

Trappings of Success: Predator Removal & Habitat Associations with Dabbling Duck Nest
Survival in Alberta Parklands

by

Emily Meagan Blythe

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences
University of Alberta

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ABSTRACT

In mallards and other upland-nesting duck species in the prairies, nest survival is the vital rate most influential to population dynamics, with 15% - 20% survival required for maintenance of stable populations. Nest survival is most limited by nest predation, which often is enhanced by anthropogenic causes including habitat fragmentation, mesopredator release, and predator subsidies. Predator removal during the nesting season has successfully increased duck nest survival on township-sized areas in agricultural ecosystems in the eastern portions of the prairie pothole region. However, predator removal has not been evaluated in western parkland habitats where three-dimensional habitat is considerably greater. During 2015 – 2017, we evaluated nest survival on control and predator-removal plots at two study areas in the central Alberta parklands. In the second year of the study, we transposed predator removal to control for habitat effects. Estimates of 34-day nest survival did not significantly differ between trapped ($\bar{x} = 20.9\%$, 95% CI = 13.2% - 33.7%) and control ($\bar{x} = 17.8\%$, 95% CI = 10.5% - 30.0%) plots in any year. Age of nest upon discovery was the most influential factor on, and had a weak positive association with, nest survival. In the final year of study, crows and ravens might have recognized investigator and nest-marking patterns, leading to exceptionally low nest survival in some plots. For one of our two study areas, the odds of nesting hen mortality were significantly higher on trapped plots (OR = 2.60, 95% CI = 1.03 – 6.58, $n = 467$), contrary to expectation. Predator removal may not have depressed nest predator populations sufficiently to improve nest survival, but potentially drove changes in predator community assemblage in favour of hen predators.

In the Canadian prairie pothole region (PPR), waterfowl management often aims to increase the productivity of duck populations through the acquisition and stewardship of nesting

habitat. Relating habitat characteristics to nest-site selection and nest predation risk can identify source and sink habitats, thereby informing management strategies for lands managed for duck production. We evaluated selection by comparing nest sites monitored in 2016 and 2017 with random locations, and evaluated habitat associations with nest survival by comparing sites of hatched and depredated nests. Based on the best model, hens nested selectively in relatively smaller patches of grassland (hay, pasture, and idle cover combined). Hens selected nest sites that were farther from aspen stands and characterized by taller vegetation that was more homogeneous in height. The best model for nest survival indicated that nests were more likely to hatch in relatively larger patches of grassland characterized by lower wetland edge-to-area ratios associated with large wetlands. Our findings indicate that smaller grassland patches are attractive sinks for upland duck nests, and do not provide evidence of adaptive habitat selection. We recommend that predator removal not be implemented in Alberta parklands due to its ineffectiveness at improving duck nest survival, and that future predator removal programs standardize and quantify removal effort. We recommend prioritization of relatively larger tracts of land for habitat acquisition and suggest management for hay rather than grazing is more effective for duck production in central Alberta parklands. Duck nest success is influenced by greater landscape composition and benefits from a greater proportion of grassland on the landscape, so we recommend greater use of easements and spring-seeded crops.

PREFACE

This thesis is an original work by Emily Meagan Blythe. Field data were collected in accordance with the Canadian Council on Animal Care guidelines and approved by University of Alberta's Animal Care and Use Committee (Protocol # AUP00001473). The DOI associated with this thesis is <https://doi.org/10.7939/DVN/PD2XCX>. Future publications by E. Blythe will be authored under the name E. O'Donovan.

For publication of Chapter 2 M.S. Boyce will be co-author. E. Blythe analysed the data and wrote most of the manuscript. M.S. Boyce provided valuable feedback throughout the analysis and writing process.

M.S. Boyce also will be co-author for publication of Chapter 3. For this manuscript, E. Blythe analysed the data and wrote most of the manuscript. M.S. Boyce provided valuable input during the analysis and writing process.

DEDICATION

I dedicate this thesis to my Dad, Darren Blythe. Thank you for being a constant source of love and support, and for all the years you worked so hard to give Quinn and I a world of opportunity. It is to your devotion I owe this accomplishment, and so much more.

ACKNOWLEDGEMENTS

No part of this project, nor all the opportunities it has afforded me, would have been possible without the support of Delta Waterfowl Foundation (DWF). DWF initially conceived the project, funded all components of the research including my stipend, provided equipment and training, and managed predator removal. Frank Rohwer, Joel Brice, Mike Buxton, Matt Chouinard, and Jim Fisher provided indispensable help with logistics and feedback throughout data analysis and writing. Land access granted by Ducks Unlimited Canada was essential to completion of this research, especially because of unexpected difficulties accessing sufficient private land. Alberta Fish and Game Association, Alberta Conservation Association, and a number of private landowners also generously granted us access. Generous funding from Mitacs Accelerate, Northern Alberta Chapter of Safari Club International, and Alberta Fish & Game Association greatly contributed to making this project a success.

To my supervisor, Mark Boyce, thank you for not letting me quit, and for knowing when I needed a kick in the ass but more often knowing when I needed a hug. Thank you for giving me the space to learn how to learn, for backing me up and supporting me when I needed guidance,

and most of all for allowing me to choose my own adventure. Perhaps the most valuable aspect of this whole experience has been the opportunity to learn through making mistakes, and I'm grateful to both DWF and Mark for sticking with me through all the bumps in the road.

Erin Bayne, Andrew Derocher, Evelyn Merrill, Stan Boutin, Colleen Cassady St. Clair, and their respective labs along with the Boyce lab, all gave me invaluable feedback that was incorporated into this thesis and contributed to my wider learning. Committee members Cindy Paszkowski and Tom Nudds provided helpful insight along the way, and also encouragement and confidence that I was doing interesting work.

I was fortunate to have outstanding technicians who worked tirelessly throughout demanding field seasons. Jessica Melsted, Talia Vilalta, Simon Andrews, Julie Hewlett, Ed Healey, and Sean O'Donovan, you gave it your all and it was a pleasure to work with each of you. Jessica and Julie went above and beyond as crew leaders, and both remained accessible to me for clarifications long after fieldwork wrapped up. Jessica generously shared her talented collection of field photos and videos and provided valuable insight on wetland dynamics. Anne Loosen did a splendid job entering a mountain of data, and Kelsey Norton and her crew collected the 2015 nest data. Hard-working trappers were just as indispensable to the completion of the research and were friendly and helpful faces in the field. Corinne and Jim Thompson not only provided a beautiful field house but invited us for cookouts that were a wonderful opportunity to all get together; your country hospitality was more than we could have hoped for. I'm not sure what to thank Roger Marcil for, because there's nothing he wouldn't have done to help. Roger is one of those rare gems who walks the walk when it comes to wildlife conservation and gives back in spades to the hunting tradition. He showed me around the region, built, installed and maintained a huge number of hen houses, helped design and build flushers, provided valuable insight, and saved me from walking between hen houses by spending a day on his quad with me. It was always a joy to chat and learn from you, and I hope you got a little joy in return watching me doggy paddle in a slough!

My dear friend Kara MacAulay brightened every day in the office and was always eager to help with anything. Annie was always a source of encouragement and wisdom – I'm glad she went first because she set an outstanding example. And thank you to the hundreds of anonymous strangers around the world who taught me R over StackOverflow; I wish I could give you more than an up-vote.

For Chapter 2, Steven Hoekman was exceedingly helpful with lambda estimates and offered thoughtful insight; he set the bar for when I may be a mentor one day. TJ Gooliaff provided insight and references regarding trapping. Meghan Beale unsparingly shared knowledge and code that was invaluable to the completion of Chapter 3. Genevieve Perkins suggested the analytical design for Chapter 3 and provided insightful and supportive feedback. Shane Roersma of Lethbridge College taught me the foundations of waterfowl management and provided insight for this work. John O'Donovan directed me to an ideal source of climate data; precipitation data was provided by the Alberta Climate Information Service, found at <https://agriculture.alberta.ca/acis>.

Dennis and Cheryl Meyer turned me on to ducks and taught me (almost) everything I know, from archery, deer, bird, and bear hunting, ice fishing, canning the bounty we brought home, and countless other skills. The hours we spent walking through the bush, driving the prairie, and freezing our butts off on windswept ice helped shape who I am, and I'll always hold those memories dear. Thank you to John and Margaret for welcoming me into their family and home, which was a respite during field season and a perfect hideaway in my last days of writing. Their support throughout this journey was as important as any. Thank you to my Grandma and Grandpa for always being just a phone call away, whether I needed you to talk me through fixing a quad, or just through a rough day. I could not have done this or many other things without you. You can finally stop asking me what a thesis is, because at long last it's what you're holding in your hands. Dominique Primeau encouraged me to "push it to the limit" and was as forgiving of my long MIA stints as only an unconditional best friend can be. Likewise, thank you to my Aunty Nan for being unwavering in your love no matter how far away I am or how little time I've given you these last few years. Quinn, I'm glad our time in Edmonton overlapped and we could make a couple of my favourite memories. Dad, you were a reliable source of measured advice throughout this project and journey, just as you've always been.

Finally, to Sean, for getting me into this mess in the first place and being an admirable peer, last-minute technician, chef, maid, mechanic, editor, contributor of creative insight, steadfast supporter and patient best friend every step of the way.

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CHAPTER 1 – GENERAL INTRODUCTION

Overexploitation and market hunting in the 1800s led to dramatic reductions in migratory bird populations across North America (Anderson et al. 2018). In 1916, after thirty years of dedicated work by organizations and individuals concerned by population declines, the Migratory Bird Treaty was ratified between Canada and the United States (Anderson et al. 2018). The Migratory Bird Treaty mandated federal regulation of migratory bird harvest in both countries and perhaps most importantly, ended spring hunting (Anderson et al. 2018). Concern about declines of waterfowl populations and their wetland habitats led to the formation of the North American Waterfowl Management Plan (NAWMP), signed by Canada and the United States in 1986 and by Mexico in 1994 (Williams and Castelli 2012, Anderson et al. 2018). NAWMP provided the framework for continental-scale improvement of waterfowl habitat quality and quantity, with the ultimate goal of restoring waterfowl populations to a high level observed in the 1970s (Williams and Castelli 2012, Anderson et al. 2018).

The Prairie Pothole Region (PPR) spans the southcentral portions of the prairie provinces into the northcentral United States, and is characterized by a high density of pothole wetlands formed by glaciation (Stewart and Kantrud 1971). The PPR is critical breeding habitat for many duck species (especially *Anas* and *Aythya* spp.), producing 50% or more of North America's ducks annually, depending on precipitation conditions (Klett et al. 1988, Crimmins et al. 2016). Because of its importance, many waterfowl conservation initiatives have focused on the PPR. Extensive wetland restoration and protection were done in large part by Ducks Unlimited (DU) throughout the 20th century (Anderson et al. 2018). In response to population declines observed in the 1980s and 1990s, intensive management to reduce duck nest predation saw the use of enclosure fencing, construction of artificial islands, installation of nesting structures, and predator trapping (Anderson et al. 2018). At the turn of the 21st century, management paradigms shifted to addressing landscapes as a whole and securing perpetual protection of prime habitat (Anderson et al. 2018).

Today, populations of most duck species are secure and spring surveys indicate that duck populations on the prairies are at their highest levels since 1955 (Anderson et al. 2018). Still, persistently low populations of northern pintail (*Anas acuta*; Devries et al. 2018), greater (*Aythya marila*) and lesser scaup (*A. affinis*; Austin et al. 2000) are cause for concern, and populations of American widgeon (*A. americana*) have failed to meet NAWMP goals (Prairie Habitat Joint

Venture 2014). Waterfowl in North America are an economic, recreational and aesthetic resource valued by nature enthusiasts and hunters (Sovada et al. 2001). Non-governmental organizations like Delta Waterfowl Foundation, DU, and Ducks Unlimited Canada play a critical role in securing duck populations for future generations through ongoing research and implementation of conservation programs.

In Alberta, the PPR consists of three ecosystems: prairie, aspen parkland, and Peace parkland (Prairie Habitat Joint Venture 2014). Alberta aspen parklands, with their semi-forested structure on the western edge of the PPR, are unique from prairie systems in their three-dimensional habitat. In Chapter 2, we present the first evaluation of predator removal for enhancement of duck nest survival in Alberta aspen parklands. This chapter will be submitted for publication in *The Journal of Wildlife Management*. In Chapter 3, we evaluate habitat associations with nest-site selection and nest success on small land parcels managed primarily for duck production. This chapter will be submitted for publication in *Avian Conservation and Ecology*. Both management tools, predator removal and land acquisition, offer approaches for addressing the same issue of low nest survival in key breeding habitats that have been changed by human land use. In Chapter 4, we summarize and compare evaluations for both approaches and provide recommendations for future management.

CHAPTER 2 - PREDATOR REMOVAL INEFFECTIVE AT IMPROVING DUCK NEST SURVIVAL IN CENTRAL ALBERTA PARKLANDS

INTRODUCTION

In mallards (*Anas platyrhynchos*) and presumably other duck species, nest survival is the most important vital rate influencing population dynamics in the Prairie Pothole Region (PPR; Hoekman et al. 2002). Maintenance of stable dabbling duck (*Anas* spp.) populations requires ~15% - 20% annual nest survival (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995); success herein defined as the hatching of at least one duckling. Low nesting success is usually attributed to the degradation of breeding habitat, including the loss of nesting cover and wetlands resulting from agricultural, industrial and residential land use (Beauchamp et al. 1996, Sovada et al. 2001). Anthropogenic habitat alteration also has led to increased nest predation (Klett et al. 1988, Beauchamp et al. 1996, Crimmins et al. 2016).

Nest predation is the strongest limiting factor of nest survival in ducks (Sargeant and Raveling 1992), and indeed most bird species (Ricklefs 1969). Mesopredator release, resulting from the loss of regulatory influence by apex predators, can contribute to enhanced richness and abundance of mid-trophic level predators (Ritchie and Johnson 2009, Suraci et al. 2016). Anthropogenic resource subsidies, provided unintentionally as food or shelter, is another phenomenon that can benefit generalist predators in highly altered habitats (Rodewald et al. 2011, Borgo and Conover 2016a) like the PPR. Loss of cover, concentration of nests in limited habitat, ease of travel by predators, and loss of landscape heterogeneity can enhance foraging efficiency of avian and mammalian predators (Clark and Nudds 1991, Pasitschniak-Arts and Messier 1995, Wirsing et al. 2012, Crimmins et al. 2016). A rich guild of nest predators, arising from anthropogenic changes to the environment, will have a diversity of foraging behaviours increasing the risk to all nests regardless of nest distribution strategy (Jiménez et al. 2007, Ringelman 2014).

Where substantial numbers of ducks breed in areas of attractive habitat, but nest survival remains suppressed due to high nest predation rates, intensive predator management can be an effective tool to mitigate nest losses (Garrettson and Rohwer 2001). The goals and policies outlined in the North American Waterfowl Management Plan (2012) aim to improve waterfowl populations across the continent using strategies based on habitat conservation. However, for

some areas, habitat-based strategies alone have proven inadequate in meeting local management goals; in such cases, short-term intensive management may be warranted and can be beneficial (Sovada et al. 2001). Predator trapping is flexible in its application in regards to space and time (Garrettson and Rohwer 2001) and has been shown to increase nest survival for waterfowl and other avian species (Drever et al. 2004, Smith et al. 2010). For example, predator removal resulted in increased dabbling duck nest survival in prairie ecosystems of Saskatchewan (Lester 2004) and North Dakota (Garrettson and Rohwer 2001, Pieron and Rohwer 2010, Pieron et al. 2012, Amundson et al. 2013), even when done at the relatively small scale of 259 ha (Chodachek and Chamberlain 2006). In the Saskatchewan parklands; however, predator removal was associated with higher dabbling duck nest survival in only one of three monitored years (Dassow 2010). Prevalence of results indicating successful implementation of predator removal may reflect publication bias towards significant results, otherwise known as the “file drawer effect” (Rosenthal 1979). Most evaluation of predator removal to improve duck nest survival has been conducted in prairie ecosystems dominated by agriculture with fewer data from parkland habitats.

Predator removal is done at substantial economic, social, and potential ecological cost, and often must be continued perpetually to maintain results (Smith et al. 2010). Documenting its effects is essential prior to implementation, to avoid unintended consequences and because predator removal can result in economic trade-offs with other initiatives such as habitat acquisition (Sovada et al. 2001, Treves et al. 2016). Potential exists for predator removal to be ineffective due to compensatory predation (Errington 1946, Boyce et al. 1999, Ellis-Felege et al. 2012), immigration (Porter et al. 2015), or increased reproductive output by predators in response to higher mortality (Sterling et al. 1983, Minnie et al. 2016). Other unintended but potential consequences of perturbing complex ecosystems with predator removal include competitive release of alternative prey (Ruscoe et al. 2011) or trade-offs within vital rates of the species meant to benefit. For example, nesting exclosures were found to be successful in increasing hatching rates of snowy plovers (*Charadrius alexandrinus*), but were associated with increased adult mortality, the vital rate to which snowy plover populations are most sensitive (Neuman et al. 2004).

Nest survival may account for nearly half (43%) of the variation in annual population growth rates of midcontinent mallards in the PPR, according to sensitivity analyses done by

Hoekman et al. (2002). However; breeding hen and duckling survival also were important vital rates accounting for 19% and 14% of variation, respectively (Hoekman et al. 2002). Outside the PPR, population growth of mallards in the Great Lakes region was most affected by non-breeding hen survival (36%), duckling survival (32%), and nest success (16%; Coluccy et al. 2008). Presumably, nest success, duckling and breeding hen survival also are important parameters for other species of upland-nesting ducks in the PPR, and possible correlation among them will further enhance their impact on population trajectories (Pearse and Lester 2007). Therefore, it is important to assess the influence of a management action on multiple population parameters (Amundson et al. 2013), especially due to the potential for opposing effects on multiple vital rates (Neuman et al. 2004, Darrah et al. 2018). Apparent competition is an example of a mechanism that may be unintentionally induced by predator removal with negative consequences for adult hen or duckling survival. Apparent competition arises when enhanced predator abundance results from an increase in a primary prey species and predation on other, secondary prey species increases collaterally (Holt 1977, Holt and Lawton 1994, DeCesare et al. 2009). McCarter (2009) found slightly higher raptor abundance on plots where mammalian predators were reduced, because raptors were possibly attracted to these plots by increased abundance of shared prey (though McCarter (2009) suggests predominance of bottom-up trophic forces). McCarter (2009) illustrates an example of how a predator community could shift in favour of principal hen and duckling predators with the removal of primarily egg predators.

