC takes into account both the minimization of log-likelihood (i.e., reduction in lack of fit) plus a penalty for the number of parameters in the model (Anderson et al. 2000). Although I had reasonably large sample sizes, I used AIC_c, which corrects AIC values for either small sample size or a large number of parameters (Anderson and Burnham 2002). I was unable to adjust for potential overdispersion of the data (i.e., by using $QAIC_c$) because PHREG does not have a mechanism to calculate $\hat{c}$. Models were compared relative to each other by considering the difference between the AIC_c value of the best fitting model (lowest AIC_c) and that of all other models (ΔAIC_c). I also calculated Akaike model weights (Franklin et al. 2000), which provide a measurement of each model's relative likelihood, as all models will sum to 1 given the data and model list (Rotella et al. 2003). Models with ΔAIC_c values ≤ 8 were included in the reported list of candidate models. Once a best model had been chosen, I used the parameter estimates (including any interacting covariates) to calculate the probabilities of selection for each of the primary covariates.

Results

Model Selection

The 308 radiomarked mallard broods selected 2,026 wetlands out of a choice set of 86,600 available wetlands. Model fit tended to improve as each of the 3 primary predictors of wetland permanency (PERM), wetland cover type (COVER), and width of flooded emergent vegetation (WIDTH) were added (Table. 3.2). The interactions between permanency and dominant vegetation (PERM * VEG) and flooded vegetation width and date (WIDTH * DATE) were also present in all candidate models. Surprisingly, the interaction between permanency and the percentage of seasonal wetlands containing water (PERM * %WET-III) was not an important predictor. However, all but 1 of the models not containing PERM * %WET-III contained the interaction of seasonal wetlands and date (PERM(III) * DATE). I believe this interaction accounted for the tendency of seasonal wetlands to become dry and unavailable late in the season. The top 2 models also contained an interaction between date and all wetland permanencies, showing that selections of wetland permanency classes other than seasonals also were date dependent.

Interactions with cover type were less consistent among the top models. The best model contained an interaction between cover type 1 and brood age (COVER(1) * AGE). The second best model was similar, but contained an interaction between age and all 5 cover types.

Width of flooded emergent vegetation was important as a primary predictor and it also interacted with date in all best models. In 3 of the top 8 models a vegetation width

Table 3.2. Ranking of hypothesized models of wetland selection by 308 mallard broods at 15 study sites in the prairie parklands of Canada between 1993 and 1997. Data include number of estimated parameters (K), Akaike's Information Criterion with small-sample correction (AIC_c), the difference between this AIC_c value and that of the top-ranked model (ΔAIC_c), and the model weight (relative likelihood of this model, given the data and model set). Only models within 8 AIC_c units of the top-ranked model are presented.

Rank	Model	K	AIC_c	ΔAIC_c	W
1)	PERM + PERM * VEG + COVER + WIDTH + PERM(I) * DATE + PERM(II) * DATE + PERM(III) * DATE + PERM(IV) * DATE + PERM(V) * DATE + PERM(VI) * DATE + PERM(VII) * DATE + COVER(1) * AGE + WIDTH * DATE	27	7693.90	0.00	0.563
2)	PERM + PERM * VEG + COVER + WIDTH + PERM(I) * DATE + PERM(II) * DATE + PERM(III) * DATE + PERM(IV) * DATE + PERM(V) * DATE +	29	7696.39	2.50	0.162

	PERM(VI) * DATE + PERM(VII) * DATE + COVER(0) * AGE + COVER(1) * AGE + COVER(2) * AGE + COVER(3) * AGE + COVER(4) * AGE + WIDTH * DATE				
3)	PERM + PERM * VEG + COVER + WIDTH + PERM(III) * DATE + COVER(1) * AGE + WIDTH * DATE	22	7697.76	3.86	0.082
4)	PERM + PERM * VEG + COVER + WIDTH + PERM(III) * DATE + WIDTH * AGE + WIDTH * DATE	22	7698.06	4.16	0.070
5)	PERM + PERM * VEG + COVER + WIDTH + WIDTH * AGE + WIDTH * DATE	21	7699.77	5.87	0.030

6)	PERM + PERM * VEG + COVER + WIDTH + PERM(III) * DATE + WIDTH * DATE	21	7700.86	6.96	0.017
7)	PERM + PERM *%WET(III) + PERM * VEG + COVER + WIDTH + WIDTH * AGE + WIDTH * DATE	22	7701.07	7.17	0.016
8)	PERM + PERM * VEG + COVER + WIDTH + PERM(III) * DATE + COVER(0) * AGE + COVER(1) * AGE + COVER(2) * AGE + COVER(3) * AGE + COVER(4) * AGE + WIDTH * DATE	24	7701.15	7.25	0.015

by brood age interaction (WIDTH * AGE) replaced the cover type 1 by age interaction (Table 3.2).

Wetland Selection

Parameter estimates from the best-fitting model were used to estimate selection probabilities for the different wetland permanencies. Since the best model contained a permanency by date interaction, selection probabilities had to be estimated separately for early (≤ 30 June) and late (> 30 June) in the brood rearing season. Alkali wetlands were strongly preferred both early (Table 3.3) and late (Table 3.4) in the season. To a lesser extent, permanent and semipermanent wetlands also were utilized extensively. Ephemeral, temporary, and tillage wetlands were avoided, as were seasonal wetlands dominated by sloughgrass. In general, an increase in permanency caused an increase in preference, and this was more pronounced late in the season (Table 3.4).

Parameter estimates from the best model were used to estimate selection probabilities for the different wetland cover types (Table 3.5). This model contained a cover type by brood age interaction, so wetland selection probabilities had to be estimated separately for both young (≤ 15 d) and old (16 – 30 d) broods. Cover type 0 (tillage) wetlands, were rare and little used, but large standard errors resulted in selection probabilities that did not differ statistically from the other 4 cover types. Other cover type selection rankings were distinct and showed a preference for open water over closed vegetation (Table 3.5). Rankings did not differ by age, but cover type 1 was less preferred by old broods than young broods (Table 3.5).

