

**BREEDING ECOLOGY OF NORTHERN PINTAILS IN PRAIRIE
LANDSCAPES: TESTS OF HABITAT SELECTION AND REPRODUCTIVE
TRADE-OFF MODELS**

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By

Terry A. Kowalchuk

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ABSTRACT

Ecologists and conservation biologists are interested in explaining why animal abundance and reproductive success vary among habitats. Initial motivation for this research arose from concerns for Northern Pintail (*Anas acuta*) populations in North America. Unlike many prairie-nesting dabbling duck populations, pintails failed to increase during periods of excellent wetland conditions, and remained below conservation goals. Low pintail populations have been linked to degraded landscape conditions on the Canadian prairies. Current habitat management for pintails aims to protect and create larger areas of perennial cover either by encouraging better management of grazing lands, by converting cropland to grassland, or by promoting adoption of fall-seeded crops like winter wheat. The central premise is that larger areas of natural grassland cover will attract breeding pintails to nest earlier in the season in low-predation-risk habitat. I studied pintail nesting ecology near the Milk River Ridge, Alberta, 2004-2006, in terms of a life-cycle perspective, from spring arrival and settling on breeding areas, to assess age and quality of nesting females, to determine timing and investment in reproduction, and finally to measure nesting success. A gradient in presumed high (grassland) to low (agriculture) habitat quality provided a landscape template for testing habitat selection models.

Pintail breeding pair densities were 1.5-3 times higher in grassland than agricultural landscapes in all three years, regardless of regional population size, with pairs occupying grassland landscapes at higher densities immediately upon arrival in early spring. Northern Shoveler (*A. clypeata*), gadwall (*A. strepera*) and blue-wing teal (*A. discors*) had similar settlement patterns as pintails, but mallard (*A. platyrhynchos*) pair density was higher in agricultural areas. Relatively more, older female pintails were captured at nests in grassland landscapes whereas yearling females were encountered more often in agricultural areas, a pattern that was not detected in female shovelers. This response suggests that older female pintails may be better able to recognize and settle in higher quality grassland habitats. Body mass of pintail females did not vary among years, decreased seasonally, and was positively related to body size index and incubation stage. Furthermore, pintail body mass did not differ between grassland (650 ± 24 g), ecotone (678 ± 27 g) and agriculture (672 ± 33 g). In female shovelers, body mass varied among years (555 ± 29 g in 2004, 481 ± 18 g in 2005, 508 ± 21

g in 2006), and increased with nesting date. Shoveler body mass did not differ between grassland (519 ± 32 g), ecotone (519 ± 44 g), or agriculture (507 ± 35 g).

Nest initiation dates did not vary by landscape for pintail, shoveler or mallard, but all species nested earlier in 2006 versus 2004. In pintail, shoveler and mallard, clutch size was negatively related to nest initiation date. Pintail and shoveler clutch sizes were generally larger in a wet year with abundant wetlands (2006) when compared with a dry year (2004), but no landscape differences were detected. Mallard clutch size did not vary by year or landscape. Female reproductive timing and investment (in terms of clutch size) were unrelated to upland habitat characteristics, counter to a hypothesis that predicts larger pintail clutch sizes in agricultural landscapes. However, pintail and shoveler invested in larger clutches in 2006, a wet year with abundant wetlands, possibly due to greater abundance of aquatic foods. Finally, nest survival rates of duck species, except mallard, tended to be higher in grassland landscapes and lower in agricultural landscapes. Pintail nest survival was consistently higher in grassland than in agricultural landscapes and was highest in 2006 when wetland conditions were excellent. Shoveler and blue-winged teal nest survival rates did not vary strongly with landscape, but were also higher in 2006, whereas mallard and gadwall nest survival estimates did not vary with landscape or year.

Overall, pintails settled at higher densities in grassland landscapes where breeding success was higher (indexed by nesting success). This suggests that pintails respond appropriately to cues that enable them to recognize suitable habitat, at least in regions where large contiguous areas of grassland habitat remain. Furthermore, assuming that findings for pintails reflect those of other grassland bird species, large remnant areas of intact natural grassland seem particularly in need of protection or restoration, and management regimes that maintain their habitat integrity. By integrating applied and theoretical aspects of pintail reproductive ecology, I attempted to provide deeper insights into the processes that could shape behavioral decisions by breeding pintails and other duck species. Older pintails may occupy wetlands in higher quality grassland habitat early in spring, forcing subordinate or later-arriving individuals into poorer quality habitat (i.e., where nesting success is lower); however, mechanisms involved in this putative process are unknown. Overall, results suggest that grassland restoration or enhancement (e.g., managing grazing intensity) could improve reproductive success of pintails and possibly other grassland bird species.

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CHAPTER 1 – GENERAL INTRODUCTION

Ecologists are interested in determining why animal abundance varies in time and space. For many species, variation in density may be associated with habitat-specific differences in survival and reproductive rates and this pattern often provides motivation to manage for increased attractiveness. Presumably, individuals that are capable of securing high quality habitat also have higher survival or reproductive rates, creating potential for selective processes to favor individuals that can recognize and exploit highly suitable habitats (Martin 1988, Clark and Shutler 1999).

The ability of individuals to distinguish and select among habitats of varying quality is one of the most significant traits possessed by an organism (Holt 1987, Jaenike and Holt 1991). Habitats may be chosen on the basis of genetic predisposition and reinforced by learning at an early age (Wecker 1964). Additionally, habitats may be selected through social facilitation when individuals are attracted to areas where other conspecifics are present (Hahn and Silverman 2006). The location of birth and previous reproductive experience may also play roles in habitat selection (Greenwood and Harvey 1982, Steele 1992, Payne and Payne 1993). Individuals may also select habitats based on previous experiences in specific habitat types. However, knowing what habitat to select is only part of the challenge; recognizing reliable cues and responding by choosing appropriate habitat are also required (Fretwell and Lucas 1970).

Habitat choices are related to proximate and ultimate factors (Cody 1985), and habitat selection is typically viewed as a hierarchical process (Johnson 1980). Proximate factors include fine level cues such as vegetative structure, or availability of food or nest sites (Verner and Willson 1966, Zimmerman 1971, Petit et al. 1988). In contrast, ultimate factors are coarse-level cues that provide key environmental stimuli, such as landscape composition (Wecker 1964). These proximate and ultimate factors represent a range of stimuli that individuals could use to recognize and settle in high suitability habitats. Factors that determine how and why individuals distribute themselves among landscapes and habitats have long been investigated (Svardson 1949, Kluyver and Tinbergen 1953, Fretwell and Calver 1970, Fretwell 1970). Interspecific and intraspecific competition are among the mechanisms underlying the patterns of individuals' distributions across habitats, but

predation also plays an important role in this process (Leonard and Picman 1987, Martin 1988, Martin and Roper 1988, Lima 1993).

1.1 Theories of Habitat Selection

Habitat selection is the process whereby individuals preferentially use or occupy available habitats (Morris 2003), i.e., they settle non-randomly. This selection has been invariably linked to population density and the associated habitats from which an individual can choose (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1988). More recently, this theory has expanded to include the effects of inter and intra-specific competition, resource distributions, spatial scale, and differences among individuals (Morris 2003). Most work has considered habitat selection at high population densities, but attention has also been paid to selection at low population densities, taking Allee effects and settlement costs into consideration (Greene and Stamps 2001). Despite advances in habitat selection theory, studies that connect habitat selection with population ecology are still limited (Morris et al. 2008).

The ideal free distribution model proposed by Fretwell and Lucas (1970) assumes that individuals are “ideal” and free to select habitats on the basis of quality (as measured by fitness metrics, e.g., survival or reproductive rates). As density increases in habitat (A), fitness of individuals decreases due to crowding and competition for resources, to the point that another habitat (B) becomes equally suitable. Thus, density of individuals in habitats A and B would eventually reach equilibrium such that individuals occupying habitats A and B have equal fitness.

An alternate model, the ideal despotic distribution, proposes that individuals must compete for access to high suitability habitat. Dominant individuals are better able to secure the best habitat, forcing subordinates into less suitable habitat (Petit and Petit 1996). In terms of reproductive success, the ideal despotic model predicts higher rates in preferred habitats over less preferred habitats. In this situation, observations suggest that a positive correlation exists between suitability and density, as predicted by the density-limiting territorial hypothesis (Fretwell 1970). Careful consideration needs to be taken when density is used as an indicator of habitat quality, especially when applied independently of some metric of reproductive success. Density could be a misleading indicator of habitat quality, especially if

it is negatively correlated with a measure of reproductive success (Van Horne 1983). Bock and Jones' (2004) review of this idea suggests that, in most cases, density is a reliable indicator of habitat quality and thus bird count data could provide an appropriate basis for making management decisions.

The primary assumption in both ideal free and despotic models is that individuals can choose between at least two habitats with different intrinsic suitability (Fretwell and Lucas 1970). Additionally, all individuals must be "ideal" and have the ability to recognize and select habitats of differing qualities (Petit and Petit 1996). Individuals select habitats that are best suited to survival and reproduction, and individuals closest to being ideal would be favored via natural selection (Fretwell and Lucas 1970); thus, populations composed of these individuals would be "adapted" to local conditions, or "ideal" for a specific area.

Dominance and territoriality play important roles in these two models of habitat selection. Territorial behavior is defined as behavior that results in defense of space or other resources by an individual against others of the same species (Bolen and Robinson 1999). Although resource defense and aggressive behaviors are obvious components of territorial behavior, they are not a requirement of Fretwell-Lucas models. However, conspicuousness is required so that other individuals are able to recognize that habitat has been claimed and is occupied. Conspicuousness may affect settlement costs associated with selection of this habitat (Greene and Stamps 2001).

Landscapes are typically composed of habitats of varying quality. In these heterogeneous environments, the number of habitats occupied by individuals of a species often varies with population size (Andr  n and Lemnell 1992). Mayr (1926) observed that common canaries (*Serinus canaria*) occupied optimal habitats first, and occurred more often in suboptimal habitats when population size increased. Kluyver and Tinbergen (1953) investigated territoriality in great tits (*Parus major*) and determined that birds in preferred habitats denied access to other individuals. These displaced individuals opted for marginal habitats, but the average reproductive success was the same in each of these habitats. In theory, only the best habitat(s) are occupied when the population size is small, with less suitable habitats being occupied more frequently or at higher densities as population size increases (Fretwell and Lucas 1970, Roughgarden 1974). This increase in occupancy of

lower quality habitats is caused by intraspecific competition, consistent with a phenomenon of density dependent habitat selection (Svardson 1949).

In some situations, anthropogenic modification of the landscape has offered a choice from which no evolutionary precedent exists and may impair individuals' abilities to recognize habitat quality (Schlaepfer et al. 2002). These modified habitats may provide some habitat requirement in greater quantity and quality (food or open water habitat) and attract individuals to settle in these areas that subsequently suffer adverse effects of poor habitat (i.e., low breeding success or adult survival). These kinds of tradeoffs may occur when habitat is being selected by ducks. Higgins (1977) observed a nest density of 0.07 nests/ha in tilled cropland in North Dakota. Devries et al. (2008) recorded a similar rate of 0.06 nests/ha and a nest survival estimate of 12% in spring-seeded crops in Saskatchewan. These estimates of nest success were higher than previously recorded and may suggest that ducks are, and have been, selecting poor quality habitats to a greater degree than expected. These areas may be operating as density independent areas and offering individuals that select these habitats the benefits of population growth under density independent conditions (Murray et al. 2010). This low nest density versus high nest survival tradeoff may be an example of where selection of poorer quality habitat may be adaptive for some individuals.

Understanding habitat selection models and the tradeoffs inherent with selection of different habitat types allows for better management decisions. If animals are settling in areas at high densities, it must be ascertained if their reproductive and survival rates are comparable to those in areas where populations occur at lower densities and are sufficient to maintain stable (or growing) population growth rates. Understanding how individuals select breeding habitat, and determining corresponding vital rates, can better guide management and conservation programs. Horn et al. (2005) examined the effects of grassland area, field size and habitat edges on daily survival of prairie duck nests; they reported that nest survival was positively related to patch and field size and shape, and these habitat features could be managed to enhance duck recruitment.

1.2 Ecology and Conservation of Northern Pintails (*Anas acuta*)

This research focused on the northern pintail (hereafter, pintail) for several reasons. First, pintail densities are usually high in the vicinity of southern Alberta's Milk River Ridge,

a landscape composed of habitats ranging from extensive tracts of natural prairie to agricultural lands dominated by spring-seeded cropland interspersed with small areas of perennial cover (grass, forage). Thus, the strong gradient of land use in this region created landscapes with (presumed) different habitat quality based on amount of upland cover and wetland density where pintails could choose to settle. These conditions also allowed for testing the habitat selection models described above. Second, the pintail is a species of special concern and a target for enhanced research and conservation efforts (Millar and Duncan 1999). Thus, understanding how landscape composition and pintail population density influence settling patterns and reproductive success could provide critical new insights for management to achieve conservation goals. Through harvest management, control of disease, and understanding and managing habitat effects on recruitment and survival, managers are attempting to increase pintail populations to the North American Waterfowl Management Plan's goal of 5.6 million breeding birds (Millar and Duncan 1999).

A single race of pintails inhabits the Northern Hemisphere, where pintails range more widely than any other species of waterfowl (Bellrose 1980). The pintail's northern breeding range includes northern Siberia, Russia, Scandinavia, Iceland and Greenland, as well northern Canada, and Alaska (Bellrose 1980, Austin and Miller 1995). In Eurasia, the southern extent of its breeding range includes southern Siberia, central Europe, the British Isles, Caspian Sea, and Transcaucasia (Bellrose 1980, Cramp 1977). In North America, the southern extent of its breeding range includes southern California, northwestern New Mexico, southern Colorado, central Kansas and the Great Lakes areas (Bellrose 1980). Key portions of breeding range include the Prairie Pothole Region of the U.S. and Canada, Alaska, and regions of northern Canada (Bellrose 1980). Pintails winter as far south as the West Indies and Columbia, with some individuals even inhabiting Palmyra Islands of the South Pacific, and Hawaii (Bellrose 1980). Major North American wintering areas are located in California, the Gulf Coast and Mexico (Austin and Miller 1995). About two thirds of Alberta-banded and half of Saskatchewan-banded pintails typically migrate to California, with the remainder wintering in Gulf Coast states and Mexico (Austin and Miller 1995).

Pintails are seasonally monogamous, sexually dimorphic, and have female-biased parental care (Austin and Miller 1995). Pairs form on wintering grounds (Sowls 1955, Oring 1964, Derrickson 1978), and weak philopatry is believed to determine female choice of

breeding grounds (Hanson and McKnight 1964). Pintails nest in sparse cover (Stoudt 1971, Dwernychuk and Boag 1972, Higgins et al. 1992) and generally farther from water than other dabbling duck species (Duncan 1987b). Nests are initiated earlier in the spring than most ducks in the *Anas* genus, and clutches also tend to be smaller (Austin and Miller 1995).

Reproductive success of pintails varies greatly over the breeding range and depends primarily on nesting success and duckling survival (Austin and Miller 1995), although estimates of adult female breeding propensity are limited and not well understood. Predation by red foxes (*Vulpes vulpes*) is believed to be a principal cause of breeding hen mortality (Sargeant et al. 1984). Nests are lost to a wide variety of mammalian species (e.g., red fox, striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*)) and birds (e.g., black-billed magpie (*Pica pica*), American crow (*Corvus brachyrhynchos*), and gulls (*Larus spp.*; Austin and Miller 1995). Pintails are harvested in annual hunting seasons across the continent (US Fish and Wildlife Service 2003).

In addition to mammalian and avian predation (Sargeant et al. 1984, Klett et al. 1988), agricultural activities such as cultivation may directly reduce nesting success (Milonski 1958, Richkus 2002). Nest success rates for pintails in the Prairie Pothole Region have typically been below the 15-20% thought necessary to sustain populations (Klett et al. 1988). Greenwood et al. (1995) recorded 7% nesting success for pintails nesting in Prairie and Parkland regions of Canada. Nesting success in upland habitat in grassland Alberta ranged from 6-18 % over a 4 year period (Guyn and Clark 2000). Overall, much previous work has revealed that nest success is variable and lower than what may be required to maintain the population (Beauchamp et al. 1996). Yet, some studies conducted on large, unbroken grassland habitat revealed an exception to the rule of low nest success. For instance, nest success for pintails based on brood observations was 45-60% in Montana (Ball et al. 1995). High nest success has also been realized on vast Conservation Reserve Program (CRP) lands in the Dakotas (Reynolds et al. 2001)

Recruitment patterns examined at large spatial scales have revealed that pintail settlement was influenced by agricultural practices rather than change in area converted to grain production (Podrutzny et al. 2002). Settlement was positively related to the amount of land left in summer fallow on the landscape and was stronger when these areas had higher wetland density (Podrutzny et al. 2002). Long-term fluctuations of pintail populations have

also displayed a synchrony with areas that are dominated by ephemeral and seasonal wetlands (Drever 2006). Devries et al. (2008) observed nest survival estimates for all duck species nesting in fall-seeded cereals (fall rye, (*Secale cereal*) and winter wheat, (*Triticum aestivum*)) ranged from 18-38% compared to 12% in spring-seeded crops in Saskatchewan. Pintails accounted for 23% of the nests in fall-seeded crops and 45% of the nests in spring-seeded crops, implying that pintails selecting spring-seeded crops have lower nest survival than individuals that select fall-seeded crops (Devries et al. 2008).

The life history strategy of pintails is thought to be characterized by long life span, small clutch size (\bar{x} = 6.9 to 7.8 eggs; Austin and Miller 1995, Bellrose 1980), and lower rates of renesting (typically < 3 renesting attempts; e.g., Richkus et al. 2005) relative to other dabbling duck species. This suggests that, among dabbling ducks, pintails may fall more towards K-selection on a r/K continuum, having delayed breeding, low reproductive output and greater parental care (Pianka 1970). Annual female survival is also higher in adult pintails (>60%) (Nicolai et al. 2005, Rice et al. 2010) compared to northern shoveler (*Anas clypeata*; 51%), gadwall (*Anas strepera*; 57%), blue-winged teal (*Anas discors*; 49%), and mallard (56%; Arnold and Clark 1996). Individuals of species characterizing K-selection increase their efficiency of resource utilization or favor a decrease in total resource use per individual, and may be associated with decreased reproductive output (Boyce 1984). In prairie dabbling ducks like pintails that are subjected to high environmental variability, niche spacing between conspecifics increases (Nudds 1983) perhaps allows for more efficient exploitation of abundant, ephemeral resources. This characteristic may enable pintails to acquire sufficient resources from habitats with high variability.

Contrary to expectations, rather than select habitats that offer characteristics of stability and constant resource availability (i.e., stable nesting habitat), pintails settle opportunistically in areas of good wetland conditions, a pattern that is different from several other prairie nesting ducks (Johnson and Grier 1988). This settling pattern is prevalent among species that use less stable wetlands and allows birds to settle in the first site that appears to offer the requisites for survival and successful breeding encountered along migration paths (Johnson and Grier 1988). Presumably, this behavior has an adaptive basis, but this somewhat contradicts other aspects of pintail life history strategy. This opportunistic settling pattern suggests pintails may be at risk of relying too strongly on cues from some

landscape variables such as wetland density, but independently of other critical landscape features such as cover quality (Porduzney 2002). Areas with abundant wetlands may create unreliable cues, attracting pintails to settle in lower quality habitat.

Pintails are also unique in their response to spring wetland habitat conditions, typically “over-flying” the prairies and nesting as far north as northern Canada (i.e., taiga, tundra) and Alaska when conditions on the prairies are unfavorable (Calverley and Boag 1977). Having the ability to nest rapidly after arrival on the prairies, pintails may be able to cope with the short nesting period presented by more northern latitudes. Evidence suggests that pintails employ this strategy to contend with the unpredictable nature of prairie habitats caused by drought (Smith 1970).

Philopatry in pintails may not be as strong as in other species. The hypothesized advantages of site familiarity would be greatly diminished for nomadic species that have evolved to exploit unpredictable environments (Anderson 1980). There may be a selective disadvantage to having a strong philopatric response if birds nest in a highly variable habitat such as the prairies of southern Canada. The disadvantage may be that pintails select unfamiliar nest sites more often than other species, which may reduce nesting success, female survival, feeding efficiency, and brood rearing success (Anderson et al. 1992). Recent evidence for mallards suggests that social factors affected settlement patterns of dispersing yearling females, but nesting success was unrelated to whether or not a female had dispersed a long versus short distance from its natal area (Coulton et al. 2011a, 2011b).

