

**MALLARD DUCKLING SURVIVAL  
AND HABITAT SELECTION  
IN THE CANADIAN  
PRAIRIE POTHOLE REGION**

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By  
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## ABSTRACT

Like life-history theory, wildlife management decisions are typically predicated on trade-offs between benefits associated with investing resources to achieve higher reproductive or survival rates versus costs or risks of achieving those goals. On the Canadian prairies, most waterfowl conservation resources are directed to policies and programs that seek to increase duck nesting success. Limited attention has focused on post-hatching life-cycle stages, yet, despite considerable recent work on duckling survival rates, many uncertainties remain concerning how abiotic and biotic factors affect duckling survival rates. The role of upland habitat characteristics may be important but has received limited attention. I evaluated hypothesized sources of variation in duckling survival for 617 mallard (*Anas platyrhynchos*) broods on 27 Canadian prairie-parkland sites, with emphasis on assessing effects of managed and remnant natural upland habitats. I contrasted suites of *a priori* and *post hoc* exploratory models that incorporated effects of landscape, weather, female and brood-related variables to explain variation in duckling survival rates. Survival was lower for ducklings that used areas with high proportions of semi-permanent wetlands, as well as for broods that travelled farther overland. Exploratory analyses revealed further that survival of ducklings was negatively related to the amount of managed hayland. In contrast, duckling survival was positively associated with the amount managed grassland. There was no evidence of trade-offs between benefits of managing habitat to enhance duck nesting success versus costs in terms of lower subsequent duckling survival.

I also addressed unresolved questions about how birds balance costs and benefits of selecting habitats by determining the survival consequences of habitat choices made during brood-rearing. In theory, fitness should be higher in preferred habitats, but this assumption is rarely tested. Fitness consequences (i.e., duckling survival) of habitat selection patterns were determined at landscape and local scales using logistic regression and information-theoretic model selection techniques. Best-approximating landscape-level models indicated that mallard females selected brood-rearing areas with a high proportion of wetland and perennial upland habitats, but duckling survival was not related to habitat selection patterns at this scale. At finer spatial scales, females selected brood-rearing areas with high proportions of wetland habitats, but, contrary to expectation, duckling survival was lower when females raised their broods in these areas. Females avoided areas with abundant perennial cover and wetlands with little vegetative cover and, consistent with prediction, duckling survival was higher when females selected areas with

low perennial cover. Thus, females did not consistently select brood-rearing habitats that conferred the highest fitness benefits. Rather, the relationship between habitat selection and duckling survival depended on spatial scale and habitats considered.

## ACKNOWLEDGEMENTS

As with many things in life, we can not do it alone and while I use the word “I” and “my” throughout this thesis, this was a team effort and I would like to give my thanks here.

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## **DEDICATION**

I dedicate this thesis to my niece and nephew; Eryca (3) and Dylan (5):

You are my inspiration and I did this for you. I hope the research we undertake to help understand wildlife-habitat relationships will ensure that the critters we see today are still there for you to enjoy as you grow up.

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# CHAPTER 1 GENERAL INTRODUCTION

## 1.1 Habitat selection theory

Habitat selection theory suggests that animals select habitats that optimize their fitness. The theoretical principle underlying the theory of habitat selection is that preferred habitats are those where reproductive success is higher (Orians and Wittenberger 1991). Since choice of habitats for breeding-season activities ultimately influences reproductive success via offspring survival, it is often assumed that habitat selection is driven by the process of natural selection (e.g., Fretwell and Lucas Jr. 1969, Rosenzweig 1981, Jaenike and Holt 1991). Trade-offs are thought to shape habitat selection decisions, since individuals must balance the benefits of gaining access to critical resources for producing offspring or ensuring self-maintenance against costs of increased risk of mortality. Similarly, life-history theory presumes that trade-offs shape the reproductive and survival rates of organisms because investment in one reproductive event or trait comes at a cost to future reproductive events or other traits (Stearns 1992). The cost of reproduction is likely the best studied life history trade-off; a hypothesis that predicts that energy allocated to reproduction is unavailable for growth, maintenance, and survival (Stearns 1989).

Habitat decisions are assumed to be adaptive but this is rarely tested and when it is, evidence remains ambiguous (Martin 1998, Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Davis 2005, Howerter et al. 2008). To understand its adaptive significance, both habitat choice and the fitness consequences of that choice must be considered (Jones 2001). Over the past decade, there has been a sharper focus on explicitly linking habitat selection patterns to fitness information in diverse taxa. For example, pattern-process relationships have been evaluated in greater sage-grouse (*Centrocercus urophasianus*; Aldridge and Boyce 2007), northern spotted owls (*Strix occidentalis caurina*; Olson et al. 2004), prairie ducks (*Anas sp.*; Clark and Shutler 1999, Howerter et al. 2008), sparrows (*Ammodramus sp.*; Gjerdrum et al. 2005), red squirrels (*Tamiasciurus hudsonicus*; Wheatley et al. 2002), and snapping turtles (*Cherydra serpentina*; Kolbe and Janzen 2002). Birds remain a popular study group for linking fitness measures to habitat selection because they are relatively easy to count and their reproductive success is easy to monitor when compared with many other organisms (Bock and Jones 2004). Often, reproductive success in birds is measured by monitoring nesting success because it can be difficult to monitor post-fledging survival due to high mobility of juveniles (Bock and Jones

2004). However, few studies combine offspring survival and habitat selection of precocial species, where young are highly mobile immediately after hatching and can be difficult to track once they leave the nest. Thus, I sought to address unresolved questions about how birds balance costs and benefits of selecting habitats by determining the offspring survival consequences of habitat choices made during brood-rearing in a precocial species (mallard, *Anas platyrhynchos*) with exclusive maternal care.

Nest-site selection in waterfowl has been well studied (e.g., Gloutney and Clark 1997, Howerter 2003) and the adaptive significance of mallard nest-site selection has been explored (Clark and Shutler 1999, Howerter et al. 2008). Nesting success has been identified as the primary breeding season vital rate influencing mallard population growth (Hoekman et al. 2002) and, as a result, much of the focus of waterfowl research has been on nest survival. However, a successfully hatched nest need not equate to recruitment (i.e., fledged young; Baldassarre and Bolen 2006). In terms of the influence of breeding season vital rates on population growth rates, duckling survival in mallards is surpassed only by nesting success and adult female survival rates (Hoekman et al. 2002).

To date, studies addressing patterns of habitat use by brood-rearing mallards have been limited to wetland habitats, have not addressed potential consequences to duckling survival of habitat selection, and have been considered at only a single spatial scale (Talent et al. 1982, Dzus and Clark 1997b, Raven et al. 2007). Habitat selection is thought to be a hierarchical process (Johnson 1980, Chalfoun and Martin 2007) and female mallards may optimize fitness by balancing choices across different spatial scales (Mack and Clark 2006). Predator communities, density of conspecifics, and food availability may be assessed at different spatial scales, and ultimately influence habitat choice. Therefore, I evaluate the offspring survival consequences of wetland and upland habitat selection at two spatial scales to resolve questions about the adaptive nature of habitat selection, using offspring survival as a metric of fitness.

## **1.2 Waterfowl management**

In the mid-1980s, concerns regarding declining waterfowl populations led to the inception of the North American Waterfowl Management Plan (NAWMP). Habitat degradation and loss since the 1960's was identified as a main driver of declining waterfowl populations. The need for habitat management on public and private lands, as well as changes in land use and agricultural

practices were identified as actions necessary to increase waterfowl populations (CWS and U.S.FWS 1986). Within NAWMP, Joint Ventures (i.e., regional, multi-agency partnerships) were created to address some of the primary species and regions of concern. The Prairie Habitat Joint Venture (PHJV) was developed to guide the protection and enhancement of waterfowl breeding habitat through upland habitat management programs and policies to improve nesting success in the prairie-parkland region of central Canada. The PHJV Assessment study (1993-2000, Figure 1.1) was designed to test the efficacy of these management programs (i.e., at attracting nesting birds to, and increasing nesting success in, managed habitats). Upland habitats (i.e., areas that can not support growth of wetland vegetation or do not hold water with any permanency) were classified in relation to the vegetation present and the agricultural activities (i.e., annual cropping, grazing or haying) performed on the land (Table 1.1). For my analyses, I did not look at individual management techniques (Table 1.2) but rather if a particular habitat type (e.g., grassland) was managed or not. I also combined shrubland and woodland into one habitat type: woody cover. Wetland habitats were classified following Stewart and Kantrud (1971), a system which bases classification on the type of vegetation present (i.e., permanency class) and the way in which emergent plants are distributed in the wetland (i.e., cover type, Table 1.3).

It is unknown whether upland habitat management for improving nesting success has a positive impact on overall waterfowl productivity. It was implicitly assumed that upland habitat composition has no negative consequences for duckling survival rates; however, this assumption has not been tested. Using the PHJV Assessment data, I address this information gap by revisiting the question of what factors influence duckling survival rates, while looking specifically at effects of managed and remnant natural upland habitats. Data from this large-scale, long term study can be used to address broad, ecological questions as well as applied, management-oriented questions for which it was designed.

### **1.3 Objectives and thesis organization**

I aimed to address two key problems with this thesis. First, in Chapter 2, I evaluated hypothesized sources of variation in duckling survival rates, with new emphasis on assessing possible effects of managed and remnant natural upland habitats. Then, in Chapter 3, I examined the adaptive nature of habitat selection by linking duckling survival rates to patterns of habitat

use by brood-rearing females. I have organized this thesis as two independent manuscripts intended for publication in peer-reviewed journals. As a result, descriptions of study sites and field methods are somewhat repetitive between the two chapters although I attempted to reduce duplication.

## 1.4 Tables

Table 1.1 Description of habitat types in the prairie-parkland region of Canada, 1993 - 2000.

<b>Habitat Type</b>	<b>Description</b>
Cropland	Areas that are tilled and planted to grain or row crops, or that are plowed and left fallow, or contain crop residue.
Grassland	Areas vegetated with native and/or introduced grasses, forbs, trees, and shrubs (aerial cover of trees and shrubs <30%). Grassland may be idled, grazed, or hayed.
Hayland	Areas seeded to grasses and/or legumes for forage production and that are hayed annually.
Wetland	All areas mapped as wetland according to Stewart and Kantrud (1971). Wetlands may be idled, grazed, or hayed.
Woody cover	Shrubland (areas with shrubs 0.5 to 6.0-m tall that have an aerial cover >30%) and woodland (areas with woody plants (trees or tall shrubs) >6.0m in height having an aerial cover >30%). Woody cover may be idled or grazed.

Table 1.2 - Description of PHJV management techniques used in the prairie-parkland region of Canada, 1993 - 2000.

<b>Management Techniques</b>	<b>Description</b>
Delayed grazing	Areas of grassland, woody cover, planted cover, and wetland that receive limited and controlled grazing pressure, usually late in the nesting season.
Delayed haying	The first hay cut is delayed until after 15 July and is restricted to 1 cut per season.
Idled hayland	Hayland that was previously cut but is now idled.
Idled parkland	Areas of idled grassland, woody cover, and wetland protected from haying, burning, grazing, plowing, or draining.
Idled pasture	Areas of grassland, woody cover, and wetland that were previously grazed but are now idled.
Planted cover	Previously cultivated areas seeded to native or introduced grasses and/or forbs and then idled.
Rotational grazing	Additional fencing used for control of grazing pressure in areas of grassland, woody cover, and wetland. Formerly cultivated areas (cropland and hayland) may also be fenced and grazed. Former cropland is seeded to a mixture of grasses and forbs prior to grazing.
Chemical fallow	Cropland fallowed using chemicals to kill vegetation.
Direct seeding	Seeding crop directly into stubble.
Fall seeded crop	Fall seeded crops (e.g., winter wheat, fall rye, canola).



Table 1.3 - Description of wetland habitat classification (follows Stewart and Kantrud 1971) used during the PHJV assessment study in the prairie-parkland region of Canada, 1993 - 2000.

<b>Wetland Habitat</b>	<b>Description</b>
<b>Permanency Classification</b>	
Seasonal (class 3)	Deepest vegetational zone dominated by shallow-marsh vegetation (e.g., whitetop river grass ( <i>Scholochloa festucacea</i> ), sloughgrass ( <i>Beckmania syzigachne</i> ), large sedges ( <i>Carex atherodes</i> ) etc.).
Semi-permanent (class 4)	Deepest vegetational zone dominated by deep-marsh vegetation (e.g., cattail ( <i>Typha spp.</i> ), hardstem bulrush ( <i>Scirpus acuta</i> ), or alkali bulrush ( <i>Scirpus paludosus</i> )).
<b>Cover type</b>	
2	5%-95% open water with dense patches or diffuse open stands of emergent vegetation.
3	5%-95% open water surrounded by a peripheral band of emergent cover averaging 2m or more in width.
4	>95% open water, or small ponds where emergent cover is restricted to marginal bands <2m in average width.

## 1.5 Figures

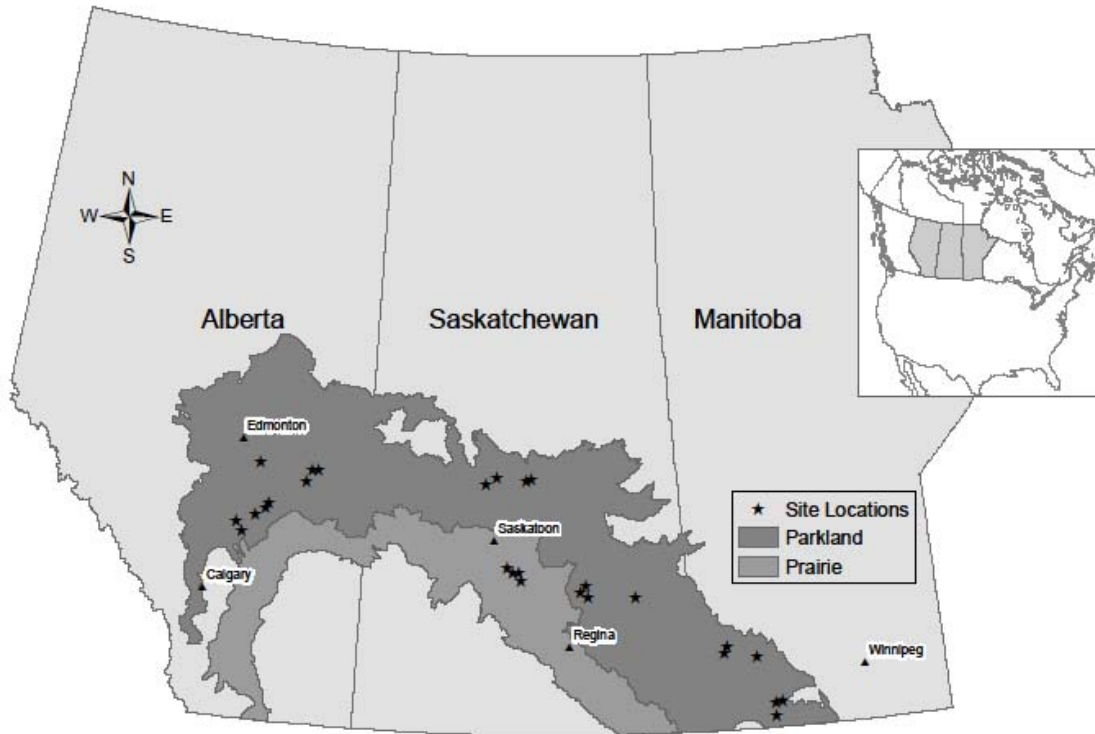


Figure 1.1 - Map showing study site locations in the prairie-parkland region of the south-central Canadian, 1993 – 2000.

