HABITAT SELECTION TRADE–OFFS, MALE QUALITY AND REPRODUCTIVE PERFORMANCE OF FEMALE MALLARDS

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By

Jennifer L. Sheppard

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ABSTRACT

Conservation programs for breeding ducks in North America are typically designed to enhance nest success by establishing or restoring attractive perennial nesting cover or promoting favourable agricultural practices. Thus, a central objective is to attract ducks to habitats where females have higher survival and reproductive rates, primarily greater nest success. Using data collected from 1993 – 2000, I investigated hypotheses proposed to explain inconsistent patterns of habitat selection detected during nesting and brood–rearing stages in free-ranging mallards (*Anas platyrhynchos*) throughout the Canadian Prairie Parklands. By simultaneously considering indices of body condition and size of male and female mallards and plumage score of males, I also evaluated the role of male quality in reproductive investment and patterns of breeding success of females. In general, wild mallards mated assortatively by body condition but not body size. Yearling females nested earlier and had higher nest survival when mated to males with better plumage quality. When paired with larger-bodied males, yearling females renested more often, whereas nest and brood survival increased among older females. I characterized the habitat composition of 100 and 500 m radius buffers surrounding nest sites and related habitat features to survival of nests, broods and females. Habitat selection trade-offs were detected among perennial habitats and planted cover, such that nest survival increased in these habitats whereas duckling survival decreased. Furthermore, at large spatial scales, nest survival decreased in areas with greater amounts of cropland whereas duckling survival increased. Survival rates of females increased with greater amounts of seasonal wetlands, but nest survival decreased in such areas. Semi-permanent wetlands were associated with decreased nest survival at larger spatial scales, but associated with higher nest success at finer scales. Benefits of increasing perennial and planted cover habitats to increase nest survival could be partly offset by costs in terms of lower duckling survival, whereas opposite patterns existed in areas of abundant seasonal. The restoration of seasonal wetlands in perennial habitats could offset these trade-offs but net impacts of habitat selection and survival trade-offs on annual reproductive success must first be evaluated.

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DEDICATION

My dog, Squid, has travelled every journey with me since I left home, travelling from field camp to field camp, province to state and back again. As I struggled through my undergraduate degree to obtain top marks, he received much fewer walks than he deserved. Yet, he still sat by my side throughout my Master's degree. He was the only thing that remained constant for me these last 9 years, keeping me company when I was homesick, and always giving me a reason to come home from the office/school at a reasonable hour. Although not much of a hunting dog, I dedicate this thesis to him, in hopes that proper habitat management techniques ensure waterfowl populations remain viable so dogs can always bond with their owners during the hunting season.

There are numerous people who deserve acknowledgement and gratitude, either for paving the way and leading me to Saskatoon for my research, or for collecting the data and creating research questions which I aimed to answer. Thanks to David Johns for allowing me to get my fill of field work every summer and to all my fellow Clarkites who made my time in the office bearable and enjoyable (and educational). I would like to thank Dr. Courtney Amundson, my mentor throughout the years, for her continued encouragement and support during my migration from field technician to graduate student, for introducing me to the life of academia, and for making me believe that I could do this. I thank my family and friends for their support throughout my entire educational experience. Finally, I give my deepest thanks to Simon, for joining me on this journey, supporting me, encouraging me, missing an entire year of school to help alleviate my stress, and for leaving your mountainous home to trek across the flatlands with me to follow my dreams; I know it couldn't have been easy for you.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 HABITAT AND HABITAT SELECTION THEORY

Orians (1980) defined habitat as a piece of terrain large enough to meet all the resource requirements of an organism, enabling it to spend at least one breeding season there, and comprised of distinguishable habitat patches which differ from one another in ways that affects its fitness. An organism must assess the current status of the habitat while predicting its value throughout the breeding season, a decision that often is made when crucial resources required later in the season may not be present (Orians 1980). Habitat selection theory suggests that animals should select habitats that optimize survival and reproductive success (Levins 1968, Orians 1980). Presumably, organisms should prefer higher quality habitats and avoid lower quality habitats, as expected if the process of habitat selection is adaptive.

Research on North American waterfowl frequently evaluates local and landscape–level factors that affect habitat use (e.g., Clark and Shutler 1999, Stephens *et al.* 2005, Howerter *et al.* 2008). Nest survival often is the most important parameter in the population dynamics of grassland nesting ducks that breed in the Prairie Pothole Region (PPR) (Cowardin *et al.* 1985, Greenwood *et al.* 1995, Hoekman *et al.* 2002, Emery *et al.* 2005, Horn *et al.* 2005, Stephens *et al.* 2005, Howerter *et al.* 2008), so conservation programs are typically designed to enhance nest success either by establishing or restoring attractive perennial nesting cover (Duebbert & Lokemoen 1976, McKinnon & Duncan 1999, Arnold *et al.* 2007) or by promoting favourable agricultural practices (Barker *et al.* 1990, Devries *et al.* 2008). Thus, a central management objective is to attract ducks to habitats where females have higher survival and reproductive rates, primarily greater nest success (Emery *et al.* 2005). But high nest survival rates and resulting high duckling densities did not always equate to increased duckling survival and recruitment (i.e., the return of yearlings into the local breeding population) due to density dependences or differences in predator communities during nesting and brood–rearing (Gunnarsson *et al.* 2006, Amundson and Arnold 2011). Measures of habitat quality must link components of an individual’s fitness (i.e., survival and reproductive success) to resources, and few studies have successfully linked critical life–stages with landscape–level drivers of reproductive success (Aldridge and Boyce 2007). Ultimately, little is known about how individual ducks use habitats during different stages of the breeding cycle.

1.2 PRAIRIE HABITAT JOINT VENTURE ASSESSMENT

In response to substantial declines in continental waterfowl populations prior to and during the mid–1980s, the North American Waterfowl Management Plan (NAWMP) was initiated to conserve continental waterfowl populations and habitats (NAWMP 1986). The Prairie Habitat Joint Venture (PHJV) is among the largest components of NAWMP, and PHJV aims to raise carrying capacity of the Canadian PPR landscapes to sustain prairie breeding waterfowl populations at levels characteristic of the mid–1970's (PHJV 2006). Low average nest success of dabbling ducks was believed to be the primary factor limiting waterfowl production in prairie Canada; consequently the PHJV initially focused strongly on managing upland cover to improve nest success (PHJV 2006).

PHJV habitat programs involved intensive wildlife management practices and extensive land–use modifications, intended to maximize waterfowl production on small parcels of land dedicated to wildlife and to enhance soil and water conservation to benefit wildlife. Thus, land was purchased or leased and planted with dense nesting cover, existing grass cover was idled, nesting structures were constructed, and cropping practices, including reductions of summer fallow, reduced tillage, promotion of fall seeding, and delayed hay cutting were implemented (PHJV 2006). To test the efficacy of these habitat management programs and evaluate whether waterfowl production was enhanced by these programs, the PHJV Assessment Study was initiated in 1993 (e.g., Emery *et al.* 2005).

From 1993 – 2000, breeding ducks were studied on 27 different study sites, throughout prairie Canada (Table 1.1; Fig. 1.1). Sites had varying areas of managed habitat and were typically 65–km^2 (except Hamiota was 78 km^2 and Punnichy was 54 km^2). Sites were only studied for a single year, and 2 – 4 sites were studied each year. Upland habitats were classified (Table 1.2), wetland permanency and vegetation was recorded (Table 1.3), and study sites were digitized for further analyses. Density and composition of duck breeding pairs, and habitat preferences and nest success of upland–nesting ducks also were recorded, but duckling and brood survival rates were only estimated for mallards (*Anas platyrhynchos*). Female mallards were captured and radio–tracked to monitor nesting and renesting events, habitat use and selection, nesting and brood–rearing success, and female survival. Consequently, the PHJV assessment provided ample opportunity for a variety of research and publications on mallards and other ducks including home–range characteristics and breeding performance (Mack and Clark 2006), nest–site selection (Howerter *et al.* 2008), landscape factors that affect nesting success and nest distribution (Howerter 2003), mallard and gadwall (*Anas strepera*) duckling survival and habitat selection (Gendron and Clark 2002, Bloom *et al.* 2012*a*), survival of male and female mallards during the breeding season (Brasher *et al.* 2006), natal dispersal (Coulton *et al.* 2010) and reproductive ecology (Devries *et al.* 2008, Arnold *et al.* 2008). Despite many novel studies arising from the PHJV assessment, several questions regarding the adaptive significance of mallard habitat selection remain unanswered, and warrant further investigation.

1.3 CONSERVATION RATIONALE

Waterfowl often demonstrate strong patterns of habitat selection during nesting (Clark and Shutler 1999, Howerter *et al.* 2008) and brood–rearing (Bloom *et al.* 2012*a*), and research on mallards has evaluated patterns, processes, and predictions of habitat selection theory during the nesting and brood–rearing phases. Despite strong patterns of habitat selection during the nesting and brood–rearing phases, mallards did not select habitats that consistently conferred reproductive benefits (Howerter *et al.* 2008, Bloom *et al.* 2012*a*, Bloom *et al.* 2013*a*). Previous studies evaluating the efficacy of NAWMP yield inconsistencies among habitat selection and reproductive performance during the nesting and brood–rearing stages. For instance, Howerter *et al.* (2008) revealed that mallards selected nest sites closer to wetland edges and preferred areas with greater amounts of planted cover and woody habitats. Yet, brood–rearing females avoided areas with greater amounts of perennial and woody cover but exhibited strong selection of brood–rearing areas with greater wetland area (Bloom *et al.* 2012*a*). Specifically, brood–rearing females selected wetlands which had at least a 2 m ring of emergent vegetation with a central expanse of open water (Cover type 3), or wetlands that are 95% open water with a band of emergent vegetation < 2 m wide (Cover type 4; Bloom *et al.* 2012*a*). Additionally, mallards selected habitats with greater amounts of woody cover, but nest survival rates were lowest in these habitat types.

Possible explanations for these inconsistencies between patterns of habitat selection and annual reproductive performance included (i) differences in stage–specific habitat–use patterns which may have different fitness consequences (Mack and Clark 2006), or (ii) the influence of parental quality on reproductive investment and success (Cunningham and Russell 2000) and, potentially, habitat selection. Results from previous studies of mallards indicate the possibility of a trade–off between benefits of nesting in fields of planted dense cover to enhance nest survival rates versus costs of lower duckling survival for broods raised in areas of abundant dense cover (Amundson and Arnold 2011, Bloom *et al.* 2013*a*). Ultimately, female mallards did not consistently select nesting and brood–rearing habitats which had the highest reproductive benefits (Howerter *et al.* 2008, Bloom *et al.* 2012*a*). Accordingly, potential trade-offs between selection of nesting habitat and survival of nests, females and ducklings, and the role of parental quality in determining reproductive investment and success of females deserved much more attention.

Large–scale conservation programs such as the PHJV may affect bird populations in numerous ways, and benefits to populations may not be observed directly. Yet, despite implications for management decisions and waterfowl production, trade–off conditions among different phases of the breeding cycle and other explanations (i.e., the role of male quality) for inconsistencies detected among habitat selection and reproductive consequences had not been adequately assessed. Thus, my broad research goal was to investigate hypotheses and predictions to explain inconsistencies between patterns of habitat selection and reproductive performance in studies of habitat selection during the nesting and brood–rearing stages in mallards.

1.3 OBJECTIVES AND THESIS ORGANIZATION

My broad objectives were to integrate existing PHJV Assessment datasets from Ducks Unlimited Canada’s Institute for Wetland and Waterfowl Research (IWWR) and address explanations for why patterns of habitat selection of female mallards did not consistently result in higher survival or reproductive rates. Specifically, in Chapter 2, I evaluated how reproductive investment and success of females was influenced by male and female quality. In Chapter 3, I addressed key hypotheses about stage–specific habitat–use patterns and evaluated the consequences of habitat choices during nesting for female survival and breeding success (i.e., fledged offspring) by examining the trade–offs between habitat selection at sequential stages of the breeding cycle (i.e., nesting and brood–rearing). Finally, in Chapter 4, I combined results from Chapter 2 and 3 to determine whether male quality influences habitat selection by females and whether higher–quality males obtained nesting and brood–rearing habitats that conferred survival and reproductive benefits.

I organized this thesis as three independent manuscripts intended for publication in peer–reviewed journals. There is redundancy in the introduction, description of study sites, and methods of some chapters, but I attempted to reduce repetition, while maintaining the independence of the individual chapters.

Table 1.1 – Twenty–seven study areas used to evaluate efficiency of habitat management programs throughout the Canadian Prairie Parklands from 1993 – 2000. All study sites were 65 km^2 (except HAM and PUN, which were 78 km^2 and 54 km^2, respectively). Each site was studied only once, corresponding to year.

Study site	Area	Year
AHE	Allan Hills East, SK	1999
AHN	Allan Hills North, SK	2000
ALW	Allan Hills West, SK	1997
BAL	Baldur, MB	1996
BEL	Belmont, MB	1994
CAM	Camp Lake, AB	1995
DAV	Davis, SK	1994
DON	Donalda, AB	1998
ELN	Elnora, AB	1997
ERS	Erskine, AB	1994
FAR	Farrerdale, SK	1998
HAM	Hamiota, MB	1993
HAY	Hay Lakes, MB	2000
HOL	Holmfield, MB	2000
JDC	Jumping Deer Creek, SK	1998
KIN	Kensella, AB	1999
KUT	Kutawa Lake, SK	1995
LEA	Leask, SK	2000
MIN	Minnedosa, MB	1998
MIX	Mixburn, AB	1997
PAR	Parkside, SK	1996
PIN	Pine Lake, AB	1996
PRI	Prince Albert, SK	2000
PUN	Punnichy, SK	1993
RED	Red Willow, AB	1999
SHO	Shoal Lake, MB	1995
WIL	Willowbrook, SK	1997

Table 1.2 – Description of habitat types in the Canadian Prairie Parklands used during the PHJV assessment study, 1993 – 2000 (modified from Bloom *et al.* 2013*b*).

Habitat Type	**Description**
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%). Grasslands may be idled, grazed, or hayed.
Hayland	Areas seeded to grasses and/or legumes for forage production and that are hayed annually.
Managed Hayland	A management technique whereby the first hay cut is delayed until after 15 July and is restricted to 1 cut per season.
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 >3–%) and woodland (areas with woody plants, trees or tall shrubs, >0.6 m in height having an aerial cover >30%). Woody cover may be idled or grazed by livestock.

Table 1.3 – Description of wetland habitat classification (follows Stewart and Kantrud 1971) used during the PHJV assessment study in the Canadian Prairie Parklands, 1993 – 2000 (modified from Bloom 2010).

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

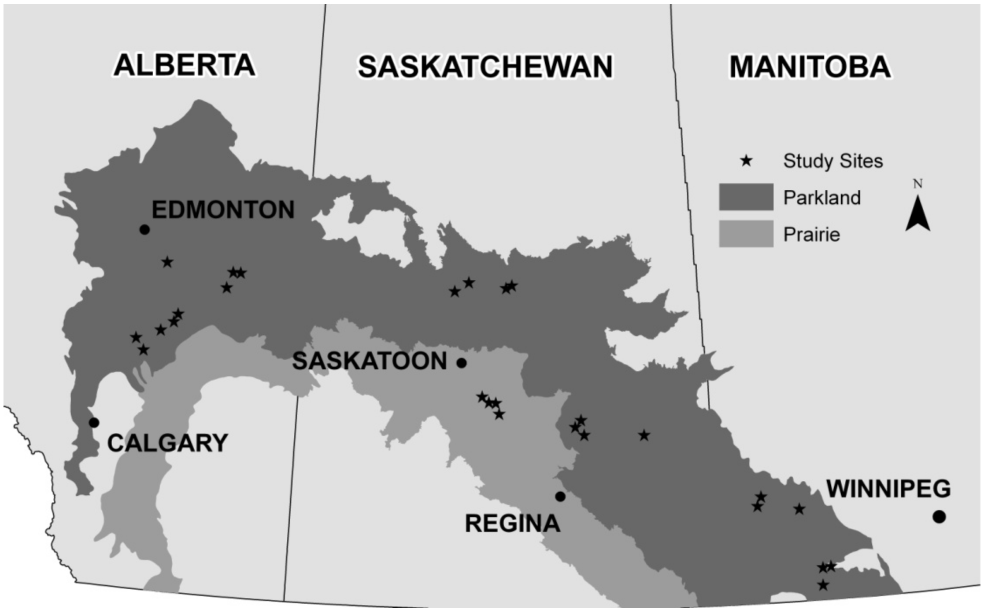

Figure 1.1 – Study sites used during the PHJV Assessment in the Canadian Prairie Parklands, 1993 – 2000, differentiating between Canadian Prairie and Parkland ecoregion.

CHAPTER 2: REPRODUCTIVE EFFORT AND SUCCESS OF WILD FEMALE MALLARDS IN RELATION TO MALE AND FEMALE QUALITY

2.1 INTRODUCTION

Life–history theory predicts that females adjust reproductive investment to reflect the costs and benefits of a given breeding attempt (Stearns 1992). Consistent with this theory, the differential allocation hypothesis states that individuals should allocate resources in response to characteristics of their mate and predicts that male attractiveness will influence the reproductive value of a female's breeding attempt (Burley 1988, Sheldon 2000). Plumage, ornaments or morphology may reliably signal a male's ability to acquire high quality habitats or increase parental care (Møller 1994, Sheldon 2000, Rowe *et al.* 2011). For instance, males with better quality plumage possibly are more aggressive and able to out-compete other males for prime habitat (Germain *et al.* 2010, Crary and Rodewald 2012). Thus, females could trade–off current and future reproduction in response to male attractiveness such that females increase their reproductive investment when mated to males perceived to be high quality (Burley 1988, Sheldon 2000). Allocating resources to increase offspring quality may increase offspring survival and subsequent lifetime reproductive success. Alternatively, when paired to low quality males, females will reduce reproductive investment to increase their reproductive lifespan (Burley 1988).

Support for differential allocation has been found in birds, insects, amphibians and mammals (Sheldon 2000). Female birds mated to more attractive males can alter their pre–hatch investment by laying larger clutches (Petrie and Williams 1993), larger eggs (Loyau *et al.* 2006, Osorno *et al.* 2006, Velando *et al.* 2006, Horváthová *et al.* 2012), or by differentially depositing concentrations of egg internal compounds (Gil *et al.* 1999, Loyau *et al.* 2006). Yet, differential allocation also could be driven by an underlying correlation between male and female quality, especially in studies of wild animals where there are alternative explanations for correlations that seem consistent with differential allocation (Sheldon 2000). For instance, in avian species with biparental care or where pair formation occurs during the breeding season, females may choose a mate based on the quality of the territory as opposed to male ornamentation, and could lay more eggs in response to abundant food resources despite male attractiveness.

In migratory waterfowl, specifically *Anas spp.*, pair dissolution generally occurs during incubation, so male ducks do not participate in brood–rearing, nor do they engage in incubation or nest–guarding (Williams 1983). Furthermore, pair formation occurs during winter, prior to arrival on the breeding grounds (Johnsgard 1960). In these systems, females do not chose mates based on the males' ability to raise offspring; moreover, the quality of breeding habitat cannot be used as a criterion for selecting a breeding partner (McKinney 1992). Thus, mate selection is based on morphology, ornaments or behaviours of males (McKinney 1992). As such, females may choose males that are more similar to themselves (i.e., mate assortatively; Cooke and Davies 1983), or select males based on qualities that signal the ability to migrate faster, obtain high–quality breeding habitat or sufficiently protect the female from forced copulations (Williams 1983, Wishart 1983). Therefore, quality of both males and females must be considered simultaneously so that correlations between male and female quality can be controlled when evaluating differential allocation in natural systems.

Seminal studies of waterfowl mating systems revealed the importance of male plumage colouration as a key predictor of female mate choice, suggesting that females preferred good–looking males, or males with better plumage quality (Klint 1980, Holmberg *et al.* 1989, Weidmann 1990). Specifically, these studies highlighted important ornaments of male mallards and suggest that preferred males possess an unmoulted green head, wide white neck–collar, uniform rusty breast, pale–grey unblotched flanks, two curled–up tail feathers, and black upper and under tail–coverts (Klint 1980, Holmberg *et al.* 1989, Weidmann 1990). Holmberg *et al.* (1989) also illustrated that females respond positively to male size and display activity, while subsequent research by Omland (1996) found correlations between pairing success and bill and plumage ornaments of male mallards; males with bright yellow–green bills and higher average plumage ornaments had greater pairing success.

Females reportedly laid larger eggs (Cunningham and Russell 2000) and increased albumen lysozyme concentrations (Giraudeau *et al.* 2011) when mated to more attractive males. Remarkably, females also may compensate for predictable deficits in offspring viability when breeding with non–preferred partners by increasing egg mass (Bluhm and Gowaty 2004). Male attractiveness is often determined based on female choice in captive populations (Cunningham and Russell 2000, Bluhm and Gowaty 2004) and ornament quality is seldom evaluated (but see

Giraudeau *et al.* 2011). Female preference for multiple ornaments of males, specifically plumage (i.e., Holmberg *et al.* 1989, Weidmann 1990, but see Omland 1996), had been studied extensively, whereas reproductive decisions of females associated with natural variation in male plumage had not been considered.

Mallards reportedly mated assortatively by body condition and age (Heitmeyer 1995), and females can adjust reproductive allocation by increasing egg mass and egg internal compounds in response to male quality (Cunningham and Russell 2000, Giraudeau *et al.* 2011). Thus, mallards are ideal for evaluating differential allocation in natural systems. First, I evaluated whether mallards mate assortatively by body size and condition by using unique data collected from a large sample of free–ranging male and female mallards. Then, I tested the hypothesis that females mated to high–quality males increase reproductive effort and have higher reproductive success by simultaneously evaluating effects of male and female quality. Specifically, I evaluated the predictions that females mated to high quality males would (i) initiate nests earlier in the breeding season, (ii) renest faster or more often following nest failure, (iii) lay larger clutches, and (iv) have greater nest and brood survival rates, than females mated to low quality males.

2.2 METHODS

2.2. 1 Study areas

During 1997–1999, data were collected at six, 65 km^2, study sites in the Canadian Prairie Parkland ecoregion of Alberta, Saskatchewan, and Manitoba (Table 2.1; Fig. 2.1). Sites were randomly selected as part of a larger study to test the efficacy of habitat management programs designed to attract and increase breeding success of upland–nesting ducks (e.g., Emery *et al.* 2005). Each site was investigated for 1 year. The primary land uses on all sites were agriculture and ranching although other land-types including patches of grass, deciduous trees, shrub land, woodland, fence lines, right-of-ways, and wetlands, were present on each study site in varied amounts (Emery et al. 2005). Study sites consisted of a mixture of managed (i.e., delayed grazing, delayed hay, planted cover) and unmanaged (i.e., cropland, hayland, pasture) cover types with some areas more intensively managed than others (Emery et al. 2005).