Pintails are among earliest species to initiate nests on the prairies (Higgins 1977, Bellrose 1980, Greenwood et al. 1995, Duncan 1987). Nesting and hatching early would allow pintails to take advantage of short-lived wetlands as brood habitat. The disadvantage of early nesting includes nest losses from unpredictable weather early in the nesting season (Greenwood et al. 1995). The overall availability of food for predators at this time may also be limited, putting greater pressure on ducks, particularly early-nesting species such as pintails.

If unsuccessful, pintail renesting effort is lower than it is in other dabbling duck species. The proportion of hens that renest after nest loss is similar for pintails and mallards (Guyn and Clark 2000, Bellrose 1980, Rotella et al. 1993); however, the total number of renesting attempts by pintails is probably lower. Mallards have been observed renesting as

many as six times (Rotella et al. 1993, Arnold et al. 2010) with averages ranging from 1.1 - 2.9 (Paquette et al. 1997). Pintails have been recorded reneesting at most twice after initial nest loss (Grand and Flint 1996, Esler and Grand 1994, Duncan 1987). Low reneesting rate may reflect an adaptation to the deteriorating habitat quality on the prairies, or as in mallards the seasonal timing of the nesting attempt (Arnold et al. 2010).

Pintails also prefer to nest in sparse vegetation relative to other ducks (Bellrose 1980). This sparse vegetation may increase predation because of poor concealment (Clark and Nudds 1991). Pintails also tend to nest in crop stubble where spring cultivation can increase nest losses compared with grassland or fall-seeded cropland (Milonski 1958, Bellrose 1980, Klett et al. 1988, Devries et al. 2008). This strategy is probably in response to the habitat selected by the species. Early nesting by pintails generally occurs before vegetation growth. A result of nesting in sparse cover, pintail hens and nests may be subjected to higher rates of predation than other prairie nesting ducks, many of which prefer nesting in heavier cover.

Sparse nesting vegetation, coupled with early season nesting may have a greater impact on pintail nest success and hen survival. Nesting earlier in the season initially allows pintails to experience lower nest densities. Low nest density coupled with lower densities of alternate prey create areas of low total prey that may be avoided by predators and afford ducks higher nest survival early in the breeding season (Brooks et al. 2008). The absolute number of predators and diversity of predator species may be a function of the habitat, and hence have greater impacts on certain prey species. Pintails may select these sparsely vegetated, homogeneous habitats to reduce effects of predator species diversity as well as increase dispersal of nests on the landscape which in turn would reduce the functional response of predators. Although controversial, nesting females may be able to recognize and possibly avoid areas with higher predation risk (Dassow et al. 2011)

1.3 Habitat Selection Models, Landscape Composition and Pintail Settling Patterns

The contrasting landscapes of southern Alberta provide a habitat template that is well-suited to testing patterns and in some cases mechanisms predicted by Fretwell-Lucas's models. Furthermore, it is hypothesized that large areas of natural grasslands provide high-suitability habitat (Sovada et al. 2000, Reynolds et al. 2001) whereas spring time direct-seeded cropland is among the least suitable landscapes. Thus, current habitat management for

pintails aims to protect and create larger areas of perennial cover either by encouraging better management of grazing lands, by converting cropland to grassland, or by promoting adoption of fall-seeded crops like winter wheat (Devries et al. 2008). The central premise is that larger areas of natural cover reduce predation rates, but other mechanisms are possible and have not been fully evaluated. For instance, better-quality habitat may be occupied earlier by higher quality birds that have higher reproductive success, regardless of predators.

From a habitat perspective, the general assumption is one of differing intrinsic suitability associated with the habitat composition of each landscape. In the Milk River Ridge area of Southern Alberta, the region where I studied pintails, this occurs as a result of differences in intensity of agricultural land use ranging from low-intensity grazing of native grasslands to intensive cultivation of small grain cereal and oilseed crops. Although landscape quality was not measured explicitly, differences in quality could be inferred based on habitat suitability characteristics such as percent native cover, density of wetlands, and predator community diversity.

1.4 Thesis Organization

This thesis has three main objectives. First, predictions arising from “ideal-free” versus “ideal-despotic” models of habitat selection were evaluated by using presumed natural gradients of habitat quality. Patterns in the distribution of breeding pintails across the landscape gradient were also determined. Nest survival was measured and used as an index of reproductive performance, enabling determination of whether settlement patterns were most consistent with ideal-free or ideal-despotic models of habitat selection. Second, putative mechanisms underlying distributional patterns such as differences in the quality of individuals occupying each landscape were examined. Third, these results were synthesized to inform management hypotheses about ways of enhancing habitat attractiveness and productivity for pintails.

The general format of the thesis is that each chapter stands alone and, as a result, there may be some duplication of information. The last paragraph of each chapter consists of a brief introduction to the next, and thus provides a logical connection between chapters. The sequence of chapters generally follows that of duck breeding chronology, beginning in Chapter 2 with an investigation of settling patterns of pintail breeding pairs in grassland,

ecotone (interspersed grassland and cropland habitats) and agriculture landscapes. Examining densities of breeding individuals, coupled with timing of settlement, enabled me to derive patterns of settlement in each landscape. More importantly, I was then able to compare observed patterns to those expected under the Fretwell-Lucas models of habitat selection, and thus to determine if despotic or ideal-free settlement is occurring for the species of interest.

The focus in Chapter 3 is reproductive potential to determine if age and body condition of nesting female pintails differed among landscape types. An integral part of overall fitness, reproductive potential may influence habitat selection as it relates to Fretwell and Lucas' models. Ideal-free conditions would predict that age and body condition would not vary with landscape, but under despotic conditions, older individuals with better body condition would be expected to select the best quality landscape.

Chapter 4 examined reproductive investment by female pintails, and assessed whether timing of breeding and reproductive investment (clutch size) varied among landscapes. Investigation of these metrics of reproductive investment provides evidence as to how habitats are settled by these species, and whether investment patterns conform to predictions of Fretwell-Lucas models. If settlement is occurring "freely", timing of breeding and clutch size would not differ with landscape, but if despotic settlement occurs, timing of breeding would be earlier and clutches would be larger in higher quality (grassland) habitats.

In Chapter 5, nest survival rates were investigated for pintails nesting in the three landscapes, along with factors affecting survival rates. Under ideal free conditions, nest success is expected to be similar among landscapes whereas under despotic conditions, nest success is expected to be higher in the best quality habitat.

Finally, throughout the thesis results for pintails are compared with those for other species of dabbling ducks (northern shovelers, mallards, blue-winged teal, and gadwall) where data permitted. Chapter 6 provides a general summary and synthesis of the main findings, along with suggestions for future work. This work was reviewed and conducted under the University of Saskatchewan, Animal Care Protocol #20040013.

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CHAPTER 2 – SPACING PATTERNS OF BREEDING DUCKS IN RELATION TO PRAIRIE LANDSCAPE COMPOSITION: TESTS OF HABITAT SELECTION MODELS

2.1 Abstract

Spatiotemporal patterns of prairie-breeding duck abundances are well-documented, but these patterns have not typically been evaluated in terms of predictions of habitat selection models. Thus, settlement patterns of breeding northern pintails (*Anas acuta*; hereafter, pintail) were investigated in southern Alberta, 2004-2006. Timing of settlement and relative pair abundances were compared among three landscapes that differed in presumed levels of habitat quality (from high to low): contiguous grassland (grassland), mixed land use (ecotone) and intensive agriculture (agriculture). Consistent with assumptions of classical models of habitat selection, pintails occurred at higher overall density (pairs per ha of wetland) in grassland landscapes in all 3 years and, furthermore, pintails occupied grassland landscapes at higher densities immediately on arrival in early spring. Northern shovelers (*Anas clypeata*; hereafter, shoveler), gadwalls (*Anas strepera*) and blue-wing teals (*Anas discors*) had settlement patterns similar to those of pintails, but mallards (*Anas platyrhynchos*) did not. These responses suggest that pintails rely on appropriate cues to select presumed high quality habitat in this region. However, further work is needed to validate the assumption that use of grassland habitat increases breeding success for pintails, as well as for other duck species.

2.2 Introduction

Numerous factors influence how animals are distributed across habitats as well as produce variation in density and fitness among individuals. Within the geographic range of a species, abundance patterns may result from environmental effects of historic and contemporary climate and habitat. At smaller scales, habitat-specific animal abundances presumably reflect differences in habitat quality, intra- and interspecific interactions, and predation. Fretwell and Lucas (1970) hypothesized that intraspecific patterns of habitat selection were related to habitat quality (presuming perfect knowledge) and population size. According to their ideal free distribution model, animals freely occupy high-suitability habitat and their fitness declines as density increases until fitness equals that of another

habitat (Morris 1989, Johnson 2007). In an ideal free distribution, all individuals are equally capable of settling in all habitats and this model predicts that equal fitness levels would be realized in all habitats, irrespective of which habitat is selected first (Fretwell 1970, Petit and Petit 1996, Skagen and Yackel Adams 2010). Alternatively, the ideal despotic distribution proposes that the highest quality habitats are occupied first by dominant individuals and subordinates are forced into sub-optimal habitat where fitness is lower (Fretwell and Lucas 1970). Thus, these models differ in fitness outcomes realized in habitats of different quality. Under the ideal despotic model, individuals occupying preferred habitats of higher quality are expected to have higher reproductive success or survival than those occupying less preferred habitats (Morris 1989); in this situation, a positive correlation between suitability and density is expected (Fretwell 1970).

A primary assumption of both models is that intrinsic habitat suitability (quality) differs among habitat options and more than one habitat is available to select from (Fretwell and Lucas 1970). Additionally, all individuals must be “ideal” and have the ability to appraise and settle in habitats of differing qualities (Petit and Petit 1996). Individuals selecting habitats that enhance their survival and reproduction would have higher relative fitness (Fretwell and Lucas 1970). Models originally proposed by Fretwell and Lucas attempted to link density of animal populations with fitness as it is influenced by habitat quality (Johnson 2007). These models have been adapted from the original intraspecific version to consider interspecific applications. Techniques such as isodar analysis have assessed deviations from ideal free distribution using repeated density measures between two habitat types, thereby eliminating the need for quantifying fitness (Morris 1987, 1988, 2003). Deviations from ideal distributions have been determined using methods which rely on measuring resource abundance in a variety of habitats (Johnson and Sherry 2001, Shochat et al. 2002). With all recent applications of the Fretwell-Lucas models, however, the fundamental link between density and habitat quality has remained constant.

Some caution is needed when density is used as a measure of habitat quality because factors such as timing of investigation, multi-annual variability and social interactions between conspecifics could create situations where density could be negatively correlated with habitat quality (Van Horne 1983). Van Horne (1983) also cautioned that habitat selection could be influenced by anthropogenic change to habitat quality and lead to higher

densities of individuals being observed in lower quality habitats. A subsequent review of this phenomenon by Bock and Jones (2004) revealed some evidence of a negative relationship between density and habitat quality, but this pattern was attributed most often to studies involving habitat disturbance. Birds are usually more abundant in habitats where reproductive success is highest, consistent with the validity of using bird counts as indicators of breeding habitat quality (Bock and Jones 2004).

How individuals distribute themselves on the landscape and factors that influence distributions have been investigated in the past (Mayr 1926, Svardson 1949, Kluyver and Tinbergen 1953, Fretwell and Calver 1970, Fretwell 1970). Intraspecific competition is one factor that influences distribution of individuals between habitats. Kluyver and Tinbergen (1953) investigated territoriality in great tits (*Parus major*) and determined that birds in preferred habitats forced excess individuals into marginal habitats, but the average reproductive success was the same in each of these habitats. Distributions of dickcissels (*Spiza sp.*) were influenced by territoriality with higher densities of males present in higher quality habitats than in lower quality habitats (Fretwell and Calver 1970). These examples of intraspecific competition provide support for the patterns of individual's distribution across habitats, and predation has also been investigated to determine its role in habitat selection (Leonard and Picman 1987, Martin 1988, Martin and Roper 1988, Lima 1993).

Habitat selection by individual duck species must consider ultimate factors that convey survival and reproduction value, and proximate cues that allow for identification of suitable habitats (Johnson and Grier 1988). Homing, opportunistic settling, and flexible settling have been identified as different patterns of settlement that are related to wetland permanency and consistency (Johnson and Grier 1988). Regardless of the settlement pattern, prairie nesting ducks settle at higher density and often experience higher recruitment during periods of greater wetland abundance (Johnson and Grier 1988, Bethke and Nudds 1995). Land use has also affected habitat selection; specifically, agricultural expansion has reduced and fragmented suitable nesting habitats (Greenwood et al. 1995) and increased predator impacts on breeding duck populations (Sovada et al. 2000). Intraspecific competition in the form of territoriality must also be considered when investigating the spacing pattern of ducks on the prairies. Within the dabbling ducks, there is variation ranging from strong territoriality in species like northern shoveler (*Anas clypeata*; hereafter, shoveler), gadwall

(*Anas strepera*), and blue-winged teal (*Anas discors*) to weak territoriality in species such as mallard (*Anas platyrhynchos*) and pintail (Anderson and Titman 1992).

Application of the Fretwell-Lucas models to duck habitat selection has been limited mainly to feeding studies. Foraging mallards distributed themselves between two patches of food in an ideal free distribution pattern; however, some individuals displayed despotic behavior which led to unequal payoffs (Harper 1982). Despite their relevance to spacing patterns, Fretwell –Lucas models have not often been considered in relation to habitat selection by ducks. Rodway (2006) investigated settlement patterns of harlequin ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia, and determined that unpaired males settle under an ideal free distribution; however, Fretwell-Lucas model predictions about reproductive success were not assessed. Nummi et al. (1994) observed that mallards in Finland and Sweden used non-preferred habitats for feeding sites when preferred sites had become occupied but again reproductive consequences were not determined. In Finland, mallards preferred wetlands with more cover, but reproductive output in terms of brood density was unrelated to wetland class (Nummi and Pöysä 1995), which is consistent with ideal free distribution. These last responses include density and reproductive output components required to discriminate between the Fretwell-Lucas models; however, the direct link between habitat and reproductive output might be skewed by brood movements, as there is no way of knowing the habitats where broods originated. Although these studies provide some insight into how ducks function within the Fretwell-Lucas framework, they do not adequately consider both habitat selection and reproductive output. Fitting observations to these models is complicated by the need for detailed information on settling patterns, population density and habitat suitability (Petit and Petit 1996, Johnson 2007), which may not be possible in most waterfowl studies.

The propensity of pintails to nest in sparse cover results in high use of agricultural landscapes. Pintails nesting in agricultural landscapes dominated by spring-seeded crops typically have low reproductive success (Devries et al. 2008). Pintail nest loss is attributed to mammalian and avian predation (Sargeant et al. 1984, Klett et al. 1988), as well as agricultural activities such as cultivation (Richkus 2002). Klett et al. (1988) observed nesting success ranging from 7-10 % for pintails in planted cover in the Dakotas and Minnesota, with the majority of loss caused by predation. Greenwood et al. (1995) recorded 7% nesting

success for pintails nesting in Prairie and Parkland regions of Canada. Nesting success in upland habitat in grassland Alberta ranged from 6-18 % over a 4 year period (Guyn and Clark 2000.) Overall, previous work has revealed that nest success is variable and lower than what may be required to maintain stable pintail populations. Studies conducted on large contiguous grassland habitat revealed an exception to the rule of low nest success; in Montana, pintail nest success was 45-60% based on estimates derived from pair-brood observations (Ball et al. 1995). High nest success has also been reported on Conservation Reserve Program (CRP) lands in the Dakotas (Reynolds et al. 2001). This trend is also seen in prairie ducks choosing larger patches of habitat, or landscapes with higher percentage of grassland cover (Phillips et al. 2003) especially if nests are initiated early (Sovada et al. 2000).

Pintail reproductive success has been linked to agricultural practices that result in increased nest survival. Recruitment at a larger spatial scale has revealed that pintail settlement occurred because of agricultural practices rather than change in area converted to grain production (Podrutzny et al. 2002). This settlement was also linked positively to the amount of summer fallow on the landscape and was stronger when these areas had higher wetland density (Podrutzny et al. 2002). Pintails also have displayed a habitat overlap with areas dominated by ephemeral and seasonal wetlands (Drever 2006). Devries et al. (2008) reported nest survival rates for all duck species nesting in winter wheat, fall rye and spring-seeded crops in Saskatchewan of 18%, 38%, and 12% respectively. Pintails accounted for 23% of the nests in fall-seeded crops and 45% of the nests in spring-seeded crops; this response suggests that pintails selecting spring seeded crops have lower nest survival than those selecting fall seeded crops (Devries et al. 2008). In southern Saskatchewan, Richkus (2002) reported that nesting pintails used cropland in proportion to availability, implying that most pintails would be exposed to high nest predation rates.

Landscape-level habitat selection may be the central issue affecting pintail populations. How pintails perceive landscape cues and select habitat is an area of possible concern. Patch size, wetland density, and cover quality cues may be similar for grassland and agricultural landscapes and may be the proximate cues used to select habitat. These cues may be based on an evolutionary adaptation to grassland landscapes (i.e., and consequences of selecting them). How pintails perceive agriculture and managed habitat landscapes is

unknown. It is possible that landscapes dominated by agricultural stubble convey the same cues as grassland landscapes (Richkus 2002). It may also be possible that agriculture landscapes are correctly perceived as secondary quality habitat, but pintails are either forced to nest there in the absence of grassland or excluded from grassland landscapes by conspecifics or other species. Either of these two hypotheses may be possible. The effect of each of these selection processes on demographic rates (e.g., adult and nest survival rates) is much different. If pintails are selecting a secondary quality habitat as a consequence of territoriality, then increasing habitat quality through management in less suitable landscapes could produce favorable demographic results. If pintails are selecting habitat that is maladaptive in landscapes that cannot be modified in ways that increase breeding success, then these areas may act as ecological traps.

My general objective was to evaluate temporal variation in settling patterns of five common species of breeding ducks across a landscape gradient in southern Alberta. Assuming that ducks occupying grassland habitat have the highest fitness (as revealed later, in Chapter 5), pair densities were expected to be consistently higher on grassland sites relative to ecotone or agricultural sites during the entire breeding season. The ideal-free model predicts that grasslands will be occupied first, followed by ecotone, and finally agriculture. Theoretically, selection of the ecotone (and subsequently agriculture) habitat would not occur until the density of ducks in grassland habitat reduced the quality of grassland habitat to the same level available in ecotone (and subsequently agriculture). Overall population density is predicted to be correlated with habitat quality and, on average, individuals in grassland, ecotone and agricultural landscapes would have similar reproductive success.

The despotic model predicts a similar pattern of habitat selection, but that dominant individuals would settle first in grassland, forcing subordinates to select ecotone and subsequently agricultural landscapes. These predictions may be more evident in territorial species such as shoveler, gadwall and blue-winged teal when compared to less territorial species such as mallard (and pintail). Therefore, pair count data for these species of dabbling ducks were also analyzed.

2.3 Study Area

Work was conducted at sites located in three landscapes south of Lethbridge, Alberta, near the Milk River Ridge (centered at 49°17'40"N, 112°36'59"W). Each of these landscapes (hereafter referred to as grassland, ecotone and agriculture) was represented by two (east and west) 41.4 km² study sites chosen to characterize the dominant landscapes in this region. The Milk River Ridge is an elevated plateau (mean altitude 1200 m above sea level) due to differential erosion, and is 250 m higher elevation than the surrounding plain. Historically, the area attracts large numbers of migrating pintails and, depending on conditions, many remain in this area during the breeding season (Miller et al. 2005). Annual ground surveys of dominant land cover were conducted on each landscape by surveying random quarter sections. These surveys were summarized to describe the difference in dominant land cover between landscapes.

The grassland landscape is composed of a mix of Fescue (*Festuca*) Grassland and Mixed Grass Prairie (Hrapko 1996), and is almost devoid of trees. The rolling topography is characterized by abundant temporary and seasonal wetlands, and the dominant land use is cattle grazing. A rest-rotation grazing system was employed to reduce overgrazing. Grazing on paddocks was limited to 50% of the annual forage growth to conserve forage for the subsequent year in the event that future drought conditions reduced plant production. The area was chosen because it is a relatively large contiguous area of natural grassland. The average vegetation cover of the 2 sites over the 3 years of the study was 100% native grassland.

The ecotone landscape consisted of a transition zone between grassland and agricultural landscapes. The area included a mix of Fescue Grassland and Mixed Grass Prairie, tame grass, and small grain (cereal and oilseed) agriculture fields. Wetland density was comparable to the grassland landscape. The average vegetation cover of the 2 sites over the 3 years of study consisted of 36% native grassland, 25% tame grass, 4 % tame forage, and 35% cultivated land dominated by spring-seeded cereal grains.