Nesting success in the Canadian PPR is generally below that seen in the American portion, due largely to differences in habitat management (Arnold et al. 2007, Drever et al. 2007, Howerter et al. 2014). At the northern extent of the PPR, the parklands of Alberta contain important nesting habitats and predator removal has not been thoroughly evaluated as a method for improving nesting success. Most studies of predator removal to enhance dabbling duck nest survival have occurred in prairie ecosystems, and the most recent evaluation in parkland habitats did not find supporting evidence warranting predator removal (Dassow 2010). Though both ecosystems are dominated by agriculture, three-dimensional habitat distinguishes the parklands from the prairies and the increased structural complexity provides more opportunity for compensatory predation. Socio-economic constraints in Alberta further reduce the probability of effectiveness of predator removal. Legal constraints necessitate partial predator removal, because species of conservation concern including long-tailed weasel (*Mustela frenata*) and American

badger (herein referred to as badger; *Taxidea taxus*) could not be removed following permit stipulations. Logistic constraints in the form of fragmentation of land tenure restrict predator removal to small, isolated land plots where access can be obtained and retained. Due to increased habitat complexity and different socio-economic forces, findings from prairie-based studies in American jurisdictions cannot be generalized to Canadian parkland habitats. It is thus imperative to investigate the use of predator removal to enhance duck nest survival in the aspen parklands prior to its proposed implementation as a management practice.

Nest survival fluctuates with nest age and initiation date (Garrettsen and Rohwer 2001), and temporal trends also may reflect seasonal changes in availability of alternative prey (Larivière and Messier 2000, Ackerman 2002), density-dependent predation (Larivière and Messier 1998), or wetland and cover conditions (Johnson et al. 1989, Greenwood et al. 1995, Emery et al. 2005). Of course, myriad habitat characteristics have been associated with nest survival and these are further discussed in Chapter 3. Observer effects can negatively affect nest survival, particularly in subsequent years of study when territorial predators have had time to learn investigator patterns and form search images for nest markers (Picozzi 1975, Buler and Hamilton 2000). Reducing frequency of nest visitation can lower predation, but “trap-lining” of nest markers by highly cognitive corvid species is a common challenge that has proven difficult to mitigate. In some cases, observer effects may positively bias nest survival; for example, nest cameras used at low density have been associated with higher nest survival, likely because they deter neophobic predators (Richardson et al. 2009).

Our primary objective in this chapter is to evaluate our hypothesis that predator removal would not improve nest survival of upland-nesting ducks in central Alberta parklands as it has in American prairie habitats. Due to enhanced potential for compensatory predation resulting from abundance of three-dimensional habitat and constraints imposed by socio-economic forces, we predicted that nest survival would not differ significantly between predator removal and control plots. In conducting our experiment, we establish baseline nest survival estimates for our study areas in the absence of predator removal. We also address the impact of marking nests on nest survival as well as the influence of predator removal on survival of nesting hens. Based on field observations, we hypothesized that a spatially and temporally explicit cohort of nests was heavily affected because corvid predation was facilitated by recognition of nest markers. Finally, we hypothesized that predation of nesting hens also would not differ significantly between predator

removal and control plots, due to challenges in achieving effective predator removal imposed by complex habitat structure and socio-economic drivers.

STUDY AREA & DESIGN

In June 2014, Delta Waterfowl Foundation biologists conducted ground and fixed-wing reconnaissance surveys of aspen parkland habitats in central Alberta. High densities of both breeding ducks (> 25 pairs/km²) and small (< 2 ha) semi-permanent and permanent wetlands were confirmed near the communities of Bashaw and Viking (Scarth and Brice 2014, unpublished data). Near each community, 30 quarter sections (~64.7 ha parcels) were selected randomly with some constraints to serve as predator removal (“trapped;” $n = 20$) and control ($n = 10$) plots. Quarter sections with more than 65% tree cover, complete absence of water or unsuitable for trapping due to an occupied dwelling were excluded. Trapped and control quarter sections were at least 3 km apart to maintain independence, a distance based on the 12-km² home range of a resident coyote (*Canis latrans*; Roy and Dorrance 1985), the farthest-ranging mammalian predator on the study areas. Within both sets of 20 predator removal plots, half were randomly chosen for nest searching (the remaining 10 were trapped without nest monitoring) and all control plots were monitored. Twenty-seven quarter sections were replaced during the study at the request of landowners. Throughout the study, predator removal was annually transposed on quarter sections provided access was retained; for example, a quarter section that was trapped in 2016 became a control plot in 2017 (figure 1).

Both study areas (Bashaw and Viking) are dominated by agriculture which consists predominantly of cattle grazing, cereal and oil seed production fragmented by a one-mile by one-mile road network and interspersed with oil and gas infrastructure. The landscape is characterized by rolling hills, stands of trembling aspen (*Populus tremuloides*), lakes and numerous pothole wetlands. Overwhelmingly, land is privately owned; however, most data were collected on land managed for duck production by Ducks Unlimited Canada (DUC). Such land was managed for maintenance of nesting cover and any grazing or haying was delayed until after July 15, when most nesting activity had ceased (Larivière and Messier 1998).

In 2015, nest searching was limited to the Bashaw study area with 45% on privately tenured land actively grazed or hayed and 55% on land managed for duck production by conservation groups. Beginning in 2016, work was expanded to the Viking study area. During 2015-2018, 61 quarter sections were nest searched; most sites were managed as rotational

pasture, with the remainder used for hay production. A total of 32 quarters were monitored for nests under both treatment conditions for at least one 3-month season each.

Dabbling ducks that were the focus of this research included mallard, northern pintail (*A. acuta*), northern shoveler (*A. clypeata*), blue-winged teal (*A. discors*), American green-winged teal (*A. crecca carolinensis*), gadwall (*A. strepera*) and American widgeon (*A. americana*). Nest or hen predators observed daily by field technicians included American crow (herein referred to as crow; *Corvus brachyrhynchos*), black-billed magpie (herein referred to as magpie; *Pica hudsonia*), red-tailed hawk (*Buteo jamaicensis*), Swainson's hawk (*B. swainsoni*), and northern harrier (*Circus cyaneus*), while common ravens (herein referred to as raven; *C. corax*) and great-horned owls (*Bubo virginianus*) also were often observed. Other nest or hen predators occurring in our study areas were striped skunks (herein referred to as skunks; *Mephitis mephitis*), raccoons (*Procyon lotor*), coyotes, red foxes (herein referred to as foxes; *Vulpes vulpes*), Franklin's ground squirrels (*Poliocitellus franklinii*), 13-lined ground squirrels (*Ictidomys tridecemlineatus*), badger, long-tailed weasel, short-tailed weasel (*Mustela erminea*), American mink (*Neovison vison*), Northern Goshawk (*Accipiter gentilis*), California gulls (*Larus californicus*) and ring-billed gulls (*Larus delawarensis*). Nest predators notably absent from our study areas include rats (*Rattus* spp.) and egg-eating snakes (Russell et al. 2000, Bourne 2015).

METHODS

One professional trapper was hired to remove nest predators in each study area, Bashaw and Viking, and predator removal took place from March 15 – July 15 of each study year. Crows, ravens, and magpies were shot and targeted with Larsen and ladder traps. Skunks, raccoons, coyotes, foxes and ground squirrels were targeted with snares, box traps, foothold traps and body-gripping traps. Trapping was not standardized, and each professional trapper chose placement, density, type of trap and use of bait based on preference. As per provincial permit guidelines, badgers were not specifically targeted because they are provincially categorized as Sensitive (Alberta Environment and Parks 2015). Weasels (*Mustela* spp.) were not targeted because the long-tailed weasel is provincially listed as May Be at Risk (Alberta Environment and Parks 2015). California gulls and ring-billed gulls are other nest predators (Sargeant et al. 1998) that were excluded from removal efforts.

Upland nest-searching was conducted on each quarter section two to three times a season between May 1 - July 15, by dragging a 30-m chain between 2 ATVs (Klett et al. 1986). Nest

searching was limited to upland areas; forested and riparian areas were not searched. Upon flushing, the hen was identified to species and the nest was marked by GPS and with a thin metal rod at the nest bowl and a painted wooden lathe 10-m north. In 2017, lathes were placed randomly at variable directions and distances ranging from 10-m to 20-m from the nest, in an effort to avoid “trap-lining” by corvids as reported by Picozzi (1975), Buler and Hamilton (2000), and others. Upon discovery and during weekly nest visits, we candled eggs to determine incubation stage (Weller 1956) and monitored clutch sizes. At detection, visual obstruction was measured with a Robel pole at the nest bowl from 4 m in four cardinal directions (Robel et al. 1970, Jiménez et al. 2007). Nests were left covered and conspicuously marked atop with vegetation to indicate investigator-induced abandonment on subsequent visits. We revisited nests every 5-7 days to track incubation, until the nest either hatched or failed due to predation or other causes. Reconyx HC600 Hyperfire Covert trail cameras were deployed opportunistically at a small subsample of 35 nests to identify predators. Cameras were deployed at both study areas on both predator removal and control plots and only on quarter sections where data for at least ten nests had been collected. To reduce abandonment risk, cameras were restricted to nests undergoing incubation (Richardson et al. 2009, Garrettson et al. 2011) and limited to one per quarter section at a time to reduce the risk of search-image formation by predators (Renfrew and Ribic 2003, Richardson et al. 2009).

Nest fates were determined from egg shell condition and other observations at the nest (Klett et al. 1986). Nests were deemed either successful or failed, and failed nests were categorized one of five ways: (1) destroyed by a predator; (2) abandoned due to a predator; (3) abandoned due to investigator activity; (4) abandoned for unknown reasons; or (5) destroyed by an investigator. Abandoned nests contained intact eggs that were cold and no longer developing when characterized as failed. Predator-induced abandonment required evidence of predator activity in the form of missing eggs, partial egg depredation or remains of depredated hens. Investigator-induced abandonment was determined when an ‘x’ made of vegetation left on the nest by investigators remained on the subsequent visit, indicating no return of the hen post-disturbance. Nests abandoned for unknown reasons were revisited by hens following the first investigator visit (ruling out investigator-induced abandonment) and were subsequently abandoned but showed no evidence of predator activity. Destroyed nests had no intact eggs remaining when failure was determined. A nest was deemed successful if evidence indicated that

at least one egg hatched. Nests abandoned during the hatching phase (i.e., all ducklings died while pipping) were categorized as failed nests. When eggs were damaged by investigators they were removed from the nest bowl to reduce olfactory cues.

Nest monitoring was approved by University of Alberta's Animal Care and Use Committee (AUP00001473) and permitted by Alberta Environment and Parks (Research Permit #57638 & Collection Licence #57639). Predator removal was implemented by Delta Waterfowl Foundation and permitted by Canadian Wildlife Service (Permit #15-AB-SC004) and Alberta Environment and Parks (Research Permit #57626 & Collection Licence #57624).

Nest-Survival Modelling

Nests that were successful, or failed through destruction or abandonment due to predators, were included in nest survival analyses; nests that failed due to investigator activity or unknown causes were excluded. Nests that were monitored by a trail camera also were excluded from analyses because the presence of a camera can positively bias nest survival by reducing predation by neophobic predators (Richardson et al. 2009).

The RMark (Laake 2013) nest survival package (White and Burnham 1999) was used to evaluate competing models describing daily survival rates (DSR) of nests as a function of individual-, group-, and time-specific covariates (Dinsmore et al. 2002, Rotella et al. 2004). This generalized linear modelling approach is equivalent to a known fate model with staggered entry, and uses the logit link to relate DSR and selected covariates (McCullagh and Nelder 1989, Rotella et al. 2004). Thus, DSR was estimated by back transformation as:

$$DSR = \frac{1}{1 + \exp\{-[\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \dots + \hat{\beta}_n x_n]\}}$$

where $\hat{\beta}_0$ is the intercept and $\hat{\beta}_i$ is the coefficient of covariate x_i for n covariates (Dinsmore et al. 2002).

An encounter history for each nest formed the input for survival analyses and each nest was described by: (1) the day it was discovered; (2) the last day it was observed to be active; (3) the last day it was observed; (4) its fate (0 = survived, 1 = failed); and (5) the number of nests sharing the same encounter history (Dinsmore et al. 2002, Rotella et al. 2004). We made five assumptions in using this nest-survival model: (1) nests were accurately aged; (2) nest fates were

attributed correctly; (3) discovery and monitoring of nests did not bias survival; (4) nest fates were independent of each other; and (5) daily survival rates were homogeneous (Dinsmore et al. 2002, Rotella et al. 2004). All analyses were carried out in R (R Core Development Team 2016) using the RMark package (Laake 2013).

Nest survival analysis was restricted to nests from quarter sections that were studied under both control and predator removal treatments ($n = 32$). Spatial and habitat differences were largely accounted for by transposing treatment, so model covariates focused on temporal variation in nest survival: initiation date, age found, seasonal trends and year. Study area (Bashaw or Viking) and treatment (trapped/control) also were included as covariates. Year was treated as a fixed effect because we were interested in the transposition of trapping, represented by the combination of year and treatment. A linear time trend was modelled to represent increasing (Garrettson and Rohwer 2001) or decreasing (Arnold et al. 2007) survival through the season. A quadratic time trend represented a peak of nest predation corresponding with a peak for nest density at mid-season (Larivière and Messier 1998), or conversely, increased survival with nest density resulting from predator swamping (Pieron and Rohwer 2010). In models including factorial covariates, the intercept was removed to avoid over-parameterization (Laake 2013). We used Pearson's r coefficient to test for collinearity and did not include covariates in the same model where $|r| > 0.6$ (Dormann et al. 2007).

Akaike information criterion corrected for small sample sizes (AICc) was used to select the most parsimonious model (Burnham and Anderson 2002) from which maximum likelihood estimates of DSRs were derived. On average, nests in our study (species pooled) took 34 days to hatch, so DSRs were raised to the power of 34 to estimate nest survival through the incubation period. To evaluate differences between predator removal and control plots, final nest-survival estimates were compared within 2015 and across 2016-2017 using a series of z-tests and application of a Bonferroni correction (Zar 2010).

Observer Impacts

High numbers of crows and ravens were noted in Viking control plots in 2017 and we suspected that nests were being targeted by corvids that had learned to recognize nest markers. We tested this prediction using chi-square tests as we were unable to quantify observer effects directly.

Observer effects could not be modelled using a time-varying covariate (Rotella et al. 2004) due

to insufficient variation in nest check intervals; particularly in 2017 Viking control plots where most nests failed to survive their first interval.

We reviewed investigator notes for all failed nests from the Viking study area and categorized nests based on descriptions of nest-predation evidence. There were three categories: (1) egg shell fragments completely absent; (2) shell fragments present; or (3) no description provided. A complete absence of egg shells is characteristic of corvid predation (Sargeant et al. 1998) because corvids commonly transport whole eggs from duck nests (Montevecchi 1976). We therefore assigned corvid predation to empty depredated nests, and assumed corvids were not responsible for depredations where egg shells remained. Comparison plots, where enhanced corvid activity was not observed, were pooled and included 2016 Viking trapped plots (spatially-paired), 2017 Viking trapped plots (temporally-paired), and 2016 Viking control plots (paired treatment). To avoid a Type II error, we examined whether collection of data about evidence of predation was similar among 2017 Viking control and comparison plots by categorizing effort for every failed nest (i.e. description of eggshell evidence provided or not). Finally, we created a test dataset where all failed nests lacking data were described as not empty (i.e. not corvid-predated) for 2017 Viking control plots and described as empty (i.e. corvid-predated) for comparison plots. Thus, our fabricated test dataset assigned missing data to the category that would lower test significance, allowing for a conservative test. Chi-square tests of independence compared the following between 2017 Viking control and comparison plots: (1) prevalence of empty depredated nests; (2) effort of data collection; and (3) prevalence of empty depredated nests using the fabricated dataset. Yates' continuity correction was applied to all chi-square tests (Yates 1934) and all analyses were carried out in R (R Core Development Team 2016).

Nesting Hen Mortality

We compared the number of nesting hens found depredated on transposed Bashaw control and trapped plots using Cochran-Mantel-Haenszel (CMH) statistics. We excluded nests from the Viking study area in hen mortality evaluation, because low trapping effort in 2016 (Appendix 1) and potential observer-enhanced nest predation in 2017 (figure 6) introduced biases. We analysed all nests from transposed quarter sections in the Bashaw study area ($n = 467$) and stratified trapped and control plots by year. The Breslow-Day test for homogeneity was used to determine whether the likelihood of hen depredation in trapped versus control plots varied significantly across years (Breslow and Day 1980). A two-tailed CMH test employing Yates'

continuity correction (Yates 1934) was used to evaluate common odds ratios and 95% confidence intervals for hen depredation in trapped versus control plots after adjusting for year (Agresti 2002). The odds ratio produced reflected odds of breeding hen mortality in the predator-removal conditions observed in our study, which we converted to probability of mortality following equation 2:

$$P = \frac{o}{o + 1}$$

where P is probability and o is odds. Analyses were carried out in R (R Core Development Team 2016) using the `vcd` and `DescTools` packages.

Hoekman et al. (2002) conducted sensitivity analyses of a stage-based matrix model describing the relationship between vital rates and population growth rate (λ) for female midcontinent mallards. We adjusted breeding hen survival for both stage classes (second year (SY) and after second year (ASY) to reflect our estimated probability of mortality in predator removal conditions. We retained Hoekman et al. (2002)'s original parameter values for all other vital rates, including nest survival (0.13 for both SY and ASY) and re-calculated the fecundity and survival transitions constituting the stage-based matrix. We then calculated stable stage distributions and projected population growth rates using stage-based matrices representing our lower, upper and mean estimates of breeding hen survival. This was done as an exercise to demonstrate and contrast population impacts of lowered breeding hen survival and was not intended to represent accurate population growth estimates for reasons discussed below. Analysis was done using the `popbio` package (Stubben and Milligan 2007) in R (R Core Development Team 2016).

RESULTS

Through 2015-2017, a total of 1,136 nests were found and monitored; of these 1,041 were suitable for analyses. Nests that were completely destroyed by investigators ($n = 25$), abandoned due to investigator activity ($n = 38$), monitored with a trail camera ($n = 35$), or found during hatching ($n = 1$), were excluded from analyses. Nests that were partially damaged by investigators ($n = 48$) were retained, as a chi-square test showed no significant difference in fates (hatch vs. failure) of damaged and undamaged nests ($\chi^2 = 1.3746$, $p = 0.241$, $df = 1$, $n = 1041$). A total of 893 nests occurred on quarter sections that had treatment transposed at least once. Blue-

winged teal nests were the most common ($n = 555$); fewer than 30 nests were found for green-winged teal, American widgeon, and northern pintail (table 1). Mean nesting period for all nests pooled was 34 days.