2.2.2 Field methods

2.2.2.1 Capture and Marking

Mallards were captured between 4 April and 5 May, before or concurrent with the earliest recorded nesting attempts, by placing decoy traps (Sharp and Lokemoen 1987) in wetlands where pairs or lone males had previously been observed. Traps were frequently moved among wetlands throughout the study site wetlands to ensure the local mallard population was represented (Brasher *et al.* 2002). Trapped birds were banded, weighed with a 1.5–kg Pesola scale (nearest 10 g), and wing chord was measured with a ruler (nearest 1 mm), from the end of the carpo–metacarpus to the tip of the longest primary feather (see Table 2.1 for sample sizes). With dial calipers, head length (nearest 0.1 mm; from the back of the head to the tip of the bill), tarsus length (nearest 0.1 mm; length of the tarsometatarsal bone) and keel length (nearest 0.1 mm, females only; from the tracheal pit to the hind margin of the sternum) was measured. Female age was classified as either second–year (SY; i.e., yearling) or after–second year (ASY; i.e., adult) by visually inspecting the greater secondary covert against a known–age sample, or measuring characteristics of the feather and performing a discriminant function analysis (adapted from Krapu *et al.* 1979). All females were equipped with a 22 g intra–abdominal radio transmitter (Model IMP/150, Telonics, Mesa, Arizona, Rotella *et al.* 1993, Paquette *et al.* 1997), tracked twice daily using vehicle–mounted, null–array antenna systems and triangulation (Kenward 1987) and monitored closely to determine reproductive histories of females (Emery *et al.* 2005, Devries *et al.* 2008). Males were radio–marked with a 9 g back–mounted radio transmitter (Model 2040, Advanced Telemetry Systems, Isanti, Minnesota; Rotella *et al.* 1993, Paquette *et al.* 1997) in 1998 and 1999, as part of an associated study by MGB (Brasher 2000, Brasher *et al.* 2002).

2.2.2.2 Determining pair status

Criteria were established *a priori* to determine pair status based on characteristics of captured birds (Table 2.2; Brasher *et al.* 2002). In 1997, it was assumed that all birds were assigned correctly as mated pairs. In 1998 and 1999, a sub–sample (n = 35) of assigned pairs were radio–tracked to confirm pair status. I validated results obtained for all presumed pairs by repeating analyses using the sub–sample of confirmed pairs when sample size was sufficient.

2.2.2.3 Plumage Characteristics

Male plumage was recorded only in 1997 at four sites for males presumed to be paired with a radio–marked female ($n = 223$; criteria in Table 2.2). Important male plumage characteristics were recorded (Klint 1980, Holmberg *et al.* 1989, Weidmann 1990, Giraudeau *et al.* 2011): (1) maximum and minimum width of the white neck ring, (2) number of places on the head and chest where feathers were missing or unmolted and, (3) number of curled tail feathers. I modified methods used by Holmberg *et al.* (1989) and Weidmann (1990) to rank each plumage characteristic according to the extent of either naturally–occurring blemishes or deviations from ideal plumage (Table 2.3), and summed individual characteristics so that smallest rank signified fewest deviations (i.e., better quality plumage).

2.2.3 Statistical analyses

2.2.3.1 Data Censoring

Five pairs were excluded from analyses either because all morphometric data were missing or birds were assigned an incorrect pair status (i.e., radio–tracking revealed female was paired with a different male or a bird was erroneously paired with two different mates during data collection; this occurred for 2% of the pairs). Missing keel lengths for four females were imputed using regression equations (F = 5.29, df = 249, $p = 0.002$) derived from the morphometric measurements (i.e., keel, wing, tarsus and head lengths) of the remaining females, and outlying tarsus lengths were similarly imputed for two males (F = 19.91, df = 249, $p < 0.001$). Ages of five females could not be determined. From the sample size of 253 pairs, plumage characteristics were collected for 217 males and 35 pairs were confirmed using radio–telemetry. Of 219 females that nested, clutch initiation dates were known for 214 females, 129 females renested at least once (renesting interval was determined for all these birds), clutch size was known for 88 nests, and brood survival was determined for 73 birds that nested successfully.

2.2.3.2 Explanatory variables

Effects of male quality could be masked by those of female or pair quality (Cunningham and Russell 2000), so I evaluated 11 *a priori* models (Table 2.4) which analyzed male and female quality simultaneously and tested for evidence of positive assortative mating by body size and condition. Because visual cues could be used differently by males and females (i.e., females likely assess mate quality, males possibly assess competitive ability), and different aspects of male quality has been reported to function differently (Edler and Friedl 2010, Crary and Rodewald 2012), I analyzed three aspects of male quality that are likely assessed by females. Body size indices of males and females were derived separately using Principal Component Analyses (PCA) based on the correlation matrix of morphometric measurements. PC1 accounted for 42% (SD = 1.29) of variation in head, wing, tarsus and keel measurements of females (coefficients of 0.58, 0.45, 0.55, 0.41, respectively) and 51% (SD = 1.26) of variation in head, wing, and tarsus measurements of males (coefficients of 0.59, 0.56, 0.58, respectively; keel length was not collected for males); thus PC1 scores were used as an index of body size in subsequent analyses. Residuals obtained from ordinary least squares regression of body mass against body size index were used as indices of body condition. Body size and condition indices were not correlated for either sex (Females: Pearson's $r = -0.003$, $n = 251$, $P = 0.96$; Males: Pearson's $r < -0.001$, $n = 251$, $P = 0.99$). To account for site–year variation in body size and condition indices, I standardized sex–specific indices by determining the average of each variable for each study site and subtracting the mean value from each measurement.

I compared body size, body condition, plumage quality indices of males, and all reproductive response variables between adult and yearling females using ANOVA. Yearling females tended to be smaller and had lower body condition indices compared to adults (see Results, section 2.3.1) and also tended to nest later than adults (Devries *et al.* 2008); thus, I analyzed reproductive data separately by female age. I tested for assortative mating by using Pearson's correlation coefficient to determine the strength of associations between indices of body size and condition for members of assigned pairs. I evaluated relationships between plumage rank, and body size and body condition indices of both males and females using Spearman's rank correlation and visually inspected plots to evaluate patterns and check for nonlinear relationships.

I measured reproductive effort using the (1) relative clutch initiation date (CID; range: 1–56), (2) number of eggs (clutch size; range: 5–12 eggs) in the first detected nest (presumed to represent the first nesting attempt), (3) interval between failure of the first nest attempt and the initiation date of the second detected nesting attempt (renesting interval; range: 2–32 days between renesting attempts), and (4) total number of times a female nested that season (renesting frequency; range: 0–6 nest attempts). For renesting intervals $\leq$ 6 days (33 nests or 13% of birds in this study), I assumed this represented a continuous laying event carried over from the initial nest attempt and that no alternative nests had been laid in the interim. I assumed a laying interval of one egg per day and that partial nest depredation had not occurred before nests were located, defining CID as the date the first egg was laid in the initial nesting attempt based on the number of eggs and stage of incubation upon discovery. To account for site–specific or annual variation in nesting chronology, I standardized CID by determining the earliest date that a clutch was initiated at each site, and assigning it as day one of the nesting season; thus, all initiation dates for a given site were scaled relative to the date of the first known nest on each site (day 1). I determined the number of days the nest survived between initiation and termination of the first detected nesting attempt (incu; range 0–36) and included this as a covariate in the analyses of renesting interval. I measured reproductive success as nest survival (≥1 egg hatched) and brood survival (≥1 duckling survived to 30 days old).

2.2.3.3 Model development and selection

To evaluate effects of male and female quality in reproductive effort and success of females, I analyzed multiple competing *a priori* models using generalized linear models. Generalized linear models do not require that response variables are continuous nor follow a Gaussian distribution, and because I was able to account for site–year differences by standardizing explanatory variables, a random effect of site–year was not necessary. I corrected for small sample size and compared candidate models using information–theoretic approaches to determine best–approximating models, and then model–averaged parameter estimates (β) and standard errors (SE) across all candidate models to obtain multi–model inferences (Burnham and Anderson 1998) based on 85% confidence intervals (Arnold 2010). To increase validity of my results and ensure relationships between male quality and reproductive investment and success of females were not confounded by other factors (i.e., CID, hatch date, or incu), I performed exploratory analyses on results which included effects of male quality in the best–approximating models. Thus, I retained models within 4 AIC (Akaike’s Information Criterion) units of the best–approximating model and compared these to exploratory variables. All statistical procedures were conducted in R, version 2.13.0 (R Core Development Team 2011).

2.3 RESULTS

2.3.1 Assortative mating

There was evidence of positive assortative mating by body condition for both age classes (adult: Pearson's $r = 0.26$, $n = 132$, $P < 0.003$; yearling: Pearson's $r = 0.26$, $n = 116$, $P < 0.005$; Fig. 2.2). Adult females did not mate assortatively by body size whereas yearling females did (adult: Pearson's $r = 0.13$, $n = 132$, $P = 0.15$; yearling: Pearson's $r = 0.25$, $n = 116$, $P = 0.006$). Assortative mating was confirmed using a subset of 35 known pairs for body condition of older and younger females (ASY: Pearson's $r = 0.67$, $n = 20$, $P = 0.001$; SY: Pearson's $r = 0.50$, $n = 15$, $p = 0.05$), whereas assortative mating by body size was not detected (ASY: Pearson's $r = 0.004$, $n = 20$, $P = 0.99$; SY: Pearson's $r = 0.12$, $n = 15$, $P = 0.95$; Fig. 2.2). Regardless of female age class, neither male and female body size, nor condition indices were correlated with male plumage score (All results: Spearman's $rho < 0.010$, $n = 217$, $P > 0.14$; Table 2.5). Compared with yearlings, adult females were larger, had better condition and were paired with larger males with better plumage quality (Table 2.6).

2.3.2 First detected nesting attempt

On average, adult females nested 6 days earlier than yearlings (Table 2.5). Neither male nor female quality indices explained clutch initiation date of adult females (Table 2.6). The best–approximating model describing CID of yearling females incorporated effects of male plumage quality ($\beta = 0.069$, SE = 0.031) and female condition ($\beta = –0.0060$, SE = 0.0013; Table 2.6); thus, as predicted, yearling females nested earlier when paired to males with good plumage quality (Fig. 2.3). Clutch size did not differ between age groups (Table 2.5), and was best explained by effects of CID (adult: $\beta = –0.010$, SE = 0.005; yearling: $\beta = –0.006$, SE = 0.005; Table 2.6).

2.3.3 Renesting

Adult females nested more often, but not faster following nest failure, than yearlings (Table 2.5). My predictions that females mated to high quality males would renest faster and more often received mixed support. Adult females had longer renest intervals when paired to males in better body condition, as indicated by the best–approximating model that included effects of male condition ($\beta = 0.0018$, SE = 0.0008) and the number of days the nest survived during the first nesting attempt ($\beta = 0.010$, SE = 0.007; Table 2.6). Conversely, neither male nor female quality influenced the renesting interval of yearling females (Table 2.6). The number of times that females renested (renesting frequency) was best explaining by effects of female body condition (β = 0.0019, SE = 0.0011) and size (β = 0.12, SE = 0.055; Table 2.6) for adult females, and effects of male size (β = 0.11, SE = 0.073; Table 2.6) for yearling females. Thus, adult females nested more often if they were larger and in better body condition, whereas yearling females paired to larger males renested more frequently (Fig. 2.4).

2.3.4 Reproductive success

Adult females initiated 2.56 nests (309 nests of 120 females), whereas yearlings initiated 1.93 (193 nests of 100 females). A total of 73 females nested successfully (adult = 44; yearling = 28; age of one female was unknown). After removing nests with evidence of investigator–induced abandonment (i.e., nest was found abandoned following damage caused by the investigator), apparent nest survival was 15% in both groups. Nest survival of adult females was positively related to male (β = 0.40, SE = 0.20) and negatively related to female (β = –0.52, SE = 0.23; Table 2.8) body sizes (Fig. 2.5). Nest survival of yearling females was best explained by effects of male plumage (β = –0.26, SE = 0.14) and female condition (β = 0.012, SE = 0.005; Table 2.8). Thus, adult females paired to larger males and yearling females paired to males with better plumage quality (low plumage scores) had higher nesting success (Fig. 2.6).

Of 73 brood–rearing females (3 females had 2 broods each), 26 had broods that survived to 30 days post–hatch. Adult females hatched 1.6 times more nests than yearlings, yet apparent brood survival of both age classes was 36%. My prediction that females mated to high quality males would have higher brood survival was only partially supported (Table 2.8). Adult females paired to larger males (β = 1.49, SE = 0.70) had greater brood survival (Fig. 2.7), but no relationships between parental quality and brood survival were detected for yearling females (Table 2.8).

2.3.5 Exploratory analyses

Yearling females initiated more nest attempts when paired to larger males (see Results section 2.3.3), however this could be explained by a higher rate of nest failure. Thus, I compared the number of nests that survived and failed between adult and yearling females to renesting frequency. Nest success only occurred during the first nesting attempt for yearlings, whereas two adult females were successful during the second attempt (Table 2.10). However, this did not provide sufficient evidence that nest failure influenced renesting frequency, so I performed an exploratory analysis and simultaneously evaluated renesting frequency and included nest survival as a covariate along with effects of male and female quality. Models which included effects of nest survival performed better than those without; thus, nest survival explained more variation in the number of renesting attempts than did male or female quality such that females experiencing nest failure renested more often ($\beta = -0.55$, SE = 0.27; Table 2.9).

Greenwood *et al.* (1995) reported poor survival of early nests, and in this study, yearling females tended to nest 6.5 days later than adults. Although this would contradict the positive relationship between male plumage and clutch initiation date of yearlings, increased nest survival of yearlings and adults could be a response to later initiation dates. Consequently, I performed an exploratory analysis to evaluate the relationship between nest survival simultaneously with effects of clutch initiation date and male and female quality indices for both age classes. The additive effect of CID did not improve model fit for either age class and models incorporating only effects of CID were 4.5 and 2.9 AICc units greater than the best–approximating model for adult and yearling female, respectively (Table 2.9; see Results section 2.3.4).

Duckling survival is greater early in the season (Rotella and Ratti 1992, Dzus and Clark 1998, Krapu *et al.* 2000, but see Gendron and Clark 2002, Davis *et al.* 2007), and could explain why adult females had greater brood survival when paired with larger males. Consequently, I simultaneously evaluated the effects of hatching date and parental quality in explaining brood survival. The additive effect of hatch date did not improve model fit and models incorporating only effects of hatch date were 7.04 AICc units higher than the best–approximating model (Table 2.9; see Results section 2.3.4).

2.4 DISCUSSION

My most important finding was the positive relationship between male body size and nest and brood survival rates of adult females. Because adult females did not mate assortatively by body size, effects of male body size were probably not confounded by effects of female quality. Moreover, as illustrated in exploratory analyses, clutch initiation and hatching dates did not appear to confound results of brood survival rates either. Adult females likely choose males based on size as opposed to plumage, a result that is consistent with research in other avian taxa (Hagelin and Ligon 2001, but see Omland 1996). Alternatively, Holmberg *et al.* (1980) found older males tended to be larger, so it is plausible that mallards mate assortatively by age; however, I did not have information to test this hypothesis. Although female quality could be affected by male condition (i.e., females could be in poor condition during pair formation but good condition during breeding because high quality males allowed them access to good food resources), Heitmeyer (1995) showed that males and females form pairs with others of relatively similar body condition and that the condition of both members tend to change at the same time between fall and spring migration. Thus, mallards in this study did mate assortatively and effects of female condition were not directly confounded by male condition or male quality.

Male quality was also positively related to clutch initiation date, renesting frequency, and nest survival of yearling females. In my exploratory analysis of nest survival, I found that models incorporating effects of male plumage and female condition performed better than models that incorporated clutch initiation date alone (ΔAICc = 0.00, 1.75 respectively); nest survival was not a consequence of nesting earlier. Additionally, negligible effects of female quality (i.e., little difference between β and SE) in the top model explaining clutch initiation date and nest survival, compared to effects of male plumage quality, suggest that male quality indices were better predictors of CID and nest survival than indices of female quality. Thus, male plumage quality, and to a lesser extent, male size are possibly important factors influencing reproductive effort and success of yearling females, whereas male size, but not male plumage, are likely important for adults.

Larger males possibly migrate faster, arrive earlier, and sequester the highest quality breeding sites or preferred brood–rearing habitats, enabling females to initiate nests and optimize use of nutrient reserves on arrival to breeding grounds. Alternatively, migration is more costly for larger individuals who must spend time during migration to replenish reserves (Bêty et al. 2003), thereby arriving later to the breeding grounds but large enough to out-compete other males for prime habitat. A male’s ability to acquire suitable environments could subsequently increase nesting and brood–rearing success by providing females with (i) sufficient resources to increase egg internal compounds or egg size; (ii) access to sufficient resources to renest more quickly following nest failure, or; (iii) access to wetland habitats with abundant food resources for ducklings, or habitats with fewer predators and competitors. I did not have sufficient data to test effects of male size on egg size or egg internal compounds, but the tendency for yearling females to nest more often following nest failure and for adult females to have greater survival of broods when paired to larger males provide support for the latter two hypotheses.

Mallards lay an average of 8–9 eggs in their first clutch (Alisauskas and Ankney 1992; Table 2.6), and females could readily commence egg laying if nest failure occurred prior to an increase in prolactin levels (prolactin increases during incubation and must decrease for rapid–follicle development to commence; Bluhm 1992). Consequently, females which experience nest failure prior to incubation typically continue egg laying immediately, whereas when a nest is destroyed during incubation the female will require an additional week to produce eggs for a replacement clutch (Bluhm 1992). As such, longer renesting intervals among adult females likely resulted from longer previous investment in incubation, which delayed the formation of a replacement clutch. This is supported by the effect of the number of days the nest survived (incu) in explaining renesting frequency. Yet, the positive relationship between renesting frequency of yearling females and nest and brood survival of adults and male size supported the hypothesis that larger males provide access to wetland habitats with abundant food resources for ducklings, and could explain why adult females paired to larger males had higher nest and duckling survival rates. Thus, the ability of a female to renest quickly was likely a response to the stage of incubation when nest failure occurred and the habitat resources secured by the male.

Titman and Lowther (1975) reported that male mallards with undamaged plumage tend to win more fights, so undamaged plumage could indicate a male’s ability to defend his mate. Additionally, female mallards prefer males with higher testosterone levels and improved mate–guarding abilities (Davis 2002), although evidence of a relationship between levels of testosterone and plumage quality is equivocal (Lindsay *et al.* 2001, Stoehr and Hill 2001, Edler and Friedl 2010). Among waterfowl, mate guarding is important to female breeding condition and success (Ashcroft 1976, Seymour and Titman 1978, Davis 2002) and protection of females may prevent injury, increased risk of predation, exposure to parasites or sexually transmitted diseases, or death resulting from forced copulations of nonmates (Goodburn 1984, Seymour 1990, Sorenson 1994, Adler 2010). Aside from donating sperm, mate guarding is the only male contribution to reproduction in many waterfowl species (Goodburn 1984, Davis 2002). If plumage represents a male’s ability to defend his mate, then females paired to males with high quality plumage will benefit from fewer forced copulation attempts by other males, higher survival during the breeding season, earlier nest initiation and have more energy to allocate to reproduction (Davis 2002, but see Cunningham 2003). This would explain why yearling females paired to males with better plumage quality nested earlier and had greater nest survival. Thus, the link between mallard plumage, testosterone level and mate–guarding ability should be further evaluated.

These results indicate that adult and yearling females likely use different cues when choosing males (i.e., adults did not mate assortatively by body size whereas yearlings females did), and likely have different objectives when choosing a mate. For instance, adult females possibly selected mates based on the male's ability to obtain high–quality breeding habitats as opposed to their mate–guarding abilities. Mate–guarding abilities could be especially important for small–bodied yearling females that are also inexperienced in either defending themselves or evading other males. The relationship between male quality, habitat acquisition, and mate–guarding and female mate–choice should be evaluated.

2.5 CONCLUSION

To my knowledge, this study was among the first to test predictions of the differential allocation hypotheses by integrating indices of male and female quality with reproductive histories in free–ranging birds. Male size was the most influential trait determining reproductive success of mallards in this study. Although this study did not provide sufficient evidence to support the differential allocation hypothesis, it did suggest that both male and female quality play important roles in avian reproductive ecology. In waterfowl, females choose breeding habitats and nest sites, but males are involved in female protection and sequestration and defense of their home–range (Anderson and Titman 1992). Although males do not participate in brood–rearing, effects of male quality is possibly manifested in a "behavioural carry–over" effect to nest and duckling survival due to the role of males in providing access to high quality wetland habitat for nesting and brood–rearing females. To further evaluate differential allocation among mallards, additional research is needed to evaluate how selection of nesting and brood–rearing habitat relates to male quality, and whether larger males can successfully acquire and defend habitats that improve the reproductive success of their mates.

Table 2.1 – Study sites, locations, and sample sizes of pairs captured in the Canadian Prairie Parklands, 1997 – 1999.

Study Site	Year	Province	Location	No. Pairs Captured	No. Pairs Censored
ALW	1997	SK	Allen Hills West	40	1
ELN	1997	AB	Elnora	61	2
MIX	1997	AB	Mixburn	69	2
WIL	1997	SK	Willowbrook	53	0
MIN	1998	MB	Minnedosa	14	0
AHE	1999	SK	Allen Hill Easst	21	0

Table 2.2 – *A priori* criteria for determining pair status of male mallards based on capture scenarios (Brasher *et al.* 2002).

Status		Criterion
Paired	A.	1 male and 1 female in same compartment; despite the presence of other mallards in or near trap
	B.	1 male and 1 female in different compartments with no other mallards in or near trap
	C.	1 male and ≥2 females in different compartments and no other mallards in or near trap
	D.	2 males and 2 females in trap; noting pairs who flew together upon release or using telemetry to determine pair status
Unpaired	A.	Males initially captured without a female, banded and released, and subsequently recaptured without a female
	B.	≥1 male in trap and no females in or near trap
	C.	≥1 male in one compartment with a male and female together in another compartment

Table 2.3 – Scoring system used to evaluate plumage characteristics of male mallards throughout the Canadian Prairie Parklands, 1997.

Characteristic	**Score**				
	0	**1**	**2**	**3**	**4**
White neck ring					
Maximum Width	11 – 14 mm	7 – 10 mm	3 – 6 mm	<3 mm	n/a
Evenness	0 mm	1 – 3 mm	4 – 6 mm	7+ mm	n/a
Interaction between width and evenness	7 + mm wide; 0 mm even	<7 mm wide; 0 mm even	7+ mm wide; <6 mm even	<7 mm wide; <6 m even	other
Number of places with missing feathers					
Head	0	1 – 3	4 – 6	6 – 9	10+
Chest	0	1 – 3	4 – 6	6 – 9	10+
Tail curls					
Number of full curls	2	1	3 or 4	0	n/a
Interaction with half curls	2 full; 0 half	2 full; any # half	1 – 3 full; any # half	No full curls	n/a

Each column was scored independently, and summed to create an overall plumage score (range 0–16).

Table 2.4 – Eleven *a priori* models used to simultaneously evaluate effects of male and female quality on reproductive investment and success of female mallards in the Canadian Prairie Parklands, 1997– 1999.

