THE ROLE OF PREDATOR REMOVAL AND DENSITY-DEPENDENCE ON MALLARD PRODUCTION IN NORTHEASTERN NORTH DAKOTA

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

COURTNEY LINDA AMUNDSON

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

ADVISOR: DR. TODD ARNOLD

MAY 2010
Acknowledgements

Funding for this research was provided by Delta Waterfowl Foundation with additional grants from the Bell Museum of Natural History, the Dennis Raveling Scholarship, and the University of Minnesota. Special thanks to F. Rohwer and L. Loos for their support and dedication to this project and my education in general. I would especially like to thank my technicians: C. Brady, J. Sheppard, C. Brown, K. Wlock, C. DeLong, J. Talotti, T. Kimmel, A. Johnson, B. Gann, A. Newman, A. Krmpotich, J. Rehar, A. Hack, N. Graff, and M. Buxton for their long hours in the field, you rocked! Permission and cooperation from hundreds of landowners, a dozen trappers, and the FWS Devil’s Lake WMD made this study possible. My committee, J. Giudice, R. Gutierrez, and D. Johnson provided project guidance and valuable comments on earlier drafts of this dissertation. Special thanks to D. Johnson for providing both the intellectual opportunity to work on analyses outside my research, and financial assistance the past 2-years. Thank you to A. Pagano, L. Beaudoin, C. Martin, J. McCarter, and especially M. Pieron for sharing data and results, and for their collaboration in and out of the field. S. Thompson, B. Meixell, E. Roche, and K. Clower helped edit chapters within this dissertation, provided logistical support, friendship, and sanity throughout the last 4-years.

I would like to thank my family and friends for encouraging and tolerating my college-induced poverty, stress, and absence …I’m finally done!

Lastly, without Todd’s calculated (and frankly, questionable) decision to take me on as a student in 2004, I wouldn’t have a PhD after my name, a fanatical love of American coots, or some of the best memories of my life. I am proud to be his first PhD graduate, and am a better person for the lessons we learned along the way. Thanks for being an amazing advisor, advocate, statistical wizard, and all around guy.
This dissertation is dedicated to

the ducks, my youth, and the friends made along the way

I’m not sure which one I’ll miss the most...
Abstract: Density-dependence is a central tenet of wildlife population dynamics and harvest management, yet the pathways and mechanisms by which density-dependence operates remain unclear. In 1994, Delta Waterfowl Foundation began trapping mesopredators in northeastern North Dakota to determine if it was a viable technique for increasing waterfowl production. Subsequent research on replicated experimental sites found that trapping predators increased nest success by about 2-fold, and nest success was the most important factor regulating population growth in previous studies of midcontinent mallards. Given the philopatric nature of most waterfowl species, higher nest success on trapped sites was predicted to lead to 36% greater annual population growth on trapped sites versus controls, which should have led to doubling of pair densities approximately every two years. This backdrop provided me with the unique opportunity to examine the role of density-dependence on waterfowl production at a local scale in North Dakota. My dissertation focuses on the role of density-dependence and predator removal on mallard duckling survival, duckling body condition, and overall mallard productivity in northeastern North Dakota from 2006-2007.

Contrary to predictions, predator removal had no beneficial effect on mallard duckling survival. Duckling density was weakly negatively associated with mallard duckling survival, but had no effect on duckling condition. Duckling survival, not nest success, was the most important factor influencing population growth and production and appeared to be functioning as the key limiting factor in our populations. Overall, predator removal did not lead to local population increases on trapped sites and added far fewer incremental ducks to the fall flight than originally predicted.

The perils of duck hunting are great - especially for the duck. -Walter Cronkite
# Table of Contents

Acknowledgements ........................................................................................................... i
Dedication ........................................................................................................................... ii
Abstract .............................................................................................................................. iii
Table of Contents .............................................................................................................. iv
List of Tables ..................................................................................................................... vi
List of Figures .................................................................................................................. vii

Prologue: History of Predator Management and Team DD ........................................ 1

## Chapter 1: Mallard Duckling Survival

1.1 Introduction ................................................................................................................. 7
1.2 Study Area .................................................................................................................. 10
1.3 Methods .................................................................................................................... 10
1.4 Results ...................................................................................................................... 18
1.5 Discussion ............................................................................................................... 19
1.6 Management Considerations ................................................................................... 24
1.7 Tables ...................................................................................................................... 26
1.8 Figures ..................................................................................................................... 30

## Chapter 2: Mallard Duckling Body Condition

2.1 Introduction ............................................................................................................... 36
2.2 Methods ................................................................................................................... 39
2.3 Results ..................................................................................................................... 44
2.4 Discussion ............................................................................................................... 46
2.5 Tables ...................................................................................................................... 52
2.6 Figures ..................................................................................................................... 54

## Chapter 3: Mallard Recruitment

3.1 Introduction ............................................................................................................... 59
3.2 Study Area ............................................................................................................... 62
3.3 Methods ................................................................................................................... 62
3.4 Results ..................................................................................................................... 69
3.5 Discussion ............................................................................................................... 71
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.6</td>
<td>Management Implications</td>
<td>77</td>
</tr>
<tr>
<td>3.7</td>
<td>Tables</td>
<td>79</td>
</tr>
<tr>
<td>3.8</td>
<td>Figures</td>
<td>82</td>
</tr>
</tbody>
</table>

**Literature Cited** | 87  

**Appendix A: Marker Effects on Mallard Ducklings**
A.1 Introduction | 101  
A.2 Methods | 102  
A.3 Results | 107  
A.4 Discussion | 109  
A.5 Tables | 112  

**Appendix B: Variable Definitions, Rationale, and Distributions** | 114
List of Tables

Chapter 1
Table 1: Weather Index Example .............................................................................. 26
Table 2: Model Selection Results ............................................................................. 27
Table 3: Analysis of Deviance Results .................................................................. 29

Chapter 2
Table 1: Covariate Rationale .................................................................................. 52
Table 2: Site-level Model Selection Results ............................................................ 53

Chapter 3
Table 1: Delta Waterfowl Foundation vital rate estimates ...................................... 79
Table 2: Vital rate estimates from our study ............................................................. 80

Appendix A
Table 1: Model selection results ........................................................................... 112
Table 2: Post-hoc model selection results .............................................................. 113
List of Figures

Chapter 1

Figure 1: Study Area ................................................................. 30
Figure 2: Mallard Density ............................................................ 31
Figure 3: Wetland Availability ..................................................... 32
Figure 4: Hatch Date by Year ...................................................... 33
Figure 5: Duckling Mass ............................................................... 34
Figure 6: Perennial Cover ......................................................... 35

Chapter 2

Figure 1: Wetland Availability ..................................................... 54
Figure 2: Perennial Cover ............................................................. 55
Figure 3: Date within Season by Duckling Age Class ..................... 56
Figure 4: Date within Season by Year .......................................... 57
Figure 5: Recent Weather Index by Year ..................................... 58

Chapter 3

Figure 1: Coefficients of determination against lambda .................. 82
Figure 2a: Coefficients of determination against fledging survival .... 83
Figure 2b: Coefficients of determination against breeding female survival ..... 84
Figure 3: Variance-stabilized sensitivities against fledging survival ....... 85
Figure 4: Coefficients of determination against hen success ............ 86
PROLOGUE: THE HISTORY OF DELTA WATERFOWL FOUNDATION AND “TEAM DD”

During the early part of the 20th century, unregulated harvest and dry conditions led to a marked decrease in waterfowl populations in North America (Baldassarre and Bolen 2006). In the 1930’s, James Ford Bell, the founder of General Mills and an avid waterfowl hunter, noticed these declines and became interested in waterfowl conservation. So, he turned his hunting camp on the Delta Marsh near Portage la Prairie, Manitoba into a hatchery, with the goal of releasing back into the wild two ducks to replace every duck that he and his guests had shot. But Bell wanted to do more, and under the advice of Aldo Leopold, he converted his field camp into a research station to study the basic ecology of North American waterfowl. It was then in 1938 that the Delta Waterfowl Research Station (hereafter Delta) was born, and under the direction of its first leader, graduate student Albert Hochbaum, Delta began a 70-year legacy of funding graduate research into basic and applied aspects of waterfowl ecology to better manage and more sustainably harvest North American waterfowl. From Delta’s first graduate student and publication, Albert Hochbaum’s The Canvasback on a Prairie Marsh, until now in 2010, Delta has given financial and logistical support to over 350 students that have published over 730 articles on waterfowl and wetland ecology (Delta Waterfowl Foundation 2010).

In the mid-1980s, drought conditions in the prairies, an increase in wetland drainage, and ongoing conversion of native prairie to agriculture led to sharp declines in waterfowl production throughout the Prairie Pothole Region (Greenwood et al. 1987). In addition to declines in available habitat, increases in mammalian predators such as
raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and red fox (*Vulpes vulpes*) further reduced waterfowl production on remaining landscapes (Sargeant et al. 1993, Beauchamp et al. 1996). In 1990, Delta shifted its focus from waterfowl and wetlands research into active management with the introduction of programs like Adopt-a-Pothole and Hen Houses, which were designed to protect small wetlands and provide safe nesting sites for mallards (*Anas platyrhynchos*).

In 1994, Delta started a predator management experiment near Devils Lake, North Dakota to determine whether removing mammalian predators on 16-mi² study sites could increase duck production. Delta paid professional trappers to remove mammalian predators using traps and snares during the waterfowl breeding season (March-July). This initial research showed a near doubling of waterfowl nest success on predator-removal sites (Garrettson and Rohwer 2001). Subsequent research evaluated waterfowl nesting success in relation to size of predator-removal areas (Hoff 1999, Chodachek and Chamberlain 2006, Pieron and Rohwer 2010), edge effects (Kuhn 2008, Pieron and Rohwer 2010), and on Canadian sites with minimal perennial cover (Lester 2004) and all of these studies consistently found higher nesting success on sites with predator-removal. Concurrent projects demonstrated that nest success benefits extended to shorebirds (Wiens 2007) and overwater nesting ducks and coots (Mense 1996), but not to songbirds (Dion et al. 1999). Duckling survival was addressed in 2 short-term studies involving northern shovelers (*Anas clypeata*; Zimmer 1996) and mallards (Pearse and Ratti 2004), but these studies suffered from low sample sizes and marker loss (Zimmer 1996). Additional research found a within season increase in small mammal populations did not
carry over to the following breeding season, possibly due to density-dependent winter mortality (Adkins 2003), which reduced concerns about an ecological release of alternative prey populations (Terborgh et al. 1999).

During July 2004, waterfowl biologists and Delta alumni gathered for a tête-à-tête at the annual Delta Waterfowl Student Research Symposium in Portage la Prairie. Over several beers and an ever increasing pitch, attendants including Dr. Todd Arnold (UMN), Dr. Tom Nudds (UGuelph), Dr. Frank Rohwer (LSU), Dr. John Eadie (UC Davis), and Dr. Mike Eichholz (SIU) discussed what an increase in production on North Dakota predator management sites might mean in terms of density-dependent regulation of waterfowl populations. Given the philopatric nature of most prairie-nesting ducks (Anderson et al. 1992), an increase in nest success and duckling survival on sites that had been continually trapped for up to 5-years should mean a substantial buildup of waterfowl populations on trapped sites relative to controls. Preliminary models using nest success estimates from prior Delta studies suggested that duck populations on predator removal sites should double every 3 years, and even faster if duckling and breeding female survival were also enhanced by predator control. If local duck populations had increased beyond what the landscape could support, predator management sites could provide a unique opportunity to observe the effects of density-dependence on waterfowl vital rates at a local scale, and that night on the Delta marsh, Delta’s density-dependence research project (affectionately dubbed “Team DD”) was born.

“There is no exception to the rule that every organic being naturally increases at so high a rate that, if not destroyed, the earth would soon be covered by the progeny of a single pair.”

-Charles Darwin 1859
Every population has the potential to exhibit density-dependent growth and
density-dependence is a central tenet in wildlife population ecology and harvest
in waterfowl has been demonstrated at a continental scale (Pospahala et al. 1974,
Kaminski and Gluesing 1987, Poysa and Pesonen 2003, Viljugrein et al. 2005); however,
few studies have examined the role of density-dependence on local reproduction
(Anderson et al. 1997), even though reproductive factors appear to be the driving force
behind population growth in waterfowl (Hoekman et al. 2002, Koons et al. 2006). In
years with a large continental population of mallards, the ratio of juveniles to adults in the
fall harvest survey tends to be low (Pospahala et al. 1974, Kaminski and Gluesing 1987).
This suggests that productivity may be lower in years when the breeding population is
high, indicating populations may have exceeded their continental carrying capacity.
However, the mechanisms by which density-dependence regulates waterfowl populations
remain unclear (Poysa and Poysa 2002). Lariviere and Messier (1998) looked at the
effects of nest density on predation of artificial waterfowl nests in southcentral
Saskatchewan and found that later in the breeding season, nests at intermediate (10
nests/ha) or high (25 nests/ha) nest densities had lower survival than nests in low (2.5
nests/ha) density areas. Additional studies in Europe found negative density-dependent
effects on mallard duckling survival (Gunnarsson et al. 2004, 2006), although densities
were manipulated by wing-clipping brooding females and were not representative of wild
populations.
In light of the general lack of knowledge about the mechanisms behind density-dependent population regulation, Delta and Team Density-dependence devised several graduate research projects assessing breeding season vital rates on trapped versus control sites in North Dakota. Matt Pieron (Louisiana State University) undertook the task of examining breeding pair abundance, territoriality among settling pairs (i.e., three-bird flights; Anderson and Titman 1992), nest success, and nesting female age. Laura Beaudoin (University of Guelph) radio-marked juvenile female mallards and examined juvenile survival, movements, and dispersal from natal breeding grounds the following spring. Finally, this dissertation summarizes my research into the role of density-dependence on duckling survival, duckling body condition, and pools Matt’s, Laura’s, and my research, as well as concurrent research on brood and pair detection (A. Pagano, UMN) and compensatory predation by raptors (C. Martin, UGuelph), to examine the contribution of predator management to waterfowl recruitment and population change in North Dakota, 2006-2007. Additionally, I estimate the cost efficiency of predator management during these years, and evaluate its potential as a management tool to increase continental waterfowl populations.

Research results from Team Density-dependence are starting to trickle in as Matt, Laura, and I near completion of our degrees. So far it appears that nest success was the only vital rate positively affected by predator management during our study (i.e., pair abundance, territoriality, juvenile survival, and dispersal were unaffected by predator removal). In response to our research, Delta Waterfowl has abandoned the sites it had trapped since the mid-nineties in favor of areas with the potential to produce larger
numbers of waterfowl (i.e., high breeding pair numbers and wetland density), but with much lower estimated productivity (e.g., less perennial cover). As more research is completed on these new sites, we may learn more about the ability of predator management to increase continental waterfowl populations.

The chapters herein are formatted for the journals to which they have or will be submitted. Chapter 1, The Effects of Predator Removal, Density-dependence, and Environmental Factors on Mallard Duckling Survival in North Dakota, was recently submitted to the Journal of Wildlife Management. Chapter 2, Factors Affecting Duckling Condition, is intended for Waterbirds. Chapter 3, The Effects of Predator Removal on Mallard Recruitment and Vital Rate Sensitivity in Northeastern North Dakota, is intended for the Journal of Wildlife Management. Appendix 1, Marker Effects on Mallard Ducklings, has been accepted for publication in the Journal of Field Ornithology. Because all chapters in this dissertation will be published with coauthors, I have used plural pronouns throughout; however, I take full responsibility for its content.
CHAPTER 1: THE EFFECTS OF PREDATOR REMOVAL, DENSITY-DEPENDENCE, AND ENVIRONMENTAL FACTORS ON MALLARD DUCKLING SURVIVAL IN NORTH DAKOTA

The conversion of native prairie to agriculture has impacted breeding waterfowl in at least 2 fundamental ways: first by limiting available habitat for nesting and brood-rearing waterfowl (Herkert et al. 2003), and second by leading to an increase in generalist predators that are likely to prey on waterfowl nests and ducklings (Johnson et al. 1989, Stephens et al. 2005). These changes have shifted the focus of waterfowl management from maintaining large tracts of grassland to maximizing productivity on fragmented and degraded habitats (Sovada et al. 2001, Phillips et al. 2003). In 1994 Delta Waterfowl Foundation began trapping mammalian meso-predators on experimental study sites in the drift prairie of northeastern North Dakota in an attempt to increase waterfowl production (Garrettson and Rohwer 2001). Subsequent research on predator-reduced areas found a dramatic increase in nest success following predator removal (Garrettson and Rohwer 2001, Pieron and Rohwer 2010). Hoekman et al. (2002) found that nest success was the most important vital rate affecting recruitment of mid-continent mallards (Anas platyrhynchos), and nest success is also the vital rate most often targeted by waterfowl managers to increase waterfowl recruitment (Cowardin et al. 1985, Emery et al. 2005). Additionally, Pearse and Ratti (2004) found that duckling survival to fledging age (30 d) increased from 0.36 on control sites to 0.52 on predator removal sites in the Saskatchewan prairies, suggesting that predator management provided an additional boost to per capita reproductive rates.
Given the strong homing nature of female waterfowl (Anderson et al. 1992), increases in nest success and duckling survival should lead to increased local duck populations over time, providing an additional boost to productivity in subsequent years if nest success and duckling survival remain high. However, population growth may force breeding ducks into higher densities, and crowding effects and habitat fragmentation could theoretically increase predator abundance and foraging efficiency (Clark and Nudds 1991, Horn et al. 2005). Together, these forces may lead to a density-dependent reduction in reproductive success in areas where duck densities are high (Kaminski and Gluesing 1987, Nichols et al. 1995), thereby eliminating or reducing any gains achieved through predator control.