A large proportion of nests were depredated or abandoned with evidence of predator activity (60.1%); see table 1 for nest fates by duck species. Within the Bashaw study area between 2016 and 2017, the number and proportion of nests hatching and failing were very similar despite the transposition of predator removal (figure 2). Private land under active hay and cattle production comprised a substantial portion (45%) of the 2015 study area, compared to 2016 and 2017 where 97.5% and 100% of quarter sections were owned by DUC, respectively. DUC delays haying or grazing until July 15, after the nesting season, so differences in management regimes affecting nests studied in 2015 eliminates a direct comparison of nest fates between 2015 and 2016-2017 (figure 2).

Through 2015-2017, 940 predators were removed. Removals consisted primarily of coyotes (17.2%), skunks (15.1%), black-billed magpies (20.9%), American crows (22.6%) and common ravens (21.7%); the latter 3 species herein referred to collectively as corvids. Red fox (0.4%), Franklin's ground squirrels (1.2%), raccoon (0.3%), American badger (0.5%), and long-tailed weasel (0.1%) were removed in negligible numbers between 2015-2017 (figure 3). See Appendix 1 for complete summary of predator removals.

Nest Cameras

Between 2016-2017, Reconyx HC600 Hyperfire Covert wildlife cameras were successfully deployed at 35 individual nests for varying amounts of time. Predators were photographed at 12 nests; near Bashaw these included corvids, striped skunks and long-tailed weasels, while 13-lined ground squirrels and striped skunks were detected near Viking (see Appendix 2 for complete summary). Predators commonly made multiple visits to a nest over hours or days, and multi-species predation events occurred at 33% of the nests where predation was photographed. Two nests were abandoned following camera deployment. Over time, vegetation often obscured the lens, and smaller predators low to the ground would not have been captured by most cameras.

Nest Survival

A total of 830 nests were used to test 13 candidate models characterizing nest survival. The top-performing model of daily survival rates included year, study area, and treatment as fixed-effects (model weight = 1.00; Appendix 3 table A 3). Mean 34-day nest survival in Bashaw control plots

in 2015, 2016 and 2017 respectively was: 27.12% (95% CI = 15.24% - 47.79%, $n = 45$); 28.79% (95% CI = 16.62% - 49.42%, $n = 39$) and 16.71% (95% CI = 11.44% - 24.31%, $n = 140$; figure 4). Mean nest survival in Bashaw trapped plots in the same respective years was: 28.71% (95% CI = 17.98% - 45.46%, $n = 59$), 19.52% (95% CI = 13.04% - 29.07%, $n = 111$) and 9.09% (95% CI = 3.47% - 23.18%, $n = 35$; figure 4). In Viking control plots in 2016 and 2017, respectively, mean 34-day nest survival was 15.76% (95% CI = 8.97% - 27.46%, $n = 65$) and 0.44% (95% CI = 0.17% - 1.16%, $n = 153$; figure 4). In the same respective years, mean nest survival in Viking trapped plots was 17.14% (95% CI = 11.11% - 25.98%, $n = 112$) and 30.30% (95% CI = 20.10% - 44.81%, $n = 71$; figure 4). See Appendix 4 for corresponding daily survival rates.

Except for the Viking 2017 control group, all 95% confidence intervals for 34-day nest survival overlap each other and include the 15% - 20% threshold required for maintenance of stable populations (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995; figure 4). Converted to 34-day nest survival, this threshold is 15.84% - 20.94%. A series of five z-tests using a Bonferroni-corrected α -value of 0.01 revealed a significant difference in mean nest survival only for the Viking 2016 trap - Viking 2017 control spatial-pairing. For this cohort, nest survival was significantly lower under control conditions ($z = 7.13$, $p < 0.001$, table 2). No other significant differences were found among the 5 pairings of nest survival estimates (table 2).

Exceptionally low nest survival in Viking 2017 control plots appeared to drive model selection, so we modelled nest survival a second time in the absence of that cohort. With the removal of these outlier values, model weight was more distributed, and five candidate models had Δ AIC values of ≤ 2 (Appendix 3 table A 4). Models containing treatment as a covariate performed poorly with model weights of ≤ 0.02 (Appendix 3 table A 4). Of the top 5 performing models, we selected nest survival as a function of nest age at the time of discovery as the most parsimonious model. Nest age upon discovery was positively skewed, with median age of 10 days (IQR = 6 - 17). Mean 34-day nest survival for nests found at 10 days of age was 21.12% (95% CI = 17.92% - 24.87%, $n = 677$). Age of nest when found was weakly associated with higher daily survival rates (figure 5), with 34-day nest survival estimates ranging from 19.60% (95% CI = 8.60% - 43.84%) to 23.55% (95% CI = 9.73% - 55.76%) with a mean of 21.66% (95% CI = 21.23% - 22.10%).

Observer Impact

For failed nests associated with predation evidence, there were significantly more depredated nests void of eggshells on 2017 Viking control plots relative to comparison plots ($\chi^2 = 50.546$, $p = 1.164 \times 10^{-12}$, $df = 1$, $n = 171$; figure 6). Evidence of predation was collected for significantly more failed nests on 2017 Viking control plots relative to comparison plots ($\chi^2 = 4.833$, $p = 0.0279$, $df = 1$, $n = 236$; figure 7). If we apply the “worst possible case scenario” in which all nests lacking data on predation history were assumed to lack eggshells for comparison plots and to contain eggshells for 2017 Viking control plots, there would still be significantly more empty depredated nests in the latter ($\chi^2 = 3.926$, $p = 0.0476$, $df = 1$, $n = 236$; figure 6) implying a link between observer activity and corvid predation.

Depredated nests were much more likely to fail in the days immediately following initial marking by observers in 2017 Viking control plots compared to all other Viking plots. The proportion of nests failing to survive their first observation interval was more than double within 2017 Viking control plots (79.1%) relative to mean proportion within 2017 predator removal plots and both 2016 Viking plots (35.0%; 95% CI = 27.6% - 42.3%; figure 8). However, the probability of increased depredation rates following initial marking are confounded by the fact that nests are less likely to survive during earlier incubation stages (Mayfield 1961, 1975).

Nesting Hen Mortality

Controlling for year and transposing treatment, the common odds of nesting hen mortality due to predation were significantly higher in trapped plots (OR = 2.60, 95% CI = 1.03 – 6.58, $n = 467$, table 3) for the Bashaw study area. The increased odds of hen mortality in trapped plots were similar in all three years (Breslow-Day $\chi^2 = 0.7133$, $p = 0.7$, $df = 2$, $n = 467$, table 3) and significantly higher relative to control plots when year is controlled (Cochran-Mantel-Haenszel $\chi^2 = 3.7413$, $p = 0.0531$, $df = 1$, $n = 467$; table 3). See Appendix 6 for a species breakdown of depredated hens.

The probability of survival for nesting hens in predator removal plots was 0.50 (95% CI = 0.28 - 0.71). Should an entire population experience the rate of breeding hen survival observed in our predator removal plots, population growth rate (λ) estimated for female midcontinent mallards would be 0.566 (95% CI = 0.320 – 0.813; figure 9). For comparison, Hoekman et al. (2002)'s λ estimate of 0.824 was based on 0.72 probability of breeding hen survival and represented an approximate population growth rate in the absence of predator removal. Our

highest estimate of breeding hen survival in predator removal conditions (0.71) results in a 1.1% lower population growth rate compared to Hoekman et al. (2002)'s benchmark estimate.

DISCUSSION

In accordance with our expectation, nest survival patterns indicated that predator removal was ineffective. In all but one study area-year combination, we found no significant difference in nest survival between control and predator removal plots (table 2). The majority of research evaluating predator removal to increase dabbling duck nest survival has found it to be effective when applied in prairie habitats (Garrettson and Rohwer 2001, Lester 2004, Chodachek and Chamberlain 2006, Pieron and Rohwer 2010, Pieron et al. 2012, Amundson et al. 2013); but publication bias towards significant results may have influenced the prevalence of positive findings (Rosenthal 1979). Ours is the third study to date demonstrating ineffectiveness of predator removal for duck nest survival in Canadian parkland habitats (Clark et al. 1995, Dassow 2010). Like Clark et al. (1995) and Dassow (2010), we conducted partial predator removal within a rich predator community characteristic of the parkland region (Sargeant et al. 1993) where ample opportunity for compensatory predation exists. Three-dimensional habitat structure and socio-economic drivers may enhance the potential for compensatory predation relative to American prairie habitats, where most successful studies have been carried out. Nest abundance and proportion of fates was largely preserved within study area across years, regardless of treatment (figure 2), indicating that nest survival was driven by habitat characteristics, which were controlled for by treatment transposition. Associations of habitat with nest predation risk are examined in Chapter 3.

A lack of response in nest survival does not necessarily preclude the depression of predator abundance because of potential compensatory nest predation by species that were not removed (Errington 1946, Boyce et al. 1999, Ellis-Felege et al. 2012). Trail camera evidence demonstrated that species that were not targeted for removal were consuming duck eggs (long-tailed weasels, 13-lined ground squirrels). Assuming effective removal of skunks, coyotes and corvids, we believe other species were responsible for compensatory nest predation which may have been facilitated through multiple mechanisms. Mesopredator release, the expansion of distribution or density of a mid-trophic level predator resulting from the decline of an apex predator (in our system, coyotes; Crooks and Soulé 1999, Prugh et al. 2009), is known to benefit foxes (e.g. Sovada et al. 1995), skunks (Crooks and Soulé 1999), ravens (Mezquida et al. 2006)

and other nest predators. Given the short four-month timeframe of predator removal each year, a distribution expansion of the community of nest predators, induced by mesopredator release, would probably occur largely through behavioural mechanisms (Lima and Dill 1990, Ritchie and Johnson 2009). The removal of more efficient nest predators may have increased opportunity afforded to less efficient species that do not key in on duck eggs as readily (Ruscoe et al. 2011, Ellis-Felege et al. 2012).

The compressed temporal and spatial scale of our predator removal plots provided ample opportunity for immigration and the creation of a core, predator-free area was unlikely (Garrettson and Rohwer 2001). The spatial scale and distribution of our predator removal was constrained by land tenure; landowner concerns about the spread of clubroot (*Plasmodiophora brassicae*), a fungal disease of canola, made accessing private land difficult. The duration of predator removal was constrained by cost; our implementation of predator removal represents the inherent logistic constraints that also would characterize a long-term predator removal program in the Alberta parklands. When applying small-scale predator removal on the prairies, Chodachek and Chamberlain (2006) increased duck nesting success on 259 ha parcels, while Sargeant et al. (1995) saw slight increases when trapping 61 – 301 ha plots. The parklands are more complex in habitat structure than prairie ecosystems and effective predator removal is challenging when conducted at small, widely distributed plots across a productive landscape supportive of high predator species richness (Sargeant et al. 1995). The Alberta parklands may be more vulnerable to the creation of a source-sink system where non-managed areas provide source populations for immigration into predator-removal areas (Novaro et al. 2005, Minnie et al. 2016). Lieury et al. (2015) suggest immigration would quickly negate the effects of reducing red foxes at scales less than 10 km², and that spring culling is more conducive to compensatory immigration than post-dispersal culling.

Wide confidence intervals preclude us from determining whether baseline nest survival in our study areas is above or below that required for population maintenance. All but one of our 10 nest survival estimates encompassed the 15.84 - 20.94% 34-day threshold required for maintenance of stable populations (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995) and none fully exceeded it (figure 4). As concluded in several other studies (Klett and Johnson 1982, Garrettson and Rohwer 2001, Dinsmore et al. 2002), nest survival increased linearly with nest age. The 2017 Viking trapped plots had the highest minimum survival estimate

at 20.10%. With a maximum estimate of 1.16% nest survival and 18 successful nests out of 153, the 2017 Viking control plot had the lowest survival. These results indicate that predator removal in the Viking area might prove effective at increasing nest survival, but this requires further investigation. In contrast, predator removal was ineffective in the Bashaw study area and does not appear to be a promising management strategy.

Based on field observations and anecdotes in other studies, we suspected exceptionally low nest survival observed in 2017 Viking control plots resulted from corvid species forming search images for investigator-marked nests (Picozzi 1975, Buler and Hamilton 2000). Recognition of the wooden lathes used to mark nests and patterns in investigator activity could have been acquired by individual crows and ravens and shared through social learning (Cornell et al. 2012), facilitating artificially high nest predation rates. Trapping and shooting of corvids in predator removal plots may have deterred trap-lining behaviour; alternatively, territorial social groups in the comparison locations may not have acquired recognition of marked nests. Our attempts to pre-empt recognition of lathes used to mark nests may have been insufficient as 10 m – 20 m may not prevent effective search image formation by crows (Picozzi 1975). Research on nests where crows, ravens and other corvids are present should include plans to minimize the potential for recognition of nest markers and enhanced nest mortality induced by investigator activity. Marking nests with a wooden lathe at a 20-m distance in variable directions as we did may not deter search image formation by corvids (Picozzi 1975). Where “trap-lining” of marked nests by corvids is observed, sporadic shooting or trapping may act as an effective deterrent by inducing fear and increasing the cost of following nest researchers.

To test if elevated nest mortality was due to corvids, we relied on evidence left at depredated nests. Inference of predator species from nest predation evidence is largely precluded by intraspecific variation and interspecific overlap in nest predation patterns, as well as the occurrence of multiple predation events (Larivière and Messier 1997, Larivière 1999). We categorized depredated nests by presence or absence of eggshells, the latter being indicative of crow predation (Montevocchi 1976) but also characteristic of nest predation by other species. In addition to corvids, significantly higher levels of depredated nests lacking shell fragments could have resulted from a spike in predation by red foxes, coyotes, Franklin’s ground squirrels, raccoons, weasels, gulls and American mink (Sargeant et al. 1998, Larivière 1999). Of these, only corvids and coyotes were effectively removed so we would expect to see a similar pattern of

predation between comparison and control plots if different species were involved. High rates of failure after initial marking and significantly more predation events consistent with corvid predation corroborate field observations of crows and ravens targeting marked nests, but uncertainty in predator identification ultimately makes our results inconclusive.

We were surprised that significantly more nesting hens were depredated on trapped plots, although low incidence and minimal influence on lambda estimates ultimately render this pattern nonsignificant. Though predator removal did not depress nest predator abundance sufficiently to improve nest survival, it appears to have influenced predator assemblage in favour of principal hen predators, thereby increasing hen mortality. Mesopredator release and competitive release may have shifted the relative abundance of mammalian predators. Coyotes were the apex predator in our system but were not principal hen predators especially in comparison to red fox (Sovada et al. 1995, Sargeant et al. 1998). Coyotes limit red fox abundance through direct killing and instilling fear, forms of interference competition (Sovada et al. 1995, Gosselink et al. 2003, Nelson et al. 2007, Ritchie and Johnson 2009). Areas where coyotes were reduced might have become attractive refuges for more important hen predators like red fox and weasels (Sargeant et al. 1998, Ritchie and Johnson 2009), resulting in increased nesting hen mortality relative to control plots. The dietary breadth of skunks is relatively high (Azevedo et al. 2006) and their niche overlaps that of red fox (Crimmins et al. 2016), so competitive release resulting from skunk removal also could have benefited weasels and foxes.

Apparent competition (Holt 1977) in the form of increased rodent abundance attracting duck predators is another potential consequence of predator removal that may have occurred to the detriment of nesting hen survival. Rodent species are an important prey item for both coyotes and skunks (Azevedo et al. 2006), the removal of which may have resulted in increased rodent abundance through both numerical and behavioural responses (Lima and Dill 1990, Henke and Bryant 1999, Ritchie and Johnson 2009). Red fox, weasel and raptor species are shared predators of rodents and adult ducks (Simms 1979, Sargeant et al. 1984, Richkus et al. 2005, Azevedo et al. 2006, Thomas et al. 2011) and an increase in their abundance is a plausible explanation for significantly higher nesting hen mortality on trapped plots. In North Dakota, McCarter (2009) observed slightly higher abundance of raptors where mammalian predators were reduced, presumably in response to increased prey.

Future evaluation of predator removal for increased duck production would be improved by the collection of additional data. Information on predator abundance is essential for evaluating the presence and degree of a decline induced by predator removal, and inferences are limited in its absence. Beyond population size, trapping harvest is influenced by effort which encompasses trapper experience, and type and placement of traps and attractants (Ruelle et al. 2003), none of which were standardized in our study design. Predator removal methods must be standardized to allow for comparisons (DeVink et al. 2011, McKelvey et al. 2011), and tracking trapping effort as well as removals over time could allow for indirect estimates of predator abundance to be made through depletion modelling (T. Arnold, personal communication). Relative importance of each nest predator species might help to elucidate aspects of compensatory predation, but such data are difficult to obtain (Hernandez et al. 1997, Larivière and Messier 1997, Larivière 1999).

The failure of predator removal programs intended to increase bird abundance because of compensatory predation is well documented (McCarter 2009), especially when predator removal does not encompass all predator species (Smith et al. 2010). Where predator removal does increase nest survival, enhancements may not translate into increases in recruitment to the local population due to a combination of low duckling survival, limitations in breeding philopatry and territorial behaviour of breeding pairs (Amundson et al. 2013, Pieron et al. 2013). A measure of recruitment is critical to truly evaluate the effectiveness of predator removal intended to increase not only nest survival but duck productivity (Amundson et al. 2013, Pieron et al. 2013). A long-term predator removal program in North Dakota has produced marginal gains in population growth at high monetary cost, in part due to low duckling survival dampening the impact of high nest survival (Amundson et al. 2013). Duckling survival benefited from predator removal in Saskatchewan (Pearse and Ratti 2004) but not in North Dakota (Amundson and Arnold 2011), where duck populations appear to be controlled predominantly by bottom-up trophic forces not addressed by predator removal (McCarter 2009). In our study, duckling survival may have been unintentionally reduced through the same mechanisms that led to a reduction in breeding hen survival. Limitations in carrying capacity due to finite food and habitat resources place constraints on recruitment that may ultimately prevent any real increases in fall flight resulting from increased nest survival (McCarter 2009, Amundson et al. 2013).

MANAGEMENT IMPLICATIONS

Predator removal was ineffective at increasing duck nesting success and at time of writing there are no plans to continue the program in the Alberta parklands. Prior to implementing any form of predator management, the benefits should be assessed using a rigorous study design and weighed against potential consequences, including those that might be unintentional or counterintuitive (Treves et al. 2016). The substantial resources required to implement predator removal could be redirected at non-lethal mitigation methods that are often more effective and less controversial (Treves et al. 2016) with less risk of inducing unintended negative consequences. Predator removal should be continuously monitored to ensure desired outcomes are being achieved. Determining prey survival at multiple life stages is important due to the potential for opposing effects on different vital rates (this study, Neuman et al. 2004, Darrah et al. 2018). Finally, retaining coyotes on the landscape might increase the success of a predator-removal program (Pieron and Rohwer 2010) because coyotes effectively control fox and other mesopredator abundance and their presence is correlated with higher nest survival (Sovada et al. 1995).