Model	Definition
Intercept	Intercept only model
Male condition	Residuals obtained by OLS regression of body mass against body size index of males
Male size	1st Principal Component derived from PCA of head, wing and tarsus length of males
Male plumage score	Total sum of ranked individual plumage characteristics according to the extent of deviations from ideal plumage
Female condition	Residuals obtained by OLS regression of body mass against body size index of females
Female size	1st Principal Component derived from PCA of head, wing, tarsus and keel length of females
Female quality	Simultaneously evaluates female body condition and body size
Male condition + female condition	Simultaneously evaluates male and female body condition index
Male size + female size	Simultaneously evaluates male and female body size index
Male plumage score + female condition	Simultaneously evaluates male plumage score and female body condition index
Male plumage score + female size	Simultaneously evaluates male plumage score and female body size index

Table 2.5 – Spearman's rank correlation (Rho; with *P* value) between male plumage quality and body size and condition of males and females (*n* = 217) for mallards in the Canadian Prairie Parklands, 1997 – 1999.

	Male Plumage Quality	
Variable	**Rho**	***p***
Female Condition (adult)	–0.036	0.71
Female Size (adult)	0.082	0.39
Female Condition (yearling)	0.076	0.45
Female Size (yearling)	0.030	0.77
Male Condition	–0.033	0.63
Male Size	–0.010	0.14

Table 2.6 – Comparison of indices of male and female quality and reproductive effort and success between adult (*n* = 132) and yearling (*n* = 116) females.

	Adult Females		Yearling Females		ANOVA
	Mean	**SD**	**Mean**	**SD**	**P**
Female quality					
Body condition index	25.3	64.8	–27.5	57.0	<0.001
Body size index	0.3	1.2	–0.2	1.3	0.024
Male quality					
Body condition index	7.9	77.3	–9.1	66.2	0.18
Body size index	0.2	1.2	–0.3	1.2	0.005
Male plumage score	8.3	2.8	9.0	2.4	0.068
Female reproductive effort					
Clutch initiation date	14.5	12.1	20.0	12.5	0.0021
Clutch size	9.3	1.7	8.6	1.7	0.20
Renesting frequency	2.1	1.4	1.4	1.0	<0.001
Renesting interval	17.9	10.7	16.8	10.8	0.60

Table 2.7 – Best–approximating *a priori* models explaining characteristics of the first detected nesting attempt and renesting by female mallards in the Canadian Prairie Parklands, 1997–1999.

Model description	**AIC$_c$**[a]	**ΔAIC$_c$**[b]	***K***	**w_i**[c]
Clutch initiation date				
Adult Females (*n* = 98)				
Intercept	262.30	0.00	2	0.22
Male size	263.08	0.78	3	0.15
Female size	263.58	1.28	3	0.12
Female condition	263.82	1.51	3	0.10
Male plumage	264.11	1.80	3	0.09
Male condition	264.27	1.96	3	0.08
Yearling Females (*n* = 83)				
Male plumage + Female condition	170.54	0.75	4	0.62
Male condition + Female condition	173.17	2.63	4	0.17
Clutch Size				
Adult Females (*n* = 28)				
Intercept (CID only)	123.41	0.00	2	0.29
Male plumage	124.90	1.50	3	0.14
Female size	125.09	1.69	3	0.13
Yearling Females (*n* = 21)				
Intercept (CID only)	94.25	0.00	2	0.32
Female size	96.36	2.11	2	0.11
Renest Interval[d]				
Adult Females (*n* = 65)				
Male condition	95.81	0.00	4	0.39
Male condition + Female condition	97.32	1.51	5	0.18
Yearling Females (*n* = 38)				
Intercept	25.59	0.00	2	0.46
Incu	27.80	2.21	3	0.15
Renest Frequency				

Adult Females (*n* = 112)				
Female quality	364.39	0.00	3	0.30
Female size	365.29	0.91	2	0.19
Male size + Female size	365.88	1.49	3	0.14
Yearling Females (*n* = 100)				
Male size	270.65	0.00	2	0.20
Intercept	270.75	0.09	1	0.19
Female size	271.34	0.69	2	0.14
Male size + Female size	272.09	1.43	3	0.10
Male Condition	272.60	1.95	2	0.07
Female condition	272.64	1.99	2	0.07

Models are ranked by differences in Akaike's Information Criterion and corrected for small sample size (ΔAIC_c). Number of parameters (*K*) includes the intercept; clutch initiation date is included in all models for clutch size only. Only models with $\Delta\text{AIC} < 2$, or the top two models, are presented.

[a] Akaike's Information Criterion corrected for small sample size.

[b] Difference in AIC_c relative to model with the lowest value.

[c] Model weight.

[d] All models (except the intercept model) include effects of the number of days the nest survived during the first detected nesting attempt (incu).

Table 2.8 – Best–approximating *a priori* models explaining reproductive success of female mallards in the Canadian Prairie Parklands, 1997–1999.

Model description	**AIC$_c$**[1]	**ΔAIC$_c$**[2]	***K***	***w$_i$***[3]
Nest survival of Adult Females (*n* = 101)				
Male size + Female size	103.74	0.00	3	0.37
Male plumage + Female size	104.86	1.12	3	0.21
Nest survival of Yearling Females (*n* = 83)				
Male plumage + Female condition	79.35	0.00	3	0.38
Female condition	81.10	1.75	2	0.16
Brood survival of Adult Females (*n* = 22)				
Male size	20.09	0.00	2	0.57
Male size + Female size	21.47	1.38	3	0.29
Brood survival of Yearling Females (*n* = 16)				
Intercept	24.22	0.00	1	0.25
Female condition	24.84	0.63	2	0.19
Male size	25.88	1.66	2	0.11

Models are ranked by differences in Akaike's Information Criterion and corrected for small sample size (ΔAIC$_c$). Number of parameters (*K*) includes the intercept. Only models with ΔAIC < 2 are presented.

[1] Akaike's Information Criterion corrected for small sample size.

[2] Difference in AIC$_c$ relative to model with the lowest value.

[3] Model weight.

Table 2.9 – Best–approximating models evaluating exploratory analyses of reproductive effort and success of female mallards in the Canadian Prairie Parklands, 1997 – 1999.

Exploratory Models	**AIC_c[1]**	**ΔAIC_c[2]**	***K***	**w_i[3]**
Renesting Frequency of Yearling Females (*n* = 83)				
Nest survival	218.81	0.00	2	0.21
Female size + Nest survival	220.19	1.38	3	0.11
Male plumage + Nest survival	220.65	1.85	3	0.08
Male size + Nest survival	220.73	1.93	3	0.08
Female condition + Nest survival	220.83	2.02	3	0.08
Male condition + Nest survival	220.91	2.10	3	0.07
Intercept	221.56	2.76	1	0.05
Nest Survival of Adults Females (*n* = 101)				
Male size + Female size	103.74	0.00	3	0.23
Male size + Female size + CID	104.08	0.34	4	0.20
Male plumage + Female size	104.86	1.12	3	0.13
Male plumage + Female size + CID	105.58	1.84	4	0.09
Female size	105.84	2.10	2	0.08
Female size + CID	106.20	2.46	3	0.07
Male plumage	107.16	3.43	2	0.04
Male size	107.28	3.54	2	0.04
Male size + CID	107.41	3.68	3	0.04
Nest Survival of Yearlings Females (*n* = 83)				
Male plumage + Female condition	79.35	0.00	3	0.26
Female condition	81.10	1.75	2	0.11
Male plumage + Female condition + CID	81.15	1.80	4	0.11
Male condition + Female condition	81.59	2.24	3	0.09
Female Condition + CID	81.92	2.57	3	0.07
Female quality	81.96	2.61	3	0.07
CID	82.25	2.90	2	0.06

Brood Survival of Adult Females ($n = 22$)				
Male size	20.09	0.00	2	0.46
Male size + Female size	21.47	1.38	3	0.23
Male size + Hatch date	21.83	1.74	3	0.19
Male size + Female size + Hatch date	23.94	3.84	4	0.07
Intercept	25.78	5.69	1	0.03
Hatch date	27.13	7.04	2	0.01

Models are ranked by differences in Akaike's Information Criterion and corrected for small sample size (ΔAIC_c). Number of parameters (K) includes the intercept.

[1] Akaike's Information Criterion corrected for small sample size.

[2] Difference in AIC_c relative to model with the lowest value.

[3] Model weight.

Table 2.10 – Number of nests that survived and failed in relation to renesting attempt (exploratory analysis of renesting frequency) for adult and yearling females in the Canadian Prairie Parklands, 1997 – 1999.

	Adult		Yearling	
Number of Nest Attempts	**Survive**	**Fail**	**Survive**	**Fail**
1	20	16	16	29
2	2	28	0	29
3	0	21	0	7
4	0	11	0	2
5	0	1	–	–
6	0	2	–	–

Figure 2.1 – Study sites used in 1997 – 1999 throughout the Canadian Prairie Parklands.

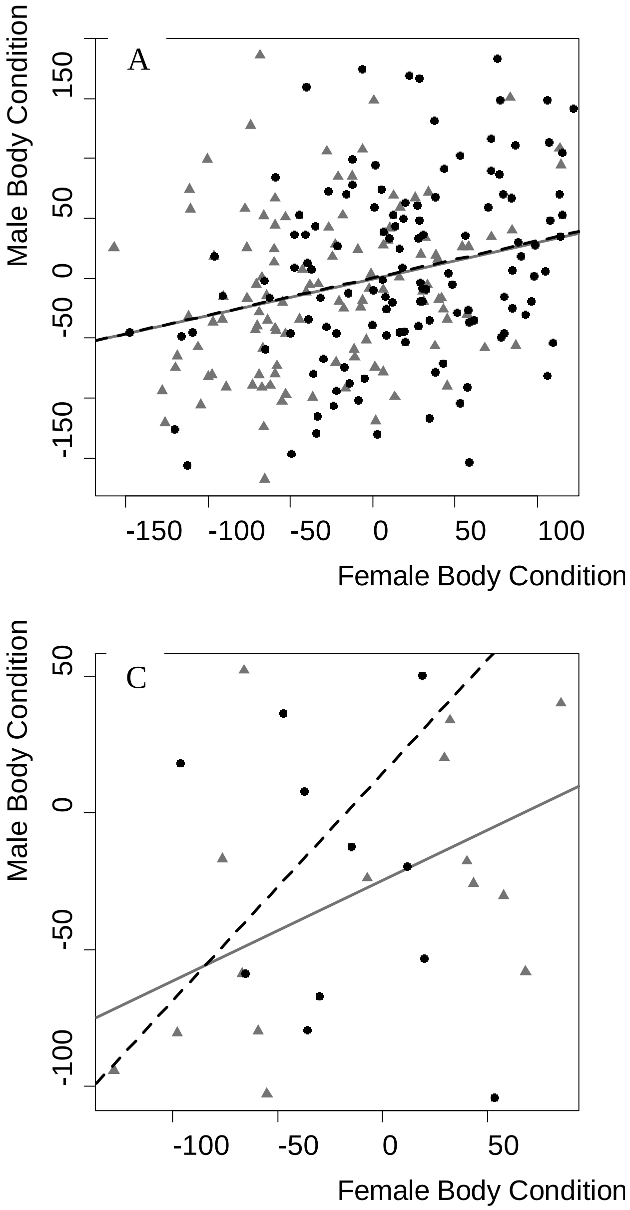

Figure 2.2 – Assortative mating of adult and yearling females by body condition for all pairs (*n* = 217;A), supported by the sub–sample of confirmed pairs (*n* = 35; C), and assortative mating of yearling females by body size (B) not supported by the sub–sample of confirmed pairs (D), for mallards in the Canadian Prairie Parklands, 1997 – 1999.

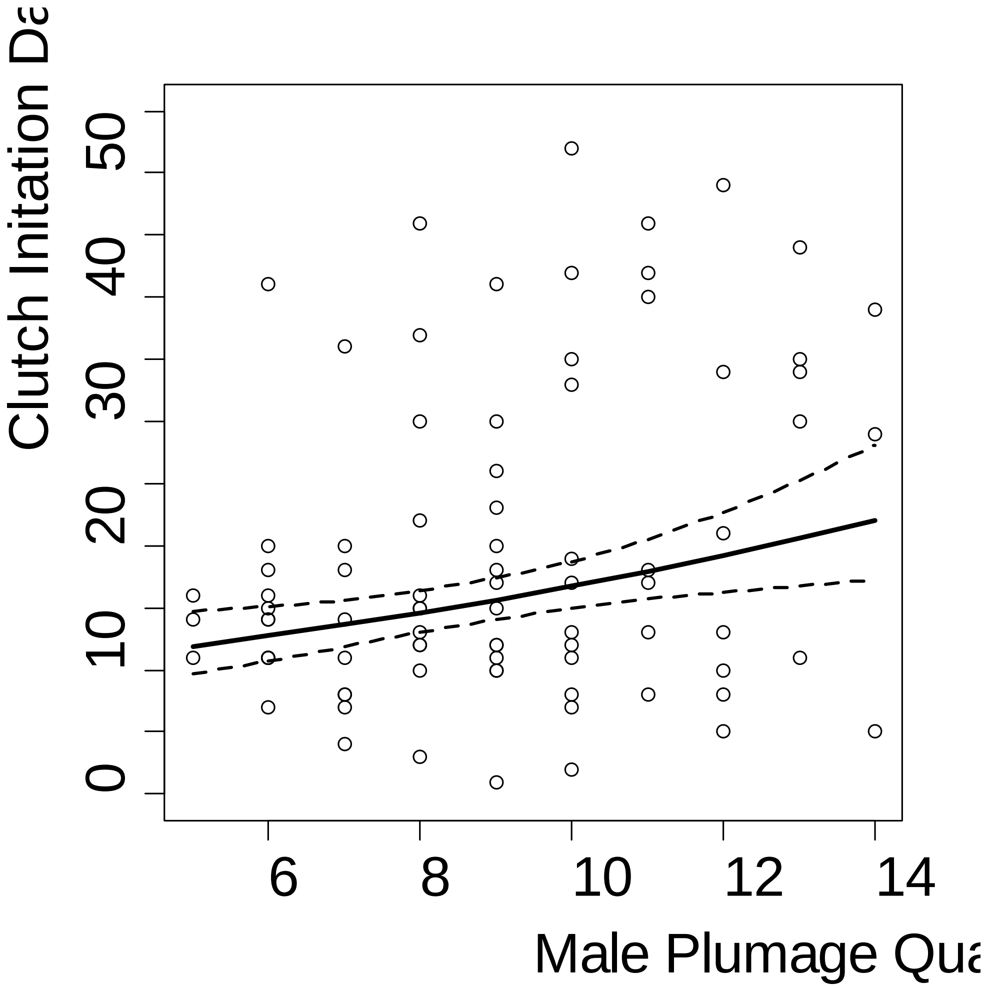

Figure 2.3 – Predicted clutch initiation date (relative to day 1; first detected nest of each site–year) of yearling females with averaged body condition indices, estimated from the best–approximating model explaining CID of yearling females in the Canadian Prairie Parklands, 1997. Low plumage scores (6) represents males with better quality plumage; higher scores (14) represents males with poor plumage. Upper and lower 85% confidence limits are represented by dashed lines, and raw data by open circles.

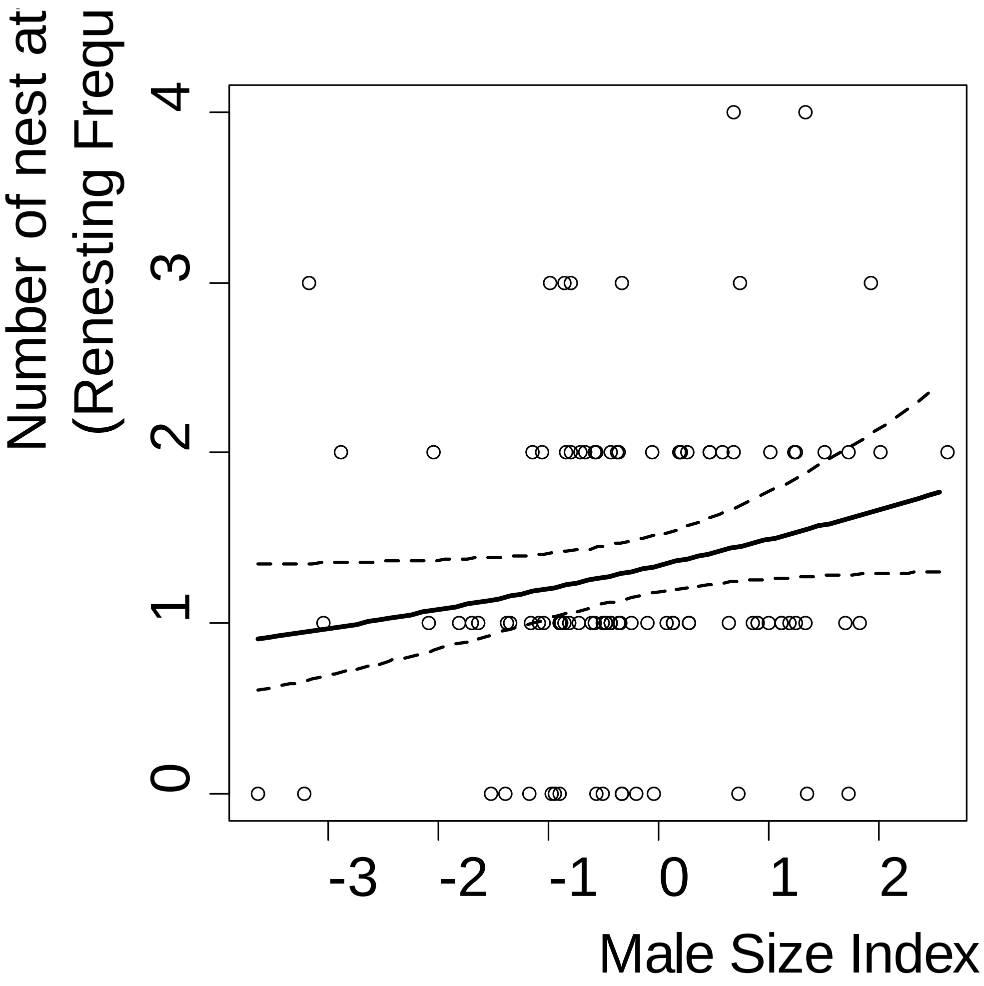

Figure 2.4 – Predicted renesting frequency of yearling females, estimated from the best–approximating model explaining renesting frequency of yearling females in the Canadian Prairie Parklands, 1997–1999. Small male body index (–3) represents smaller males; larger size index (2) represents large males. Upper and lower 85% confidence limits are represented by dashed lines, and raw data by open circles.

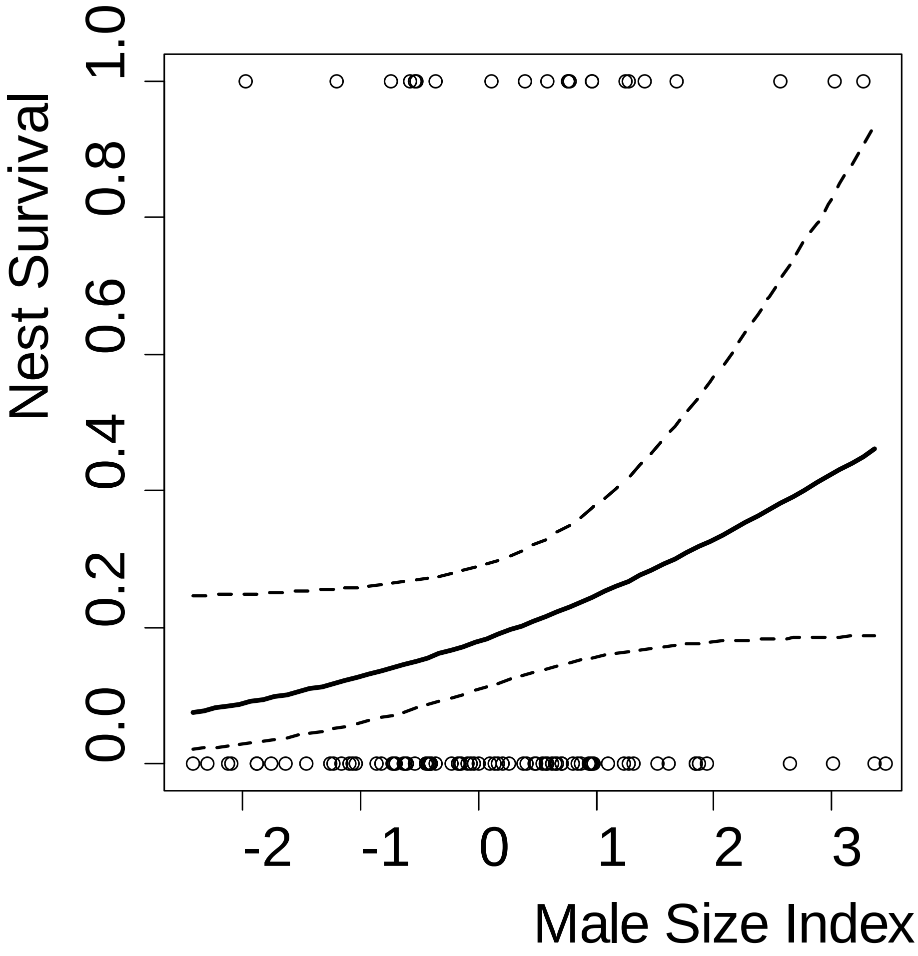

Figure 2.5 – Predicted nest survival of adult females with averaged body size, estimated from the best–approximating model explaining nest survival of adult females in the Canadian Prairie Parklands, 1997–1999. Small male body index (–2) represents smaller males; larger size index (3) represents large males. Upper and lower 85% confidence limits are represented by dashed lines, and raw data by open circles.

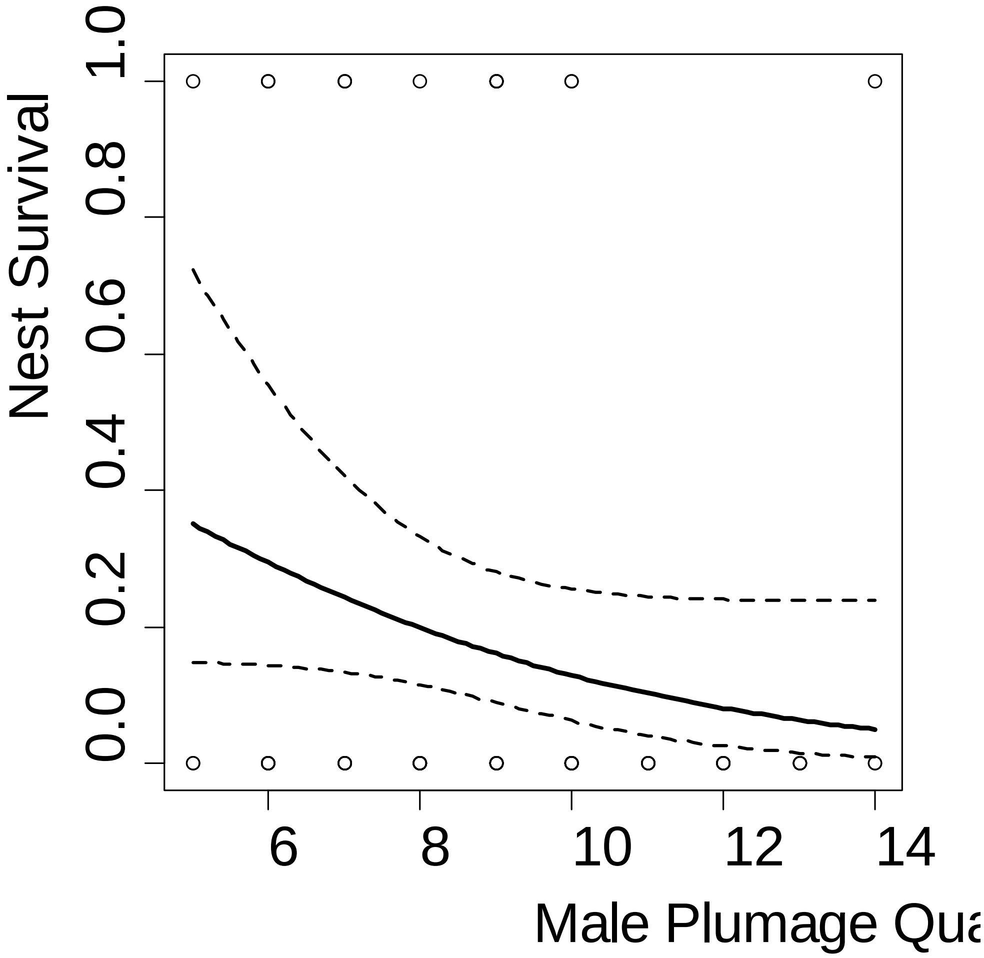

Figure 2.6 – Predicted nest survival of yearling females with averaged body condition, estimated from the best–approximating model explaining nest survival of yearling females in the Canadian Prairie Parklands, 1997. Small plumage rank (6) represents males with better quality plumage (less blemishes); large plumage ranks (14) represent males with poor plumage quality. Upper and lower 85% confidence limits are represented by dashed lines, and raw data by open circles.