# **CHAPTER 2    LANDSCAPE-LEVEL CORRELATES OF MALLARD DUCKLING SURVIVAL: IMPLICATIONS FOR CONSERVATION PLANNING**

## **2.1    Introduction**

North American waterfowl management agencies currently invest millions of dollars annually in habitat conservation programs. The success of these programs hinges not only on attracting birds to managed habitat but also on increasing breeding success in these areas. To increase duck reproductive success on managed lands in the Prairie Pothole Region (PPR), habitat management planning has typically focused on improving nesting success. However, duck recruitment does not depend solely on successfully hatched nests but also on survival of ducklings through the brood-rearing period (Baldassarre and Bolen 2006). In terms of the influence of breeding season vital rates on population growth rates, duckling survival in mallards is surpassed only by nesting success and adult female survival rates (Hoekman et al. 2002). Therefore, brood requirements also should be considered when managing for waterfowl productivity. This lack of consideration for brood survival in management planning may be due to the perception that many factors affecting duckling survival cannot be modified by direct management programs. However, it is unknown whether upland habitat management for improving nesting success has an impact on other vital rates, including duckling survival.

Here, I evaluate hypothesized sources of variation in duckling survival, with new emphasis on assessing possible effects of managed and remnant natural upland habitats. Hypotheses and associated predictions are described below and listed in Table 2.1.

### **2.1.1    Female and brood attributes**

Older females with more brood-rearing experience could provide better care. Conversely, younger females might hatch broods later in the season and provide poor care due to their inexperience and/or an increased need to regain nutrients lost during egg laying and incubation or to moult. Duckling survival was unrelated to female age in mallards (Krapu et al. 2000,

Hoekman et al. 2004) but was higher for wood duck (*Aix sponsa*) ducklings raised by older females in the southern United States (Davis et al. 2007).

Evidence for seasonal variation in duckling survival has been equivocal. Duckling survival decreased with later hatch date in some cases (Orthmeyer and Ball 1990, Rotella and Ratti 1992b, Krapu et al. 2000) but not in others (Leonard et al. 1996, Gendron and Clark 2002, Davis et al. 2007). Suggested hypotheses for seasonal variation in duckling survival include 1) declining wetland abundance or quality (Rotella and Ratti 1992b, Dzus and Clark 1998), 2) decreased invertebrate numbers (Cox Jr. et al. 1998), 3) increasing salinity in wetlands as water levels decrease (Mitcham and Wobeser 1988), 4) increased predation as alternate prey availability decreases (Grand and Flint 1995), and 5) reduced maternal care (Krapu et al. 2000).

In contrast to the evidence for seasonal variation in survival, evidence for a relationship between duckling survival and duckling age has been consistent. Ducklings are most susceptible to mortality events in the first week of life (Talent et al. 1983, Sayler and Willms 1997, Gendron and Clark 2002). The incomplete thermoregulatory ability of ducklings in their first week of life makes them more susceptible to weather events than older ducklings (Sedinger 1992), suggesting potential for an interaction between age and weather events. Indeed, Krapu et al. (2006) found that survival of ducklings <7 days old was reduced by rain events whereas survival of older ducklings was not. Sayler and Willms (1997) suggested that mortality may be a result of inclement weather (i.e., high winds, rain and large waves) or long overwater moves that result in increased energy use and decreased foraging time. Young ducklings may also be more susceptible to predation events (Talent et al. 1983, Sayler and Willms 1997).

Evidence for a relationship between duckling survival and brood size has been inconsistent. In a brood size manipulation study, mallard duckling survival rates were lower in enlarged broods than in control broods; relatively fewer ducklings were effectively concealed and warmed by females attending larger broods (Dzus and Clark 1997a). However, in other studies with mallards, duckling survival was unrelated to brood size (Krapu et al. 2000, Gendron and Clark 2002). Northern pintail (*Anas acuta*) and wood duck ducklings in smaller broods had higher survival rates (Guyn and Clark 1999, Davis et al. 2007, respectively). Conversely, females might be more prone to abandon the smallest broods resulting in brood loss (e.g., Barrow's goldeneye, *Bucephala islandica*; Eadie and Lyon 1998). These counteracting forces set up the possibility of stabilizing selection on brood size.

### 2.1.2 Wetland and upland habitats

Duckling survival is influenced by the quality of wetland habitat encountered during the brood-rearing period (e.g., Rotella and Ratti 1992b, Dzus and Clark 1998, Krapu et al. 2000; 2006). Wetland habitat quality may be related to several attributes including wetland permanency, vegetative cover, and density.

Wetland permanency (Stewart and Kantrud 1971) may influence duckling survival and, although it is still debated which is most significant, both seasonal and semi-permanent wetlands provide important brood habitat via vegetative protection from predators and the elements, and food availability (Duebber and Frank 1984, Rotella and Ratti 1992a, Dzus and Clark 1997b, Krapu et al. 2006). Indeed, Krapu et al. (2006) found that >90% of wetlands used by mallard broods in the U.S. PPR were seasonal and semi-permanent wetlands. In terms of areal extent, seasonal and semi-permanent wetlands are the predominant wetland types in the PPR (Stewart and Kantrud 1971). Spatiotemporal variability inherent in prairie wetland dynamics, and their abundance on the landscape, may influence whether seasonal or semi-permanent wetlands are most important for ducklings. During a prairie drought, mallard broods used semi-permanent wetlands more than seasonal wetlands and following drought, brood use of seasonal wetlands increased while use of semi-permanent wetlands decreased (Krapu et al. 2006). Rotella and Ratti (1992a) also found that during dry years, mallard broods spent more time on large semi-permanent wetlands. Krapu et al. (2000) found that duckling survival was higher when seasonal wetlands were abundant.

Wetland vegetation (cover type; Stewart and Kantrud 1971) likely provides protection from predators and adverse weather, however selection patterns have been inconsistent. Talent et al. (1982) and Raven (2004) found that brood-rearing hens preferred cover type 3 wetlands, which typically have a >2 m peripheral ring of emergent vegetation and a central area of open water. Talent et al. (1982) found that brood-rearing hens also preferred cover type 2 wetlands, these having scattered vegetation intermixed with pockets of open water, while Raven (2004) observed a preference for cover type 4 wetlands, these wetlands having 95% of the basin as open water with a peripheral band of emergent vegetation <2 m wide.

Overland travel is necessary for most broods, at least for initial movements from nest to wetland. Some researchers have reported that overland travel lowers duckling survival (Ball et

al. 1975, Rotella and Ratti 1992a), whereas others have not (Talent et al. 1983, Dzus and Clark 1997b). Duckling survival rates may be directly related to wetland density (Rotella and Ratti 1992a, Dzus and Clark 1998) because broods are able to make shorter overland moves when there are more wetlands nearby.

Loss and fragmentation of perennial cover is known to reduce nesting success (Greenwood et al. 1995). However, effects of perennial cover fragmentation and upland management efforts on duckling survival are not known. Krapu et al. (2000) did not detect an effect of the amount of perennial cover within the study site on brood survival. Here, I revisit this question by considering the effects of both perennial and managed habitats on duckling survival. Unlike Krapu et al. (2000), I consider habitat features within the immediate vicinity of the brood to determine if management techniques and/or landscape composition have an impact on duckling survival.

### **2.1.3 Weather**

Duckling mortality can be influenced by inclement weather, which can include either cold, rainy, windy conditions or above-normal temperatures (see review in Johnson et al. 1992). Daily minimum temperature and precipitation have been used as indices of weather condition and may have a negative effect on duckling survival, particularly within the first week of life (Krapu et al. 2006).

## **2.2 Methods**

### **2.2.1 Data Collection**

I tested key hypotheses (Table 2.1) using data collected during the Prairie Habitat Joint Venture Assessment Study, an eight-year, multi-province investigation conducted by Ducks Unlimited Canada's (DUC) Institute for Wetland and Waterfowl Research (IWWR; Anderson et al. 1995). Between 1993 and 2000, 27 unique sites were studied across the aspen (*Populus tremuloides*) parkland (23) and mixed-grass prairie (4) ecoregions of the Canadian PPR (see Emery et al. 2005). This study was designed to study mallard breeding ecology and assess the effectiveness of PHJV habitat programs delivered in the PPR.

#### *2.2.1.1 Study Site Selection*

Study sites were randomly selected across the PPR from within the primary PHJV target areas (areas with wetland densities capable of supporting  $>7.7$  mallard pairs/km<sup>2</sup>). Sites were stratified into high, medium and low treatment categories, depending on the amount and type of PHJV treatments present. Twenty-five study sites were 66 km<sup>2</sup> (two others were 80 km<sup>2</sup> and 55 km<sup>2</sup>) and each site was examined once over the course of the study. Study sites are described in detail by Emery et al. (2005).

#### *2.2.1.2 Capture and marking*

More than 3,500 female mallards were trapped and marked with radio transmitters (111 and 123 on the two sites in 1993 and 135-137 on all subsequent sites). Most females were decoy trapped (Sharp and Lokemoen 1987, Ringelman 1990) in the spring (between 4 April and 5 May), implanted with a 22-g abdominally-implanted (Telonics IMP/150; Olsen et al. 1992, Rotella et al. 1993) or a 4- or 8-g back-mounted radio-transmitter (Advanced Telemetry Systems models 357 and 2040, respectively; Mauser and Jarvis 1991) and subsequently tracked using vehicle-mounted null array antenna systems and triangulation. To increase the number of radio-marked broods for duckling survival analysis, most nests that were found incidentally while conducting other study activities and a sample of nests found through traditional nest searching methods, had predator-deflection fences erected around them. Just prior to estimated hatch dates nests were revisited and females captured either by mist net, dip net, spring-loaded purse traps or walk in traps and then outfitted with back-mounted radio-transmitters. The University of Saskatchewan's Committee on Animal Care and Supply approved animal handling procedures (Protocol No. 920007).

#### *2.2.1.3 Brood observations*

Duckling counts were attempted immediately after hatch and every 7 days thereafter until a brood was lost (i.e., all ducklings were dead or abandoned) or was 30 days old. This resulted in 850 broods and 3,440 brood observations over the 8 years of the study. The number of broods per site ranged from 18 to 60.

#### *2.2.1.4 Habitat classification*

In July, wetlands were classified by permanency class and vegetative cover type at each site (Stewart and Kantrud 1971) and the dominant vegetation types and presence of flooded emergent

vegetation (extent of flooding) were recorded. Detailed notes regarding upland habitat use for each study site were collected during the field season and digitized using 1:5,000 air photos taken late in the field season (i.e., July – August). Digitized habitat maps were imported into SPANS geographic information system (GIS; PCI Geomatics, Richmond Hill, Ontario, Canada).

## **2.2.2 Data Preparation**

### *2.2.2.1 Female and brood locations*

I digitized brood locations in ArcMap 9.3 (ESRI, Redlands, CA) by cross-referencing radio telemetry field maps (created during the field season) with digitized habitat layers. Since triangulation provides an estimate of the actual hen location and there is error associated with each location (Podruzny 1996, Simpson 2005), I used pond centers as the location when a brood hen was found on ponds <5 ha. If the pond was >5 ha, I digitally placed the location on the pond as it had been recorded on the original field map (Raven 2004). Podruzny (1996) used sites from the PHJV assessment study (along with other sites in the U.S. PPR) to determine error ellipses associated with triangulation methods.

### *2.2.2.2 Data censoring*

Females periodically take breaks from their broods to feed and rest (Håland 1983, Talent et al. 1983, Rotella and Ratti 1992a, Pietz and Buhl 1999). Therefore, some telemetry locations could be a lone hen rather than a hen with her brood. Prior to creating brood routes, I established censoring rules to remove possible brood breaks. A move >300 m followed by a return to the previous pond location, was identified as a brood break (Raven 2004). In the absence of a visual confirmation of status (alone or with brood), this censoring rule served to remove potentially erroneous location data. Only females that spent the entire brood-rearing period on the study site were considered for analysis because I wanted to include only those broods that had a complete history of habitat use.

Duckling counts were recorded as being full (complete duckling count), partial (complete duckling count uncertain) or mixed (ducklings of various ages or species within brood). When a mixed brood (i.e., brood contained ducklings of various ages or species) was observed, I censored the data to the observation prior to the mixed count. I omitted partial counts from the dataset because they do not provide reliable count data. For females with confirmed total brood



loss (i.e., observed without their brood at multiple locations), I “rolled back” to a location where the female had been found for >1 day or to the previous brood observation (whichever occurred first). This was necessary because the location where total brood loss was visually confirmed was likely not where loss occurred. Erratic movements by females signaled the possibility of total brood loss, and led to a visual confirmation that the female had lost her brood. For females with only 1 observation (where total brood loss was confirmed) and who did not stay on a pond for >1 day prior to being observed, data only included the nest location; here, I assumed that the buffer around the nest would capture habitats used by the brood in the first few days of life. Broods that increased in size from one full count observation to the next were removed from the dataset.

If a brood was abandoned or the female died before the brood reached 30 days of age, I assumed the brood perished. However, some abandoned ducklings may have survived (Gendron and Clark 2002) and, as a result, survival estimates could be biased low.

#### *2.2.2.3 Brood routes*

I created apparent brood routes using Hawth’s Analysis Tools (Beyer 2004) within ArcGIS 9.3 (ESRI, Redlands, CA) by drawing a straight line from nest to first female location and between subsequent locations. These are apparent routes because I only had daily locations and some moves may have been missed. I assumed a straight-line trajectory between locations because the actual path taken during inter-wetland moves was not known. I separated each route into two duckling age classes: 0-7 and 8-30 days old because duckling mortality risk is greatest in the first week of life (Talent et al. 1983, Saylor and Willms 1997, Gendron and Clark 2002).

#### *2.2.2.4 Habitat features*

I determined upland and wetland habitat attributes for each age class of a broods’ route using 500 m radius buffers, created using the buffer tool in ArcGIS. I selected a 500 m radius because 80% of first moves made by brood females were <500 m. Therefore, the buffer would represent all habitats where the brood may have travelled between telemetry locations. This buffer size also allows for triangulation error that is inherent in telemetry studies (Podruzny 1996, Simpson 2005). I extracted the amount of habitat within each buffer from digitized wetland and upland habitat layers using the intersect tool in ArcGIS. Prior to determining if the 500 m was an

appropriate spatial scale, I also considered a 250 m radius buffer size. However, models using habitat variables collected from 500 m radius buffers were better supported than those with a 250 m radius. Therefore, I focus on the results of the 500 m radius buffer analysis and draw inferences from these models.

### **2.2.3 Data Analysis**

#### *2.2.3.1 Explanatory variables*

I included fourteen *a priori* variables (10 had 2 age-specific values and 2 had values specific to the <7 day old age class), six exploratory variables (each having 2 age-specific values), and seven 2-way interactions in the final analysis. I included female age (second year (SY) and after second year (ASY)), hatch date and the quadratic effect of hatch date. Brood-related variables included duckling age and brood size (the number of ducklings at hatch and at day 8).

Landscape variables included, for each age class, the proportion of perennial cover (i.e., native grassland, hay, trees, shrubs, planted nesting cover and road rights of way), wetland density (the number of wetlands holding water in July (i.e., flooded) divided by buffer area), distance from nest to first wetland, the proportion of flooded permanency class III and IV wetlands, and the proportion of flooded cover type 2, 3 and 4 wetlands in each buffer (Stewart and Kantrud 1971). Exploratory variables related to PHJV upland habitat management programs included the proportion of managed perennial habitat, and the proportions of managed cropland, hayland, grassland and planted nesting cover within each buffer.

I calculated overland travel by summing the distance of the upland sections of the each brood route. To adjust for the effect of the number of days alive on route length (i.e., longer lived broods have the potential to move farther or more often than do short lived broods), I used the back-transformed residuals derived by regressing log-transformed route length against log-transformed number of days alive for each brood.

I obtained weather data from the five Environment Canada weather stations closest to each study site. I used inverse distance weighting to create an estimate of the weather at each study site, with closer stations contributing more heavily to the estimate than those located farther away. I created a weather index for each brood's first week of life using principal component analysis (PCA; PROC PRINCOM; SAS Institute Inc. 1999). Weather variables used in the PCA included the number of days below 10°C, minimum 7-day temperature, average daily

temperature, average daily precipitation, and maximum 7-day precipitation. I selected the second principal component (Prin2) as the weather index since it best represented the trend I was characterizing: warm/dry versus cold/wet conditions (coefficients: 0.18, -0.20, -0.19, 0.67, 0.67 corresponding to number of days below 10°C, minimum 7-day temperature, average daily temperature, average daily precipitation and maximum 7-day precipitation, respectively). Prin2 accounted for 35.2% of the total original variance in weather data.