In conclusion, current nest survival in the central Alberta parklands might be lower than that required for maintenance of stable populations (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995) but our results do not indicate that nest survival would benefit from predator removal. Our observations of a possible increase in nesting hen mortality on predator removal sites raise new concerns and add to a growing body of literature suggesting minimal gains from predator removal intended to increase duck production (McCarter 2009, Amundson and Arnold 2011, Amundson et al. 2013, Pieron et al. 2013). Habitat-based management alternatives might be a more effective approach for reducing nest-predation risk (Chapter 3).

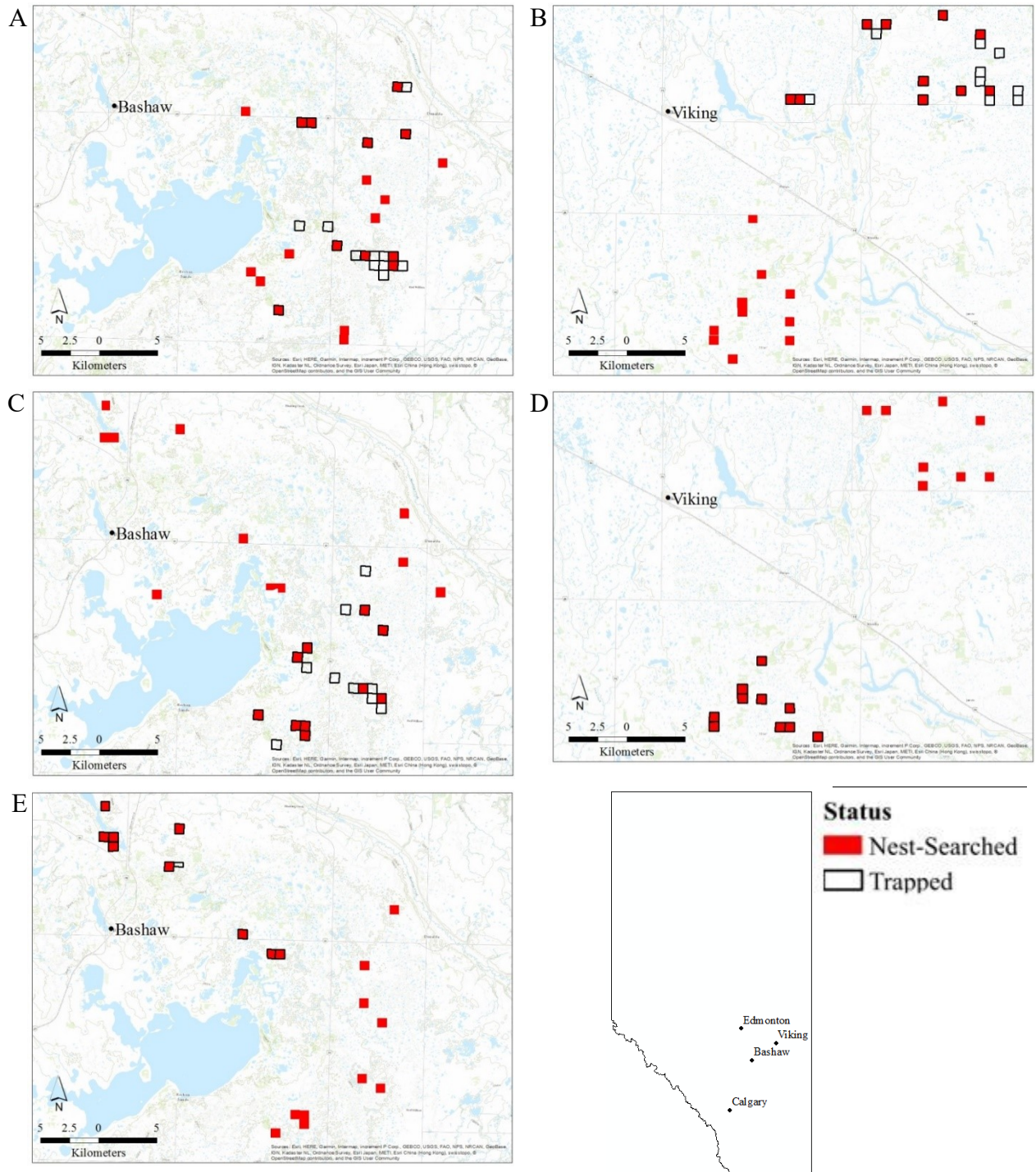


Figure 1: Maps of Bashaw and Viking study areas through 2015 – 2017, where (A) Bashaw 2015; (B) Viking 2016; (C) Bashaw 2016; (D) Viking 2017; and (E) Bashaw 2017. Red indicates nest-searched areas; black borders indicate predator removal.

Table 1: Species composition of fates and total count of nests monitored in Bashaw and Viking study areas, 2015 – 2017. Nests abandoned or destroyed due to investigator activity not included. Reason for nest abandonment was attributed to predator if there was evidence of predator activity, and as unknown cause otherwise.

Species	Destroyed	Hatched	Abandoned		Total
			Predator	Unknown	
American green-winged teal	1	4	0	0	5
American widgeon	8	4	1	2	15
Blue-winged teal	275	192	41	47	555
Gadwall	57	49	15	7	128
Mallard	58	30	10	8	106
Northern pintail	1	0	0	0	1
Northern shoveler	94	58	22	7	181
Unidentified	41	4	2	3	50
					1041

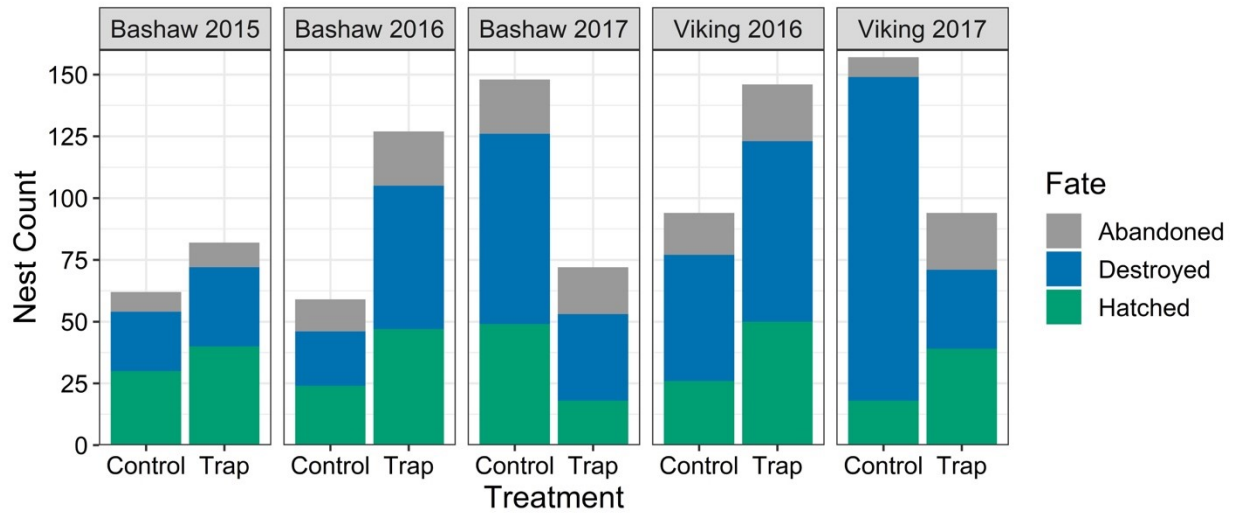


Figure 2: Fates of duck nests (abandoned, destroyed by predator, or hatched) in central Alberta parklands by study area, year and treatment ($n = 1041$).

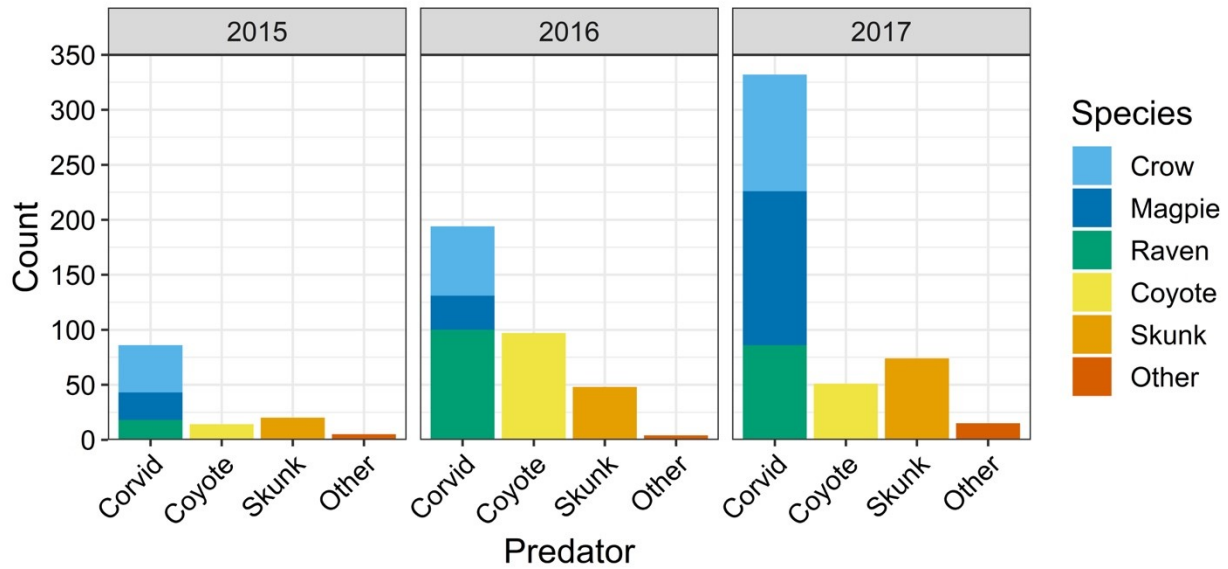


Figure 3: Nest predator species removed through 2015 - 2017 from Bashaw and Viking, Alberta study areas ($n = 940$).

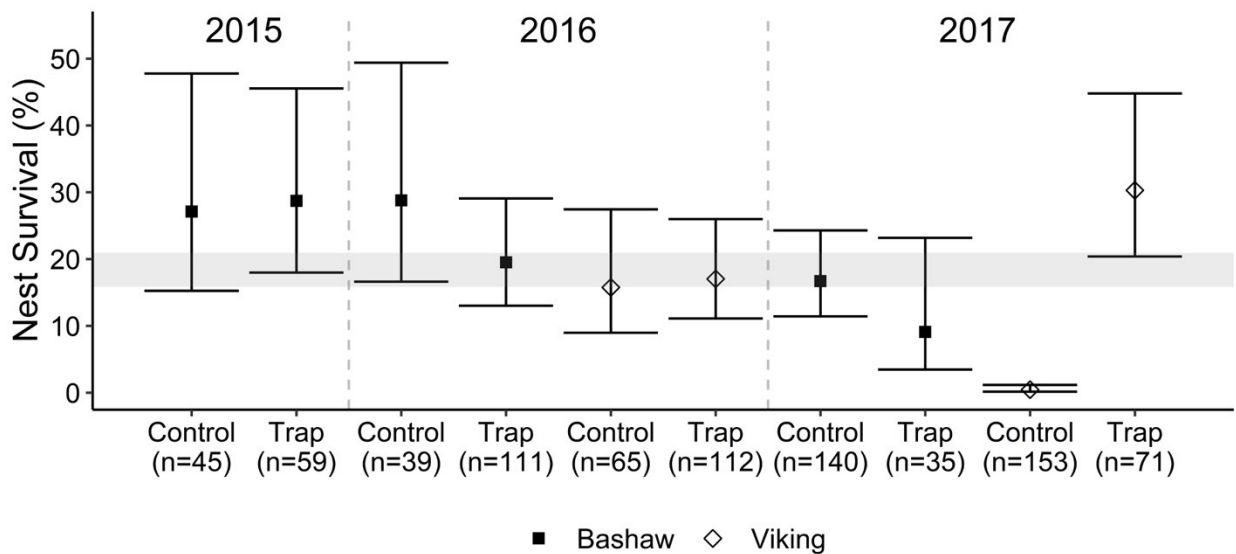


Figure 4: 34-Day nest survival on trapped and control plots (trapping transposed between years) over 3 years in the central Alberta parklands. Threshold for stable population maintenance of 15 - 20% nest survival (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995) converted to 34-day nest survival shown in grey. Confidence intervals = 95%, $n = 830$.

Table 2: Statistics generated from five z-tests comparing mean nest survival within 2015 and across transposed 2016 & 2017 treatments, using a Bonferroni correction of $\alpha = 0.01$.

Study area	Year-treatment pairing	z-score	p-value
Bashaw	2015 control - 2015 trapped	-0.16	0.88
	2016 control - 2017 trapped	2.12	0.03
	2016 trapped - 2017 control	0.56	0.57
Viking	2016 control - 2017 trapped	-1.92	0.06
	2016 trapped - 2017 control	7.13	0.00

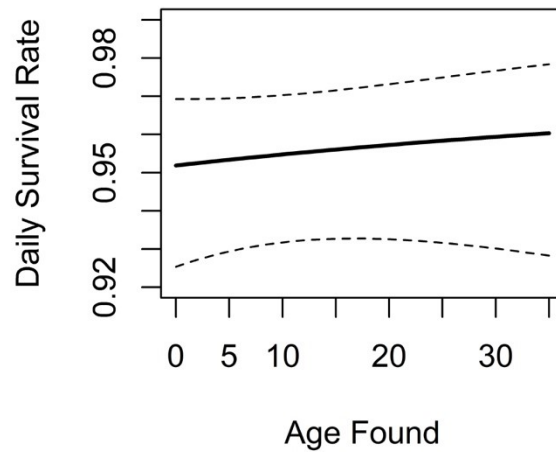


Figure 5: Daily survival rate (DSR) as a function of nest age when found, derived from the top-performing model when 2017 Viking control nests were excluded. Solid line is mean DSR; dashed lines represent 95% confidence intervals.

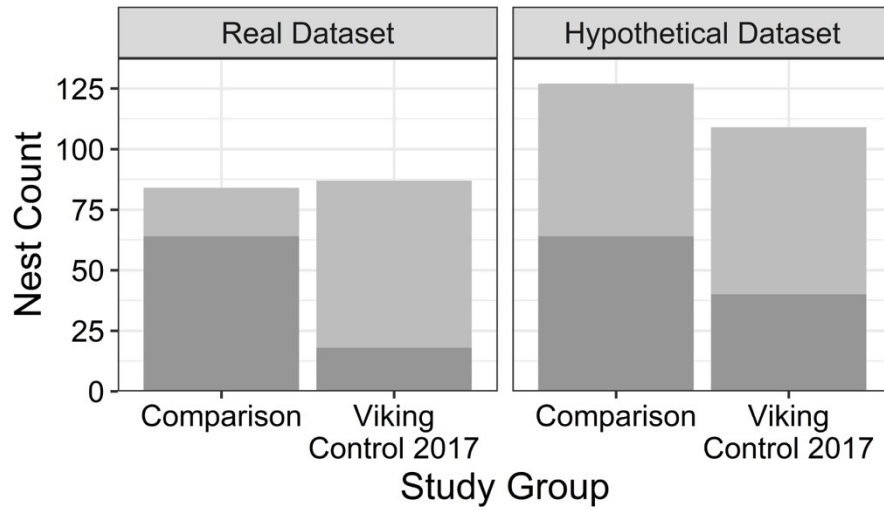


Figure 6: Counts of depredated nests based on predation evidence for comparison areas (2016 & 2017 Viking trapped plots and 2016 Viking control plots, pooled) and 2017 Viking control plots. Light grey represents depredated nests with no eggshells in or near the nest; dark grey represents nests where eggshells were found. Real dataset refers to field data; the hypothetical dataset was fabricated to account for unequal data collection.

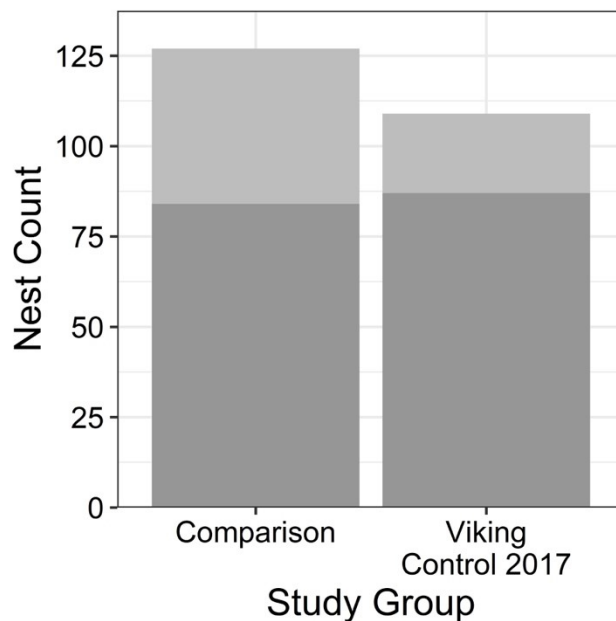


Figure 7: Counts of nests by data collection effort regarding predation evidence for comparison areas (2016 & 2017 Viking trapped plots and 2016 Viking control plots, pooled) and 2017 Viking control plots. Light grey represents an absence of data collection regarding the presence/absence of egg shells; dark grey represents nests for which such data were collected.