Parameter estimates from the best model were used to estimate the effect that width of flooded emergent vegetation had on wetland selection by mallard broods. The

Table 3.3. Ranking of mallard brood selection probabilities for wetland permanency and dominant emergent vegetation during the early (≤ June 30th) brood rearing season in the Canadian prairie parklands. Selection probabilities sum to 100% and assume equal availability of each permanence/vegetation category.

Permanence (Early)	Parameter Estimate	Standard Error	Probability (%)	Unique ID	Not Different [a]
III(BESY)	-0.942	0.286	0.31	A	C
II	-0.079	0.313	0.74	B	C,E,F,D,H
I	-0.062	0.737	0.76	C	B,A,E,G,F,D,L, I,H
III(other)	0	0	0.80	D	C,B,E,H
III(CAAT)	0.095	0.124	0.88	E	F,D,H,C
III(SCFE)	0.281	0.159	1.07	F	C,B,E,H
III(GLGR)	0.684	0.167	1.60	G	C,K,L,I,J,H
VII	0.750	1.036	1.70	H	C,B,E,G,F,D,K L,N,I,J,M
IV(TYSP)	0.788	0.207	1.77	I	C,G,K,L,J,H
IV(other)	0.897	0.163	1.97	J	G,K,L,I,H
IV(CAAT)	0.911	0.214	2.00	K	G,L,I,J,H
IV(SCFE)	0.947	0.279	2.07	L	C,G,K,I,J,H
V	1.736	0.220	4.57	M	N,H
IV(SCSP)	1.909	0.214	5.43	N	M,H
VI	4.526	0.779	74.32	O	

[a] Not different column represents lack of overlap in confidence intervals.

Table 3.4. Ranking of mallard brood selection probabilities for wetland permanency and dominant emergent vegetation during the late (> June 30th) brood rearing season in the Canadian prairie parklands.

Permanence (Late)	Parameter Estimate	Standard Error	Probability (%)	Unique ID	Not Different[a]
VII	-10.986	181.696	0.00	A	B,C,D,E,F,G,H,I,J, K,L,M,N,O
III(BESY)	-0.942	0.286	0.36	B	A,C,D
I	-0.324	1.460	0.68	C	A,B,D,E,F,G,H,I,J, K,L
II	-0.215	0.491	0.75	D	A,B,C,E,F,G
III(other)	0	0	0.93	E	A,C,D,F
III(CAAT)	0.095	0.124	1.03	F	A,C,D,E,G
III(SCFE)	0.281	0.159	1.24	G	A,C,D,F
III(GLGR)	0.684	0.167	1.85	H	A,C,I,J,K,L
IV(TYSP)	0.937	0.243	2.38	I	A,C,H,J,K,L
IV(other)	1.046	0.207	2.66	J	A,C,H,I,K,L
IV(CAAT)	1.060	0.249	2.70	K	A,C,H,I,J,L
IV(SCFE)	1.096	0.274	2.79	L	A,C,H,I,J,K
IV(SCSP)	2.058	0.249	7.31	M	A
V	2.686	0.346	13.69	N	A,O
VI	4.190	1.258	61.63	O	A,N

[a] Not different column represents lack of overlap in confidence intervals.

Table 3.5. Ranking of mallard brood selection probabilities for wetland cover type by young (≤ 15 days old) and old (> 15 days old) mallard broods on the Canadian prairie parklands.

Cover Type	Parameter Estimate	Standard Error	Probability (%)	Unique ID	Not Different[a]
Young Broods					
0	-10.490	377.000	0.00	A	B,C,D,E
1	0	0	6.16	B	A
2	1.101	0.116	18.52	C	A
4	1.611	0.176	30.85	D	A
3	1.977	0.112	44.47	E	A
Old Broods					
0	-10.490	377.000	0.00	A	B,C,D,E
1	-0.429	0.198	4.10	B	A
2	1.101	0.116	18.93	C	A
4	1.611	0.176	31.53	D	A
3	1.977	0.112	45.44	E	A

[a] Not different column represents lack of overlap in confidence intervals within each age class.

best model contained an interaction with date, so results had to be examined separately for early and late season wetland selections. There was a 31% increase in wetland selection probability for each additional 10 meters of flooded emergent vegetation in the early season, but the effect was reduced to 21% during the late season (Table 3.6).

Exploratory Analysis

The extremely high selection probabilities for alkali (VI) wetlands (Tables 3.3 and 3.4) were surprising, as alkali wetlands are not known as exceptional brood habitat, at least not for mallards (Swanson et al. 1984). Hence, before concluding that alkali wetlands were strongly preferred by mallard broods, I conducted some additional post-hoc analysis of where and how alkali wetlands were selected. Upon further inspection, I found that approximately 85% of all alkali wetland selections were made on the Baldur study site by just 3 broods. These broods were moving back and forth between 2 adjacent alkali wetlands on nearly a daily basis. Consequently, I re-ran the best models from Table 3.2 after excluding alkali wetlands from the data to determine whether my other results were robust (Table 3.7). Parameter estimates for the other wetland permanency classes were almost unchanged from the original model (Tables 3.8, 3.9), but selection probabilities were obviously much higher after excluding alkali wetlands. Semipermanent and permanent wetlands became the most important wetland classes after excluding alkali wetlands.

Discussion

Model Selection

Important variables for predicting wetland selection by mallard broods were consistent throughout most of my top-fitting models. Hence, my results were unlikely to

Table 3.6. Seasonal effect of a 10m-width increase of flooded emergent vegetation on wetland selection by mallard broods in the Canadian prairie parklands.

Season of Selection	Parameter Estimate	Standard Error	10m Effect [a]
Early (≤ June 30)	0.0267	0.0023	30.54
Late (> June 30)	0.0187	0.0037	20.56

[a] Percentage increase in wetland use that would be associated with a 10 m increase in width of flooded emergent vegetation.