Several studies have examined the role of density on nest predation in waterfowl (Hill 1984, Kantrud 1993, Ackerman et al. 2004), but few have assessed the role of density on duckling survival (Kaminski and Gluesing 1987, Gunnarsson et al. 2004, Gunnarsson et al. 2006). Duckling density may increase duckling survival (i.e., positive density-dependence) by satiating local predators and diluting predation risk, enhancing predator detection by broods, or by increasing detection of food locations by broods (Afton and Paulus 1992, Leonard et al. 1996). Such potential benefits are widely implicated in studies of post-hatch brood amalgamation (Kehoe 1989), wherein the young of several females combine to form a single large crèche. Canvasback (Aythya valisineria) ducklings had higher survival in an area of experimentally increased brood densities (Leonard et al.1996), as did mallard ducklings (Hill et al. 1987). Conversely, Makepeace and Patterson (1980) found that brood-rearing common shelduck (Tadorna
*tadorna*) females often exhibited aggression toward other females and that increased interactions between broods at higher densities resulted in greater mortality when ducklings became separated from the female or mixed with other broods. Additionally, Gunnarsson et al. (2006) experimentally increased mallard brood density on Swedish lakes by releasing broods tended by wing-clipped female mallards and found that lakes with higher duckling densities had lower duckling survival.

Duckling age, environmental factors, and female characteristics may also impact duckling survival. Several studies have demonstrated that younger ducklings were less likely to survive than older ducklings (Guyn and Clark 1999, Pietz et al. 2003, Chouinard and Arnold 2007), presumably due to reduced ability to escape from predators, limited foraging skills, or an inability to thermoregulate (Caldwell 1973, Drever et al. 2004). Harsh or inclement weather early in life may therefore reduce survival through acute exposure, or by increasing energetic demands of ducklings that in turn may worsen body condition and lead to increased mortality from proximate causes such as predation or starvation. Additionally, studies have documented the importance of wetland inundation, particularly of seasonal wetlands, on duckling survival (Talent et al. 1982; Krapu et al. 2006; M. Anderson, Institute for Wetlands and Waterfowl Research [hereafter IWWR], unpublished data). Hatch date and female characteristics (age, body condition) were also found to influence duckling survival (Dzus and Clark 1998, Guyn and Clark 1999, Pietz et al. 2003), but predation was the most important proximate cause of mortality in all studies that determined cause of death using radio-marked ducklings (Mauser et al. 1994, Korschgen et al. 1996, Chouinard and Arnold 2007).
The main objective of our study was to measure duckling survival to 30 days of age in relation to experimental predator removal on township-sized (92.3 km²) study sites. An ancillary objective was to determine how survival varied in relation to spatiotemporal variation in duckling density, because we believed a priori that predator removal would lead to greatly enhanced brood densities. Finally, we were interested in determining how additional environmental and brood-specific factors such as duckling age, initial brood size, duckling mass at hatch, female age and body condition, breeding pair density, hatch date, weather, and local habitat conditions affected survival of mallard ducklings.

**STUDY AREA**

We conducted research on 8 township-sized (93.2 km²) study sites located in the Devil’s Lake Wetland Management District, North Dakota (Fig. 1). All study sites were characterized by moderate to high densities of seasonal and semipermanent wetlands that would have harbored high densities of breeding mallards and other dabbling ducks in all but extreme drought years (Artmann et al. 2001, Garrettson and Rohwer 2001). The landscape was highly fragmented, consisting primarily of small grain and row crop agriculture, with lesser amounts of pasture and hayland. Very little native grassland remained, although there were relatively large amounts of idle perennial cover in the form of Conservation Reserve Program grasslands. From 15 March to 15 July of each year, mammalian predators were experimentally reduced via lethal trapping on 4 sites (all but 1 were randomly selected) and the remaining 4 sites were used as controls (Pieron
and Rohwer 2010). In 2006, we removed one trapped site from our analyses due to small samples sizes (see Results section).

METHODS

Field Work

Beginning in late April of each year, search crews looked for mallard nests on each study area using methodology similar to Klett et al. (1986). From these nests, we attempted to capture late-incubating females according to typical hatching chronology using mist nets, drop-door traps, and walk-in traps (Weller 1957, Bacon and Evrard 1990, Dietz et al. 1994). We took morphometric measurements (head length, culmen length, tarsus length, ± 0.1 mm using digital calipers; and flattened wing chord, ± 1 mm using a metal ruler), pulled a number 2 greater secondary covert feather to assess female age (Krapu et al. 1979, Pieron 2010), and fitted females with a 9-g prong-and-suture radio-transmitter equipped with a mortality sensor (Advanced Telemetry Systems, Isanti, MN; Pietz et al. 1995). We dosed females intravenously with 0.1 mg/kg Propofol (Schering-Plough Corporation, Kenilworth, NJ) immediately after processing to reduce nest abandonment (Machin and Caulkett 1998). Anesthetized birds were placed back on their nests and researchers quickly left the area to allow females to experience a soft recovery (Hepp and Manlove 2001). We visited nests on the estimated day of hatch to capture, weigh (± 1g), measure (head and tarsus length; ± 0.1 mm), and band ducklings with plasticine-filled U.S. Fish and Wildlife Service metal leg bands (Blums et al. 1999). Estimating hatch
date was imprecise and ducklings often hatched somewhat asynchronously; consequently several broods were missed or partially banded. In 2006 we also placed 1.8-g transmitters on 2 ducklings per brood (Appendix A, Mauser and Jarvis 1991). All capture and handling methods were approved by University of Minnesota Institutional Animal Care Permit # 0512A78586.

We located broods of radiomarked females via triangulation using a truck-mounted, null-peak antennae system (Kenward 1987). We monitored females daily until 10 days post-hatch and every second day from 11-30 days post-hatch or until female mortality, total brood mortality, or radio failure occurred, whereas broods were located using homing telemetry every third day for the first 12 days post-hatch and then every 7-10 days until 30 days post-hatch. Upon locating broods, we used spotting scopes or binoculars to try to count the number of surviving ducklings. At approximately 30 days of age or whenever total brood failure was suspected, more invasive techniques were used (i.e., beating wetland vegetation with sticks to flush broods into open water) in attempt to get a final brood count (Paquette et al. 1997, Pearse and Ratti 2004). We made an additional attempt to see the entire brood when we suspected brood counts were incomplete (e.g., ducklings in thick vegetative cover, or brood seen only briefly).

We estimated duckling abundance for each site and year using roadside surveys of wetlands located <150 m from roads (Pagano and Arnold 2009). We conducted brood surveys in early June and early July to account for early hatching versus late-hatching broods. Each survey consisted of 3 replicate counts conducted on a single day, which we treated as 3 sampling occasions in a mark-recapture survey (Pagano and Arnold 2009).
We used the Huggins’ closed-capture model (Huggins 1989) as implemented in Program MARK (ver. 6.0; White and Burnham 1999) including covariates in the best-approximating model from Pagano and Arnold (2009) to estimate detection probabilities, and we used the Horvitz-Thompson estimator (Horvitz and Thompson 1952) to derive estimates of duckling abundance (Pagano and Arnold 2009). Ducklings <30 days of age during the second survey were added to total ducklings from the first survey to derive estimates of total duckling abundance for each site-year.

We digitized all inundated wetlands based on annual aerial photographs, and then classified each basin by permanence class (Cowardin et al. 1979) using National Wetland Inventory data verified by ground-truthing. We derived total inundated wetland area (km$^2$) per site by summing all digitized wetland areas. Estimated total duckling density was the ratio of estimated duckling abundance ($Anas$ spp.) to total surveyed wetland area.

We also estimated mallard duckling density because conspecifics are likely the most direct competitors for resources and may have a more pronounced density-dependent effect than all dabbling duck species combined (Danielson and Gaines 1987, Carrete et al. 2006).

We derived a brood-specific weather index for the first 10-days of life using standardized measures of wind chill and precipitation. We obtained weather data from stations near each study site (range: 0-13 km from study site boundary) from the North Dakota Agricultural Weather Network (NDAWN 2010). We calculated estimates of daily wind chill using minimum daily temperature (Fahrenheit; $T$) and average daily wind speed (mph; $V$; NOAA 2010; Eq. 1).
Wind Chill = 13.112 + 0.6215 \times T − 11.37 \times (V^{0.16}) + 0.3965 \times T \times (V^{0.16}) \quad \text{Eq. 1}

We then subtracted the annual mean and divided by the annual standard deviation to obtain a standardized wind chill for each day of the brood-rearing season. Daily total rainfall (cm) was multiplied by -1 so that higher scores represented better weather for duckling survival (Korschgen et al. 1996); we then subtracted mean daily rainfall and divided by the standard deviation to obtain standardized values. We added together standardized wind chill (SWC) and standardized daily rainfall (SDR) to obtain a daily weather score. For each brood, we weighted daily weather scores for the first 10 days post-hatch by assigning higher weights earlier in life and reducing weight as a linear function of age (w; range: 0.19 on day 1, 0.17 on day 2, ... to 0.01 on day 10) since ducklings are better able to thermoregulate with increasing age (Caldwell 1973). Finally, we summed daily indices to produce the final weather index score for each brood (Eq. 2; see Table 1 for worked example).

\[ Weather_{Brood} = \sum_{age \ 1-10} [SWC + SDR]_{age} \times (0.21 - 0.02 \times age) \quad \text{Eq. 2} \]

We considered 3 potential wetland variables: total area (km$^2$) per study site of seasonal wetlands (WET3), total area of semipermanent wetlands (WET4), and total combined area of seasonal plus semipermanent wetlands (WET[3+4]). Wetland permanency classes were derived from Cowardin et al.'s (1979) classification scheme, and we considered the 2 classes that have been most frequently identified as providing important habitat for mallard broods (Talent et al. 1982, Raven et al. 2007). Because these 3 variables were highly correlated ($r > 0.62$), only 1 wetland variable was allowed in any single model. Aerial photos were taken during spring, so wetland variables are an
index of wetland availability for each site-year and do not measure within-year trends in water levels.

We estimated female body condition (COND) using residuals from an ordinary least squares regression of body mass versus the first principal component score (PROC PRINCOMP; SAS Institute 2009) obtained from the correlation matrix of female morphometric measurements (Schulte-Hostedde et al. 2005). We visited nests after hatch to determine initial brood size (BS) based on previous clutch size minus any unhatched eggs. Other potential covariates included mean duckling mass at hatch (MASS), Julian hatch date (DATE), year (YEAR), study site (SITE), duckling age (AGE = days post-hatch), estimated number of mallard breeding pairs on each site (PAIR), female age (HENAGE) estimated as second-year (SY) or after-second-year (ASY) based on feather criteria (Pieron 2010), and proportion of perennial cover on each site (COVER). Full descriptions of each covariate and rationale for inclusion are provided in Appendix B.

**Statistical Analyses**

We estimated duckling survival to 30 days post-hatch using the nest survival module in Program MARK (i.e., ragged telemetry; Rotella et al. 2004). Model selection was based on Akaike’s Information Criterion adjusted for small sample size and overdispersion (QAIC<sub>c</sub>; Burnham and Anderson 2002). We sequentially tested biologically feasible combinations of parameters in 3 stages: 1) duckling age, 2) year and site-level effects, and 3) brood-level covariates. The best supported model from each stage was used as a template for examining additional parameters in the subsequent stage (Chouinard and Arnold 2007, Fondell et al. 2008). Models with 1 additional parameter
were considered competitive only if they resulted in QAIC$_c$ scores that were lower than the simpler model (Burnham and Anderson 2002:131). We used an analysis of deviance approach (Ballerini et al. 2009) to estimate the relative contribution of each covariate to total deviance explained by the most saturated model. The use of ragged telemetry for estimating duckling survival does not account for potential dependence among broodmates; therefore we estimated overdispersion (ĉ) using the methods of Bishop et al. (2008). We conducted 5,000 simulations in Program MARK using a highly-parameterized ($K = 30$) model that incorporated effects of duckling age, year × study site, hatch date, female age, duckling mass, and marker effects (plasticine bands and transmitters). Both marker types had deleterious effects on survival (Appendix A). We therefore statistically removed effects due to marking ducklings by including covariates for both marker types in all models, using the best supported parameterization for marker effects, and setting covariate values for both effects to 0.

We reported cumulative survival and parameter values using 85% confidence limits because they are more compatible with AIC-based model selection than traditional 95% limits (Arnold 2010). Asymmetric confidence limits around cumulative survival estimates were derived in Program MARK from 5,000 bootstrap simulations that were based on individual ducklings and models were corrected for overdispersion.

In stage 1, we estimated daily survival rates ($S_i$) for a fully age-dependent model ($S(\text{AGE}_{\text{full}})$) wherein ducklings were assumed to have a separate survival probability for each day of age from 1-30. We then considered biologically feasible simplifications (e.g., pooling survival estimates for very young or very old ducklings) in an effort to
reduce model parameters. Previous investigators split the brood-rearing period into 2 intervals based on expected differences in survival probabilities (Orthmeyer and Ball 1990, Krapu et al. 2000) or treated survival as a continuous logistic function of age (Mehl and Alisauskas 2007). Therefore, we considered 4 additional age-structured models: 1) constant survival independent of age \{S(.)\}; 2) age grouped into 1-10 days versus 11-30 days \{S(AGE_{1-10}, 11-30)\}, which was consistent with our weather index; 3) age grouped into 1-15 days versus 16-30 days \{S(AGE_{1-15}, 16-30)\}, which reflected a commonly used split in previous research; and 4) a model that treated survival as a logistic function of age \{S(AGE_{\text{logistic}})\} (Table 2).

In stage 2, we added year and site-level covariates to our best-supported age-structure model (Table 2). In the model incorporating all 15 site-years \{S(Age \times YEAR \times SITE)\}, small sample sizes in 2 site-years resulted in inestimable parameters. Therefore, for those 2 sites we constrained the regression coefficients to be equal in 2006 and 2007. To investigate potential causes of spatiotemporal variation, we replaced site-year effects with covariates measured at the site-level (e.g., TRAP, COVER) or site-year (e.g., PAIRS, BROODS, WET3). We had only 8 sites and 15 site-years; therefore, we restricted our models to include a maximum of 1 site-level or 2 site-year covariates. Because predator control was an experimentally applied treatment and determining if it affected duckling survival was our primary research objective, we utilized a likelihood ratio test (Lebreton et al. 1992) to evaluate the null hypothesis that trapping had no effect on survival.
In the third and final stage, we added brood-level covariates (e.g., DATE, COND, MASS) and a priori 2-way interactions (e.g., DATE×YR) to the best-supported model from stage 2 (Table 2). Using a forward-selection approach, we sequentially considered each brood-level covariate and if the covariate did not lead to a reduction in QAIC\(_c\) over the simpler model from the second stage, it was not considered further. We used the same forward selection approach to consider models that included \(\geq2\) brood-level covariates and interactions provided they led to further reductions in QAIC\(_c\).

**RESULTS**

Our analysis included 68 radio-marked female mallards with 510 ducklings in 2006 and 100 females with 765 ducklings in 2007 (\(\bar{x}_{\text{Brood Size}} = 8.0\); range: 2 – 12), for an effective sample size of 9,287 “duckling exposure days”. We excluded 1 site-year (Harlow-2006) because we were unable to obtain model-based survival estimates due to small samples (3 broods experienced total brood loss and 1 brood was censored). Sixty-five percent of the 168 radio-marked females experienced total brood loss, and apparent survival of brood females was 95.8% (7 females died). Our estimated value of \(\hat{e}\) was 3.60.

Our sequential modeling approach led us to examine 29 total models: 5 models of age structure, 16 models that included year- and site-level effects, and 8 models that included brood-level covariates or interactions (Table 2). Our best-approximating model had an Akaike weight of 0.63 and the top 3 models (which were hierarchically simpler versions of the top-ranked model) had cumulative Akaike weights of 0.95. Daily survival probabilities increased as a logistic function of duckling age, and cumulative 30-day survival was higher in 2007 (\(\hat{S}_{30\text{-day}}^{2007} = 0.264\); 85% CI: 0.193 – 0.355) than 2006.
Mallard brood density was not a covariate in our stage-3 model set, but we found a weak negative association between MALLD and log-odds of survival ($\beta_{\text{MALLD}} = -0.009; \text{85\% CI: } -0.015 \text{ to } -0.004; \text{Fig. 2}$) in our stage-2 model \{$S(\text{AGE} \times \text{YEAR} + \text{MALLD})\}$, where it explained 10\% of spatiotemporal variation in duckling survival (Table 3). However, percent variation explained by MALLD was <1\% when WET(3+4) and COVER were in the model. Duckling survival probabilities were positively correlated with total km$^2$ of inundated seasonal and semipermanent wetlands (WET[3+4]) in each site-year ($\beta_{\text{WET[3+4]}} = 0.054; \text{85\% CI: } 0.021 \text{ to } 0.087; \text{Fig. 3}$). Conversely, survival probabilities were negatively associated with proportion perennial cover ($\beta_{\text{COVER}} = -1.345; \text{85\% CI: } -1.939 \text{ to } -0.750$). We also found a negative association between log-odds of survival and hatch date in 2006 ($\beta_{\text{DATE}*2006} = -0.420; \text{85\% CI: } -0.606 \text{ to } -0.233$) but not in 2007 ($\beta_{\text{DATE}*2007} = -0.022; \text{85\% CI: } -0.152 \text{ to } 0.108; \text{Fig. 4}$). Additionally, the log-odds of survival increased with mean duckling mass at hatch ($\hat{\beta} = 0.134, \text{85\% CI: } 0.033 \text{ to } 0.234; \text{Fig. 5}$). Our stage-3 models did not contain a covariate for predator removal, but stage-2 model \{$S(\text{AGE} + \text{YEAR} + \text{TRAP} + \text{AGE} \times \text{YEAR})\}$ suggested that predator removal did not lead to increased log-odds of daily survival ($\hat{\beta}_{\text{Trapped}} = -0.148; \text{85\% CI: } -0.346 \text{ to } 0.050$). Likewise, a likelihood-ratio test of the hypothesis that predator removal increased duckling survival received no support ($D = 0.68, 1 \text{ df}, P = 0.71$).