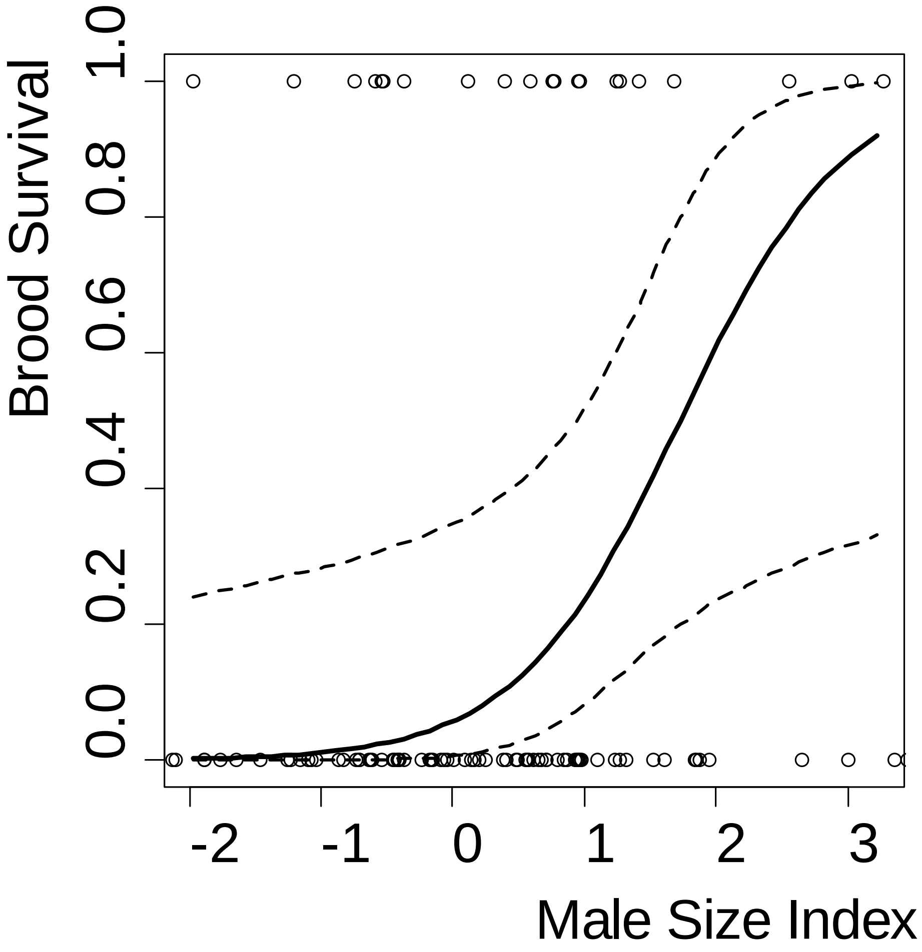

Figure 2.7 – Predicted brood survival of adult females, estimated from the best–approximating model explaining brood survival of adult females in the Canadian Prairie Parklands, 1997–1999. Small male body index (–2) represents smaller males; larger quality index (3) represents large males. Upper and lower 85% confidence limits are represented by dashed lines, and raw data by open circles.

CHAPTER 3: INVESTIGATING EQUIVOCAL EVIDENCE OF ADAPTIVE NEST–SITE SELECTION IN MALLARDS

3.1 INTRODUCTION

Habitat selection theory suggests that animals should select habitats that optimize their fitness (Levins 1968, Orians 1980). Presumably, organisms should prefer higher–quality habitats and avoid lower–quality habitats, as expected if habitat selection is adaptive. To fully understand habitat selection, Clark and Shutler (1999) suggested that researchers take three crucial steps to link habitat choices to fitness consequences. First, the *pattern* of habitat selection must be identified, i.e., to determine whether differences exist between used and available habitat. Second, understanding the *process* of habitat selection is necessary, by asking whether and how unsuccessful and successful sites differ. Third, conclusions about the potential adaptive basis for habitat choice should be validated by testing whether characteristics which increase survival *predict* habitat preferences (Clark and Shutler 1999). However, organisms may have evolved strategies to minimize risks and maximize fitness while moving among habitat patches and using different habitats at various life cycle stages (Levin *et al.* 1984, Nichols 1996, Paasivaara and Pöysä 2008) or by valuing one breeding season vital rate over another. Moreover, anthropogenic landscape changes may decouple formerly–reliable evolved cues used to select habitats, resulting in maladaptive habitat choices (Schlaepfer *et al.* 2002, Chalfoun and Martin 2007, Howerter *et al.* 2008, Chalfoun and Schmidt 2012). In either case, evidence for adaptive habitat selection may be equivocal (Howerter *et al.* 2008); thus a crucial fourth step in understanding habitat selection would be to *link* processes of habitat selection at one breeding (or life cycle) stage to offspring and adult survival during subsequent stages.

Waterfowl often demonstrate strong patterns of habitat selection during nesting (Clark and Shutler 1999, Howerter *et al.* 2008) and brood–rearing (Bloom *et al.* 2013*a*), and research on mallards has evaluated patterns, processes, and predictions of habitat selection during the nesting phase. For instance, mallard nest success increases with greater amounts of wood–shrub and planted cover and lower amounts of seasonal and semipermanent wetlands within the home–range (Mack and Clark 2006). Furthermore, nest–site selection is strongest for planted cover, followed by woodlands, despite low nest survival rates in woodland habitats (Howerter *et al.* 2008). Additionally, mallards tend to select small habitat patches close to wetlands, regardless of higher predation rates associated with these spatial conditions (Howerter *et al.* 2008). Although mallards demonstrated strong selection during the nesting phase, they did not consistently select habitats that confer reproductive benefits, suggesting conflicting evidence about the adaptive basis for nest–site selection (Howerter *et al.* 2008). Similar results have been detected in various avian families and research has indicated that over 50% of studies on habitat selection yield inconsistencies between nest site preferences and nest success (Chalfoun and Schmidt 2012)

Similarly to research on nest–site selection, studies of brood–rearing habitat also reveal that females did not consistently select habitats that confer the highest benefits. For example, Bloom *et al.* (2012*a*) reported that duckling survival was highest when a greater proportion of the surrounding landscape was composed of wetlands characterized by a central expanse of open water and a peripheral ring of flooded emergent vegetation (cover type 4 wetland), and negatively related to increasing proportions of managed hayland. But, at larger scales, females that demonstrated stronger selection for areas with more wetlands with large expanses of open water (cover type 3 or 4 wetland) had lower duckling survival rates, whereas at finer scales, females selected areas with high proportions of wetlands at no cost to survival (Bloom *et al.* 2013*a*). Yet, females were able to fledge more ducklings when avoiding woody perennial habitats (Bloom *et al.* 2013*a*).

Presumably, selection should favor females that are able to contend with stage–specific habitat selection trade–offs and fledge more offspring. If different selective pressures operate when females are nesting versus raising broods, an integrated assessment of trade–offs during different stages of the breeding cycle could explain ambiguities about the adaptive basis of habitat selection (Howerter *et al.* 2008). Possibly, female waterfowl select nest sites to minimize female mortality as opposed to maximizing nest survival rates (Chalfoun and Martin 2007, Howerter *et al.* 2008), or alternatively, to maximize duckling survival (Pöysä *et al.* 2000). Previous research of habitat selection by mallards have shown that increased amounts of wood–shrub and planted cover within the home range increase nest survival (Mack and Clark 2006), whereas avoidance of woody cover increased duckling survival (Bloom *et al.* 2012*a*, 2013*a*). Additionally, mallards select nest sites closer to wetland edges where nest survival is reduced (Howerter *et al.* 2008) yet overland travel is dangerous for ducklings (Bloom *et al.* 2012*a*). Remarkably, duckling survival has not been linked to features of the nesting habitat, and habitat selection in earlier stages of the breeding cycle has not been related to reproductive performance in subsequent stages.

Here, I evaluate hypothesized habitat selection trade–offs at sequential stages of the breeding cycle. Specifically, I test the prediction that habitats selected to favour nest survival result in lower adult female or duckling survival rates. I compare survival of females, nests, and ducklings to selection of nesting habitat, using an extensive 8–year dataset for free–ranging mallards collected throughout the Canadian Prairie Parklands.

3.2 METHODS

3.2. 1 Study areas

Breeding female mallards were studied on 27 study sites (Table 1.1; Fig. 1.1) in the Canadian Prairie Parkland ecoregion of Alberta (8 sites), Saskatchewan (12 sites), and Manitoba (7 sites), 1993–2000. Sites were typically 65 km^2, and had varying areas of managed habitat. These sites were selected randomly to test the efficacy of habitat management programs designed to attract and increase breeding success of upland–nesting ducks. Study sites are described in detail by Emery *et al.* (2005). Each site was investigated for 1 year. The primary land uses on all sites were agriculture and ranching although other land-types including patches of grass, deciduous trees, shrub land, woodland, fence lines, right-of-ways, and wetlands, were present on each study site in varied amounts (Emery et al. 2005). Study sites consisted of a mixture of managed (i.e., delayed grazing, delayed hay, planted cover) and unmanaged (i.e., cropland, hayland, pasture) cover types with some areas more intensively managed than others (Emery et al. 2005).

3.2.2 Field methods

3.2.2.1 Capture and Marking

Over 3,500 female mallards (111–137 females per site during 4 April – 5 May each year; Table 3.1) were trapped and marked with radio–transmitters. Most birds were trapped by placing decoy traps (Sharp and Lokemoen 1987) in wetlands where pairs or lone males had previously been observed. Traps were frequently moved throughout study site wetlands to ensure the local mallard population was represented (Brasher *et al.* 2002). To increase the number of radio–marked brood–rearing females for duckling survival analyses, traditional nest searching methods were used to locate nests and predator–deflection fences were placed around nests to prevent predation. Females were captured just prior to estimated hatch dates using either a mist net (Bacon and Evrard 1990), spring–loaded purse trap (modified from Coulter 1958), automatic nest trap (Weller 1957), or walk–in trap (Dietz *et al.* 1994). Female age was classified as either second–year (yearling) or after–second year (adult) by visually inspecting the greater secondary covert against a known–age sample, or measuring characteristics of feathers and performing a discriminant function analysis (adapted from Krapu *et al.* 1979). All females were equipped with either a 22 g intra–abdominal (Model IMP/150, Telonics, Mesa, Arizona, Rotella *et al.* 1993, Paquette *et al.* 1997) or a 4 or 8 g back–mounted radio-transmitter (Models 357 and 2040, respectively, Advanced Telemetry Systems, Isanti, Minnesota, Mauser and Jarvis 1991) and were subsequently radio–tracked using vehicle–mounted, null–array antenna systems and triangulation (Kenward 1987) to determine reproductive histories and habitat use of females (Devries *et al.* 2003).

Females were monitored daily until a 30–day brood count was obtained for females that nested successfully, the female was seen unpaired and flocked in early July, or the female died. Birds that disappeared within 2 weeks of marking or birds that disappeared following nest failure and could no longer be located were censored (accounting for 8% of the females). Nests were revisited every 6–10 days until nest fate was determined, and were classified as successful if $\geq$1 egg hatched (Klett *et al.* 1986).

3.2.2.2 Habitat Classification

Wetlands were classified (Stewart and Kantrud 1971; Table 1.3), and dominant vegetation types and presence of flooded emergent vegetation (extent of flooding) were recorded. Detailed notes regarding upland habitat type and landuse 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 in late July or early August in the field season. Digitized habitat maps were imported into SPANS Geographic Information System (GIS; PCI Geomatics, Richmond Hill, Ontario, Canada). Using the buffer and intersect tools in ArcGIS, I created a 100 m and 500 m buffer around each nest and summarized the upland and wetland habitat attributes within each buffer (Fig. 3.1).

3.2.3 Statistical analyses

3.2.3.1 Data censoring

I removed females that were marked with a back-mounted transmitter prior to nest initiation (n = 145) due to negative effects of these transmitters on duckling survival (Bloom *et al.* 2012*b*). Additional females or nesting attempts were excluded if: a female's transmitter was lost during the study (n = 25 females); nest fate could not be determined (n = 29 nests of 22 females); nest failure was due to nest parasitism or investigator activity (n = 352 nests of 285 females); clutch initiation date was unknown (n = 80 nests); clutch initiation date and termination date did not make biological sense (n = 5 nests); or, habitat information was not available (i.e., nest occurred outside the study area; n = 345 nests of 260 females). Thus, nest survival was estimated using 3819 nesting attempts by 2213 females (see Table 3.1 for sample sizes). To reduce pseudoreplication, I averaged the habitat variables between all nest attempts for a given individual (range 1–6), and only considered the CID and distance to nearest wetland of the first nest attempt for each female; thus, I estimated female and nest survival using 2213 females. Following censoring criteria used by (Bloom 2012*a*), duckling survival was estimated using 596 females that nested successfully.

3.2.3.2 Spatial Scale

Habitat selection is a hierarchical process (Johnson 1980) and previous research on mallards had indicated that different patterns of habitat selection emerge with different spatial scales (e.g., Howerter 2003, Bloom *et al.* 2013*a*). Moreover, nest predators likely respond to landscape characteristics at different scales (Stephens *et al.* 2005). Thus, I conducted my analyses at two spatial scales to increase the probability of detecting relationships between nesting habitat variables and survival of females, nests and ducklings. I used a 100 m radius buffer to represent local (fine scale) nest habitat characteristics and to minimize overlap with the brood–rearing area, and a 500 m radius buffer to represent nesting and brood–rearing areas (coarse scale).

3.2.3.3 Fitness consequences of breeding habitats

To test the hypothesis of habitat selection trade–offs among sequential stages of the breeding cycle, I wanted to take a direct, integrated analytical approach. Previous analyses using the same dataset highlighted 16 different habitat and wetland variables selected by mallards during nesting (Mack and Clark 2006, Howerter *et al.* 2008) or brood–rearing (Bloom 2012*a*, Bloom *et al.* 2013*a*; Table 3.2). Thus, I created 22 *a priori* models based on the 16 aforementioned habitat and wetland covariates as well as the best–approximating models that described nest or duckling survival from previous studies (Mack and Clark 2006, Howerter *et al.* 2008, Bloom *et al.* 2012*a*, Bloom *et al.* 2013*a*; Table 3.3). I separately evaluated variation in survival rates of females, nests and ducklings in relation to factors describe by 22 *a priori* models and compared results to identify trade-offs between the different life–stages.

3.2.3.4 Model Development and Selection

I used case–control logistic regression to relate the strength of nest–site selection to nest, female and duckling survival rates for each spatial scale. I incorporated fixed effects of clutch initiation date and female age, and random effects of study area in all models. I used generalized linear mixed models to evaluate competing models of daily female and duckling survival rates because generalized linear models do not require that response variables are continuous nor follow a Gaussian distribution (Proc Genmod, SAS Institute 2011); random effects of study area accounted for additional variation in female and duckling survival rates due to site–year effects. I used nonlinear mixed models to evaluate competing models of daily nest survival rates assuming a binominal distribution and logit link function (Proc NLMIXED, SAS Institute Inc. 2011).

I compared candidate models using information–theoretic approaches to determine best–approximating models, and model–averaged parameter estimates (β) and standard errors (SE) that were within 4 AIC (Akaike's Information Criterion) units of the top model to obtain multi–model inferences (Burnham and Anderson 1998) based on 85% confidence intervals (Arnold 2010). Results derived from models of female survival were overdispered ($\hat{c}$ = 1.6) and were likely caused by lack of independence among nesting attempts; thus, I used the quasi-likelihood form of AIC to determine best-approximating models describing female survival (QAIC: Burnham and Anderson 1998). I did not find evidence of overdispersion when modeling duckling survival ($\hat{c}$ =1.07); thus, I did not use QAIC. I did not correct for small sample size because the sample size was large enough that such adjustments were inconsequential. All statistical procedures were conducted in SAS, version 9.3.

3.3 RESULTS

3.3.1 Fine spatial scale (100 m buffer)

Nest survival increased with greater amounts of perennial cover and wetland habitat within the buffer, as indicated by the best approximating model which incorporated effects of the proportion of cover type 4 wetlands, wetland habitat and perennial habitat (NumCov4: β = 0.035, SE = 0.13; WLarea: β = 0.29, SE = 0.12; Pern: β = 0.25, SE = 0.08, respectively; Table 3.4). Female survival was positively related to the proportion of seasonal wetlands within the 100 m buffer, as indicated by the best–approximating model explaining daily female survival which incorporated effects of woody cover, and the proportion of seasonal and semi-permanent wetlands (Wood: β = -0.27, SE = 0.39; AreaClass4: β = 0.17, SE = 0.47; AreaClass3: β = 2.34, SE = 1.20 Table 3.4). Daily survival rate of ducklings was best explained by the amount of perennial cover within the buffer (Table 3.4). Duckling survival decreased as perennial and planted cover increased (Pern: β = –0.119, SE = 0.067; DNC: β = –0.116, SE = 0.078).

3.3.1.1 Trade–offs between breeding stages and habitat variables

Habitat selection trade–offs were detected between three habitat covariates. Greater amounts of DNC and perennial cover were associated with increased nest, but decreased duckling, survival rates (Table 3.5). Increasing amounts of seasonal wetlands were associated with lower nest survival but higher female survival, with no relationship with duckling survival (Table 3.5; Fig. 3.2).

3.3.2 Coarse spatial scale (500 m buffer)

As expected, nest survival rate increased with greater amounts of perennial cover within the buffer (β = 0.32, SE = 0.11; Table 3.4). Nest survival rate also tended to increase with the amount of planted cover (β = 0.23, SE = 0.14), but decreased when nests were located closer to wetlands (β = –0.0010, SE = 0.0005). Female survival rate increased with managed hayland as indicated by the best–approximating model describing daily female survival which incorporated effects of the proportion of cover type 4 wetlands and managed hayland (AreaCov4: β = 0.23, SE = 1.92; Mg_Hay: β = 2.11, SE = 1.89; Table 3.4). The best–approximating model describing daily duckling survival rate contained effects of perennial cover (β = –0.26, SE = 0.10; Table 3.4); as expected, duckling survival decreased as perennial cover increased within the buffer.

Duckling survival increased with increasing amounts of cropland (Crop: $\beta = 0.18$, SE = 0.09) but decreased with planted cover (DNC: $\beta = –0.24$, SE = 0.12).

3.3.2.1 Trade–offs between breeding stages and habitat variables

Habitat selection trade–offs were detected between three habitat covariates. Consistent with fine scale results, perennial cover and DNC were associated with greater nest survival but lower duckling survival, whereas female survival remained unaffected (Table 3.5; Fig 3.3). Nest survival decreased as the amount of cropland increased within the buffer, but duckling survival was higher and female survival was unaffected (Table 3.5; Fig. 3.4).

3.4 DISCUSSION

My most important finding was evidence of a trade–off between nest and duckling survival rates in relation to perennial habitat, cropland, and planted cover. Perennial cover includes native grassland, hayland, trees, shrubs, and planted nesting cover, as such, correlations between perennial and planted cover (Pearson's $r = 0.59$, $n = 3219$, $P < 0.001$) likely led to similar results between these variables, whereas negative correlations between perennial cover and cropland (Pearson's $r = –0.70$, $n = 3219$, $P < 0.001$) likely accounted for the opposing results between these habitat types. Also, brood–rearing females avoid perennial cover (Bloom *et al.* 2013*a*); thus, the positive relationship between duckling survival rate and cropland is possibly a function of females avoiding perennial cover as opposed to selecting cropland habitat. Alternatively, seasonal wetlands in cropland habitat could attract fewer predators because of generally lower staple prey abundance in cropland or these wetlands possibly contain more aquatic invertebrate food resources due to runoff and nutrient enrichment from agricultural processes. This could explain the positive relationships between seasonal wetlands and female survival and subsequent relationships between duckling survival and cropland; ideas that should be explored further. Regardless, females that demonstrated the strongest selection for high quality nesting habitat (perennial cover and planted cover) had higher nest survival at the cost of reduced duckling survival. Benefits of selecting nest–sites in areas of greater perennial or planted cover if the nest–site is near high–quality brood–rearing habitat could outweigh the costs associated with predation rates near habitat edges. This would explain why Howerter *et al.* (2008) found that ducks nest near edges when selecting grassland habitat, despite low nest survival closer to edges (Howerter 2003).

Females that select strongly for areas with greater amounts of semi–permanent wetlands during nesting are likely to endanger themselves and their ducklings due to the association between semi–permanent wetlands and mink. Seasonal and semi–permanent wetlands are negatively correlated (Pearson's $r = –0.67$, $n = 3219$, $P < 0.001$), thus females that strongly select for seasonal wetlands would avoid predators associated with semi–permanent wetlands thereby enhancing female and duckling survival rates. Alternatively, seasonal wetlands provide plentiful food sources for nesting and brood–rearing females, yet the abundance of seasonal wetlands may be associated with an increase in small mammals and mesocarnivores (Walker 2013). For instance, red fox (*Vulpes vulpes)* are reportedly one of the most important nest predators and are more numerous in areas of abundant seasonal wetlands (Johnson *et al.* 1989, Phillips *et al.* 2003), which likely explains the negative relationship between nest survival and seasonal wetlands.