#### 2.2.3.2 *Transmitter effect*

Three transmitter-trap combinations were used on female mallards during the PHJV assessment study: decoy-trapped females equipped with abdominal implant or back-mounted transmitters and nest-trapped females outfitted with back-mounted transmitters. Decoy trapping occurs in the spring, prior to nest initiation while nest trapping occurs late in incubation. As a result, decoy-trapped females outfitted with back-mounted transmitters carried the transmitter for much longer than those females trapped on nests. Back-mounted transmitters were deployed on decoy-trapped females on five study sites early in the project. Concerns that transmitter discomfort caused females to preen excessively, potentially decreasing maternal care and ultimately duckling survival, led researchers to discontinue use of the backpack transmitter/decoy trap combination (D. Howerter, Ducks Unlimited Canada, unpublished data). I tested for a nuisance effect of transmitter type on duckling survival before proceeding with main analyses.

#### 2.2.3.3 *Model development and selection*

Care was taken to develop a biologically defensible set of candidate models, rather than consider all possible combinations of covariates (Anderson and Burnham 2002). I coded *a priori* predictions about factors influencing survival variation by including specific explanatory variables (covariates) in competing statistical models (Appendix 1). I included covariates with support from previous studies and, where conflicting results exist in the literature, I developed competing models. I also developed exploratory models to determine if variables that have not previously received attention (i.e., upland habitat features) are related to survival, provided there was a biological rationale for their inclusion. I included biological null (duckling age and

intercept) and statistical null (intercept only) models in the candidate set. During my analysis, I looked for, and guarded against, effects of exceptional study sites.

I used nonlinear mixed modeling techniques with SAS (SAS Institute Inc. 1999), and an information-theoretic approach to determine best-approximating models (Burnham and Anderson 1998). The surviving number of ducklings was treated as binomially distributed, conditional on the number of ducklings observed during the previous brood count. I calculated the variance inflation factor,  $\hat{c}$ , from the most parameterized (global) model in my candidate set of models using the Pearson chi square statistic (Anderson et al. 2001), and adjusted the number of estimable parameters to include the estimation of  $\hat{c}$  (Anderson and Burnham 2002). Due to the evidence of overdispersion ( $\hat{c} = 3.98$ ) likely caused, in part, by lack of independence in the fates of brood-mates, differences between study sites, or both, I used the quasi-likelihood form of Akaike's Information Criterion (QAIC: Burnham and Anderson 1998).

I conducted a *post hoc* exploratory analysis to investigate the influence of natural upland habitats and PHJV managed habitats on mallard duckling survival. In separate analyses, I added managed perennial cover, total perennial cover, planted nesting cover, managed cropland, managed hayland, and managed grassland to the best-approximating *a priori* model.

## **2.3 Results**

A total of 617 broods with complete habitat information and that were tracked reliably until they died or were 30 days old remained after the data were censored. The number of broods per site ranged from 11 to 46 (median = 20).

### **2.3.1 Transmitter effect**

Ducklings of females that were decoy trapped in the spring and outfitted with back-mounted transmitters had lower predicted 30-day duckling survival rates (0.332, SE = 0.048) than ducklings from either decoy-trapped females with abdominal transmitters (0.523, SE = 0.009) or nest-trapped females with back-mounted transmitters (0.539, SE = 0.014). Therefore, ducklings attended by decoy-trapped females marked with back-mounted transmitters were excluded from further analyses.

### 2.3.2 Duckling age

As expected, predicted daily duckling survival rates were lower in the first week of life (0.952, SE = 0.001) versus later (0.988, SE = 0.001) supporting the *a priori* hypothesis that survival is positively related to duckling age.

### 2.3.3 Performance of *a priori* models

The best-approximating *a priori* model included duckling age (included in all models;  $\beta_{<7} = 3.408$ ,  $SE_{<7} = 0.090$ ,  $\beta_{>7} = 4.451$ ,  $SE_{>7} = 0.102$ ), distance travelled overland ( $\beta_{<7} = -0.047$ ,  $SE_{<7} = 0.043$ ,  $\beta_{>7} = -0.092$ ,  $SE_{>7} = 0.023$ ), and the proportion of wetlands in the buffer that were class IV (i.e., semi-permanent:  $\beta_{<7} = -0.680$ ,  $SE_{<7} = 0.116$ ,  $\beta_{>7} = 0.006$ ,  $SE_{>7} = 0.148$ ; Table 2.2).

The prediction that overland travel reduces duckling survival was supported for both young and old ducklings, though with only weak evidence for young ducklings (Figure 2.1b). Young ducklings were negatively influenced by the abundance of class IV wetlands in the buffer area, whereas older ducklings were not (Figure 2.2b).

Parameter estimates from models with  $\Delta Q A I C$  values  $<4$  were model-averaged due to low model weights ( $<0.13$ ) and high model selection uncertainty. Effects of duckling age (both age classes), and abundances of semi-permanent and seasonal wetlands (young ducklings only) had the most support, as indicated by 95% confidence intervals that excluded 0 (Table 2.3). All other variables appearing in the top model set had confidence intervals overlapping 0, indicating little support for hypothesized effects of these factors.

### 2.3.4 Exploratory analyses

The addition of both managed hayland ( $\beta_{<7} = 0.064$ ,  $SE_{<7} = 0.691$ ,  $\beta_{>7} = -3.834$ ,  $SE_{>7} = 0.757$ ) and managed grassland ( $\beta_{<7} = 3.408$ ,  $SE_{<7} = 0.979$ ,  $\beta_{>7} = 2.642$ ,  $SE_{>7} = 1.409$ ) improved the best-approximating *a priori* model, with managed hayland producing the strongest increase in model weight (Table 2.4). Survival of older duckling was negatively related to the amount of managed hayland but this had a negligible influence on young ducklings (Figure 2.3b). The amount of managed grassland positively influenced the survival of ducklings of all ages (Figure 2.4b). Neither the addition of managed cropland nor planted nesting cover superseded performance of the *a priori* best-approximating model.

Similar to the *a priori* analysis, parameter estimates from exploratory models (with  $\Delta\text{QAIC} < 4$ ) were model-averaged due to model selection uncertainty (weights  $< 0.14$ ). Duckling age, managed hayland, class IV (semi-permanent) and class III (seasonal) wetlands, and overland travel had the most support, as indicated by 95% confidence intervals that did not overlap 0 (Table 2.5). All other variables appearing in the top model set had confidence intervals overlapping 0, indicating little support for these parameters.

## 2.4 Discussion

Although upland habitat management programs aim to increase duck nesting success, it has been unknown how, or even if, duckling survival is affected by these programs. My exploratory analysis demonstrated the importance of the amount of managed grassland and managed hayland on mallard duckling survival. A simpler classification of managed perennial habitats which combined managed hayland, grassland and planted nesting cover, did not appear as an important predictor of mallard duckling survival probably because the strong positive influence of managed grassland and a strong negative influence of managed hayland masked the effects of individual habitat types. Krapu et al. (2000) also failed to detect an effect of perennial habitat, measured at the study site level, on mallard duckling survival. There is no evidence of a trade-off between benefits of managing perennial upland habitats to enhance nesting success and costs in terms of lower duckling survival. The negative effect of managed hayland on older ducklings, however, should be investigated further.

Here, duckling survival was negatively related to distance travelled overland for ducklings. These results support the findings of Ball et al. (1975) and Rotella and Ratti (1992a, b), but contradicts other researchers who reported that overland travel has no effect on duckling survival (Talent et al. 1983, Dzus and Clark 1997b). Previous studies that considered the effect of overland travel on mallard duckling survival had small sample sizes (25-52 broods) and were conducted on single study sites within the Canadian and U.S PPR, therefore site-specific predator communities and wetland conditions could explain variation between studies. The large sample size and wide range of upland and wetland habitat conditions of the PHJV Assessment dataset helps make my results robust and applicable across the PPR. Since I did not have radio-marked ducklings, I do not know if mortality events occurred before, during, or after overland moves. Increased vulnerability to predators, especially upland-foraging mammals, during

overland travel could result in lower survival rates; however, I was unable to evaluate this directly. Shorter (or less frequent) moves could be a correlate of wetland density (i.e., in regions of high wetland density overland moves can be shorter), but wetland density did not appear as an important predictor of duckling survival, supporting Rotella and Ratti (1992b) who found that a negative effect of overland travel on duckling survival regardless of wetland density. Nesting success improves with increased distance from wetlands (Howerter 2003) therefore, nesting females are faced with the trade-off between nesting far from wetlands to maximize nesting success and close enough to maximize survival during inter-wetland moves.

Both semi-permanent and seasonal wetlands were important in explaining variation in survival rates of mallard ducklings. The number of wet, semi-permanent wetlands is an important, but negative, predictor of young duckling survival. Brood use of semi-permanent wetlands has been documented for mallards (Duebber and Frank 1984, Dzus and Clark 1997b), but no negative effect between the number of days spent on semi-permanent wetlands and duckling survival was observed (Dzus and Clark 1997b). I did not consider individual wetland use but rather a landscape perspective of the proportion of wetlands in the brood-rearing area that were semi-permanent. The negative effect of semi-permanent wetlands on duckling survival may be due to a lack of seasonal wetlands in the landscape or to the occurrence of mink (*Mustela vison*), a known predator of ducklings with a preference for semi-permanent wetlands (Talent et al. 1983, Korschgen et al. 1996, Krapu et al. 2004). The positive effect of seasonal wetlands on duckling survival has been well documented (Talent et al. 1982, Krapu et al. 2000) and was further supported for young ducklings by the model averaged results.

Survival rates for young (0-7 days old) ducklings were lower than for older (8-30 days old) ducklings. Mortality is higher in the first week of life (Talent et al. 1983, Sayler and Willms 1997, Gendron and Clark 2002) when ducklings are most vulnerable to adverse weather conditions. While weather did not appear in any top models, it is evident that younger ducklings are more susceptible to the combined impacts of all mortality events than are older ducklings. Surprisingly, weather did not appear as a strong predictor of survival in mallard ducklings here. However, weather conditions were not recorded at each study site; instead I used information from nearby Environment Canada weather stations to estimate weather conditions during each broods first week of life. Prairie weather is highly variable and the weather index I created likely

did not accurately estimate weather conditions at each study site. As a result, the influence of weather on duckling survival may have been underestimated.

Female age was not a strong predictor of duckling survival, supporting previous research for mallards (Krapu et al. 2000, Hoekman et al. 2004). In southern Ontario, older brood-rearing mallard females were more successful at raising broods than younger females, but the effect was very weak (Hoekman et al. 2004). Conversely, older wood duck females had higher success at raising broods than their younger counterparts (Davis et al. 1997) however these are cavity nesting ducks in the southern U.S. and may not be comparable to ground nesting, prairie mallards.

Similar to Gendron and Clark (2002), hatch date was not a strong predictor of duckling survival. This contradicts many other reports of duckling survival decreasing with later hatch dates (Rotella and Ratti 1992b, Dzus and Clark 1998, Krapu et al. 2000). Gendron and Clark (2002) suggested that high quality wetland conditions throughout the breeding season mediated the relationship between hatch date and duckling survival. They also suggested that wetland condition is a better predictor of duckling survival than hatch date (Gendron and Clark 2002). Their suggestions are supported by my results since hatch date was not an important predictor of duckling survival but wetland condition (i.e., proportion wetlands in the brood-rearing area that are semi-permanent or seasonal) was.

Although duckling survival has been relatively well studied, my study was unique because it reconsidered mallard duckling survival using a large dataset spanning a wide geographical area and variety of PHJV management intensities. The impact of upland habitat management on ducklings has been missing in current waterfowl research. My results help fill that gap and also will contribute to robust habitat management planning tools. Future work should be directed at other waterfowl species or at specific management practices. For example, fall seeded croplands, planted to increase nesting success of pintails, should be assessed for a potential influence on duckling survival because young ducklings may be forced to travel long distances overland to reach brood-rearing wetlands.

#### **2.4.1 Management implications**

Typically, evaluations of upland habitat management programs focus on determining whether such programs enhance use and improve nesting success, and have not given



consideration to possible effects on duckling survival. My results imply that existing habitat management programs do not negatively impact mallard duckling survival.

Grassland habitats managed to enhance nesting success had a positive impact on survival of ducklings (Figure 2.4a). Management and protection of grassland habitats should continue as a primary method for increasing mallard productivity. Grasslands that are idled or lightly grazed have higher productivity (i.e., product of nest density and success) than more heavily grazed fields (Warren et al. 2008), therefore, by working directly with farmers and ranchers to improve pasture practices, through rotational grazing and reduced grazing intensity, habitat managers can achieve landscape scale impacts. Focusing management activities on grassland habitats should have positive gains for both nest and duckling survival. Other grassland bird species also will benefit from such management actions since areas with high waterfowl density support higher richness and abundance of avian species than areas of low waterfowl density (Skinner and Clark 2008).

With the addition of information on how duckling survival is influenced by current upland management practices, managers should be able to make better informed decisions about how to allocate limited resources. These decisions should ensure that both nesting success and duckling survival are positively impacted by management activities, leading to greater waterfowl productivity.

## 2.5 Tables

Table 2.1 - Covariates used in a priori and exploratory models to explain variation in mallard duckling survival across prairie Canada, 1993-2000. Predicted results are expressed as  $\beta > 0$  if a positive effect is predicted and the opposite when a negative effect is predicted.

Variable name	Definition	Expected response
<i>Wetland Attributes:</i>		
Class3	proportion of wetlands in the buffer that are seasonal (class III)	$\beta > 0$
Class4	proportion of wetlands in the buffer that are semi-permanent (class IV)	$\beta > 0$
Cover2	proportion of wetlands in the buffer that are cover type 2	$\beta > 0$
Cover3	proportion of wetlands in the buffer that are cover type 3	$\beta > 0$
Cover4	proportion of wetlands in the buffer that are cover type 4	$\beta > 0$
<i>Brood-related attributes:</i>		
Dage	age of ducklings (number of days alive)	$\beta > 0$
Bsize	size of brood at hatch and on day 8	$\beta < 0$
<i>Female-related attributes:</i>		
Henage	age of brood hen (ASY/SY)	$\beta > 0, \beta = 0$
Hatdate	date of hatch	$\beta < 0, \beta > 0, \beta = 0$
Hatdate2	quadratic form of hatch date	$\beta < 0, \beta > 0, \beta = 0$
<i>Environmental attributes:</i>		
Weather	weather index for first week of life (characterizes warm/dry versus cold/wet conditions)	$\beta > 0$
<i>Landscape attributes:</i>		
Pern_cov	proportion of the buffer that is perennial cover	$\beta = 0$
Travel	distance travelled overland, adjusted for number of days alive	$\beta < 0, \beta = 0$
Dist_to_first_wetl	distance from nest to first wetland (m)	$\beta < 0$
Density	wetland density (#wetlands/m <sup>2</sup> )	$\beta > 0$
<i>Exploratory landscape attributes:</i>		
Mng_pern	proportion of the buffer that is managed perennial cover	
Mng_crop	proportion of the buffer that is managed cropland	
Mng_hay	proportion of the buffer that is managed hayland	
Mng_grass	proportion of the buffer that is managed grassland	
DNC	proportion of the buffer that is planted nesting cover	

Table 2.2 - Best-approximating *a priori* models ( $\Delta\text{QAIC} < 2.0$ ) explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. The “best” model ( $\Delta\text{QAIC} = 0.00$ ) has the lowest QAIC value and the highest model weight ( $w_i$ ). The table includes model description, the number of estimable parameters (K) in each model, -2loglikelihood (-2logLK), QAIC score (estimated using  $\hat{c} = 3.98$ ), and the difference in QAIC score from the highest ranked model ( $\Delta\text{QAIC}$ ). Duckling age was included in all models.