The agricultural landscape, located north of the Milk River Ridge, was dominated by agriculture crops; mainly spring-seeded wheat (*Triticum sp.*), barley (*Hordeum sp.*), and canola (*Brassica sp.*). The area has low seasonal wetland density, and permanent wetlands have been drained to allow for centre pivot or rolling irrigation systems to be used. Road and

trail edges, abandoned farm yards, creeks and irrigation canals are common. The average vegetation cover of the two sites over the three years consisted of 4% native grassland, 36% tame grassland, 13 % tame forage, and 47% cultivated land dominated by spring-seeded cereal grains.

2.4 Methods

2.4.1 Waterfowl Transects

Waterfowl density transects were created on each landscape (grassland, ecotone, agriculture) study site (east and west) in 2004. Transects were selected to include wetlands of varying permanency and represent wetland types present (i.e., natural ponds, dugouts, canal nodes, impoundments) in each landscape study site. Transect lengths varied (6.8-12.3 km) and continued until approximately 30 wetlands containing water were obtained for each study site in each landscape. Transects in 2005 (7.5-12.9 km) and 2006 (6.7-13.1 km) followed the same route as 2004, but differed in length based on wetland abundance differences between years.

Wetland water level was recorded on a 6-point scale (range = 0 [dry], 1 [vestigial-pools or puddles remain], 2 [recessional-water levels have receded into central zone], 3 [intermediate- some water level recession], 4 [full] to 5 [flooded]) at each visit (Canadian Wildlife Service 1989). Water levels for each wetland were ground-truthed on 1998 aerial photographs on the first visit and used to determine wet area for each wetland. Wet area was determined by planimetry using Ozi-explorer™ software from ground-truthed aerial photos. Wet area was recalculated for each year of the study.

2.4.2 Indicated Breeding Pair Surveys

All wetlands on transects were visited three times during three, 1-week survey periods in mid-April, mid-May and mid-June, 2004-2006 (9 visits total for the season). All ducks counted on wetlands (using 8-10x binoculars or 10x spotting scopes) were assigned to a social grouping (i.e., pairs, lone females, lone males, groups [<6 birds] and flocks [>5 birds]). An indicated breeding pair was the total of paired ducks and lone males for each species (Dzubin 1969). Due to differences in arrival times and settlement on the study sites, emphasis will be placed on early season (mid-April and mid-May) counts to assess

landscape-specific settling patterns of pintail, mallard and shoveler, while late season counts will be emphasized (mid-May and mid-June) to assess patterns for gadwall and blue-winged teal. Each survey included three counts of indicated breeding pairs and allowed for a mean, median or maximum count to be used for each survey. Correlation analysis on mean, maximum and median counts was conducted to determine which metric best described bird abundance, and, as a result, the median value of three pair counts conducted for each survey period (i.e., resulting in three monthly estimates each year) was retained for analyses.

2.4.3 Statistical Analysis

Variation in indicated breeding pairs was modeled using year (YEAR: 2004, 2005, 2006), landscape (LAND: grassland, ecotone and agricultural), study replicate (REP(LAND): replicate sites nested within landscapes), survey (SURV: April, May, June), and the interactions of year by landscape, landscape by survey, year by survey, and year by survey by landscape. These variables were considered in the global model, and an *a priori* candidate set also included less complex models. Data were analyzed using log-linear models (SAS Instit. 2009, PROC GENMOD) with Poisson error distribution (appropriate for count data), a log link function, and an offset variable to adjust for effects of wetland area. Goodness of fit was determined for all models by calculating variance inflation factors. The variance inflation factor (\hat{c}) derived from the global model was used in all subsequent models to adjust for overdispersion and calculate quasi-Akaike's Information Criterion (QAIC_c) values (Burnham and Anderson 2002). Using backwards elimination, the least predictive covariate based on likelihood ratio and chi-squared test was removed from the model and the resulting model was reexamined. This process continued until no further elimination of covariates was possible. Models were ranked using QAIC_c and model weights, with retention of covariates of interest (Burnham and Anderson 2002).

When interactions were retained in the best approximating model(s), data were sorted by variables in the interaction to further explore how indicated breeding pairs varied in relation to explanatory variables. Models were assessed for performance at each step using Akaike's Information Criterion using QAIC_c (Burnham and Anderson 2002). Model parameter (β) and standard error (SE) estimates are presented.

2.5 Results

A total of 434 basins was surveyed for waterfowl breeding pairs in 2004 to 2006. In general, wetland numbers and areas were similar across grassland, ecotone and agriculture landscapes, with a tendency for more small wetlands in ecotone relative to the other landscapes (Table 2.1). Study area size was consistent between the three years, but wet basin density was lowest in 2004 and increased in the subsequent years, so that more wet basins were present in all landscapes in 2006. Wet basins used in waterfowl surveys were more permanent in nature in 2004 when compared to 2005 and 2006. In 2005 and 2006, these same permanent and seasonal basins were surveyed, but because of improved water conditions in 2005 and especially in 2006, more temporary basins were added to the surveys. These temporary basins in 2005 and 2006 became dry on the second and third surveys and explain the wider range in numbers of basins surveyed in these years.

A total of 2,726 (median count) indicated pairs was recorded for the five most abundant breeding duck species. Pintails, gadwalls, blue-winged teal and shovelers were most numerous on wetlands in the grassland landscape, while mallards were most numerous on agricultural wetlands (Table 2.2).

Table 2.1. Minimum and maximum number of flooded wetland basins (maximum area of water, ha) surveyed for ducks in each landscape from 2004-2006, southern Alberta.

Year	GRASSLAND	ECOTONE	AGRICULTURE	Total
2004	33-37 (59.4)	49-52 (54.8)	33-33 (67.3)	116-122 (181.5)
2005	38-39 (61.5)	41-41 (27.4)	44-45 (61.8)	123-125 (150.7)
2006	47-59 (64.7)	62-63 (26.4)	54-65 (61.0)	163-187 (152.1)

Table 2.2. Median indicated breeding pairs (and range between three surveys) of mallard (Mall), gadwall (Gadw), blue-winged teal (Bwte), northern shoveler (Nsho) and northern pintail (Nopi) based on median count data in grassland, ecotone and agriculture landscapes, 2004-2006, in southern Alberta.

Year	Grassland					Ecotone					Agriculture				
	Mall	Gadw	Bwte	Nsho	Nopi	Mall	Gadw	Bwte	Nsho	Nopi	Mall	Gadw	Bwte	Nsho	Nopi
2004	14 (6-21)	63 (12-72)	20 (0-37)	37 (36-57)	28 (20-35)	18 (5-20)	19 (6-23)	30 (0-35)	24 (21-32)	14 (11-16)	40 (25-51)	18 (9-45)	12 (2-46)	27 (23-42)	6 (5-12)
2005	9 (2-10)	26 (25-28)	14 (14-24)	24 (15-38)	17 (14-31)	6 (4-18)	10 (8-12)	5 (4-12)	17 (3-17)	19 (2-23)	30 (28-44)	17 (17-20)	6 (3-12)	28 (19-28)	21 (3-25)
2006	13 (3-13)	42 (30-48)	32 (16-43)	38 (18-57)	38 (9-48)	9 (0-9)	3 (3-10)	14 (5-17)	14 (10-18)	16 (1-20)	29 (21-44)	12 (8-12)	9 (7-10)	29 (8-47)	17 (3-26)

2.5.1. All Duck Species

Initial analysis conducted on all species determined that the best model describing variation in indicated breeding pairs contained the covariates for species, landscape, year, and sites nested within landscapes, as well as interactions of landscape by year, landscape by species, year by species and landscape by year by species ($w_i = 1.000$). As a result of the effect of species (and some interactions involving species) on indicated breeding pairs, data were analyzed separately by species.

2.5.2 Northern pintail

Overall, densities were significantly higher in grasslands when compared with ecotone and agriculture landscapes when all years were considered. The global model used to assess pintail pair density included the variables for landscape, replicate nested within landscape, year, survey, landscape by survey interaction, year by landscape interaction, year by survey interaction and year by survey by landscape interaction. The best-approximating model contained effects of landscape, year, survey, landscape by survey interaction, and year by landscape interaction (Table 2.3). Pintail density was higher in grassland than in either agriculture ($\beta = -1.69 \pm 0.40$) or ecotone ($\beta = -1.54 \pm 0.37$), a pattern that was most pronounced in 2006 (Fig. 2.1). Density declined seasonally on all landscapes from April to June ($\beta = -0.84 \pm 0.18$) and May to June ($\beta = -0.42 \pm 0.19$) (Fig. 2. 1). Because of the interaction between landscape and survey, and year and landscape in the previous model, further analyses were conducted for each year to contrast the differences amongst landscapes. The global model in this analysis contained the covariates for landscape, survey, and landscape by survey interaction.

In 2004, the best-approximating model included the covariate for survey ($w_i = 0.634$), but pintail density did not differ among the three surveys. Because of the interest in landscape effects on pintail density and the weight ($w_i = 0.344$) of the landscape-only model, it too was investigated. Pintail density was higher in grassland than in either agriculture ($\beta = -1.32 \pm 0.61$) or ecotone ($\beta = -0.99 \pm 0.32$).

Table 2.3. Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), survey (SURV), and selected interaction effects on northern pintail indicated breeding pair densities, Milk River Ridge, Alberta, 2004-2006. QAIC_c is the quasi-Akaike's information criterion that adjusts models on the basis of the variance inflation factor ($\hat{c} = 1.066$) derived from global model.¹

Model	K	-2logL	QAIC _c	Δ_i	w_i
LAND, YEAR, SURV, LAND*SURV, YEAR*LAND	28	1360.69	86.35	0.00	0.960
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*SURV	34	1345.63	92.75	6.40	0.040
LAND, REP(LAND), YEAR, SUR, LAND*SURV, YEAR*LANDS, YEAR*SUR	43	1337.27	108.35	22.00	0.000
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV, YEAR*SURV*LAND	70	1418.76	200.66	114.31	0.000

¹ K = number of parameters; -2logL = -2 log-likelihood value; Δ_i =QAIC_c difference between the best-approximating model and the model shown; w_i = model weight.

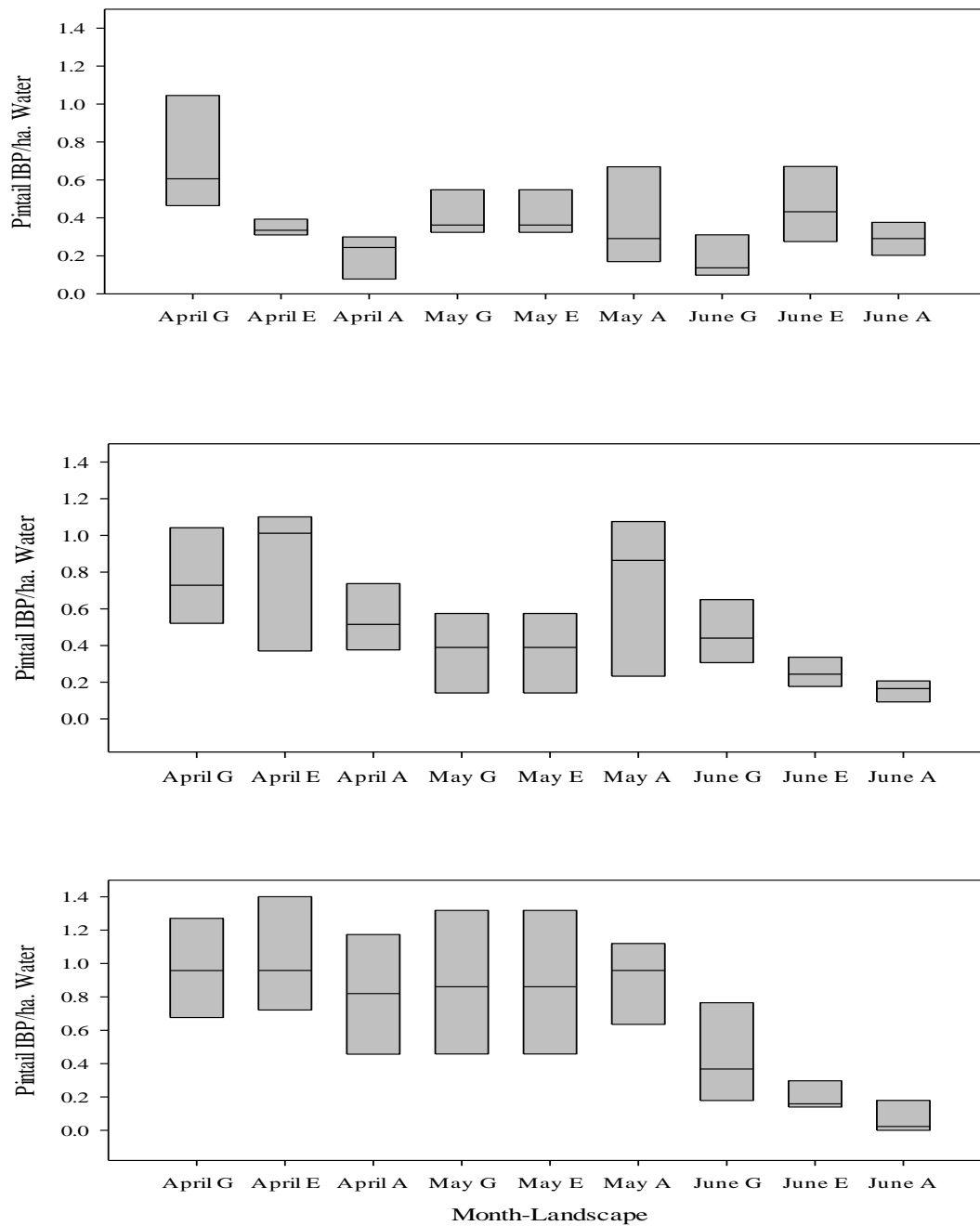


Figure 2.1. Northern pintail indicated breeding pair (IBP) density (median pairs/ha water surveyed) for each landscape (G, Grassland; E, Ecotone; A, Agriculture) on the Milk River Ridge, Alberta, during April, May and June 2004 (top panel), 2005 (middle) and 2006 (bottom). Horizontal lines within the box plots represent median pintail density, with 25 and 75 percentile values at the bottom and top, respectively.

In 2005, the best model describing variation in pintail density included the covariate for landscape ($w_i = 0.551$); however, pintail density did not differ among landscapes. The competing model containing the covariate survey also received support ($w_i = 0.421$). In this model pintail density was higher in April than in June ($\beta = 1.40 \pm 0.30$) as well as higher in May than in June ($\beta = 1.13 \pm 0.27$).

In 2006, the best model describing variation in pintail density included the covariate for landscape ($w_i = 0.858$). Pintail density was higher in grassland than ecotone ($\beta = -0.78 \pm 0.31$) or agriculture ($\beta = -0.80 \pm 0.31$). Other models were not well supported and not considered further.

To focus on possible temporal changes in patterns of settlement across landscapes, data were analyzed by survey period. In the April and May surveys (Table 2.4), pintail density was higher in grassland than ecotone and agriculture in 2004 and 2006 but not in 2005. In the June survey, pintail density was higher in grassland than agriculture and ecotone in 2004 and 2006, but not in 2005.

Table 2.4. Summary of northern pintail pair density comparisons among landscapes (G=Grassland, E=Ecotone, A=Agriculture), for each survey period (April, May, June) and year (2004-2006), Milk River Ridge, Alberta. Density estimates are shown in Fig. 2.1.

Year	April	May	June
2004	G>E (p=0.002) G>A (p=0.009)	G=E (p=0.13) G>A (p=0.002)	G>E (p=0.001) G>A (p=0.001)
2005	G=E (p=0.28) G=A (p=0.43)	G=E (p=0.42) G=A (p=0.91)	G>E (p=0.001) G>A (p=0.001)
2006	G>E (p=0.008) G>A (p=0.022)	G>E (p=0.048) G>A (p=0.006)	G>E (p=0.001) G>A (p=0.001)

2.5.3 Northern shoveler

The best-approximating model describing shoveler pair density incorporated effects of landscape, year, survey, landscape by survey interaction, and year by survey interaction (Table 2.5). Shoveler density was higher in grassland than ecotone ($\beta = -0.91 \pm 0.25$), but did not differ between grassland and agriculture ($\beta = -0.07 \pm 0.34$) (Fig 2.2). Shoveler density varied by year, with higher density in 2004 ($\beta = 1.44 \pm 0.31$) than 2006, but not between 2005 ($\beta = -0.45 \pm 0.32$) and 2006. Seasonally, shovelers declined between April and June ($\beta = -1.48 \pm 0.30$) and from May to June ($\beta = -1.00 \pm 0.26$).

Because of the interactions between landscape and survey, and year and survey in the previous model, further analyses were conducted for each year to contrast the differences amongst landscapes. The global model in this analysis contained the covariates for landscape, survey, and the landscape by survey interaction.

In 2004, the best-approximating model ($w_i = 0.874$) included effects of landscape. Shoveler density was higher in grassland than ecotone ($\beta = -0.84 \pm 0.14$) or agriculture ($\beta = -0.33 \pm 0.13$). In 2005, the best model describing variation in shoveler density included the covariate for survey ($w_i = 0.590$). Shoveler density was higher in both April ($\beta = 0.81 \pm 0.19$) and May ($\beta = 0.60 \pm 0.20$) than in June. In 2006, the best model included the covariates for landscape and survey ($w_i = 0.775$). Shoveler density was higher in grassland than ecotone ($\beta = -0.88 \pm 0.17$) or agriculture ($\beta = -0.39 \pm 0.14$), and higher in April ($\beta = 1.30 \pm 0.19$) and May ($\beta = 1.00 \pm 0.20$) than in June. Further separation of the data by year and survey was warranted because landscape, survey, and landscape and survey covariates were present in models for each of the 3 years.

In April (Table 2.6), shoveler density was higher in grassland than ecotone, but not agriculture, in all years. In May, shoveler density in grassland and ecotone did not differ in 2004 and 2005, but was higher in grassland than ecotone in 2006. In May, no difference was observed in shoveler density between grassland and agriculture in all years. In June, shoveler density was higher in grassland than ecotone in 2004 and 2005 but not in 2006. Density was higher in grassland than agriculture in 2006, but not in 2004 or 2005.

Table 2.5. Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), survey (SURVEY), and selected interaction effects on northern shoveler indicated breeding pair densities, Milk River Ridge, Alberta, 2004-2006. QAIC_c is the quasi-Akaike's information criterion that adjusts models on the basis of the variance inflation factor ($\hat{c} = 1.317$) derived from global model.¹

Model	K	-2logL	QAIC _c	Δ_i	w_i
LAND, YEAR, SURV, LAND*SURV, YEAR*SURV	28	1374.00	91.82	0.00	0.985
LANDS, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*SURV	34	1358.69	100.24	8.43	0.015
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV	43	1357.78	116.90	25.10	0.000

¹ K = number of parameters; -2logL = -2 log-likelihood value; Δ_i =QAIC_c difference between the best-approximating model and the model shown; w_i = model weight.