The positive relationship between duckling survival and greater amounts of managed hayland at larger spatial scales was intriguing and contradict Bloom *et al.*'s (2012*a*) report that survival of older ducklings was negatively related to the amount of managed hayland. This may be because I did not differentiate between duckling age classes in my analyses, whereas Bloom *et al.* (2012*a*) separated younger versus older ducklings. Moreover, Howerter (2003) found that nest survival in hayland was influenced by clutch initiation date, such that nests initiated later in the season had lower survival, but those initiated early had high survival. Possibly, high nest success earlier in the season in hayland contributed to higher duckling survival rates documented in this study. Regardless, of the 15 habitat variables evaluated in this study, the proportion of managed hayland and semipermanet wetlands (AreaClass4) within the buffer were the only two habitat variables that were not associated with lower survival or reproductive success. Conversely, Bloom *et al.* (2012*a*) detected a negative effect of semi–permanent wetlands on duckling survival, but suggested this was attributable to a preference for these wetland types by mink (*Neovison vison*). Whether managed hay and semipermanent wetlands is beneficial to mallard survival and recruitment is uncertain but should be evaluated further.

Bloom *et al.* (2013*a*) found that females avoided brood–rearing areas with greater proportions of perennial habitats and select areas with greater proportions of wetland habitat at finer scales, but did not detect any consequence for duckling survival. The best–approximating model explaining daily nest survival rate in this study included effects of the proportion of cover type 4 wetlands, perennial cover, and wetland habitats within the 100 m buffer (Table 3.4); however, only the latter two covariates influenced survival (i.e., CIs did not include zero). These results suggested that nest survival increased with perennial and wetland habitat, but similar to Bloom *et al.* (2013*a*), this additive effect had no influence on duckling survival, nor did it influence female survival; yet, at finer scales, brood–rearing females select these habitats (Bloom *et al.* 2013*a*). Although this does not indicate a trade–off per se, it does explain why brood–rearing females select habitats that appear to have no direct benefit for ducklings. Thus, mallards likely select habitats to increase nest survival with neutral or trivial consequences for duckling survival. Considering the high sensitivity and elasticity of mallard population growth rates in variation in nest success during the life–cycle (Cowardin and Johnson 1979, Hoekman *et al.* 2002), mallards likely “value” safe nest–sites more than safe brood–rearing sites.

3.5 MANAGEMENT IMPLICATIONS

Although several studies have investigated daily survival rates of mallards at specific breeding stages (e.g., Stephens *et al.* 2005, Mack and Clark 2006, Bloom *et al.* 2012*a,* Bloom *et al.* 2013*a*), to my knowledge, none have simultaneously evaluated habitat selection at one breeding stage and related it to survival rates across subsequent stages of the breeding cycle. Although Clark and Shutler (1999) suggested that understanding patterns, processes and predictions are crucial to studies of habitat selection, linking habitat choices across subsequent stages of the annual cycle, or breeding cycle, is equally important in discerning the processes that shape patterns of habitat selection and making better–informed management decisions.

My results suggest that mallards select habitats to increase nest survival while simultaneously forecasting the quality of brood–rearing habitat. Although habitat selection at one breeding stage (i.e., nesting) may appear counterproductive, these habitat choices sometimes increase or decrease subsequent breeding phase vital rates (i.e., duckling survival). This study suggests that mallards likely prefer to nest in habitats known to increase nest survival, but in close proximity to high–quality brood–rearing habitats. These results demonstrated that selecting nest sites in areas of greater perennial and planted cover had a detrimental effect on duckling survival. Greater amounts of managed hayland increased duckling survival rates; however, equivocal results between this study and Bloom *et al.* (2012*a*) should be re-examined to better inform hayland management decisions. Furthermore, I showed that wetland habitats have important consequences for survival rates throughout the breeding period, including for female survival. Thus, seasonal wetlands should be maintained and restored to promote female and duckling survival rates, but semi–permanent wetlands must also be present to enhance nest survival. As such, habitat managers should continue implementing habitat management regimes which include a mosaic of habitats of varying sizes of perennial and planted cover while maintaining sufficient amounts of wetland habitats within the landscape. The juxtaposition of habitats surrounding high–quality nesting locations is crucial to duckling survival and ultimately recruitment, thus managers should consider implementing habitat programs which positions high-quality brood habitat (i.e., managed hayland and croplands) near high-quality nesting habitat (i.e., perennial and planted cover).

Table 3.1 – Study sites and sample sizes of female mallards captured in the Canadian Prairie Parklands, 1993 – 2000

Study Site	Year	Province	Location	No. Birds Captured	No. Birds Retained[a]
AHE	1999	SK	Allan Hills East	135	103
AHN	2000	SK	Allan Hills North	135	85
ALW	1997	SK	Allan Hills West	135	108
BAL	1996	MB	Baldur	135	131
BEL	1994	MB	Belmont	135	122
CAM	1995	AB	Camp Lake	137	84
DAV	1994	SK	Davis	135	112
DON	1998	AB	Donalda	135	93
ELN	1997	AB	Elnora	135	116
ERS	1994	AB	Erskine	135	64
FAR	1998	SK	Farrerdale	135	96
HAM	1993	MB	Hamiota	111	56
HAY	2000	MB	Hay Lakes	135	106
HOL	2000	MB	Holmfield	135	113
JDC	1998	SK	Jumping Deer Creek	135	118
KIN	1999	AB	Kensella	135	80
KUT	1995	SK	Kutawa Lake	135	81
LEA	2000	SK	Leask	135	70
MIN	1998	MB	Minnedosa	135	123
MIX	1997	AB	Mixburn	135	123
PAR	1996	SK	Parkside	135	102
PIN	1996	AB	Pine Lake	135	127
PRI	2000	SK	Prince Alberta	135	105
PUN	1993	SK	Punnichy	123	75
RED	1999	AB	Red Willow	135	96
SHO	1995	MB	Shoal Lake	127	95
WIL	1997	SK	Willowbrook	135	126

[a] The number of birds retained for analysis following censoring.

Table 3.2 – List of variables and predicted effects of habitat selection during nesting on nest survival rates of mallards in the Canadian Prairie Parklands, 1993 – 2000. Predicted effect on survival is expressed as β > 0 for a positive effect and β < 0 for a negative effect.

Covariates	**Definition**	**Predicted effect on nest survival**[1]
Landscape attributes		
Crop	Proportion of the buffer that is crop.	$\beta < 0$
DNC	Proportion of the buffer that is planted nesting cover.	$\beta > 0$
Mg_Hay	Proportion of the buffer that is managed hayland.	$\beta > 0$
Pern	Proportion of the buffer that is perennial (includes managed and unmanaged habitats).	$\beta > 0$
Wood	Proportion of the buffer that is woody cover.	$\beta < 0$
WLarea	Proportion of the buffer that is wetlands.	$\beta < 0$
Wet_dist	Distance from nest to the nearest wetland.	$\beta < 0$[a]
WLdensity	Wetland density (number of wetlands/buffer area).	$\beta > 0$
Wetland attributes		
AreaClass3	Proportion of the buffer that is seasonal wetlands (Class3).	$\beta < 0$
AreaClass4	Proportion of the buffer that is semipermanent wetlands (Class4).	$\beta > 0$
AreaCov3	Proportion of the buffer that is cover type 3 wetlands (5% – 95% open water surrounded by a peripheral band of emergent cover averaging 2m or more in width).	$\beta > 0$
AreaCov4	Proportion of the buffer that is cover type 4 wetlands (>95% open water, or small ponds where emergent cover is restricted to marginal bands <2 m in average width).	$\beta < 0$
NumClass3	Proportion of the wetlands in the buffer that are seasonal (Class3).	$\beta < 0$
NumClass4	Proportion of the wetlands in the buffer that are semi–permanent (Class4).	$\beta > 0$
NumCov4	Proportion of the wetlands in the buffer that are cover type 4.	$\beta < 0$

[1] Predicted survival of females and ducklings are opposite predictions for nest survival

[a] Nest survival will decrease closer to wetlands

Table 3.3 – List of 22 *a priori* models used to determine survival rates of nests, females and broods in relation to nesting patterns of habitat selection of mallards in the Canadian Prairie Parklands, 1993–2000.

	Model	Support for model
1	Intercept	Intercept only model.
2	Crop	Howerter *et al.* (2008) found an interaction between crop and habitat type.
3	Mg_Hay	Duckling survival was negatively related to greater proportions of managed hayland (Bloom *et al.* 2012*a*).
4	DNC	Nest–site selection was highest for planted cover (Howerter *et al.* 2008).
5	Pern	Avoidance of perennial habitats increase duckling survival (Bloom *et al.* 2013*a*).
6	Wood	Nest–site selection was second highest for trees (Howerter *et al.* 2008); Unsuccessful broods preferred woody cover (Bloom *et al.* 2013*a*).
7	WLarea	Mallards selected brood–rearing areas with greater wetland coverage at local scales (Bloom *et al.* 2013*a*).
8	Wet_dist	Mallards tended to nest closet to wetlands (Howerter *et al.* 2008).
9	WLdensity	Mallards selected brood–rearing areas with greater wetland density at landscape scales, but experienced brood failure (Bloom *et al.* 2013*a*).
10	AreaClass3	Increased duckling survival (Bloom *et al.* 2012*a*).
11	AreaClass4	Decreased duckling survival (Bloom *et al.* 2012*a*).
12	AreaCov3	At fine scales, duckling survival is decreased with increased amounts of AreaCov3 (Bloom *et al.* 2013*a*).
13	AreaCov4	Duckling survival increased with AreaCov4 (Bloom *et al.* 2012*a*).

14	NumClass3	Bloom *et al.* (2012*a*) found a positive effect when model–averaged.
15	NumClass4	Bloom *et al.* (2012*a*) found a negative effect when model–averaged.
16	NumCov4	At fine scale, duckling survival decreased with increased amounts of NumCov4 (Bloom *et al.* 2013*a*).
17	AreaCov4 + Mg_Hay	Top exploratory model explaining duckling survival (Bloom *et al.* 2012*a*).
18	AreaClass3 + AreaClass4	Mack and Clark (2006) found that successful nesters had greater amounts of class 3–4 wetlands within their home–range.
19	Pern + *Wetlands	Top model explaining duckling survival at finer scales (Bloom *et al.* 2013*a*).
20	NumCov4 + AreaCov3	At landscape scales, brood lost was greater when females preferred areas with greater NumCov4 and AreaCov3 (Bloom *et al.* 2013*a*).
21	NumCov4 + WLarea + Pern	At local scale, these covariates were contained in best–approximating model explaining brood survival (Bloom *et al.*2013*a*).
22	Wood + AreaClass3 + AreaClass4	Nest survival increased with greater amounts of wood–shrub and lower amounts of class3–4 wetlands within home–range (Mack and Clark 2006).

*NumClass4 + NumCov3 + NumCov4 + WLdensity + AreaClass3 + AreaClass4 + AreaCov3 + AreaCov4

Table 3.4 – Best–approximating *a priori* models explaining variation in survival rates in relation to nest habitat of breeding mallards in the Canadian Prairie Parklands, 1993 – 2000.

Model	K	AIC[1]	ΔAIC[2]	w_i[3]
100 m buffer				
Daily Nest Survival				
NumCov4 + WLarea + Pern	34	17090.21	0.00	0.92
NumClass4	32	17095.85	5.65	0.05
Mg_Hay	32	17098.10	7.89	0.02
Daily Female Survival				
Wood + AreaClass3 + AreaClass4	35	1032.50	0.00	0.65
AreaClass3 + AreaClass4	34	1034.14	1.63	0.29
AreaClass3	33	1038.55	6.05	0.03
Daily Duckling Survival				
Pern	33	452.09	0.00	0.15
DNC	33	452.83	0.74	0.10
Intercept	32	453.21	1.12	0.09
500 m buffer				
Daily Nest Survival				
Pern	32	18415.80	0.00	0.99
DNC	32	18426.20	10.40	0.01
Wet_dist	32	18427.48	11.67	0.00
Daily Female Survival				
AreaCov4 + Mg_Hay	34	5944.77	0.00	0.93
Mg_Hay	33	5950.18	5.42	0.06
Pern + All wetlands	41	5954.35	9.53	0.008
Daily Duckling Survival				
Pern	33	492.50	0.00	0.34
DNC	33	494.61	2.11	0.12
Crop	33	495.25	2.75	0.09

Models are ranked by differences in Akaike's Information Criterion (AIC). Number of parameters (*K*) includes the intercept; nest age (for daily nest survival only), study area (*n* =27), hen age, and nest initiation date are included in all models. Only models with ΔAIC < 2 of the top model or the top three models are presented.

[1] Used QAIC for female survival.

[2] Difference in AIC (or QAIC for female survival) relative to model with the lowest value.

[3] Model weight.

Table 3.5 – Results of covariates used in *a priori* models to explain variation in nest survival of mallards across the Canadian Prairie Parklands, 1993 – 2000, with 85% confidence intervals. β > 0 if there is a positive effect, β < 0 is a negative effect, and β = 0 implies no effect; positive and negative effects are highlighted in bold.

	100 m			500 m		
Habitat	**Nest**	**Female**	**Duckling**	**Nest**	**Female**	**Duckling**
Crop*	**β < 0** -0.39, -0.17	β = 0	β = 0	**β < 0** -0.34, -0.07	β = 0	**β > 0** 0.04, 0.31
Hay	β = 0	β = 0	β = 0	β = 0	β = 0	**β > 0** 0.08, 1.16
DNC*	**β > 0** 0.04, 0.32	β = 0	**β < 0** -0.23, -0.01	**β > 0** 0.29, 0.43	β = 0	**β < 0** -0.42, -0.08
Pern*	**β > 0** 0.17, 0.38	β = 0	**β < 0** -0.22, -0.02	**β > 0** 0.17, 0.48	β = 0	**β < 0** -0.41, -0.11
Wood	β = 0	β = 0	β = 0	β = 0	β = 0	β = 0
Wlarea	**β > 0** 0.03, 0.26	β = 0	β = 0	β = 0	β = 0	β = 0
Wet_dist	β = 0	β = 0	β = 0	**β < 0** -0.002, -0.004	β = 0	β = 0
WLdensity	β = 0	**β > 0** 157, 3360	β = 0	β = 0	β = 0	β = 0
AreaClass3	β = 0	**β > 0** 0.46, 3.71	β = 0	β = 0	β = 0	β = 0
AreaClass4	**β > 0** 0.04, 0.36	β = 0	β = 0	β = 0	β = 0	β = 0
AreaCov3	β =0	β = 0	β = 0	β = 0	β = 0	β = 0
AreaCov4	β = 0	β = 0	β = 0	β = 0	β = 0	β = 0
NumClass3*	**β < 0** -0.22, -0.06	**β > 0** 0.17, 0.76	β = 0	β = 0	β = 0	β = 0
NumClass4	β = 0	β = 0	β = 0	**β < 0** -0.22, -0.009	β = 0	β = 0
NumCov4	β = 0	β = 0	β = 0	β = 0	β = 0	β = 0

***** Habitats for which tradeoffs exist

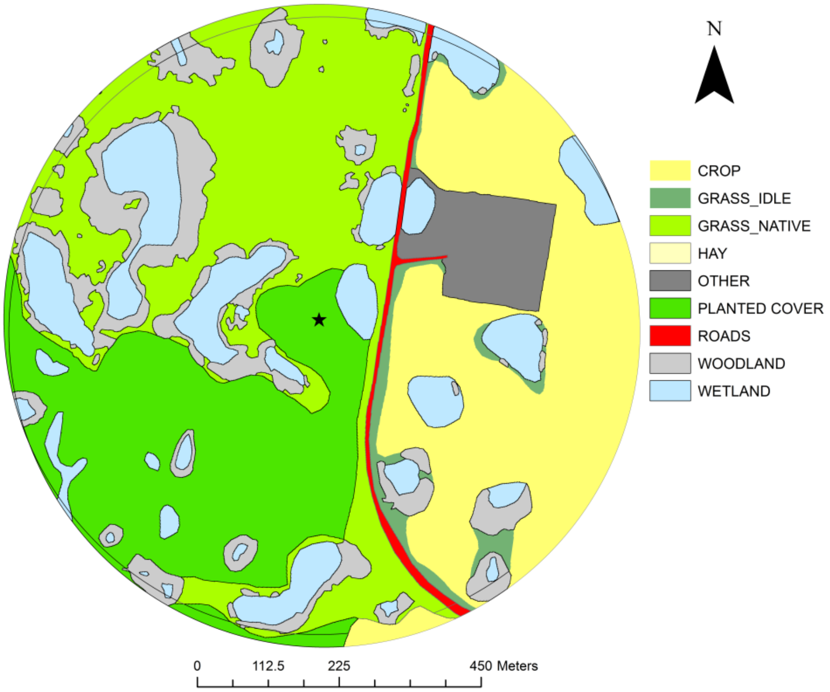

Figure 3.1 – Illustration of a 500 m radius buffer surrounding the nest site (black star), identifying the nine habitat variables used to determine nesting habitat of mallard females in the Canadian Prairie Parklands, 1993 – 2000.

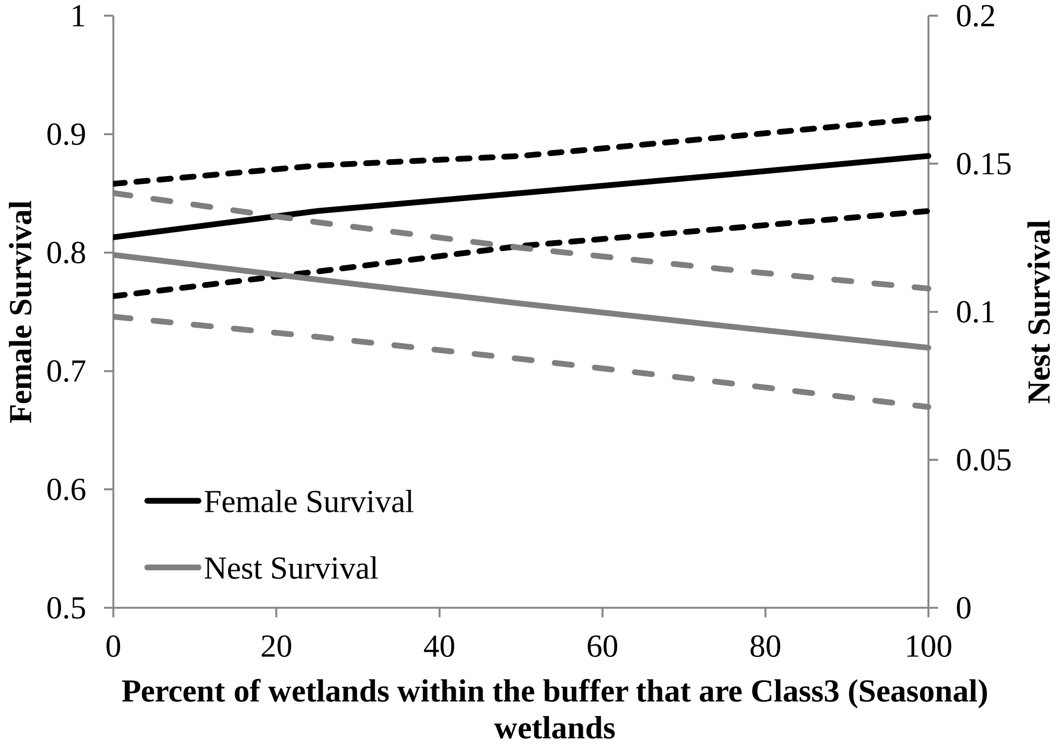

Figure 3.2 – Predicted survival rates of females (black) and nests (grey) in relation to the percent of wetlands within the 100 m buffer around nests that are seasonal (the best-approximating model explaining female survival), for female mallards breeding in the Canadian Prairie Parklands, 1993 –2000; dashed lines represent 85% confidence intervals.

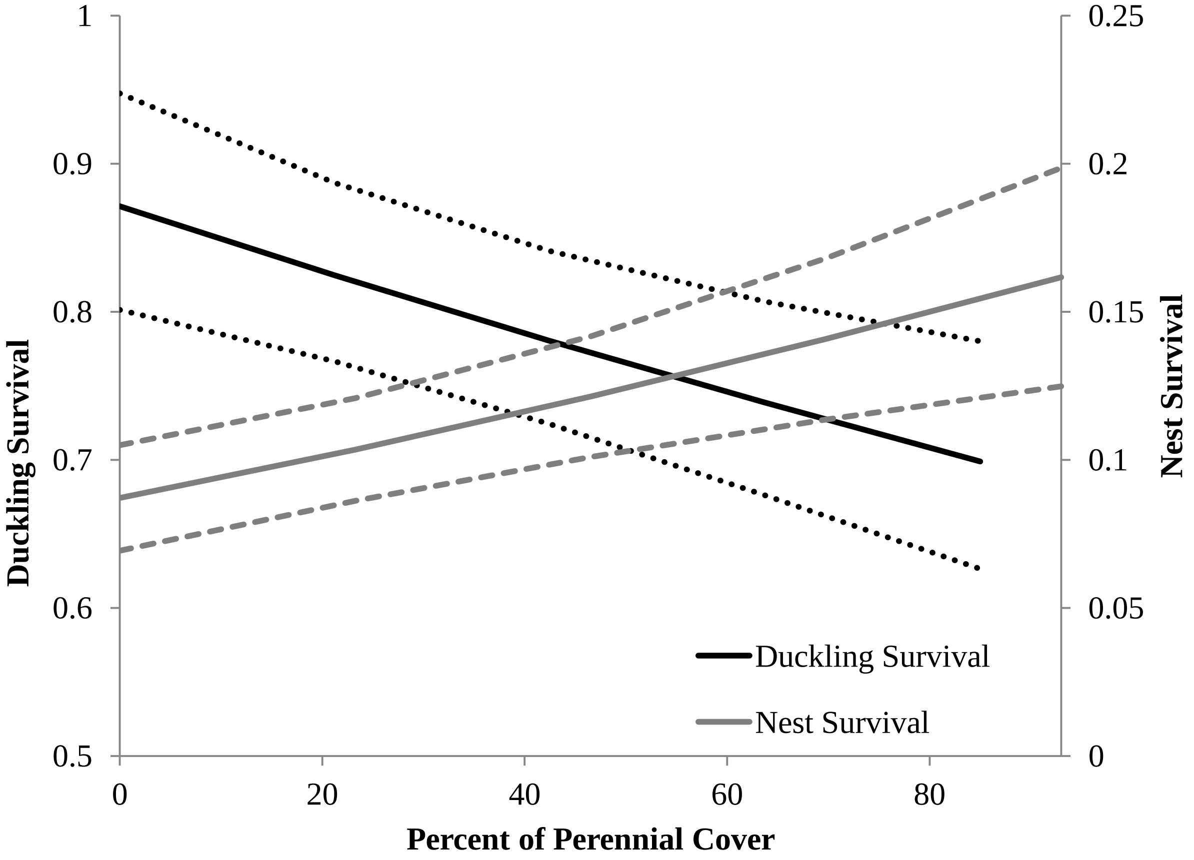

Figure 3.3 – Predicted survival rates of ducklings (black) and nests (grey) in relation to the percent of perennial cover within the 500 m buffer around nests (the best–approximating model explaining daily nest and duckling survival), for female mallards breeding in the Canadian Prairie Parklands, 1993 –2000; dashed lines represent 85% confidence intervals.