Model description <sup>a</sup>	K	-2logLK	QAIC	$\Delta\text{QAIC}$	$w_i$
Travel + class4	7	8110.35	2053.14	0.00	0.13
Travel + cover4 + class3	9	8097.48	2053.91	0.76	0.09
Henage + cover4 + class4	9	8100.50	2054.67	1.52	0.06
Class4 + DNC	7	8116.46	2054.68	1.53	0.06
Henage + class4	7	8116.63	2054.72	1.58	0.06

<sup>a</sup>Travel is the distance travelled overland, adjusted for number of days alive, class3 and class4 are the proportion of wetlands within the buffer that are class III (seasonal) or IV (semi-permanent), cover4 is the proportion of wetlands within the buffer that are cover type 4, henage is the age of the female, and DNC is the proportion of the buffer that is composed of planted nesting cover.

Table 2.3 - Model-averaged parameter estimates from variables appearing in the best-approximating *a priori* models ( $\Delta QAIC < 4$ ) explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. Unconditional standard error, 95% confidence intervals and the coefficient of variation (CV) are given for each parameter.

Parameters <sup>a</sup>	Model-averaged effect estimate	Unconditional standard error	95% confidence interval		CV
			lower	upper	
Dage <7	2.622	0.459	1.703	3.540	0.18
Dage >7	3.707	0.606	2.495	4.920	0.16
Class4 <7	-0.542	0.214	-0.971	-0.113	0.40
Class3 <7	0.522	0.225	0.072	0.972	0.43

<sup>a</sup> Dage is duckling age and class3 and class4 are the proportion of wetlands within the buffer that are class III (seasonal) or IV (semi-permanent). The <7 indicates ducklings that are 1-7 days old and >7 indicates ducklings between 8-30 days old.

Table 2.4 - The top exploratory models explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. The addition of the exploratory variables managed hay and managed grass outperformed the best-approximating *a priori* model. The “best” model ( $\Delta\text{QAIC} = 0.00$ ) has the lowest QAIC value and the highest model weight ( $w_i$ ). The table includes model description, the number of estimable parameters (K) in each model,  $-2\log\text{LK}$ , QAIC score (estimated using  $\hat{c} = 3.98$ ), the difference in QAIC score from the highest ranked model ( $\Delta\text{QAIC}$ ). Duckling age was included in all models.

Model description <sup>a</sup>	K	$-2\log\text{LK}$	QAIC	$\Delta\text{QAIC}$	$w_i$
Travel + class4 + managed hay <sup>b</sup>	9	8089.47	2051.89	0.00	0.13
Travel + class4 + managed grass <sup>b</sup>	9	8090.82	2052.23	0.34	0.11
Travel + class4	7	8110.35	2053.14	1.25	0.07
Travel + cover4 + class3	9	8097.48	2053.91	2.01	0.05

<sup>a</sup> Travel is the distance travelled overland, adjusted for the number of days alive, class3 and class4 are the proportion of wetlands within the buffer that are class III (seasonal) or IV (semi-permanent), managed hay is the proportion of the buffer that is managed hayland, managed grass is the proportion of the buffer that is managed grassland, and cover4 is the proportion of wetlands within the buffer that are cover type 4.

<sup>b</sup> Exploratory variables.

Table 2.5 - Model-averaged parameter estimates for parameters found in the best-approximating exploratory models ( $\Delta\text{QAIC} < 4$ ) explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. Unconditional standard error, 95% confidence interval and the coefficient of variation are given for each parameter.

Parameters <sup>a</sup>	Model-Averaged Effect Estimate	Unconditional Standard Error	95% Confidence Interval		CV
			lower	upper	
Dage > 7	4.467	0.260	3.946	4.987	0.06
Dage < 7	3.267	0.304	2.660	3.874	0.09
Class4 < 7	-0.680	0.235	-1.150	-0.210	0.35
Managed hay >7	-3.834	1.511	-6.855	-0.813	0.39
Class3 < 7	0.623	0.248	0.126	1.120	0.40
Travel > 7	-0.092	0.046	-0.183	-0.001	0.50

<sup>a</sup> Dage is duckling age, class3 and class4 are the proportion of wetlands within the buffer that are class III (seasonal) or class IV (semi-permanent), managed hay is the proportion of the buffer that is managed hayland, and travel is the distance travelled overland, adjusted for the number of days alive. The <7 indicates ducklings that are 1-7 days old and >7 indicates ducklings between 8-30 days old.

## 2.6 Figures

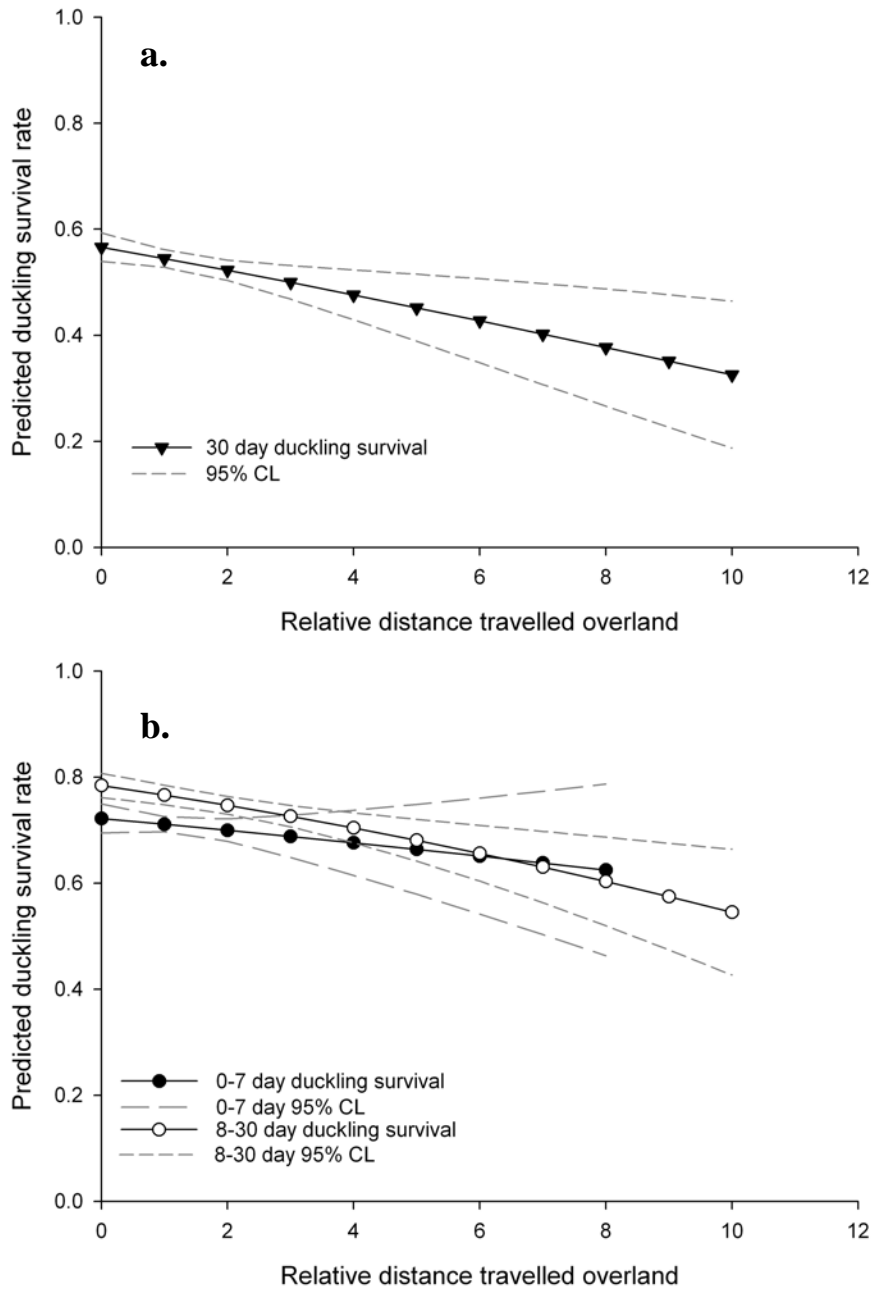


Figure 2.1 - Relationship between distance travelled overland (corrected for the number of days alive) and a) predicted 30-day duckling survival (filled triangles) and b) survival of younger (filled circles) and older (open circles) ducklings, estimated from the best-approximating model explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. Upper and lower 95% confidence limits are represented by dashed lines. Larger values indicate longer distances travelled overland, corrected for the age of the ducklings.

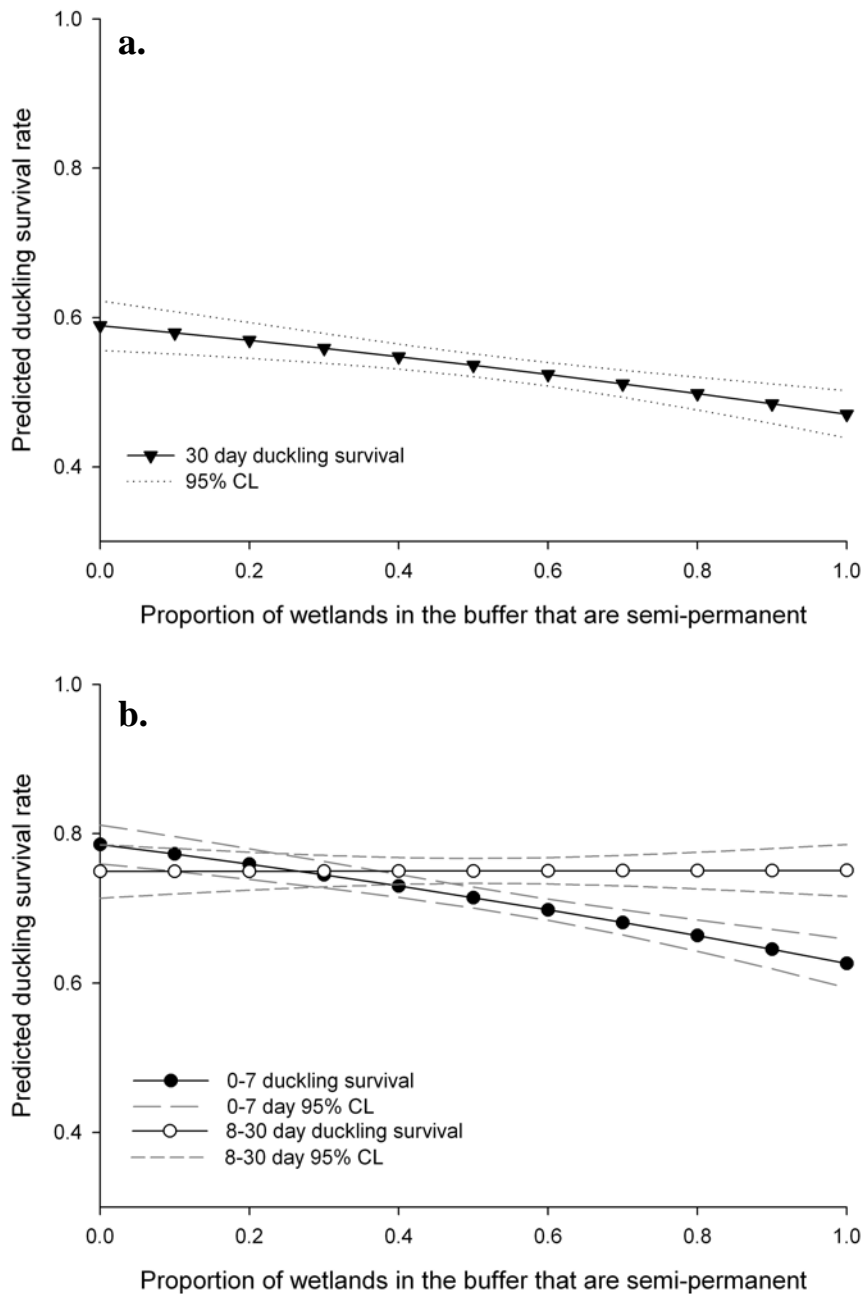


Figure 2.2 - Relationship between amount of semi-permanent (class IV) wetland and a) predicted 30-day duckling survival (filled triangles) and b) survival of younger (filled circles) and older (open circles) ducklings, estimated from the best-approximating model explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. Upper and lower 95% confidence limits are represented by dashed lines.



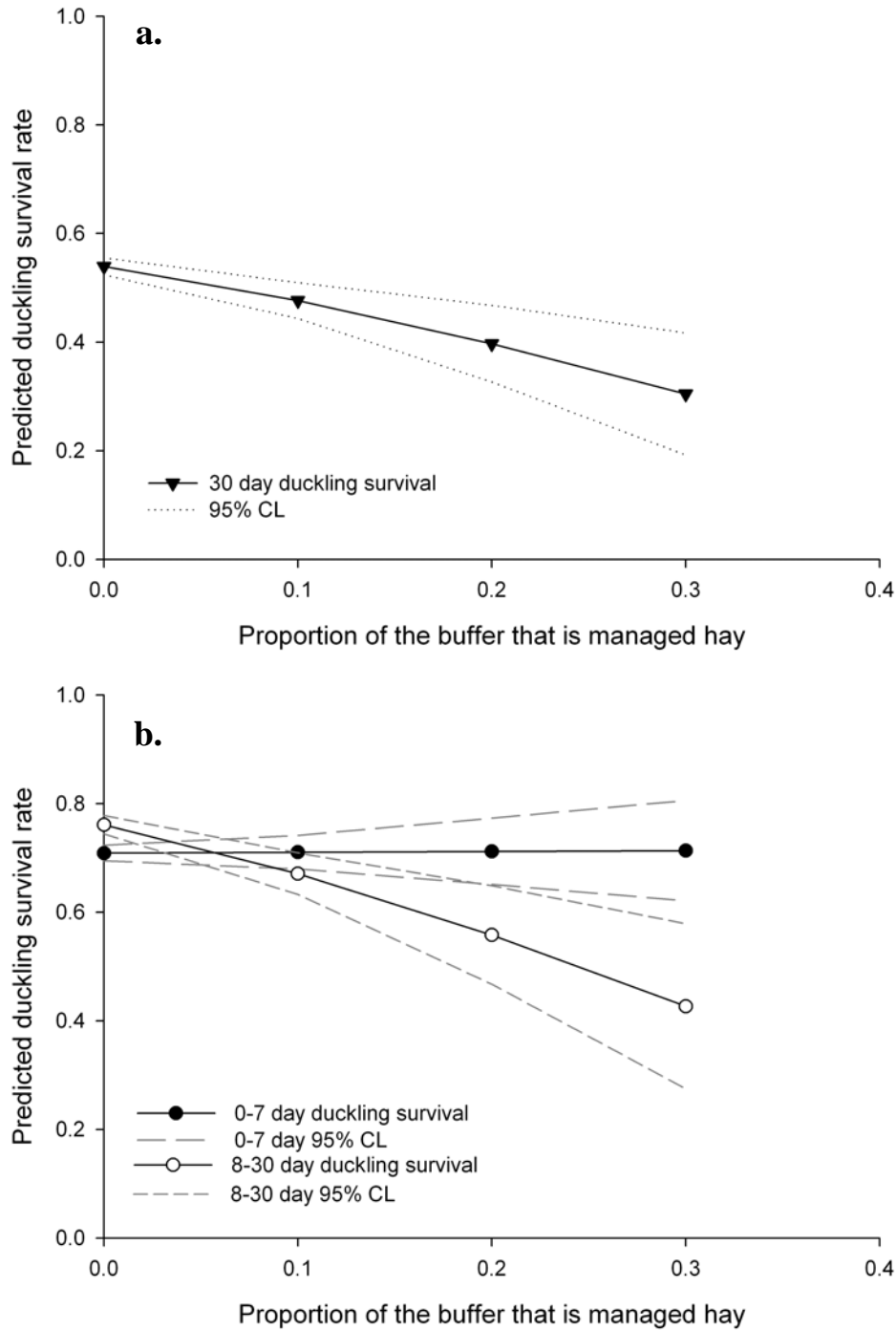


Figure 2.3 – Relationship between amount of managed hayland and a) predicted 30-day duckling survival (filled triangles) and b) survival of younger (filled circles) and older (open circles) ducklings, estimated from the exploratory model containing the managed hayland variable explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. Upper and lower 95% confidence limits are represented by dashed lines.