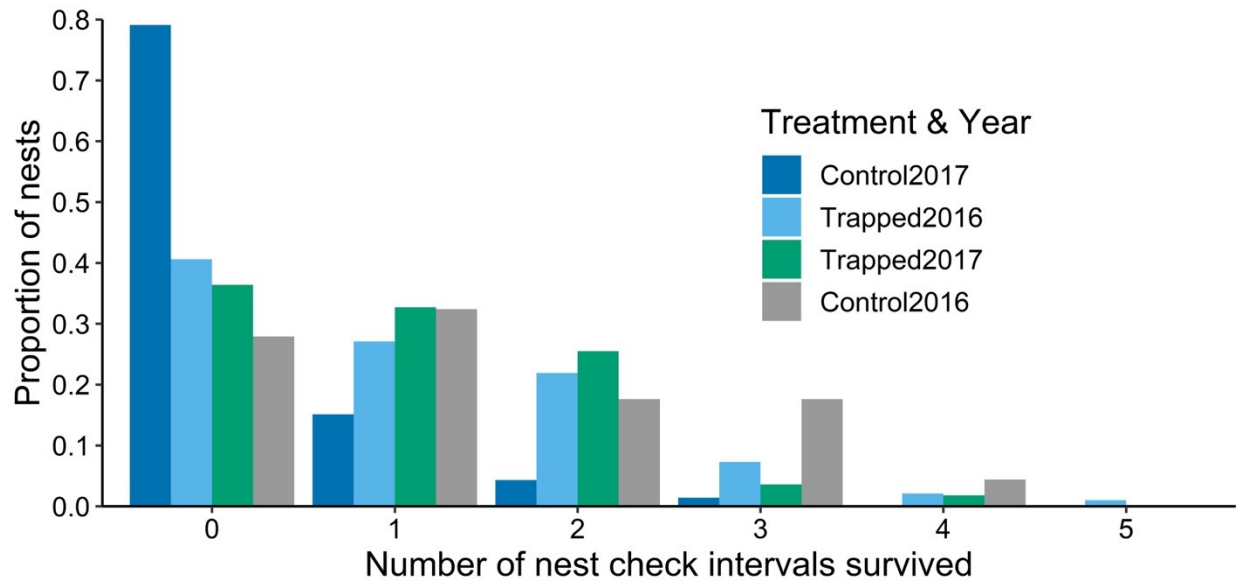


Figure 8: Proportion of failed nests surviving 0-5 nest check intervals within control and trapped plots in 2016 – 2017 near Viking, Alberta. Nest check interval zero occurs between initial nest discovery and first re-visit.

Table 3: Counts of surviving and depredated nesting hens by treatment and year from transposed plots near Bashaw, Alberta.

		Year	2015	2016	2017
Treatment	Hen Killed				
Predator Removal	Yes		4	9	5
	No		60	115	33
Control	Yes		1	2	6
	No		50	40	142

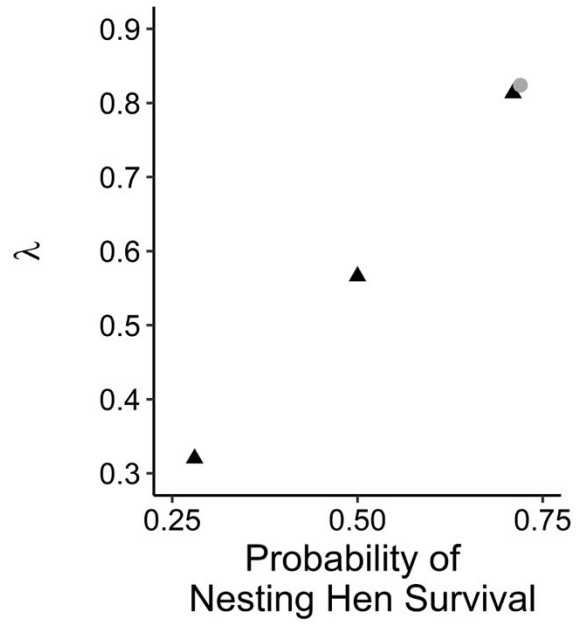


Figure 9: Population growth rate (λ) as a function of nesting hen survival. Black triangles represent our estimates from predator removal plots, and the grey circle represents estimate by Hoekman et al. (2002), for reference

CHAPTER 3 – HABITAT ASSOCIATIONS WITH NEST PREDATION RISK IN CENTRAL ALBERTA

INTRODUCTION

Habitat conservation has been a keystone of waterfowl management in North America since the 1930s (Anderson et al. 2018) and is the principal tenet of the North American Waterfowl Management Plan (NAWMP; Sovada et al. 2001, North American Waterfowl Management Plan 2012). In the United States, the Conservation Reserve Program successfully increased recruitment by an estimated 12.9 million ducks through protection of existing cover and conversion of 1.9 million ha of cropland to perennial cover (Reynolds et al. 2001, Howerter et al. 2014). In the absence of a similar broad-scale program in the Canadian prairie pothole region (PPR), abundance of nesting cover is predominantly influenced by cattle markets and the resulting demand for tame forage and pasture relative to cropland (Prairie Habitat Joint Venture 2014). The Prairie Habitat Joint Venture (PHJV) is responsible for implementing conservation programs under NAWMP in Canada (Howerter et al. 2014), and from 2007 – 2012 over half its habitat retention budget was allocated to land acquisition (Prairie Habitat Joint Venture 2014). While conservation easements and land-use agreements also play an important role in conservation of Canadian PPR habitats (Prairie Habitat Joint Venture 2014), land ownership by conservation organizations is a primary method of conserving duck nesting habitat.

The relationship between habitat and nest predation risk has long been a focus of waterfowl research, but findings are often incongruent across studies because risk is area-specific and fluid with time (Williams 1997). At a continental scale, duck populations vary with fluctuations in annual precipitation and availability of wetland and upland habitat limits populations when climatic conditions are optimal (Howerter et al. 2014, Anderson et al. 2018). However, at finer spatial scales it is difficult to elucidate consistent patterns of nest survival, the most influential vital rate in duck population dynamics (Hoekman et al. 2002). Nest predation risk, the greatest factor limiting nest survival (Ricklefs 1969, Sargeant and Raveling 1992), can be influenced by nesting cover (e.g. Emery et al. 2005), edge effects (Lahti 2001), patch size (e.g. Sovada et al. 2000), duck species (e.g. Beauchamp et al. 1996), availability of alternative prey (e.g. Schmidt and Whelan 1999), and climatic conditions (Beauchamp et al. 1996, Drever et al. 2004). Habitat associations with nest predation risk are inherently variable and fluid both

temporally and spatially. If a stable pattern arises it can quickly dissolve as predators adjust their foraging behaviours (Conover 2007, Jiménez et al. 2007). Likewise, ducks and other birds are constantly adapting to the strategies of their predators (Conover 2007). This “arms race” of predator-prey dynamics prevents consistent prediction of nest survival based on correlations with habitat characteristics across spatial and temporal scales (Conover 2007, Jiménez et al. 2007, Borgo and Conover 2016b). For example, evidence for association of habitat attributes with nest survival often varies across studies, and even within a single study, relationships are often inconsistent across years (Jiménez et al. 2007). Associations between habitat and nest survival are thus site-specific, may reflect climatic conditions, predator community and alternative prey dynamics, and can be temporally variable.

Predator foraging modalities and the effectiveness of visual and olfactory cues are influenced by habitat features, and features that hinder predator searching ability may be associated with higher nest survival (Rangen et al. 1999, Conover 2007). Mammalian carnivores are primarily olfactory oriented but may switch to visual cues at close range, while avian predators, including corvids and diurnal raptors, are visually oriented (Conover 2007). Olfaction is most effective when odour plumes are concentrated and detectable, as occurs in an open field without obstacles; updrafts and turbulence dilute odours and are induced by surface roughness, such as scattered trees (Conover 2007, Borgo and Conover 2016b). Visual cues include the nest itself but also hen behaviour and patterns in site characteristics that form the basis of search images (Conover 2007, Borgo and Conover 2016b). Relationships between habitat features and nest survival may identify successful and unsuccessful nesting strategies and also provide information on the relative importance of predators using olfactory versus visual cues (Rangen et al. 1999, Conover 2007). Nest-site attributes that are optimal for avoiding detection by olfactory predators often are not equally conducive for avoiding visual predators, and vice versa; in such a case intermediate sites might provide the best protection (Conover 2007). Spatial scale interacts with foraging ability and can provide another strategy for avoiding a suite of predators employing multiple foraging modalities. For instance, olfaction is most affected at a patch scale where habitat structure affects atmospheric turbulence and updrafts, while visual concealment is most effective at the immediate nest-site (Conover 2007). Thus, nest-site selection at multiple scales can influence predation risk.

The process through which an animal chooses a resource is known as selection, and it is commonly assumed that animals select high-quality resources to increase their fitness (Manly et al. 2003). Selection of a nest-site reflects how the environment is perceived and the ability of a hen to evaluate information about her environment (Clark and Shutler 1999). Nest-site selection by hens can be influenced by genetic, imprinted, or learned preferences (Clark and Shutler 1999); factors beyond nest-site security, (i.e. ability to meet nutritional requirements) also may be influential (Sovada et al. 2000). It is unclear how birds assess predation risk at a nest site, and how effective they are at doing so (Møller 1988, Sieving and Willson 1998, Conover 2007). Within a season, Pinyon jays (*Gymnorhinus cyanocephalus*) reacted to nest predation by cats by re-nesting higher in the canopy, and to predation by American crows (*Corvus brachyrhynchos*) by re-nesting lower in the canopy (Marzluff 1988). However, there was no evidence that past nest losses informed nest locations in subsequent years (Marzluff 1988, Conover 2007). Dassow (2010) posited that female ducks might be able to acquire information about predator densities and space use by detecting predator urine through ultra-violet vision. Another means of assessing risk is for a bird to scout widely and spend time at a potential nest-site prior to nesting; if her activity quickly attracts predators, she can select a different site (Nolan 1978, Conover 2007).

The selection of a nest-site has important ramifications for both hen and nest survival (Clark and Shutler 1999), two of the most influential factors in duck population dynamics (Hoekman et al. 2002). Trade-offs between nest and hen survival might influence nest-site selection (Götmark et al. 1995, Wiebe and Martin 1998, Conover 2007, Devries et al. 2018). Borgo and Conover (2016b) found that blue-winged teal (*Anas discors*) selected sites in shorter vegetation, possibly because reduced concealment provided greater ability for the hen to detect and avoid predators (Götmark et al. 1995, Borgo and Conover 2016b). Nest-site selection also can be influenced by hen age and experience. Lokemoen et al. (1990) reported that previously successful mallard (*A. platyrhynchos*) and gadwall (*A. strepera*) hens selected the same cover type the subsequent year, and mallards nested closer to previously successful nest sites. In areas with ubiquitous generalist predators, the optimal strategy might be to counter search-image formation by random selection of nest sites (Conover 2007, Jiménez et al. 2007, Borgo and Conover 2016b).

Areas identified as frequently used by a species of interest often are assumed to be high quality, but when selected areas are burdened by high mortality risk they are called attractive

sinks, or ecological traps (Dwernychuk and Boag 1971, Donovan et al. 1995, Delibes et al. 2001, Battin 2004, Nielsen et al. 2006). Attractive sinks have been associated with human-dominated landscapes (Battin 2004, Nielsen et al. 2004, Nielsen et al. 2006, Aldridge and Boyce 2007). In contrast, a high-use area with low mortality risk can be considered a high-quality source (Naves et al. 2003, Nielsen et al. 2004, Nielsen et al. 2006), and attractive sinks are maintained by immigration from source habitats (Pulliam 1988). There also can be areas where mortality risk is high but use is low, resulting in an avoided sink (Delibes et al. 2001, Battin 2004). A less explored phenomenon with potential to limit populations is a ‘perceptual trap;’ areas of high-quality habitat that are avoided because they are perceived as less attractive (Patten and Kelly 2010). Failure to assess fitness in conjunction with habitat selection can lead to misidentification of sink habitats as sources, potentially leading to misguided management actions (Clark and Shutler 1999, Nielsen et al. 2004, Aldridge and Boyce 2007).

Because of the potential for sink dynamics, it is crucial to examine not only nest-site selection but also differences in successful and unsuccessful nests to identify optimal (i.e. productive source) habitats (Clark and Shutler 1999, Naves et al. 2003, Nielsen et al. 2004). Selection of suboptimal nest-sites may occur if an individual is incapable of identifying appropriate sites, or if optimal sites are not available (Clark and Shutler 1999). Territoriality may not play a role in nest-site selection by dabbling ducks (Clark and Shutler 1999, but see Devries et al. 2018), so unavailability of optimal nest sites can mostly be attributed to extensive habitat degradation across the PPR (Higgins 1977, Sugden and Beyersbergen 1984, Greenwood et al. 1995, Miller and Nudds 1996). Nest-site selection and nest success may be disconnected if site selection, formed by long-term natural selection pressures, results in maladaptive responses to short-term predation pressures that are ever-changing both spatially and temporally (Clark and Shutler 1999). Potential for maladaptive nesting strategies increases on human-altered landscapes that no longer function like the ecosystems in which nesting birds evolved (Schlaepfer et al. 2002, Bock and Jones 2004).

Rotella and Ratti (1992) suggest that substantial portions of the PPR function as ecological traps, attracting large numbers of nesting ducks that fail to produce enough fledglings to offset annual mortality. Small, isolated grassland fragments likely function as sinks, because they are attractive to nesting hens but are frequently used by nest predators like foxes and skunks (Sovada et al. 2000) and are efficiently searched (Nams 1997, Jiménez et al. 2007). Due to high

predation and destruction of nests by farming activities, researchers have suggested that spring-seeded crops act as an ecological trap for northern pintails (*A. acuta*), because they are attracted to them (Miller and Duncan 1999, Richkus 2002, Richkus et al. 2005, Devries et al. 2018). Ecological sink dynamics also might occur where a trade-off is made in selection. Devries et al. (2018) found evidence of sink dynamics near wetland margins, but the attracting feature may have been reduced risk to duckling survival because of a shorter distance required to travel overland when broods fledge.

Our objective is to explore associations between habitat and nest-site selection and nest survival on small parcels of land managed for duck production in the central Alberta parklands, part of the PPR. In doing so, we will identify source and sink habitats to inform how conservation lands may be best configured and managed. To evaluate nest-site selection, we will compare nest locations with random locations, and we hypothesize that differences exist in habitat characteristics between nests and random sites. We predict habitat selection patterns will parallel patterns in nesting success as expected if adaptive selection is occurring (Clark and Shutler 1999, Devries et al. 2018). The null hypothesis (i.e., no habitat difference between nest sites and random locations) would indicate random nest placements, possibly the best strategy when birds nest among ubiquitous predators that use search images to locate prey (Conover 2007, Jiménez et al. 2007, Borgo and Conover 2016b).

To evaluate habitat associations with nest success, we compare habitat characteristics between hatched and failed nests. We hypothesize a suite of habitat characteristics is associated with higher probabilities of nest success and predict that those characteristics will impede visual- and olfactory-based foraging efforts of nest predators. The null hypothesis, no difference in habitat characteristics among hatched and depredated nests, might occur if stabilizing selection is operating, and successful and failed nests share the same mean traits (Clark and Shutler 1999). Alternatively, a lack of habitat differences between hatched and failed nests supports the hypothesis that a stable, long-term pattern does not exist among nest characteristics because predators quickly adapt their search strategies based on cues associated with successful nests (Jiménez et al. 2007).

STUDY AREA

For three seasons 2015-2017, we searched for and monitored duck nests at two study areas in the central Alberta parklands, near the communities of Bashaw and Viking. The parklands are

characterized by rolling hills, lakes, numerous permanent and ephemeral pothole wetlands, and stands of deciduous trees, primarily consisting of trembling aspen (*Populus tremuloides*). Both study areas are within an agricultural ecosystem dominated by the production of cereal and oil seed crops, livestock grazing, and oil and gas infrastructure. Land is partitioned into quarter section (~64.75 ha) parcels and the majority is privately owned. The landscape is highly fragmented and has a high density of linear features including a one-mile by one-mile road network, railroads, and transmission lines.

Beginning in 2016 nest searching was restricted to lands that were managed primarily for duck production by delay of haying or grazing until after July 15, when most nesting activity was concluded (Larivière and Messier 1998). We monitored nests and collected data describing available nest sites at 45 quarter sections (figure 10), all owned and managed by Ducks Unlimited Canada. In 2017 for all quarter sections, the landcover type of the neighboring eight land parcels had cover consisting of 0 -100% (\bar{x} = 50%) crop (predominantly cereal or canola, but also corn and legumes) and 0 -100% (\bar{x} = 46%) grassland (hay, active and idle pasture combined). Large water bodies (0 -13%, \bar{x} = 1%) and large deciduous tree stands (0 -25%, \bar{x} = 3%) less commonly abutted the quarter sections we studied. Amalgamation of adjacent quarter sections resulted in the creation of 36 distinct patches, ranging from ~64.75 – ~194.25 ha in size. Within these patches, area covered by deciduous tree stands ranged from 0.31 – 50.89 ha (\bar{x} = 15.95) and area in permanent wetlands ranged from 1.34 – 27.48 ha (\bar{x} = 10.4). The remaining area was upland managed as tame grassland used for hay or grazing; upland area ranged from 14.49 - 27.48 ha (\bar{x} = 66.83; figure 10) and was variably comprised of predominantly crested wheat (*Agropyron cristatum*), common timothy (*Phleum pratense*), smooth brome (*Bromus inermis*), and alfalfa (*Medicago sativa*). Precipitation trends were similar at both of our study areas throughout 2015-2017; 2016 was the wettest year with a mean of 472 mm annual precipitation. Mean annual precipitation in 2015 (392 mm) and 2017 (404 mm, figure 11; Alberta Climate Information Service 2018) was comparable. From 2013-2017, there has been a general trend in both studies areas of increasing annual precipitation (figure 11; Alberta Climate Information Service 2018).

Both study areas were characterized by a high diversity of generalist predators known to prey on duck eggs and nesting hens (Sargeant et al. 1998). Avian predators inhabiting our study areas include American crows, common ravens (*C. corax*), black-billed magpies

(*Pica hudsonia*), red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*B. swainsoni*), great-horned owls (*Bubo virginianus*), California gulls (*Larus californicus*) and ring-billed gulls (*L. delawarensis*; Sargeant et al. 1998). Mammalian predators include striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), Franklin's ground squirrels (*Poliocitellus franklinii*), American badgers (*Taxidea taxus*), long-tailed (*Mustela frenata*) and short-tailed weasels (*M. erminea*). Important nest predators notably absent from our study areas were rats (*Rattus* spp.) and egg-eating snakes (Russell et al. 2000, Bourne 2015). Research targeted upland-nesting (dabbling) ducks, and focused on mallard, northern pintail, northern shoveler (*A. clypeata*), blue-winged teal, American green-winged teal (*A. crecca carolinensis*), gadwall, and American widgeon (*A. americana*).

METHODS

From May 1 – July 15 during the years 2015-2017, we used the chain-drag method (Klett et al. 1986) to find duck nests on upland, non-forested areas of our study sites. We identified hen species and marked nests with GPS waypoints, a metal rod at the nest site and a painted wooden lathe 10-m north of the nest. In 2017 lathes were placed in variable directions and at greater distances to prevent recognition by predators. Also upon nest discovery, we measured visual obstruction at a distance of 4-m and a height of 1-m in four cardinal directions using a Robel pole (Robel et al. 1970, Jiménez et al. 2007). We revisited nests weekly to track incubation stage via candling (Weller 1956) until we could determine their fates (hatched, depredated or abandoned) from egg shell condition and other observations (Klett et al. 1986). Nest monitoring was permitted by Alberta Environment and Parks (Research Permit #57638 & Collection Licence #57639) and approved by University of Alberta's Animal Care and Use Committee (AUP00001473).