**DISCUSSION**

Surprisingly, predator removal had no effect on duckling survival. This is contradictory to several published studies on the importance of predation on duckling survival (Krapu
et al. 2004, Pietz et al. 2003), including the only other experimental study of predator
removal on duckling survival (Pearse and Ratti 2004). Traditional trapping methods
focus primarily on nest predators including striped skunks (*Mephitis mephitis*), raccoons
(*Procyon lotor*), and red foxes (*Vulpes vulpes*), but of these species only foxes are
thought to be an important brood predator (Sargeant et al. 1993). During our study, red
fox densities were extremely low and constituted only 2.1% of the total animals removed
by trappers (Pieron and Rohwer 2010). Low red fox populations have been attributed to
a relatively recent outbreak of sarcoptic mange and an influx of coyotes (*Canis latrans*)
to the area (Pieron and Rohwer 2010). Pietz et al. (2003) found that skunks, raccoons,
and red fox accounted for only 7.5% of known predator-related deaths of radio-marked
ducklings, whereas the vast majority of duckling mortality was from raptors (25.0%) or
American mink (*Neovison vison*; 67.5%). Several species of raptors including red-tailed
hawk (*Buteo jamaicensis*), northern harrier (*Circus cyaneus*), great-horned owl (*Bubo
virginianus*), and Swainson’s hawk (*Buteo swainsoni*) were present on our study areas
(Martin 2009).

Mink densities are often higher in areas of permanent or semipermanent water
(Pietz et al. 2003, Krapu et al. 2004). During the years of our study the drift prairie of
North Dakota had experienced above-average water levels for more than a decade, which
may have led to high densities of mink (Krapu et al. 2004). Additionally, mink can be
difficult to trap and often require specific trapping effort to reduce densities (North
Dakota Furtakers Association 1997, Bonesi and MacDonald 2004). In our study, mink
comprised 5.2% of total predators removed from treatment sites (Pieron and Rohwer
2010) and were frequently observed on both trapped and control sites, which may help explain the lack of a predator removal effect on duckling survival on our sites. Pearse and Ratti (2004) reported few observations and only incidental trapping of 4 mink (0.8% of total predators trapped) on their study sites, which could suggest lower mink densities in their site-years than we observed.

Part of the rationale for our research was the prediction that predator removal would lead to higher recruitment, and female philopatry would lead to higher pair and brood densities on trapped areas in subsequent years. Inconsistent with our predictions, duckling survival was not affected by breeding-pair density. Mallard brood density had a weak negative effect on duckling survival; however, habitat variables (i.e., WET [3+4] and COVER) were better predictors of daily survival probabilities. However, concurrent research on our study areas found that numbers of breeding pairs did not build to higher levels on trapped sites, suggesting density-dependence at some earlier stage of the life-cycle (e.g., via duckling survival or spring settling choices of one year-old females; Pieron 2010; L. Beaudoin, University of Guelph, unpublished data). All of our study sites had extremely high densities of breeding pairs (range: 11 to 23 mallard pairs/ wetland km$^2$) and broods (range: 6 to 75 mallard ducklings/ wetland km$^2$), and all but one study site (Alsen: 12%) had 20 - 40% perennial cover and similar wetland area (WET[3+4]). It is possible our sample did not include enough range in pair and duckling densities, especially at higher density levels, to detect a more pronounced effect of density on duckling survival.
Although density-dependence in duckling survival has been demonstrated when broods were manipulated to artificially high densities in oligotrophic systems (Gunnarsson et al. 2006), no studies have demonstrated it in natural settings. Density-dependence in duckling survival could be intermittent and detectable only in years where resources become extremely limiting (e.g., during drought; Anderson et al. 1997).

Although 2006 was considered a very dry breeding season (National Drought Mitigation Center 2009), conditions may not have been bad enough to induce strong effects of resource limitation on our study sites.

Consistent with previous studies, the area of seasonal and semipermanent wetlands in each study area was positively correlated with duckling survival (Krapu et al. 2006; M. Anderson, IWWR, unpublished data). However, contrary to our predictions, upland perennial cover had the opposite effect, with greater amounts of cover being associated with lower duckling survival. Several studies found that increasing the amount of grass in the landscape improves nest success (Reynolds et al. 1994, Stephens et al. 2005, Arnold et al. 2007), suggesting that large tracts of cover may provide sanctuary from predators or reduce predator foraging efficiency. We are unable to explain why an increase in grassland cover would negatively impact duckling survival, but researchers observed a similar association between duckling survival and certain types of upland perennial cover (e.g., idle hayland) in the Canadian Parklands (D. Howerter, Ducks Unlimited Canada, pers. comm.) and forest cover in the Great Lakes (Simpson et al. 2007). Additionally, increased perennial cover could be associated with higher tree and shrub densities, which provide nesting sites and perches for avian
predators (Martin 2009). Concurrent research on our study sites found raptors, especially ground-nesting raptors (e.g., Northern Harrier, *Circus Cyaneus*) were abundant in our site years and populations were higher on trapped sites than controls (Martin 2009).

Heavier ducklings, which presumably hatched from larger eggs, had higher survival probabilities in our study, which is consistent with previous studies on factors affecting duckling survival (Anderson and Alisauskas 2001, Pelayo and Clark 2003, Traylor and Alisauskas 2006). Larger ducklings may have higher survival due to an increase in energy reserves for thermoregulation and increased homeothermic efficiency (Rhymer 1988, Anderson and Alisauskas 2001). Additionally, larger body mass may provide an advantage for procuring food during the first days of life, when survival is lowest (Rhymer 1988). Larger ducklings also may have better locomotion, which could help ducklings evade predators, reduce energy expenditure during overland travel, and more efficiently dive and forage for food (Anderson and Alisauskas 2001).

Ducklings from late-hatching broods had lower survival probabilities than ducklings from early hatching broods, but this effect was only evident in 2006. Although 2006 began as a wet spring, there was little rainfall during the brood-rearing period and our study sites experienced a pronounced drop in water levels, which may explain the effect of hatch date in 2006. A similar study in southwestern Manitoba found mallard duckling survival was highest in wet years when wetland densities were high (Rotella and Ratti 1992). Increased survival with wetland availability may be related to reduced food availability late in the breeding season (Cox et al. 1998). Additionally, predation rates may increase as the season progresses due to fluctuations in alternate prey availability.
and increased prey consumption from nursing females and young-of-the-year (Grand and Flint 1996).

Our 30-day duckling survival estimates (range among site-years: 1% – 34%) are among the lowest ever reported for the Prairie Pothole Region (Lokemoen et al. 1990, Pietz et al. 2003, Krapu et al. 2004, Stafford and Pearse 2007). Stafford and Pearse (2007) reported 42 – 77% survival of radio-marked mallard ducklings hatched from overwater nesting cylinders in eastern South Dakota. In North Dakota, Krapu et al. (2004) estimated 31% cumulative survival of mallard ducklings in the early 1990’s and Pietz et al. (2003) estimated 32 – 57% 30-day survival of gadwall (Anas strepera) ducklings, depending on seasonal wetland availability. Our results are also surprising given high nest success estimates from these same sites (\( \bar{x}_{2006-2007} = 42.3\% \); Pieron and Rohwer 2010), which previous studies have suggested may be positively correlated with duckling survival (Pearse and Lester 2007; M. Anderson, IWWR, unpublished data). In our study, duckling markers (transmitters and plasticine bands) lowered duckling survival in the first few days after hatch (Appendix A), but we statistically adjusted our survival estimates to account for marker effects. Although we cannot explain why our estimates of duckling survival are lower than others have reported, we suspect that high densities of mink and raptors may have contributed to low survival probabilities.

**Management Implications**

Predator management has historically been used to increase avian productivity, particularly for ground-nesting species (Côté and Sutherland 1997, Shwiff et al. 2005). Although many studies have reported positive impacts of predator removal on nest
success, little evidence exists for comparable benefits to other vital rates (e.g., duckling survival; but see Pearse and Ratti 2004). Mallard pair densities, perennial-cover abundance, and nest survival were extremely high in our study, and under these conditions the benefits of predator removal may be greatly diminished due to compensatory losses during other stages of the annual cycle (e.g., brood rearing). Under such conditions managers may want to focus predator removal efforts on landscapes where nest success is low but potential productivity is high (e.g., low perennial cover but high wetland densities). Although nest success is widely accepted as the most important factor affecting recruitment for prairie-nesting mallards (Hoekman et al. 2002), other vital rates (e.g., female or duckling survival) may be more important to population change in areas where nest success is higher or other vital rates are lower (Hoekman et al. 200*, Collucy et al. 200*). Also, we emphasize the importance of assessing other factors affecting duckling survival, including brood-specific predators not traditionally removed through predator management. Given that abundance of seasonal and semipermanent wetlands positively affected duckling survival, we recommend that waterfowl managers continue to focus their attention on wetland conservation in conjunction with other management actions to maximize waterfowl recruitment.
Table 1. A worked example of calculating a weather index score for a brood hatched 22 May 2007 (Julian date 142). Weather was factored in for the first 10-days post hatch (Duckling Age), where minimum daily temperature (degrees Fahrenheit; T), average wind speed (mph; V), and total daily rainfall (in cm; TDR) were reported from the nearest weather station. We first estimated Wind Chill (Eq. 1), and then multiplied wind chill and negative TDR, standardized across all dates used in our study-year (SWS). That score was then weighted (w) by a linearly declining function of age, where weather effects were strongest for newly hatched ducklings. The overall weather score is then the weighted sum of daily standardized weather scores ($\sum_{Duckling\ Age} SWS \times w$).
Table 2. Model selection results from a sequential analysis of factors affecting mallard duckling survival in northeastern North Dakota, 2006-2007. We selected models sequentially in a 3-stage design with the best supported model serving as a template for the next stage. We ranked models based on Akaike’s Information Criterion corrected for overdispersion (\( \hat{c} = 3.60 \)) and small sample size (QAIC\(_c\)). Deviations from the best supported model in each stage are reported as \( \Delta \text{QAIC}_c \). Model weights (\( w_i \)) are reported by stage as well as the number of model parameters (\( K \)) and quasi-deviance (Qdev). The number of parameters (\( K \)) includes additive effects for 2 additional covariates (TRANS and BAND) used to adjust survival estimates for estimated marker effects.

<table>
<thead>
<tr>
<th>Model</th>
<th>( \text{QAIC}_c )</th>
<th>( w_i )</th>
<th>( K )</th>
<th>Qdev</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stage 3: Brood-level effects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{DATE} \times \text{YEAR} + \text{MASS} )</td>
<td>0.00(^a)</td>
<td>0.63</td>
<td>11</td>
<td>609.93</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{DATE} \times \text{YEAR} )</td>
<td>1.72</td>
<td>0.27</td>
<td>10</td>
<td>613.65</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{DATE} )</td>
<td>5.20</td>
<td>0.05</td>
<td>9</td>
<td>619.15</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{MASS} )</td>
<td>6.95</td>
<td>0.02</td>
<td>9</td>
<td>620.89</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) )</td>
<td>8.07</td>
<td>0.01</td>
<td>8</td>
<td>624.01</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{HENAGE} )</td>
<td>9.04</td>
<td>0.01</td>
<td>9</td>
<td>622.98</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{BS} )</td>
<td>9.43</td>
<td>0.01</td>
<td>9</td>
<td>623.37</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{WEATHER} )</td>
<td>9.55</td>
<td>0.01</td>
<td>9</td>
<td>623.49</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{COND} )</td>
<td>9.89</td>
<td>0.00</td>
<td>9</td>
<td>623.84</td>
</tr>
<tr>
<td><strong>Stage 2: Year and site-level effects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) )</td>
<td>0.00</td>
<td>0.47</td>
<td>8</td>
<td>624.01</td>
</tr>
<tr>
<td>( \text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}(3+4) + \text{MALLD} )</td>
<td>1.99</td>
<td>0.17</td>
<td>9</td>
<td>624.00</td>
</tr>
</tbody>
</table>
AGE\textsubscript{logistic}×\text{YEAR} + COVER & 2.12 & 0.16 & 7 & 628.13 \\
AGE\textsubscript{logistic}×\text{YEAR} + \text{WET}(3+4) & 2.53 & 0.13 & 7 & 631.12 \\
AGE\textsubscript{logistic}×\text{YEAR} + 4\text{WET} & 5.94 & 0.02 & 7 & 631.96 \\
AGE\textsubscript{logistic}×\text{YEAR} + \text{MALLD} & 6.82 & 0.02 & 7 & 632.84 \\
AGE\textsubscript{logistic}×\text{YEAR}×\text{SITE} & 7.66 & 0.01 & 30 & 587.49 \\
AGE\textsubscript{logistic}×\text{YEAR} + \text{BROODS} & 8.55 & 0.01 & 7 & 634.57 \\
AGE\textsubscript{logistic}×\text{YEAR} & 10.56 & 0.01 & 6 & 638.58 \\
AGE\textsubscript{logistic}×\text{YEAR} + \text{TRAPPED}×\text{YEAR} & 11.41 & 0.00 & 8 & 637.42 \\
AGE\textsubscript{logistic} & 11.55 & 0.00 & 4 & 643.57 \\
AGE\textsubscript{logistic}×\text{YEAR} + 3\text{WET} & 11.80 & 0.00 & 7 & 637.82 \\
AGE\textsubscript{logistic}×\text{YEAR} & 12.44 & 0.00 & 6 & 640.46 \\
AGE\textsubscript{logistic}×\text{YEAR} + \text{PAIRS} & 12.56 & 0.00 & 7 & 638.58 \\
AGE\textsubscript{logistic}×\text{YEAR} + \text{SITE} & 12.62 & 0.00 & 14 & 616.57 \\
AGE\textsubscript{logistic}×\text{TRAPPED}×\text{YR} & 12.65 & 0.00 & 10 & 632.65 \\

\textit{Stage 1: Age effects}

\begin{tabular}{llll}
\text{AGE\textsubscript{logistic}} & 0.00 & 0.94 & 4 \\
\text{AGE\textsubscript{full}} & 5.67 & 0.06 & 32 \\
\text{AGE\textsubscript{1-10,11-30}} & 31.18 & 0.00 & 4 \\
\text{AGE\textsubscript{1-15,16-30}} & 67.18 & 0.00 & 4 \\
\text{AGE\textsubscript{null}} & 148.50 & 0.00 & 3 \\
\end{tabular}

\textsuperscript{a} QAIC\textsubscript{c} = 631.96
Table 3. The proportion of variation in duckling daily survival explained by covariates from an Analysis of Deviance. We used \{S(\text{AGE}_{\text{logistic}})\} as our base model for determining the proportion of variation explained by \text{YEAR}. For site-level effects we used base model \{S(\text{AGE}_{\text{logistic}} \times \text{YEAR})\} and for brood-level effects we used based model \{S(\text{AGE}_{\text{logistic}} \times \text{YEAR} + \text{COVER} + \text{WET}[3+4])\}.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Proportion</th>
<th>Covariate</th>
<th>Proportion</th>
<th>Covariate</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Brood-level effects</strong></td>
<td></td>
<td><strong>Site-level effects</strong></td>
<td></td>
<td><strong>Year effect</strong></td>
<td></td>
</tr>
<tr>
<td>DATE×YEAR</td>
<td>0.18</td>
<td>COVER</td>
<td>0.19</td>
<td>YR</td>
<td>0.09</td>
</tr>
<tr>
<td>HD</td>
<td>0.09</td>
<td>WET(3+4)</td>
<td>0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MASS</td>
<td>0.06</td>
<td>MALLD</td>
<td>0.10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HENAGE</td>
<td>0.02</td>
<td>BROODS</td>
<td>0.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WEATHER</td>
<td>0.01</td>
<td>PAIRS</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BS</td>
<td>0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>COND</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Map of 93.2 km\(^2\) study sites located in northeastern North Dakota. Sites in black were treatments (mammalian meso-predators reduced each season) and cross-hatched sites were controls (no predator removal). County names are listed for reference.
Figure 2. Model-based estimates of cumulative 30-day survival with 85% confidence interval (dashed lines) of mallard ducklings in northeastern North Dakota in relation to mallard brood density (per wetland km\(^2\)) in 2007. Average mallard brood density was 30.3 ducklings/wetland km\(^2\). Estimates are derived from the stage-2 model \{S(AGE + YEAR + AGE\times YEAR + MALLD + TRANS + BAND)\} with covariates other than MALLD and YEAR set to mean values, and marker effects set to zero.
Figure 3. Model-based estimates of cumulative 30-day survival with 85% confidence interval (dashed lines) of mallard ducklings in northeastern North Dakota in relation to total area of inundated seasonal and semipermanent wetlands (WET[3+4]) in 2007. Average wetland area inundated was 12.4 km$^2$ per 93.2 km$^2$ study site. Estimates are derived from model \{S(AGE + YEAR + AGE$\times$YEAR + COVER + WET[3+4] + DATE + DATE$\times$YEAR + MASS + TRANS + BAND)\} with covariates other than WET(3+4) and YEAR set to mean values, and marker effects set to zero.
Figure 4. Relationship between hatch date (Julian) and estimated cumulative 30-day survival probabilities with 85% confidence interval of mallard ducklings in northeastern North Dakota in 2006 (dashed lines) and 2007 (solid lines; 145 = 25 May and 175 = 24 Jun). Estimated survival was based on model \(S(\text{AGE} + \text{YEAR} + \text{AGE} \times \text{YEAR} + \text{COVER} + \text{WET}[3+4] + \text{DATE} + \text{DATE} \times \text{YEAR} + \text{MASS} + \text{TRANS} + \text{BAND})\) with covariates set to mean values and marker effects set to zero. Mean hatch date was later in 2007 than in 2006 (13 June vs. 9 June, respectively).
Figure 5. Cumulative 30-day survival with 85% confidence interval (dashed lines) of mallard ducklings in northeastern North Dakota in 2007 as a function of mean duckling mass (g) per brood at hatch. Estimated survival was based on model \{S(AGE + YEAR + AGE×YEAR + COVER + WET[3+4] + DATE + DATE×YEAR + MASS + TRANS + BAND)\} with covariates set to mean values and marker effects set to zero. Mean duckling mass among all marked broods was 34.2 g in 2007.
Figure 6. Cumulative 30-day survival with 85% confidence interval (dashed lines) of mallard ducklings in northeastern North Dakota in 2007 as a function of proportion of perennial cover in each 93.2 km$^2$ study site. Estimated survival was based on model \{S(AGE + YEAR + AGE×YEAR + COVER + WET[3+4] + DATE + DATE×YEAR + MASS + TRANS + BAND)} with covariates set to mean values and marker effects set to zero. Cover proportions ranged from 11.2% of the Leeds Study site to 86.2% of the Cando site.
CHAPTER 2: FACTORS AFFECTING DUCKLING BODY CONDITION