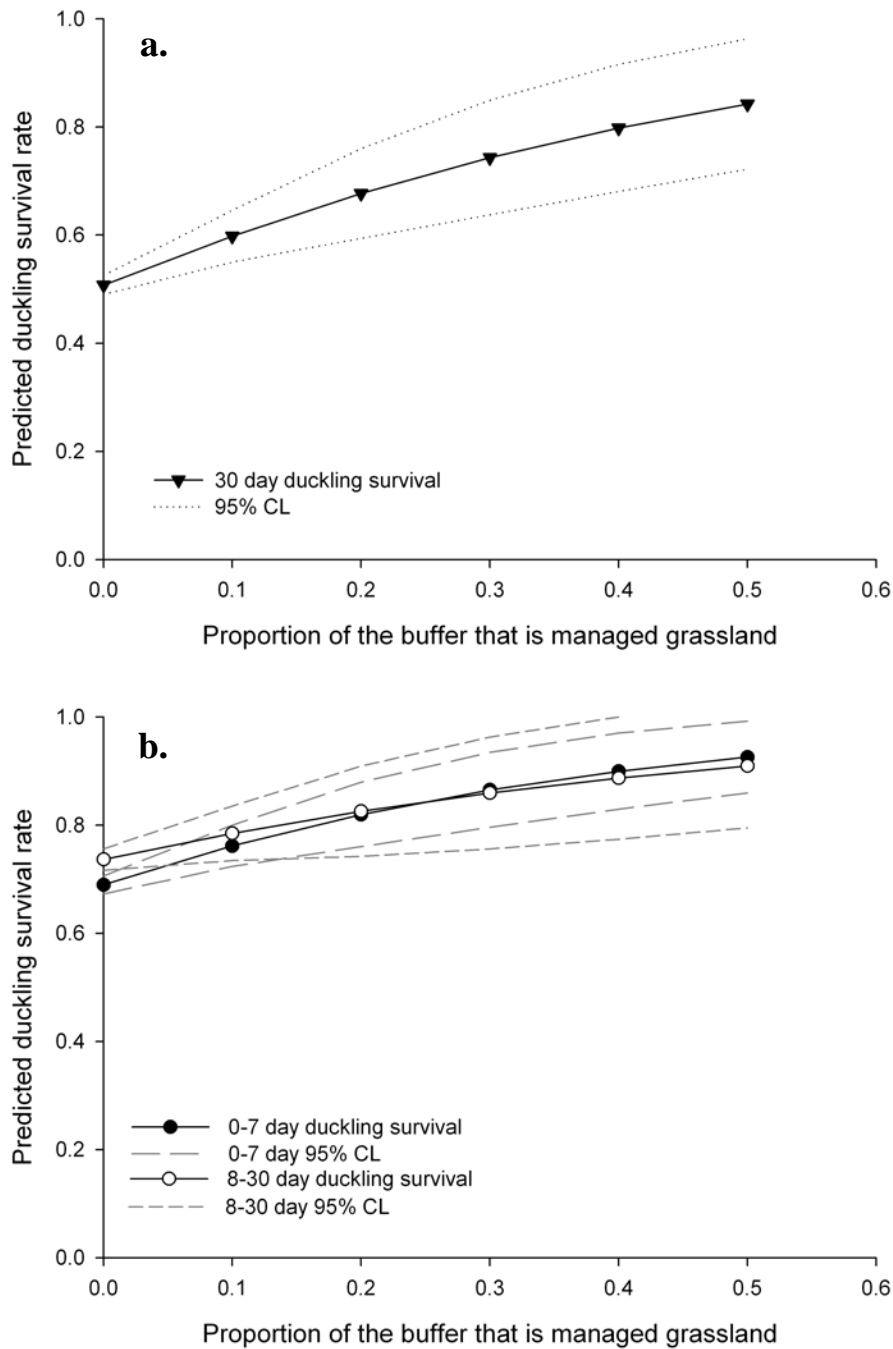


Figure 2.4 – Relationship between the amount of managed grassland and a) predicted 30-day duckling survival (filled triangles) and b) survival of younger (filled circles) and older (open circles) ducklings, estimated from the top exploratory model containing the managed grassland variable explaining predicted mallard duckling survival rates across prairie Canada, 1993-2000. Upper and lower 95% confidence limits are represented by dashed lines.

# **CHAPTER 3    CONSEQUENCES OF HABITAT SELECTION FOR OFFSPRING SURVIVAL: SCALE-DEPENDENT TRADE-OFFS IN A PRECOCIAL SPECIES.**

## **3.1 Introduction**

Trade-offs occur when investment of time or energy into one trait or reproductive event comes at a cost to other traits or future events (Stearns 1992). The cost of reproduction is likely the best known life history trade-off, a hypothesis that predicts that energy allocated to reproduction is unavailable for growth, maintenance, and survival (Stearns 1989).

Overinvestment in reproduction reduces the time or energy available for future reproduction, predator avoidance and/or protection against disease. However, fitness is also influenced by decisions regarding the amount of parental care provided, timing of reproduction, and habitats chosen for foraging and breeding. Presumably, an individual's choice of habitat also reflects trade-offs that balance benefits of gaining access to critical resources for producing offspring or ensuring self-maintenance against costs of higher mortality risk.

Understanding both how species use habitats, and if that use is selective (non-random), has been a key driver of habitat conservation for decades (Lack 1933). It is often assumed that fitness is higher in preferred habitats (i.e., that habitat selection is adaptive) but this is rarely tested (Martin 1998). To understand its adaptive significance, there are two aspects of habitat selection to consider: habitat choice and the fitness consequences of that choice (Jones 2001). Many studies describe habitat selection patterns, but few determine whether and why these patterns affect fitness (Jones 2001).

Selection of specific habitats need not equate to improved fitness. Animals may make “bad habitat choices” if they are restricted from gaining access to optimal habitats or are subject to mismatched environmental cues (Van Horne 1983, Pulliam 1988). So-called ecological traps occur when individuals preferentially forage or breed in non-productive (sink) habitats (Battin 2004, Bock and Jones 2004). Sink habitats are those that attract individuals but where fitness is too low to be self-sustaining (Pulliam 1988). Without considering fitness consequences of habitat selection, researchers may unwittingly advocate for protection of ecological trap habitats with detrimental effects on populations (Martin 1998).

Birds are a popular study group for habitat selection studies because they are relatively easy to count and their reproductive success easy to monitor when compared with many other organisms (Bock and Jones 2004). Nesting success is commonly used to indicate reproductive success since nests are relatively easy to find and monitor. Success of hatched young has received less attention because of the difficulty in tracking pre-fledging young, particularly in precocial birds whose young are quite mobile (Bock and Jones 2004). While nest-site selection and nesting success have been well studied for waterfowl, brood habitat selection and duckling survival have not. Mallard ducklings depart the nest within 24 hours after hatching and are highly mobile in the pre-fledging period making their survival difficult to monitor. Mallard nest-site selection did not correspond with increased nesting success (Howerter et al. 2008, but see Clark and Shutler 1999). It is possible that mallards choose nest sites that lead to higher duckling survival rates by “anticipating” conditions during brood-rearing (Pöysä et al. 2000).

Here, I evaluate how a precocial bird balances costs and benefits of selecting specific habitats, by determining the pre-fledging offspring survival consequences of habitat choices made by female mallards during the brood-rearing period. Females select habitats for brood-rearing and must balance their own needs versus those of their offspring, and this trade-off could affect overall fitness. Decisions regarding where and when to nest, where to raise their young and how much energy to invest in brood-rearing are important determinants of offspring survival.

### **3.1.1 Hypotheses and Predictions**

My objective was to test the hypothesis that female mallards select brood-rearing habitats (wetland and surrounding uplands) that lead to survival of ducklings (i.e., that habitat selection is adaptive). Non-random use of brood-rearing wetland habitats by mallards has been documented (Talent et al. 1982, Rotella and Ratti 1992a, Raven et al. 2007 but see Mulhern et al. 1985) but, to my knowledge, surrounding upland habitats have never been considered in brood habitat selection studies nor have the potential consequences for duckling survival.

I compared used and available habitats (i.e., to measure “selection” *pattern*) and considered the influence of habitat selection patterns on survival of ducklings (i.e., to measure selective mechanisms or “*processes*”). Presumably, preferred habitats are those where ducklings experience lower mortality rates; to my knowledge, this prediction has not been tested. Predicted

habitat selection patterns and predicted effects on duckling survival are outlined in Table 3.1.

## **3.2 Methods**

I used data collected during the Prairie Habitat Joint Venture (PHJV) Assessment Study. Habitat use was compared to availability at two scales: areas used by females and their broods versus the scales of (1) the entire study site (landscape) and (2) a randomly oriented area of equal size and shape to the brood-rearing area (local). I defined used habitat as those habitats found within the brood-rearing area.

### **3.2.1 Data Collection**

Between 1993 and 2000, mallards were studied on 27 sites across the aspen-parkland and mixed-grass prairie ecoregions of the PPR. The PHJV Assessment study was designed to investigate mallard breeding ecology and assess the effectiveness of PHJV habitat management programs being delivered in the PPR. These programs aim to attract breeding waterfowl to high quality habitats and increase nesting success rates.

#### *3.2.1.1 Site Selection*

Sites were randomly selected across the PPR from within the primary PHJV target areas (areas with wetland densities capable of supporting  $>7.7$  mallard pairs/km<sup>2</sup>). Sites were stratified into high, medium and low management categories, depending on the amount and type of PHJV habitat management program (e.g., planted nesting cover (DNC), delayed hay, idle parkland, rotational grazing systems) being delivered on the site. Most (25) study sites were 66 km<sup>2</sup> (two were 80 km<sup>2</sup> and 55 km<sup>2</sup>) and each site was examined once over the course of the study. Study sites are described in detail by Emery et al. (2005).

#### *3.2.1.2 Capture and Marking*

Over 3,500 female mallards were trapped and marked with radio transmitters (typically 135-137 per site) over the course of the study. Most females were decoy trapped (Sharp and Lokemoen 1987, Ringelman 1990) in the spring (between 4 April and 5 May), implanted with a 22-g abdominally-implanted (Telonics IMP/150; Olsen et al. 1992, Rotella et al. 1993), or a 4- or 8-g back-mounted (Advanced Telemetry Systems models 357 and 2040, respectively; Mauser

and Jarvis 1991), radio-transmitter and subsequently tracked using vehicle-mounted null array antenna systems and triangulation. To increase the number of radio-marked broods, most nests that were found incidentally while performing other study activities and a sample of nests found through traditional nest searching methods, had predator-deflection fences erected around them. Just prior to their estimated hatch dates, nests were revisited and the females captured either by mist net, dip net, spring-loaded purse traps or walk in traps and then outfitted with back-mounted radio-transmitters.

#### *3.2.1.3 Brood Observations*

Duckling counts were attempted immediately after hatch and every 7 days thereafter until a brood was lost (i.e., all ducklings were dead or abandoned) or was 30 days old. Over 8 years, this resulted in 850 broods and 3,440 brood observations. The number of broods per site ranged from 18 to 60.

#### *3.2.1.4 Habitat Classification*

Wetlands were classified (Stewart and Kantrud 1971), and dominant vegetation types and presence of flooded emergent vegetation (extent of flooding) were recorded. Detailed notes regarding upland habitat use for each study site were collected during the field season and used to inform the creation of a digitized map derived using 1:5,000 air photos taken late in the field season. Digitized habitat maps were imported into SPANS Geographic Information System (GIS; PCI Geomatics, Richmond Hill, Ontario, Canada).

### **3.2.2 Data Preparation**

#### *3.2.2.1 Female and brood locations*

I digitized brood locations in ArcGIS 9.3 (ESRI, Redlands, CA) by cross-referencing radio telemetry field maps (created during the field season) with digitized habitat maps (above). Triangulation provided an estimate of the females' location but there is error associated with each location (Podruzny 1996, Simpson 2005); consequently, the center of a wetland was used as the brood location when a female was located on ponds <5 ha. If the pond was >5 ha, the location was digitally placed on the pond, as shown on the original field map.

### 3.2.2.2 *Data Censoring*

Females take periodic breaks from their broods to feed and rest (Håland 1983, Talent et al. 1983, Rotella and Ratti 1992a, Pietz and Buhl 1999), so some telemetry locations could represent a lone female. Prior to creating brood routes, I established censoring rules to remove possible brood breaks. A move >300 m followed by a return to the previous pond location was identified as a brood break. In the absence of a visual confirmation of status (alone or with brood), this censoring rule served to reduce potentially erroneous location data. Only females that spent the entire brood-rearing period within the boundaries of the study site were considered for analysis because I wanted to include only those broods that had a complete history of habitat use.

Duckling counts were recorded as being complete (i.e., ducklings were highly visible to the observer who believed that all ducklings were reliably counted), partial (an incomplete duckling count was possible) or mixed (ducklings of various ages or species were detected within a brood). I removed mixed broods from the dataset since complete survival data were not available for them. I omitted partial counts from the data set because they did not provide reliable counts. Broods that increased in size from one complete count to the next were removed from the dataset. For females with confirmed total brood loss (i.e., observed without their brood at multiple locations), I used either the most recent location where the female had been found for >1 day or the previous brood observation, whichever was most recent. This was necessary because the location where total brood loss was visually confirmed was likely not that where loss occurred. Erratic movements by females signaled the possibility of total brood loss, and led to a visual confirmation that the female had lost her brood. If a brood was abandoned or the female died before the brood reached 30 days of age, I assumed the brood was dead. However, I recognize that some abandoned ducklings may have survived (Gendron and Clark 2002) and, as a result, survival estimates could be biased low. I removed broods that died at the nest since a random route could not be created (i.e., the random route would be identical to the nest buffer).

### 3.2.2.3 *Brood Routes*

I created brood routes using Hawth's Tools (Beyer 2004) in ArcGIS by drawing a straight line from nest to first female location and between subsequent locations. These are apparent routes because I had only daily locations and some moves could have been missed. I assumed a straight line trajectory between locations but it is unknown what actual path was used by the

female during inter-wetland moves. Complete routes (from nest to last known location) were used for this analysis because I wanted to compare broods that survived to 30 days to those that did not.

I created random routes by randomizing the direction of the original route while keeping it anchored on the nest site and maintaining the original route shape. I used the ‘randomize route location and orientation’ option in Alternate Animal Movements (Jenness 2005) in ArcView 3.2 (ESRI, Redlands, CA). Random routes were anchored on the nest location to allow nest-site selection to remain consistent. Since the female had already chosen to create her nest in a certain habitat and brood-rearing habitats are constrained by nest location, I wanted to consider fine-scale habitat selection patterns by comparing the route she used to another available route from that point.

#### *3.2.2.4 Habitat Summation*

I created 500 m buffers around each original and random route and summarized the upland and wetland habitat attributes within each buffer, using the buffer and intersect tools in ArcGIS, respectively. The 500 m radius was selected because 80% of first moves made by brood females were <500 m and this buffer size accommodated inherent telemetry error (Podruzny 1996, Simpson 2005).

By anchoring the random route on the nest, complete buffer overlap was unavoidable within a 500 m radius around the nest site (Figure 3.1a). I was concerned that this overlap could partly mask patterns of habitat selection, particularly for short-lived broods with small buffers, and that this could potentially be an artifact caused by methodology rather than an actual lack of selection. I, therefore, split the 500 m buffer around the nest into two equal parts (Figure 3.1b); with each half of the buffer allotted as either used or random (Figure 3.1c). I created this split by drawing a straight line through the buffer from the point where the two buffers diverged. Any remaining buffer overlap was permitted.

### **3.2.3 Data Analysis**

#### *3.2.3.1 Explanatory Variables*

I analysed wetland habitat variables that have been reported previously in mallard habitat use and selection studies. Raven et al. (2007) found (using a subset of the dataset I analyzed) that



broods preferred wetlands with vegetative cover types 3 (patches of open water intermixed with vegetative cover; Stewart and Kantrud 1971) and 4 (>95% open water and/or a <2m fringe of emergent vegetation; Stewart and Kantrud 1971), semi-permanent wetlands (class IV) with bulrush (*Scirpus* spp.) dominance (and avoidance for semi-permanent wetlands dominated by cattails (*Typha* spp.)), and seasonal wetlands (class III) with tall manna grass dominance (and avoidance of seasonal wetlands dominated by slough grass (*Beckmannia syzigachne*)). They did not find a preference for whitetop river grass (*Scolochloa festucacea*) dominated seasonal wetlands, as did Talent et al. (1982). Thus, I included vegetative cover type and both seasonal and semi-permanent wetlands as explanatory variables in my analyses. I also included wetland density and wetland area (see definitions in Table 3.1).