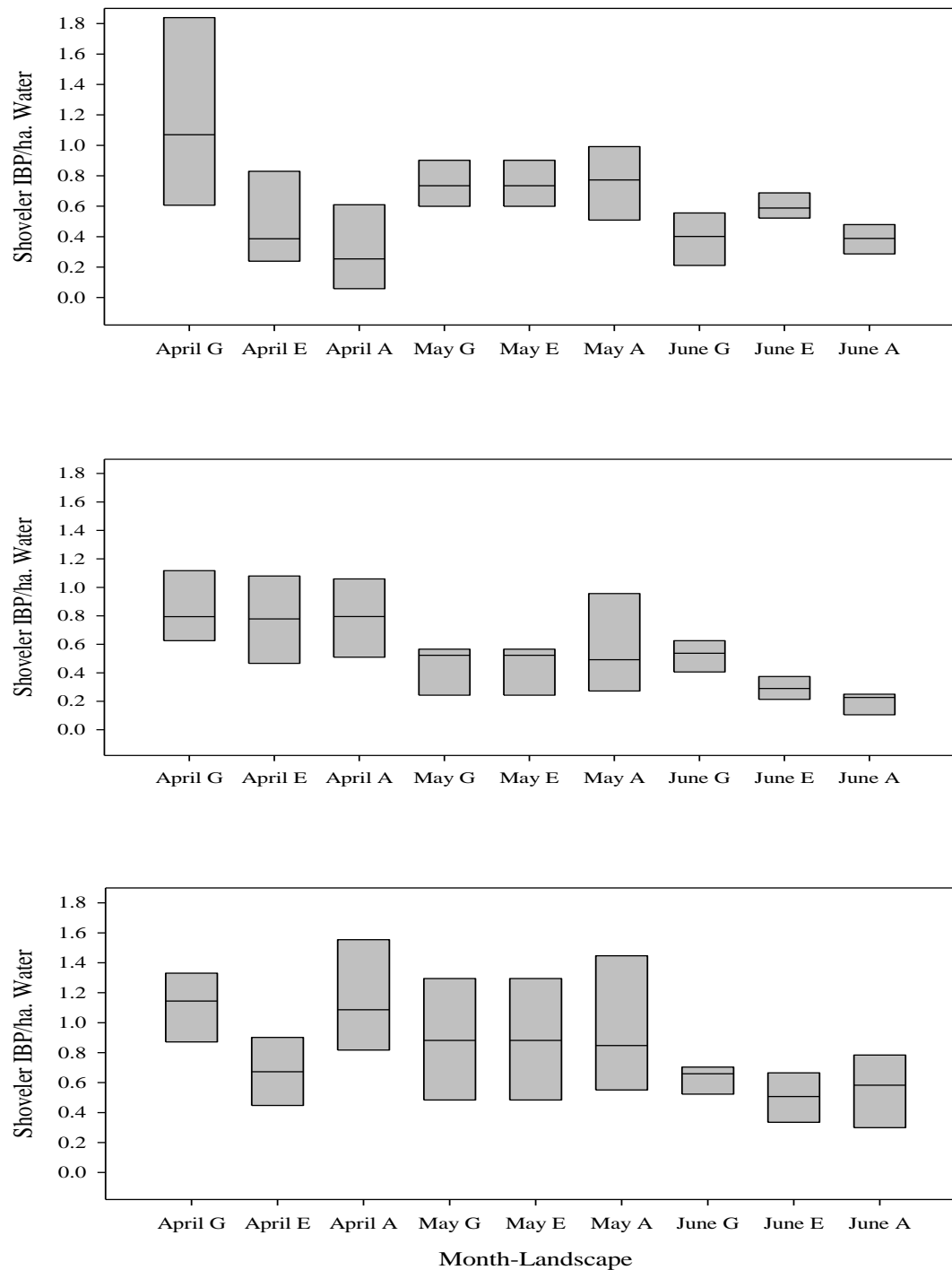


Figure 2.2. Shoveler indicated breeding pair (IBP) density (median pairs/ha water surveyed) for each landscape (G, Grassland; E, Ecotone; A, Agriculture) on the Milk River Ridge, Alberta, during April, May and June surveys in 2004 (top panel), 2005 (middle) and 2006 (bottom). Horizontal lines within the box plots represent median pintail density, with 25 and 75 percentile values at the bottom and top, respectively.

Table 2.6. Summary of northern shoveler density comparisons among landscapes (G=Grassland, E=Ecotone, A=Agriculture), for survey period (April, May, June) and year (2004-2006), Milk River Ridge, Alberta.

Year	Survey 1 (April)	Survey 2 (May)	Survey 3 (June)
2004	G>E (p=0.004) G=A (p=0.064)	G=E (p=0.29) G=A (p=0.19)	G>E (p=0.015) G=A (p=0.50)
2005	G>E (p=0.034) G=A (p=0.098)	G=E (p=0.96) G=A (p=0.29)	G>E (p=0.013) G=A (p=0.84)
2006	G>E (p<0.001) G=A (p=0.352)	G>E (p=0.019) G=A (p=0.079)	G=E (p=0.130) G>A (p=0.001)

2.5.4 Mallards

The best-approximating model for mallard pair density incorporated effects of landscape, year, survey, and landscape by survey interaction (Table 2.7). Mallard density was lower in grassland than agriculture ($\beta = 2.04 \pm 0.30$), but did not differ between grassland and ecotone ($\beta = -0.26 \pm 0.42$) (Fig 2.3). Mallard density varied by year, with higher densities in 2004 ($\beta = 0.77 \pm 0.10$) than 2006, and higher in 2005 ($\beta = 0.38 \pm 0.11$) than 2006. Seasonally, mallards declined between April and June ($\beta = -1.42 \pm 0.32$) and May and June ($\beta = -1.22 \pm 0.32$). Because of the interaction between landscape and survey in the previous model, further analyses were conducted for each year to contrast the differences amongst landscapes. The global model in this analysis contained the covariates for landscape, survey, and the landscape by survey interaction.

In 2004, the best-approximating model included the covariate for landscape ($w_i = 0.586$). Mallard density was lower in grassland than agriculture ($\beta = 1.06 \pm 0.13$) but did not differ between grassland and ecotone ($\beta = -0.30 \pm 0.16$). The competing model containing landscape and survey ($w_i = 0.414$) also received considerable support. In this model, mallard density was lower in grassland than agriculture ($\beta = 1.05 \pm 0.13$), and higher in grassland than ecotone ($\beta = -0.31 \pm 0.16$). Mallard density was higher in April ($\beta = 0.67 \pm 0.12$) than June but did not differ between May ($\beta = 0.14 \pm 0.14$) and June.

In 2005, the best model describing variation in mallard density included landscape ($w_i = 0.823$). Mallard density was lower in grassland than agriculture ($\beta = 1.41 \pm 0.17$), but did not differ between grassland and ecotone ($\beta = 0.36 \pm 0.21$). The model containing landscape and survey received some support ($w_i = 0.177$). In this model, mallard density was lower in grassland than agriculture ($\beta = 1.41 \pm 0.17$) but not between grassland and ecotone ($\beta = 0.36 \pm 0.21$). Mallard density was higher in April ($\beta = 0.48 \pm 0.16$) than June and May ($\beta = 0.59 \pm 0.15$) than June.

In 2006, the best model included the covariates for landscape, survey, and landscape by survey interaction ($w_i = 0.775$). Because of the interaction, data were separated into survey and reanalyzed. In April, mallard density was lower in grassland than agriculture ($\beta = 1.14 \pm 0.30$), but not between grassland and ecotone ($\beta = -0.28 \pm 0.43$). In May, mallard density was lower in grassland than agriculture ($\beta = 0.73 \pm 0.29$), but not between grassland

and ecotone ($\beta = -0.40 \pm 0.40$). In June, mallard density was lower in grassland than agriculture ($\beta = 1.88 \pm 0.43$) but not between grassland and ecotone ($\beta = -1.01 \pm 0.80$).

Table 2.7. Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), survey (SURVEY), and selected interaction effects on mallard indicated breeding pair densities, Milk River Ridge, Alberta, 2004-2006. QAIC_c is the quasi-Akaike's information criterion that adjusts models on the basis of the variance inflation factor ($\hat{c} = 0.937$) derived from global model.¹

Model	K	-2logL	QAIC _c	Δ_i	w_i
LAND, YEAR, SURV, LAND*SURV	19	1693.07	190.29	0.00	1.000
LAND, REP(LAND), YEAR, SURV, LAND*SURV, LAND*YEAR*SURV	51	1658.37	246.35	56.06	0.000
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV, LAND*YEAR*SURV	70	1553.04	249.16	58.87	0.000
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*SURV, LAND*YEAR*SURV	60	1657.37	266.02	75.73	0.000

¹ K = number of parameters; -2logL = -2 log-likelihood value; Δ_i =QAIC_c difference between the best-approximating model and the model shown; w_i = model weight.

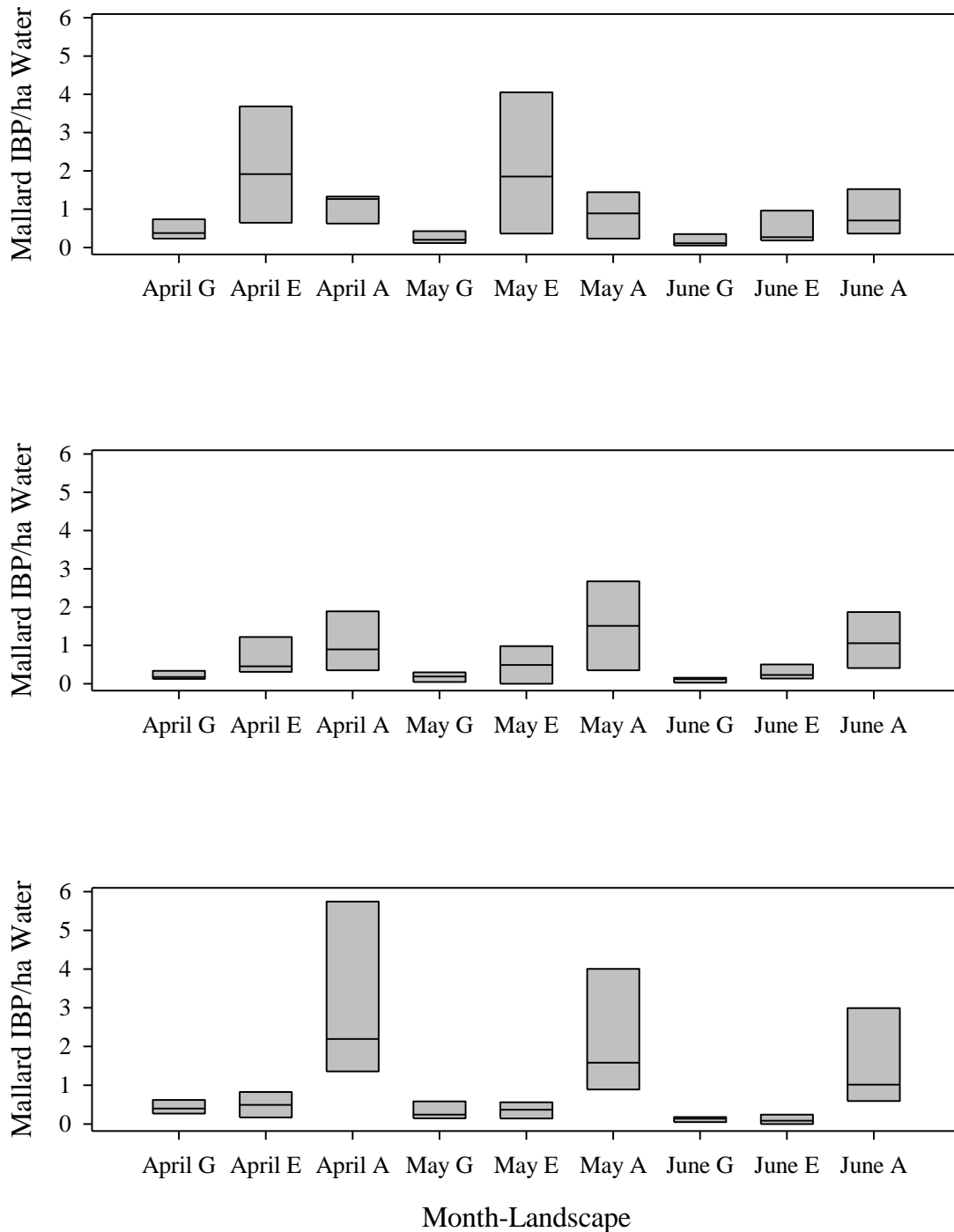


Figure 2.3. Mallard indicated breeding pair (IBP) density (median pairs/ha water surveyed) for each landscape (G, Grassland; E, Ecotone; A, Agriculture) on the Milk River Ridge, Alberta, during April, May and June surveys in 2004 (top panel), 2005 (middle) and 2006 (bottom). Horizontal lines within the box plots represent median pintail density, with 25 and 75 percentile values at the bottom and top, respectively.

2.5.5 Gadwall

The best-approximating model describing variation in gadwall breeding pairs incorporated effects of landscape, year, survey and year by survey interaction (Table 2.8). Gadwall density was higher in grassland than ecotone ($\beta = -0.85 \pm 0.13$), and agriculture ($\beta = -1.42 \pm 0.16$) (Fig 2.4). Gadwall density varied by year, with higher density in 2004 ($\beta = 1.29 \pm 0.22$) than 2006, but not between 2005 ($\beta = 0.28 \pm 0.26$) and 2006. Seasonally, gadwall density did not change between April and June ($\beta = 0.18 \pm 0.27$), and May and June ($\beta = -0.26 \pm 0.24$).

In order to contrast differences amongst landscapes, further analysis by year was conducted. The global model in this analysis contained the covariates for landscape, survey, and the landscape by survey interaction.

In 2004, the best-approximating model included the covariate for landscape and survey ($w_i = 0.999$). Gadwall density was higher in grassland than ecotone ($\beta = -1.40 \pm 0.15$) or agriculture ($\beta = -0.70 \pm 0.13$). Gadwall density increased seasonally, with higher density in June when compared to both May ($\beta = -1.59 \pm 0.19$) and April ($\beta = -0.29 \pm 0.12$). In 2005, the best model describing variation in gadwall density included the covariate for landscape ($w_i = 0.940$). Gadwall density was higher grassland than either agriculture ($\beta = -0.55 \pm 0.16$) or ecotone ($\beta = -1.00 \pm 0.20$). In 2006, the best model included the covariates for landscape, survey, and landscape by survey interaction ($w_i = 0.955$). Because of the interaction, data were separated into survey and reanalyzed. In April, Gadwall density was higher in grassland than agriculture ($\beta = -0.99 \pm 0.32$), and ecotone ($\beta = -2.21 \pm 0.57$). In May, Gadwall density was also higher in grassland than agriculture ($\beta = -1.46 \pm 0.31$) and ecotone ($\beta = -1.48 \pm 0.34$). In the June survey, Gadwall density followed the same trend and was higher in grassland than agriculture ($\beta = -1.73 \pm 0.35$) and ecotone ($\beta = -2.26 \pm 0.48$).

Table 2.8. Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), survey (SURVEY), and selected interaction effects on gadwall indicated breeding pair densities, Milk River Ridge, Alberta, 2004-2006. QAIC_c is the quasi-Akaike's information criterion that adjusts models on the basis of the variance inflation factor ($\hat{c} = 1.347$) derived from global model.¹

Model	K	-2logL	QAIC _c	Δ_i	w_i
LAND, YEAR, SURV, YEAR*SURV	19	811.15	-222.59	0.00	1.000
LAND, REP(LAND), YEAR, SURV, YEAR*LAND, YEAR*SURV	34	795.80	-200.02	20.57	0.000
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV	43	792.42	-185.27	37.33	0.000
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV, YEAR*SURV*LAND	70	1060.88	35.31	257.90	0.000

¹ K = number of parameters; -2logL = -2 log-likelihood value; Δ_i =QAIC_c difference between the best-approximating model and the model shown; w_i = model weight.

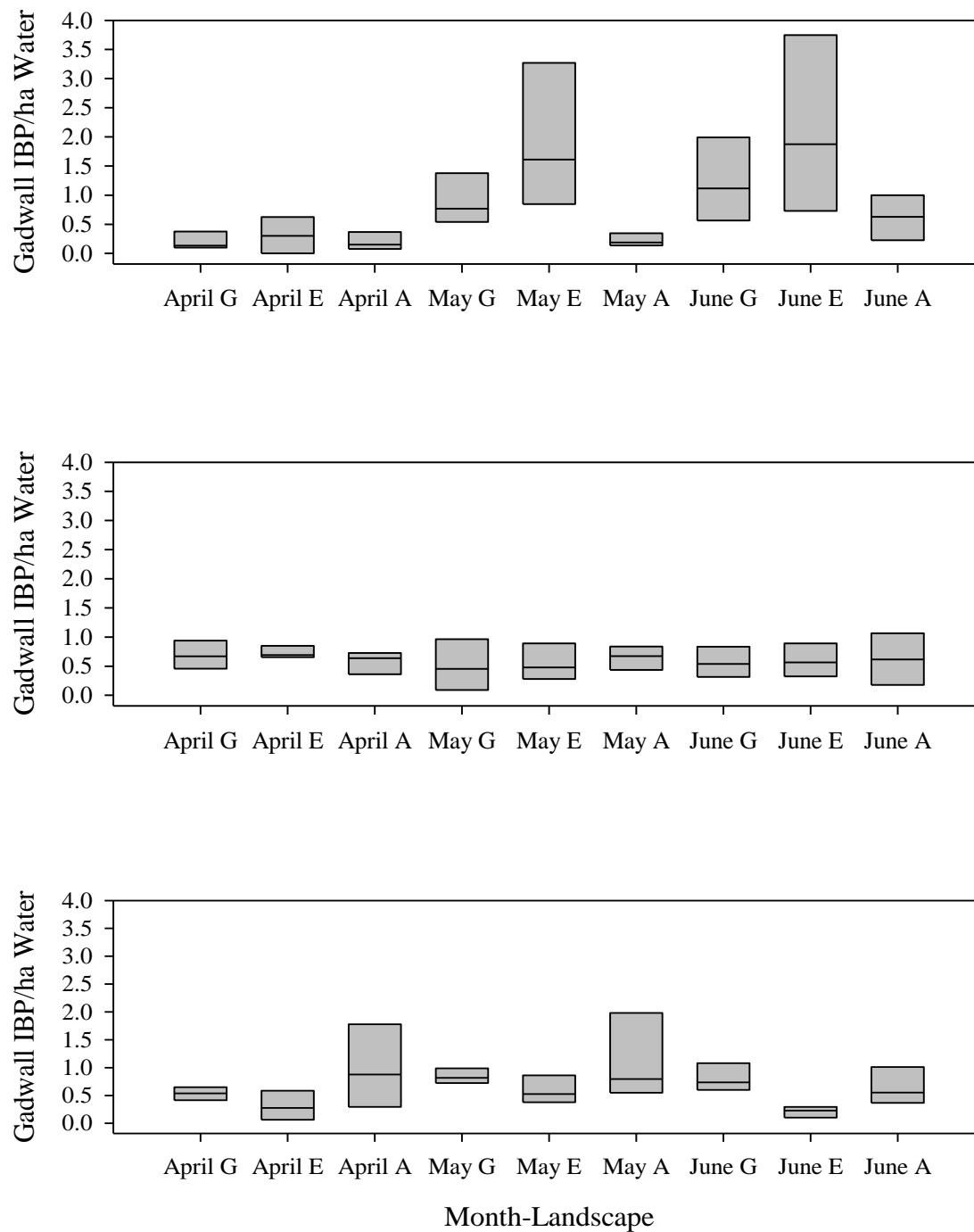


Figure 2.4. Gadwall indicated breeding pair density (IBP) (median pairs/ha water surveyed) for each landscape (G, Grassland; E, Ecotone; A, Agriculture) near the Milk River Ridge, Alberta, during April, May and June surveys in 2004 (top panel), 2005 (middle) and 2006 (bottom). Horizontal lines within the box plots represent median pintail density, with 25 and 75 percentile values at the bottom and top, respectively.

2.5.6 Blue-winged teal

The best-approximating model for teal breeding pairs incorporated effects of landscape, replicate nested within landscape, year, survey, landscape by survey interaction, year by landscape interaction, year by survey interaction (Table 2.9). Teal density, based on this model, was higher in grassland than ecotone ($\beta = -1.51 \pm 0.29$), and agriculture ($\beta = -0.98 \pm 0.27$) (Fig 2.5). Blue-winged teal density varied by year, with higher densities in 2004 ($\beta = 0.41 \pm 0.19$) than in 2006, but not between 2005 ($\beta = 0.03 \pm 0.22$) and 2006. Seasonally, blue-winged teal density was higher in June than April surveys ($\beta = -0.70 \pm 0.24$), but not between May and June ($\beta = 0.12 \pm 0.19$).

Because of the interaction between year and survey and year and landscape in the previous model, further analyses were conducted for each year to contrast the differences amongst landscapes. The global model in this analysis contained the covariates for landscape, replicate nested within landscape, survey, and the landscape by survey interaction.

In 2004, the best-approximating model included the covariate for survey ($w_i = 0.923$). Blue-winged teal density did not differ between June and April, but was higher in June than the May ($\beta = 0.52 \pm 0.14$). The best model containing the covariate for landscape, included landscape and survey ($w_i = 0.076$). In this model, blue-winged teal densities were the same as in the survey-only model. Blue-winged teal density was did not differ between grassland and agriculture ($\beta = -0.07 \pm 0.17$) or grassland and ecotone ($\beta = 0.23 \pm 0.17$).

In 2005, the best model describing variation in blue-winged teal density included the covariate for landscape, survey and landscape by survey interaction. To determine the effect of survey on landscape, data were sorted by survey and reanalyzed. In April, blue-winged teal density was higher in grassland than agriculture ($\beta = -1.71 \pm 0.56$), but not between grassland and ecotone ($\beta = -0.76 \pm 0.43$). In May, blue-winged teal density was again higher in grassland than agriculture ($\beta = -1.02 \pm 0.42$), but not between grassland and ecotone ($\beta = -0.35 \pm 0.37$). In June, blue-winged teal density was higher in grassland than both agriculture ($\beta = -0.86 \pm 0.32$) and ecotone ($\beta = -1.70 \pm 0.49$).