Body condition is typically defined as the amount of energy reserves an individual carries relative to its body size (Johnson et al. 1985; Hill et al. 2003), and it is frequently estimated by using the residuals of a regression of body mass on structural size (Green 2001). Ducklings in better condition presumably have greater energy reserves and can better tolerate inclement weather, temporary food shortages, and long overland movements between wetlands. Body condition is often an important predictor of survival during the pre- and post-fledging periods, and yet it remains one of the least studied aspects of waterfowl biology (Sedinger 1992; Hill et al. 2003). Pre-fledging condition may affect recruitment of individuals into the breeding population through effects on hunting susceptibility (Hepp et al. 1986; Hill et al. 2003), age-specific breeding propensity (Sedinger et al. 2004), and hatch-year survival (Christensen 1999; Cooch 2002; Hill et al. 2003). Dufour et al. (1993) showed that Mallards (Anas platyrhynchos) in poorer condition during pre-season banding were more likely to be shot by hunters. Additionally, wintering American Black Ducks (Anas rubripes) and Canvasbacks (Aythya valisineria) in poor condition had lower overwinter survival (Haramis et al. 1986; Conroy et al. 1989). Black Brant (Branta bernicla nigricans) goslings in the Yukon-Kuskokwim Delta, Alaska that were larger and hatched earlier were more likely to become breeders the following year (Sedinger et al. 2004). Higher pre-fledging survival in heavier and better conditioned offspring has been demonstrated in Canvasbacks (Anderson et al. 1997), Spectacled Eiders (Somateria fischeri; Flint et al. 2006), and several species of goose (Barnacle Goose, Branta leucopsis, Owen and Black
Dabbling duck (tribe: Anatini) ducklings eat primarily aquatic invertebrates for the first few weeks of life and spend considerable time foraging (Ringelman and Flake 1980). Given their rapid growth rate and high metabolic demands relative to other precocial birds (Sedinger 1992), food limitation among pre-fledged waterfowl may occur whenever food availability is low, competition for food resources is high, or individual behavior reduces foraging or increases metabolic demands. Cox et al. (1998) found Mallard duckling growth rates and survival increased with invertebrate availability, suggesting food limitation may influence survival. Additionally, Flint et al. (2006) reported that condition of Spectacled Eider ducklings increased survival to 30 days post-hatch, and condition was linked to available foraging habitat. Factors such as high brood density, low wetland availability, inclement weather, atypical hatch date, or disturbance from predators could also induce food limitation for waterfowl ducklings, which could negatively affect their growth rates, body condition, and ultimately, survival.

There is some evidence that density-dependence may affect body condition and survival during the pre-fledging stage. Body condition was lower when more broods were present in studies of Black Brant goslings on the Yukon-Kuskokwim Delta, Alaska (Sedinger et al. 1998), and Lesser Snow Geese at LaPerouse Bay, Manitoba (Williams et al. 1993). Mallard duckling survival was lower in lakes with experimentally increased brood density in Scandinavia (Gunnarsson et al. 2006), and a weak negative effect of
density on duckling survival was also apparent on our study sites in North Dakota (Chapter 1, this document). Antagonistic encounters among broods have been observed in several studies (Newton and Campbell 1975; Titman and Lowther 1975; Savard 1984), which may result in increased brood movements in areas of high brood density.

Makepeace and Patterson (1980) found that brood-rearing Common Shelducks (*Tadorna tadorna*) often exhibited aggression toward other females and that increased interactions between broods (caused by higher density) resulted in more ducklings becoming lost or mixing with other broods. Both these activities may lower duckling survival and have the potential to increase metabolic rates while decreasing time spent foraging (Makepeace and Patterson 1980).

Several environmental factors have been shown to affect duckling survival, and if these factors operate primarily through energetic pathways, then these same factors should negatively affect duckling condition. Inclement weather patterns may reduce foraging ability and food abundance, and increase energetic demands for thermoregulation (Caldwell 1973; Mendenhall and Milne 1985; Flint et al. 2006), which is especially important for young ducklings. Duckling survival is lowest early in life (Guyn and Clark 1999; Pietz et al. 2003; Chouinard and Arnold 2007), and this has been attributed to the limited ability of young ducklings to thermoregulate, locomote, and forage (Anderson and Alisauskas 2001). Wetland availability has been shown to increase duckling survival (Yerkes 2000; Chapter 1, this document), which is related to overall food availability and inter-wetland movements of ducklings. Moving between wetlands has been shown to decrease survival in canvasback ducklings (Leonard et al. 1996), but
that relationship has been ambiguous in Mallards (Dzus and Clark 1997; Chouinard and Arnold 2007). Several studies have shown hatch date negatively influences duckling survival (Dzus and Clark 1998; Guyn and Clark 1999), and ducklings that hatch later have lower age corrected mass than early hatched ducklings (Flint et al. 2006).

We examined the role of density-dependence, and environmental factors on the body condition of dabbling ducklings by relating size corrected body mass (condition) to brood density, wetland density, amount of perennial grass in the landscape, capture date, approximate hatch date, duckling age, and recent weather conditions. If energetic limitations are a primary driving force behind patterns of duckling mortality, we predicted that duckling condition should increase with wetland density and duckling age and decrease with brood density, capture date, and inclement weather, especially among younger ducklings (Cox et al. 1998).

METHODS

Study Site

Our study took place on eight, township-sized (93.2 km²) sites in the Devils Lake Wetland Management District in northeastern North Dakota in 2006-2007 (only four sites were evaluated in 2006). Our study sites consisted of predominately small grain agriculture, with some pasture and relatively large amounts of idle perennial cover (20-95%) in the form of Conservation Reserve Program or Waterfowl Production Areas. Five of our study sites had mammalian meso-predators removed as part of Delta Waterfowl Foundation’s predator management program and the other three sites had no
predator trapping. Densities of breeding mallard pairs were exceptionally high in both years ($\bar{x} = 56$ pairs per km$^2$); 2006 was characterized by a wet spring and dry summer, whereas 2007 had more precipitation during brood rearing (mean deviation from long-term average$_{\text{June-August}} = -2.64$ cm and $-0.05$ cm, respectively; NDAWN 2010).

**Data Collection and Covariate Formation**

We conducted 2–3 rounds of duckling trapping from 10 June to 5 August in 2006-2007. Five swim-in bait traps (Evrard and Bacon 1998) per site were placed in randomly selected roadside wetlands and checked twice daily for seven days. Seasonal, semipermanent, or permanent wetlands that contained water at the time of trapping, had $>10\%$ emergent vegetation, were located within 100m of a road, and were capable of supporting multiple broods during the breeding season were considered for trapping locations. Traps were baited with barley inside the trap and along the edge to lure ducklings into the trap and bait was replenished daily or as needed.

Captured ducklings were weighed ($\pm 1-5$ g with a Pesola scale), measured (head and tarsus length, $\pm 0.01$ mm), sexed, and aged according to plumage development (Gollop and Marshall 1954). We fit each captured duckling with either a plasticine or adult metal (age class IIA+) U.S. Fish and Wildlife Service (FWS) band (Blums and Davis 1999). Duckling age classes were pooled for the oldest two classes (IIC and III = IIC+) since some species were not captured in the oldest age class. Ducklings were released together as broods onto the same wetland immediately after data collection. Recaptured ducklings were not measured to avoid confounding of condition with prolonged exposure to supplemental grain.
We obtained estimates of brood abundance for each site using roadside brood surveys that utilized all wetlands located <150 m from the road (Pagano and Arnold 2009). We conducted 2 rounds of surveys (early June and early July) to account for early-hatching versus late-hatching broods. Each survey round comprised 3 replicate surveys conducted over a single day, which we treated as a closed population mark-recapture survey (Pagano and Arnold 2009). Ducklings <30 days of age during the second survey were added to total ducklings from the first survey to derive estimates of total duckling abundance for each site-year.

We took aerial photos of each study site in each year, digitized all inundated wetlands using ArcGIS (version 9.2, ESRI, Redlands, CA) and created a land-use data layer. We classified each wetland basin by permanence class (Cowardin et al. 1979) using National Wetland Index (NWI) data verified by ground-truthing. We derived total inundated seasonal and semipermanent wetland area (WET; km$^2$; Cowardin et al. 1979) for each site by summing digitized wetland areas over all wetlands. We considered only semipermanent and seasonal wetlands since they are the two classes that have been most frequently identified as providing important habitat for Mallard broods (Talent et al. 1982; Raven et al. 2007). Total duckling density (DUCKD) was the ratio of estimated dabbling duck (Anas spp.) ducklings to total surveyed wetland area. We used our land use layer, verified by ground-truthing (Pieron 2010) to derive the proportion of perennial cover (COVER) in each site.

We derived a date-specific weather index (WEATHER) for the 7 days prior to trapping using standardized measures of wind chill and precipitation. We obtained
weather data from stations near each study site (range: 0-13 km from study site boundary) from the North Dakota Agricultural Weather Network (NDAWN 2010). Wind chill was multiplied by $-1 \times$ standardized daily total rainfall to obtain a daily weather score. Daily total rainfall was multiplied by -1 so higher scores referenced ‘better’ (e.g., higher wind chill and less precipitation) weather for that day. We then standardized scores based on the seasonal average and summed daily weather scores for the 7 days prior to trapping. See Chapter 1 of this document for complete methodology and worked example of our weather covariate, however, we did not employ a tapering effect for the weather covariate in this chapter.

**Statistical Analyses**

We estimated body condition by conducting a Principle Components (PC) analysis (Proc PRINCOMP; SAS Institute Inc. 2009) on the correlation matrix of raw tarsus and head length measurements to obtain an index of body size (SIZE) for each species examined. Duckling mass was log transformed to adjust for nonlinearity in our data. We then examined a nested suite of 6 linear models that predicted log duckling mass as a function of size, sex, species and their two-way interactions, and selected the model with minimal AIC$_c$ as the best approximating model. We adjusted mass by sex and species since we were not directly interested in sex and species differences in condition and these variables may explain variation in mass (Hill et al. 2003). Residuals from this regression were retained as our index of body condition (Schulte-Hostedde et al. 2005).
We analyzed data with General Linear Mixed Models (PROC MIXED; SAS Institute 2009) using maximum likelihood estimation (METHOD=ML; Littell et al. 2006). We started with a ‘full’ model consisting of all main effects and biologically reasonable 2-way interactions (Table 1). We selected models using an AIC framework, adjusted for small sample size (AIC_c; Burnham and Anderson 2002) using a hierarchical selection approach (Lebreton et al. 1992) where the model with the lowest AIC_c score was best supported by the data. We first compared the most highly parameterized individual structure plus all possible 1 and 2-variable combinations of COVER, DENSITY, and WETLAND. We did not consider perennial cover and duckling density in the same model because they were highly correlated (r = 0.80). The best supported site-level model was then used to select the best supported suite of individual duckling effects. We also conducted an ad-hoc Analysis of Deviance (ANODEV; Ballerini et al. 2009) to determine how well our site-level covariates explained geographic variation in duckling condition by comparing deviance from a fully parameterized model including a dummy site effect (SITE; levels 1 - 8) to our fixed site-level covariates.

We selected duckling-level effects by removing one fixed effect term at a time from the most parameterized model from stage 1 and comparing model fit. Interactions and main effects were considered removable terms, however, main effects were not removed if the model still contained 2-way interactions involving that effect. Any terms removed from the model that resulted in a lower AIC_c score or was within 2 AIC_c units of the best supported, more parameterized model were then considered in the next stage. The next stage had one additional term removed and was then compared to the previous
best supported model. This selection continued until all models that removed one additional term from did not further reduce $\text{AIC}_c$ score (Lebreton et al. 1992). Inference was made from the model with the lowest $\text{AIC}_c$ score. We report supported model effects using model-predicted condition estimates, $\text{AIC}_c$ weight ($w_i$), and least square means (LSMEANS; SAS Institute 2009) with 85% confidence intervals since they are more aligned with AIC model selection (Arnold 2010).

RESULTS

We captured 663 ducklings from 6 species including 231 Mallards, 111 Gadwalls (Anas strepera), 290 Blue-winged Teal (Anas discors), 5 Lesser Scaup (Aythya affinis), 8 American Wigeon (Anas americana), 13 Northern Shovelers (Anas clypeata), and 5 Northern Pintails (Anas acuta). Sample sizes ranged from 34 ducklings at the Whitman site to 196 ducklings at the Cando site. We captured approximately equal numbers of males ($n = 290$) and females ($n = 250$). We trapped more birds in 2007 ($n = 463$) than 2006 ($n = 200$), and on average, ducklings were trapped 16 days earlier in 2007 (12 July) than in 2006 (28 July). We restricted our analysis to Mallards, Gadwalls, and Blue-winged Teal since sample sizes were low for all other species. We excluded an additional 69 observations due to missing mass and size measurements, resulting in an effective sample size of 563 ducklings.

Eigenvalues from PC1 of our Principle Components analyses were 1.74, 1.77, and 1.92 for Blue-winged Teal, Gadwalls, and Mallards, respectively. Log-transformed
duckling mass (LN\_MASS) was best explained by the following model ($w_i = 0.87$), which essentially resulted in separate regressions for each species:

$$LN\_MASS = \text{intercept} + \text{SPECIES} + \text{SIZE} + \text{SPECIES} \times \text{SIZE}$$

Our best approximating model explained 87.8% of the variation in LN\_MASS. Log mass increased with structural size ($\hat{\beta} = 0.60$, 85% CI: 0.59 – 0.62), and backtransformed mass was lower for Gadwall ($\bar{x}_{\text{mass}} = 125.45$, 85% CI: 120.93 – 130.14) than for Blue-winged Teal ($\bar{x}_{\text{mass}} = 188.95$, 85% CI: 185.03 – 192.96), or Mallards ($\bar{x}_{\text{mass}} = 210.95$, 85% CI: 206.04 – 215.96). Mallards had the largest increase in mass per unit size (SPECIES\_\text{SIZE}), for example, a 1 unit increase in the size variable increased mass by 1.83 g in Mallards, 1.47 g in Gadwall, and 1.41 g in Blue-winged Teal. Residuals from this regression were used as our index of body condition.

Wetland density best explained patterns of site-level variation (Table 2) and this variable was retained for examination of duckling-level effects. Perennial cover also had some support as a site-level covariate in comparison to the null model with no site-level effects; however, the COVER + WETLAND model was not an improvement over the WETLAND only model (Table 2). Duckling condition increased with wetland density ($\hat{\beta} = 0.01$, 85% CI: 0.00 – 0.01; Fig. 1) and condition decreased with increasing amounts of perennial cover in the landscape ($\hat{\beta} = -0.15$, 85% CI: -0.226 – -0.07; Fig. 2). Duckling density had virtually no effect on duckling condition ($\Delta\text{AIC}_c$ from null model = 1.44, $w_{\text{DUCKD}} = 0.001$).

The SITE variable improved model fit ($\Delta\text{AIC}_c = -33.71$) over our best supported site-level model (WETLAND). Wetland density explained 23.2% of the variation in
duckling body condition associated with our fully parameterized model, perennial cover explained 10.9%, and together they explained 25.4% of the variance. However, duckling density accounted for only 1.4% of the site-level variation in duckling condition and was clearly unimportant.

Our best supported model included effects of WETLAND, AGE, DATE, WEATHER, YEAR (2006 or 2007), WEATHER × YEAR, AGE × DATE, and DATE × YEAR (w_i = 0.45, K = 22, Eq. 1).

\[
\text{Condition} = \text{Intercept} + \text{WETLAND} + \text{AGE} + \text{DATE} + \text{WEATHER} + \text{YEAR} + \text{WEATHER} \times \text{YEAR} + \text{AGE} \times \text{DATE} + \text{DATE} \times \text{YEAR} \quad \text{Eq. 1}
\]

Mean trap date was 27 July 2006 (x_julian = 207.51, 85% CI: 207.78 – 209.25) and 13 July 2007 (x_julian = 193.51, 85% CI: 192.75 – 194.27). Mean weather scores were 1.30 (85% CI: 1.09 to 1.51) in 2006 and 0.40 (85% CI: 0.10 to 0.70) in 2007. Condition was generally lowest for younger ducklings (Fig. 3), and being younger later in the season decreased condition for IB ducklings, but increased condition for all other age classes (Fig. 3). Condition increased throughout the season, and this effect was more pronounced in 2006 (Fig. 4) and for older ducklings (Fig. 3). Condition decreased with better weather in 2006 and had a weak, positive association in 2007 (Fig. 5).

**DISCUSSION**

Contrary to our predictions, we found no support for density-dependence in duckling body condition. This contradicts previous research that found evidence of food and habitat limitation on duckling condition in spectacled eiders (Flint et al. 2006), and
smaller body size in years with high numbers of Black Brant broods in Alaska (Sedinger et al. 1998). Most body condition research has focused on semi-colonial or colonial nesting goslings that tend to more completely utilize available forage within brood-rearing areas (Schmutz 1993; Cooch 2002; Slattery and Alisauskas 2002). Territoriality among settling breeding pairs in the spring may act as a spacing mechanism to avoid density-dependent effects (e.g., food limitation) on offspring condition and survival (Anderson and Titman 1992). Therefore, density-dependence in offspring condition of prairie-nesting species is most likely only experienced in years with wet springs that attract high densities of breeding pairs, followed by drought periods that result in food limitation during the brood rearing period. Although 2006 was drier during the brood-rearing period than the long term average (NDAWN 2010), this may not have been enough to induce density-dependence in duckling condition. Additionally, our estimates of duckling density were measured at the site-level (93.2 km²), which might be too crude to detect density-dependence on a more local scale (e.g., within a wetland).