Table 3.7. AIC_c rankings for the exploratory models used to relate wetland habitat features to mallard brood selection on 15 study sites in the prairie parklands of Canada (conventions as in Table 3.2). Alkali wetlands were excluded from this analysis.

Rank	Model	K	AIC_c	ΔAIC_c
1)	PERM + PERM * VEG + COVER + WIDTH + PERM(I) * DATE + PERM(II) * DATE + PERM(III) * DATE + PERM(IV) * DATE + PERM(V) * DATE + PERM(VII) * DATE + COVER(1) * AGE + WIDTH * DATE	25	7649.38	0
2)	PERM + PERM * VEG + COVER + WIDTH + PERM(I) * DATE + PERM(II) * DATE + PERM(III) * DATE + PERM(IV) * DATE + PERM(V) * DATE + PERM(VII) * DATE + COVER(0) * AGE + COVER(1) * AGE + COVER(2) * AGE + COVER(3) * AGE + COVER(4) * AGE + WIDTH * DATE	27	7651.69	2.30

3)	PERM + PERM * VEG + COVER + WIDTH + WIDTH * AGE + WIDTH * DATE	20	7657.45	8.06
4)	PERM + PERM * VEG + COVER + WIDTH + PERM(III)*DATE + COVER(1) * AGE + WIDTH * DATE	21	7658.31	8.92
5)	PERM + PERM * VEG + COVER + WIDTH + PERM(III) * DATE + WIDTH * AGE + WIDTH * DATE	21	7659.09	9.70

Table 3.8. Ranking of mallard brood selection probabilities for wetland permanency classes and dominant emergent vegetation during the early (≤ June 30th) brood rearing season in the Canadian prairie parklands. Alkali wetlands were not included in this analysis.

Permanence (Early)	Parameter Estimate	Standard Error	Probability (%)	Unique ID	Not Different[a]
III(BESY)	-0.943	0.286	1.22	A	C
II	-0.083	0.313	2.89	B	C,D,E,F,H
I	-0.059	0.737	2.96	C	A,B,D,E,F,G,H,I
III(other)	0	0	3.14	D	B,C,E,H
III(CAAT)	0.093	0.124	3.45	E	B,C,D,F,H
III(SCFE)	0.289	0.159	4.19	F	B,C,E,H
III(GLGR)	0.684	0.167	6.23	G	C,H,I,J,K,L
VII	0.751	1.036	6.66	H	B,C,D,E,F,G,I,J,K, L,M,N
IV(TYSP)	0.793	0.207	6.95	I	C,G,H,J,K,L
IV(other)	0.898	0.163	7.71	J	G,H,I,K,L
IV(CAAT)	0.911	0.214	7.81	K	G,H,I,J,L
IV(SCFE)	0.918	0.242	7.87	L	G,H,I,J,K
V	1.733	0.220	17.79	M	H,N
IV(SCSP)	1.905	0.214	21.12	N	H,M

[a] Not different column represents lack of overlap in confidence intervals.

Table 3.9. Ranking of mallard brood selection probabilities for wetland permanency classes and dominant emergent vegetation during the late (> June 30th) brood rearing season in the Canadian prairie parklands. Alkali wetlands were not included in this analysis.

Permanence (Late)	Parameter Estimate	Standard Error	Probability (%)	Unique ID	Not Different[a]
VII	-10.988	182.846	0.00	A	B,C,D,E,F,G,H,I,J,K,L,M,N
III(BESY)	-0.943	0.286	0.94	B	A,C,D
I	-0.323	1.460	1.75	C	A,B,D,E,F,G,H,I,J,K,L
II	-0.213	0.491	1.96	D	A,B,C,E,F,G
III(other)	0	0	2.42	E	A,C,D,F
III(CAAT)	0.093	0.124	2.66	F	A,C,D,E,G
III(SCFE)	0.289	0.159	3.23	G	A,C,D,F
III(GLGR)	0.684	0.167	4.80	H	A,C,I,J,K,L
IV(TYSP)	0.938	0.243	6.19	I	A,C,H,J,K,L
IV(other)	1.042	0.207	6.87	J	A,C,H,I,K,L
IV(CAAT)	1.055	0.249	6.96	K	A,C,H,I,J,L
IV(SCFE)	1.063	0.274	7.01	L	A,C,H,I,J,K
IV(SCSP)	2.050	0.249	18.82	M	A
V	2.708	0.346	36.36	N	A

[a] Not different column represents lack of overlap in confidence intervals.

have been influenced by the fortuitous close fit of a biologically inappropriate model. Wetland permanence was included in all 8 of my top models. Wetland cover type and width of flooded emergent vegetation also were included, showing that configuration and quantity of vegetation were important attributes of wetland selection. An interaction between date and width of flooded emergent vegetation also appeared in all of the best models. Finally, my top 8 models all included an interaction between wetland permanence and the dominant species of vegetation.

Wetland Permanence

Researchers have widely recognized that permanency is an important predictor of wetland selection by broods (Talent et al. 1982, Rotella and Ratti 1992b, Dzus and Clark 1997), and it appeared in all of my final models. This seems obvious, as a wetland's ability to provide the necessities of life for an aquatic duck brood clearly depends on its ability to hold water. Mallard ducklings depend on aquatic habitats for foraging, locomotion, and escape cover. Hence, the ability of a wetland to retain water throughout the brood-rearing season may be the most important wetland characteristic selected by mallard broods.