In 2006, the best model describing variation in blue-winged teal density included the covariate for landscape only. Blue-winged teal density was higher in grassland than agriculture ($\beta = -1.32 \pm 0.20$), and higher in grassland than ecotone ($\beta = -0.84 \pm 0.18$).

Table 2.9. Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), survey (SURVEY), and selected interaction effects on blue-wing teal indicated breeding pair densities, Milk River Ridge, Alberta, 2004-2006. QAIC_c is the quasi-Akaike's information criterion that adjusts models on the basis of the variance inflation factor ($\hat{c} = 0.940$) derived from global model.¹

Model	K	-2logL	QAIC _c	Δ_i	w_i
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV	43	1498.08	172.07	0.00	0.521
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND, YEAR*SURV, YEAR*SURV*LAND	70	1060.88	172.25	0.18	0.477
LAND, REP(LAND), YEAR, SURV, LAND*SURV, YEAR*LAND	34	792.42	184.65	12.57	0.001

¹ K = number of parameters; -2logL = -2 log-likelihood value; Δ_i =QAIC_c difference between the best-approximating model and the model shown; w_i = model weight.

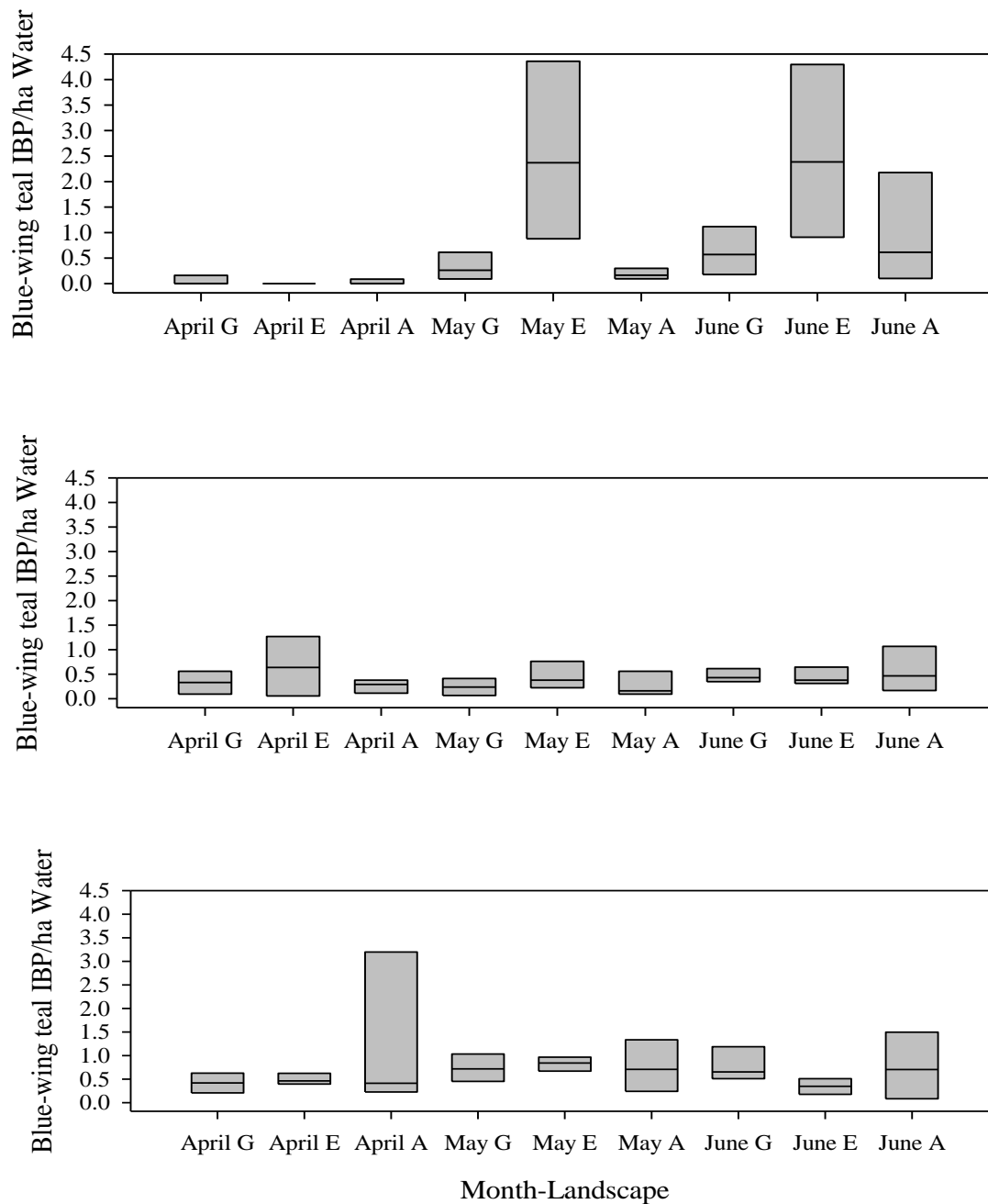


Figure 2.5. Blue-winged teal indicated breeding pair (IBP) density (median pairs/ha water surveyed) for each landscape (G, Grassland; E, Ecotone; A, Agriculture) on the Milk River Ridge, Alberta, during April, May and June surveys in 2004 (top panel), 2005 (middle) and 2006 (bottom). Horizontal lines within the box plots represent median pintail density, with 25 and 75 percentile values at the bottom and top, respectively.

2.6 Discussion

If habitat selection by pintails conforms with Fretwell-Lucas models, I predicted that habitats of highest quality (grassland) would be occupied first in spring, followed by habitats of lower quality such as ecotone and agriculture habitats. Seasonally, pintail density in April was higher in grassland than in ecotone or agriculture in 2 of 3 years of study. The May (and June) surveys revealed the same trend for pintails. Pintails appear to arrive on the breeding grounds, and given an opportunity to choose from all available habitat types, prefer grassland over ecotone and agricultural areas. As the breeding season progresses, pintail density in grassland did not change significantly, suggesting that grassland habitat remains occupied at consistently high levels, perhaps to capacity, which is also consistent with the idea that grassland habitat is preferred. Pintail density increased in ecotone and agriculture during later spring survey periods, suggesting that pintails may be forced to select vacant territories in presumed low-quality habitat as the breeding season progresses. Although these patterns conform to our general understanding of habitat preferences in pintails, as well as theoretical expectations, the exact mechanism(s) that produce these patterns are unknown.

An assumption of the present study was all individuals were able to assess and select from among all habitats in all landscapes. In waterfowl, philopatry can influence selection of breeding sites (Anderson et al. 1992) and may affect which landscape is selected. If habitat selection is determined by previous natal or breeding experience and site fidelity, free settlement may be constrained, perhaps violating this assumption of Fretwell-Lucas models. I was not able to measure site fidelity and assumed that it was comparable in all landscapes.

In the models of habitat selection tested, the highest quality habitat is predicted to have higher densities of breeding pairs than lower quality habitats for either despotic or free distributions. Pintails exhibited this pattern with higher overall density in grassland when compared to ecotone and agriculture when all years were considered. The same pattern was observed for all years in gadwall and blue-winged teal, with higher densities occurring in grassland. Shovelers exhibited a different pattern with higher densities in grassland when compared with ecotone, but not to agriculture. Mallards revealed an opposite pattern with highest densities in agriculture when compared with grassland and ecotone. In pintail, gadwall and blue-winged teal, the pattern of habitat selection observed matched the predicted pattern of habitat distribution (selection of best available). Information about spacing

mechanisms and reproductive success are needed to more fully discriminate between the ideal-free and ideal-despotic models. However, further investigation into the timing of settlement can provide some insights into possible mechanisms underlying the distribution patterns of breeding individuals.

If the settlement patterns of ducks reflect habitat quality, then measurements of reproductive success, like nest success, could be used to infer how pair settlement patterns should develop. In pintails, preferential settlement on grassland sites was generally consistent with the higher nest success recorded on grassland sites (Chapter 5). Shoveler settlement follows a different pattern from pintails and appears to settle on grassland and agriculture equally throughout the season, but at a higher rate than ecotone. Mallards displayed an opposite trend with seasonal selection favoring agricultural areas compared to grasslands. Gadwall and blue-winged teal follow similar selection patterns to pintails and seasonally select grassland before agriculture indicating a preference for the higher quality habitat. Nest success for these four species however, did not differ between landscapes (Chapter 5). These patterns of seasonal settlement suggest that pintails, gadwall, and blue-winged teal are selecting habitat consistent with Fretwell and Lucas models. Shovelers did not demonstrate a pattern of preference for any habitat type, while mallards demonstrated a preference for agricultural landscapes.

Selection patterns were not consistent for all years which suggest that other variables such as regional population size and wetland density may have affected pintail distribution patterns. Sizes of local populations may affect selection of habitat by increasing or decreasing intra and interspecific competition for territories. According to Fretwell and Lucas, the among-habitat density distribution patterns are expected to change as local populations vary, especially among species with strong territoriality. Limited high quality sites would be in greater demand when local populations are larger leading to selection earlier in the breeding season. Under ideal free conditions, habitats would be less affected by regional population levels as sites in secondary or tertiary habitats may be available and offer comparable reproductive output. The regional (southern Alberta) and local (Stratum 29) populations for these species varied over the 3 years (Table 2.10) and may have affected landscape-specific settlement rates. Estimated regional population sizes of all species

fluctuated across years, but pintail populations increased most dramatically, especially from 2005 to 2006.

Pintails exhibited a pattern that suggests despotic habitat selection and that appears to be related to local population density. In all 3 years, pintails settled initially in grassland habitat and maintained relatively high density in that habitat throughout the season. As local pintail populations increased from 2004 to 2005, the same level of settlement was observed in grassland, but higher pair densities occurred in ecotone and agriculture in 2005. The trend continued with even higher densities in ecotone and agriculture in 2006 relative to the earlier years. These general findings are consistent with predictions under an ideal-despotic distribution model.

Shovelers did not exhibit the same pattern of habitat selection as pintails. Increases in the local population between 2004 and 2005 did produce increases in secondary and tertiary habitats being selected, suggesting that a free distribution pattern of habitat selection is occurring. Mallards exhibited a different pattern of selection as it relates to local population change. Mallards were observed having higher settlement in agriculture (preferred by mallards) in 2006 compared to 2005, but not in any of the other landscapes. The observed pattern in mallards suggests that the local population is not affecting settlement patterns. Gadwall and blue-winged teal did not exhibit any pattern of habitat selection in relation to differences in local population change.

These settlement patterns observed by pintails suggest that the best quality habitat is selected. This pattern is similar for other species examined except mallards that display a preference for agricultural landscapes. The mechanisms driving selection are unknown but patterns appear to suggest that pintails are settling in habitats in a manner consistent with despotism, a conclusion that is supported by some of the evidence concerning reproductive potential (Chapter 3) and investment (Chapter 4) patterns, as well as breeding success (Chapter 5). Therefore, in the next chapter, I evaluate whether older females and birds with better body condition (i.e., indices of individual quality) are more likely to settle in grassland habitat.

Table 2.10. Estimated population sizes (in thousands) for five species of ducks in stratum 29 and southern Alberta 2004-2006. Source: Huggins, 2006.

	2004		2005		2006	
	Stratum	S.	Stratum	S.	Stratum	S.
	29	Alberta	29	Alberta	29	Alberta
Northern pintail	53.4	161.3	44.7	282.3	122.7	611.0
Northern shoveler	57.7	384.6	84.0	547.6	61.4	700.8
Mallard	101.6	600.1	106.5	671.4	139.1	900.7
Gadwall	68.5	289.9	38.2	338.2	64.9	455.2
Blue-winged teal	56.3	360.2	77.4	649.2	66.0	864.3

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CHAPTER 3 – FEMALE AGE AND BODY CONDITION OF NORTHERN PINTAIL AND NORTHERN SHOVELER IN RELATION TO LANDSCAPE CHARACTERISTICS

3.1 Abstract

Reproductive timing and investment patterns in ducks and many other bird species are related to female quality and environmental conditions, including habitat quality. Female age and measures of female body size and condition were compared for nesting birds in 3 landscapes of differing habitat quality (from higher to lower): grassland, ecotone, and agriculture. Body mass of northern pintail females (*Anas acuta*) varied among years and by nesting date, and was positively related to body size index, but mass did not differ among landscapes. In female northern shovelers (*Anas clypeata*), body mass varied among years and by nesting date; females nesting in agricultural landscapes had greater body mass in 1 of 3 years. Relatively more older female pintails were captured at nests in grassland landscapes whereas yearling females were encountered more often in agricultural areas, a pattern that was not detected in female shovelers. This response suggests that older female pintails are better able to recognize and settle in higher quality grassland habitats. An alternative hypothesis is that yearling pintails are forced into suboptimal habitat by older birds, as expected under an ideal-despotic model of habitat selection.

3.2 Introduction

Determining factors that influence the distribution of animals across habitats is a fundamental problem for ecologists and conservation biologists because of unequal fitness payoffs typically associated with use of different habitats. Fretwell-Lucas models predict how individuals should select habitats of varying quality based on ideal-free or ideal-despotic processes (Fretwell and Lucas 1970, Petit and Petit 1996). Ideal-free distributions occur when individuals settle optimally across habitats unconstrained by the presence of other individuals, while ideal despotic distributions form when some individuals are prevented by others from settling in the highest quality habitat (Holmes et al. 1996). Thus, the two models differ in terms of how reproductive success is related to habitat use.

Single or multiple mechanisms could produce patterns of habitat use, including habitat preferences related to an individual's age or quality (Ost and Steele 2010, Bearhop et

al. 2004, Marra and Holmes 2001). Previously (Chapter 2), I demonstrated that grassland landscapes were occupied consistently earlier in the breeding season and at higher densities than were agricultural landscapes in both northern pintails (hereafter, pintail) and northern shovelers (hereafter, shoveler). Here, I begin to examine mechanisms that could account for these habitat use patterns, by testing whether higher quality females are found more often breeding in grassland landscapes.

Older and heavier ducks have greater survival and reproductive potential than do younger, light-weight ducks; consequently, selection of older, good-quality mates is probably advantageous (Heitmeyer 1995). In waterfowl, older females generally breed earlier, produce larger eggs and have larger clutches than do younger individuals (Rohwer 1992, Blums et al. 1997). Likewise, older pintails nest earlier and have larger clutches than younger birds (Duncan 1987a, 1987b). In shovelers there is evidence that older birds nest earlier and produce larger ducklings, but not necessarily larger clutches (Blums et al. 1997, Blums et al. 2002). However, this does not necessarily imply selection of better quality habitat by older females.

Direct evidence of age-specific habitat selection is lacking for waterfowl, but has been demonstrated in black-throated blue warblers (*Dendroica caerulescens*; Holmes et al. 1996), prothonotary warblers (*Protonotaria citrea*; Petit and Petit 1996), and Eurasian jays (*Garrulus glandarius*; Andron 1990). In waterfowl, older dominant individuals could force subordinates into lower quality habitat resulting in a disproportionately higher number of older females nesting in higher quality grassland habitat.

Higher quality individuals may be able to sequester resources earlier and begin breeding as soon as the highest quality habitats are available in spring (e.g., Blums et al. 2005). Body reserves are used for egg laying and incubation by temperate-nesting waterfowl which nest shortly following migration, and these reserves are critical in meeting the energy demands during this period of the annual cycle (Alisauskas and Ankney 1992, MacCluskie and Sedinger 1999). Body reserves may be important in pintails as they tend to nest early and sometimes before food resources are widely available. Body condition might also influence the selection of habitat in pintails because birds in better condition may be able to select from an array of habitats with varying qualities, whereas birds in poor condition may need to select higher quality areas to meet energy demands for nesting. This body condition

hypothesis suggests that poorer-condition birds would be found in the best (grassland landscape) quality habitat, and better-condition birds could be found across various habitats. A competing hypothesis suggests that better-condition birds would be able to secure better quality habitat (grassland landscape) and poor-conditioned birds would be forced to use lower quality habitat (agriculture landscape). My main objective was to determine if female age and body mass differed between agricultural (and ecotone) landscapes when compared with adjacent grassland landscapes. Under an ideal-free distribution, no differences in female age or body condition among landscapes are expected. Alternatively, the ideal-despotic distribution model predicts that older, better-condition females would breed in high-quality grassland landscapes.

3.3 Study Area

Work was conducted at sites located in three landscapes located to the south of Lethbridge, Alberta, near the Milk River Ridge (centered at 49°17'40"N 112°36'59"W). Each of these landscapes (hereafter referred to as grassland, ecotone and agriculture) was represented by two (east and west) 41.4 km² study sites chosen to characterize the dominant landscapes in this region. The Milk River Ridge is an elevated plateau (mean altitude, 1200 m above sea level) due to differential erosion, and is 250 m higher elevation than the surrounding plain. The area also is on a historic flyway and with high numbers of pintails moving through the area during the breeding season (Miller et al. 2005). General vegetation and land use features of the three landscapes are described in greater detail in Chapter 2.

3.4 Methods

3.4.1 Age and Body Mass of Breeding Hens

Nest searches began in late April and concluded in early July, 2004-2006. Nests were located by flushing females using standard cable-chain nest searching techniques (Klett et al. 1986), and occurred from 08:00-14:00 during favorable weather (Gloutney et al. 1993). Nests were defined as bowls or scrapes consisting of ≥ 1 egg. Flushed birds were identified visually, and confirmed using characteristics of eggs, down, and breast feathers in the bowl. Nests were marked with a bamboo stake (1-1.3 m tall, 0.5 to 1 cm diameter) placed 4 m from the nest bowl in a randomly selected cardinal direction. Date found, species, number of eggs,

stage of incubation (Weller 1956), and visual obstruction readings (Robel et al. 1970) were recorded for each nest. Universal Transverse Mercator (UTM) coordinates were determined for each nest site and used to aid in relocation.

Alternate nests were assigned to one of two sample groups, being either (1) reproductive investment (Chapter 4, 5) or (2) reproductive potential nests. Females attending nests assigned to the reproductive potential study were captured at approximately 15 days of incubation throughout the nesting season (determined *a posteriori* on the basis of nest initiation date distributions) using a modified Weller trap (Weller 1957). Traps were set during early to mid-morning and revisited in mid-afternoon; traps were not set overnight to reduce predation risk. Captured birds were removed from traps and marked with a standard aluminum United States Fish and Wildlife Service (USFWS) leg band (Lokemoen and Sharp 1985). Prior to release, body mass (nearest 5 g using a Pesola scale), flattened wing cord length (nearest 1 mm using a ruler), and tarsus, head and bill lengths (nearest 0.1 mm using dial calipers) were recorded.

Female age in pintails was determined by inspecting the fifth greater secondary covert for internal or no markings, or markings that were contiguous with the edge to allow for aging to second year (juvenile), and after second year (adult), following Duncan (1985). Two independent observers assigned age to these feathers in a double-blind process to determine female age. Results of the two estimations were compared to confirm age. In cases of initial disagreement, further assessment was conducted to determine age by consensus.

To reduce nest abandonment (Smith et al. 1980, Rotella and Ratti 1990), females were given an intravenous injection of propofol to induce anesthesia (10 mg/kg of anesthetic over a 1 min period), following Machin and Caulkett (2000). Depth of anesthesia was determined by opening the bill and pulling the tongue forward to determine reaction (Machin and Caulkett 2000); heart and respiration rate were monitored with a stethoscope and visually. When breathing and heart rate were stabilized, females were placed on the nest to complete recovery from the anesthetic. Hens were observed from a distance until consciousness (movement was observed) was regained (15-60 min) and to ensure that mortality did not occur.

3.4.2 Statistical Analysis

Differences in female ages (AGECLASS, i.e., adult versus yearling) among landscapes were evaluated using logistic regression (PROC LOGISTIC, SAS Instit. 2009). *A priori* models considered effects of landscape (LAND), site replicates nested within landscape (REP(LAND)), year (YEAR) and the interaction between year and landscape. Models were ranked using Akaike's Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002). To control for the possible effects of structural differences in body size on body mass, principle component analysis (Proc Princomp, SAS Instit. 2009) was conducted on measurements of head, wing and tarsus lengths to derive an index of structural size in both pintails and shovelers. The first principle component (PC1) for both pintails and shovelers produced a positive correlation among variables with coefficients ranging from 0.32 to 0.43 for pintails and 0.34 to 0.43 for shovelers. The PC1 eigenvalues for pintails and shovelers were 1.29 and 1.30 and explained 74.9% and 77.0% of variance, respectively. The PC1 score was used as an index of body size in subsequent analyses.