Landscape Covariates

In 2017, for each quarter section where nest-searching took place, we recorded the landcover type for each of the eight surrounding quarter sections and categorized them as crop, forest, water or grassland (hay and pasture combined). In July of 2017 on each study site, we mapped the perimeter of every wetland still containing water via GPS-tracking on foot or by ATV. Thus, wetlands used in our analyses represent water bodies that remained permanent throughout the nesting season in an average year relative to the last decade (figure 11; Alberta Climate Information Service). Also in July of 2017, we measured visual obstruction at 983

stratified random locations within our study sites using a Robel pole (Robel et al. 1970) and the same protocol used at nest sites. Visual obstruction measurements were limited to upland areas that were nest searched and locations were chosen in the field and stratified by topography so that one-third each were taken on hilltops, slopes, and low-lying areas. Measurements on slopes were divided equally between north and south aspects. We attempted to distribute locations evenly throughout each study site; 30 measurements provided good coverage on a lightly forested quarter section, and 15 were sufficient on a heavily forested quarter section. We established this protocol based on sampling guidelines for achieving representative samples intended for spatial interpolation via kriging (Fortin and Dale 2005). For both nest sites and random locations, we quantified visual obstruction by mean and coefficient of variation (SD/\bar{x}). To accommodate vegetation growth and account for the fact that reference values of visual obstruction were only collected at peak growth, we included Julian day in models and allowed for an interaction with visual obstructions.

We further characterized the landscape using GIS-based human-use, vegetation and landscape covariates analysed in the WGS 1984 UTM Zone 12N projected coordinate system within ArcMap (version 10.6.1, Environmental Systems Research Institute, Redlands, CA). Our study sites were delineated using the Alberta Township System spatial layer available from Alberta Environment and Parks through Altalis (v4.1, 2017; <https://beta.altalis.com/map?id=119>). Spatial data for roads were also obtained through Altalis from Alberta Environment and Parks (2017; <https://beta.altalis.com/map?id=201>) and all classes of road (highway, gravel, etc.) were pooled. Wetland spatial data created by GPS-tracking was edited in ArcMap (version 10.6.1, Environmental Systems Research Institute, Redlands, CA) and wetland perimeter was divided by area to calculate edge-to-area ratios (figure 12). Spatial data describing vegetation were created manually to obtain the resolution required for fine-scale analyses. Stands of trees and tall shrubs, predominantly consisting of trembling aspen and herein referred to as “aspen stands”, were digitized at a 1:2000 scale from 0.5-m resolution imagery collected between 2010-2014 by DigitalGlobe (World Imagery, Environmental Systems Research Institute, Redlands, CA). Upland area was created by removing aspen stands and wetlands from our study sites, so that all remaining area was categorized as upland. Where data were missing for surrounding landcover, we supplemented it using the most recent DigitalGlobe imagery (World Imagery, Environmental Systems Research Institute, Redlands, CA) available for the area in question. Spatial covariates

were quantified in R (version 3.5.1, R Core Team 2018) using packages *arcgisbinding* (Esri 2018), *sp* (Pebesma and Bivand 2005, Bivand et al. 2013), *spatstat* (Baddeley and Turner 2005, Baddeley et al. 2013, Baddeley et al. 2015), *raster* (Hijmans 2018), *sf* (Pebesma 2018), and others at one of two spatial scales: nest-site and patch. An individual patch represented a single unit that was searched for nests, such that adjacent nest-searched quarter sections were amalgamated; patch size thus varied from ~64.75 ha to ~194.25 ha. Refer to table 4 for a complete list of covariates, metrics, data sources, and spatial scale categories.

Habitat Modelling

Categorical variables were study area, species, and individual nest and all were treated as random effects. We tested for significant differences ($p \leq 0.05$) in response variables among levels of categorical variables using proportion tests. We used proportion tests and pairwise comparisons to test for significant differences ($p \leq 0.05$) in values of continuous variables among levels of categorical variables. Among continuous predictor variables, collinearity was examined using Pearson's r coefficient; we did not include covariates in the same model where $|r| > 0.6$ (Dormann et al. 2007). All predictor covariates were standardized ($\bar{x} = 0$, $SD = 1$).

Our analysis was two-part: evaluation of habitat associations with (a) nest-site selection and (b) nest success. We used the same covariates and candidate models for both analyses (Devries et al. 2018), grouped into two spatial scales: individual nest-site and patch (table 4). We evaluated nest-site selection by comparing nests sites from 2016 and 2017 to available locations (Manly et al. 2003) where visual obstruction had been measured in 2017. For nest-site selection, to ensure nests from both years could be combined, we tested for significant differences in the means of each predictor covariate between years using t-tests and corrected for multiple testing with a Bonferroni correction (Zar 2010). We used logistic regression and the logit link to model the binary response of interest ((a) nest present and (b) nest hatched) following the equation:

$$\pi = \frac{e^{a+\beta_1X_1+\beta_2X_2+\dots+\beta_nX_n}}{1 + e^{a+\beta_1X_1+\beta_2X_2+\dots+\beta_nX_n}}$$

where π is event probability, a is the Y intercept and β_i is the regression coefficient for covariate X_i in a series of n covariates (McCullagh and Nelder 1989, Peng et al. 2002). Intercepts and regression coefficients were estimated using the maximum likelihood method (McCullagh and

Nelder 1989). For both analyses, we determined the appropriate structure of random effects by first modelling the response variable as a function of only random effects: study area (Bashaw or Viking), individual nest, and in analysis of nest success, year. We then estimated models including fixed effects and used the resulting candidate models to reflect competing hypotheses. The same set of predictor covariates were used for each set of candidate models in analysis of both nest-site selection and nest success.

We identified the most parsimonious models using Akaike information criterion corrected for small sample size (AICc) and considered models with $\Delta\text{AICc} < 2$ to be equally plausible (AICc; Burnham and Anderson 2002). Because the response variable of used/available in the analysis of nest-site selection is not discrete (i.e., data were not mutually exclusive), we evaluated the predictive ability of the top-performing model using k-fold cross validation (Fielding and Bell 1997, Boyce et al. 2002). We divided the data into five folds and within each created ten equal-interval bins of predicted probabilities. For each fold, we tested the association between area-adjusted frequencies and bin ranks using Spearman's rank correlation coefficient (r_s), and averaged the five correlations (\bar{r}_s) to quantify predictive success (Boyce et al. 2002). For nest success models, because the response variable of hatched/failed was mutually exclusive, we evaluated model performance using area under the receiver operating characteristic curve (AUROC; Hanley and McNeil 1982). The AUROC indicates the probability that model predictions match observed values and varies from 0.5 (no better than chance) to 1 (perfect predictive ability).

RESULTS

Nest-site selection

Of 1,136 nests found and monitored through 2015-2017, 690 were suitable for analysis of nest-site selection. We excluded nests that had been damaged by investigators regardless of fate and nests with no data for visual obstruction; the latter necessitated exclusion of all nests monitored in 2015. From that subset, we retained only nests that hatched ($n = 254$) or failed due to depredation or abandonment attributed to predator activity ($n = 436$). Duck species were pooled, because significantly unequal proportions of predation events only occurred among 'unidentified' species (pairwise $p = 0.01$). This collinearity was accepted because reduced opportunity to observe and confidently identify a hen was inherent in nests that failed early in observation; therefore we would expect a higher proportion of failures among unidentified nests.

We compared nest sites with 983 available locations for which visual obstruction had been measured in July 2017. No significant differences in the means of predictor covariates existed among 2016 and 2017 nests (table 5), so both years were pooled for comparison to available locations.

Modelling to determine appropriate structure of random effects revealed that both study area and individual nest overfit the data (variance and SD = 0, table A5) so no random effects were retained. We selected the only model with $\Delta\text{AICc} < 2$ that included no uninterpretable predictors (β spanning 0, $p > 0.05$; table A6) as the top-performing model. The top model for nest-site selection included percent surrounding grassland ($\beta = -0.18$, 95% CI = -0.28 - -0.07), coefficient of variance of visual obstruction interacting with Julian day ($\beta = -0.15$, 95% CI = -0.24 - -0.05), distance to aspen stand ($\beta = 0.20$, 95% CI = 0.09 - 0.30), and mean visual obstruction interacting with Julian day ($\beta = 0.27$, 95% CI = 0.17 - 0.37; figure 13). The mean Spearman-rank correlation (\bar{r}_s) between area-adjusted frequencies and bin ranks was 0.79 (mean $p = 0.01$).

Nest success

For analysis of nest success, we chose a subset of the nests used in analysis of nest-site selection. We excluded a cohort of nests ($n = 133$) demonstrated to have been disproportionately impacted by investigator-enhanced predation due to corvids recognizing nest markers (refer to Chapter 2 for more detail). Thus, there were 557 nests suitable for analysis of habitat associations with nest success, 233 that were successful and 324 that failed.

All combinations of potential random effects (year, study area and individual nest) overfit the data (variance and SD = 0, table A7). Proportion tests indicated no significant differences in response (hatch/fail) among levels of individual random effects, so we included only fixed effects in candidate models. The only model with $\Delta\text{AICc} < 2$ that included no uninterpretable predictors (β spanning 0, $p > 0.05$; table A6) was selected as the top-performing model. The top model for nest success included percent surrounding grassland ($\beta = 0.29$, 95% CI = 0.11 - 0.49) and wetland edge-to-area ratio ($\beta = -0.26$, 95% CI = -0.46 - -0.69; figure 14). The AUROC for the top model was 0.61 (figure 15).

DISCUSSION

In our study areas, nesting hens selected relatively smaller patches of contiguous grassland and within these patches nest sites that were farther from aspen stands and characterized by relatively

taller, more uniform, vegetation. More specifically, hens selected quarter sections where a lower proportion of immediately surrounding landcover was grassland (hay or pasture); by default, these preferred nesting patches were bordered by a greater proportion of cultivated cropland. We were surprised that smaller grassland patches were selected because if selection were adaptive we would expect hens to select larger patches because increased patch size reduces nest predation by diluting nest density or reducing predator foraging efficiency (Clark and Nudds 1991, Larivière and Messier 1998). However, the effect of patch size on duck nest success in agricultural ecosystems is mediated by greater landscape composition, specifically proportion of grassland (Andrén 1994, Donovan et al. 1997, Kuehl and Clark 2002, Horn et al. 2005). Some researchers have concluded no effect of patch size on duck nest survival (Clark and Nudds 1991, Jiménez et al. 2007). Alternatively, apparent selection for smaller grassland patches might have been confounded by our definition of ‘grassland’ which included pooling of idle and active pasture. In nesting northern pintails, Devries et al. (2018) found evidence for avoidance of pasture and selection for idle grassland. If hens perceived actively grazed grassland as poor habitat, they might have selected against it and because we combined idle and active pasture, selection against active grazing may erroneously appear as selection for smaller patches.

Selection for sites at a greater distance from aspen was in accordance with our predictions, because trees attract raptors and corvids that use perches to detect visual cues for hunting (Conover 2007). Greater distance from forest edges also might offer protection from mammalian predators known to frequent edge habitats (Gates and Gysel 1978, Niemuth and Boyce 1997). Selection for greater visual concealment also was unsurprising because of the protection provided against visual-oriented predators. For blue-winged teal, northern shoveler, and mallard, Clark and Shutler (1999) found cover to be the most important variable in nest-site selection, and in their review of other studies found cover to be the most frequently cited difference between successful and failed nests. However, visual obstruction does not appear to contribute appreciably to protection from mammalian predators (Clark and Nudds 1991, Jiménez et al. 2007). Selection for homogeneous cover, indicated by a lower coefficient of variance of visual obstruction, may reduce the ability of predators to form effective visual search images by increasing potential prey sites (Martin 1993).

If nest-site characteristics of greater distance from trees and cover homogeneity scale up to be consistent at the patch scale, there would be evidence for a trade-off in selection between

visual and olfactory concealment (Conover 2007). Many of the aspen stands in our study area are small, and scattered trees provide turbulence and updraft that hinder detection by olfactory predators (Conover 2007). Similarly, an open-field with a smooth structure allows scent to travel efficiently (Conover 2007, Borgo and Conover 2016b), benefiting olfactory-oriented predators. Visual concealment is most effective at the nest-site scale while olfactory concealment functions at the patch scale, where updrafts and turbulence are affected (Conover 2007). Thus, to mitigate risk from both visual- and olfactory-oriented predators, a hen should select nest sites with good visual protection within patches offering olfactory concealment (Conover 2007). Our evidence suggests hens are selecting nest-site characteristics that provide visual concealment, but models containing covariates related to olfactory concealment were not supported. The rolling topography of our study areas might reduce the need for hens to seek out olfactory concealment relative to flat prairie.

In our study areas, nests were more likely to hatch if they were located in relatively larger patches of contiguous grassland that contained relatively more large wetlands (characterized by lower edge-to-area ratios). A quarter section surrounded by crop land and containing numerous small wetlands (resulting in a higher wetland edge-to-area ratio) would be the least likely location for a nest to hatch. We were not surprised that larger grassland patches were associated with greater nest success because several other studies have concluded the same, possibly because large patches cannot be as effectively searched by predators (Kantrud 1993, Ball et al. 1995, Horn et al. 2005). Sovada et al. (2000) found activity indices of red foxes to be greatest in small patches, and higher activity indices of coyotes in large patches. Because foxes are a relatively more important nest predator and are subordinate to coyotes (Sovada et al. 1995), relatively higher use of large patches by coyotes may mediate nest predation risk in large patches (Sovada et al. 2000). However, the positive trend between patch size and nest survival found by Sovada et al. (2000) was ultimately inconclusive because it varied annually and with nest initiation date.

There was an inverse relationship with nest success and wetland edge-to-area ratio, but our interpretation of wetland edge in our study areas relates to wetland type rather than conventional edge functions. In forest ecosystems, edges are associated with increased nest parasitism and enhanced nest predation due to abundance of predators using edge for travel and foraging (Gates and Gysel 1978, Andrén 1995, Niemuth and Boyce 1997). Edge effects are

weaker in prairie agricultural ecosystems, possibly because of reduced contrast in vegetative structure among cover types during the growing season (Phillips et al. 2003). Wetland perimeters are primary hunting areas for predators like skunks, American minks (*Neovison vison*), and raccoons (Kantrud 1993, Larivière and Messier 2000, Phillips et al. 2003, Phillips et al. 2004). Duck nests in these areas are at risk of incidental predation (Andrén 1995). The vegetative structure and productivity of a wetland perimeter varies in relation to the permanence, depth, salinity, and surrounding land use of the wetland (Stewart and Kantrud 1971). Permanent or alkali ponds and lakes are more likely to have perimeters consisting of open water and bare soil, relative to ephemeral and temporary wetlands which are often characterized by vegetated perimeters (Stewart and Kantrud 1971). Permanent or alkali ponds and lakes tend to be larger than other classes of wetlands with more productive edges, and so would have a relatively lower edge-to-area ratio. Thus, we interpret the negative relationship with wetland edge-to-area ratio as reflecting higher rates of incidental nest predation where more wetlands with productive edges, which also happen to be smaller in size, occur. Large wetlands, with a greater tendency to have bare soil perimeters (Stewart and Kantrud 1971), would not be attractive foraging areas for predators and would thus be associated with lower incidental predation of duck nests. Alternatively, larger water bodies may be associated with higher nest success because of the olfactory concealment provided at night, when many mammalian nest predators are most active. Large water bodies retain heat longer than the surrounding land, resulting in updrafts that would disperse odorants from nests (Conover 2007).

Our results suggest that adaptive selection was not occurring because there is no agreement between nest-site selection and nest success. Further, our results provide evidence of an attractive sink and possibly a perceptual trap. Selection for small patches of grassland associated with lower nest success is evidence of an attractive sink (Nielsen et al. 2006). Sovada et al. (2000) also identified small, isolated patches of grassland as ecological sinks for ducks, because they are attractive to nesting hens but are frequently visited by important nest predators like red fox. Other habitat features selected by nesting hens (greater distance from aspen and taller, homogeneous cover) appear to have no consequence to nest survival. This aspect of our findings is similar to that of (Borgo and Conover 2016b), who found selection for nest sites with greater visual concealment but no related advantage to nest success. Because visual concealment of nests does not effectively prevent detection by olfactory-oriented predators, the lack of a

relationship between visual concealment and nest success may indicate greater predation by mammals relative to avian predators (Borgo and Conover 2016b). Finally, nesting hens did not appear to alter their selection in response to lower nest success in areas with higher wetland edge-to-area ratios. Lack of selection for habitats characterized by low wetland edge-to-area ratios might be the result of a perceptual trap, where high-quality patches are not selected because they are perceived as unattractive (Patten and Kelly 2010).

Patterns of both nest-site selection and nest success are often temporally fluid, changing within and among nesting seasons (Sovada et al. 2000, Devries et al. 2018). Analysis at a smaller temporal scale may reveal development of an adaptive response, if nest-site selection changed over time in response to nest success (Clark and Shutler 1999, Devries et al. 2018). An indication of an adaptive response would be increased nest density in areas associated with higher nest success (Clark and Shutler 1999, Morris et al. 2008), and a within-season response may occur later in the nesting season, when re-nesting occurs (Devries et al. 2018). Particularly in fragmented habitats, patterns in selection and nest success are influenced by greater landscape composition (Andr n 1994, Donovan et al. 1997, Devries et al. 2008, Devries et al. 2018). For example, Horn et al. (2005) found differential edge effects among landscapes that varied in their proportion of grassland. The accuracy of our models could be improved by determining whether the influence of our predictor covariates changes with landscape composition. Nest-site selection (Borgo and Conover 2016b) and success also can vary among species; Clark and Shutler (1999) found differential patterns in nest success among duck species. However, our collective analysis of all duck species allowed us to evaluate interspecific pressures likely to arise from the community of generalist predators characterizing our study area (Sargeant et al. 1993, Clark and Shutler 1999).

Though territoriality among breeding ducks is debated, nest-site selection may be constrained by density-dependent mechanisms (Devries et al. 2018). Especially in areas of limited suitable habitat, prey density and distribution can act as a cue to predators and increase their foraging efficiency (Conover 2007). Determining whether nest predation was density dependent may further clarify the patterns we observed in nest-site selection and success, because density dependence or lack thereof can be indicative of primary predator guilds (Schmidt and Whelan 1999, Ringelman 2014). Evaluating density dependence of nest predation may support or refute our interpretation that incidental predation is the cause of higher nest

mortality on patches with higher wetland edge-to-area ratios. Nest predation rates by incidental predators should be density independent, because incidental nest predators would not actively return to areas of high nest density (Wirsing et al. 2012).