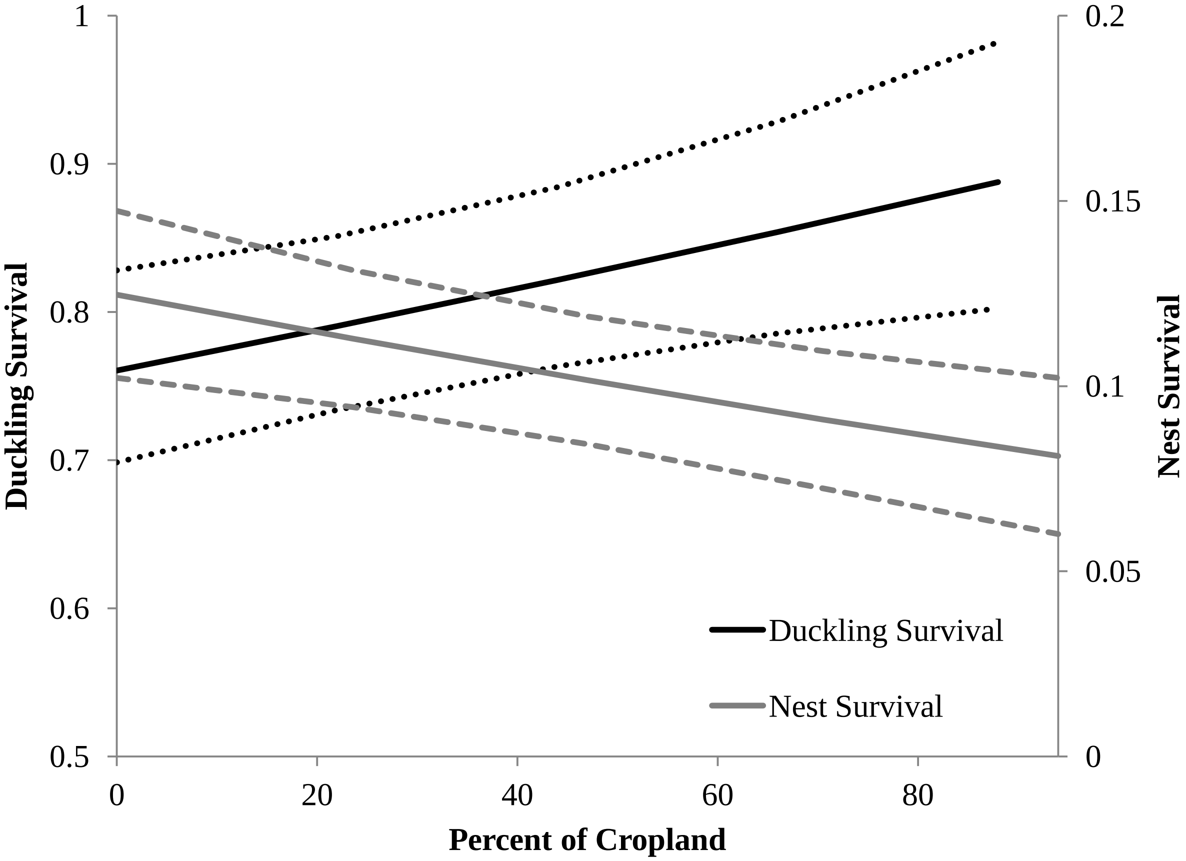

Figure 3.4 – Predicted survival rates of ducklings (black) and nests (grey) in relation to the percent of cropland within the 500 m buffer, for mallard females in the Canadian Prairie Parklands, 1993 –2000; dashed lines represent 85% confidence intervals.

CHAPTER 4: MALE QUALITY AND HABITAT SELECTION BY NESTING FEMALE MALLARDS

4.1 INTRODUCTION

Choice of breeding habitat has a profound impact on reproductive rates in birds and other animals (Cody 1985, Danchin *et al.* 1998), and habitat selection theory suggests that animals choose habitats to optimize fitness and prefer habitats where survival or reproductive rates are higher (Levins 1968, Orians 1980). Waterfowl often demonstrate strong patterns of habitat selection during nesting (Clark and Shutler 1999, Howerter *et al.* 2008) and brood–rearing (Bloom *et al.* 2012*a*, 2013*a*), and research on mallards have evaluated predictions of habitat selection theory during the nesting and brood–rearing phases. Howerter *et al.* (2008) revealed that nesting female mallards select nest sites closer to wetland edges and prefer areas with greater amounts of planted cover and woody habitats. Subsequent research by Bloom *et al.* (2012*a*) suggested that brood–rearing females avoid areas with greater amounts of perennial and woody cover but exhibit strong selection for brood–rearing areas with greater wetland area, specifically wetlands with expanses of open water surrounded by bands on emergent vegetation (Cover type 3 and 4 wetlands). Despite strong patterns of habitat selection during the nesting and brood–rearing phases, mallards did not select habitats that consistently confer reproductive benefits (Howerter *et al.* 2008, Bloom *et al.* 2013*a*; Chapter 3). For instance, during nesting, mallards selected habitats with greater amounts of woody cover, but nest survival rates are lowest in these habitat types (Howerter *et al.* 2008)

Possible explanations for inconsistencies among patterns of habitat selection and subsequent reproductive performance include: (i) differences in stage–specific habitat–use patterns that may have different trade–off consequences (Mack and Clark 2006), or (ii) the role of parental quality in determining reproductive investment (Cunningham and Russell 2000) and, potentially, habitat selection. In Chapter 3, I demonstrated that habitat–specific trade–offs occur between sequential breeding stages in response to the amount of perennial habitat, planted cover, cropland, and seasonal wetlands. For instance, greater amounts of perennial and planted cover within the vicinity of the nest increased nest survival but reduced duckling survival. Previously, I also demonstrated an additive effect of male and female quality on reproductive investment and success of females (Chapter 2). Specifically, yearling females nested earlier and had higher nest survival when mated to males with better plumage scores. Furthermore, when paired with larger–bodied males, yearling females renested more often, whereas nest and brood survival increased among adult females. During the breeding season, pairs establish territories that are usually quite large, nest within the defended area or close by and often forage extensively within the defended area (Anderson and Titman 1992). Although males do not participate in brood–rearing, females may choose higher–quality males, especially larger males, due to their ability to successfully acquire and defend habitats that improve reproductive success (Chapter 2). Male quality has been linked to higher-quality breeding habitat in red-winged blackbirds (*Agelaius phoeniceus*; Yaukawa 1981), northern wheatears (*Oenanthe oenathe*; Pärt 2001), and winter territories of American redstarts (*Setophaga ruticilla*; Germain *et al.* 2010). However, in waterfowl, the relationship between male quality and habitat acquisition has not yet been considered.

Here, I evaluate the role of males in habitat use and reproductive success of female mallards. Specifically, I investigate how selection of nesting and brood–rearing habitat relates to measurements of male quality known to influence reproductive investment decisions of females (Chapter 2), by using an extensive data set collected from free–ranging birds. These data provided a unique opportunity to test whether (i) females paired to high quality males select preferred nesting and brood–rearing habitats identified by Howerter *et al.* (2008) and Bloom *et al.* (2012*a*, 2013*a*), respectively, and (ii) larger males acquire higher–quality breeding habitat (i.e., habitats for which trade–offs among female, nest and duckling survival either did not exist or brood survival increased; Chapter 3).

4.2 METHODS

4.2.1 Study areas

During 1997–1999, data were collected at six, 65 km^2 study sites in the Canadian Prairie Parkland ecoregion of Alberta, Saskatchewan, and Manitoba (Chapter 2; Table 2.1; Fig. 2.1). Sites were selected randomly as part of a larger study to test the efficacy of habitat management programs designed to attract and increase breeding success of upland–nesting ducks (e.g., Emery *et al.* 2005). Each site was investigated for 1 year. The primary land uses on all sites were agriculture and ranching although other land-types including patches of grass, deciduous trees, shrub land, woodland, fence lines, right-of-ways, and wetlands, were present on each study site in varied amounts (Emery et al. 2005). Study sites consisted of a mixture of managed (i.e., delayed grazing, delayed hay, planted cover) and unmanaged (i.e., cropland, hayland, pasture) cover types with some areas more intensively managed than others (Emery et al. 2005).

4.2.2 Field methods

4.2.2.1 Capture and marking

Mallards were captured during 4 April – 5 May each year, before or concurrent with the earliest recorded nesting attempt, by placing decoy traps (Sharp and Lokemoen 1987) in wetlands where pairs or lone males had previously been observed (see Chapter 2; Table 2.1 for sample sizes). Traps were frequently moved among wetlands throughout the study site to ensure the local mallard population was represented (Brasher *et al.* 2002). Trapped birds were banded, weighed with a 1.5–kg Pesola scale (nearest 10 g), and wing chord was measured with a ruler (nearest 1 mm), from the end of the carpo–metacarpus to the tip of the longest primary feather. With dial calipers, head length (nearest 0.1 mm; from the back of the head to the tip of the bill), tarsus length (nearest 0.1 mm; length of the tarsometatarsal bone) and keel length (nearest 0.1 mm, females only; from the tracheal pit to the hind margin of the sternum) was measured. Female age was classified as either second–year (yearling) or after–second year (adult) by visually inspecting the greater secondary covert against a known–age sample, or measuring characteristics of the feather and performing a discriminant function analysis (adapted from Krapu *et al.* 1979). All females were equipped with a 22 g intra–abdominal radio-transmitter (Model IMP/150, Telonics, Mesa, Arizona, Rotella *et al.* 1993, Paquette *et al.* 1997), tracked intensively using vehicle–mounted, null–array antenna systems and triangulation (Kenward 1987) and monitored closely to determine reproductive histories of females (Emery *et al.* 2005, Devries *et al.* 2008). Males were radio–marked with a 9 g back–mounted radio transmitter (Model 2040, Advanced Telemetry Systems, Isanti, Minnesota; Rotella *et al.* 1993, Paquette *et al.* 1997) in 1998 and 1999, as part of another study (Brasher 2000, Brasher *et al.* 2002).

Females were monitored daily until a 30–day brood count was obtained for females that nested successfully, the female was seen unpaired and flocked in early July, or the female died. Birds that disappeared within 2 weeks of marking following nest failure and could no longer be located were censored. Nests were revisited every 6–10 days until nest fate was determined, and were classified as successful if $\geq$1 egg hatched (Klett *et al.* 1986).

4.2.2.2 Parental quality and reproductive investment and success

Criteria were established *a priori* to determine pair status based on characteristics of captured birds (Chapter 2: Table 2.2; Brasher *et al.* 2002). In 1997, I assumed that all birds were assigned correctly as mated pairs. In 1998 and 1999, a sub–sample of assigned pairs were radio–tracked (*n* = 35) to confirm pair status. I validated results obtained for all presumed pairs by repeating analyses using the sub–sample of confirmed pairs when sample size was sufficient.

Male plumage was recorded only in 1997 at 4 sites for males presumed to be paired with a radio–marked female (*n* = 223; criteria in Chapter 2; Table 2.2). Important male plumage characteristics were recorded (Klint 1980, Holmberg *et al.* 1989, Weidmann 1990, Giraudeau *et al.* 2011): (1) maximum and minimum width of the white neck ring, (2) number of places on the head and chest where feathers were missing or unmolted and, (3) number of curled tail feathers. I modified methods of Holmberg *et al.* (1989) and Weidmann (1990) to rank each plumage characteristic according to the extent of either naturally–occurring blemishes or deviations from ideal plumage (Chapter 2: Table 2.3), and summed individual characteristics so that smallest rank signified fewest deviations (i.e., better quality plumage).

4.2.2.3 Habitat classification

Wetlands were classified (Stewart and Kantrud 1971; Chapter 1; Table 1.3), 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 in late–July or early–August. Digitized habitat maps were imported into SPANS Geographic Information System (GIS; PCI Geomatics, Richmond Hill, Ontario, Canada). Using the buffer and intersect tools in ArcGIS, I created a 100 m and 500 m buffer around each nest and summarized the upland and wetland habitat attributes within each buffer (Chapter 3; Fig. 3.1). To avoid pseudoreplication, I averaged the habitat variables between all nest attempts for a given individual (range 1 – 6), and only considered the CID and distance to nearest wetland of the first nest attempt of reach female.

4.2.4 Data censoring

Five pairs were excluded from analyses either because data were missing or birds were assigned an incorrect pair status (i.e., radio–tracking revealed female was paired with a different male or a bird was erroneously paired with two different mates during data entry). Missing keel lengths for four females were imputed using regression equations ($F = 5.29$, $df = 249$, $p = 0.002$) derived from the morphometric measurements (i.e., keel, wing, tarsus and head lengths) of the remaining females, and outlying tarsus lengths were similarly imputed for two males ($F=19.91$, $df= 249$, $p< 0.001$). Ages of five females could not be determined. From a sample size of 253 pairs, plumage characteristics were collected for 217 males, 35 pairs were confirmed using radio–telemetry, 30 pairs did not nest, and habitat information was not available for 23 females (i.e., these females nested outside the study area). Thus, reproductive histories and habitat composition was available for 88 adult and 71 yearling females.

4.2.5 Statistical analyses

Body size indices of males and females were derived separately using Principal Component Analyses (PCA) based on the correlation matrix of morphometric measurements. PC1 accounted for 42% (SD = 1.29) of variation in head, wing, tarsus and keel measurements of females (coefficients of 0.58, 0.45, 0.55, 0.41, respectively) and 51% (SD = 1.26) of variation in head, wing, and tarsus measurements of males (coefficients of 0.59, 0.56, 0.58, respectively); thus, PC1 scores were used as an index of body size in subsequent analyses. Residuals obtained from ordinary least squares regression of body mass against body size index were used as indices of body condition. To account for site–year variation in body size index, I standardized sex–specific indices by determining the average body condition and size index for each study site and subtracting the mean value from each measurement.

To evaluate whether higher quality males acquire preferred brood–rearing habitats, I related patterns of habitat use of females and measurements of male quality to: (1) preferred nesting and brood–rearing habitats, and (2) habitats that increase reproductive success (Howerter *et al.* 2008, Bloom *et al.* 2013*a*, Chapter 3). I identified 9 habitat variables that female mallards select during nesting and brood–rearing, or for which habitat–specific trade–offs have been illustrated between the nesting and brood–rearing stages, and predicted that higher quality males would procure habitats that benefit brood–rearing females (Table 4.1).

Adult female mallards mate assortatively by body condition, whereas yearling female mate assortatively by body size and body condition (Chapter 2). Thus, correlations between male and female quality should be controlled to properly evaluate habitat selection. Moreover, yearling females tend to nest later than adults (Devries *et al.* 2008) and age–specific mate selection likely differs depending on how females perceive males (Chapter 2), as such it was essential to simultaneously evaluate both male and female quality to fully understand the role of males in decisions of habitat selection of females. I evaluated 9 *a priori* models which simultaneously considered attributes of male quality which influence reproductive investment and success of females (Chapter 2), with measures of female quality (Table 4.2).

I analyzed reproductive data separately by female age to account for differences in age–specific female mate preferences. I included a binomial variable for nest survival (hatched or failed) when evaluating habitats selected during nesting and a binomial variables for brood survival (fledged, failed) when evaluating habitats selected during brood–rearing. I used generalized linear models to evaluate competing models which related male quality to habitat selection of females (Proc GENMOD, SAS Institute Inc. 2011). I corrected for small sample sizes and compared candidate models using information–theoretic approaches to determine best–approximating models within the candidate set. I model–averaged parameter estimates (β) and standard errors (SE) across all candidate models to obtain multi–model inferences (Burnham and Anderson 1998) based on 85% confidence intervals (Arnold 2010). To increase validity of my results and ensure that relationships between male quality and habitat selection were not confounded by other factors, I performed exploratory analyses to incorporate effects of clutch initiation and nest survival in the best–approximating models, and then compared these results to those from models with effects of both male and female quality. All statistical procedures were conducted in SAS, version 9.3.

4.3 RESULTS

Contrary to predictions, male quality was not related to the amounts of planted cover, woody cover, perennial cover and cropland within 100 m or 500 m of the nests of yearling or adult mallards. Instead, smaller-bodied yearling females had greater amounts of perennial and woody cover but smaller amounts of cropland surrounding the nest site (Table 4.3). My prediction that females would obtain nest sites closer to wetlands was only partially supported, as indicated by the best–approximating models explaining distance to the nearest wetland (consistent across both spatial scales) which included only effects of male size index for both age classes (Adults: $\beta = 3.98$, SE = 2.25; Yearlings: $\beta = -13.99$, SE = 3.96; Table 4.3). In particular, yearling females nested closer to wetlands when paired to larger males (Fig. 4.1). Large-bodied yearling females paired to larger males obtained areas with a greater proportion of wetland habitat (100 m: Male Size: β = 0.024, SE = 0.010; Female Size: β = 0.019, SE = 0.010; Table 4.3). Contrary to predictions, at the 100 m scale, small-bodied adult females paired to larger males (Male Size: β = –0.042, SE = 0.018; Female Size: β = 0.048, SE = 0.019; Table 4.3), and yearling females paired to males with better plumage quality (β = 0.021, SE = 0.012) had smaller amounts of cover type 4 wetlands (NumCov4) within the nest buffer (Table 4.3). Consistent with predictions, adult females paired to larger males tended to have greater amounts of seasonal wetlands within the 500 m buffer (β = 0.028, SE = 0.017; Table 4.3; Fig. 4.3).

4.3.1 Exploratory analyses

Although results suggest that female quality does not confound effects of male quality in explaining NumCov4 wetlands within 100 m of the nest of yearling females (Table 4.3), yearling females nest earlier and have greater nest survival when paired to males with better plumage quality (Chapter 2). Additionally, effects of NumCov4 wetlands were contained within the best–approximating model explaining daily nest survival at the 100 m scale (Chapter 3). Thus, the relationship between male plumage and NumCov4 wetlands within the buffer could be a result of nesting earlier (i.e., birds that settle earlier select higher–quality habitats; Fretwell and Lucas 1970), or may interact with nest survival. To determine whether effects of male plumage quality were confounded by clutch initiation date or nest survival, I performed additional exploratory analyses to evaluate effects of male plumage, clutch initiation date, and an interaction between male plumage and nest survival. However, the best–approximating model explaining the proportion of cover type 4 wetlands within 100 m of nests of yearling females, only contained effects of male plumage (β = 0.021, SE = 0.012; Table 4.4).

4.4 DISCUSSION

My most important findings were the relationships between male body size and habitat selection of adult females, and male plumage quality and habitat selection of yearling females. Specifically, the distance from the nest to the nearest wetland, the proportion of cover type 4 wetlands and the proportion of seasonal wetlands within the buffer were best explained by effects of male quality after I controlled for female quality. I predicted that females paired to high–quality males would obtain nest sites surrounded by greater amounts of habitats that increase duckling survival rates and those predictions were partially supported. Specifically, yearlings nested closer to wetlands, and adults had great amounts of seasonal wetlands within 500 m of nests, when paired to high quality males. Results are consistent with my previous prediction that larger males can sequester higher quality brood–rearing habitat (Chapter 2; i.e., areas with greater amounts of seasonal wetlands and nest–sites closer to wetlands; Bloom *et al.* 2012*a*) or provide access to wetland habitats with abundant food resources for ducklings, resulting in greater brood survival among adult females.

Adult females nested further from wetlands when paired to larger males (Fig. 4.1). This was opposite from my prediction that females paired to higher quality males would nest closer to wetlands to increase brood survival. If adult females value brood survival over nest survival (as suggested in Chapter 2 and by Pöysä *et al.* 2000), and larger males are better quality, then it is expected that females will choose males which can sequester upland nesting habitats near suitable wetlands. One possible explanation for this inconsistency could be the wetland type that the nest was closest to. Possibly, adult females nested further from high–quality brood–rearing wetlands to ensure nest survival, or nested further from wetlands associated with duckling predators (i.e., semi–permanent wetlands). Alternatively, adult females likely “value” safer nest–sites over safer brood–rearing habitats (Chapter 3). As predicted, yearling females nested closer to wetlands when paired to larger males. The tendency for yearlings to nest closer to wetland edges likely reduced the probability of nest survival (Howerter *et al.* 2008) and could explain why yearling females paired to larger–bodied males renested more often (Chapter 2). To fully understand the relationship between brood survival and distance from nest to nearest wetland in relation to parental quality, wetland permanency and cover class should be considered simultaneously with wetland distance, while considering female age classes separately.

In this study, male quality was only related to wetland habitats, thus predictions that females paired to higher quality males would obtain greater amounts of beneficial upland cover (i.e., perennial and woody cover) within nest buffers was not supported. Additionally, my prediction that females paired to high quality males would procure areas with greater amounts of NumCov4 wetlands was not supported, whereas adult females paired to larger males obtained nest-sites with greater amounts of seasonal wetlands. NumCov4 wetlands are negatively correlated with the proportion of seasonal wetlands within the nest buffer (Pearson’s $r = –0.23$, n

= 151, *P* = 0.005). Possibly, females are faced with a trade–off between greater amounts of cover type 4 wetlands versus seasonal wetlands. Thus, habitat selection of contrasting landscapes which increase duckling survival (i.e., areas with greater amount of NumCov4 wetlands vs. seasonal wetlands) should be further evaluated. If female mallards select males based on their ability to secure high–quality brood–rearing habitats then results suggest that mallards valued duckling survival over nest survival and that female mallards forecasted the quality of brood–rearing habitats when selecting nesting sites.

4.5 CONCLUSION

To my knowledge, this is among the first study to integrate measures of male quality in the evaluation of habitat selection of females during nesting and brood–rearing in free–ranging waterfowl. Male quality was important in determining the percent of wetland habitats, which reportedly improve brood survival, within 100 m and 500 m buffers of the nest site, but did not influence habitat decisions in relation to upland habitats shown to increase nest survival. Male size was the most influential trait determining the distance of the nest to the nearest wetland and the proportion of seasonal wetlands within the 500 m nest buffer of adult females. Male plumage quality was important also in determining the proportion of cover type 4 wetlands in the 100 m nest buffer of yearling females. This study suggested that effects of female quality is also important in determining the habitat composition and wetland habitats of nest buffers and revealed that smaller-bodied yearling females had smaller amounts of cropland but greater amounts of perennial and woody cover surrounding the nest site.

Results from Chapter 2 suggested that adult females paired to larger males had greater brood survival and predicted that higher quality males are better able to procure high–quality brood–rearing areas. Results from this study demonstrated that male mallard quality is related to wetland habitats previously identified to influence brood survival, but not upland habitats reported to increase nest survival. As suggested by Pöysä *et al.* (2000), mallards possibly value duckling survival over nest survival and could explain why females chose males based on their abilities to secure high–quality brood–rearing habitats as opposed to nesting habitat. Thus, female mallards possibly forecasted the quality of brood–rearing habitats when selecting nesting sites; an idea that should be explored.

Table 4.1 – List of habitat variables, predicted effects and justification for prediction, of habitat selection during nesting in relation to male quality of mallards in the Canadian Prairie Parklands, 1997 – 2000.