Alkali wetlands (permanency class VI) had selection probabilities of 74.3 and 61.6% early and late in the brood-rearing season, respectively, implying that if all 15 permanence/vegetation types were equally abundant (i.e., an availability of 100/15 = 6.7%), then alkali wetlands would be used at rates 11.1 and 9.2 times greater than their availability. This overwhelmingly strong preference for alkali wetlands prompted me to conduct additional post hoc analysis. Most selection events involving alkali wetlands were attributable to just 3 broods moving on an almost daily basis between 2 alkali wetlands on a single study area (Baldur, MB), so I suspect that these results were fortuitous. Since alkali wetlands were rare, this potentially atypical behaviour by a few broods could have seriously inflated the selection probabilities for alkali wetlands across my entire data set. Thus, I am unwilling to conclude that alkali wetlands represent the most preferred wetland class by mallard broods, and I recommend that the topic receive additional investigation in areas where alkali wetlands are more abundant.

Upon removal of alkali wetlands from analysis, the relative rankings of other wetland classes did not change greatly, but the selection probabilities increased substantially (Tables 3.8 and 3.9). Because alkali wetlands were so rare, and because their preference ranking seemed to be inflated by the aberrant behaviour of 3 broods, I believe that the final model excluding alkali wetlands is most representative of habitat selection preferences by mallard broods in most areas of the Canadian prairie parklands. Thus, in the following discussion of permanency preferences, I have based my conclusions on the results from the exploratory analysis (Tables 3.7 - 3.9).

Selection probabilities for permanent wetlands (permanency V) were high, especially during the late brood-rearing period (36%). As their name implies, permanent wetlands hold water year round, even during dry years. Late in the brood-rearing season and especially during dry years, permanent wetlands may have provided the only available surface water for mallard broods, as other wetlands became nearly or totally dry. Nevertheless, permanent wetlands also were used extensively (selection = 18%) in the early part of the brood-rearing season when less-permanent water was presumably more abundant, so other reasons must exist for their preference. Permanent wetlands are typically large in comparison to other available wetlands, and often have many other ducks and broods occupying them. Hence, broods using permanent wetlands may have been seeking safety in numbers. Although permanent wetlands often contain a large percentage of open water, they usually contain considerable cover for broods around their periphery. As ducklings age and become less susceptible to avian predators, the large expanses of open water may become more attractive. From the middle of a large permanent wetland, ducklings likely could readily see terrestrial predators approaching and may be easily able to avoid them.

Prior to my study, most research indicated that seasonal wetlands were most preferred by mallard broods (Talent et al. 1982, Duebbert and Frank 1984, Mauser et al. 1994b, Krapu et al. 1997). Nevertheless, I found that semipermanent wetlands were the most important brood habitat, accounting for 51 and 46% of the pooled selection probabilities during early and late brood rearing, respectively (results are pooled over 5 dominant vegetation types; Tables 3.8 and 3.9). Semipermanent wetlands were consistently preferred over seasonal wetlands during both the early and late season; pooled selection probabilities for seasonal wetlands were just 18 and 14%, respectively. This was likely due, at least in part, to actual wetland availability. Many seasonal wetlands that were included in the choice set were nevertheless dry or nearly dry, and therefore unavailable as brood habitat. For example, the driest site (Camp Lake, AB) had only 19% of its seasonal wetlands that retained water during wetland classification (conducted from 19 June to 11 July, inclusive), whereas 81% of its semipermanent wetlands retained water at this time. Averaged over all 15 sites, 53% of seasonal wetlands held water during classification (range 19-88%), versus 91% of semipermanents (range 79-99%) (Appendix 1). Hence seasonal wetlands were less available than semipermanent wetlands, but I could not simply exclude seasonal wetlands that were dry during classification, because many of them would have contained water during some portion of the brood-rearing period.

Not surprisingly, broods exhibited low selection probabilities for ephemeral, temporary, and tillage wetlands, although confidence intervals were large and thus rates did not always differ significantly from other more permanent wetland types (Tables 3.8 and 3.9). Selection probabilities were low for these wetland classes even though I excluded basins that did not retain water until the end of the summer. Although these wetland classes were abundant early in the nesting season, few of them held water when broods began hatching, and thus they were probably not available at all during the brood-rearing period. On average, only 15% of temporary wetlands were flooded during wetland classification (range 0 - 72%), and of the 2 sites where > 25% of the temporary basins were flooded (Elnora and Mixburn; Appendix 1), both received abundant late summer rains which likely caused many of these wetlands to be re-flooded.

A priori, I had suspected that the interaction between wetland permanence and percent of seasonal basins that were flooded during classification would help resolve some of the selection uncertainty pertaining to when wetlands actually became dry, but this interaction was not included in any of the top models. However, some of the effect of wetlands drying up during the brood-rearing season seems to have been accounted for with the permanence by date interaction. In general, selection probabilities were higher for more ephemeral wetlands earlier in the season, and for more permanent wetlands later in the season. Likely, drying wetlands are the principle reason for a temporal change in permanency preferences by broods, but if this was the only reason then the site-level moisture indicator (%WET-III) should have been a superior predictor of this trend. This was not the case, and I therefore believe that additional factors such as food availability also must influence this relationship.

Wetland Cover Type

Although configuration of emergent vegetation has been mentioned in previous studies of mallard brood habitat (Talent et al. 1982), I am not aware of any specific analyses to determine how wetland preferences vary across emergent cover types (as defined by Stewart and Kantrud 1971). Emergent cover can be very important to broods, as predation is the principle determinant of overall duckling survival (Rotella and Ratti 1992a). Because cover type is a good predictor of the amount of concealment that a wetland can provide for broods, it should be included in any analysis of brood habitat preferences.

Wetlands with cover type 1 have emergent vegetation covering the entire wetland basin. Although it might seem that such wetlands would provide the best cover and would be most preferred, at least by young broods, these wetlands had the lowest use by mallard broods. I believe that this was at least partially due to the greater tendency for cover type 1 wetlands to become dry. Thus, the low preference for cover type 1 may have been partly due to inflated availability (i.e., inability to exclude dry wetlands from the choice set), rather than actual avoidance.