In the United States, two programs implemented in the American prairie pothole region with a goal of improving waterfowl production demonstrate the impact of scale in land management for conservation purposes. In the first program, nearly 112,000 ha of upland habitat were purchased and managed by the U.S. Fish and Wildlife Service; these parcels are known as Waterfowl Production Areas (WPA). The second initiative, the Conservation Reserve Program (CRP), began in 1985 and incentivized landowners to convert cropland to perennial cover; by 1995 14.7 million ha had been enrolled in the program (Reynolds et al. 2001). In the 1980s, despite cover management, nest success on many WPA lands was below the threshold required to maintain stable populations (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995) and lower than that found on CRP lands (Kantrud 1993). Low nest success on WPA lands was partially attributed to their isolation within a largely cultivated landscape (Klett et al. 1988, Reynolds et al. 2001). In the 1990s, nest success on WPA lands increased and was comparable to that of CRP lands, but the improvement was attributed to the increased proportion of grassland across the landscape resulting from CRP (Reynolds et al. 2001). Similarly, on the Canadian prairies Greenwood et al. (1995) found duck nest success decreased as the proportion of the landscape under cultivated crop increased. In Montana, nest success was found to be higher on larger patches of intact grassland (Ball et al. 1995). Even at a scale of 65 km², habitat mitigations in the Canadian PPR were insufficient to substantially impact mallard recruitment (Howerter et al. 2014). The extent of grasslands on the landscape seems to be the determining factor in duck nest survival, and the success of intensive management of small land parcels is constrained by greater landscape composition.

MANAGEMENT IMPLICATIONS

Continuous monitoring of nest-site selection and nest success on small land parcels managed for duck production can allow for detection of attractive sinks. Mapping of selection and success could identify sinks at the patch scale (Nielsen et al. 2006) and could form the basis for intensive vegetation management used to mitigate attractive sinks and increase factors associated with nest success. For example, selection could be influenced through grazing management; hens are selecting for taller and more homogeneous cover, which is more likely to

form under haying than grazing. Selection cues could be manipulated, so that patches characterized by attributes associated with high survival could be made more attractive by conversion to hay fields (Patten and Kelly 2010). Likewise, patches acting as sinks could be made less attractive by strategically reducing vegetation height and increasing heterogeneity through grazing during the nesting season. Multiple contiguous parcels of land are better for upland duck nest success because smaller patches of grassland are acting as attractive sinks.

Areas with sufficient wetlands and large tracts of contiguous grassland are likely the most productive for ducks (Sovada et al. 2000), but such a landscape is unlikely to develop in the absence of an incentive program similar to the CRP. Where nesting habitat exists in small, isolated fragments across the landscape, as is the case in the central Alberta parklands, intensive management is likely required to mitigate the effects of ecological traps and ensure duck productivity (Sovada et al. 2000). A better alternative may be to increase the proportion of fall-seeded crops across the landscape. Fall-seeded crops, like winter wheat and fall rye, are relatively under-utilized in the Canadian PPR but support high nest success (Devries et al. 2008, Devries et al. 2018). Protection of large patches of idle grassland and wider use of fall-seeded crops at a landscape scale where densities of nesting ducks are high represent perhaps the best option to increase duck nesting success (Reynolds et al. 2001, Devries et al. 2018).

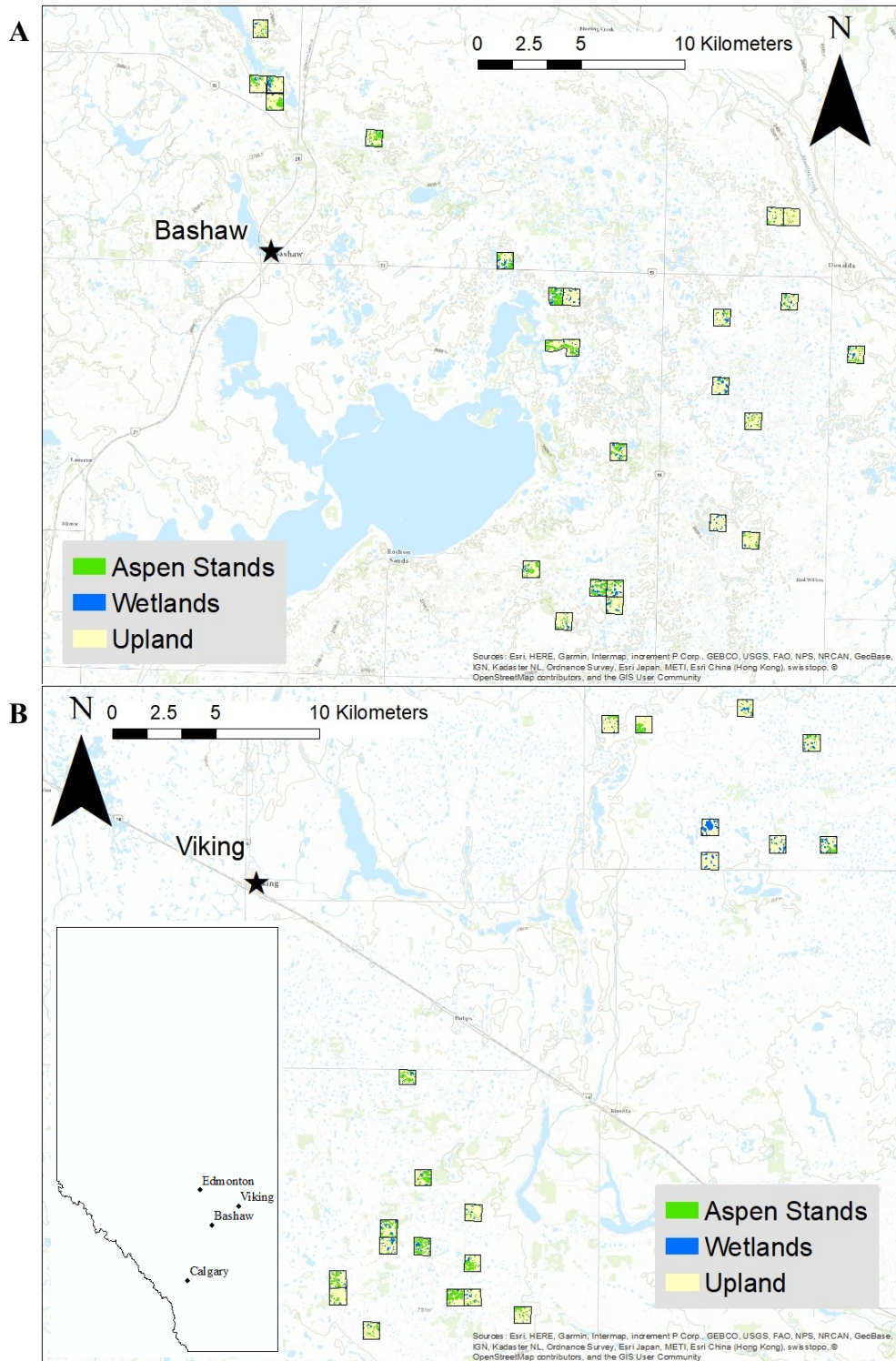


Figure 10: Maps depicting landcover of 45 study sites at (a) Bashaw and (b) Viking study areas in the central Alberta parklands, 2016-2017.

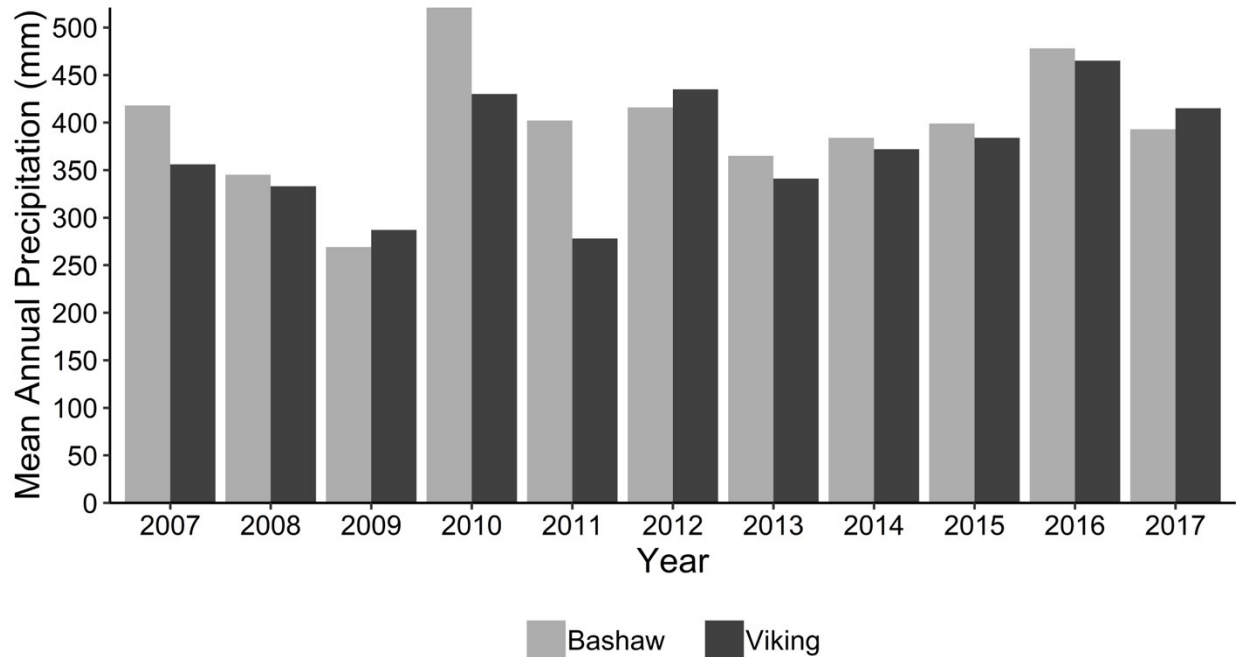


Figure 11: Annual precipitation (mm) averaged over two townships for both Bashaw (T41R19W4 and T42R21W4) and Viking (T46R12W4 and T48R10W4) study areas. Interpolated data provided by Alberta Agriculture and Forestry, Alberta Climate Information Service (ACIS; <https://agriculture.alberta.ca/acis>).

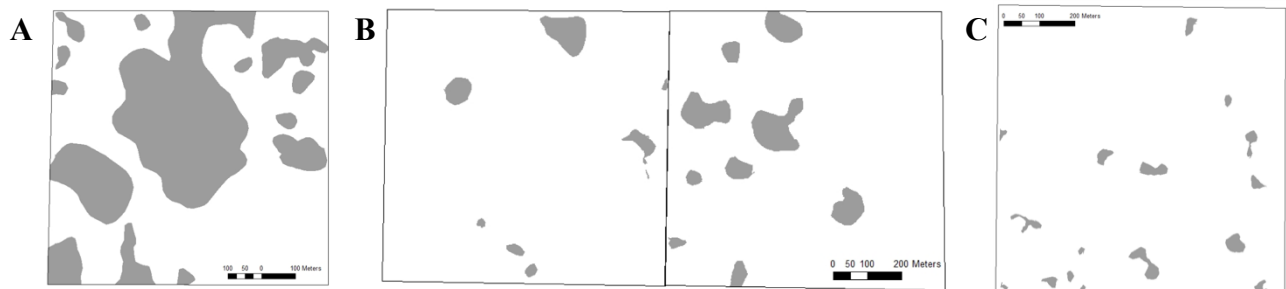


Figure 12: Depictions of (A) minimum (259), (B) median (598), and (C) maximum (1619) values of wetland edge-to-area ratio in our central Alberta parklands study areas. Wetlands displayed in grey.

Table 4: Covariates used for logistic regression models of nest-site selection and nest success. Covariates were grouped into two spatial scales, nest-site and patch, using 3 data themes: human-use, landscape, and vegetation. All GIS-based data were vector data.

Covariate	Source	Spatial Scale
Human-use		
Roads	Altalis	
<i>Distance to road (m)</i>		nest-site
Surrounding landcover	Field data (2017), supplemented by DigitalGlobe Imagery	
<i>Grassland quarters abutting focal quarter-section (% out of 8)</i>		patch
Landscape		
Wetlands	Mapped by GPS (July 2017)	
<i>Distance to nearest wetland edge (m)</i>		nest-site
<i>Edge (m) to area (ha) ratio</i>		patch
Vegetation		
Aspen stands	Digitized from DigitalGlobe Imagery	
<i>Distance to nearest aspen edge (m)</i>		nest-site
<i>Total perimeter (m)</i>		patch
Upland	Area not classified as wetland or aspen	
<i>Area (ha)</i>		patch
Visual Obstruction	Robel pole measurements (July 2017)	
<i>Mean (cm)</i>		nest-site
<i>Coefficient of Variance (cm)</i>		nest-site

Table 5: Statistics comparing mean covariate values between nests found in 2016 and 2017, using a Bonferroni correction of $\alpha = 0.005$.

Predictor covariate	t-value	df ¹	<i>p</i> -value
Aspen perimeter	0.59	634.79	0.56
Distance to aspen	-0.51	632.80	0.61
Distance to road	0.43	669.61	0.67
Distance to wetland	1.11	634.40	0.27
Julian date of discovery	2.37	640.78	0.02
Percent adjacent grassland	0.65	624.20	0.52
Robel - coefficient of variance	-0.40	655.89	0.69
Robel - mean	-1.31	665.07	0.19
Upland area	-0.01	665.03	0.36
Wetland edge-to-area ratio	-0.78	687.73	0.44

¹df = degrees of freedom

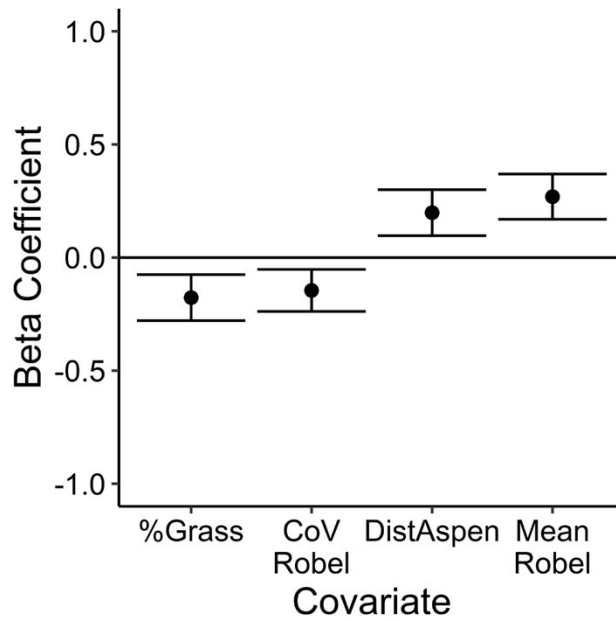


Figure 13: Scaled beta coefficients from top-performing logistic regression model for site selection of duck nests ($n = 690$) compared to available sites ($n = 983$) in central Alberta parklands in 2016 – 2017. Error bars represent 95% confidence intervals.

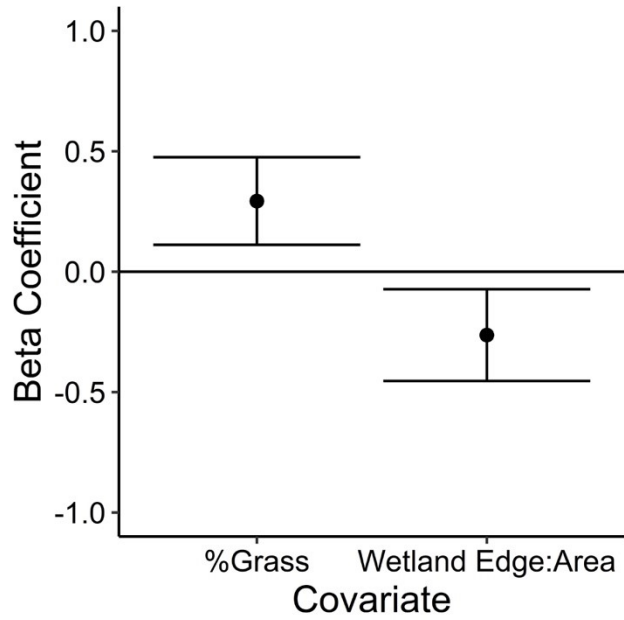


Figure 14: Scaled beta coefficients from top-performing logistic regression model for fate (hatched/depredated) of duck nests ($n = 557$) in central Alberta parklands in 2016 – 2017. Error bars represent 95% confidence intervals.

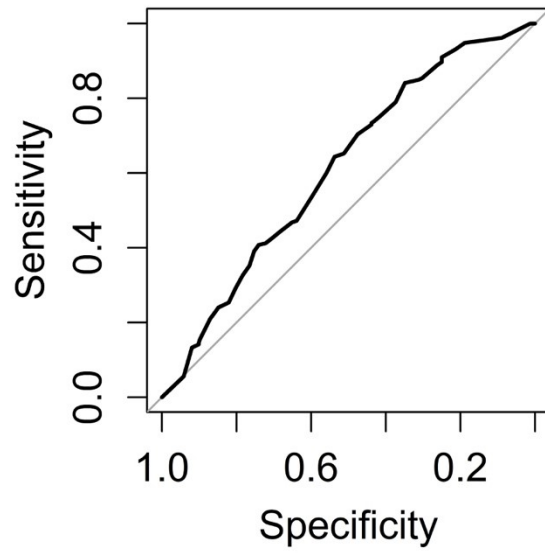


Figure 15: ROC curve for top-performing logistic regression model for fate (hatched/depredated) of duck nests ($n = 557$) in central Alberta parklands in 2016 – 2017. AUROC = 0.6131; diagonal line represents AUROC = 0.50.

CHAPTER 4 - CONCLUSION

We have demonstrated that predator removal is ineffective at increasing nest success in the central Alberta parklands and identified attractive sinks for nest survival on land parcels owned and managed for duck production. Our estimates indicate that nest survival in the central Alberta parklands may be insufficient to maintain stable populations (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995). These findings present a paradox, because predator removal is perhaps best applied to alleviate ecological traps that habitat-based strategies fail to mitigate in the short-term (Garrettson and Rohwer 2001, Sovada et al. 2001). Without predator removal as a viable option, the tools available to address sink dynamics on land managed for duck production are limited, and may include adjustments to grazing regimes (Ignatiuk and Duncan 2001) or provision of artificial nesting structures (Chouinard et al. 2005). Mapping of attractive sink habitats on individual quarter sections would provide fine-scale information that could be used for habitat manipulation on a case-by-case basis (Nielsen et al. 2004).