Variation in body mass (MASS) of breeding pintails and shovelers was assessed with respect to the effect of landscape (LAND), year (YEAR), capture date (CAPD), incubation stage when captured (INCSTG), body size index (PCA1), age (AGE, in pintails only), clutch size (CSIZE) and the interaction between year and landscape. Data were analyzed using mixed models (SAS Instit. 2009, PROC MIXED) with LSMEANS (SAS Instit. 2009) used to produce body mass estimates (g) and 95 % confidence intervals. Model parameter estimates and standard errors are presented. To control the effects of study replicate clustering, a random statement including the interaction between replicate and landscape was added. Models were ranked using models weights (w_i), with retention of covariates of interest based on AIC_c values (Burnham and Anderson 2002). When year by landscape interaction was retained in the best-approximating model, data were sorted by variables in the interaction to explore effects of individual variables. Model parameter (β) estimates and standard error (SE) values are presented.

3.5 Results

3.5.1 Age

Totals of 79 pintails and 81 shovelers were captured over 3 years (Table 3.1) and were used to determine whether female age and body condition varied by landscape conditions. The global model used to determine variation in age class included covariates for year, landscape, site replicate nested within landscape and the interaction between year and landscape. The best approximating model describing variation in age class included the covariate for landscape ($w_i = 0.648$; Table 3.2). A greater proportion of adult female pintails was captured on nests in grassland than in agriculture. The proportion of adults in grassland compared to ecotone did not differ.

Chi-squared analysis comparing observed and expected ratios of adults to yearlings was conducted to compare the distribution of pintail females among landscapes and years. The ratio of adult:yearling pintails was significantly higher in grassland (28:5) and ecotone (23:4), whereas similar numbers of adults and yearlings (8 vs 9) were captured in agricultural areas ($\chi^2 = 10.65$, $df=2$, $p = 0.005$) (Figure 3.1). No yearlings were captured in 2004 when poor wetland conditions prevailed (Figure 3.2); the ratios of adult:yearling pintails nearly differed among years ($\chi^2 = 5.87$, $df = 2$, $p = 0.06$), and were 19.5:0 in 2004, 28.6:13.0 in 2005 and 28.6:10.4 in 2006.

Table 3.1. Total numbers of female pintails and shovelers captured on nests in each landscape (grassland, ecotone and agriculture) during 2004-2006, Milk River Ridge, Alberta.

Year	Pintails			Shoveler		
	Grassland	Ecotone	Agriculture	Grassland	Ecotone	Agriculture
2004	9	4	3	2	6	2
2005	12	13	7	12	7	21
2006	7	17	7	5	14	12

Table 3.2. Models used to assess the effect of year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)) and landscape by year interaction on age of female pintails nesting on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2LogL	AICc	Δ_i	w_i
LAND	4	74.23	6.85	0.00	0.648
LAND, YEAR	7	64.26	8.07	1.22	0.352
LAND, YEAR, REP(LAND)	16	53.84	20.32	13.48	0.001
LAND, YEAR, REP(LAND), LAND*YEAR	25	51.19	36.85	30.01	0.000

K=number of parameters, -2logL=-2 log likelihood value, AICc=corrected Akaike's information criterion value, Δ_i =AIC_c difference, w_i =model weight

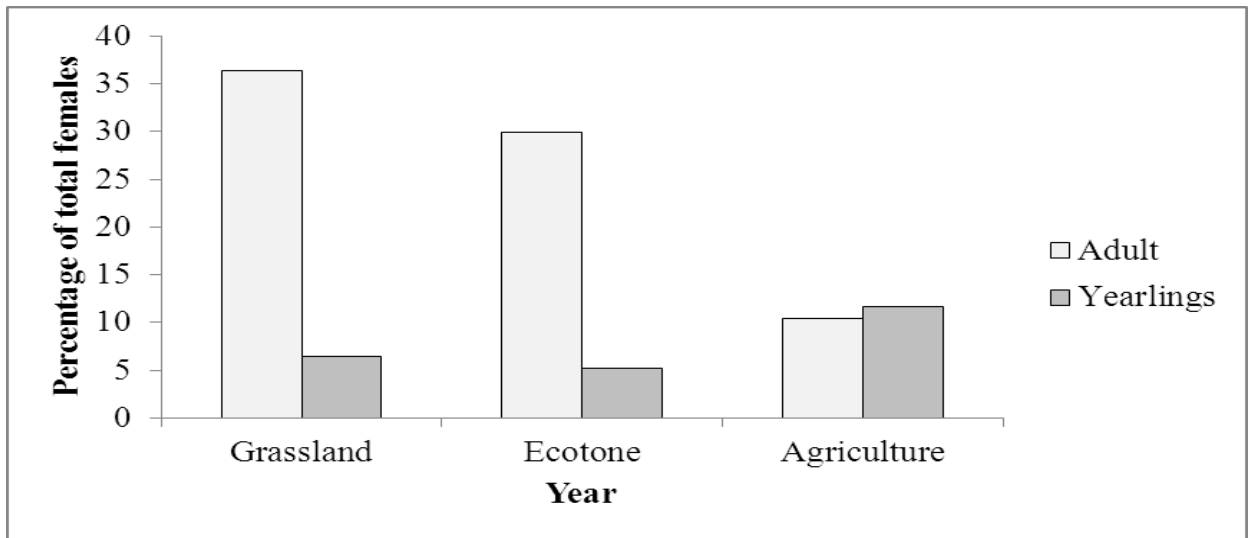


Figure 3.1 Percentage of adult (n = 59) and yearling (n = 18) female pintails captured at nests in grassland (n =33), ecotone (n =27), and agricultural (n =17) landscapes on the Milk River Ridge, Alberta, 2004-2006.

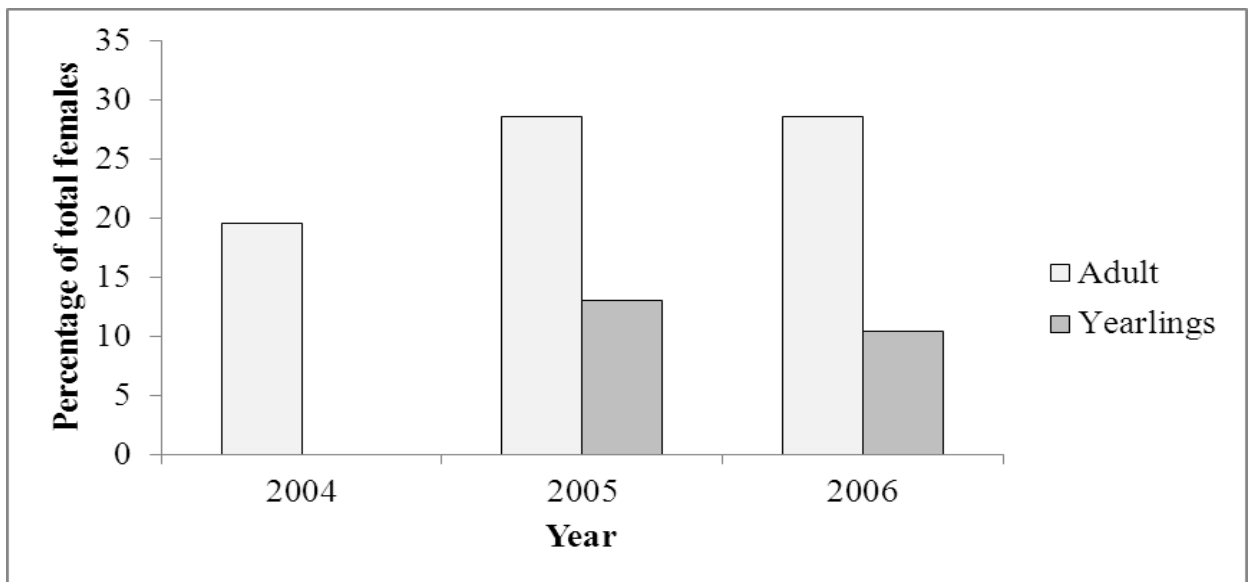


Figure 3.2 Annual percentages of adult and yearling pintail females across all years, captured at nests on the Milk River Ridge, Alberta, in 2004 (n = 15 females), 2005 (n = 32) and 2006 (n = 30).

3.5.2 Body Mass

Body mass of female pintails was best described by a model containing effects of capture date, landscape, year, incubation stage and body size index ($w_i = 0.999$) (Table 3.3). Body mass declined with capture date ($\beta = -0.61 \pm 0.34$), but increased with body size index ($\beta = 12.40 \pm 5.78$) and incubation stage ($\beta = 2.90 \pm 1.26$). Pintails differed weakly in body mass between grassland and ecotone ($\beta = 28.05 \pm 14.03$) but not agriculture ($\beta = 21.52 \pm 15.27$). Body mass estimates for pintails were 650 ± 24 g in grassland, 678 ± 27 g in ecotone and 672 ± 33 g in agriculture. Compared with 2006, body mass did not differ in 2005 ($\beta = -25.35 \pm 13.04$), or 2004 ($\beta = 26.15 \pm 15.85$). Body masses of pintails in 2004, 2005 and 2006 averaged 693 ± 25 g, 641 ± 18 g, and 667 ± 19 g, respectively. Overall, an intercept-only model produced a body mass estimate of 659 ± 8 g.

The best-approximating model describing body mass in female shovelers included the covariates for capture date, landscape, year, incubation stage and the interaction between year and landscape ($w_i = 0.610$) (Table 3.4). In the best model, body mass decreased with capture date ($\beta = -1.70 \pm 0.35$), and increased with incubation stage ($\beta = 2.31 \pm 0.96$). Relative to grassland, body mass of shovelers did not differ in ecotone ($\beta = -47.11 \pm 25.27$) or agriculture ($\beta = -33.34 \pm 20.16$). Body mass estimates in grassland, ecotone and agriculture were 519 ± 32 g, 519 ± 44 g, and 507 ± 35 g, respectively. Female shovelers had greater body mass in 2006 and 2004 when compared to 2005 ($\beta = -64.44 \pm 16.61$), with no difference being detected between 2006 and 2004 ($\beta = 15.20 \pm 17.27$). Shoveler body mass estimates were 555 ± 29 g in 2004, 481 ± 18 g in 2005, and 508 ± 21 g in 2006. The intercept-only model produced an estimate of 506 ± 7 g.

Because of the year by landscape interaction being present in the best model, data were sorted by year and re-analyzed to isolate annual landscape differences. In 2004, the effect of capture date on body mass was negligible ($\beta = -0.28 \pm 1.50$), and body mass did not differ between grassland, ecotone ($\beta = -4.05 \pm 54.19$) or agriculture ($\beta = -38.20 \pm 37.10$). Body mass estimates in grassland, ecotone and agriculture were 517 ± 29 g, 515 ± 40 g, and 504 ± 33 g, respectively, in 2004. In 2005, body mass decreased with relative clutch initiation date ($\beta = -1.14 \pm 0.34$). Relative to grassland, body mass did not differ in ecotone ($\beta = 12.68 \pm 25.24$) and agriculture ($\beta = 10.53 \pm 23.10$). Body mass estimates for 2005 in grassland, ecotone and agriculture were 462 ± 52 g, 475 ± 47 g, and 473 ± 38 g, respectively.

In 2006, the pattern remained the same as in 2005, with decreasing body mass with relative capture date ($\beta = -2.13 \pm 0.64$). Body mass estimates in 2006 did not differ between grassland, ecotone ($\beta = -41.72 \pm 20.10$) and agriculture ($\beta = -27.11 \pm 15.35$) and were 552 ± 29 g, 510 ± 48 g, and 525 ± 31 g, respectively.

Table 3.3. Models used to assess the effect of landscape (LAND) year (YEAR), capture date (CAPD), incubation stage when captured (INCSTG), principle component 1 (PCA1), age (AGE), clutch size (CSIZE) and the interaction between year and landscape on body mass of pintails on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2LogL	AICc	Δ_i	w_i
CAPD, LAND, YEAR, INCSTG, PCA1	10	772.10	94.43	0.00	0.999
CAPD, LAND, YEAR, INCSTG, PCA1, LAND*YEAR	19	730.10	112.62	18.18	0.001
CAPD, LAND, YEAR, INCSTG, PCA1, AGE, LAND*YEAR	21	709.60	116.67	22.23	0.000
CAPD, LAND, YEAR, INCSTG, PCA1, AGE, CSIZE, LAND*YEAR	22	704.90	118.47	24.04	0.000

K=number of parameters, -2logL=-2 log likelihood value, AICc=corrected Akaike's information criterion value, Δ_i =AICc difference, w_i =model weight

Table 3.4. Models used to assess the effect of landscape (LAND) year (YEAR), capture date (CAPD), incubation stage when captured (INCSTG), principle component 1 (PCA1), clutch size (CSIZE) and the interaction between year and landscape on body mass of shovelers on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2LogL	AICc	Δ_i	w_i
CAPD, LAND, YEAR, INCSTG, LAND*YEAR	18	726.70	113.49	0.00	0.610
CAPD, LAND, YEAR, INCSTG, CSIZE, LAND*YEAR	19	717.90	115.08	1.59	0.275
CAPD, LAND, YEAR, INCSTG, PCA1, CSIZE, LAND*YEAR	20	712.40	116.83	3.34	0.115

K=number of parameters, -2logL=-2 log likelihood value, AICc=corrected Akaike's information criterion value, Δ_i =AICc difference, w_i =model weight

3.6 Discussion

In dabbling ducks, female age has been linked to greater survival and reproductive potential in terms of nesting success (Duncan 1987a, Heitmeyer 1995, Devries et al. 2008) and offspring recruitment (Blums et al. 2002). Additionally, in many duck species, older females nest earlier in the season, have higher nesting propensity, lay larger clutches, and renest more persistently (Rohwer 1992, Arnold 2010). Because of the link between age and reproductive output, investigating relationships between age and habitat selection could be instructive because this could help to understand patterns of habitat selection by breeding waterfowl.

In terms of nesting patterns, relatively more adult female pintails were captured on nests in grassland and ecotone landscapes whereas relatively more yearlings were captured at nests in agricultural landscapes. Pintail pairs occurred at higher densities on grassland landscapes; in general, pair density was highest on wetlands in grassland landscapes in early spring in all years (Chapter 2). Older, experienced females may be better able to recognize and settle in higher quality habitat. The mechanism(s) driving settlement of these landscapes by pairs is unclear, but there may also be a competitive advantage of being older, with paired adult females possibly forcing yearling females into lower quality agricultural landscapes. This hypothesis may be more plausible if high-quality females mate with high-quality males; positive assortative mating by quality has not been determined in pintails, but has been reported in wild mallards and other birds (Wishart 1983, Holmberg et al 1989). This settlement pattern, where higher proportions of adults occur in grassland and ecotone areas, could produce landscape differences in reproductive output. It was not possible to determine the age of birds upon arrival in the spring, but older birds typically arrive on breeding grounds before younger ones in some species (Smith and Moore 2005). Temporally, it appears that adults selected all habitats, in each year, while yearlings only occurred in habitats in 2005 and 2006. In 2004, a year with fewer wetlands, only adult female pintails were found nesting in all landscapes, suggesting age-related effects of landscape and wetland conditions on reproductive decisions may be occurring. Younger female ducks are known to reduce nesting effort when wetland conditions are generally poor (Afton 1984, Dufour and Clark 2002), but whether this represents reproductive constraint or restraint remains unknown.

Body mass of female pintails declined with capture date, but not incubation stage or structural index measurements even though females were captured late in incubation. This trend is consistent with previous work that reported the same pattern of body mass variation in pintails (Duncan 1987a, Guyn and Clark 2000). However, female body mass did not differ among landscapes in either pintails or shovelers. Although older pintails were encountered more often in grassland and ecotone than agriculture, these females did not differ in body mass from birds nesting in agriculture. Shovelers, for all years of the study combined, did not demonstrate any difference between birds settling in any of the three habitat types. When analyzed by year, body mass of pintails did not differ between landscapes in any of the 3 years of the study. Part of the reason for the lack of body mass effect may be due to small sample size and the fact that birds were captured throughout the breeding season rather than on their arrival to the breeding grounds. It seems unlikely that a lack of difference in body masses between females nesting in grassland and agricultural areas was due to higher egg investment by birds in grasslands because clutch sizes did not differ among landscapes in either species.

Overall for these two species, landscape effects on body mass are not clear. The landscape selected may not be affected by the body mass of the birds, but at this coarse level of assessment it may not have been detected. It is reasonable to assume that in the case of pintails, a trend to higher body mass in better quality habitat would be evident. As an early-season nester and a species that depends on endogenous resources, this conclusion is reasonable (MacCluskie and Sedinger 1999). On the other hand, shovelers may not exhibit the same trend due to their nesting ecology. As an early to mid-season nester and a species that requires higher use exogenous reserves for egg formation, determining this trend may be more difficult. For pintails in particular, there could be a tradeoff that allows the selection of lower quality nesting habitat because of the ability to increase or maintain body condition through the acquisition of waste grain present in agricultural landscapes.

Returning to the Fretwell-Lucas models of habitat selection, some evidence suggests that older pintails – possibly those individuals with higher reproductive potential - are selecting grasslands. On the other hand, there was no evidence that grassland-nesting female pintails or shovelers were higher quality birds, as indexed by body mass. Given that grasslands attract older, more experienced females, grassland could represent higher quality

habitat. Therefore, I evaluated whether female reproductive investment patterns differed among landscapes and, more specifically, I determined whether female pintails nesting in grassland habitat produced larger clutches, earlier, when compared with females nesting in agricultural and ecotone landscapes (Chapter 4).

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CHAPTER 4 – TIMING OF NESTING AND REPRODUCTIVE INVESTMENT PATTERNS IN PRAIRIE-NESTING DUCKS: RELATIONSHIPS WITH HABITAT QUALITY

4.1 Abstract

Reproductive investment patterns of female northern pintails (*Anas acuta*), assessed in terms of nest initiation date and clutch size, were investigated on the Milk River Ridge of Alberta. To test models of habitat selection, reproductive investment variables were compared between three landscapes of differing habitat qualities (from higher to lower): grassland, ecotone, and agriculture. Annual and landscape-level variation in reproductive measurements were also considered for northern shovelers (*A. clypeata*) and mallards (*A. platyrhynchos*). For clutch initiation date, effects of species, year, and species by year interaction were detected, but there were no differences among landscapes for any species. Pintails nested significantly earlier (17 May \pm 3 days) than did shovelers (24 May \pm 3 days), but not mallards (19 May \pm 4 days) for all years combined, and nesting dates of mallards and shovelers did not differ. Clutches of all three species were initiated earlier in 2006 (11 May \pm 3 days) than in 2004 (24 May \pm 4 days), and 2005 (23 May \pm 3 days). In all 3 species of ducks, clutch size was negatively related to nest initiation date. In northern pintails, clutch size was larger in 2006 (a wet year with abundant wetlands) than in 2004 (dry year) but not 2005, and did not differ between landscapes. Northern shoveler clutch size was larger in 2006 and 2005 than in 2004, but did not differ among landscapes. Mallard clutch size did not vary by year or landscape. In general, these findings indicate that female reproductive timing and investment (in terms of clutch size) were unrelated to upland habitat characteristics. However, female northern pintails and northern shovelers may invest in larger clutches in wet years with abundant wetlands, possibly due to greater abundance of aquatic foods.

4.2 Introduction

Timing of nest initiation and clutch size may be influenced by the quality of habitats selected by breeding birds. In waterfowl, hypotheses linking nest initiation date to habitat quality and energetics include incubation energetics (i.e., wherein energy shortage delays incubation), laying delay (egg production requires energy), and optimal rearing hypotheses

(timing of hatch coincides with highest food abundance) (Rohwer 1992). A common thread in all of these is the connection to energy needs associated with breeding and production of young. Quality of habitat selected by breeding individuals may influence energy acquisition and may affect reproductive investment, and subsequent offspring recruitment (Alisauskas and Ankney 1991).

Energy for breeding can be obtained on the wintering grounds and carried as endogenous reserves to the breeding grounds for use in reproduction (egg production). Additional exogenous energy is obtained on the breeding grounds, but may be influenced by timing of arrival (Tome 1991, Bond et al. 2007). Ducks arriving on the Canadian prairies in the spring should select habitats that will maximize fitness (e.g., reproductive success and survival), and selection presumably should focus on the highest quality habitat(s) available. Because these species are abundant in the area, and have similar reproductive strategies, I investigated habitat selection and reproductive investment patterns of northern pintail (hereafter, pintail), northern shoveler (hereafter shoveler), and mallard in southern Alberta.

Pintails and mallards are among the earliest duck species to initiate nests on the prairies (Higgins 1977, Bellrose 1980, Duncan 1987, Greenwood et al. 1995). Shovelers initiate nests midway between the earliest and latest species (e.g., gadwall, *Anas strepera*) of prairie nesting ducks (Afton 1980). Early nesting may be a response to the temporary nature of the wetlands on the prairies. The disadvantage of early nesting includes nest losses because of unpredictable weather early in the nesting season (Greenwood et al. 1995). There is evidence that early nesting increases fitness in prairie waterfowl (Krapu et al. 2000), and earlier nest initiation would also offer more time for renesting attempts in the event of nest loss (Arnold et al. 2010).