To my knowledge, upland habitat variables have never been considered in mallard brood-rearing habitat selection so I used results from the first chapter to guide model development. I considered both managed and unmanaged perennial upland habitats. Perennial habitat includes hayland, grassland, planted nesting cover (managed only), and woody cover.

### 3.2.3.2 *Spatial Scale*

Because habitat selection is thought to be a hierarchical process and prior decisions made by females may constrain current (or future) options (Johnson 1980), I considered two spatial scales for my analysis. At the local scale, an approach equivalent to Thomas and Taylor's (2006) study design IV of paired individual use vs. individual availability was implemented because random routes were anchored on the nest site making each used and random route a matched pair. At the landscape scale, habitat variables within the buffered brood routes were compared to those within the study area. This is equivalent to a design II approach of individual use vs. collective (study site) availability (Thomas and Taylor 2006).

### 3.2.3.3 *Model Development and Selection*

I used case-control logistic regression to compare used and available habitats. I used PROC GLIMMIX (SAS Institute Inc. 1999) assuming a binomial distribution and a logit link (i.e., logistic regression). I excluded the intercept term from the model (Compton et al. 2002, Wilson and Martin 2008). I developed a candidate set of 22 models (Table 3.2) by specifying biologically-sound reasons for including variables in the same model rather than simply

considering all possible combinations of covariates (Anderson and Burnham 2002). I used information-theoretic techniques to determine best-approximating models (Burnham and Anderson 1998).

There was no evidence of overdispersion (variance inflation factor,  $\hat{c} = 1.02$ ) and no need to adjust for small sample size ( $n = 582$ ), so I used Akaike's Information Criterion (AIC; Burnham and Anderson 1998). At the landscape scale,  $\hat{c}$  values were high ( $>12$ ) in any models including wetland density. Three females on a single study site (MIX) with very high wetland density who raised broods in areas of relatively low wetland density caused the inflation of  $\hat{c}$  values. Removal of these females resulted in more moderate  $\hat{c}$  values ( $\hat{c} = 0.79$ ), but since model rank did not change with their exclusion, these females were retained for all analyses. AIC values were not adjusted for overdispersion in this case.

I initially considered a random effect of study area to account for error associated with differences between study sites (27 different sites over 8 years). However, estimates for the variance components were less than the standard error, indicating weak evidence that effects of habitat variables vary by study site (models without the random effect variable had lower AIC values and thus, more explanatory power). I therefore used models that excluded a random effect of study area for all analyses and inferences are made from these models.

To perform a simultaneous test of strength of selection and fitness consequences (i.e., duckling survival), I considered an interaction term between each habitat covariate and the proportion of ducklings in the brood that survived to 30 days. To determine which interaction terms to include in the analyses, I started by fitting a global model of main effects. Each interaction term was then added, individually, to the global model and, if its addition lowered the AIC score, it was retained for further analyses. I included only those interactions that lowered the AIC scores.

Five *post hoc* models were created from the best-approximating *a priori* model to explore the effect of perennial habitat. Managed and unmanaged perennial habitat variables were removed from the top model and substituted with individual perennial habitat variables (i.e., unmanaged and managed hayland, unmanaged and managed grassland, woody cover, and DNC) and their interactions with the proportion of ducklings in the brood that survived to 30 days. The survival interaction terms for unmanaged hay, managed hay, and managed grass did not lower the AIC score and were not included in the exploratory models.

### 3.3 Results

After censoring the data set, a total of 582 broods with complete survival information (i.e., from hatch to death or to 30 days) remained for analyses, with the number of broods per site ranging from 11 to 45 (median = 19).

#### 3.3.1 Landscape Scale

The best-approximating model describing fitness consequences of habitat selection at the landscape-scale was the global (most parameterized) model (Table 3.3). Females selected brood-rearing habitats with more abundant semi-permanent wetlands, perennial cover, and with higher wetland area and densities than found on respective study sites (Table 3.4). The interspersion of wetland vegetation also affected brood habitat selection, with areas characterized by high proportions of sparsely vegetated wetlands being selected over those with denser vegetative cover (Table 3.4; Stewart and Kantrud 1971).

The addition of interaction terms between habitat variables and the proportion of ducklings in the brood that survived to 30 days to the top *a priori* model did not lower the AIC score, suggesting that duckling survival is unrelated to habitat selection patterns at the landscape scale.

Exploratory inclusion of individual perennial habitat variables did not improve the top *a priori* model. DNC appeared in the second best model; however, this model was 5 AIC units below the best-approximating model (Table 3.5).

#### 3.3.2 Local Scale

The best-approximating model describing fitness consequences of habitat selection at the local scale contained vegetative cover type 4 wetlands, managed perennial habitat and interactions between proportion of ducklings in the brood that survived to 30 days and (a) wetland area and (b) unmanaged perennial habitat (Table 3.3). Females avoided brood-rearing areas containing higher proportions of wetlands with little vegetative cover (cover type 4; Stewart and Kantrud 1971) and higher proportions of managed perennial habitats (Table 3.4). Unsuccessful broods showed strong selection for brood-rearing areas with greater wetland area than found in their random route (Figure 3.2). Successful broods avoided unmanaged perennial habitats (Table 3.4).

The *post hoc* addition of woody cover to the top *a priori* model improved the AIC score (Table 3.5), indicating that avoidance of perennial habitats by brood-rearing females at the local scale may be driven by an avoidance of woody cover (i.e., trees and shrubs). Successful broods are those that show strong avoidance of woody cover (Figure 3.3).

Although mallard females select brood-rearing habitats with higher wetland area than are available at both the landscape and local scales, there appears to be a scale-dependent trade-off between duckling survival and wetland habitat selection. Landscape-scale selection for wetland area did not appear to influence duckling survival, while selection at the local scale had a negative influence on survival. To further explore the apparent mismatch between selection for brood-rearing areas with high wetland area and poor duckling survival, I performed a *post hoc* analysis to determine if wetland availability on the study site influences local-scale decisions by brood-rearing females. I sorted study sites into low, medium and high wetland availability (i.e., wet wetlands / total wetlands) and compared the local-scale selection of wetland area and its interaction with duckling survival between these three groups (Table 3.6). Selection of wetland area by non-surviving broods was well estimated at the three levels of wetland availability and only surviving broods on sites with high wetland availability demonstrated avoidance of brood-rearing areas with high wetland coverage (Figure 3.4). Thus, females raising broods on sites with high wetland availability and selecting brood-rearing area with greater wetland area have lower survival than females that chose brood-rearing areas with lower wetland area than was available.

### **3.4 Discussion**

The sequence of decisions that animals use to choose habitats is considered to be a hierarchical process (Johnson 1980). I, therefore, considered two spatial scales to determine if brood-rearing females select habitats differently at each scale. Brood-rearing female mallards may first decide to breed in a specific landscape, and then choose habitat(s) for nesting and brood-rearing at finer scales. However, females may assess habitats for nesting and brood-rearing simultaneously, complicating observed patterns of selection. Because mallard nesting success is typically low (Arnold et al. 1993, Greenwood et al. 1995) and females are most vulnerable to predators when nesting (Kirby and Cowardin 1986), habitat selection decisions made during the critical nesting phase to enhance clutch and female survival may constrain

brood-rearing habitat choices later in the breeding season. Further evaluation of such breeding phase trade-offs would be informative.

Mallard females selected brood-rearing habitats with high wetland area at both spatial scales, however, at the local scale; females that demonstrated the strongest selection for wetland area were those that did not successfully raise broods. Similarly, mallard females that successfully hatched nests had home ranges with fewer wetlands than were available on the study site (Mack and Clark 2006). Breeding females, in both the nesting and brood-rearing stages of the breeding season that minimize wetlands in their immediate surroundings have better success of both nests and broods.

The availability (i.e., the proportion of wetlands on the study site holding water) of wetlands on the landscape influences decisions made by brood-rearing mallards. Females on sites with high wetland availability that selected brood-rearing areas of relatively high wetland coverage (i.e., compared to random) had poorer duckling survival than those females that did not. Thus, it appears that a trade-off exists in regions of high wetland availability (i.e., it is important to have wetlands on the landscape, but not too many). Females likely make trade-offs in terms of the benefits of accessing wetlands necessary for brood-rearing against the costs of increased encounter rates with predators that associate with wetlands. The mismatch between selection for areas of high wetland coverage and duckling survival could have important implications for management strategies and planning. Depending on pair settlement and nesting success rates, perhaps wetland conservation should be focused more on areas of moderate rather than highest wetland coverage.

Wetland variables were calculated using ponds that were holding water in July, when wetland classification took place. Some wetlands may have held water early in the breeding season and were actually available to broods throughout a portion of the breeding season. As a result, the values of wetland area, wetland availability, and other wetland specific variables could be lower than was actually available.

Perennial habitats were selected at the landscape scale, but avoided at the local scale. Nesting success is positively associated with perennial cover (Greenwood et al. 1995, Mack and Clark 2006), so it is plausible that landscape patterns are indicative of nest-site selection while local-scale patterns are indicative of brood-rearing. Woody cover was the important driver of perennial habitat avoidance at the local scale, and broods that demonstrated the strongest avoidance

patterns had the highest survival of ducklings, showing consistent support for habitat selection patterns conferring with survival. The interaction between survival of ducklings and avoidance of woody cover may be related to increased risk of predation by aerial predators near woody habitats. Nesting females select woody cover for nest sites despite low nest survival in these habitats (Howerter 2003), presumably to increase their own survival during incubation, though this needs to be determined.

Patterns of habitat selection may be driven by the process of natural selection (Clark and Shutler 1999). For natural selection to produce patterns in habitat selection, selected habitats should be those that result in higher survival. I found inconsistent evidence of habitat selection patterns conferring enhanced survival. Selective patterns at the landscape scale had no apparent consequences to duckling survival. At the local scale, habitat selection patterns influenced survival of ducklings, although they did not always confer improved fitness benefits. Females that demonstrated the strongest selection for wetland area were those that unsuccessfully fledged ducklings while females that demonstrated the strongest avoidance of woody cover were those with the highest duckling survival. Hence, there is inconsistent support for the hypothesis that brood-rearing mallard females select habitats that confer the highest fitness benefits. Similarly, endangered greater sage-grouse (*Centrocercus urophasianus*) do not always select habitats that result in highest chick survival (Aldridge and Boyce 2008), highlighting the importance of assessing both habitat selection and fitness within selected habitats so that management actions target the most productive habitats.

However, I do not know if brood-rearing habitats are chosen on the basis of innate (genetic) behaviour or develop as a result of learning or experience. Female mallards and their daughters frequently reuse brood-rearing or natal wetlands (when available), respectively, in subsequent years, so habitat choices may be related to previous experience and success (Clark et al. 2005). Strength of fidelity to reused wetlands was not related to previous brood-rearing success in mallards (Clark et al. 2005), but further work is needed to rigorously test this idea.

Lack of consistent evidence that brood-rearing habitat selection is adaptive could be due to the scale used for habitat comparisons. The local scale could be too fine since random route buffers could overlap original route buffers. Using randomly placed route buffers or comparing used routes to home ranges may have better exposed selection patterns. Alternatively, ambiguous evidence that brood-rearing habitat selection maximizes fitness could be a result of the generalist

nature of mallards. The prairies are a dynamic ecosystem and mallards are well adapted for this type of environment. Unpredictable, dynamic environments may favour a flexible response (Mulhern et al. 1985, Fryxell 1997). Inconsistency in selection patterns could be evidence of plastic habitat selection (i.e., used habitats are statistically different than available habitats but not consistent over time) may be a result of variability in prairie wetland habitats through space and time (Mulhern et al. 1985). Predation pressures are also known to fluctuate on the prairies (Clark and Shutler 1999, Davis 2003) and could result in survival not conferring with habitat selection patterns (Davis 2005, Fontaine and Martin 2006). As a result, selection patterns may appear neutral or as not having an adaptive nature but over the long term they may be optimal. Further studies should focus on assessing the influence of both reproductive survival parameters (i.e., female, nest, and offspring survival) as well as demographic parameters (e.g., clutch size, nesting attempts) on habitat selection at multiple spatial scales to determine if habitat selection patterns are being driven by finding safe nest or brood-rearing sites and/or food availability.

### 3.5 Tables

Table 3.1 - List of variables, predicted habitat selection patterns and predicted effects of selection on mallard duckling survival in the Canadian prairies, 1993-2000.

Variable	Definition	Predicted selection pattern	Predicted effect on survival
wetland permanency:			
class3	the proportion of wetlands in the buffer that are seasonal	+	$\beta > 0$
class4	the proportion of wetlands in the buffer that are semi-permanent	+	$\beta < 0$
vegetative cover type:			
cover2	the proportion of wetlands in the buffer that are cover type 2; scattered vegetation intermixed with pockets of open water	+	$\beta > 0$
cover3	the proportion of wetlands in the buffer that are cover type 3; >2 m ring of emergent vegetation and a central area of open water	+	$\beta > 0$
cover4	the proportion of wetlands in the buffer that are cover type 4; 95% of the basin as open water with a <2 m band of emergent vegetation	+	$\beta > 0$
density	density of wetlands in the buffer	+	$\beta > 0$
area	the proportion of the buffer that is wetland	+	$\beta > 0$
um_ern	the proportion of the buffer that is unmanaged perennial cover	-	$\beta < 0$
mg_ern	the proportion of the buffer that is managed perennial cover	-	$\beta < 0$
<i>Exploratory upland variables:</i>			
um_hay	the proportion of the buffer that is unmanaged hayland	-	$\beta < 0$
mg_hay	the proportion of the buffer that is managed hayland	-	$\beta < 0$
um_grass	the proportion of the buffer that is unmanaged grassland	+	$\beta > 0$
mg_grass	the proportion of the buffer that is managed grassland	+	$\beta > 0$
DNC	the proportion of the buffer that is planted nesting cover	-	$\beta < 0$
wood	the proportion of the buffer that is trees and shrubs	-	$\beta < 0$



Table 3.2 - List of models used to determine mallard brood-rearing habitat selection in the Canadian prairies, 1993-2000.

<b>Model #</b>	<b>Model<sup>a</sup></b>
1a-b	class, cover2,3,4, density, area, um_pern, mg_pern, (area*fledge,
global	um_pern*fledge, cover3*fledge)
2 a-b	class
3 a-c	cover, ( cover3*fledge)
4	area, (area*fledge)
5	density
6	um_pern, (um_pern*fledge)
7	mg_pern
8	density, um_pern, mg_pern, (um_pern*fledge)
9	area, um_pern, mg_pern, (area*fledge, um_pern*fledge)
10 a-b	class, um_pern, mg_pern, (um_pern*fledge)
11 a-f	class, cover, ( cover3*fledge)
12 a-b	class, area, (area*fledge)
13 a-b	class, density
14 a-b	class, DNC, (DNC*fledge)
15 a-b	class, mg_hay
16 a-b	class, mg_grass
17 a-b	class, area, um_pern, mg_pern, (area*fledge, um_pern*fledge)
18 a-b	class, density, um_pern, mg_pern, (um_pern*fledge)
19 a-b	class, cover, area, (area*fledge, cover3*fledge)
20 a-b	class, cover, density, (cover3*fledge)
21 a-b	cover, area, um_pern, mg_pern, (area*fledge, um_pern*fledge, cover3*fledge)
22 a-b	cover, um_pern, mg_pern, (um_pern*fledge, cover3*fledge)
<b>Exploratory</b>	
101	cover4, area, mg_hay, um_hay, (area*fledge)
102	cover4, area, mg_grass, um_grass, (area*fledge, um_grass*fledge)
103	cover4, area, wood, (area*fledge, wood*fledge)
104	cover4, area, DNC, (area*fledge, DNC*fledge)
105	cover4, area, DNC, wood, (area*fledge, DNC*fledge, wood*fledge)

<sup>a</sup> Class3 and class4 are the proportion of wetlands within the buffer that are class III (seasonal) or IV (semi-permanent), cover2, 3, or 4 is the proportion of wetlands within the buffer that are cover type 2, 3, or 4, area is the proportion of the buffer that is wet wetland, density is the density of wet wetlands in the buffer, um\_pern is the proportion of the buffer that is unmanaged perennial habitat, mg\_pern is the proportion of the buffer that is managed perennial habitat, um\_grass is the proportion of the buffer that is unmanaged grassland, mg\_grass is the proportion of the buffer that is managed grassland, um\_hay is the proportion of the buffer that is unmanaged hayland, mg\_hay is the proportion of the buffer that is managed hay, DNC is the proportion of the buffer that is planted nesting cover, wood is the proportion of the buffer that is woodland, and fledge is the proportion of the brood that survived to 30 days.