Cover types 3 and 4 were most preferred by mallard broods. Usually these cover types occur in semipermanent or permanent wetlands, where deep water in the central portion of the basin often precludes emergent vegetation. Therefore, even though cover types 3 and 4 do not have as much cover as cover types 1 or 2, they usually coincide with larger and deeper wetlands that are more likely to retain water, and are thus selected more frequently by broods.

Width of Flooded Emergent Vegetation

Like cover type, the width of flooded emergent vegetation also influences the amount and quality of concealment that a wetland can provide. Flooded cover is superior to upland cover because ducklings can feed freely while remaining protected from various predators. The width of flooded emergent vegetation may have been a better measure of concealment cover than was cover type. Although both variables describe vegetation and its configuration within a wetland, the width of flooded emergents can only be > 0 if a wetland still contained water at classification time. Therefore, wetlands with positive values for flooded emergent width almost certainly contained water during the brood-rearing period. Consequently, it should have been a better variable than cover type, which can also describe the vegetation arrangement in an otherwise dry wetland.

In my analyses, width of flooded emergents was more important early in the brood rearing season than late. In the early part of the season, wetlands had less vegetative growth, so available cover may have been at more of a premium. In addition, as broods become older they forage less and spend more time in the open (Ringelman and Flake 1980), thus emergent cover becomes less important.

Species of Vegetation

Species composition of wetland vegetation has not been widely studied with regard to brood habitat. Talent et al. (1982) believed that mallard broods had a preference for whitetop rivergrass ponds, but selection preferences were not quantified in relation to other vegetation types. The large sample of broods and available wetlands in this study allowed me to conduct a thorough analysis of dominant vegetation species and their relative preference by mallard broods. Because wetland vegetation is dependent on the seasonal hydrology of a wetland (Stewart and Kantrud 1971, Grosshans 2001), the dominant plant species were somewhat dependent on wetland permanence and could only be considered as an interacting variable with wetland permanency (i.e., a seasonal wetland could not be dominated by cattails, because cattail dominance is a defining characteristic of semipermanent wetlands). The importance of this species-by-permanence interaction to wetland selection was obvious, as shown by its presence in all of the top-fitting models. Possible reasons for vegetation type playing an important part in wetland selection by broods could be the quality of protective cover it provides or its function in providing substrate for aquatic invertebrates, the most important food source of mallard ducklings (Chura 1961).

From my results, it appears that mallards prefer semipermanent wetlands dominated by bulrush, and avoid semipermanents dominated by cattail. I believe preference for bulrush over cattail is due to the physiognomy of each species. There is sufficient space between bulrush stems to allow ducklings to maneuver and remain in contact with their mother and broodmates, while still providing adequate overhead protection from aerial predators. On the other hand, cattail usually grows in very dense stands that make maneuvering difficult. Also in dry years, cattail ponds seem to have less sufficient water than do bulrush ponds.

Contrary to Talent et al. (1982), I detected no preference for seasonal wetlands dominated by whitetop rivergrass versus other seasonal vegetation. However, I did observe a preference for tall manna grass on seasonal wetlands. Mallard broods also seemed to avoid seasonal wetlands dominated by sloughgrass. Sloughgrass often grows in thick stands that completely cover seasonal wetlands during the latter portion of the season. Sloughgrass wetlands are very abundant on the prairie parkland landscape and so their apparent availability to broods is high. However, many of these wetlands have little water by the time broods have left the nest, and moreover they are usually relatively small basins (e.g., < 0.1 ha). I believe the apparent avoidance of sloughgrass wetlands by broods is a result of these wetlands not offering sufficient space or resources for broods, and not due to the vegetative qualities of sloughgrass per se.

General Conclusions

Because wetland permanence, cover type, width of flooded emergents, and dominant plant species are interrelated and do not vary independently, it is difficult to focus on a single variable while excluding the other 3. Moreover, since I could not reliably exclude dry wetlands because inundation levels were usually recorded late in the brood-rearing period, actual availability of wetlands across these 4 variable sets may have differed substantially, and these availabilities likely changed as the season progressed. Thus, it is probably best to view all relevant variables in concert to obtain an accurate picture of the habitat preferences exhibited by mallard broods.

In general, mallard broods preferred more permanent wetlands with a mixture of flooded emergent vegetation and open water. Vegetation types that promoted open stands (e.g. bulrush) seemed to be preferred over vegetation that occurred in dense, potentially impenetrable stands (e.g. cattail and sloughgrass). The availability of adequate water seemed to be the overriding factor, especially late in the brood-rearing season, but other factors clearly were at work.

CHAPTER 4: SUMMARY AND RECOMMENDATIONS

To manage habitats for the benefit of brood survival, it is important to understand how mallard broods move and select habitat within landscapes. Many studies point to the importance of early hatched broods for producing new recruits into the breeding population (Sayler and Willms 1997, Dawson and Clark 2000, Krapu et al. 2000, Anderson et al. 2001, Blums et al. 2002; but see Mauser et al. 1994a). Therefore, management for brood habitat should especially focus on conditions in the early portion of the brood rearing season. Although there were seasonal changes in model parameters and absolute selection probabilities, the relative patterns of movement and wetland selection did not differ greatly between early and late season. Generally speaking, a good brood wetland in the early season also was good in the late season.

Although mallard broods clearly preferred certain wetlands over others, they used almost all varieties of wetland to at least some extent. Providing breeding waterfowl with landscapes containing a high density of wetlands would ensure that suitable basins were always nearby, thereby minimizing potentially dangerous overland movements. Hence, management should further focus on landscapes that contain a wide diversity of wetlands. Permanent and semipermanent wetlands are especially important for ensuring that some brood habitat is nearby and available, even during dry years or drier portions of the breeding season (i.e. later in the summer).