If unsuccessful, pintails do not renest as frequently as other dabbling duck species. The proportion of females that renest after nest loss is similar for pintails and mallards (Bellrose 1980, Rotella et al. 1993, Guyn 2000), but the total number of renesting attempts by pintails is believed to be much lower. Mallards may renest as many as six times (Rotella et al. 1993) with an average ranging from 1.1 to 2.9 (Paquette et al. 1997). Mallards exhibit a high propensity to renest after loss, particularly if initial nesting occurs early in the breeding season (Arnold et al. 2010). Pintails are less likely to renest than mallards and have been observed renesting only twice after initial nest loss (Duncan 1987, Esler and Grand 1994,

Grand and Flint 1996b). This low renesting rate may be an adaptation to the declining quality of wetland habitats on prairies due to natural drawdown (Raveling and Heitmeyer 1989). Shovelers renesting rates in Alberta have been reported at 75% but the number of renesting attempts is unknown (Bellrose 1980). This variation in propensity and timing of renesting could affect the mean nest initiation date, and vary with habitat quality.

Clutch sizes of most species of birds decline during the nesting season (Lack 1968, Krapu et al. 2004), including waterfowl that breed in temperate regions of North America (Rohwer 1992). Mean clutch size of pintails in Alberta has been reported as 6.9 ± 0.1 (SE) eggs with no difference detected between age classes (Duncan 1987). Guyn and Clark (2000) reported similar findings in Alberta where the mean clutch size was 7.2 ± 0.15 (SE) eggs, with no difference detected between years. Duncan (1987) also hypothesized that, despite generally low renesting rates, pintails have smaller clutches on grassland habitats because conditions in this habitat (food limitation or female quality) were less suitable than other habitat types where food abundance is higher.

Comparisons of clutch sizes between habitats for pintails are lacking. Duncan (1987) reported a larger clutch size in captive pintails than in wild birds, perhaps suggesting that clutch size varies with habitat quality (i.e., food) or that low clutch size of wild birds is related to higher predation rates (i.e., high frequency of smaller replacement clutches). In common goldeneyes (*Bucephala clangula*) nesting on lakes with high and low food production, clutch mass was greater for females nesting on lakes with higher food production (Mallory 1994). Common eiders (*Somateria mollissima*) exhibited the same trend with larger clutches in higher quality habitat (Kilpi and Lindstrom 1997). These examples suggest that there is a link between habitat quality and clutch size. Whether this same link between habitat quality and reproductive investment of nesting ducks selecting habitats of differing qualities exists is yet untested.

One hypothesis regarding habitat quality is that agricultural landscapes (dominated by small grain farming practices) may provide habitat tradeoffs that attract pintails and lead to the selection of these areas in which to breed. Agriculture landscapes might provide richer resources due to agricultural waste grains and fertilizer inputs to wetlands which produce greater abundance of macro-invertebrate foods important for energy acquisition (Duncan 1987). These landscapes may also provide open water earlier because of differential rates of

melting and water flow due to cultivation and ditching practices. This hypothesis predicts that timing of nesting may be earlier, and clutch size may be larger because of increased resources available due to agrochemical inputs into the system. An alternative hypothesis is that timing is earlier and clutch size is larger in higher quality habitat. The early settlement at higher densities by breeding pairs on grassland (dominated by perennial grasses) landscapes suggests that pintails could perceive grassland landscapes as being high quality nesting habitat (Chapter 1). Furthermore, given that relatively more adult females were captured on nests in grassland landscapes (Chapter 2), I predicted that pintails nest earlier and lay larger clutches in grasslands.

My objective was to investigate how nest initiation dates and clutch sizes differed between agricultural and ecotone landscapes when compared with adjacent grasslands of presumed higher quality. Investigation of these metrics of reproductive investment could yield insights into how habitats are settled and whether investment patterns conform to predictions of Fretwell-Lucas models.

4.3 Study Area

Work was conducted at sites located in three landscapes south of Lethbridge, Alberta, near the Milk River Ridge (centered at 49°17'40"N 112°36'59"W). Each of these landscapes (hereafter referred to as grassland, ecotone and agriculture) was represented by two (east and west) 41.4 km² study sites chosen to characterize the dominant landscapes in this region. The Milk River Ridge is an elevated plateau (mean altitude, 1200 m above sea level) due to differential erosion, and is 250 m higher elevation than the surrounding plain. The area also is on a historic flyway and with high numbers of pintails moving through the area during the breeding season (Miller et al. 2005). A more detailed description of study sites are given in Chapter 2.

4.4 Methods

Nests were found using standard nest-searching techniques (Klett et al. 1986). Searches began in late April and concluded in early July each year, and were conducted daily from 8:00 to 14:00 during favorable weather conditions (Gloutney et al. 1993). Most females attending nests were identified visually to species when flushed from their nests by the cable-

chain or during subsequent nest visits, or by using egg and down feathers present in nest bowls. Number of eggs was recorded along with stage of laying or incubation. To determine incubation stage, at least 2 eggs from each nest were field candled to determine embryonic development. If development was detected, clutches were considered to be complete. If nests were found with eggs that did not have embryonic development, full clutch was determine on subsequent visits(s), typically about 7-10 days later. Clutches >12 and <4 eggs were removed from the sample to reduce possible effects of parasitism and partial clutch predation, respectively. Nest initiation date was calculated for pintail, shoveler and mallard nests by subtracting the number of days associated with clutch production (1 day/egg) and incubation stage from the date the nest was found.

4.4.1 Statistical Analysis

The most parameterized model for nest initiation date (NESTIN) included effects of species (SPECIES), year (YEAR), landscape (LAND), site-replicate nested within landscape (REP(LAND)), and the interactions species by year, species by landscape, year by landscape, and species by year by landscape. Thereafter, additional *a priori* candidate models of lower complexity were used to assess nest initiation date variation in all species (details below).

Nest initiation date data were analyzed using mixed models (PROC MIXED) in SAS (SAS Institute 2009) with LSMEANS used to produce nest initiation date estimates and 95% confidence limits, adjusted for covariate effects. To control the effects of clustering of nests within sites in each landscape, a random statement was included to account for site-replicate effects being nested within landscapes. Models were ranked using models weights, with retention of covariates of interest (and a common set of random effects, as above) using Akaike's Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002). Where interactions were included in the best-approximating model, data were sorted by variables in the interaction to better resolve effects of individual variables.

Initial analysis of clutch size (CSIZE) data was completed using generalized linear models (SAS Institute. 2009, PROC GENMOD) with LSMEANS function to produce estimates of clutch size and 95% confidence intervals. A scale parameter (\hat{c}) was estimated in most parameterized model and used in all subsequent models to control for overdispersion (i.e., QAIC_c). The most parameterized model incorporated effects of species (SPECIES),

nest initiation date (NESTIN), year (YEAR), landscape (LAND), study site replicate nested within landscape REP(LAND), and the interactions between nest initiation date and species, nest initiation date and year, nest initiation date and landscape, year and species, landscape and species, landscape and year. Simpler *a priori* candidate models were created to assess sources of variation in clutch size. Models were ranked using models weights, with retention of covariates of interest using Akaike's Information Criterion (Burnham and Anderson 2002). Parameter estimates (β) and standard error (SE) values are presented. Nonlinear effects of initiation date on clutch size were not detected during initial analyses, and were not considered further.

When interactions were retained in the best-approximating model, data were sorted by variables in the interaction to explore effects in greater detail. When a year effect was present in the best model and produced differences in clutch size, data were standardized and reanalyzed using relative clutch initiation date. Relative nest initiation standardized nest initiation to the date that 5% of each year's nests were initiated. Relative nest initiation date (RCID) replaced nest initiation date in the candidate set of models, and data were re-analyzed. The landscape covariate is of particular interest in these models because it is an index of habitat quality and was retained to determine the landscape effect on the dependent variable(s) being assessed.

4.5 Results

Nest initiation date analyses were conducted on 242 pintail, 348 shoveler, and 169 mallard nests. A sub-sample of 206 pintail, 274 shoveler, and 122 mallard nests with complete clutches (i.e., incubation had started) was used in clutch size analyses. All other species were excluded because nest searching activities were curtailed before late nesting species had completed nesting.

Median nest initiation date varied by year, and was also generally earlier for pintails nesting in grassland when compared to ecotone and agriculture. Shoveler median nest initiation date varied by year but did not vary by landscape. Finally, mallard median initiation date varied by year, and was generally earlier in agriculture than grassland (Table 4.1).

Table 4.1. Median nest initiation date and 95% confidence interval for Mallard (Mall), Shoveler (Nsho) and Pintail (Nopi) nesting in grassland, ecotone and agriculture landscapes, 2004-2006, in southern Alberta.

Year	Grassland			Ecotone			Agriculture		
	Mall	Nsho	Nopi	Mall	Nsho	Nopi	Mall	Nsho	Nopi
2004	27 May n = 5 (27 May- 27 May)	26 May n = 21 (9 May- 12 Jun)	19 May n = 14 (8 May- 30 May)	24 May n = 9 (18 May- 30 May)	30 May n = 21 (9 May- 20 Jun)	21 May n = 24 (28 Apr- 12 Jun)	23 May n = 21 (6 May- 9 Jun)	27 May n = 13 (21 May- 2 Jun)	27 May n = 7 (24 May- 29 May)
2005	13 May n = 10 (15 Apr- 10 Jun)	1 Jun n = 23 (5 May- 28 Jun)	20 May n = 31 (25 Apr- 14 Jun)	25 May n = 10 (9 May- 10 Jun)	30 May n = 40 (2 May- 27 Jun)	9 May n = 32 (11 Apr- 6 Jun)	23 May n = 20 (23 Apr- 21 Jun)	1 Jun n = 57 (9 May- 24 Jun)	2 Jun n = 23 (3 May- 1 Jul)
2006	13 May n = 25 (21 Apr- 4 Jun)	9 May n = 44 (17 Apr- 31 May)	30 Apr n = 47 (4 Apr- 26 May)	18 May n = 8 (11 May- 24 May)	10 May n = 29 (25 Apr- 24 May)	11 May n = 35 (11 Apr- 10 June)	8 May n = 61 (7 Apr- 8 Jun)	7 May n = 100 (7 Apr- 6 Jun)	9 May n = 35 (10 Apr- 7 June)

4.5.1 Nest Initiation Date

Initial analysis of nest initiation date was conducted on all duck species (pintail, shoveler and mallard). The best-approximating model included effects of species, year, and species by year interaction (Table 4.2). Pintails nested significantly earlier (17 May \pm 3 days) than did shovelers (24 May \pm 3 days), but not mallards (19 May \pm 4 days) for all years combined, and nesting dates of mallards and shovelers did not differ. Clutches of all three species were initiated earlier in 2006 (11 May \pm 3 days) than in 2004 (24 May \pm 4 days), and 2005 (23 May \pm 3 days). Due to the inclusion of a species (and interaction) effect in the best-approximating model, data were reanalyzed for each species of interest.

In pintails, the best-approximating model describing nest initiation date included the covariate for year (Table 4.3). Pintail clutches were initiated earlier in 2006 (10 May \pm 6 days) than in 2005 (22 May \pm 6 days), but not 2004 (21 May \pm 7 days). No difference was observed in nest initiation date between 2004 and 2005.

Because of the interest in landscape effect on nest initiation date the best model containing the covariate for landscape was also examined. This model contained the covariate for landscape and year ($w_i = 0.064$). Pintails nest initiation dates did not differ annually (2006, 10 May \pm 6 days; 2005, 21 May \pm 6 days; 2004, 21 May \pm 7 days), nor did it differ between grassland (14 May \pm 11 days), ecotone (17 May \pm 14 days) or agricultural (21 May \pm 10 days) areas. Variation in nest initiation date between years was controlled by using relative nest initiation date and data were reanalyzed. In the model of relative nest initiation date containing covariates for landscape, again, mean relative nest initiation date did not differ between grassland (24 \pm 10 days), ecotone (27 \pm 13 days) or agriculture (32 \pm 10 days).

Table 4.2. Models used to assess the effect of species (SPECIES), year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)), species by year, species by landscape, year by landscape, and species by year by landscape interactions on nest initiation date of all ducks on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	AIC _c	ΔAIC _c	w _i
SPECIES, YEAR, SPECIES*YEAR	16	6201.30	716.21	0.00	0.942
SPECIES, YEAR, LAND, SPECIES*YEAR	19	6193.10	721.78	5.58	0.058
SPECIES, YEAR, LAND, SPECIES*YEAR, SPECIES*LAND	28	6168.60	738.52	22.31	0.000
SPECIES, YEAR, LAND, SPECIES*YEAR, SPECIES*LAND, YEAR*LAND	37	6148.20	755.47	39.26	0.000
SPECIES, YEAR, LAND, SPECIES*YEAR, SPECIES*LAND, YEAR*LAND, SPECIES*YEAR*LAND	64	6095.40	806.73	90.52	0.000

K=number of parameters, -2logL=-2 log likelihood value, AIC_c =corrected Akaike's information criterion value, ΔAIC_c=AIC_c difference, w_i=model weight

Table 4.3. Models used to assess the effect year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)), year by landscape interactions on nest initiation date of pintails on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	AIC _c	ΔAIC _c	w _i
YEAR	4	2054.1	231.80	0.00	0.936
LAND, YEAR	7	2041.7	237.18	5.38	0.063
LAND, YEAR, LAND*YEAR	16	2013.6	253.78	21.98	0.000

K=number of parameters, -2logL=-2 log likelihood value, AIC_c =corrected Akaike's information criterion value, ΔAIC_c=AIC_c difference, w_i=model weight

The best approximating model describing nest initiation date in shovelers included the covariate for year ($w_i = 0.941$) (Table 4.4). Shoveler nests were initiated earlier in 2006 (11 May \pm 3 days) than 2005 (30 May \pm 4 days) and 2004 (29 May \pm 4 days). No difference was observed in nest initiation date between 2004 and 2005.

The second best-approximating model describing nest initiation date included the covariates for year and landscape ($w_i = 0.059$). Shovelers nested earlier in 2006 (12 May \pm 4 days) than 2005 (30 May \pm 4 days) and 2004 (28 May \pm 5 days) but there was no difference between grassland (24 May \pm 6 days), ecotone (24 May \pm 8 days) or agricultural (22 May \pm 7 days) areas. Seasonal variation in nest initiation date between years was controlled by using relative nest initiation date and data were reanalyzed. In the model of relative nest initiation date containing covariates for landscape, mean relative nest initiation date did not differ between grassland (19 \pm 7 days), ecotone (22 \pm 9 days), or agriculture (18 \pm 7 days).

The best-approximating model describing nest initiation date in mallards included the covariate for year ($w_i = 0.936$) (Table 4.5). Mallard clutches were initiated earlier in 2006 (12 May \pm 5 days) than 2004 (23 May \pm 6 days) but not 2005 (21 May \pm 6 days). No difference was observed in nest initiation date between 2004 and 2005.

The second best supporting model describing nest initiation included the covariate for year and landscape ($w_i = 0.065$). Mallard nest initiation did not differ between 2006 (12 May \pm 5 days), 2005 (22 May \pm 6 days) or 2004 (23 May \pm 7 days). Mallard nest initiation did not differ between grassland (19 May \pm 7 days), ecotone (19 May \pm 8 days), or agriculture (18 May \pm 8 days). Finally, in a model of relative clutch initiation date that contained covariates for landscape, mean relative clutch initiation date did not differ between grassland (28 \pm 7 days), ecotone (30 \pm 8 days), or agriculture (27 \pm 10 days).

Table 4.4. Models used to assess the effect year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)), year by landscape interactions on nest initiation date of shovelers on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	AICc	ΔAIC_c	w_i
YEAR	4	2735.7	314.50	0.00	0.941
LAND, YEAR	7	2727	320.04	5.54	0.059
LAND, YEAR, LAND*YEAR	16	2707.1	337.00	22.50	0.000

K=number of parameters, -2logL=-2 log likelihood value, AIC_c =corrected Akaike's information criterion value, ΔAIC_c = AIC_c difference, w_i =model weight

Table 4.5. Models used to assess the effect year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)), year by landscape interactions on nest initiation date of mallards on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	AICc	ΔAIC_c	w_i
YEAR	4	1398.4	161.18	0.00	0.935
LAND, YEAR	7	1385.4	166.53	5.35	0.064
LAND, YEAR, LAND*YEAR	16	1360.4	183.29	22.11	0.000

K=number of parameters, -2logL=-2 log likelihood value, AIC_c = corrected Akaike's information criterion value, ΔAIC_c = AIC_c difference, w_i =model weight

4.5.2 Clutch Size

In general, nest numbers increased seasonally across the three years of the study (Table 4.6), especially in grassland and agricultural areas, and corresponded with increasing wetland densities and improving habitat conditions (Huggins 2006). Pintail nests were more common on grassland areas, whereas shoveler and especially mallard nests were more abundant on agricultural sites.

Initial analysis was conducted for pintails, shovelers, and mallards combined. The best-supported model describing variation in clutch size included the covariates for nest initiation date, species, year and landscape (Table 4.7). Overall, clutch size declined with nest initiation date ($\beta = -0.030 \pm 0.003$). Relative to shovelers (9.6 ± 0.2 eggs), pintails (7.0 ± 0.2 eggs, $\beta = -2.65 \pm 0.12$) and mallards (8.8 ± 0.2 eggs, $\beta = -0.82 \pm 0.14$) had smaller clutches, after adjusting for initiation date. Clutch sizes for all species were lower in 2004 than 2005 ($\beta = 0.26 \pm 0.13$) or 2006 ($\beta = 0.76 \pm 0.15$); no difference was detected between 2005 and 2006. Clutch sizes for all ducks were larger in grassland versus agriculture ($\beta = -0.30 \pm 0.13$), but not larger than in the ecotone landscape ($\beta = -0.01 \pm 0.14$). Data were reanalyzed to better determine species-specific relationships.

For pintails, nest initiation date described most variation in clutch size (Table 4.8), and clutch size declined with date ($\beta = -0.030 \pm 0.005$). The best-supported model that contained the effects of nest initiation date, year and landscape was also investigated. Clutch size declined with nest initiation date ($\beta = -0.030 \pm 0.005$), and clutch size was larger in 2006 (7.3 ± 0.2 eggs) than in 2004 (6.8 ± 0.4 eggs; $\beta = -0.51 \pm 0.24$), but not 2005 (7.2 ± 0.3 eggs; $\beta = -0.18 \pm 0.19$). Clutch sizes did not differ among the grassland (7.1 ± 0.3 eggs), ecotone (7.3 ± 0.3 eggs; $\beta = 0.18 \pm 0.19$), or agricultural (6.9 ± 0.3 eggs; $\beta = -0.24 \pm 0.21$) landscapes.

Table 4.6. Number of nests with complete (i.e., incubated) clutches for mallard, northern shoveler and northern pintail, Milk River Ridge, Alberta, 2004-2006. Number in parentheses represents total number of nests found for each species and year.