Variable	**Prediction**	**Justification**
	Higher quality males will procure:	
DNC	Areas with smaller amounts of planted cover.	Mallards exhibited a preference for planted cover (Howerter *et al.* 2008), and a trade–off existed between nest and duckling survival (Chapter 3).
Wood	Areas with smaller amounts of woody cover.	Preference for woody cover was 2nd highest in a study of habitat selection of mallards (Howerter *et al.* 2008) and avoidance of woody cover increased duckling survival (Bloom *et al.* 2013*a*).
Wet_Dist	Nest sites closer to wetlands.	Mallards tended to nest closer to wetlands than by chance alone (Howerter *et al.* 2008). Less overland travel was beneficial to duckling survival (Bloom *et al.* 2012*a*).
Num_Cov4	Areas with greater number of wetlands with cover type 4.	Mallards exhibited greater selection for cover type 4 wetlands during brood–rearing (Bloom *et al.* 2012*a*).
Area_Cov3	Areas with greater amounts of cover type 3 wetlands.	Mallards exhibited preference for a greater coverage of cover type 3 wetlands during brood–rearing (Bloom *et al.* 2012*a*).
WLArea	Areas with greater proportion of wetland habitat.	Mallards selected areas with greater proportion of wetland habitat (Bloom *et al.* 2012*a*).
Pern	Areas with lower amounts of perennial cover.	Brood–rearing females avoided areas with greater amounts of perennial habitat (Bloom *et al.* 2013*a*), and a trade–off existed between nest and duckling survival in relation to perennial cover (Chapter 3).

Crop	Areas with greater amounts of cropland.	Trade–off existed between nest and duckling survival in relation to cropland at coarse spatial scales (Chapter 3).
Num_Class3	Areas with greater amounts of Class3 wetlands.	Trade–off existed between nest and duckling survival in relation to seasonal wetlands at fine spatial scales (Chapter 3).

Table 4.2 – Nine *a priori* models used to simultaneously evaluate effects of male and female quality on patterns of habitat selection of female mallards in the Canadian Prairie Parklands, 1997 – 1999.

Model	**Definition**
Intercept	Intercept only model.
Male size	1^{st} Principal Component derived from PCA of head, wing, and tarsus length of males.
Male plumage score	Total sum of ranked individual plumage characteristics according to the extent of deviations from ideal plumage.
Female condition	Residuals obtained by OLS regression of body mass against body size index of females.
Female size	1^{st} Principal Component derived from PCA of head, wing, tarsus and keel length of females.
Female quality	Simultaneously evaluated female condition and female size.
Male size + female size	Simultaneously evaluates male and female body size index.
Male plumage score + female condition	Simultaneously evaluates male plumage score and female body condition index.
Male plumage score + female size	Simultaneously evaluates male plumage score and female body size index.

Table 4.3 – Best–approximating *a priori* models explaining variation in nesting habitat of breeding mallards in the Canadian Prairie Parklands, 1997 – 2000.

Model description	**AIC_c[1]**	**ΔAIC_c[2]**	***K***	**w_i[3]**
Adult Females (n = 88)				
Distance to Nearest Wetlands (both spatial scales)[a]				
Male Size	835.84	0.00	3	0.28
Intercept	836.73	0.89	2	0.18
Male Size + Female Size	836.76	0.92	4	0.18
Num_Cov4 (100 m scale)[b]				
Male Size + Female Size	-17.30	0.00	4	0.59
Female Size	-14.37	2.93	3	0.14
Num_Class3 (100 m scale)[b]				
Female Size	70.28	0.00	3	0.38
Male Plumage + Female Size	71.97	1.69	4	0.16
Male Size + Female Size	72.15	1.87	4	0.15
Area_Cov3 (500 m scale)[b]				
Female Condition	-305.48	0.00	3	0.25
Male Plumage + Female Condition	-304.53	0.95	4	0.16
Intercept	-304.32	1.16	2	0.14
Male Size + Female Condition	-304.05	1.43	4	0.12
Num_Class3 (500 m scale)[b]				
Male Size	-22.82	0.00	3	0.25
Intercept	-22.38	0.45	2	0.20
Male Size + Female Size	-21.65	1.17	4	0.14
Yearling Females (*n* = 71)				
Distance to Nearest Wetlands (both spatial scales)[a]				
Male Size	724.62	0.00	3	0.55
Male Size + Female Size	725.15	0.53	4	0.42
Male Plumage + Female Size	732.89	8.27	4	0.01
Woody Cover (100 m scale)[a]				
Female Size	-14.06	0.00	3	0.28

Male Plumage + Female Size	-12.80	1.25	4	0.11
Intercept	-12.51	1.55	2	0.10
Male Size + Female Condition	-12.42	1.63	4	0.09
Num_Cov4 (100 m scale)[b]				
Male Plumage	-14.02	0.00	3	0.26
Intercept	-13.28	0.73	2	0.18
Male Plumage + Female Condition	-12.87	1.15	4	0.15
Female Condition	-12.06	1.95	3	0.10
Male Plumage + Female Size	-11.83	2.19	4	0.09
Pern (100 m scale)[a]				
Female Size	41.06	0.00	3	0.37
Male Size + Female Size	42.09	1.02	4	0.22
Male Plumage + Female Size	42.88	1.81	4	0.15
Male Size + Female Condition	43.03	1.97	4	0.14
Wetland Area (100 m scale)[b]				
Male Size + Female Size	-118.25	0.00	4	0.48
Male Size	-117.03	1.22	3	0.26
Cropland (100 m scale)[a]				
Female Size	32.43	0.00	3	0.41
Male Plumage + Female Size	34.25	1.82	4	0.17
Male Size + Female Size	34.36	1.93	4	0.16
Woody Cover (500 m scale)[a]				
Female Size	-62.13	0.00	3	0.29
Intercept	-61.22	0.91	2	0.18
Area_Cov3 (500 m scale)[b]				
Male Plumage + Female Condition	-217.75	0.00	4	0.55
Intercept	-214.91	2.84	2	0.13
Perennial Cover (500 m scale)[a]		_		
Female Size	-5.42	0.00	3	0.40
Male Size + Female Size	-3.68	1.74	4	0.17
Cropland (500 m scale)[a]				

Female Size	10.14	0.00	3	0.29
Male Size + Female Size	11.51	1.37	4	0.15
Intercept	11.77	1.63	2	0.13
Male Plumage + Female Size	12.13	1.98	4	0.11

Models are ranked by differences in Akaike's Information Criterion and corrected for small sample size (ΔAIC_c). Number of parameters (*K*) includes the intercept and a binomial value for nest or brood survival.

[1] Akaike's Information Criterion corrected for small sample size.

[2] Difference in AIC relative to model with the lowest value.

[3] Model weight.

[a] Nest survival is included as a covariate.

[b] Brood survival is included as a covariate.

Table 4.4 – Best–approximating exploratory models explaining variation in the proportion of cover type 4 wetlands within the 100 m nest buffer of yearling female mallards (*n* = 71) in the Canadian Prairie Parklands, 1997 – 2000.

Model	**Deviance**	***K***	**AIC_c[1]**
Male Plumage	2.69	3	–14.01
Intercept	2.82	2	–13.07
Male Plumage + CID	2.64	4	–12.79
Male Plumage + Male Plumage*succ	2.67	4	–11.93
CID	2.82	3	–10.88
Male Plumage + CID + Male Plumage*CID	2.63	5	–10.58
CID + CID*succ	2.81	4	–8.60

Models are ranked by differences in Akaike's Information Criterion and corrected for small sample size (ΔAIC_c). Number of parameters (*K*) includes the intercept and a binomial variable for nest survival.

[1] Akaike's Information Criterion corrected for small sample size.

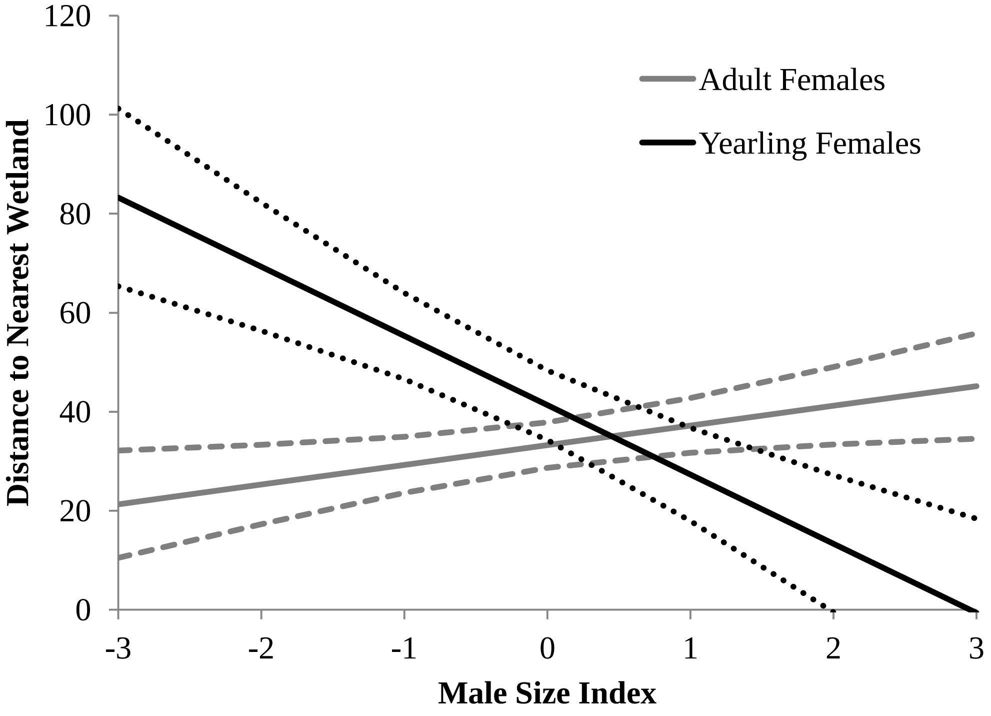

Figure 4.1 – Predicted distance from nest to nearest wetland in relation to male size index for adult (grey; *n* = 88) and yearling (black; *n* = 71) female mallards in the Canadian Prairie Parklands, 1997 – 2000; dashed lines represent 85% confidence intervals. Negative values of the body size index represent small–bodied males and positive values signify large–bodied males.

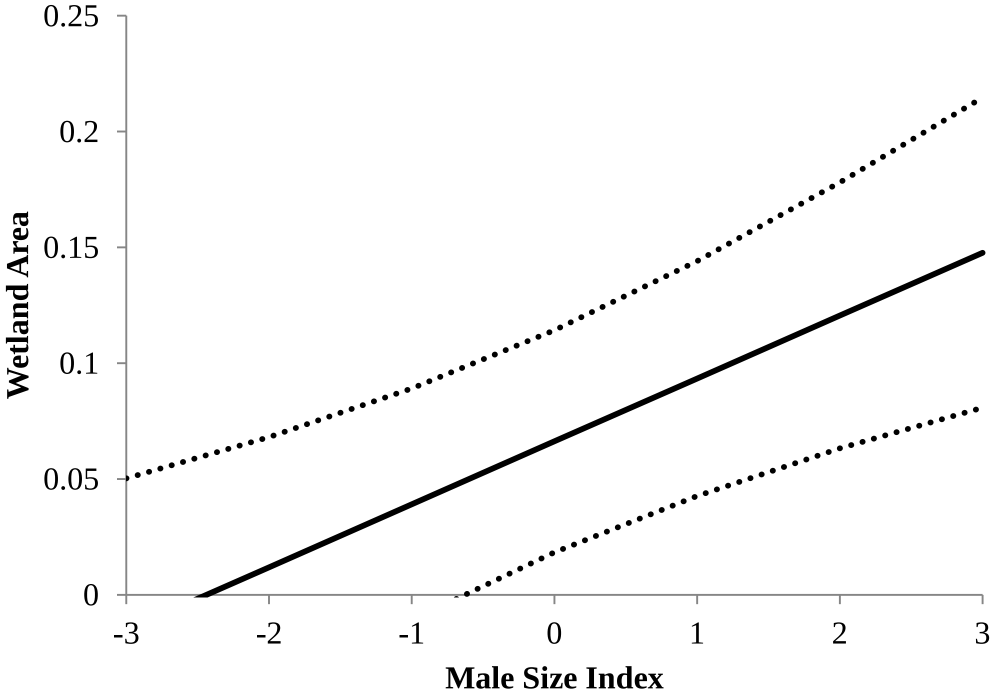

Figure 4.2 – Predicted wetland area within the 100 m nest buffer in relation to male size index for yearling female mallards (n = 71) in the Canadian Prairie Parklands, 1997 – 2000, dashed lines represent 85% confidence intervals. Negative values of the size index represent small–bodied males and positive values signify large–bodied males.

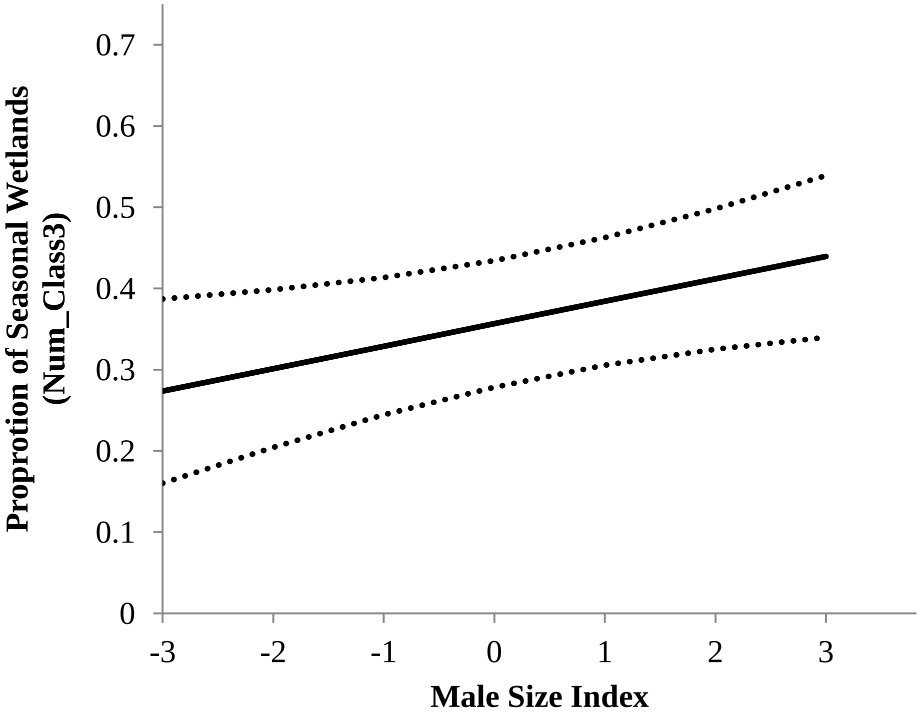

Figure 4.3 – Predicted proportion of seasonal wetlands (Class3) within the 500 m nest buffer in relation to male size index for adult female mallards (n = 88) in the Canadian Prairie Parklands, 1997 – 2000, dashed lines represent 85% confidence intervals. Negative values of the size index represent small–bodied males and positive values signify large–bodied males.

CHAPTER 5: SYNTHESIS

5.1 CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

In studies of habitat selection theory, it is often assumed that habitat selection is adaptive and researchers expect that organisms select higher–quality, and avoid lower–quality, habitats (Levins 1968, Orians 1980). However, when evaluating patterns of habitat selection it is essential to link fitness consequences of habitat choices to substantiate the putative adaptive basis for habitat selection (Clark and Shutler 1999). Poor habitat choices made during critical life–stages of an organism (i.e., during breeding) may have detrimental effects on individual survival or lifetime reproductive success. Moreover, failure to properly test whether habitat selection is adaptive (even in a phenotypic sense) could promote retention, restoration and management of unfavourable habitats and could reduce effectiveness of conservation programs.

Recent studies of habitat selection during breeding in mallards and other avian species have tested for congruence between habitat preferences and reproductive success. Yet, different studies of specific breeding–stages illustrated that habitats that benefit mallards during one stage of the breeding cycle (i.e., during nesting) may not benefit mallards during subsequent stages (i.e., during brood–rearing; Howerter *et al.* 2008, Bloom *et al.* 2013*a*). Thus, to help guide management decisions aimed at increasing population growth rates, it is essential to understand the factors influencing patterns of habitat selection at major stages of the breeding cycle. Using data collected during the PHJV Assessment study, I was able, for the first time, to address questions about potential habitat–specific trade–offs between subsequent stages of the breeding cycle and female survival and explore the importance of male quality in determining reproductive investment, success, and decisions of habitat selection of female mallards. Overall, my main findings: (1) provide valuable new knowledge for habitat managers to consider when designing conservation programs and (2) improve current knowledge about differential allocation and habitat selection theories.

The differential allocation hypothesis states that individuals should allocate resources in response to characteristics of their mate and predicts that male attractiveness will influence the reproductive value of a female's breeding attempt (Burley 1988, Sheldon 2000). Females are expected to trade–off current and future reproduction in response to male attractiveness, such that females increase their reproductive investment when mated to high–quality males (Burley

1988, Sheldon 2000). However, differential allocation could also be driven by an underlying correlation between male and female quality, especially in studies of wild animals where there could be many alternative explanations for correlations that seem consistent with differential allocation (Sheldon 2000); consequently, differential allocation is rarely considered in wild populations. Yet, in waterfowl mating systems, mate selection is based on morphology, ornaments or behaviours of males as opposed to the ability of a male to raise offspring or in response to male territory (McKinney 1992). Thus, by considering the quality of both males and females simultaneously to control for correlations between male and female quality, I demonstrated how differential allocation can be evaluated in natural systems. Although results from my research did not provide sufficient evidence to support the differential allocation in free–ranging mallards, it did suggest that both male and female quality play important roles in avian reproductive ecology. Thus, researchers should consider effects of both male and female quality in future studies, a step I applied in Chapters 2 and 4.

In waterfowl, females choose breeding habitats and nest sites, thus male quality is rarely considered when evaluating reproductive ecology or habitat selection. However, males are involved in female protection and sequestration and defense of their home–range (Anderson and Titman 1992), so male quality is probably important to reproductive investment decisions and habitat selection of females. To determine the role of males in reproductive investment and success of females, I related measurements of male quality that have been demonstrated to influence mate choice of females (i.e., Klint 1980, Holmberg *et al.* 1989, Weidmann 1990), to reproductive histories of their partners. I found that male body size was positively related to survival rates of nest and broods of adult females, independent and additive to effects of female quality. Moreover, male quality was positively related to clutch initiation date, renesting frequency, and nest survival of yearling females. In response to these results (Chapter 2), I hypothesized that larger males provide access to wetland habitats with abundant food resources for ducklings; this would explain why adult females paired to larger males had higher nest and duckling survival.

My results also indicated that adult and yearling females likely use different cues when choosing males (i.e., adults did not mate assortatively by body size whereas yearlings females did). For instance, adult females likely selected mates based on the male’s ability to obtain high–

quality breeding habitats, whereas mate–guarding abilities could be especially important for small–bodied yearling females. These results highlighted the importance of differentiating between different age classes and this approach should be considered in future studies of waterfowl. From my analysis of Chapter 2, I was unable to determine the relationship between male quality, habitat acquisition, and mate–guarding and female mate–choice; however I was able to evaluate correlates of male quality and habitat acquisition in Chapter 4. Thus, I demonstrated that male quality influences reproductive investment and success of females and should be considered when evaluating reproductive ecology of waterfowl. Yet, whether males with better plumage quality provide yearlings with sufficient protection or whether larger males can migrate faster and procure preferred breeding habitat should be evaluated in future studies.

Nest survival is considered the most important parameter in the population dynamics of upland nesting waterfowl that breed in the PPR (Cowardin *et al.* 1985, Greenwood *et al.* 1995, Hoekman *et al.* 2002, Emery *et al.* 2005, Horn *et al.* 2005, Stephens *et al.* 2005, Howerter *et al.* 2008) and conservation programs are typically designed to increase nest success. Thus, management objectives have focused on attracting ducks to habitats where nest success is greater (Emery *et al.* 2005). Yet, Bloom *et al.* (2013*a*) evaluated patterns of habitat selection of brood–rearing females and found that habitats which reportedly improve nest survival (Howerter *et al.* 2008) did not always benefit ducklings. Moreover, Howerter *et al.* (2008) demonstrated that females did not always select nesting habitats that increase nest survival.

To address inconsistent patterns of habitat selection between the nesting and brood–rearing stages, I linked processes of habitat selection during nesting to survival rates of females, nests and ducklings. My analyses focused on high–quality nesting and brood–rearing habitats that reportedly influenced survival of nests or broods (Howerter *et al.* 2008, Bloom *et al.* 2012*a*, 2013*a*). I found evidence of habitat–specific trade–offs between the nesting and brood–rearing stage and between survival of nests and females. Specifically, upland nesting habitats that increased nest survival (i.e., greater amounts of DNC, perennial cover or lower amounts of cropland) were negatively associated with duckling survival but unrelated to female survival. Similarly, wetland habitats that reportedly benefited duckling survival (i.e., greater amounts of seasonal wetlands; Bloom *et al.* 2012*a*) were negatively associated with nest survival. Results from finer spatial scales (100 m) revealed that wetland habitats that impacted nest survival (i.e., seasonal and semi–permanent wetlands) but not duckling survival tended to have the opposite effect on female survival rates. For instance, seasonal wetlands increased female survival but negatively impacted nest survival. Results from Chapter 3 suggested that mallards selected habitats that increased nest survival while simultaneously forecasting preferred brood–rearing habitat. Stage–specific survival (i.e., survival of nests, females or broods) in relation to wetland composition surrounding nest sites could be a consequence of wetland associated predators or plentiful food resources found in wetlands, and should be considered in subsequent research.

Female waterfowl choose nest sites and pair dissolution occurs during incubation (Williams 1983). Because of the lack of participation of male ducks in brood–rearing, incubation or nest guarding, male quality is rarely considered when evaluating habitat selection of nesting females. Yet, the ability of a male to procure high–quality breeding habitats and defend the home range could have important implications of habitat choices and subsequent breeding success of females. To test predictions arising from results of Chapter 2, I evaluated how male quality related to habitat selection of females during nesting and how these habitat decisions affected subsequent duckling survival. I found no indication that male quality was important in determining upland habitat composition surrounding nest sites but male quality was related to acquisition of high–quality brood–rearing habitats. Larger males likely sequestered high quality brood–rearing habitats or provided access to wetland habitats with abundant food resources for ducklings; however, a larger sample size of brood-rearing females with detailed habitat information is required to substantiate this finding. Additionally, male body size was the most important variable determining the distance from the nest to the nearest wetland such that adult females nested further, whereas yearling females nested closer, to wetlands when paired to larger males. Although results from yearling females were consistent with predictions, the tendency for yearlings to nest closer to wetland edges increases the probability of nest failure (Howerter *et al.* 2008). This likely explained why yearling females paired to larger–bodied males renested more often (Chapter 2). Additionally, opposite to my predictions, adult females likely nested further from high quality brood–rearing wetlands to increase female or nest survival. Thus, to fully understand the relationship between male quality and distance to nearest wetland, wetland permanency and cover class should be considered simultaneously with habitat–specific trade–offs, while considering female age classes separately.

Results of Chapter 3 suggested that female's valued safer nest sites over brood survival, but subsequent analyses (Chapter 4) lead to the conclusion that mallards possibly value duckling survival over nest survival and may explain why females choose males based on their abilities to secure high–quality brood–rearing habitats as opposed to nesting habitat. Because females are particularly vulnerable to predators during incubation, females likely value "safer" nesting sites. However, males do not protect the nest site or female during incubation, instead high quality males likely secure high quality wetlands where the pair will feed and meet prior to incubation and females possibly take their ducklings to these wetlands upon nest exodus. Additionally, by providing suitable brood-rearing wetlands males likely ensure their own lifetime reproductive success. To further evaluate patterns of habitat selection of nesting females, additional research is needed to determine how females use the habitats males procure and whether mallards value brood survival rates over nest survival rates.