Table 3.3 - Top models ( $\Delta AIC < 2$ ) describing habitat selection patterns in mallards by comparing buffers around used brood routes to a) the study site (landscape scale) or b) random brood routes (local scale) in the Canadian prairies, 1993-2000.

<b>Model Description<sup>a</sup></b>	<b>-2logLK</b>	<b>AIC</b>	<b>K</b>	<b><math>\Delta AIC</math></b>	<b><math>w_i</math></b>
<b>a) Landscape Scale:</b>					
class4, cover2, cover3, cover4, area, density, unmanaged perennial, managed perennial	413.14	429.14	8	0.00	1.00
class3, cover2, cover3, cover4, area, density, unmanaged perennial, managed perennial	425.62	441.62	8	12.48	0.00
<b>b) Local Scale:</b>					
cover4, area, unmanaged perennial, managed perennial, unmanaged perennial *fledge, area*fledge	749.72	761.72	6	0.00	0.32
cover3, area, unmanaged perennial, managed perennial, unmanaged perennial *fledge, area*fledge	748.92	762.92	7	1.20	0.18
area, unmanaged perennial, managed perennial, unmanaged perennial *fledge, area*fledge	753.08	763.08	5	1.36	0.16

<sup>a</sup> Class3 and class4 are the proportion of wetlands within the buffer that are class III (seasonal) or IV (semi-permanent), cover 3 or 4 is the proportion of wetlands within the buffer that are cover type 3 or 4, area is the proportion of the buffer that is wet wetland, um\_ pern is the proportion of the buffer that is unmanaged perennial habitat, mg\_ pern is the proportion of the buffer that is managed perennial habitat, and fledge is the proportion of ducklings in the brood that survived to 30 days.

Table 3.4 - Coefficients and odds ratios (OR) for variables in the best-approximating models used to determine patterns of habitat selection by mallards by comparing used brood routes to a) study sites (landscape scale) and b) random routes (local scale) in the Canadian prairies, 1993-2000. Fledge indicates the proportion of the brood surviving after 30 days.

Variable <sup>a</sup>	Estimate	95% CI		Odds Ratio <sup>b</sup>	95% CI for OR	
		lower	upper		lower	upper
<b>a) Landscape Scale:</b>						
Class4	4.73	3.85	5.60	1.60	1.47	1.75
Cover2	2.87	1.71	4.04	1.33	1.19	1.50
Cover3	4.74	3.67	5.81	1.61	1.44	1.79
Cover4	6.03	4.03	8.02	1.83	1.50	2.23
Wetland area	10.66	8.60	12.73	2.91	2.36	3.57
Wetland density	20.89	18.67	23.10	8.07	6.47	10.08
Managed perennial	2.32	1.43	3.20	1.26	1.15	1.38
Unmanaged perennial	3.04	1.87	4.21	1.36	1.21	1.52
<b>b) Local Scale:</b>						
Cover4	-2.43	-3.78	-1.08	0.78	0.69	0.90
Wetland area, when fledge = 0.0	9.58	7.92	11.23	2.61	2.21	3.07
Wetland area, when fledge = 1.0	0.90	-2.77	4.58	1.09	0.76	1.58
Unmanaged perennial, when fledge = 0.0	-0.63	-1.25	-0.01	0.94	0.88	0.99
Unmanaged perennial, when fledge = 1.0	-4.19	-6.13	-2.25	0.66	0.546	0.80
Managed perennial	-1.14	-1.90	-0.37	0.89	0.83	0.96

<sup>a</sup> Class4 is the proportion of wetlands within the buffer that are class IV (semi-permanent), cover2, 3, or 4 is the proportion of wetlands within the buffer that are cover type 2, 3, or 4, wetland area is the proportion of the buffer that is wet wetland, wetland density is the density of wet wetlands in the buffer, unmanaged perennial is the proportion of the buffer that is unmanaged perennial habitat, managed perennial is the proportion of the buffer that is managed perennial habitat, and fledge is the proportion of the brood that survived to 30 days.

<sup>b</sup> Odds ratio for a 0.1 change in proportion of habitat.

Table 3.5 - Top exploratory model ( $\Delta AIC < 2$ ) describing habitat selection patterns by mallards by comparing buffers around used brood routes to a) the study site (landscape scale) and b) random brood routes (local scale) in the Canadian prairies, 1993-2000.

<b>Model Description</b> <sup>a</sup>	<b>-2logLK</b>	<b>AIC</b>	<b>K</b>	<b><math>\Delta AIC</math></b>	<b><math>w_i</math></b>
<b>a) Landscape scale:</b>					
Class4, cover2, cover3, cover4, area, density, unmanaged perennial, managed perennial	413.14	429.14	8	0.00	0.82
Class4, cover2, cover3, cover4, area, density, DNC <sup>b</sup>	420.29	434.29	7	5.15	0.06
<b>b) Local Scale:</b>					
cover4, area, wood, area*fledge, wood*fledge <sup>b</sup>	750.76	760.76	5	0.00	0.26
cover4, area, unmanaged perennial, managed perennial, area*fledge, unmanaged perennial *fledge	749.72	761.72	6	0.96	0.16

<sup>a</sup> Class4 is the proportion of wetlands within the buffer that are class IV (semi-permanent), cover2, 3, or 4 is the proportion of wetlands within the buffer that are cover type 2, 3, or 4, area is the proportion of the buffer that is wet wetland, density is the density of wet wetlands in the buffer, unmanaged perennial is the proportion of the buffer that is unmanaged perennial habitat, managed perennial is the proportion of the buffer that is managed perennial habitat, DNC is the proportion of the buffer that is planted nesting cover, wood is the proportion of the buffer that is woodland, and fledge is the proportion of the brood that survived to 30 days.

<sup>b</sup> exploratory model

Table 3.6 - Parameter estimates for the interaction between wetland area and proportion of ducklings in the brood that survived to 30 days (fledge) on sites with low, medium, or high wetland availability. Estimates were calculated from the best-approximating *a priori* model used to determine patterns of habitat selection by brood-rearing mallards in the Canadian prairies, 1993-2000.

<b>Study Site Wetland Availability</b>	<b>Variable</b>	<b>Estimate</b>	<b>SE</b>
low	wetland area when fledge = 0.0	13.718	3.597
	wetland area when fledge = 1.0	11.195	10.57
medium	wetland area when fledge = 0.0	4.567	2.298
	wetland area when fledge = 1.0	2.584	5.058
high	wetland area when fledge = 0.0	12.746	2.932
	wetland area when fledge = 1.0	-9.163	8.247

### 3.6 Figures

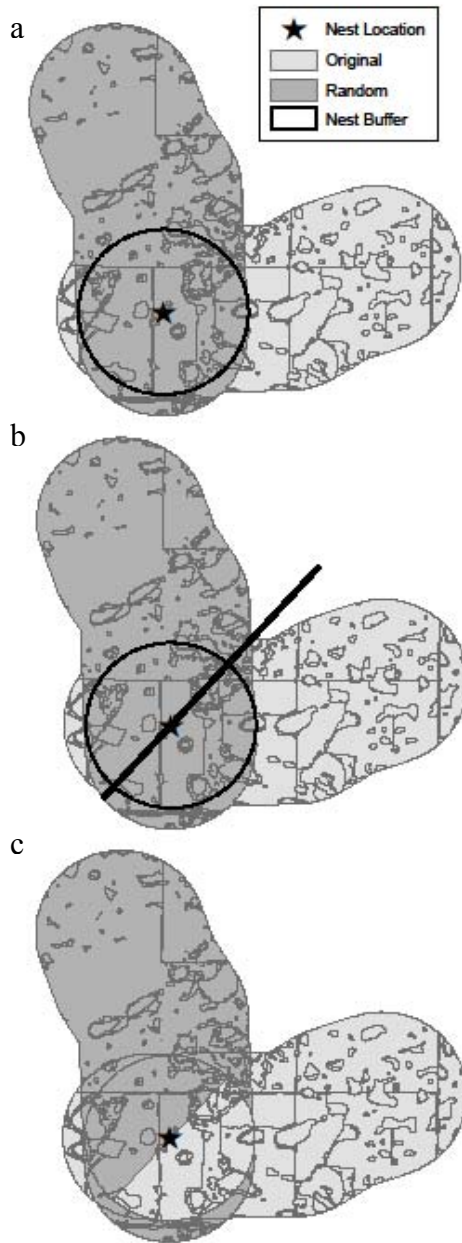


Figure 3.1 - Methods used for dividing buffer overlap between used and random mallard brood route buffers in the Canadian prairies, 1993-2000. A 500 m radius around the nest has complete overlap between used and random buffers (a), split line determined by drawing a line from point of divergence through nest (b), half of nest buffer allotted as used and half to random (c). Any remaining overlap was permitted and varies randomly with each brood.

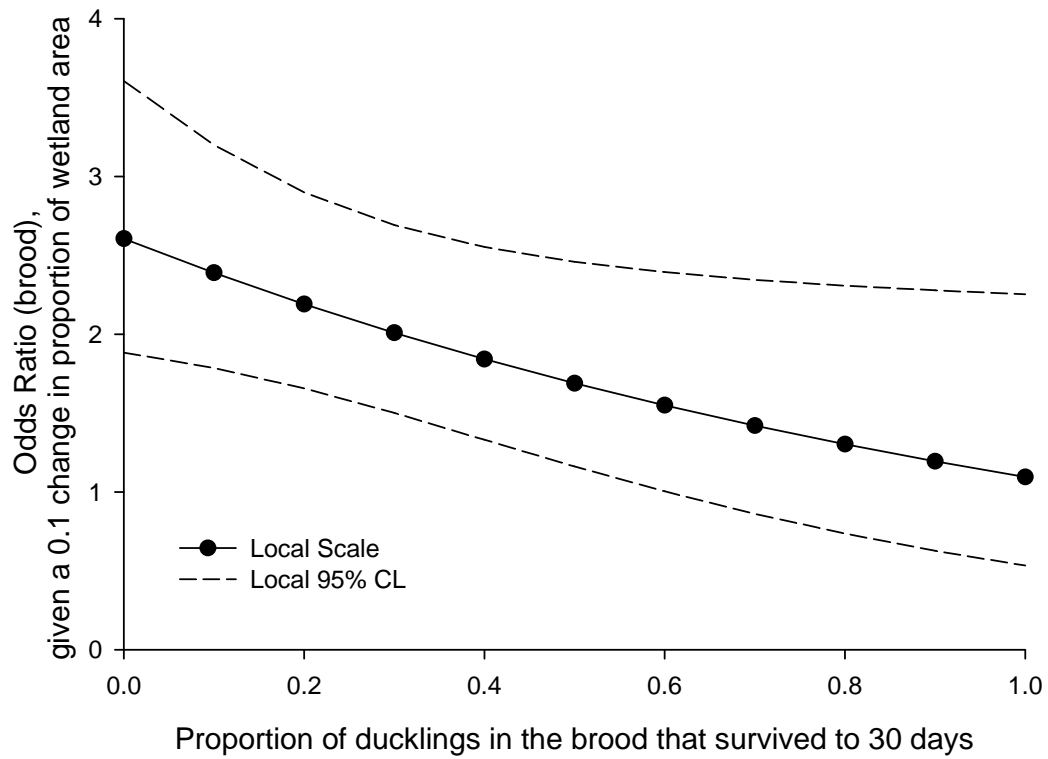


Figure 3.2 - Relationship between duckling survival and local-scale selection of brood-rearing areas with high wetland area for mallard ducklings in the Canadian prairies, 1993-2000. Odds ratios >1 indicate selection for wetland area. Odds ratios (for a 0.1 change in proportion of habitat) were estimated from the best-approximating, local scale, a priori model. Upper and lower 95% confidence limits are represented by dashed lines.

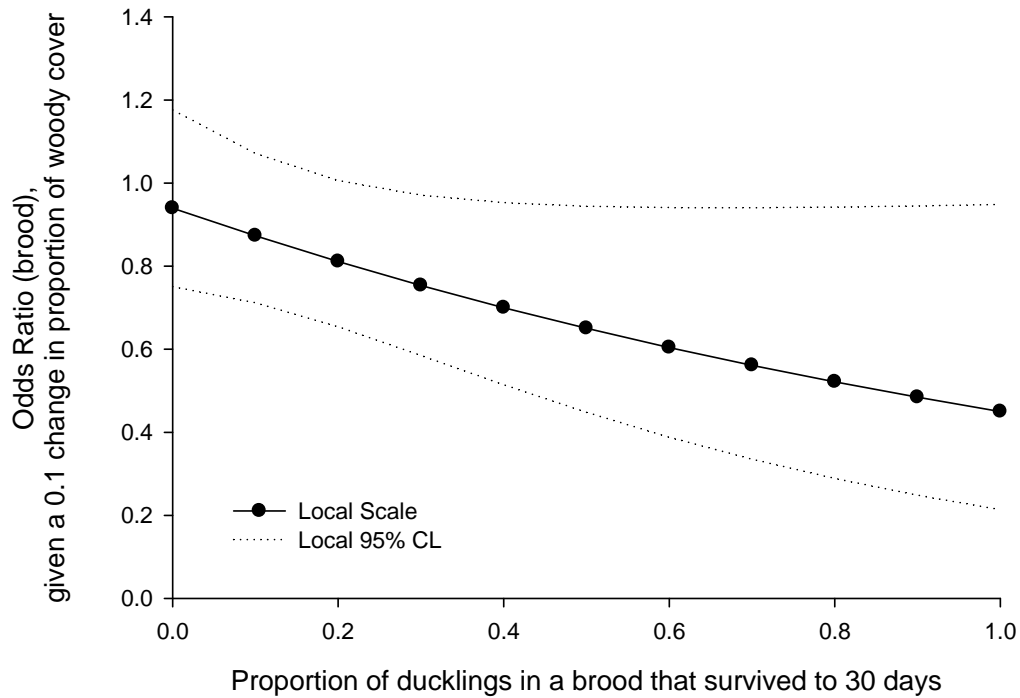


Figure 3.3 - Relationship between duckling survival and local-scale avoidance of brood-rearing areas with woody for mallard ducklings in the Canadian prairies, 1993-2000. Odds ratios <1 indicate avoidance of woody cover. Odds ratios (for a 0.1 change in proportion of habitat) were estimated from the best-approximating, local scale, exploratory model. Upper and lower 95% confidence limits are represented by dashed lines.