Landscape management should continue to focus primarily on nesting habitat, as hatching rates are the most important determinant of annual recruitment in mallards (Hoekman et al. 2002). But the Prairie Habitat Joint Venture (PHJV) strategy for managing nesting habitat closely parallels the requirements of broods. Throughout the prairie pothole region, duck densities are highest in areas with high wetland densities (Reynolds et al. 2001). These are also the areas where the most PHJV programs have been implemented for increasing nest success. To maximize recruitment, future nest habitat management should target these same landscapes, but also should consider the quality of brood rearing habitat. Permanent cover provided for nesting ducks also may benefit early hatched broods during overland moves, thereby reducing risk of brood predation. Coincidentally, Howerter (2003) found that areas with permanent cover were preferred by early nesting ducks and provided higher hatching rates.

Managers should not only consider waterfowl and wetland densities when securing habitat, but also the permanence of local wetlands. An abundance of successful nests and young broods will not enhance recruitment if broods can not survive (Sayler and Willms 1997). Attracting ducks to successfully nest in managed landscapes with low brood survival could act as a population sink. However, if these landscapes can be jointly managed for high brood survival along with high nest success, results could be doubly favorable. Further, by securing nesting habitat containing favorable brood-rearing wetlands, even more hens can be attracted to nest in managed nesting areas.

Selection analysis showed that vegetation plays a very important role in wetland selection by mallard broods. Configuration of vegetation on wetlands should be considered when rating landscapes for brood habitat. The amount of flooded emergent vegetation a wetland contains can heavily influence habitat choices of broods. The greater the width of flooded emergent vegetation, the more likely a wetland was chosen, especially early in the brood-rearing season. Nevertheless, a central expanse of open water also was important to selection. Finally, species of vegetation appeared to explain a great deal of selection for wetlands of the same permanence. Cattail ponds, although abundant in the prairie parklands, were the least preferred of the semipermanent wetlands, whereas bulrush ponds were highly preferred. Broods strongly avoided seasonal wetlands with sloughgrass as the dominant vegetation.

Brood ponds should normally be within 500 m of a nest site to be considered available to a brood. Minimizing the distance a brood must travel for adequate habitat should be emphasized, and targeting areas with high wetland densities for nesting habitat management can help achieve this. Duckling mortality is very high shortly following hatch (Ball et al. 1975, Talent et al. 1983, Mauser et al. 1994a), and distance of overland moves is thought to be negatively correlated with survival (Ball et al. 1975), so good brood habitat should always be in close proximity to nesting areas. A landscape in the prairie parkland region should always contain permanent or at least semipermanent wetlands in order to be considered good brood habitat for mallards. These wetlands should also contain abundant flooded emergent vegetation along with areas of open water. Given the choice, vegetation types promoting more open stands such as bulrush should be favored over vegetation types occurring in dense, potentially impenetrable stands (e.g., cattail and sloughgrass).

For results from habitat selection studies to be useful, landscape managers must assume that habitat selection decisions are positively correlated with survival or reproductive success (Clark and Shutler 1999). Natural selection should favor broods that select the best wetlands to ensure their survival to fledging age. Historically this assumption was undoubtedly true, but in today's heavily modified landscapes this may not be the case (Orians and Wittenberger 1991). Nevertheless, merely linking survival with habitat is not always useful if the habitat is not chosen by the organism or is not available (Pribil 1998, Howerter 2003). Consequently, relating movement patterns with selection studies would help managers ensure that preferred habitat is accessible to broods. Linking both of these with survival would give even more strength to claims that managing a landscape for certain habitat features will indeed increase population growth, and future analyses are intended for these data (D. Howerter, unpubl. data).

This study represented a compilation of data acquired from 15 different study sites in 5 different years, and I was not able to influence how the data were collected from each potential wetland. Nevertheless, with the benefit of hindsight and for the benefit of future studies, I believe it is worth identifying additional variables that might have been useful in analysis. A measurement of distance from the prior location to each available wetland could have been included to examine the importance of proximity in a brood's ultimate choice of wetland (i.e., rather than assume all wetlands within 500 m were equally available, availability could have been modeled as a function of proximity). Also, measurements of wetland size (e.g., basin area or perimeter) may have been helpful. Although size information was potentially available from our GIS layer, it was not readily linked to the other attribute data. Moreover, because aerial photo delineation took place after field work was completed, there was not complete agreement between basins delineated in the GIS layer and wetland attributes collected from the ground (i.e. a peanut-shaped wetland may have been identified as one large pond in the GIS layer, but as 2 smaller ponds from the ground). Additionally, it would have been very helpful to have "real-time" data on wetland inundation (i.e. measured biweekly throughout the brood-rearing period), and to have had more information available than just "wet" or "dry" (i.e., wet basins could have been recorded as 1/4, 1/2, 3/4, or completely full). Finally, it would be useful to revisit some landscapes where alkali wetlands are much more abundant in order to validate or invalidate the apparently strong preference for alkali wetlands that I observed in this study.

My study reveals some key and formerly misunderstood factors relating to movement patterns and wetland selection by mallard broods. I believe managers can use these results to make better decisions concerning procurement or enhancement of potential managed nesting habitat. Good brood habitat can translate into increased duckling survival and subsequently higher recruitment rates for managed landscapes.

Appendix 1. Wetland covariates for 15 PHJV Assessment study areas in the Canadian prairie parklands.