Whether mallards mate assortatively by age is unknown, but could explain why adult and yearling females choose mates differently. I did not have information on male age but this should be considered in further research evaluating waterfowl reproductive ecology. I did not have sufficient data to determine whether females increase egg mass when mated to larger males, but in accordance to the differential allocation hypothesis, it is expected that females would increase egg mass when paired to high quality males. The relationship between habitat quality, male quality and egg investment would provide useful insights into differential allocation of mallards. Omland (1996) and Girardeau *et al.* (2011) used male bill colour as a key predictor of male quality. Alternative, reliable, measures of male quality could help strengthen results found here and clarify unresolved questions about patterns of habitat selection of female mallards in response to male quality.

5.2 MANAGEMENT IMPLICATIONS

The habitats evaluated here have been documented as preferred or demonstrated as high–quality (i.e., shown to increase offspring survival) nesting or brood–rearing habitats of mallards in the Canadian PPR (Howerter *et al.* 2008, Bloom *et al.* 2012*a*). Although conservation efforts have primarily focused on increasing perennial and planted cover habitats to increase nest survival, I demonstrated that selection of nest–sites in areas of greater perennial and planted cover can lower subsequent duckling survival. Furthermore, I showed that increased amounts of seasonal wetlands and cropland found close to nests could have a positive effect on survival of ducklings and females, while negatively affecting nest survival. Because of stage–specific habitat trade–offs associated with perennial cover and cropland habitats, it is recommended that the costs and benefits of these habitats and subsequent reproductive success of mallards be carefully considered. Whether cropland and perennial habitats increase recruitment is not known, but should be considered. Thus, efforts to covert annual cropland to perennial grassland and planted cover could be re-evaluated when the associations between upland habitat and wetland class are better understood. For instance, cropland may only be beneficial to duckling survival when sufficient amounts of seasonal wetlands are retained within the landscape. Thus, the suitability of seasonal wetlands to duckling survival (i.e., whether these wetlands have abundant food resources), should be investigated. Continued crop management practices with the restoration of seasonal wetlands within the landscape is a suitable management recommendation, but predator complexes and food resources must first be evaluated before robust management recommendations are made.

Additionally, I highlight the importance of male quality in reproductive investment decisions, reproductive success and habitat selection of females. I showed that females increase reproductive investment and success when paired to larger males and that female mallards paired to these males select nesting habitats with greater amounts of high–quality brood–rearing habitats. Thus, management techniques which focus on increasing nest survival based on habitat selection during nesting should be modified to recognize the ability of females to select nesting habitats which subsequently benefit ducklings. Thus, continued management and restoration of high–quality wetland habitats for brood–rearing females is recommended.

The Canadian Prairie Parklands (PPR) is a complex landscape and habitat selection of mallards may vary depending on female age and the spatial scale at which selection is evaluated. The habitat selection decisions that female mallards make during nesting are not as clearcut as simply selecting the highest quality nesting habitats. Instead, females likely forecast favourable brood–rearing areas and likely rely on their mate to sequester suitable territories for nesting and brood-rearing. Furthermore, complex predator communities and dynamic wetland conditions within the PPR likely influence decisions about habitat selection. Thus, continued consideration of how habitat selection decisions are affected by anthropogenic changes (i.e., wetland drainage, residual run–off of pesticides into wetland and the resulting changes in nutrient input into wetlands), and how duckling survival is impacted by these factors are important for future management planning.

LITERATURE CITED

Adler, M. 2010. Sexual conflict in waterfowl: why do females resist extrapair copulations? Behav. Ecol., 21: 182 – 192.

Aldridge, C.L. and Boyce, M.S. 2007. Linking occurrence and fitness to persistence: habitat–based approach for endangered Greater sage–grouse. Ecol. App., 17: 508 – 526.

Alisauskas, R.T. and Ankney, C.D. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. and Krapu, G.L. (Eds.), Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, U.S.A, pp. 30 – 61.

Amundson, C.L. and Arnold, T.W. 2011. The role of predator removal, density–dependence, and environmental factors on mallard duckling survival in North Dakota. J. Wildl. Manage., 75: 1330 – 1339.

Anderson, M.G. and Titman, R.D. 1992. Spacing patterns. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. and Krapu, G.L. (Eds.), Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, U.S.A, pp. 251 – 289.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criteria. J. Wildl. Mange., 74: 1175 – 1178.

Arnold, T.W., Craig–Moore, L.M., Armstrong, L.M., Howerter, D.W., Devries, J.H., Joynt, B.L., Emery, R.B. and Anderson, M.G. 2007. Waterfowl use of dense nesting cover in the Canadian Parklands. J. Wildl. Manage., 71: 2542 – 2549.

Ashcroft, R.E. 1976. A function of the pairbond in the common eider. Wildfowl, 24: 101 – 105.

Bacon, B.R. and Evrard, J.O. 1990. Horizontal mist net for capturing upland nesting ducks. North American Bird Bander, 15: 18 – 19.

Barker, W.T., Sedivec, K.K., Messer, T.A., Higgins, K.F. and Hertel, D.R. 1990. Effects of specialized grazing systems on waterfowl production in south–central North Dakota. Transactions of the North American Wildlife and Natural Resources Conference, 55: 462 – 474.

Bêty, J., Gauthier, G. and Giroux, J.F. 2003. Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. Am. Nat., 162: 110 – 121.

Bloom, P.M. 2010. Mallard duckling survival and habitat selection in the Canadian Prairie Pothole Region. MSc thesis, Biology, University of Saskatchewan, Saskatoon

Bloom, P.M., Clark, R.G., Howerter, D.W. and Armstrong, L.M. 2012*a*. Landscape–level correlates of mallard duckling survival: implications for conservation programs. J. Wildl. Manage., 76: 813 – 823.

Bloom, P.M., Clark, R.G., Howerter, D.W. and Armstrong, L.M. 2013*a*. Multi–scale habitat selection affects offspring survival in a precocial species. Oecologia, IN Press.

Bloom, P.M., Howerter, D.W., Devries, J.H., Armstrong, L.M. and Clark, R.G. 2012*b*. Radiomarking brood–rearing mallard females: implications for juvenile survival. Wildl. Soc. Bull., 36: 582 – 586.

Bloom, P.M., Howerter, D.W., Emery, R.B. and Armstrong, L.M. 2013*b*. Relationships between grazing and waterfowl production in the Canadian Prairies. J. Wildl. Manage., 77: 534 – 544.

Bluhm, C.K. 1992. Environmental and endocrine control of waterfowl populations. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. and Krapu, G.L. (Eds.), Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, U.S.A, pp. 323 – 364.

Bluhm, C.K. and Gowaty, P.A. 2004. Reproductive compensation for offspring viability deficits by female mallards, *Anas platyrhynchos*. Anim. Behav., 68: 985 – 992.

Brasher , M.G., Arnold, T.W., Devries, J.H. and Kaminski, R.M. 2006. Breeding–season survival of male and female mallards in Canada’s Prairie–Parklands. J. Wildl. Manag., 70: 805 – 811.

Brasher, M.G., Kaminski, R.M. and Burger Jr., L.W. 2002. Evaluation of indicated breeding pair criteria to estimate mallard breeding populations. J. Wildl. Manage., 66: 985 – 992.

Burley , N. 1988. The differential allocation hypothesis: an experimental test. Am. Nat., 132: 611 – 628.

Burnham, K.P. and Anderson, D.R. 1998. Model selection and inference: an information theoretic approach. Springer, New York, U.S.A.

Chalfoun, A.D. and Schmidt, A.S. 2012. Adaptive breeding-habitat selection: is it for the birds? Auk, 129: 589 – 899.

Chalfoun, A.D. and Martin, T.E. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. J. App. Ecol., 44: 983 – 992

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

Cody, M.L. 1985. Habitat selection in birds. Academic Press Inc. Orlando, Florida, U.S.A.

Cooke, F. and Davies, J.C. 1983. Assortative mating, mate choice and reproductive fitness in Snow Geese. In: Bateson, P (Eds.), Mate choice. Cambridge University Press, Cambridge, pp. 279 – 295.

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

Coulton, D.W., Clark, R.G. and Hebert, C.E. 2010. Determining natal origins of birds using stable isotopes (δ^{34}S, δD, δ^{15}N): model validation and spatial resolution for mid–continent mallards. Waterbirds, 33: 10 – 21.

Cowardin, L.M. and Johnson, D.H. 1979. Mathematics and mallard management. J. Wildl. Manage., 43: 18 – 35.

Cowardin, L.M., Gilmer, D.S. and Shaiffer, C.W. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildl. Monog., 92: 1 – 37.

Crary, A.K. and Rodewald, P.G. 2012. Plumage coloration and ornamentation as predictors of nest survival and number of young fledged in Yellow Warblers. J. Field Ornithol., 83: 130 –140.

Cunningham, E.J.A. 2003. Female mate preferences and subsequent resistance to copulation in the mallard. Behav. Ecol., 14: 326 – 333.

Cunningham, E.J.A. and Russell, A.F. 2000. Egg investment is influenced by male attractiveness in the mallard. Nature, 404: 74 – 77.

Danchin, E., Boulinier, T. and Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of Coloniality. Ecol., 79: 2415 – 2428.

Davis, B.J., Cox, R.R., Kaminski, R.M. and Leopold, B.D. 2007. Survival of wood duck ducklings and broods in Mississippi and Alabama. J. Wildl. Manage., 71: 507 – 517.

Davis, E.S. 2002. Female choice and the benefits of mate guarding by male mallards. Anim. Behav., 64: 619 – 628.

Devries, J.H., Citta, J.J., Lindberg, M.S., Howerter, D.W. and Anderson, M.G. 2003. Breeding–season survival of mallard females in the Prairie Pothole Region of Canada. J. Wildl. Manage., 67: 551 – 563.

Devries, J.H., Brook, R.W., Howerter, D.W. and Anderson, M.G. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk, 125: 618 – 628.

Dietz, N.J., Bergmann, P.J. and Flake, L.D. 1994. A walk–in trap for nesting ducks. Wildl. Soc. Bull., 22: 19 – 22.

Donham, R.S., Dane, C.W. and Farner, D.S. 1976. Plasma luteinizing–hormone and development of ovarian follicles after loss of clutch in female mallards (*Anas platyrhynchos*). Gen. Comp. Endocrinol., 29: 152 – 155.

Duebbert, H.F. and Lokemoen, J.T. 1976. Duck nesting in fields of undisturbed grass–legume cover. J. Wildl. Manag., 40: 39 – 49.

Dzus, E.H. and Clark, R.G. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. Auk, 115: 311 – 318.

Edler, A.U. and Friedl, T.W.P. 2010. Individual quality and carotenoids–based plumage ornaments in male red bishops (*Euplectes orix*): plumage is not all that counts. Biol. J. Linn. Soc., 99: 384 – 397.

Emery, R.B., Howerter, D.W., Armstrong, L.M., Anderson, M.G., Devries, J.H. and Joynt, B.L. 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian prairies. J. Wildl. Manage., 69: 1181 – 1193.

Fretwell, S.D. and Lucas, J.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica, 19: 16 – 36.

Gendron, M. and Clark, R.G. 2002. Survival of gadwall and mallard ducklings in southcentral Saskatchwean. J. Wildl. Manage., 66: 170 – 180.

Germain, R.R., Marra, P.P., Kyser, T.K. and Ratcliffe, L.M. 2010. Adult–like plumage coloration predicts winter territory quality and timing of arrival on the breeding grounds of yearling male American redstarts. Condor, 112: 676 – 682.

Goodburn, S.F. 1984. Mate guarding in the mallards *Anas platyrhynchos*. Ornis Scandinavica, 15: 261 – 265.

Gil, D., Graves, J., Hazon, N. and Wells, A. 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. Sci., 286: 126 – 148.

Giraudeau, M., Duval, C., Czirjak, G.A., Bretagnolle, V., Eraud, C., McGraw, K.J. and Heeb, P. 2011. Maternal investment of female mallards is influenced by male carotenoid–based coloration. Proc. R. Soc. Lond. B Biol. Sci., 278: 781 – 788.

Greenwood, R.J., Sargeant, A.B., Johnson, D.H., Cowardin, L.W. and Shaffer, T.L. 1995. Factors associated with duck nest success in the Prairie Pothole region of Canada. Wildl. Mono., 128: 3 – 57.

Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H. and Nummi, P. 2006. Experimental evidence for density–dependent survival in mallard (*Anas platyrhynchos*) ducklings. Oecologia, 149: 203 – 213.

Hagelin, J.C. and Ligon, J.D. 2001. Female quail prefer testosterone–mediated traits, rather than the ornate plumage of males. Anim. Behav., 61: 465 – 476.

Heitmeyer, M.E. 1995. Influences of age, body condition, and structural size on mate selection by dabbling ducks. Can. J. Zool., 73: 2251 – 2258.

Hoekman, S.T., Mills, L.S., Howerter, D.W., Devries, J.H. and Ball, I.J. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. J. Wildl. Manage., 66: 883 – 900.

Hoekman, S.T., Gabor, T.S., Murkin, H.R., Maher, R.H. and Armstrong, L.M. 2004. Factors affecting survival of Mallard ducklings in southern Ontario. Condor, 106: 485 – 495.

Holmberg, K., Edsman, L. and Klint, T. 1989. Female mate preferences and male attributes in mallard ducks *Anas platyrhynchos*. Anim. Behav., 38: 1 – 7.

Horn, D.J., Philips, M.L., Koford, R.R., Clark, W.R., Sovada, M.A. and Greenwood, R.J. 2005. Landscape composition, patch size, and distance to edges: interactions affecting duck reproductive success. Ecol. App., 15: 1367 – 1376.

Horváthová, T., Nakagawa, S. and Uller, T. 2012. Strategic female reproductive investment in response to male attractiveness in birds. Proc. R. Soc. Lond. B Biol. Sci., 279: 163 – 170.

Howerter, D.W. 2003. Factors affecting duck nesting in the Aspen Parklands: a spatial analysis. PhD dissertation, Biological Sciences, Montana State University, Bozeman, Montana

Howerter, D.W., Rotella, J.J., Anderson, M.G., Armstrong L.M. and Devries, J.H. 2008. Mallard nest–site selection in an altered environment: predictions and patterns. Israel J. Ecol. Evol., 54: 435 – 457.

Johnsgard, P.A. 1960. Pair–formation mechanisms in *Anas* (Anatidae) and related general. Ibis, 102: 616 – 618.

Johnson, D.H. 1980. The comparison of usage and availability measurement for evaluating resource preference. Ecology, 61: 65 – 71.

Johnson, D.H., Sargeant, A.B. and Greenwood, R.J. 1989. Importance of individual–species of predators on nesting success of ducks in the Canadian Prairie Pothole region. Can. J. Zool., 67: 291 – 197.

Kenward, R. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. Academic Press, London.

Klett, A.T., Dubbert, H.F., Faanes, C.A. and Higgins, K.F. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. United States Fisheries and Wildlife Resources Publication 158.

Klint, T. 1980. Influence of male nuptial plumage on mate selection in the female mallard (*Anas platyrhynchos*). Anim. Behav., 28: 1230 – 1238.

Krapu, G.L., Johnson, D.H. and Dane, C.W. 1979. Age determination of mallards. J. Wildl. Manage., 43: 384 – 393.

Krapu, G.L., Pietz, P.J., Brandt, D.A. and Cox, R.R. Jr. 2000. Factors limiting mallard brood survival in Prairie Pothole landscapes. J. Wildl. Manage., 64: 553 – 561.

Levin, S.A., Cohen, D. and Hasting, A. 1984. Dispersal strategies in patchy environments. Theo. Popul. Biol., 26: 165 – 191.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, U.S.A.

Lindsay, W.R., Webster, M.S. and Schwabi, H. 2011. Sexually selected male plumage color is testosterone dependent in a tropical passerine bird, the red–backed fairy–wren (*Malurus melanocephalus*). PLoS ONE, 6: e26067.

Loyau, A., Jalme, M.S., Mauget, R. and Sorci, G. 2007. Male sexual attractiveness affects the investment of maternal resources into the eggs in peafowl (*Pavo cristatus*). Behav. Ecol. Sociobiol., 61: 1043 – 1052.

Mack, G.G. and Clark, R.G. 2006. Home–range characteristics, age, body size, and breeding performance of female mallards (*Anas platyrhynchos*). Auk, 123: 467 – 474.

Mauser, D.M. and Jarvis, R.L. 1991. Attaching radio transmitters to 1–day–old mallard ducklings. J. Wildl. Manag., 55: 488 – 491.

McKinney, F. 1992. Courtship, pair formation, and signal systems. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. and Krapu, G.L. (Eds.), Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, Minnesota, U.S.A, pp. 214 – 250.

McKinnon D.T. and Duncan, D.C. 1999. Effectiveness of dense nesting cover for increasing duck production in Saskatchewan. J. Wildl. Manag., 63: 382 – 389.

Møller, A.P. 1994. Symmetrical male sexual ornaments, paternal care, and offspring quality. Behav. Ecol., 5: 188 – 194.

Nichols, J.D. 1996. Sources of variation in migratory movements of animal populations: statistical inference and selective review of empirical results for birds. In: Rhodes, O.E., Chesser, R.K. and Smith, M.H. (Eds.), Population Dynamics in Ecology Space and Time. The University of Chicago Press, Chicago. pp. 147 – 197.

[NAWMP] North American Waterfowl Management Plan. 1986. North American Waterfowl Management Plan: A strategy for cooperation. Unpublished report. Environment Canada, Ottawa.

Omland, K.E. 1996. Female mallard mating preferences for multiple male ornaments I: natural variation. Behav. Ecol. Sociobiol., 39: 353 – 360.

Orians, G.H. 1980. Habitat selection: general theory and applications to human behaviour. In: Lockard, J.S. (Ed.), The Evoluntion of Human Social Behaviour. Elsevier, New York, U.S.A. pp. 49 – 66.

Osorno, J.L., Morales, J., Moreno, J., Merino, S., Tomás, G. and Vásquez, R.A. 2006. Evidence for differential maternal allocation to eggs in relation to manipulated male attractiveness in the pied flycatcher (*Ficedula hypoleuca*). J. Ornithol., 147: 605 – 611.

Paasivaara, A. and Pöysä, H. 2008. Habitat–patch occupancy in the common goldeneye (*Bucephala clangula*) at different stages of the breeding cycle: implications to ecological processes patchy environments. Can. J. Zool., 86: 744 – 755.

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

Pärt, T. 2001. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenathe oenathe*. Anim. Behav., 62: 379 – 388.

Petrie, M. and Williams, A. 1993. Peahens lay more eggs for peacocks with larger trains. Proc. R. Soc. Lond. B Biol. Sci., 251: 127 – 131.

Phillips, M.L., Clark, W.R., Sovada, M.A., Horn, D.J., Koford, R.R. and Greenwood, R.J. 2003. Predator selection of prairie landscape features and its relation to duck nest success. J. Wildl. Manage., 67: 104 – 114.

Pöysä, H., Elmberg, J., Sjöberg, K. and Nummi, P. 2000. Nesting mallards (*Anas platyrhynchos*) forecast brood–stage food limitation when selecting habitat: experimental evidence. Oecologia, 122: 585 – 586.

[PHJV] Prairie Habitat Joint Venture. 2006. PHJV Strategic Plan 2006 – 2011. A partnership that provides solutions for wildlife, the landscape and people. Unpublished report. Prairie Habitat Joint Venture, Edmonton.

R Core Development Team, 2011. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Rotella, J.J. and Ratti, J.T. 1992. Mallard brood survival and wetland habitat conditions in Southwestern Manitoba. J. Wildl. Manag., 56: 499 – 507.

Rotella, J.J., Howerter, D.W., Sankowski, T.P. and Devries, J.H. 1993. Nesting effort by wild mallards with 3 types of radio transmitters. J. Wildl. Manage., 57: 690 – 695.

Rowe, M., Czirják, G. Á., McGraw, K.J. and Giraudeau, M. 2011. Sexual ornamentation reflects antibacterial activity of ejaculates in mallards. Biol. Lett., 7: 740 – 742.

SAS Institute Inc. 2011. SAS OnlineDoc® 9.3. Cary, NC: SAS Institute Inc.

Schlaepfer, M.A., Runge, M.C. and Sherman, P.W. 2002. Ecological and evolutionary traps. Trends Ecol. Evol., 17: 474 – 480.

Seymour, N.R. 1990. Forced copulation in sympatric American black ducks and mallards in Nova Scotia. Can. J. Zool., 68: 1691 – 1696.

Seymour, N.R. and Titman, R.D. 1978. Changes in activity patterns, agonistic behavior, and territoriality of black ducks (*Anas rubripes*) during the breeding season in Nova Scotia tidal marsh. Can. J. Zool., 56: 1179 – 1785.

Sharp, D.E. and Lokemoen, J.T. 1987. A decoy trap for breeding–season mallards in North Dakota. J. Wildl. Manage., 51: 711 – 715.

Sheldon, B.C. 2000. Differential allocation: tests, mechanisms and implications. Trends Ecol. Evol., 15: 397 – 402.

Sorenson, L.G. 1994. Forced extra-pair copulation and mate guarding in the white-checked pintail: timing and tradeoffs in an asynchronously breeding duck. Anim. Behav., 48: 519 – 533.

Stearns, S.C. 1992. The evolution of life histories. Oxford, UK: Oxford University Press.

Stephens, S.E., Rotella, J.J., Lindberg, M.S., Taper, M.L. and Ringelman, J.K. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. Ecol. App., 15: 2137 – 2149.

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

Stoehr, A.M. and Hill, G.E. 2001. The effects of elevated testosterone on plumage hue in male house finches. J. Avian Biol., 32: 153 – 158.

Titman, R.D. and Lowther, J.K. 1975. The breeding behavior of a crowded population of Mallards. Can. J. Zool., 53: 1270 – 1283.

Velando, A., Beamonte–Barrientos, R. and Torres, R. 2006. Pigment–based skin colour in the blue–footed booby: an honest signal of current condition used by females to adjust reproductive investment. Oecologia, 149: 535 – 542.

Walker, J. 2013. Understanding waterfowl: seasonal wetlands and breeding ducks. Ducks Unlimited. Retrieved April 2013, from http://www.ducks.org/conservation/waterfowl–biology/understanding–waterfowl–seasonal–wetlands–and–breeding–ducks.

Weidmann, U. 1990. Plumage quality and mate choice in mallards (*Anas platyrhynchos*). Anim. Behav., 115: 127 – 141.

Weller, M.W. 1957. An automatic nest–trap for waterfowl. J. Wildl. Manage., 21: 456 – 458.

Williams, M. 1983. Mate choice in the Mallard. In: Bateson, P (Ed.), Mate Choice. Cambridge University Press, Cambridge, pp. 297 – 309.

Wishart, R.A. 1983. Pairing chronology and mate selection in the American wigeon (*Anas americana*). Can. J. Zool., 61: 1733 – 1743.

Yasukawa, K. 1981. Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). Ecol., 62: 922 – 929.