Although condition did not decrease with increasing duckling density, body condition increased with wetland availability. This suggests that food availability may have played a role in body condition; however, our lack of density-dependence weakens this hypothesis. Besides food availability, an increase in seasonal and semipermanent wetlands may provide protection from predators that are not adept at swimming or obtaining prey on the water (e.g., red fox, raptors). Predator avoidance may be energetically expensive, especially for younger ducklings (Sedinger 1992; Chapter 1, this document), and may lower condition in areas with less available wetland area.
Additionally, Mallard duckling survival increased with wetland availability in our study site-years (Chapter 1, this document), and Simpson et al. (2007) showed Mallard duckling survival increased with the amount of vegetated wetland used by broods. Alternatively, ducklings may have had to move less often or not as far in areas with high wetland density, which may have conserved energy and allowed an increase in condition. Longer inter-wetland movements, and especially distance from the nest to the first natal wetland has been shown to decrease mallard duckling survival in Manitoba (Rotella and Ratti 1992), although these effects have been ambiguous in other studies (Yerkes 2000; Simpson et al. 2007).

Duckling movements may be related to our unexpected negative effect of perennial cover on condition, which had some support in our first stage analysis. Although one might expect an increase in wetland area to be correlated with perennial cover since wetland drainage is higher in agriculture, these two covariates were weakly negatively correlated (r = -0.28). Movement through perennial cover may be more energetically costly due to thick underbrush, or may have influenced predation risk by influencing movement routes of broods and females. We are unable to decipher why perennial cover negatively influenced duckling body condition in our study, but it also decreased mallard duckling survival in our site-years (Chapter 1, this document). Additionally, researchers observed a similar effect of delayed and idle hayland on mallard duckling survival in the Canadian Parklands, although the overall effect of perennial cover was positive (P. Bloom, unpublished data).
Condition was lowest for younger age classes, which varied within season (Fig. 3). Age-specific variation in condition may have implications for survival since early age classes are most vulnerable to predation and inclement weather (Caldwell 1973; Pietz et al. 2003; Drever et al. 2004; Pearse and Ratti 2004). Our condition estimates could have been biased by the consumption of grain, especially since we found an increase in condition for older age classes. After palpating the crops of several ducklings and conducting necropsies of duckling trap mortalities, we observed very little, if any grain in young (< IIA) ducklings. We speculate they followed feeding females into the traps. Older ducklings were variable, and most contained little grain, but necropsies measured upwards of 30 g of grain in the crop of age class IIB blue-winged teal (C. Amundson, unpublished data). Therefore, our estimates of body condition for older age classes may have been biased high for older ducklings, but we doubt there was any bias by species or site-level effects since all species and age classes appeared to consume grain similarly among sites and all sites were baited in the same manner. Future research should include an index of grain consumption if using baited swim-in traps.

Hatching later (being a younger age class later in the season; DATE × AGE) lowered body condition for age class IB ducklings, and increased condition in other age classes (Fig. 3). The more pronounced negative effect of hatch date on condition in young ducklings is consistent with research that found decreased food availability as the season progresses (Cox et al. 1998). The anomaly with extremely young and old age classes maybe partially explained by the range of dates we trapped each age class (Fig. 3). We trapped very few IA ducklings late in the season (x̄ IA = 194), and very few IIC+
ducklings early in the season ($\bar{x}_{126}$ = 206.5), and there may have been insufficient range in trap date to accurately assess effects of hatch date at these age classes.

Condition was slightly higher in 2006, but increased throughout the season in 2006 and stayed relatively constant in 2007 (Fig. 4). This could be an artifact of trapping schedules between years since we did not trap ducklings before July 17th in 2006. Additionally, although previous literature found a decrease in food availability as the season progresses (Cox et al. 1998), which could lower condition later in the season, most ducklings are older later in the year, and our results also found older ducklings had higher condition (Fig. 3).

Contrary to our predictions, duckling condition only increased slightly with weather in 2007 (Fig. 5) and was not age-dependent. Additionally, ducklings in 2006 had markedly lower condition in better weather, which may be explained by the relatively narrow range of weather in 2006 (range: -4.12 to 4.99). It is possible that only extreme recent weather days may negatively affect duckling condition, although 2007 had a larger range in weather conditions (range: -7.90 to 9.66) surrounding trapping, and trends were weakly positive (Fig. 5).

We did not account for overdispersion in our analysis since broods were often caught without a female in sight, in large groups of similarly aged ducklings (>12 ducklings), and with ducklings of mixed ages and species (which may have been a mixed brood). We acknowledge, however, that condition may not be independent within a brood due to similarities among broodmates, and the behavior and foraging patterns of
individual females, which may lead to biased estimates of precision (i.e., underestimating variance) and overfit best supported models (Flint et al. 1995).

We have shown that duckling condition varies by wetland availability, date within season, and weather trends; and these trends may be year and age-specific. However, the mechanism for this variation remains unclear, and may involve a combination of duckling bioenergetics, the tradeoff between growth and maintenance, as well as female and brood behavior, and wetland movements. Future research into density-dependence, and upland cover are needed at finer scales to fully ascertain their role on duckling condition. Duckling mass at hatch (a proxy for hatchling condition) had a positive effect on mallard duckling survival, and duckling survival was the most important vital rate to mallard recruitment and population growth during our study (Chapter 1 and 3, this document). Therefore, examining factors affecting condition may provide insight into mechanisms driving survival and ultimately recruitment of ducks into the breeding population.
Table 1. Definitions and rationale for variables included in models of factors affecting duckling body condition in northeastern North Dakota.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition and rationale</th>
</tr>
</thead>
<tbody>
<tr>
<td>AGE</td>
<td>Age categories based on Gollop and Marshall (1954). Growth rates vary with age, so condition may also vary in relation to overall body mass and effects of weather in relation to body mass.</td>
</tr>
<tr>
<td>DATE</td>
<td>Body condition may vary temporally not only with age, but as food availability and wetland conditions change through time.</td>
</tr>
<tr>
<td>WEATHER</td>
<td>Poor weather may reduce foraging time, especially for younger ducklings, and invertebrate hatches are more common in warm weather, which may make food more available</td>
</tr>
<tr>
<td>YEAR</td>
<td>There may be annual variation in condition related to variables not measured in this study.</td>
</tr>
<tr>
<td>SITE</td>
<td>There may be geographic variation in condition not explained by our site-level covariates.</td>
</tr>
<tr>
<td>COVER</td>
<td>Inter-wetland movements may be energetically expensive, and this may be variable depending on whether the predominant land use is row crop agriculture or perennial grass (with more dense low-ground vegetation).</td>
</tr>
<tr>
<td>WETLAND</td>
<td>Wetland availability is related to brood movement frequency, distance, and food availability, which all may influence duckling condition.</td>
</tr>
<tr>
<td>DENSITY</td>
<td>Duckling density may limit food availability and cause territorial behavior in brooding females, which could influence duckling condition.</td>
</tr>
<tr>
<td>YEAR × DATE</td>
<td>Seasonal variation in duckling condition may vary with environmental conditions in a given year.</td>
</tr>
<tr>
<td>YEAR × AGE</td>
<td>Age effects may vary by year due to environmental variation in resources and climatic conditions.</td>
</tr>
<tr>
<td>YEAR × WEATHER</td>
<td>Weather effects may vary by year.</td>
</tr>
<tr>
<td>DATE × AGE</td>
<td>Temporal variation in condition may be greater for younger ducklings (i.e., hatched later in the season).</td>
</tr>
<tr>
<td>AGE × WEATHER</td>
<td>Weather effects may have more pronounced effects on condition in younger ducklings that lack full thermoregulation.</td>
</tr>
</tbody>
</table>
Table 2. Model selection results from a sequential analysis of site-level factors affecting duckling condition in northeastern North Dakota from 2006-2007. We ranked models based on Akaike’s Information Criterion corrected for small sample size (AIC\(_c\)). Deviations from the best fit model are reported as ΔAIC\(_c\). Model weights (\(w_i\)) are reported as well as the number of parameters (K). The best supported model from this analysis was carried over to examine duckling-level factors affecting body condition (see Table 5).

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAIC(_c)</th>
<th>(w_i)</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site-level covariates added to the most parameterized duckling-level model(^a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WETLAND</td>
<td>0.00</td>
<td>0.51</td>
<td>40</td>
</tr>
<tr>
<td>WETLAND + COVER</td>
<td>0.93</td>
<td>0.32</td>
<td>41</td>
</tr>
<tr>
<td>WETLAND + DUCKD</td>
<td>2.23</td>
<td>0.17</td>
<td>41</td>
</tr>
<tr>
<td>COVER</td>
<td>8.10</td>
<td>0.01</td>
<td>39</td>
</tr>
<tr>
<td>NULL</td>
<td>12.88</td>
<td>0.00</td>
<td>39</td>
</tr>
<tr>
<td>DUCKD</td>
<td>14.30</td>
<td>0.00</td>
<td>40</td>
</tr>
</tbody>
</table>

\(^a\) Global duckling-level model CONDITION = INT + AGE + DATE + WEATHER + YEAR + AGE×DATE + AGE×WEATHER + DATE×YEAR + WEATHER×YEAR + AGE×YEAR

\(^b\) AIC\(_c\) for best supported model = -164.62
Figure 1. Model-based estimates of duckling (Blue-winged Teal, Gadwall, and Mallard) body condition in relation to seasonal and semipermanent wetland area (km²) per study site in North Dakota, 2006 - 2007. Linear trend lines are based on model predicted trends and are plotted against the original data to illustrate fit. Average wetland area was 12.43 km² per site.
Figure 2. Model-based estimates of duckling (Blue-winged Teal, Gadwall, and Mallard) body condition in relation to the proportion of each study site covered in perennial grass (excluding pasture) in North Dakota, 2006 - 2007. Linear trend lines are based on model predicted trends and are plotted against the original data to illustrate fit. Average proportion perennial cover was 0.43.
Figure 3. Model-based trends in duckling (Blue-winged Teal, Gadwall, and Mallard) body condition in relation to date trapped (Julian date) in North Dakota, 2006 - 2007. Each trend was examined for linearity and age class IIC+ was better explained by a quadratic effect. Trends are plotted by age class only within the spectrum of observed trapped dates. Mean trap date was 17 July (Julian date = 198).
Figure 4. Model-based trends in duckling (Blue-winged Teal, Gadwall, and Mallard) body condition in relation to date trapped (Julian date) in North Dakota, 2006 and 2007. Model-predicted trends are plotted by year only within the spectrum of observed trapped dates and against the original data to illustrate fit. Mean trap date was 27 July (Julian date = 208) in 2006, and 13 July (Julian date = 194) in 2007.
Figure 5. Trends in duckling (Blue-winged Teal, Gadwall, and Mallard) body condition in relation to a combined weather index for the 7-days prior to trapping (higher score = better weather) in North Dakota, 2006 and 2007. Linear trend lines are based on model predicted trends and are plotted against the original data to illustrate fit. Mean weather score was 1.30 in 2006 and 0.40 in 2007.
CHAPTER 3: THE EFFECTS OF PREDATOR REMOVAL ON MALLARD POPULATION DYNAMICS AND VITAL RATE SENSITIVITY IN NORTH DAKOTA

The Prairie Pothole Region is the most important breeding area for many species of North American waterfowl (Reynolds 2000). As prairies and wetlands have been converted to agriculture, waterfowl biologists and land managers have struggled to increase waterfowl productivity on fragmented landscapes with abundant predators and minimal escape cover for nesting females and broods (Drever et al. 2007). Although numerous factors influence waterfowl productivity, predation is widely implicated as the most important factor affecting survival of nests, ducklings, and breeding females (Sovada et al. 2001; Pietz et al. 2003; Brasher et al. 2006; Pieron and Rohwer 2010). Predator communities of the Prairie Pothole Region are dominated by medium sized mammalian carnivores such as striped skunk (Mephitis mephitis), raccoon (Procyon lotor), and red fox (Vulpes vulpes). These species are efficient nest predators, and red fox are an important predator of nesting females (Sargeant et al. 1993). A change in the predator community, in combination with a reduction in perennial nesting cover and wetland area, has led to a long-term decline in waterfowl production (Sargeant et al. 1993, Beauchamp et al. 1996, Drever et al. 2007) and is thought to represent the major bottleneck impeding waterfowl population growth in the Prairie Pothole Region (Hochbaum and Caswell 1978, Hoekman et al. 2002).

Several studies have examined the relative importance of different vital rates in driving annual variation in recruitment (i.e., the number of females produced in year $t$ that also survive to breed in year $t+1$; Johnson et al. 1987, Hoekman et al. 2002, Koons et al. 2006) and population change in waterfowl (Wisdom et al. 2000, Hoekman et al.
From these studies, nest success appears to be the most important vital rate dictating population change in waterfowl and waterfowl managers often focus their efforts on increasing the number of nests hatched in the landscape (Rohwer and Fisher 2007), although studies have also noted the importance of female and duckling survival (Cowardin et al. 1985, Johnson 1987, Hoekman et al. 2002).

Habitat management has been the mainstay of waterfowl management for decades (Kadlec and Smith 1992). Waterfowl managers have tried to increase breeding pair populations by restoring and protecting wetlands and to increase nesting success by increasing perennial cover on the landscape (Turner et al. 1987, Reynolds et al. 2001). However, the amount of perennial cover and wetland area needed to sustain waterfowl populations may not be economically or logistically feasible (Reynolds et al. 2001, Pieron and Rohwer 2010) and therefore, some focus has shifted to increasing productivity on existing landscapes primarily by excluding or removing predators (e.g., predator fences and trapping; Cowardin et al. 1998, Pieron and Rohwer 2010), or by providing nesting structures that offer protection from predators (Coulton 2008, Stempka 2009).

Since 1994, Delta Waterfowl Foundation (Delta) has trapped mammalian mesopredators in northeastern North Dakota during the spring and summer in an attempt to increase waterfowl nest success and subsequent production. Since then, multiple studies have demonstrated that removing predators results in near doubling of nest success (Garrettson and Rohwer 2001, Chodachek and Chamberlin 2006, Pieron and Rohwer 2010), and mallard duckling survival was positively influenced by predator reduction in a Saskatchewan study (Pearse and Ratti 2004; but see Chapter 1, this document).
However, recent research found breeding pair numbers were not higher on predator managed sites (Pieron 2010), and non-target predators (e.g., raptors, mink) may still influence vital rates and key in on areas where target predators have been reduced (Martin 2009; Chapter 1, this document).

From previous research on predator removal sites, Delta Waterfowl Foundation derived rough predictions of “incremental ducks” added to the fall population as a result of predator management (Table 1). However, many of the vital rates used for these projections were guesstimates or were obtained piecemeal from other studies in varying times and locations. Here, we present an assessment of the impact of operational predator management on mallard production with most breeding season vital rate estimates obtained from the same study areas from 2006-2008. We focused on mallards since they are abundant, tractable, and the most widely harvested species of waterfowl in North America (Baldassarre and Bolen 2006). Mallards have also been the subject of numerous previous population modeling efforts (Cowardin and Johnson 1979, Johnson et al. 1987, Hoekman et al. 2002, Coluccy et al. 2008).

To evaluate the efficacy of predator management for increasing mallard production in North Dakota’s drift prairie we: 1) built a matrix model to estimate mallards added to the fall population on trapped and control sites using site-specific estimates of breeding pairs, nest success, duckling survival, and juvenile (post-fledging) survival, 2) conducted a sensitivity analysis to explore the relative contribution of each vital rate to overall variation in mallard recruitment, and 3) estimated the cost of predator management per incremental duck produced. We focus on additions to the fall flight,
rather than population growth rate ($\lambda$) because predator control is aimed primarily at increasing harvest, so the gains only need to persist until the beginning of fall hunting season.

**STUDY AREA**

We modeled fecundity parameters with estimates from 8 township-scale (93.2 km$^2$) sites in the Devils Lake Wetland Management District in northeastern North Dakota during 2006-2007 (one additional control site was used to estimate fledging survival). Our study sites were located in the drift plain biogeographic province and consisted of predominately small grain agriculture, with some pasture and relatively large amounts of perennial cover due to enrollment in the Conservation Reserve Program (CRP). Five of our study sites had mammalian meso-predators removed as part of Delta Waterfowl’s predator management program and the other three had no predator trapping and served as controls (16 site-years). Trapped sites had been trapped consecutively for 2-8 years. See Chapter 1 of this document for a detailed description of our study sites.

**METHODS**

**Vital Rates**

We conducted annual spring pair counts to estimate breeding pair numbers on sampled wetlands, which we then used to develop a generalized mixed linear model for predicting pair abundance ($P$; pairs) per study site adjusted for wetland type and area (Pieron 2010). We estimated mallard nest success using a logistic-exposure model that accounted for initiation date, and nest age effects (Pieron and Rohwer 2010). Because female mortality was modeled separately, we adjusted nest success upward by 5% to
account for nests that failed concurrent with female mortality. Hoekman et al. (2002) used a 10% upward adjustment factor, which we revised to 5% based on more recent analysis (Arnold et al. 2010 found that 205 out of 4,112 radiomarked mallard nests in prairie Canada failed due to female mortality). We then converted nest success (NS) to hen success (H) to account for renesting using the equation $H = NS \times e^{(1-NS)^2}$ (Cowardin and Johnson 1979). Arnold et al. (2010) showed this equation provided a reliable estimate of hen success adjusted for renesting. We estimated initial brood size (BS) by visiting nests post-hatch and subtracting the number of unhatched eggs from the pre-hatch clutch size (C. Amundson, unpublished data). We derived estimates of duckling survival to 30 days post-hatch from periodic resightings of radio-marked females with broods using the nest survival module in Program MARK (Rotella et al. 2004). Duckling survival was estimated for 15 site-years (4 trapped sites in both years, 3 control sites in 2006 and 4 control sites in 2007). Best supported models did not include a predator-removal effect (Chapter 1, this document); so treatment specific estimates were derived from the most highly parameterized model that included site effects and were then averaged across trapped and control sites. We extended duckling survival estimates from 30 days of age to 1 August (approximately 54 days old) by taking the mean mallard hatch date (HD) per site from 2006-2007 (Pieron, unpublished data), adding 30 days to account for our duckling survival estimates, then taking the daily survival rate (DSR) on day 30 to the $n_{days}$th power, where $n_{days} = 1$ August – (mean HD + 30). We estimated post-fledging survival rates (J) using a Cormack-Jolly-Seber survival analysis of abdominally implanted juvenile female mallards from 2007-2008 using
Program MARK (White and Burnham 1999, L. Beaudoin, unpublished data). We estimated juvenile survival to the beginning of resident waterfowl hunting season (22 September) on 6 sites (5 trapped, 1 control) in 2007-2008. Estimates were pooled by year and across treatment since predator removal ended mid-July in all years and fledged juveniles often flew beyond the borders of our study sites.