Our results demonstrating ineffectiveness of predator removal to increase nest survival confirmed our prediction based on enhanced potential for compensatory predation because of three-dimensional habitat and socioeconomic forces dictating small-scale partial predator removal. Predator removal often increases nest survival in prairie systems (Garrettson and Rohwer 2001, Lester 2004, Chodachek and Chamberlain 2006, Pieron and Rohwer 2010, Pieron et al. 2012), but our results demonstrate the importance of rigorous evaluation prior to initiating a predator-removal program in novel habitats or socioeconomic conditions. Predator removal requires substantial resources that could be directed at other conservation initiatives like habitat protection (Sovada et al. 2001), so it was imperative to test its ability to effectively increase nest survival in Alberta parklands prior to implementation. Aspen parkland habitats have rich predator communities (Sargeant et al. 1993), and legal restrictions necessitate partial predator removal, greatly complicating the implementation of successful nest predator removal (Smith et al. 2010). Additionally, fragmentation of land ownership logistically constrains predator removal to small spatial scales where it may be less effective (Lieury et al. 2015). Predator removal in the Alberta parklands is thus complicated not only by biological challenges, but anthropogenic constraints.

Both management approaches that we evaluated were small in scale and inherently limited in their ability to substantially contribute at a population level. Increasing the proportion

of secure nesting habitat across the landscape through conversion of cropland, protection of existing grassland, and greater use of spring-seeded crops is perhaps the most effective means of increasing duck production (Reynolds et al. 2001, Devries et al. 2008, Devries et al. 2018). Continued restoration and protection of wetlands across the PPR also is critical to maintaining healthy duck populations (Prairie Habitat Joint Venture 2014, Anderson et al. 2018). Evaluating conservation efforts by the single vital rate of nest survival can lead to erroneous conclusions, and a measure of recruitment is crucial to determine the true effect of any management effort on population dynamics (McCarter 2009, Amundson and Arnold 2011, Amundson et al. 2013, Pieron et al. 2013).

Future challenges for waterfowl conservation include threats from climate change, agricultural and urban expansion, and public apathy towards the intrinsic value of wildlife and ecosystems (Anderson et al. 2018). Grasslands are the least protected biome on the planet (Hoekstra et al. 2004) and work continues to reduce and mitigate conversion of both grasslands and wetlands of the PPR (Prairie Habitat Joint Venture 2014). Low nest survival arising from habitat degradation and artificially high populations of nest predators (Klett et al. 1988, Beauchamp et al. 1996, Sovada et al. 2001, Crimmins et al. 2016) persists and is a continuous challenge to waterfowl managers. In this thesis I have evaluated both predator removal and fine-scale habitat management as methods to increase duck nest success in crucial breeding habitat, the Alberta aspen parklands. In doing so, I have demonstrated the challenges of mitigating low nest survival at a local scale when aggravating factors operate at a landscape and continental scale, beyond the influence of any one management organization. Fortunately, waterfowl conservation is a success story of cooperation across multiple levels of government (Anderson et al. 2018) and organizations like Delta Waterfowl Foundation and Ducks Unlimited ensure ongoing support for research and on-the-ground initiatives.

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APPENDICES

APPENDIX 1. PREDATOR REMOVALS

Table A 1. Total nest predators removed from Bashaw and Viking trapped sites, 2015 – 2017.

Species	2015	2016		2017		Total
	Bashaw	Bashaw	Viking	Bashaw	Viking	
Coyote	14	64	33	35	16	162
Franklin's Ground Squirrel	0	0	0	0	11	11
Red Fox	0	0	1	3	0	4
Raccoon	1	0	1	0	1	3
Skunk	20	20	28	31	43	142
Badger*	4	1	0	0	0	5
Raven	18	95	5	54	32	204
Magpie	25	28	3	63	77	196
Crow	43	63	0	43	63	212
Long-tailed weasel*	0	1	0	0	0	1
Total	125	272	71	229	243	940

*incidental

APPENDIX 2. TRAIL CAMERA SUMMARY

Table A 2. Summary of wildlife trail cameras deployed at individual nests and predator species photographed.

Study area & year	N ¹	n ²	Predator species
Bashaw 2016	8	3	Striped skunk, black-billed magpie American crow or common raven Striped skunk
Bashaw 2017	15	5	Unidentified corvid Striped skunk, black-billed magpie Long-tailed weasel (post-hatch) Unidentified furbearer (possibly weasel) Long-tailed weasel
Viking 2016	9	4	Striped skunk, 13-lined ground squirrel, unidentified rodent 13-lined ground squirrel Striped skunk Striped skunk, 13-lined ground squirrel
Viking 2017	3	0	N/A

¹N = individual nests with cameras

²n = nests with predator photographed

APPENDIX 3. AIC VALUES

Table A 3. RMark nest survival models for daily survival rates of duck nests ($n = 830$) on plots where predator removal was transposed over > 2 years in central Alberta parklands in 2015 - 2017, ranked by corrected Akaike's Information Criterion (AICc).

Model	K ¹	AICc ²	Δ AICc ³	w _i ⁴	Deviance
S(~1 + treatment:StudyArea:year)	10	2093.94	0.00	1.00	2073.91
S(~1 + treatment:year)	6	2160.84	66.90	0.00	2148.83
S(~1 + StudyArea:year)	5	2166.58	72.64	0.00	2156.57
S(~1 + AgeDay1 + StudyArea:year)	6	2168.15	74.21	0.00	2156.14
S(~year)	3	2179.72	85.78	0.00	2173.72
S(~AgeDay1 + year)	4	2181.72	87.78	0.00	2173.71
S(~StudyArea)	2	2186.03	92.09	0.00	2182.03
S(~treatment)	2	2186.13	92.19	0.00	2182.13
S(~Time * Time)	2	2193.44	99.49	0.00	2189.43
S(~Time)	2	2193.44	99.49	0.00	2189.43
S(~AgeFound)	2	2204.64	110.70	0.00	2200.64
S(~1)	1	2204.96	111.02	0.00	2202.96
S(~AgeDay1)	2	2206.76	112.82	0.00	2202.76

¹K = number of model parameters

²AICc = Akaike information criterion corrected for small sample sizes

³ Δ AICc = difference in AIC value from top model

⁴w_i = model weight

Table A 4. RMark nest survival models for daily survival rates of duck nests on plots where predator removal was transposed over > 2 years in central Alberta parklands in 2015 - 2017, excluding Viking Control 2017 plots. Ranked by corrected Akaike's Information Criterion (AICc).

Model	K ¹	AICc ²	ΔAICc ³	w _i ⁴	Deviance	Beta Value
S(~-1 + StudyArea:year)	5	1803.43	0	0.26	1793.42	+
S(~AgeFound)	2	1803.79	0.36	0.22	1799.79	+
S(~Time * Time)	2	1805.20	1.77	0.11	1801.20	-/+
S(~Time)	2	1805.20	1.77	0.11	1801.20	-/+
S(~-1 + AgeDay1 + StudyArea:year)	6	1805.43	2.00	0.10	1793.42	-/+
S(~1)	1	1806.50	3.07	0.06	1804.50	
S(~year)	3	1807.11	3.68	0.04	1801.11	
S(~treatment)	2	1808.32	4.88	0.02	1804.31	
S(~AgeDay1)	2	1808.39	4.95	0.02	1804.38	
S(~StudyArea)	2	1808.51	5.07	0.02	1804.50	
S(~-1 + treatment:StudyArea:year)	9	1808.53	5.10	0.02	1790.51	
S(~AgeDay1 + year)	4	1808.96	5.52	0.02	1801.00	
S(~-1 + treatment:year)	6	1811.85	8.42	0.00	1799.84	

¹K = number of model parameters

²AICc = Akaike information criterion corrected for small sample sizes

³ΔAICc = difference in AIC value from top model

⁴w_i = model weight

Table A 5. Logistic regression models containing only random effects for site selection of duck nests ($n = 690$) compared to available sites ($n = 983$) in central Alberta parklands in 2016 - 2017, ranked by corrected Akaike's Information Criterion (AICc).

Model	Intercept	df ¹	LL ²	AICc ³	Δ AICc ⁴	w _i ⁵
U(~1)	-0.35	1	-1133.85	2269.7	0	0.54
U(~1 nest)	-0.35	2	-1133.85	2271.7	2	0.2
U(~1 StudyArea)	-0.35	2	-1133.85	2271.7	2	0.2
U(~1 nest + 1 StudyArea)	-0.35	3	-1133.85	2273.7	4.01	0.07

¹df = degrees of freedom

²LL = log likelihood

³AICc = Akaike information criterion corrected for small sample sizes

⁴ Δ AICc = difference in AIC value from top model

⁵w_i = model weight

Table A 6. Logistic regression models containing only random effects for fate (hatched/depredated) of duck nests ($n = 557$) in central Alberta parklands in 2016 - 2017, ranked by corrected Akaike's Information Criterion (AICc).

Model Number	Model	Intercept	df ¹	LL ²	AICc ³	Δ AICc ⁴	w _i ⁵
9	H(~1)	-0.33	1	-378.62	759.24	0.00	0.37
1	H(~1 nest)	-0.33	2	-378.62	761.25	2.01	0.14
3	H(~1 StudyArea)	-0.33	2	-378.62	761.25	2.01	0.14
2	H(~1 year)	-0.33	2	-378.62	761.25	2.01	0.14
8	H(~1 year/StudyArea)	-0.32	3	-378.43	762.91	3.67	0.06
7	H(~1 nest + 1 year)	-0.33	3	-378.62	763.28	4.04	0.05
6	H(~1 nest + 1 StudyArea)	-0.33	3	-378.62	763.28	4.04	0.05
5	H(~1 StudyArea + 1 year)	-0.33	3	-378.62	763.28	4.04	0.05
4	H(~1 nest + 1 StudyArea + 1 year)	-0.33	4	-378.62	765.30	6.07	0.02

¹df = degrees of freedom

²LL = log likelihood

³AICc = Akaike information criterion corrected for small sample sizes

⁴ Δ AICc = difference in AIC value from top model

⁵w_i = model weight

Table A 7. Logistic regression models for site selection of duck nests ($n = 690$) compared to available sites ($n = 983$) in central Alberta parklands in 2016 - 2017, ranked by corrected Akaike's Information Criterion (AICc).

Model	Intercept	df ¹	LL ²	AICc ³	Δ AICc ⁴	w _i ⁵
U(~-percentgrass+DistRoad+DistAspen-DistPonds+meanrobel:JulianD-JulianD:covRobel)	-0.45	7	-1089.66	2193.39	0.00	0.48
U(~-percentgrass+DistRoad+DistAspen+meanrobel:JulianD-JulianD:covRobel)	-0.45	6	-1091.15	2194.36	0.97	0.30
U(~-percentgrass+DistAspen+meanrobel:JulianD-JulianD:covRobel)	-0.45	5	-1092.65	2195.33	1.93	0.18
U(~-aspen_m+ponds_EDmha-percentgrass+DistRoad+DistAspen-DistPonds+upland_ha+meanrobel:JulianD-JulianD:covRobel)	-0.45	10	-1089.37	2198.87	5.48	0.03
U(~-percentgrass+DistAspen+meanrobel:JulianD)	-0.43	4	-1097.60	2203.23	9.84	0.00
U(~-aspen_m+DistRoad+DistAspen+meanrobel:JulianD-JulianD:covRobel)	-0.45	6	-1097.31	2206.68	13.28	0.00
U(~-ponds_EDmha-percentgrass-DistPonds-upland_ha+meanrobel:JulianD-JulianD:covRobel)	-0.45	7	-1098.50	2211.07	17.68	0.00

U(~~ponds_EDmha-percentgrass- DistPonds+meanrobel:JulianD)	-0.42	5	-1104.25	2218.54	25.15	0.00
U(~~ponds_EDmha-percentgrass+meanrobel:JulianD)	-0.43	4	-1105.37	2218.77	25.38	0.00
U(~~percentgrass)	-0.36	2	-1125.89	2255.78	62.39	0.00
U(~~percentgrass-ponds_EDmha)	-0.36	3	-1125.58	2257.17	63.78	0.00
U(~1)	-0.35	1	-1133.85	2269.69	76.30	0.00
U(~~ponds_EDmha)	-0.35	2	-1133.80	2271.60	78.21	0.00

¹df = degrees of freedom

²LL = log likelihood

³AICc = Akaike information criterion corrected for small sample sizes

⁴ Δ AICc = difference in AIC value from top model

⁵w_i = model weight

Table A 8. Logistic regression models for fate (hatched/depredated) of duck nests ($n = 557$) in central Alberta parklands in 2016 - 2017, ranked by corrected Akaike's Information Criterion (AICc).

Model	Intercept	df ¹	LL ²	AICc ³	Δ AICc ⁴	w _i ⁵
H(~ponds_EDmha+percentgrass-meanrobel:JulianD)	-0.29	4	-364.64	737.35	0.00	0.40
H(~percentgrass-ponds_EDmha)	-0.35	3	-366.03	738.10	0.75	0.28
H(~ponds_EDmha+percentgrass-DistPonds-meanrobel:JulianD)	-0.29	5	-364.47	739.06	1.71	0.17
H(~aspen_m-ponds_EDmha+percentgrass+DistRoad-DistAspen-DistPonds+upland_ha-meanrobel:JulianD-JulianD:covRobel)	-0.29	10	-360.62	741.65	4.30	0.05
H(~ponds_EDmha+percentgrass-DistPonds-upland_ha-meanrobel:JulianD-JulianD:covRobel)	-0.30	7	-364.19	742.58	5.23	0.03
H(~percentgrass+DistRoad+DistAspen-meanrobel:JulianD-JulianD:covRobel)	-0.28	6	-365.70	743.55	6.20	0.02
H(~percentgrass)	-0.34	2	-369.88	743.79	6.44	0.02
H(~percentgrass+DistRoad+DistAspen-DistPonds-meanrobel:JulianD-JulianD:covRobel)	-0.28	7	-364.98	744.15	6.81	0.01
H(~percentgrass+DistAspen-meanrobel:JulianD)	-0.28	4	-368.09	744.26	6.91	0.01
H(~percentgrass+DistAspen-meanrobel:JulianD-JulianD:covRobel)	-0.28	5	-367.93	745.97	8.62	0.01

H(~ponds_EDmha)	-0.34	2	-371.11	746.24	8.89	0.00
H(~aspen_m+DistRoad+DistAspen- meanrobel:JulianD-JulianD:covRobel)	-0.29	6	-372.03	756.20	18.86	0.00
H(~1)	-0.33	1	-378.62	759.24	21.89	0.00

¹df = degrees of freedom

²LL= log likelihood

³AICc = Akaike information criterion corrected for small sample sizes

⁴ Δ AICc = difference in AIC value from top model

⁵w_i = model weight

APPENDIX 4. DAILY SURVIVAL RATES

Table A 9. Daily survival rate (DSR) and standard error (SE) derived from top-performing RMark nest survival model for daily survival rates of duck nests on plots where predator removal was transposed over > 2 years in central Alberta parklands in 2015 – 2017.

Study Area/Year/Treatment	DSR ¹	SE ²
Bashaw 2015 Control	0.9623486	0.0080840
Bashaw 2016 Control	0.9640390	0.0077220
Viking 2016 Control	0.9471145	0.0077928
Bashaw 2017 Control	0.9487335	0.0052604
Viking 2017 Control	0.8527007	0.0121859
Bashaw 2015 Trapped	0.9639663	0.0065871
Bashaw 2016 Trapped	0.9530781	0.0056207
Viking 2016 Trapped	0.9492815	0.0059268
Bashaw 2017 Trapped	0.9318947	0.0130123
Viking 2017 Trapped	0.9653167	0.0056134

¹DSR = daily survival rate

²SE = standard error

APPENDIX 5. BETA COEFFICIENTS

Table A 10. Beta coefficients from top-performing RMark nest survival model for daily survival rates of duck nests on plots where predator removal was transposed over > 2 years in central Alberta parklands in 2015 – 2017.

Covariate	β^1	SE ²	lcl ³	ucl ⁴
Control:Bashaw:2015	3.24	0.22	2.80	3.68
Trap:Bashaw:2015	3.29	0.19	2.91	3.66
Control:Bashaw:2016	3.29	0.22	2.85	3.73
Trap:Bashaw:2016	3.01	0.13	2.76	3.26
Control:Viking:2016	2.89	0.16	2.58	3.19
Trap:Viking:2016	2.93	0.12	2.69	3.17
Control:Bashaw:2017	2.92	0.11	2.71	3.13
Trap:Bashaw:2017	2.62	0.21	2.21	3.02
Control:Viking:2017	1.76	0.10	1.57	1.95
Trap:Viking:2017	3.33	0.17	3.00	3.66

¹ β = beta coefficient

²SE = standard error

³lcl = lower confidence limit

⁴ucl = upper confidence limit

Table A 11. Beta coefficients from top-performing logistic regression model for site selection of duck nests ($n = 690$) compared to available sites ($n = 983$) in central Alberta parklands in 2016 – 2017.

Covariate	β^1	SE ²	p -value	lcl ³	ucl ⁴
Percent grassland	-0.1775	0.0519	0.0006	-0.2813	-0.0736
Distance to aspen	0.1983	0.0518	0.0001	0.0947	0.3019
Mean visual obstruction with Julian day interaction	0.2691	0.0510	1.35E-07	0.1670	0.3712
Coefficient of variance of visual obstruction with Julian day interaction	-0.1453	0.0474	0.0022	-0.24	-0.0505

¹ β = beta coefficient

²SE = standard error

³lcl = lower confidence limit

⁴ucl = upper confidence limit

Table A 12. Beta coefficients from top-performing logistic regression model for fate (hatched/depredated) of duck nests ($n = 557$) in central Alberta parklands in 2016 – 2017.

Covariate	β^1	SE ²	p -value	lcl ³	ucl ⁴
Percent grassland	0.2932	0.0927	0.0016	0.1077	0.4786
Wetland edge-to-area ratio	-0.2637	0.0971	0.0066	-0.4579	-0.0695

¹ β = beta coefficient

²SE = standard error

³lcl = lower confidence limit

⁴ucl = upper confidence limit

APPENDIX 6. SPECIES OF DEPREDATED HENS

Table A 13. Counts of depredated nesting hens ($n = 27$) by species and treatment plot on which they were found.

Species	Control	Predator Removal
American green-winged teal	1	0
American widgeon	0	1
Blue-winged teal	3	10
Gadwall	3	1
Northern shoveler	2	6