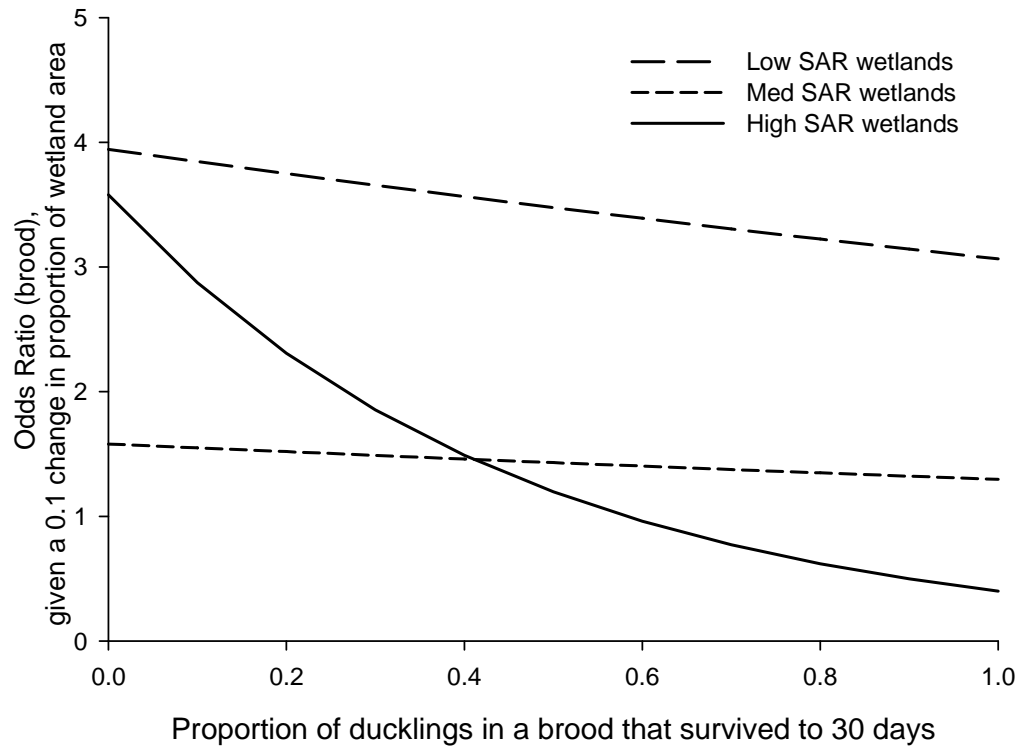


Figure 3.4 - Relationship between duckling survival and local-scale selection of brood-rearing areas with high wetland area by brood-rearing mallards in the Canadian prairies, 1993-2000 on study sites (SAR) with low (long dash), medium (short dash), and high (solid) wetland availability. Odds ratios >1 indicate selection for wetland area. Odds ratios (for a 0.1 change in proportion of habitat) were estimated from the best-approximating, local scale, a priori model.

## CHAPTER 4 SYNTHESIS

An important challenge for animal ecologists is to explain why there is so much variation in population size, and central to this objective is to understand why reproductive and survival rates vary so much. Furthermore, understanding what factors influence survival rates (i.e., habitat choices or factors such as weather, experience, or the surrounding landscape) provides a cornerstone for wildlife management by helping guide management activities aimed at increasing population growth rates. Using data collected during the Prairie Habitat Joint Venture (PHJV) Assessment study, I addressed questions regarding both variation in duckling survival rates and the adaptive nature of habitat selection. Specifically, I employed a conceptual framework similar to that of life-history theory, one that explicitly considered the potential for trade-offs to exist between (i) management actions designed to benefit birds at different life-cycle stages (i.e., nesting versus brood-rearing) and (ii) the consequences of habitat choices made by birds at different spatial scales (i.e., landscape versus brood-rearing area). Overall, my main findings have important implications for conservation programs on the Canadian prairies and for theoretical advances in habitat selection theory. Below, I elaborate on each of these topics, and provide suggestions for future research.

Upland habitat management has been the primary method used to increase waterfowl nesting success in the Canadian PPR since the PHJV was conceived in 1986, although similar objectives pervade strategies in the U.S. PPR as well (Reynolds et al. 2001). While these programs aim to increase nesting success, it has been unknown what, if any, effect these programs have on duckling survival. In response to this information gap, I evaluated hypothesized sources of variation in mallard duckling survival, with a particular emphasis on managed and remnant natural upland habitats (Chapter 2). I considered the effects of upland and wetland habitats, female and brood-related variables and weather on variation in duckling survival rates. I found that survival was lower for ducklings that travelled farther overland and used areas with a high proportion of semi-permanent wetlands. Duckling survival was positively associated with managed grasslands and negatively related, for older ducklings, to managed hayland. There was no evidence of trade-offs between benefits of managing habitat to enhance nesting success and costs in terms of lower subsequent duckling survival. I was, however, unable to assess whether the density of broods in areas with high management activity had an impact on duckling survival

rates through, for example, increased competition between females for brood space or between broods for limited food resources, or perhaps increased predator activity in areas of high prey (i.e., brood) abundance. Survival of mallard ducklings in Sweden is negatively density dependent, however the mechanisms behind these patterns remain unclear (Elmberg et al. 2005, Gunnarsson et al. 2006).

Weather variables did not appear in any of my top models, contradicting previous work on this subject. Weather conditions (i.e., daily temperature and precipitation values) were not recorded at each study site; instead, I used information from nearby weather stations to estimate weather conditions for each brood. Prairie weather is highly variable and the weather index I created likely did not accurately estimate weather conditions at each study site. As a result, the influence of weather on duckling survival may have been underestimated.

Precocial young that must travel overland in search of food resources and for predator avoidance likely are subjected to similar mortality pressures. Indeed, similar to my results, sharp-tailed grouse (*Tympanuchus phasianellus*) chick survival declined with longer distances travelled from the nest (Goddard and Dawson 2009). Contrary to my results, but conferring with other studies on waterfowl, sharp-tailed grouse chick survival declined with poor weather in the first seven days of life (Goddard and Dawson 2009).

Female age did not have a strong impact on duckling survival, which is similar to other mallard duckling survival studies (Krapu et al. 2000, Hoekman et al. 2004). However, mallard nesting success is related to female age, with older mallard females having higher nesting success than younger females (Devries et al. 2008). Perhaps female age is most important during the nesting phase of reproduction when experience in nest site selection is critical but becomes less important during brood rearing relative to other factors. Female age is, however, an important predictor of duckling survival for cavity nesting wood ducks in the southern U.S. (Davis et al. 2007). In other precocial species this trend has also been observed; older female white-tailed and willow ptarmigan (*Lagopus leucurus* and *L. lagopus*) also were more successful at raising broods than younger females (Wiebe and Martin 1998).

My results suggest that upland habitat management programs that aim to increase nesting success have either a positive or no impact on duckling survival rates. Consideration of how these programs affect breeding female survival could make programs even more robust. Regular evaluation of programs is important for ensuring that management dollars are being spent

effectively. Evaluation of the impact of outreach programs (i.e., programs designed to influence landowner land management practices) in affecting mallard population growth rate is also critical to determine their efficacy. The PHJV assessment study was designed for mallards, but other waterfowl, other bird species, mammals and invertebrates may be positively influenced by these management activities (e.g., Skinner and Clark 2008).

Research studies are often confined to a handful of study sites over a few years or one study site over many years. It is unusual to have a large scale study that spans a large geographical area over a relatively long time frame. The PHJV Assessment study was unique in its size and scope and provides a landscape-level perspective on waterfowl ecology. Smaller, more focused studies are valuable since they can more easily consider temporal variation at the same locations. However, generalizing the results of the PHJV Assessment study across an entire landscape is, perhaps, more applicable for management planning. The PHJV Assessment study could have been improved by incorporating a temporal component (i.e., by revisiting sites), and recording seasonal change in wetland quality and availability, site-specific weather data, and detailed predator community information. Predation is an important cause of duckling mortality (Pearse and Ratti 2004) and predation risk varies by region and conditions such as alternate prey availability. I was unable to control for the effect of predators on duckling survival rates.

The assumption that selected habitats are high quality habitats (i.e., where reproductive success and, thus, fitness are higher) is common in ecological studies of habitat selection for a wide variety of taxa (Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Howerter et al. 2008). In Chapter 3, I addressed unresolved questions about how birds balance costs and benefits of selecting habitats by determining the survival consequences of habitat choices made by brood-rearing mallards. At the landscape scale, females selected brood-rearing areas with a high proportion of wetland and perennial upland habitats, but duckling survival was not related to habitat selection patterns at this scale. At finer scales, females also selected brood-rearing areas with high proportions of wetland habitats, but, contrary to expectation, duckling survival was lower when females raised their broods in these areas. The availability of wetlands on the landscape influences decisions made by brood-rearing mallards. Females on sites with high wetland availability that selected brood-rearing areas of relatively high wetland coverage had poorer duckling survival than those females that did not. Thus, it appears that a trade-off exists in regions of high wetland availability. At the local scale, woody cover (trees and shrubs) was

avoided by brood-rearing females, and indeed, females that showed the strongest avoidance of woody cover had the highest duckling survival rates. Thus, females did not consistently select brood-rearing habitats that conferred the highest fitness benefits; rather, the relationship between habitat selection and fitness depended on spatial scale and the habitats considered. Benefits of selective use of landscapes with higher wetland area may be counterbalanced by lower offspring survival in brood-rearing areas characterized by abundant wetlands.

During the breeding season, decisions made regarding where and when to nest, what path to take during inter-wetland moves and which wetlands to occupy are likely the result of a series of trade-offs. Females must balance the costs and benefits of each decision while trying to optimize both their own survival and the survival of their young. It is often assumed that decisions regarding habitat selection should result in the greatest survival of young; however, this was not always the case here. I found that habitat choices made by female mallards did not always confer fitness benefits through increased survival. This has been a common pattern, as reported in some other studies that tested for adaptive habitat selection (Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Howerter et al. 2008). This may be because we often attempt to link one component of reproductive success (i.e., nesting or fledging success) with one spatial scale of habitat features. However, decisions regarding habitat choices are likely made at multiple scales to optimize overall fitness payoffs. Chalfoun and Martin (2007) addressed this concern by comparing various fitness metrics (nesting success, number of young fledged per year) and demographic parameters (clutch size, clutch mass, nestling mass, and number of nest attempts) of Brewer's sparrow (*Spizella breweri*) at three different spatial scales and found that nesting success was not higher in preferred habitats. Habitat preferences did accord with higher nestling mass and number of nesting attempts in Chalfoun and Martin's study, suggesting that habitats may be chosen in response to food availability. To increase survival of self or young, habitat choices likely also take into account predator abundance, food availability and other factors. Decisions made to maximize nest survival could constrain offspring survival after nest exodus. Future work in this area should consider multiple features of reproductive success, along with demographic parameters, at multiple spatial scales to attempt to tease apart these patterns and processes.

For habitat decisions to be adaptive they must have a genetic basis, however, it remains unclear if habitat selection has a genetic basis or is developed via learning or experience (Clark

and Shutler 1999). Evidence of phenotypic correlation between habitat preference and fitness has been demonstrated in arthropods and molluscs (Jaenike and Holt 1991). Habitat choices may be related to previous experience and success; female mallards and their daughters frequently reuse brood-rearing or natal wetlands (when available), respectively, in subsequent years (Clark et al. 2005). However, strength of fidelity to reused wetlands was not related to previous brood-rearing success (Clark et al. 2005); a problem that should be evaluated again with larger samples of sites and broods.

#### **4.4 Management implications**

Intensive efforts have been made by many conservation agencies to increase nesting success of waterfowl in the Canadian PPR. While the focus of these programs has been on nesting success, little has been known about how, or if, upland habitat management influences survival of ducklings. I found that managed grasslands had a positive effect on duckling survival. Management activities aimed to protect and enhance grasslands will benefit both nesting success and duckling survival and should lead to greater waterfowl productivity. Continued efforts to protect the native grasslands that remain in the Canadian PPR, to convert annual cropland back into perennial grassland, and to encourage and aid farmers and ranchers to practice good pasture management are recommended.

Females that selected brood-rearing areas with abundant wetlands on sites with high wetland availability were those that had the poorest duckling survival. This mismatch between selection for areas of high wetland coverage and duckling survival could have important implications for management strategies and planning. Similarly, mallard females that successfully hatched nests had home ranges with fewer wetlands than were available on the study site (Mack and Clark 2006). Depending on pair settlement, female survival and nesting success rates, perhaps wetland conservation should be focused more on areas of moderate rather than highest wetland coverage. However, this suite of trade-off needs rigorous evaluation before robust management recommendations can be made.

Females that avoided brood-rearing areas with abundant woody cover (trees and shrubs) had a higher likelihood of successfully raising their broods. Furthermore, nesting females select woody cover for nest sites despite low nest survival in these habitats (Howerter 2003), presumably to increase their own survival during incubation, although this last idea needs to be determined. This would suggest that focusing wetland management actions in areas with less

woody cover could have a positive impact on productivity. But trees and shrubs are ubiquitous in the Canadian aspen parklands and avoiding these areas in management planning may not be feasible or cost-effective. Over the past century, aspen populations have expanded, perhaps due to the extirpation of Plains bison (*Bison bison bison*) or the suppression of natural fire regimes (Campbell et al. 1994). Thus, there are costs and benefits associated with different habitats at different scales and for different life-cycle stages. Continued consideration of how habitat selection at different spatial scales influences adult female survival, nesting success, and duckling survival is important for future management planning.

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## APPENDIX 1

Complete list of *a priori* and exploratory models developed to estimate mallard duckling survival rates across prairie Canada, 1993-2000. Exploratory models were created by adding exploratory variables to the best-approximating *a priori* model.

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### Model description

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Dage

Statistical null

Dage + bsize + travel + henage + hatdate + class + cover + density + weather + DNC

Dage + bsize + travel + henage + hatdate + class + cover + density + weather + pern\_cov

Dage + hatdate + density

Dage + henage + density

Dage + hatdate + density + henage

Dage + hatdate + density + henage + DNC

Dage + hatdate + density + henage + pern\_cov

Dage + hatdate + density + DNC

Dage + hatdate + density + pern\_cov

Dage + hatdate + density + DNC + DNC\*density

Dage + hatdate + density + pern\_cov + pern\_cov\*density

Dage + hatdate + bsize

Dage + hatdate + bsize + travel

Dage + hatdate + bsize + weather

Dage + hatdate + bsize + henage

Dage + hatdate + bsize + henage + travel

Dage + hatdate + bsize + travel + weather

Dage + travel + hatdate

Dage + dist\_to\_first\_wetl + hatdate

Dage + dist\_to\_first\_wetl + hatdate + hatdate2

Dage + dist\_to\_first\_wetl + hatdate + dist\_to\_first\_wetl\*hatdate

Dage + travel + weather

Dage + dist\_to\_first\_wetl + weather

Dage + hatdate + weather

Dage + travel + hatdate + weather

Dage + travel + density

Dage + travel + density + DNC

Dage + travel + density + pern\_cov

Dage + travel + henage

Dage + travel + henage + density

Dage + travel + henage + DNC

Dage + travel + henage + pern\_cov

Dage + travel + henage + density + DNC  
 Dage + travel + henage + density + percov  
 Dage + travel + henage + hatdate  
 Dage + travel + henage + hatdate + DNC  
 Dage + travel + henage + hatdate + percov  
 Dage + henage + bsize  
 Dage + henage + DNC  
 Dage + henage + percov  
 Dage + hatdate + henage + DNC  
 Dage + hatdate + henage + percov  
 Dage + travel + cover  
 Dage + travel + class  
 Dage + travel + cover + class  
 Dage + henage + cover  
 Dage + henage + class  
 Dage + henage + cover + class  
 Dage + henage + travel + cover  
 Dage + henage + travel + class  
 Dage + henage + travel + cover + class  
 Dage + bsize + cover  
 Dage + bsize + cover + travel  
 Dage + cover + weather  
 Dage + class + DNC  
 Dage + class + percov  
 Dage + travel + DNC  
 Dage + dist\_to\_first\_wetl + DNC  
 Dage + travel + percov  
 Dage + dist\_to\_first\_wetl + percov  
 Dage + hatdate + DNC  
 Dage + hatdate + percov  
 Dage + hatdate + DNC + DNC\*hatdate  
 Dage + hatdate + percov + percov\*hatdate  
 Dage + travel + hatdate + DNC  
 Dage + dist\_to\_first\_wetl + hatdate + DNC  
 Dage + travel + hatdate + percov  
 Dage + dist\_to\_first\_wetl + hatdate + percov  
 Dage + travel + DNC + DNC\*travel  
 Dage + travel + pern\_cov + pern\_cov\*travel  
 Dage + class + DNC  
 Dage + class + pern\_cov  
 Exploratory models:  
 Dage + travel + class4 + mng\_cov  
 Dage + travel + class4 + pern\_cov



Dage + travel + class4 + mng\_pern

Dage + travel + class4 + DNC

Dage + travel + class4 + mng\_grass

Dage + travel + class4 + mng\_hay

Dage + travel + class4 + mng\_crop

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