We modeled adult breeding season survival (B), the probability a settled pair initiated a nest (nesting propensity; NP), and their associated process variance using data from the Prairie Habitat Joint Venture (PPJV) Assessment conducted in the Canadian parklands by Ducks Unlimited Canada’s Institute for Wetland and Waterfowl Research (IWWR; Hoekman et al. 2002; M. Anderson, IWWR, unpublished data). Winter survival (W) was estimated by taking annual survival rates of midcontinent female mallards from Chu and Hestbeck (1989) and dividing by the breeding season survival rate (Hoekman et al. 2002; IWWR, unpublished data); our estimates of process variance were obtained from Hoekman et al. (2002), who used the delta method to decompose annual process variance into breeding and winter components.

**Production Model**

Differences in vital rates among age classes (second year or after second year) were minimal (Hoekman et al. 2002; M. Pieron, C. Amundson, and L. Beaudoin, unpublished data), or derived from pooled parameters (winter survival; Hoekman et al. 2002). Therefore, we averaged vital rate estimates across age classes and years, and then pooled them into trapped (predator reduced) and control (untrapped) sites for treatment specific production estimates. Incremental mallards per female added to the fall population (MP;
i.e., number of mallards of both sexes produced per female mallard that survived to fall hunting) was a product of adult breeding survival (B), nesting propensity (NP), hen success (H), hatched brood size (BS), fledging success (FS) and post-fledging survival of juveniles (J) where:

\[ MP = (B \times NP \times H \times BS \times FS \times J) \]

We estimated recruitment into the breeding population as the product of winter survival (W) and the number of hatch-year female mallards added to the fall flight (MP/2; assuming a 50:50 sex ratio):

\[ Recruitment = \frac{MP}{2} \times W \]

We estimated the relative population growth rate (\( \lambda \)) for each treatment as the proportion of adults that survived plus the number of surviving female recruits (Sandercock et al. 2008) where:

\[ \lambda = (B \times W) + Recruitment \]

To derive 95% confidence intervals on our production estimates, we conducted 10,000 bootstraps on mean vital rates incorporating process variance and associated distributions using the Poptools add-in (Hood 2003) for Excel (Microsoft Office 2007, Microsoft, Redmond, WA). We partitioned total variance (empirical standard deviation) into process and sampling variance using a SAS (SAS Institute 2009) macro (L. Armstrong, Ducks Unlimited Canada, personal communication) for vital rates estimated in North Dakota (i.e., H, BS, JS, J). We simulated each vital rate from a beta distribution except initial brood size, which was simulated from a normal distribution since it was not restricted to values between 0 and 1.
Sensitivity Analyses

We conducted a modified sensitivity analysis (Link and Doherty 2002) and life-stage simulation analysis (LSA; Wisdom et al. 2000) of lower vital rates to examine the extent each parameter influenced changes in \( \lambda \). We used a stage-based matrix model that combined a birth-pulse population with a pre-breeding census. Given no evidence of age-specific variation in survival or fecundity, our 2-stage projection matrix was identical across age classes

\[
\begin{bmatrix}
B \times NP \times H \times BS \times D \times FS \times J & B \times NP \times H \times BS \times D \times FS \times J \\
B \times W & B \times W
\end{bmatrix}
\]

We used Matlab (version 7.8; The Mathworks, Natick, MA) to generate 10,000 simulated population estimates using vital rates that varied from mean values by associated process variance. Vital rates estimated in the same time and place may be subject to some level of correlation and so we generated a Pearson correlation matrix for our estimates of nest, duckling and juvenile survival, and initial brood size as a proportion of the maximum site-specific mean brood size to constrain brood size to a beta distribution (e.g., if maximum mean brood size = 4.5 female ducklings/female, and mean \( BS_{\text{site}} = 4.2 \) female eggs/female, the proportion of the max = \( 4.2/4.5 = 0.933 \)). Process variance for brood size was recalculated using these proportions. We drew a random sample from beta distributed correlated variables and associated process variance by using Betarv software (Western EcoSystems Technology, Cheyenne, WY) developed by Tadeu et al. (2008). Betarv first produces uniformly distributed random variables between 0 and 1 with required correlations and beta shape parameters, then converts them to standard beta random variables using the inverse of the beta distribution function. This
method is fairly accurate except for very high and very low correlations when beta and normal correlations diverge. Correlation strength ranged from -0.05 for brood size and fledging survival to -0.15 for hen success and fledging survival, which we deemed an acceptable range (Fig. 2 in Tadeu et al. 2008). Simulated BS proportions were then multiplied by the maximum mean brood size to estimate fecundity and calculate sensitivity.

Several papers have discussed the use of sensitivities versus elasticities (e.g., Horvitz et al. 1997, de Kroon et al. 2000, Link and Doherty 2002); and here we present variance-stabilized sensitivities (VSS; Link and Doherty 2002) that address the problem with analytical sensitivities that proportional changes in vital rates are of different scales (Horvitz et al. 1997). VSS works by scaling parameters so that the magnitude of change is independent of the mean value of the parameter, while also providing equal ranks on the importance of complementary rates, which is a shortcoming of traditional elasticity analysis (Link and Doherty 2002). Additionally, elasticity is uninformative since fecundity in our model is the product of lower-level vital rates (e.g., breeding propensity, duckling survival), which result in identical elasticities for each vital rate.

We calculated VSS for each run of our simulation model by applying the arcsine square root transformation to beta distributed parameters, log-transforming the normally distributed parameter, and applying the following equation:

\[ VSS_q(\lambda, \theta) = Sensitivity(\log \lambda, q(\theta)) \]

where \( q \) is the choice transformation for parameter \( \theta \) (Link and Doherty 2002).
We plotted VSS estimates against their vital rate inputs to assess which sources of process variance are contributing the most to population change. Although useful to address the shortcomings of traditional sensitivities, VSS can be difficult to interpret with respect to management considerations so we also conducted a life stage simulation analysis. An LSA uses coefficients of determination ($r^2$) between 10,000 simulated estimates of $\lambda$ and randomly drawn vital rates from respective distributions across their range of process variance to indicate the amount of variation in population growth attributable to the range of variation in each parameter. Parameters with the highest $r^2$ have the greatest impact on population dynamics (Beissinger et al. 2008). For vital rates deemed important from our VSS and LSA, we further explored their contribution to $\lambda$ across the range of each parameter by plotting 1) loess-smoothed trends of VSS estimates against their vital rate inputs (M. Anderson, IWWR, unpublished data) and 2) coefficients of determination as a function of a single vital rate while holding all other vital rates constant at mean values (Hoekman et al. 2002).

**Cost Estimates**

We estimated the cost of predator management per incremental mallard produced by using the approximate cost of predator removal (PRED; Delta Waterfowl Foundation, unpublished data) per site divided by the total breeding pairs per site that were mallards (MALLPROP; Pieron 2010) to estimate the cost of predator removal associated with mallards. We divided this cost by the average number of mallards produced per site (MP×P) to obtain the cost of predator removal per incremental mallard (MC).

$$MC = \left( \frac{PRED}{MALLPROP} \right) \div (MP \times P)$$
RESULTS

North Dakota Vital Rates

Pair abundance (Pieron 2010), initial brood size (two-tailed t-test; \( t = -1.32, P = 0.21 \)), and fledging survival (two-tailed t-test; \( t = -0.22, P = 0.83 \)), were not statistically different between trapped and control sites. However, adjusted hen success was 16.5% higher on trapped sites, whereas pair abundance and initial brood size were slightly higher on control sites (76 pairs and 0.41 ducklings, respectively; Table 2). Finite rate of population change (\( \lambda \)) averaged slightly higher on trapped sites (\( \lambda = 0.81; 95\%\ CI: 0.55 – 1.20 \)) than control sites (\( \lambda = 0.76; 95\%\ CI: 0.53 – 1.11 \)) and our model predicted declining populations for both treatments in these years.

Sensitivity Results

Vital rate estimates were pooled across treatments for sensitivity analyses (Table 2, “Overall”). Results from our LSA found over half of the variation in \( \lambda \) was explained by fledging survival (\( r^2 = 0.56 \)). Breeding season survival of females, winter survival of females and juveniles, and to a lesser extent hen success were also important (\( r^2 = 0.24, 0.12 \) and 0.073, respectively); and brood size (\( r^2 = 0.01 \)), juvenile survival (\( r^2 = 0.00 \)), and nesting propensity (\( r^2 = 0.00 \)) had negligible effect on population change (Fig. 1). Fledging survival and hen success explained approximately 94% of the variation in production (MP; \( r^2 = 0.83 \) and 0.11, respectively). To maintain population size (\( \lambda = 1.00 \)), an adjustment of one parameter would require fledging survival \( \geq 0.35 \), or breeding season survival \( \geq 0.91 \). No other single vital rate could increase \( \lambda \) enough to stabilize the population. We plotted coefficients of determination (\( r^2 \)) as a range of loess
smoothed vital rates for fledging survival and female breeding season survival, holding all other rates to mean values. Fledging survival is most important when it is less than 0.64, at which point hen success becomes the strongest predictor of population growth (Fig 2a). Breeding season survival was the most important parameter affecting lambda when it was less than 0.43, after which fledging survival became the most important parameter (Fig 2b).

Consistent with our LSA, fledging survival had the highest mean VSS (1.58), followed by breeding season survival (0.79), winter survival (0.63), hen success (0.56), initial brood size (0.36), juvenile survival (0.29), and nesting propensity (0.12). Plotting vital rate sensitivity across the range of process variation in fledging survival showed a general decline in sensitivity of survival rates as fledging survival increased and an increase in reproductive rate sensitivity (Fig. 3).

Cost evaluation

During the years of our study predator removal cost approximately $40,000 per site (F. Rohwer and J. Brice, personal communication). Mallards constituted 26% of the breeding pairs on each site (Pieron 2010), which translated to $10,400 per site spent on mallard production. Delta originally predicted trapped sites produced 3.58 mallards (of both sexes) per female compared to 1.40 mallards per female on control sites (Table 1). Our revised estimates predicted trapped sites produced 0.59 mallards per female (95% CI: 0.10 – 1.40) compared to 0.46 mallards per female on control sites (95% CI: 0.07 – 1.16). Our model predicted 0.12 additional mallards per female (95% CI: 0.74 fewer – 0.99 more) on trapped sites, at an average cost of $82.12 (95% CI: $7.92 – $10,400) per
mallard. These production estimates are 18.1 times lower than Delta’s original production estimate of 2.17 incremental mallards per female and 12.9 times more expensive than their predicted cost of $6.39 per incremental duck.

Delta’s entire North Dakota predator management program (7 sites in 2006-2007) contributed an average of 887 additional mallards (95% CI: 7,440 less – 9,215 more) of both sexes annually to the fall flight in 2006-2007.

DISCUSSION

Our research into the production and recruitment of mallards in North Dakota resulted in several major findings. First, mallard populations in 2006-2007 declined by an average of 20.3% annually, suggesting our estimates of vital rates were either biased low or below sustainable levels for reasons beyond the scope of this paper. Second, our results were inconsistent with the tenet that nest success is the most important vital rate for mallard population growth (Hoekman et al. 2002). Results indicate that during our study, fledging success, not hen success, was the most important factor regulating mallard population growth followed by breeding season and winter survival (Fig. 1). Finally, our results suggest the benefits of predator management to mallard production have not materialized in North Dakota, even with a substantial increase in nest success.

Our model predicted declining populations in 2006-2007, although 95% confidence intervals of λ overlapped 1.0 and pair abundance was similar from 2006-2008 (Pieron 2010). A recent sensitivity analysis conducted from the PPJV assessment (1993-2000) reported declining mallard populations in the prairie-parklands (λ = 0.95, M. Anderson, IWWR, unpublished data), and Hoekman et al. (2002) also predicted declining
populations of midcontinent mallards ($\lambda = 0.82$) using much of the same data. Further examination of our vital rates found fledging and female breeding season survival were the only two vital rates that could be individually manipulated to increase $\lambda \geq 1$. This would require a 15% increase in fledging survival or a 19% increase in breeding season female survival.

Although we attempted to estimate as many vital rates as possible from our study site-years, survival and breeding propensity estimates were derived from the literature and may not be directly applicable to our study sites. Estimates of annual survival are from 1960-1985, and given the dependence of waterfowl survival to environmental stochasticity and annual weather patterns (Krementz et al. 1997), these results may not reflect current levels of survival and, to our knowledge, no more recent estimates exist for midcontinent mallards. Additionally, estimates of breeding season survival and nesting propensity were taken from the PPJV assessment in the Canadian prairie-parklands, which may not be relevant to the drift prairie since predator communities may differ in these two areas (Sargeant et al. 1993).

Hen success, breeding pair abundance, and duckling survival estimates in our study site-years were atypical and heavily influenced our rates of production and population growth. Nest success (uncorrected for renesting and female survival) averaged 42% on control sites in 2006-2007, which is much higher than estimates from smaller experimental sites in our general study area in 1994-1996 (23%; Garretson and Rohwer 2001) and 2001-2002 (29%; Chodachek and Chamberlin 2006), and was well above what is necessary to maintain populations in areas with higher duckling survival
(Cowardin et al. 1985). Pieron and Rohwer (2010) speculated that low fox abundance during 2006-2007, and high perennial cover on all sites may have contributed to our exceptionally high estimates of nest success. Mallard breeding pair density was, on average, 15 pairs/km$^2$ (38 pairs/mi$^2$), which translates to roughly 56 pairs of all species per km$^2$ (146 pairs/mi$^2$). These estimates are well above the approximately 80-100+ pairs/mi$^2$ of the 5 most common dabbling duck species predicted across our study sites (HAPET 2008). However, a post-hoc LSA found overall breeding pairs (simulated with empirical standard error since they were an expanded count) explained only 1% of the variation in the number of ducklings produced ($MP \times P$) per site. Mean duckling survival to 30 days post-hatch ($\bar{x} = 0.203$; Chapter 1, this document) is among the lowest ever reported in the prairies (Lokemoen et al. 1990, Pietz et al. 2003, Krapu et al. 2004, Stafford and Pearse 2007), which could be a result of brood predation by high densities of raptors and mink (Chapter 1, this document). Chapter 1 of this document found duckling survival was best explained by a logistic function of age that reached an asymptote at approximately 30 days-old. Realistically, survival may still increase slightly from 30-54 days of age as ducklings become better at locomotion and gain experience in foraging and predator avoidance (Anderson and Alisauskas 2001). Therefore, we extended our day 30 estimate of DSR out to 54 days post-hatch, which is probably biased low. Using constant survival from 30 to 54 days old estimated 4.9% lower survival to 1 August than using juvenile survival rates for the same number of days. By taking the mean of these two survival estimates (90.9%), fledging survival would have increased by approximately 0.5%, and the number of ducks produced by 10 birds per site. Therefore, assuming
constant survival from 30 to approximately 54 days of age may have lowered our estimates of production slightly, but would not have changed differences between treatment-specific production rates.

Fledging survival was the most important factor affecting population change in our study, followed by breeding season and winter survival. At first glance our results are inconsistent with Johnson et al. (1987) and Hoekman et al. (2002), who found that nest success was the most important vital rate affecting population change in midcontinent mallards. However, Hoekman et al. (2002) noted that as nest success reached approximately 40%, duckling survival became the most important vital rate. Nest success was, on average, above that threshold in our site-years, whereas our estimates of duckling survival were much lower, causing duckling survival to be the most important vital rate in our model. At current fledging survival rates, manipulating hen success in an LSA had little effect on $\lambda$ at any level, and when nest success was lower (< 35%), breeding season survival explained the most variation in population change (Fig. 5). These results are also consistent with Koons et al. (2006), who found that survival parameters were most important to lesser scaup population growth.

Our site and time-specific estimates of increased production on predator management sites in North Dakota are 8% of what Delta Waterfowl Foundation originally predicted, and the entire predator management program in North Dakota contributed a trivial amount (0.008%) to the fall flight of midcontinent mallards (FWS 2007). Predator management had no effect on duckling survival to 30 days of age (Chapter 1, this document), which is inconsistent with a previous study that found an
increase in duckling survival on predator managed sites in Saskatchewan (Pearse and Ratti 2004). Chapter 1 of this document hypothesized that this effect could be partially explained by the abundance of mink (*Neovison vison*) and raptors, which are not effectively removed by traditional trapping. Additionally, once nest success was converted into hen success and corrected for nest failure due to female mortality, the difference in hen success between trapped (0.690) and control sites (0.525) was much smaller than the near doubling in nest success reported in the literature (Garretson and Rowher 2001, Chodachek and Chamberlin 2006, Pieron and Rohwer 2010).

Unfortunately, we were unable to assess the effects of predator management on summer female survival. Breeding season survival may have increased under predator management, but a significant reduction is unlikely since red fox populations were so low during these years (Pieron and Rohwer 2010), and alternative hen predators (e.g. raptors) were unaffected by predator control.

Incremental mallards produced on predator management sites comprised 0.008\% (95\% CI: 0 – 0.092\%) of the mean midcontinent mallard population in 2006-2007 (10.65 million birds, FWS 2007). To estimate the scale and cost needed to increase waterfowl populations on a continental scale, we estimated the number of sites and cost associated with increasing the Midcontinent fall flight of mallards by 1\%. A 1\% increase in the fall flight would most likely provide additional hunting opportunity, but is still well below minimum detectable levels of population change at this scale (2006-2007 fall flight index was reported with a 95\% CI of 9.4\%). It would take 840 (lower bound of 95\% CI = 81 sites) predator management sites (4,500 mi$^2$ total) at an annual expense of $33.6 million
USD (lower bound of 95% CI = $3.24 million USD) to increase the midcontinent mallard fall flight by 1%. However, conducting predator management on this scale would be infeasible for logistical reasons including obtaining landowner permission and availability of highly skilled trappers. Additionally, enacting lethal predator control on this scale could be subject to public backlash from anti-hunting and animal-rights organizations (Messmer et al. 1999).