Study Area	Area (km^2)	Temporary Density / km^2	Seasonal Density / km^2	Semipermanent Density / km^2	Temporary Inundated (%)	Seasonal Inundated (%)	Semipermanent Inundated (%)
Allan Hills	65.50	1.05	8.99	8.05	10.00	59.22	80.96
Baldur	67.17	2.47	2.47	3.45	23.49	61.81	87.05
Belmont	65.10	6.84	5.16	4.84	13.03	42.21	89.09
Camp Lake	65.90	5.84	21.84	6.30	0.78	19.21	81.15
Davis	67.66	6.84	9.52	5.97	0.00	41.52	98.48

Elnora	65.95	8.49	20.64	2.49	36.07	74.69	93.10
Erskine	66.03	5.13	9.71	4.42	1.47	31.85	87.13
Hamiota	80.38	0.75	10.21	0.45	6.67	37.30	98.70
Kutawa	67.05	0.98	19.82	3.74	22.73	78.92	99.34
Mixburn	65.72	7.29	28.81	15.02	72.44	88.31	96.10
Parkside	66.03	0.32	4.30	2.14	0.00	41.08	87.18
Pine Lake	65.61	1.34	21.35	5.11	10.07	76.41	94.65
Punnichy	55.44	2.78	16.45	3.12	5.19	40.98	91.46
Shoal Lake	67.42	4.97	9.88	1.16	20.60	69.19	95.71
Willowbrook	66.83	6.79	16.40	4.94	2.64	36.56	78.57

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. B. N. Petrox and F. Csaki, editors. Second International Symposium on Information Theory. Akedemiai Kiado, Budapest, Hungary.

Anderson, D. R. and K. P. Burnham. 2002. Avoiding pitfalls when using information – theoretic methods. Journal of Wildlife Management 66(3):912-918.

_____, _____, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64(4):912-923.

Anderson, M. G., R.B. Fowler and J.W. Nelson. 1995. Northern grassland conservation and the prairie joint venture. Proceedings of the North American Wildlife and Natural Resources Conference 60:404-412.

Anderson, M. G., M. S. Lindberg, and R. B. Emery. 2001. Probability of survival and breeding for juvenile female canvasbacks. Journal of Wildlife Management 65:385-397.

Bacon, B. R., and J. O. Evrard. 1989. Horizontal mist net for capturing upland nesting ducks. North American Bird Bander 15:18-19.

Ball, I. J., D. S. Gilmer, L. M. Cowardin and J .H. Riechmann. 1975. Survival of wood duck and mallard broods in northcentral Minnesota. Journal of Wildlife Management 39:776-780.

Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. Pages 204-227 in A. Van Der Valk, editor. Northern prairie wetlands. Iowa State University Press, Ames, Iowa.

Beauchamp, W. D., R. R. Koford, T. D. Nudds, R. G. Clark, and D. H. Johnson. 1996. Long term declines in nest success of prairie ducks. Journal of Wildlife Management 60:247-257.

Berg, P. 1956. A study of waterfowl broods in eastern Montana with special reference to movements and the relationship of reservoir fencing to production. Journal of Wildlife Management 20:253-262.

Biondini, M. E., A. A. Steuter, and R. G. Hamilton. 1999. Bison use of fire-managed prairies. Journal of Range Management 52:454-461.

Blums, P., G. Clark, and A. Mednis. 2002. Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. Journal of Animal Ecology 71:280-295.

Canadian Wildlife Service and U. S. Wildlife Service. 1986. North American Waterfowl Management Plan: a strategy for cooperation. Canadian Wildlife Service, Ottawa, ON, Canada and U. S. Fish and Wildlife Service, Washington, D. C., USA.

Chura, N. J. 1961. Food availability and preferences of juvenile mallards. Transactions of the North American Wildlife Conference 26:121-134.

Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. Wildlife Society Bulletin 19:534-543.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80:272-287.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80:566-575.

Coulter, M. W. 1958. A new waterfowl nest trap. Bird Banding 29:236-241.

Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monograph 92.

_____, and D. H. Johnson. 1979. Mathematics and mallard management. Journal of Wildlife Management. 43:18-35.

_____, _____, T. L. Shaffer, and D. W. Sparling. 1988. Applications of a simulation model to decisions in mallard management. U. S. Fish and Wildlife Service, Fish and Wildlife Technical Report 17.

Dawson, R. D., and R. G. Clark. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. Condor 102:930-935.

Dietz, N. J. 1994. A walk-in trap for nesting ducks. Wildlife Society Bulletin 22:19-22.

Duebbert, H. F., and A. M. Frank. 1984. Value of prairie wetlands to duck broods. Wildlife Society Bulletin 12:27-34.

Dzubin, A. and J. B. Gollop. 1972. Aspects of mallard breeding ecology in Canadian parkland and grassland. Pages 113-152 in Population ecology of migratory birds - a symposium. U.S. Fish and Wildlife Service, Wildlife Resource Report 2.

Dzus, E. H. and R. G. Clark. 1997. Overland travel, food abundance, and wetland use by mallards: relationships with offspring survival. Wilson Bulletin 109:504-515.

Evans, C. D., and K. E. Black. 1956. Duck production studies on the prairie potholes of South Dakota. U.S. Fish and Wildlife Service Special Science Report on Wildlife 32.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539-590.

Giudice, J. H. 2001. Visibility bias in waterfowl brood surveys and population ecology of dabbling ducks in central Washington. Ph.D., University of Idaho, Moscow, Idaho, USA.

Grosshans, R. E. 2001. Long-term vegetation dynamics following water level stabilization in a prairie marsh. Dissertation, University of Manitoba, Winnipeg, Manitoba, Canada.

Hamilton, R. G. 1996. Using fire and bison to restore a functional tallgrass prairie landscape. Transactions of the North American Wildlife and Natural Resources conference 61:208-214.

Higgins, K. F., L. M. Kirsch, H. G. Duebbert, A. T. Klett, J. T. Lokemoen, H. W. Millar, and A. D. Kruse. 1977. Construction and operation of cable-chain drag for nest searches. U.S. Fish and Wildlife Service, Wildlife Leaflet 512.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analysis of the life cycle of mid-continent mallards. Journal of Wildlife Management 66:883-900.

Howerter, D. W. H. 2003. Factors affecting duck nesting in the aspen parklands: a spatial analysis. Dissertation, Montana State University, Bozeman, Montana, USA.

Johnson, D. H., D. W. Sparling, and L. M. Cowardin. 1987. A model of the productivity of the mallard duck. Ecological Modeling 38:257-276.

Keith, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildlife Monographs 6.

Klett, A. T., H. F. Duebbert, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairies Pothole Region. U.S. Fish and Wildlife Service Resource Publication 158.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. Bioscience 49:39-50.