If predator management is not a viable option to maintain and increase waterfowl populations, what are the alternatives? Traditional waterfowl management has focused on permanent habitat and wetland protection, which may appear more cost effective since once land is purchased, it is conserved in perpetuity. However, there are substantial maintenance and monitoring costs associated with habitat acquisition (Hollevoet and Dixon 2007), and it is estimated that in some areas greater than 40% of the landscape must be in perennial cover to reach nest success levels that could maintain populations (Reynolds et al. 2001). There is a large gap in our knowledge of the cost-efficiency of waterfowl management programs, and to date we know of only two cost-benefit analyses have been completed for waterfowl management (Lokemoen 1984, Rashford and Adams 2007). Both studies found direct management activities (e.g., predator management) were more cost-effective than primary land-use activities (e.g., CRP, wetland restoration). However, estimates of cost efficiency are highly dependent on available vital rate data, and as our study illustrates, these can be spatially and temporally variable. Additional research into demographic rates and the cost-effectiveness of waterfowl
management programs is needed to better estimate the relative costs of waterfowl
management techniques.

In terms of production, U.S. agriculture policy (e.g., CRP, “Swampbusters”) has
been the most effective tool in waterfowl conservation on a continental scale (Reynolds
et al. 2001). These provisions, however, were not originally intended as wildlife
conservation programs, and as global markets increase demands for food, livestock feed,
and biofuel, their future is uncertain (Higgins et al. 2002). From 2007-2009, North
Dakota lost over 20% of its 3.4 million acres of CRP to row crop agriculture (USDA
2010), and recent federal estimates suggest the loss of CRP would result in the loss of
grass and wetlands that add 6.2 million ducks annually to the fall flight (HAPET 2009).

MANAGEMENT IMPLICATIONS

Although suggested as a cost effective management tool (Lokemoen 1984, Rashford and
Adams 2007), predator management may have diminishing returns in areas where duckling
survival is low but nest success levels are already high (Cowardin et al. 1985). Changing
site-selection criteria to target areas with low perennial cover (low potential nesting success)
but high wetland densities (good potential brood survival) may provide an increase in overall
recruitment. However, recent research in Saskatchewan found predator management in a
highly fragmented landscape with little (< 15%) perennial cover did not result in increased
nest success, possibly due to increased predation and decreased trapping efficiency in highly
fragmented landscapes (J. Dassow, Southern Illinois University, personal communication).

Managers shouldn’t assume that high nest success = high production. Our study
illustrates the need for local assessment of vital rates in order to a) determine which vital
rates drive population growth, and b) what management actions may increase those rates. In our site-years, wetland density was positively correlated with duckling survival (Chapter 1, this document), and wetland conservation may be more important to recruitment, especially in areas with nest success above threshold levels (Cowardin et al. 1985). However, although hen success and duckling survival were weakly negatively correlated ($r = -0.15$), higher hen success results in a shift toward earlier hatch dates for mallards, which has been shown to increase duckling survival (Dzus and Clark 1998, Guyn and Clark 1999, Pietz et al. 2003). Breeding season female survival is most likely a direct result of predation rates, and although we doubt predator management increased female survival substantially in our study, increasing perennial cover may reduce predator foraging efficiency (Reynolds et al. 1994, Stephens et al. 2005, Arnold et al. 2007), and a decrease in woody vegetation may reduce raptor populations (Murphy 1993, Martin 2009).
Table 1. Vital rate estimates used by Delta Waterfowl Foundation (F. Rohwer, personal communication) to estimate the number of mallards produced per 93.2 km² (36 mi²) site where densities of mammalian predators were reduced during the breeding season (Trapped) versus untrapped control sites (Control). Their estimates did not incorporate juvenile or breeding female survival.

<table>
<thead>
<tr>
<th>Vital Rate</th>
<th>Trapped</th>
<th>Control</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding Pairs (P)(^a)</td>
<td>749</td>
<td>749</td>
<td>Reynolds et al. (1996); assuming 20.8 mallard pairs per mi(^2)</td>
</tr>
<tr>
<td>Hen Success (H)(^b)</td>
<td>0.624</td>
<td>0.393</td>
<td>Garretson and Rohwer (2001), Johnson (1979)</td>
</tr>
<tr>
<td>Clutch Size(^c) (CS)</td>
<td>10</td>
<td>10</td>
<td>Alisauskas and Ankney (1992)</td>
</tr>
<tr>
<td>Duckling Survival (DS)</td>
<td>0.573</td>
<td>0.357</td>
<td>Pearse and Ratti (2004); to 30 days post-hatch.</td>
</tr>
<tr>
<td>Mallards Produced (MP)</td>
<td>2,678</td>
<td>1,051</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Pair numbers are corrected for the proportion of all breeding pairs that were mallards (total pairs × 0.26; Pieron 2010)

\(^b\) Mean nest success (NS) estimates from trapped and control sites (0.473 0.211, respectively; Garretson and Rohwer 2001) corrected for renesting using \(H = NS \times e^{(1-NS)^2}\) (Cowardin and Johnson 1979).

\(^c\) Clutch size was not corrected for probability of egg hatch.

\(^d\) Not incorporated
Table 2. Vital rate estimates, process variance (σ), and data sources used to estimate the number of mallards produced per 93.2 km² (36 mi²) site in northeastern North Dakota, 2006-2007. Densities of mammalian predators were reduced during the breeding season on 5 sites (Trapped), treated as an experimental control on 3 sites (Control; 4 sites for fledging survival), or were pooled across all sites (Overall).

<table>
<thead>
<tr>
<th>Vital Rate</th>
<th>Trapped</th>
<th>σ</th>
<th>Control</th>
<th>σ</th>
<th>Overall</th>
<th>σ</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding Pairs (P)</td>
<td>1,327</td>
<td>104.81a</td>
<td>1,403</td>
<td>160.57</td>
<td>1,356</td>
<td>86.21</td>
<td>Pieron 2010</td>
</tr>
<tr>
<td>Nesting Propensity (NP)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.97</td>
<td>0.02</td>
<td>Hoekman et al. 2002; IWWR, unpublished data</td>
</tr>
<tr>
<td>Breeding season survival (B)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.72</td>
<td>0.07</td>
<td>Hoekman et al. 2002; IWWR, unpublished data</td>
</tr>
<tr>
<td>Hen Success (H)b</td>
<td>0.69</td>
<td>0.04</td>
<td>0.53</td>
<td>0.07</td>
<td>0.63</td>
<td>0.10</td>
<td>Pieron and Rohwer 2010, Arnold et al. 2010</td>
</tr>
<tr>
<td>Brood Size (BS)</td>
<td>7.85</td>
<td>0.56</td>
<td>8.26</td>
<td>0.24</td>
<td>4.00</td>
<td>0.26</td>
<td>Amundson, unpublished data, Pieron 2010</td>
</tr>
<tr>
<td>Fledging Survival (FS)c</td>
<td>0.18c</td>
<td>0.10</td>
<td>0.18</td>
<td>0.11</td>
<td>0.18</td>
<td>0.10</td>
<td>Chapter 1, this document</td>
</tr>
<tr>
<td>Juvenile Survival (J)d</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.86</td>
<td>0.03</td>
<td>L. Beaudoin, unpublished data</td>
</tr>
<tr>
<td>Winter Survival (W)c</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.80</td>
<td>0.05</td>
<td>Hoekman et al. 2002; IWWR, unpublished data</td>
</tr>
</tbody>
</table>

---

* Standard errors were not available on per site estimates of breeding pair abundance, so SE is from all 15 site-year estimates and is not process variance alone.
b Hen success is nest success corrected for renesting and upward adjusted by 5% to account for nests that failed due to female mortality that was already accounted for in breeding season survival.

c to approximately 54 days post-hatch. Thirty-day estimates (Chapter 1, this document) were extended by taking day 30 DSR out to August 1 ($\bar{x} = 24$ days).

d Juvenile survival is from fledge to the average start of resident hunting season in 2006-2007 (September 22)

e $W = \frac{\text{Annual survival (Chu and Hestbeck 1989)}}{\text{Breeding Season survival (Hoekman et al. 2002; IWWR, unpublished data)}}$
Figure 1. Coefficients of variation ($r^2$, sum = 1) from a life-stage simulation analysis on demographic vital rates affecting finite population change ($\lambda$) in mallards in North Dakota, 2006-2007. Fledging success (FS) explained the most variation in population growth, followed by female breeding season survival (B), winter survival (W), and hen success (H). We pooled less important vital rates (Other).
Figure 2. Results from a life-stage simulation analysis of female mallards in northeastern North Dakota, 2006-2007 across the range of process variation in fledging survival (a), and breeding female survival (b). Other parameters are held at mean values. We present loess smoothed coefficients of determination ($r^2$) with finite population change ($\lambda$) of the 4 most important (highest $r^2$) vital rates ($FS =$ fledging survival, $B =$ breeding female survival, $H =$ hen success, and $W =$ wintering female survival). Vertical dotted lines represent mean values of the varied parameters ($\bar{x}_{FS} = 0.18$, $\bar{x}_B = 0.72$).
Figure 3. Loess smoothed plots of 10,000 simulated variance-stabilized sensitivities of female mallards in northeastern North Dakota, 2006-2007 across the range of process variation in fledging survival. Other parameters are held at mean values. We present the 4 vital rates with the highest sensitivities (FS = fledging survival, B = breeding female survival, H = hen success, and W = wintering female survival). Mean fledging success in our site-years was 0.18.
Figure 4. Results from a life-stage simulation analysis of female mallards in northeastern North Dakota, 2006-2007, across the range of process variation in hen success. Other parameters are held at mean values. We present loess smoothed coefficients of determination ($r^2$) with finite population change ($\lambda$) of the 4 most important (highest $r^2$) vital rates (FS = fledging survival, B = breeding female survival, H = hen success, and W = wintering female survival). Mean hen success was 0.59 (vertical dotted line).
LITERATURE CITED


Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and T. L. Shaffer. 1993. Distribution and abundance of predators that affect duck production in the Prairie Pothole


APPENDIX A: EFFECTS OF RATIO-TRANSMITTERS AND PLASTICINE BANDS ON MALLARD (ANAS PLATYRHYNCHOS) DUCKLING SURVIVAL

Individualized markers are vital to understanding the behavior and demography of birds, yet few studies have tested the fundamental assumption that markers do not influence survival (Murray and Fuller 2000). Marking of hatchling waterfowl is often necessary to quantify survival, cause-specific mortality, or movements after leaving nests (Sedinger 1992). For survival analysis, plasticine bands and radio-transmitters have been widely used to individually mark day-old waterfowl.

Plasticine-filled leg bands are USGS metal bands engraved with contact information. The inside of each band is filled with non-drying clay designed to fit the tarsus of hatchling ducks (Blums et al. 1997). The clay erodes as the duckling grows, eventually providing a small snug-fitting tarsal band for the fully-grown duck. Plasticine bands were first developed in Latvia (Blums et al. 1999) and have gained popularity in North America in recent years as an alternative to web tags (Davis et al. 2001, Stafford and Pearse 2007, Coulton and Clark 2008). Blums et al. (1999) compared survival rates of Wood Duck (Aix sponsa) ducklings marked with plasticine bands versus web tags and found no deleterious effects of plasticine bands on survival. Additionally, plasticine bands had almost perfect retention in a study comparing retention of web tags and plasticine bands in several species of ducks (Blums et al. 1994).

Radio-tagging ducklings can provide information about brood-mixing and cause-specific mortality (Mauser et al. 1994, Chouinard and Arnold 2007). Several investigators have used prong-and-suture radio-transmitters (Mauser and Jarvis 1991) on day-old ducklings and found no effects on survival (Krementz and Pendleton 1991,
Mauser et al. 1994, Chouinard and Arnold 2007, Stafford et al. 2002). However, Pietz et al. (2003) and Krapu et al. (2004) found that survival rates of radio-marked Gadwall (Anas strepera) and Mallard (Anas platyrhynchos) ducklings were lower than for unmarked siblings.

During a two-year investigation of Mallard (Anas platyrhynchos) duckling survival in North Dakota, we marked day-old ducklings with either plasticine-filled leg bands or prong-and-suture transmitters. Because we also had radio-transmitters on attendant females and were able to locate and determine the fates of unmarked ducklings, we were able to compare daily survival rates and cumulative fledging probability of marked and unmarked ducklings. Our objectives were to test for effects of markers on survival and measure the extent of any associated biases.

METHODS

Our study was conducted at nine 92.3-km² study sites in the Drift Prairie eco-province in the Devils Lake Wetland Management District in northeastern North Dakota. Two sites were only used in one year (Harlow 2006, Alsen 2007), giving us a total of 16 site-years. Our sites were part of a study designed to assess the effects of brood density and predator removal on Mallard duckling survival (Amundson 2010) and five sites had mammalian meso-predators, primarily striped skunk (Mephitis mephitis) and raccoon (Procyon lotor), removed during the waterfowl breeding season while the remaining four sites served as controls (Amundson 2010). Sites had 6.5 – 20.6 km² of seasonal and semi-permanent wetlands with 37 - 119 breeding waterfowl pairs per km² (Amundson
2010, Pieron 2010). Our study area was predominately small grain or row crop agriculture, but contained > 20% perennial cover via Conservation Reserve Program (CRP) lands and Waterfowl Production Areas (Pieron and Rohwer 2010).

**Data collection.** In 2006 and 2007, we captured female Mallards on their nests during late incubation and marked them with 9-g prong-and-suture transmitters. We visited nests on the estimated day of hatching to mark ducklings with plasticine-filled metal leg bands (Blums and Davis 1999). We adjusted outer band diameter after attachment to between 9.0 and 9.5 mm. We used a 50% Roma Plastilina #1 (Sculptor House Inc., Skillman, NJ), 50% DaVinci Soft (Chavant Professional Plasteline Inc., Farmingdale, NJ) mixture early in the season (prior to 11 June) and then switched to 60% Roma Plastilina, 40% Chavant DaVinci for the duration of the season (P. Blums, pers. comm.). We pre-filled bands with clay and refrigerated them when not in use. In 2006, we also fit two randomly selected ducklings per brood with 1.8-g prong-and-suture transmitters (covariate TRANS; Advanced Telemetry Systems, Isanti, MN) equipped with a mortality sensor (Mauser and Jarvis 1991). Due to imperfect prediction of hatching times, some broods were completely missed or only partially banded (i.e., broods left nests before they could be banded or 1-4 eggs had not yet hatched when brood mates were banded). Because we could not distinguish between banded and unbanded ducklings during subsequent visual observations, our measure of a banding effect (covariate BAND) was the proportion of non-radiomarked ducklings per brood that received plasticine bands (e.g., if 7 of 8 non-radiomarked ducklings were banded, BAND
= 0.875 for all ducklings in that brood). Radio-marked ducklings did not receive plasticine bands (BAND = 0, TRANS = 1).

We estimated locations of brood-rearing females by null-peak triangulation (Kenward 1987) using Location of a Signal software (LOAS; Ecological Software Solutions LLC 2009). We monitored radio-marked females every day until 10 d post-hatching and every second day from 11-30 d post-hatching, or until female mortality, total brood mortality, or radio failure. We located broods using homing telemetry of the female transmitter every third day for the first 12 d post-hatch and then every 7-10 d until 30 d post-hatching and we opportunistically attempted to count the number of ducklings. We observed broods from a distance (>50 m) using spotting scopes to avoid disturbance until the final count (approx. 30 d) when we used more invasive techniques (e.g., beat-outs; Paquette et al. 1997, Pearse and Ratti 2004). We made an additional attempt to see the entire brood when we suspected brood counts were incomplete (e.g., ducklings in thick vegetation or brood seen only briefly). We located duckling signals with the same protocol used for adult transmitters, although we frequently located females first before picking up weaker signals from duckling transmitters. When we detected a mortality signal, we located ducklings to confirm mortality.

**Statistical analyses.** Because we had uneven intervals between resightings of broods, we estimated duckling survival using the nest survival module in Program MARK (i.e., ragged telemetry; Dinsmore et al. 2002, Colwell et al. 2007). This method uses maximum-likelihood methods rather than a mid-point assumption to estimate when mortality occurred for ducklings that disappeared between observations (Dinsmore et al.
2002). We structured our capture histories based on duckling age rather than calendar date, included site and year effects by recognizing a unique attribute group for each site-by-year combination, included individual and brood-specific covariates to account for variation in hatch date and marking methods, and employed a logit link function for all models. All ducklings at one site (Harlow 2006, N = 3 broods) died or had to be censored before the first resighting following radio failure and we were unable to estimate survival or variance for this site, so we censored data for this location (Stafford and Pearse 2007).

We used a hierarchical approach for model selection (Lebreton et al. 1992, Chouinard and Arnold 2007). Amundson (2010) found no evidence of a predator-removal effect on survival and so we did not include a predator-removal term in our models. Also, age effects were best explained by modeling daily duckling survival ($S_i$) as a linear-logistic function of duckling age ($\text{logit}[S_i] = \beta_0 + \beta_1 \cdot \text{Age}$, where Age = 1-30 d), so we employed this age structure to all models (Amundson 2010).

The logit transformation allowed flexibility to fit models where daily survival was an asymptotically increasing function of duckling age, which represents a more biologically realistic approach than pooling survival into arbitrary periods (Chouinard and Arnold 2007). We considered four models incorporating general spatial and temporal variation because survival varied among sites and between years (Amundson 2010): 1) Age*Site*Yr, 2) Age*Yr, 3) Age*Site, and 4) Age+Site+Yr, where * and + denote factorial versus additive relationships between variables, respectively. We ranked models based on Akaike’s information criterion (AIC) corrected for small sample size.
and over-dispersion ($\text{QAIC}_c$; Burnham and Anderson 2002). We accounted for over-
dispersion ($c$) due to non-independence among brood mates by setting $\hat{c} = 3.60$
(Amundson 2010), using methods outlined in Bishop et al. (2008).

Using the best-supported model of year and site effects as a base model, we added
hatch date and year-by-hatch date as brood-specific covariates to account for potentially
confounding effects of hatch date on survival (transmitters were only used in 2006, and
there was a weak negative correlation between hatch date and the probability of receiving
bands or transmitters: $r = -0.16$ and -0.15, respectively). We retained hatch date and
year-by-hatch date if each variable led to a net reduction in QAIC$_c$ (Burnham and
Anderson 2002:131). Finally, to this best-approximating base model, we added the
effects of banding and radio-marking as simple additive covariates (i.e., affecting survival
of ducklings of all ages at all sites equally on the logit scale) and retained each variable if
it led to a net reduction in QAIC$_c$. Additionally, we examined a year-specific banding
effect and applied a radio-marker effect to 2006 data only because transmitters were only
used that year.

From our best supported model, we report year-specific geometric mean
cumulative survival to 30 d of age as well as a standard error based on process variation
($\sigma$) from all 15 site-years. Process variation represents an estimate of the real
spatiotemporal variation in survival after partitioning out variation due to sampling error
(White 2000). We report 85% confidence intervals (CI) rather than the more typical
95% CI because they are more compatible with AIC-based model selection (Arnold
2010).
RESULTS

We radio-marked 82 ducklings from 43 broods and banded 572 ducklings from 85 broods, including all non-radiomarked ducklings from 58 broods and 1 - 8 ducklings per nest from 27 broods that were partially banded. Our unmarked sample included 77 ducklings from 27 partially-banded broods and 544 ducklings from 83 broods that were unbanded (N = 621 total unmarked ducklings from 110 broods). Our effective sample size, based on total exposure intervals, was 9287.

Our best supported a priori model of daily duckling survival included a linear-logistic effect of duckling age, site effects on both the intercept and slope of this relationship, additive effects of year, hatch date, and their interaction, and additive effects of plasticine bands and radio-transmitters (Table 1). Although there was some model-selection uncertainty regarding whether to include one or both marker effects, models that included some form of deleterious effect of either plasticine bands or radio-transmitters comprised 93% of the cumulative model weights (Table 1). Both radio-transmitters and plasticine bands had deleterious effects on duckling survival (β_{TRANS} = -0.82, 85% CI = -1.32 to -0.33 and β_{BAND} = -0.29, 85% CI = -0.55 to -0.03). Geometric mean cumulative survival was 0.22 (σ = 0.11) and 0.20 (σ = 0.11) for unmarked ducklings, whereas cumulative survival to 30 days of age for banded ducklings was 0.14 (σ = 0.09) and 0.13 (σ = 0.09) in 2006 and 2007, respectively. Cumulative survival to 30 d was 0.04 (σ = 0.03) for radio-marked ducklings in 2006.
We conducted a *post-hoc* analysis to better estimate the persistence of marker effects. We assumed that marker effects would be strongest for newly hatched ducklings and would diminish with age, eventually becoming small enough that they were negligible and non-detectable. We therefore tested nine additional models where the effects of plasticine bands and radio-transmitters declined linearly over the first 30, 21, 14, or 7 d of life. Radio-marker effects were also allowed to decline over the first 4 d of life because dead ducklings were discovered shortly after death, whereas documentation of mortality for banded ducklings relied on resightings that had longer intervals between detection. We first examined models that hypothesized a tapering in radio-marker effects, holding banding effects constant. Then, using the best supported radio-marker effect, we tested models positing tapering effects of bands over shorter intervals. These models were fit using the product function in the design matrix of program MARK, where the 4-d transmitter effect would be implemented by using product(1,TRANS), product(0.75,TRANS), product(0.5,TRANS), and product(0.25,TRANS) for the first 4 d of life and product(0,TRANS) for 5-30 d of age. All nine post-hoc models outperformed the model with constant band and transmitter effects (Table 2), with the greatest support accruing to a model where radiomarker effects disappeared after 4 d and banding effects disappeared after 7 d, but there was considerable model-selection uncertainty about how long banding effects persisted ($\Delta Q_{AIC_c} = 0.16$; Table 2).

**DISCUSSION**
Back-mounted radio-transmitters have been widely used to mark newly-hatched ducklings, but we found that transmitters markedly decreased the survival prospects of Mallard ducklings. Krapu et al. (2004) found that radio-marked Mallard ducklings had lower 30-d survival rates than unmarked ducklings, and Pietz et al. (2003) found that survival rates also decreased for radio-marked Gadwall ducklings. However, other investigators have examined the effects of radio-transmitters on Mallard ducklings and found no difference in survival of marked and unmarked ducklings (Krementz and Pendleton 1991, Mauser et al. 1994, Stafford et al. 2002, Chouinard and Arnold 2007). Additionally, Davis et al. (1999, 2001) found no effect of transmitters on duckling survival or nest box exodus rates in Wood Ducks.

Our study is the first to report deleterious effects of plasticine bands. Blums et al. (1999) found no effect of plasticine bands on duckling survival in six waterfowl species including Mallards, but their study had relatively low power (36-60%) to detect an effect of the magnitude observed in our study (Blums et al. 1999: Table 5).

Several factors likely affect the sensitivity of ducklings to external markers, including morphology, energetic constraints, and habitat use. Radios used in our study were approximately 6% and bands approximately 4% of initial body mass. Although Blums et al. (1999) were skeptical about plasticine bands with weights up to 3.6% of duckling mass affecting duckling survival, we argue that, for species such as Mallards that often have long (≥ 1 km; Dzus and Clark 1997) overland movements to initial and subsequent wetlands, even relatively light markers might be deleterious. In addition, it might not be the weight of bands per se, but the potential for bands to become entangled
in dense vegetation that reduces duckling survival in upland-nesting Mallards. Although several studies have revealed no effects of radio transmitters or plasticine-bands on survival, most of these studies were either conducted in large wetlands where overland movements were minimal once broods reached water (Blums et al. 1999, Chouinard and Arnold 2007) or involved ducks nesting on islands or in artificial nesting structures where overland movements by broods were minimal (Blums et al. 1999, Davis et al. 2001, Stafford et al. 2002, Coulton and Clark 2008). Our study areas and those of Krapu et al. (2004) consisted of numerous isolated wetlands that required sometimes long initial movements (up to 2 km; C. Amundson, unpubl. data) from the nest to wetlands, especially during dry years like 2006 when duckling survival was lower. Additionally, Rotella and Ratti (1992) found a negative association between distance moved and Mallard duckling survival in southwestern Manitoba and found that ducklings moved the greatest distances during the first week post-hatching. Our post-hoc analysis further supports an overland-movement induced marker effect because ducklings over 4-days old appeared to suffer no negligible effects from radios, presumably because older ducklings move less or are more capable of carrying a 1.8-g transmitter.

We did not randomly assign plasticine bands to broods in our study, but rather marked all ducklings that had hatched and were present in nests during our nest visits. Although this could potentially bias results if missed or partially marked broods represent a biased sample, we accounted for study site, year, and hatch date effects in our model to account for the most likely confounding variables (these were the only variables that varied with respect to rates of banding or radio-marking). Additional bias may result
from differential survival of later-hatched ducklings within a brood because those that were missed were the latest to hatch. However, evidence suggests that last-hatched ducklings are least likely to survive (Erikstad et al. 1998), so our estimates of banding effects are likely conservative.

Biologists rely on marked individuals to examine population dynamics, answer ecological questions, and evaluate management actions. However, if markers impact fecundity, survival, or behavior, inferences made from such studies may be biased. Although other investigators have suggested that anchor-suture radio-transmitters and plasticene leg bands can provide unbiased estimates of survival (e.g., Blums et al. 1999, Chouinard and Arnold 2007), our results indicate that both types of markers reduced duckling survival. Although it is often not feasible to recapture ducklings after they leave the nest, our post-hoc analysis suggests that waiting to mark ducklings until they are at least 1 week old may negate most adverse effects (we are unable to discount the possibility that the marking process itself caused lower survival for the first few days, and such an effect might occur even if ducklings were marked at later ages). For studies where offspring must be marked in the nest, we recommend continued use of web tags (Haramis and Nice 1980). Investigators using either plasticine bands or anchor-suture transmitters on day-old waterfowl should be aware of likely biases to survival estimates and attempt to incorporate marker effects into estimates of survival.
Table 1. Model-selection results from a priori analyses of Mallard duckling survival in relation to age (1-30 d), site (9 townships in North Dakota), year (YR: 2006 or 2007), Julian hatch date (HD), plasticine bands (BAND), and radiotransmitters (TRANS). Models were ranked according to differences in Akaike’s information criterion (ΔQAICₜ) corrected for overdispersion (ĉ = 3.60) and effective sample size (n = 9287), Akaike model weights (wᵢ), number of estimable parameters (K), and quasi-deviance (QDev = -2log(Likelihood)/ĉ).

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔQAICₜ</th>
<th>wᵢ</th>
<th>K</th>
<th>Qdev</th>
</tr>
</thead>
<tbody>
<tr>
<td>(AGE<em>SITE) + (YR</em>HD) + BAND + TRANS</td>
<td>0.00</td>
<td>0.40</td>
<td>21</td>
<td>593.39</td>
</tr>
<tr>
<td>(AGE<em>SITE) + (YR</em>HD) + TRANS</td>
<td>0.61</td>
<td>0.30</td>
<td>20</td>
<td>596.01</td>
</tr>
<tr>
<td>(AGE<em>SITE) + (YR</em>HD) + (BAND*YR) + TRANS</td>
<td>1.72</td>
<td>0.17</td>
<td>22</td>
<td>593.11</td>
</tr>
<tr>
<td>(AGE<em>SITE) + (YR</em>HD) + BAND</td>
<td>3.66</td>
<td>0.06</td>
<td>20</td>
<td>599.06</td>
</tr>
<tr>
<td>(AGE<em>SITE) + (YR</em>HD)</td>
<td>5.16</td>
<td>0.03</td>
<td>19</td>
<td>602.57</td>
</tr>
<tr>
<td>(AGE<em>SITE) + (YR</em>HD) + (BAND*YR)</td>
<td>5.64</td>
<td>0.02</td>
<td>21</td>
<td>599.03</td>
</tr>
<tr>
<td>(AGE*SITE) + YR</td>
<td>8.40</td>
<td>0.01</td>
<td>17</td>
<td>609.83</td>
</tr>
<tr>
<td>(AGE*SITE)</td>
<td>10.49</td>
<td>0.00</td>
<td>16</td>
<td>613.93</td>
</tr>
<tr>
<td>(AGE<em>SITE</em>YR)</td>
<td>12.84</td>
<td>0.00</td>
<td>30</td>
<td>588.13</td>
</tr>
<tr>
<td>(AGE*YR)</td>
<td>16.23</td>
<td>0.00</td>
<td>4</td>
<td>643.72</td>
</tr>
</tbody>
</table>

*QAICc of top-ranked model = 635.49
Table 2: Model selection results from post-hoc models examining the duration of marker effects on Mallard ducklings. Banding effects (BAND, TRANS) were modeled to decline linearly over 7, 14, 21, or 30 d post-hatch; radiomarker effects were also allowed to decline over 4 d. Models were ranked according to differences in Akaike’s information criterion (ΔQAICc) corrected for overdispersion (c = 3.60) and effective sample size (n = 9287), Akaike model weights (wi), number of estimable parameters (K), and quasi-deviance (QDev = -2log(Likelihood)/c).

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔQAICc</th>
<th>wi</th>
<th>K</th>
<th>Qdev</th>
</tr>
</thead>
<tbody>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND7d + TRANS4d</td>
<td>0.00a</td>
<td>0.20</td>
<td>21</td>
<td>584.42</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND + TRANS4d</td>
<td>0.16</td>
<td>0.18</td>
<td>21</td>
<td>584.58</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND30d + TRANS4d</td>
<td>0.31</td>
<td>0.17</td>
<td>21</td>
<td>584.73</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND14d + TRANS4d</td>
<td>0.46</td>
<td>0.16</td>
<td>21</td>
<td>584.88</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND21d + TRANS4d</td>
<td>0.49</td>
<td>0.16</td>
<td>21</td>
<td>584.91</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND+ TRANS7d</td>
<td>1.87</td>
<td>0.08</td>
<td>21</td>
<td>586.29</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND + TRANS14d</td>
<td>4.41</td>
<td>0.02</td>
<td>21</td>
<td>588.83</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND + TRANS21d</td>
<td>5.72</td>
<td>0.01</td>
<td>21</td>
<td>590.14</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND + TRANS30d</td>
<td>6.68</td>
<td>0.01</td>
<td>21</td>
<td>591.10</td>
</tr>
<tr>
<td>(AGE<em>SITE)+(YR</em>HD)+ BAND + TRANS</td>
<td>8.97</td>
<td>0.00</td>
<td>21</td>
<td>593.39</td>
</tr>
</tbody>
</table>

a QAICc of top model = 626.52
APPENDIX B. VARIABLE DEFINITIONS, RATIONALE, AND DISTRIBUTIONS

YEAR – 2006 or 2007: Annual variation in duckling survival is often pronounced (e.g., Rotella and Ratti 1992, Mauser et al. 1994) and the two years of this study were very different in terms of wetland conditions.

TRAPPED – Whether or not a study site was trapped (had mammalian meso-predators removed); two groups derived from sites. This variable was experimentally administered. Previous research suggests predator removal increases duckling survival (Pearse and Ratti 2004).

SITE – Dummy variables to account for potential study area effects (93.2 km$^2$) (Attribute group 1-9; same 7 sites used in both 2006 and 2007, plus 1 new site in 2007; 1 2006 site was dropped due to insufficient data). Previous studies suggest that geographic variation may impact duckling survival and this variable captures all the differences among study sites, including possible factors we did not measure.

COVER – Proportion idle perennial cover in each site (primarily Conservation Reserve Program and Waterfowl Production Areas; pastures and haylands not included). Habitat composition has been shown to effect predator density and behavior and may impact duckling survival (Simpson et al. 2007, Paasivaara 2008). Distribution of observed values among all site-years: min = 0.11, median = 0.30, max = 0.72.

PAIR – Block-level pair density (all species per 93.2 km$^2$). Higher pair densities may indicate better brood habitat (positive effect), or act to create density-dependence in brood survival by increasing competition for limited food resources for broods (negative effect on survival). Distribution of observed values among all site-years: min = 889, median = 1,324, max = 2,884.

WET3 – Area (km$^2$) of seasonal (Cowardin et al. 1979) wetlands in each 93.2 km$^2$ study block that were inundated in the year of study. An abundance of seasonal wetlands may increase survival by providing additional preferred habitat for broods (Talent et al. 1982). Distribution of observed values among all site-years: min = 1.39, median = 4.87, max = 12.11.

WET4 – Area (km$^2$) of Class IV (Cowardin et al. 1979) semipermanent wetlands in each 93.2 km$^2$ study site that were inundated in the year of study. An abundance of class IV-wetlands may increase survival by providing additional preferred habitat for broods (Raven et al. 2007). Distribution of observed values among all site-years: min = 0.55, median = 5.79, max = 8.74.
WET(3+4) – Area (km\(^2\)) of combined seasonal and semipermanent wetlands (Cowardin et al. 1979) in each 93.2 km\(^2\) study site that were inundated in the year of study. Distribution of observed values among all site-years: min = 6.49, median = 12.71, max = 20.60.

DATE – Hatch Date; date ducklings left the nest. Numerous studies suggest a benefit of early hatching (Guyn and Clark 1999, Pearse and Ratti 2004), but see Dzus and Clark (1998). Distribution of observed values among all site-years: min = 19 May, median = 10 June, max = 3 July.

COND – Index of residual scores from regression of female body mass against size. Size estimates were combined from several morphometric measurements (head length, culmen length, head width, bill width, tarsus length, and wing chord) using a Principal Components Analysis. Females in better condition should have better fledging rates than females in poor condition and this effect may be more pronounced later in the season (Devries et al. 2008). Distribution of observed values among all marked brood females: min = -103.41, median = -0.61, max = 160.30.

BS – Brood size; number of ducklings that leave the nest with a female. Pietz et al. (2003) found ducklings from larger broods survived better than those from small broods. Distribution of observed values among all site-years: min = 2, median = 8, max = 12.

MASS – Average duckling mass within a brood (g). Heavier broods may be less subject to catastrophic events or temporary food shortages than lighter broods (Flint et al. 2006). Distribution of observed values among all site-years: min = 25.18, median = 34.21, max = 41.36.

WEATHER – Index score derived from summing standardized (based on season-long average) values of minimum wind chill (WC = 35.74 + 0.6125\times T – 35.75\times (V^{0.16}) + 0.4275\times T\times (V^{0.16})) and total precipitation. Wind chill estimates were summed with total precipitation (multiplied by -1) to obtain daily scores. Higher scores infer better weather conditions. Scores for the first 10-days post-hatch were weighted based on duckling age (assigning higher weights earlier in life) and then summed to produce the final index score. Distribution of observed values among all site-years: min = -2.43, median = 0.22, max = 1.23.

AGE – Duckling age from 1 – 30 days post-hatch. Numerous studies have shown that most duckling mortality occurs shortly after hatch (e.g., Guyn and Clark 1999, Pietz et al. 2003, Chouinard and Arnold 2007).
DD – Duckling density (all species) per km$^2$ for each study site. An increase in duckling density may lower survival due to increased competition for habitat and food resources (Gunnarrsson et al. 2004), or dilute predator effects leading to an increase in survival (Larivière and Messier 1998). Distribution of observed values among all site-years: min = 74.88, median = 306.55, max = 1095.33.

MALLD – Mallard duckling density per km$^2$ for each study site. An increase in duckling density may lower survival due to increased competition for habitat and food resources and conspecifics are the most direct competitors. Distribution of observed values among all site-years: min = 5.63, median = 29.52, max = 75.61.

HENAGE – Bivariate; 1-year old, 2+ years old; older females have larger clutches, and might be more successful at rearing broods than younger females (Guyn and Clark 1999).