Krapu, G. L., R. J. Greenwood, C. P. Dwyer, K. M. Kraft, and L. M. Cowardin. 1997. Wetland use, settling patterns, and recruitment in mallards. Journal of Wildlife Management 61:736-746.

Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox. 2000. Factors limiting mallard brood survival in prairie pothole landscapes. Journal of Wildlife Management 64:553-561.

Lands Directorate. 1986. Wetlands in Canada: a valuable resource. Fact Sheet 86-4. Environment Canada, Ottawa, Canada.

Lokemoen, J. T. 1973. Waterfowl production on stock-watering ponds in the northern plains. Journal of Range Management 26:179-184.

Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44:695-699.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Discrete choice models with changing availability. Pages 150-163 in Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands

Mauser, D. M., and R. L. Jarvis. 1991. Attaching radio transmitters to 1-day-old mallard ducklings. Journal of Wildlife Management 55:488-491.

_____, _____, and D. S. Gilmer. 1994a. Survival of radio-marked mallard ducklings in northeastern California. Journal of Wildlife Management 58:82-87.

_____, _____, and _____. 1994b. Movements and habitat use of mallard broods in northeastern California. Journal of Wildlife Management 58:88-94.

Morris, D. W., and D. L. Davidson. 2000. Optimally foraging mice match patch use with habitat difference in fitness. Ecology 81:2061-2066.

Mulhern, J. H., T. D. Nudds, and B. R. Neal. 1985. Wetland selection by mallards and blue-winged teal. Wilson Bulletin 97:473-485.

National Wetlands Working Group. 1988. Wetlands of Canada. Ecological Land Classification Series, No. 24. Environment Canada, Sustainable Development Branch, Ottawa, Canada.

Olsen, G. H., J. F. Dein, G. M. Haramis, and D. G. Jorde. 1992. Implanting radio transmitters in wintering canvasbacks. Journal of Wildlife Management 56:325-328.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29-S49.

Orthmeyer, D. L., and I. J. Ball. 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. Journal of Wildlife Management 54:62-66.

Paquette, G. A., J. H. Devries, R. B. Emery, D. W. Howerter, B. L. Joynt, and T. P. Sankowski. 1997. Effects of transmitters on reproduction and survival of wild mallards. Journal of Wildlife Management 61:953-961.

Pietz, P. J., and D. A. Buhl. 1999. Behaviour patterns of Mallard Anas platyrhynchos pairs and broods in Minnesota and North Dakota. Wildfowl 50:101-122.

Prairie Habitat Joint Venture. 1986. Canadian Wildlife Service.

Pribil, S. 1998. Reproductive success is a misleading indicator of nest-site preference in the red-winged blackbird. Canadian Journal of Zoology 76:2227-2234.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. Journal of Wildlife Management 65:765-780.

Ringelman, J. K. 1990. Decoy trap for ducks. U.S. Fish and Wildlife Service Leaflet 13.

_____, and L. D. Flake. 1980. Diurnal visibility and activity of blue-winged teal and mallard broods. Journal of Wildlife Management 44:822-829.

Rotella, J. J., D. H. Howerter, T. P. Sankowski, and J. H. Devries. 1993. Nesting effort by wild mallards with 3 types of radio transmitters. Journal of Wildlife Management 57:690-695.

_____, and J. T. Ratti. 1992a. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. Journal of Wildlife Management 56:499-507.

_____, and _____. 1992b. Mallard brood movements and wetland selection in southwestern Manitoba. Journal of Wildlife Management 56:508-515.

_____, R. G. Clark, and A. D. Afton. 2003. Survival of female lesser scaup: effects of body size, age, and reproductive effort. The Condor 105:336-347.

Sargeant, A. B., A. D. Kruse, and A. D. Afton. 1974. Use of small fences to protect ground bird nests from mammalian predators. The Prairie Naturalist 6:60-63.

_____, and D. G. Raveling. 1992. Mortality during the breeding season. Pages 396-422 in Ecology and management of breeding waterfowl. B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. University of Minnesota Press, Minneapolis, MN, USA.

SAS Institute. 1996. SAS/STAT changes and enhancements through version 6.12. SAS Institute, Cary, North Carolina, USA.

Sayler, R. D., and M. A. Willms. 1997. Brood ecology of mallards and gadwalls nesting on islands in large reservoirs. Journal of Wildlife Management 61:808-815.

Sharp, D. E., and J. T. Lokemoen. 1987. A decoy trap for breeding season mallards in North Dakota. Journal of Wildlife Management 51:711-715.

Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated pothole region. U.S. Fish and Wildlife Service Resource Publication 92.

Stoudt, J. H. 1971. Ecological factors affecting waterfowl production in the glaciated prairie region. U.S. Fish and Wildlife Service Resource Publication 92.

Swanson, G. A., V. A. Adomaitis, F. B. Lee, J. R. Serie, and J. A. Shoesmith. 1984. Limnological conditions influencing duckling use of saline lakes in south-central North Dakota. Journal of Wildlife Management 48:340-349.

Talent, L. G., R. L. Jarvis, and G. L. Krapu. 1983. Survival of mallard broods in south-central North Dakota. Condor 85:74-78.

______, G. L. Krapu, and R. L. Jarvis. 1982. Habitat use by mallard broods in south central North Dakota. Journal of Wildlife Management 46:629-635.

Turner, B. C., G. S. Hochbaum, F. D. Caswell, and D. J. Nieman. 1987. Agricultural Impacts on Wetland Habitats on the Canadian Prairies 1981-1985. Transactions of the Fifty-second North American Wildlife and Natural Resources Conference. 206-215.

Weller, M. W. 1957. An automatic nest-trap for waterfowl. Journal of Wildlife Management 21:456-458.

______. 1964. The reproductive cycle. Pages 35-79 *in* The waterfowl of the world, Volume 4. Country Life, London, England.