	Grassland			Ecotone			Agriculture		
	Mall	Nsho	Nopi	Mall	Nsho	Nopi	Mall	Nsho	Nopi
2004	3 (4)	14 (21)	10 (14)	7 (9)	16 (21)	21 (24)	14 (21)	8 (13)	7 (7)
2005	7 (10)	18 (23)	25 (31)	4 (10)	30 (40)	26 (32)	15 (20)	51 (57)	18 (23)
2006	17 (25)	40 (44)	44 (47)	7 (8)	20 (29)	29 (35)	48 (61)	77 (100)	26 (35)

Table 4.7. Models used to assess the effect of nest initiation date (NESTIN), species (SPECIES), year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)), nest initiation by species, nest initiation by year, nest initiation by landscape, year by species, landscape by species, landscape by year, nest initiation by landscape by species, and landscape by year by species interactions on clutch size of ducks on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAIC _c	ΔQAIC _c	w _i
NESTIN, SPECIES, YEAR, LAND	11	1946.13	328.08	0.00	0.940
NESTIN, SPECIES, YEAR, LAND, NESTIN*SPECIES	14	1942.50	333.60	5.52	0.059
NESTIN, SPECIES, YEAR, LAND, REP(LAND), NESTIN*SPECIES	22	1938.29	349.06	20.98	0.000
NESTIN, SPECIES, YEAR, LAND, REP(LAND), NESTIN*SPECIES, SPECIES*LAND	31	1935.96	366.76	38.69	0.000
NESTIN, SPECIES, YEAR, LAND, REP(LAND), NESTIN*SPECIES, SPECIES*LAND, NESTIN*LAND	34	1932.59	372.32	44.24	0.000
NESTIN, SPECIES, YEAR, LAND, REP(LAND), NESTIN*SPECIES, SPECIES*LAND, NESTIN*LAND, NESTIN*YEAR	37	1931.46	378.18	50.10	0.000

Variance inflation factor derived from global model $\hat{c}=1.5954$, k =number of parameters, $-2\log L=-2 \log$ likelihood value, $QAIC_c$ =corrected quasi-Akaike's information criterion value, $\Delta QAIC_c$ =QAIC_c difference, w_i =model weight

Table 4.8. Models used to assess the effect of nest initiation date (NESTIN), year (YEAR), landscape (LAND), replicate nested within landscape (REP(LAND)), nest initiation by year, and nest initiation by landscape interactions on clutch size of pintails on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAIC _c	ΔQAIC _c	w _i
NESTIN	2	649.51	106.55	0.00	0.996
NESTIN, YEAR, LAND	8	642.47	117.62	11.07	0.004
NESTIN, YEAR, LAND, NESTIN*LAND	11	641.99	123.57	17.02	0.000
NESTIN, YEAR, LAND, REP(LAND), NESTIN*LAND	19	636.25	138.82	32.28	0.000
NESTIN, YEAR, LAND, REP(LAND), NESTIN*LAND, NESTIN*YEAR	22	635.97	144.80	38.26	0.000

Variance inflation factor derived from global model $\hat{c}=1.4503$, k=number of parameters, -2logL=-2 log likelihood value, QAIC_c=corrected quasi-Akaike's information criterion value, ΔQAIC_c=QAIC_c difference, w_i=model weight

In shovelers, nest initiation date accounted for the largest amount of variation in clutch size ($w_i = 0.991$). Clutch size in shovelers declined with date ($\beta = -0.040 \pm 0.004$). The second best model ($w_i = 0.009$) describing clutch size in shovelers included covariates for nest initiation date, year, and landscape ($w_i = 0.009$) (Table 4.9). Clutch size declined with nest initiation date ($\beta = -0.03 \pm 0.01$). Clutch sizes for shovelers in 2006 (10.0 ± 0.2 eggs) were similar to 2005 (9.6 ± 0.3 eggs; $\beta = -0.36 \pm 0.19$), but higher than in 2004 (9.0 ± 0.4 eggs; $\beta = -0.95 \pm 0.24$). Clutch sizes did not differ between grassland (9.7 ± 0.3 eggs), ecotone (9.5 ± 0.3 eggs; $\beta = -0.21 \pm 0.21$), or agriculture (9.3 ± 0.2 eggs; $\beta = -0.43 \pm 0.18$).

Year effects were controlled by standardizing clutch initiation date and clutch size was reexamined to determine the effect of landscape, relative clutch initiation date, replicate nested within landscape, and the interaction between relative clutch initiation date and landscape. The best model contained the effects of relative clutch initiation date ($w_i = 0.936$; $\beta = -0.04 \pm 0.01$). The second best model contained the effects of relative clutch initiation date and landscape ($w_i = 0.064$). Clutch size declined with relative clutch initiation date ($\beta = -0.04 \pm 0.01$). Clutch sizes did not differ between grassland (9.9 ± 0.3 eggs), ecotone (9.5 ± 0.3 eggs; $\beta = -0.38 \pm 0.22$), or agriculture (9.6 ± 0.2 eggs; $\beta = -0.33 \pm 0.19$).

In mallards, nest initiation date described the largest amount of variation in clutch size ($w_i = 0.996$) and, again, clutch size declined with date ($\beta = -0.04 \pm 0.01$). The second-best model included covariates for nest initiation date, year, and landscape ($w_i = 0.005$) (Table 4.10). Clutch size declined with nest initiation date ($\beta = -0.04 \pm 0.01$). Clutch sizes for mallards did not differ between 2006 (9.2 ± 0.4 eggs) and 2005 (9.1 ± 0.6 eggs; $\beta = -0.03 \pm 0.34$) or 2004 (8.3 ± 0.4 eggs; $\beta = -0.83 \pm 0.36$). Clutch sizes did not differ between grassland (9.0 ± 0.6 eggs), ecotone (8.9 ± 0.7 eggs; $\beta = -0.08 \pm 0.45$), or agriculture (8.7 ± 0.4 eggs; $\beta = -0.32 \pm 0.33$).

Table 4.9. Models used to assess the effect of nest initiation date, year, landscape, replicate nested within landscape, nest initiation by year, and nest initiation by landscape interactions on clutch size of shovelers on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAIC _c	ΔQAIC _c	w _i
NESTIN	2	876.77	142.12	0.00	0.991
NESTIN, YEAR, LAND	8	858.11	151.62	9.50	0.009
NESTIN, YEAR, LAND, NESTIN*LAND	11	853.32	156.98	14.86	0.001
NESTIN, YEAR, LAND, REP(LAND), NESTIN*LAND	19	852.95	172.96	30.84	0.000
NESTIN, YEAR, LAND, REP(LAND), NESTIN*LAND, NESTIN*YEAR	22	840.08	177.19	35.07	0.000

Variance inflation factor derived from global model $\hat{c}=1.3919$, k=number of parameters, -2logL=-2 log likelihood value, QAIC_c = corrected quasi-Akaike's information criterion value, ΔQAIC_c=QAIC_c difference, w_i=model weight

Table 4.10. Models used to assess the effect of nest initiation date, year, landscape, replicate nested within landscape, nest initiation by year, and nest initiation by landscape interactions on clutch size of mallards on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAIC _c	ΔQAIC _c	w _i
NESTIN	2	771.10	114.51	0.00	0.997
NESTIN, YEAR, LAND	8	768.02	126.26	11.75	0.003
NESTIN, YEAR, LAND, NESTIN*LAND	11	767.77	132.26	17.75	0.000
NESTIN, YEAR, LAND, REP(LAND), NESTIN*LAND	19	760.05	147.59	33.09	0.000
NESTIN, YEAR, LAND, REP(LAND), NESTIN*LAND, NESTIN*YEAR	22	759.82	153.59	39.09	0.000

Variance inflation factor derived from global model $\hat{c} = 2.0478$, k = number of parameters, -2logL = -2 log likelihood value, QAIC_c = corrected quasi-Akaike's information criterion value, ΔQAIC_c = QAIC_c difference, w_i = model weight

4.6 Discussion

4.6.1 Timing of breeding

For all species combined, variation in mean nest initiation date was best described by annual and landscape effects. Yearly variation had significant effects on nest initiation date in all species, likely due to annual changes in habitat (wetland density) and weather conditions. The earliest mean nest initiation occurred in 2006, which also corresponded with higher breeding densities of ducks and excellent wetland conditions early in the nesting season (Huggins 2006). A later mean nest initiation date was observed in 2005 when habitat conditions early in the season were below optimal with lower wetland densities that improved as the season progressed. The latest mean nest initiation date occurred in 2004 which had the lowest wetland densities of the 3 years and was affected by a late spring snow event that destroyed all nest initiated to that point. Landscape had no effect on mean nest initiation when all three species were combined.

For pintails, the difference in mean nest initiation date observed across the 3 years was probably due to variation in habitat conditions. Seasonal variation in nest initiation date on this study spanned 12 days, and is comparable to the seasonal variation of 7 days reported by Duncan (1987) studying pintails in Alberta from 1982-1984. The span of nest initiation depends upon the local temperature and water conditions and an individual pintail's physiology and renesting propensity (Bellrose 1980). Early season nesters such as pintails and mallards, may be restricted from earlier nesting by temperature and weather events (Smith 1968).

Seasonal variation in clutch size may also be linked to body condition, but I did not find that body mass of pintails changed seasonally (Chapter 3). In captive pintails, genetic variation has been hypothesized as a possible explanation for variation in nest initiation date (Duncan 1987) and has been observed in other birds (van Noordwijk et al. 1980). This was not considered as an explanatory variable in this study.

The link between presumed habitat quality and mean nest initiation date was not evident in this study. This may be due to the species selected to test the hypothesis. Early season nesters such as pintail and mallard may not require exogenous energy to initiate clutches due to the higher initial amounts of endogenous energy available to them (MacCluskie and Sedinger. 1999), and thereby precluding the need to select higher quality

habitat to initiate egg production. Pietz et al. (2000) observed that reproductive output of mallards (early season nesters) was not affected by habitat conditions, while gadwall (late season nesters) clutch size was correlated with habitat conditions. Using early season nesting birds may have prevented the detection of a quality difference between landscapes. If early season nesting by pintails and mallards is not affected by initial habitat quality, it may explain why selection of habitats of lower quality occurs or why there is not difference in nest initiation date between habitats of differing qualities.

I was unable to account for female age effects because relatively few female pintails were classified to age (Chapter 3), female age was not determined in shovelers and no female mallards were captured. No yearling pintails were captured at nests in 2004, yet nesting averaged ~8 days earlier on grassland than agricultural sites. In other years, yearling females nested about 4 days later than did adults. However, mean clutch initiation dates were not later in agricultural areas despite more yearling females nesting in agricultural landscapes (Chapter 3).

Advantages of early nesting include increased opportunity to renest in the event of nest loss (Arnold et al. 2010), and increased recruitment (Dawson and Clark 2000). Although not significant, there was a tendency for grassland females to nest earlier, and this may afford some advantage over other habitats. The effect of landscape on nest initiation date was not supported in this study and suggests finer level variables outside the scope of this study may be affecting nest initiation.

4.6.2 Clutch Size

For all species, clutch size declined with nest initiation date, a finding that is consistent with many other studies (Duncan 1987, Krapu et al. 2004). Species-specific differences in clutch size were also observed. The interspecific variation in clutch size can be attributed to differences in body size, diet, and timing of lipid acquisition and nesting which can affect the amount of lipid available for egg production (Krapu et al. 2004). Annual variation in clutch size was observed for all ducks with higher clutch sizes in 2005 and 2006 when compared to 2004. The increase in clutch size may be a response to the improved habitat conditions across all landscapes in 2005 and 2006 when compared to 2004 (Huggins 2006). Higher nest survival in these years also may have impacted clutch size estimates.

Nest survival in 2004 was the lowest of the three years (Chapter 5), so a higher frequency of smaller replacement clutches would result in lower mean clutch sizes. Differences between landscapes were not evident in this study for all species of ducks combined.

As expected, variation in clutch size for pintails was best explained by the effect of nest initiation date. Clutch sizes I recorded were consistent with other estimates for pintails in Alberta (Duncan [1987], 6.9 ± 0.1 eggs; Guyn and Clark [2000], 7.2 ± 0.1 eggs). Variation in clutch size between years and landscapes was not evident. Contrary to Duncan's speculation, landscape effects did not explain clutch size in pintails. The similarity of clutch size between landscapes for pintail may be tied to their energetic requirements. Early nesting species such as pintails may depend on endogenous reserves more so than exogenous reserves to initiate first clutches and this may emancipate females to select habitat independent of quality. No age effect on clutch size was observed. This is consistent with work conducted in Alaska (Esler and Grand 1994) which found the nutrient reserves used in clutch formation did not differ as a result of hen age.

Clutch size in shovelers and mallards followed the same trend as pintails, with variation in clutch size being explained by initiation date. Shovelers exhibited an annual effect with smaller clutches in 2004 when compared with 2005 and 2006. As above, smaller clutches in 2004 could be indicative of the low nest survival (Chapter 5) and the inclusion of more small clutch sizes as a result of renesting. Mallards did not exhibit this seasonal trend. Overall clutch size did not vary between landscapes for these species and is consistent with clutch size estimates reported in previous work (Bellrose 1980). This work contradicts Ball et al. (2002) who found that clutch size of mallards in artificial nesting structures was larger in landscapes dominated by grassland as compared to cropland.

When considered in the Fretwell-Lucas models of selection, it appears that the timing of breeding and reproductive investment patterns are similar across a presumed habitat quality gradient. Fretwell-Lucas models of habitat selection consider selection of habitats on the basis of multiple habitat characteristics and measurements of animals' quality in terms of fitness (Petit and Petit 1995). In the previous chapters, settling patterns of breeding pairs and reproductive potential (body mass and age of pintails and shovelers) were described. To better understand which of the Fretwell- Lucas models of habitat selection pintails and shovelers are employing, fitness parameters like reproductive success and survival must also

be investigated and linked to settlement patterns of these two species. Specifically, if pintails (and shovelers) recognize and settle earlier in the breeding season and at higher densities in high-quality habitat, I predict that measurements of reproductive success will be highest in grassland habitat. Thus, in Chapter 5, I evaluate how duck nesting success varies with landscape composition.

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CHAPTER 5 – NESTING SUCCESS OF PRAIRIE-BREEDING DABBING DUCKS IN RELATION TO LANDSCAPE COMPOSITION

5.1 Abstract

Nesting success of northern pintails (*Anas acuta*) and four other dabbling duck species was investigated in southern Alberta, on areas ranging in composition from intensive agriculture to large expanses of grassland with low-intensity grazing. I tested whether pintail nesting success was higher in grassland landscapes, as suggested in some recent studies, and looked for similar patterns in other dabbling ducks. In general, nest survival rates of all species tended to be higher in grassland landscapes and lowest in agricultural landscapes. Pintail nest survival was consistently higher in grassland than in agricultural landscapes and higher in 2006, a year with abundant wetlands, than in 2004, when wetland abundance was lower. Northern shoveler (*Anas clypeata*) nest survival did not vary by landscape type but was higher in 2006 than 2004. Blue-winged (*Anas discors*) teal nest survival did not differ among landscapes, but was higher in 2006 than 2005. Mallard (*Anas platyrhynchos*) and gadwall (*Anas strepera*) nest survival estimates did not vary with landscape or year. These findings suggest that grassland restoration or enhancement could improve nesting success of pintails and possibly other dabbling duck species.

5.2 Introduction

Nest predation is the most important process affecting breeding success of most bird species (Ricklefs 1969, Martin 1995). In the past decade, significant advances have occurred in our understanding of predation and how landscape composition mediates predator-prey interactions in boreal, Prairie and Parkland ecosystems (Wiens 1994, Donovan et al. 1997, Keyser et al. 1998, Stephens et al. 2003). Two separate but inter-related habitat changes, habitat loss and fragmentation, are principal causes of low avian breeding success and population declines in several ecosystems (Saunders et al. 1991, Greenwood et al. 1995, Beauchamp et al. 1996, Donovan et al. 1997). Nest losses are generally higher in smaller areas of natural habitat, possibly because these remnant areas are more easily searched by predators and brood parasites (Johnson and Temple 1990), or nests are more easily detected near edges because edge:area ratios are greater in smaller patches (Gates and Gysel 1978, Temple 1986, Lariviere and Messier 2000). Nest predation in a habitat patch is also affected

strongly by the composition of surrounding lands or matrix (Johnson and Temple 1990, Winter et al. 2000). Thus, the success of habitat restoration and protection programs for increasing avian breeding success probably depends critically on habitat size, shape and placement as well as characteristics of the adjacent matrix (Clark and Nudds 1991, Stephens et al. 2003, Horn et al. 2005).

On the North American prairies, duck nest success is also strongly affected by these predator-landscape interactions. Nest success tends to be very low in small fields of remnant and planted cover (Cowardin et al. 1983, Greenwood et al. 1995, Sovada et al. 2000), but on average much higher in grass-dominated areas (Reynolds et al. 2001). Currently, the prairie region of North America is composed of large areas where breeding success and survival appear to be insufficient to maintain locally stable populations (i.e., a “sink”; Pulliam 1988) and smaller “source” areas where sufficient numbers of birds are produced to offset local annual losses and possibly to emigrate to sinks (Miller 2000). Immigration to sinks could produce unreliable assessments of population status and perhaps even a false perception of growing population trends over time, suggesting “demographic rescue” in sinks by individuals from source areas (Coulton and Clark 2008).

The principal cue (e.g., spring wetland abundance) that ducks used over evolutionary time scales to select breeding areas may no longer be reliable because present-day upland habitat (i.e., natural or agricultural) cannot provide safe nesting cover, regardless of wetland abundance (Greenwood et al. 1995, Bethke and Nudds 1995, Schlaepfer et al. 2002). These demographic-landscape processes, and management actions designed to ameliorate them, form the central conceptual framework for this study.

Nesting success rates for pintails in the Prairie Pothole Region are frequently below the 10-20% level thought necessary to sustain stable population of most duck species (Klett et al. 1988). Klett et al. (1988) reported nest success rates ranging from 7 to 10% for northern pintails (hereafter pintail) in planted cover in the Dakotas and Minnesota, with the majority of nest losses from predation. Greenwood et al. (1995) recorded 7% nesting success for pintails nesting in Prairie and Parkland regions of Canada. Nesting success in upland habitat in grassland Alberta ranged from 6 to 18 % over a 4 year period (Guyn and Clark 2000).

Studies conducted on large contiguous grassland habitat revealed an exception to the rule of low nest success. In Montana, nest success for pintails based on brood/pair ratio observations ranged from 45-60% on large contiguous grassland habitat (Ball et al. 1995), suggesting that high recruitment is possible. Settlement by breeding pairs at a larger spatial scale has revealed that pintail settlement was due to agricultural practices rather than a change in area converted to grain production (Podrutzny et al. 2002). This settlement was also linked positively to the amount of summer fallow on the landscape and was stronger when these areas had higher wetland density (Podrutzny et al. 2002). Pintails also display a habitat affinity for areas that are dominated by ephemeral and seasonal wetlands (Drever 2006). Devries et al. (2008) observed nest survival for all duck species nesting in winter wheat, fall rye and spring-seeded crops in Saskatchewan was 18%, 38%, and 12%, respectively. Pintails accounted for 23% of the nests in fall-seeded crops and 45% of the nests in spring-seeded crops, implying that pintails selecting spring-seeded crops have lower nest survival than those selecting fall-seeded crops (Devries et al. 2008).

Additionally, nesting success may be influenced by the timing of nesting, visual concealment and plant species at the nest site. Earlier nest initiation may be possible in higher quality habitat, and affect which habitat is selected. If this is the case, we would predict the selection of grassland landscapes over others available. Visual concealment of pintail nests is lower than other prairie nesting ducks such as mallards (Richkus 2002), and suggests that preference for nest sites is not based on concealment alone. Species composition (i.e., grasses, forbs, shrubs) may play a larger role in affecting nest choices and survival rates. Vegetation that creates physical impediments to predator movement or reduces nest detection ability (e.g., blocks odours) have produced higher nest survival (Sugden and Beyersbergen 1986, Guyn and Clark 1997, Johnson et al. 2005); natural grasslands with the mix of grass and shrubs, may provide more physical impediments to predators.

Collectively, pintail nesting success should be highest on large areas of contiguous grassland, these being relatively pristine habitats where pintails settled historically for reproduction (Keith 1961, Stoudt 1971). This general observation also forms the basis for conservation decisions to retain and restore grassland habitat and to convert spring-seeded cropland to perennial cover or fall-seeded cereal crops. However, few studies have evaluated

pintail nesting success in the same years with habitat conditions representing a locally strong land use gradient from large grassland areas to those of intensive grain farming.

My main objective was to address this deficiency by investigating how reproductive success of ducks on the Milk River Ridge, Alberta, was related to nest site and landscape characteristics. Duck nesting success was investigated to determine if nesting success would be highest on areas of large, contiguous grasslands and lowest in remnant or restored natural habitats embedded in areas of intensive spring-seeded crop production, as is currently assumed by current habitat conservation programs. According to Fretwell-Lucas's (1970) "ideal-free" model, habitat-specific densities are adjusted such that individuals have equal reproductive success in all habitats. By contrast, under the "ideal-despotic" model, preferred habitats are occupied by dominant individuals that obtain higher reproductive success. Earlier, I reported that more older female pintails nested in grassland habitat (Chapter 3) where consistently higher densities of breeding pairs were also observed (Chapter 2). Here, I complete a stronger assessment of the ideal-despotic model, by testing whether pintail nesting success was higher in grassland than in non-grassland landscapes.

5.3 Study Area

Work was conducted at sites located in three landscapes south of Lethbridge, Alberta, near the Milk River Ridge (centered at 49°17'40"N 112°36'59"W). Each of these landscapes (hereafter referred to as grassland, ecotone and agriculture) was represented by two (east and west) 41.4 km² study sites chosen to characterize the dominant landscapes in this region. The Milk River Ridge is an elevated plateau (mean altitude, 1200 m above sea level) due to differential erosion, and is 250 m higher elevation than the surrounding plain. The area also is on a historic flyway and with high numbers of pintails moving through the area during the breeding season (Miller et al. 2005). A more detailed description of study sites are given in Chapter 2.

5.4 Methods

Nests were located by flushing females using standard nest searching techniques (Klett et al. 1986). Searches began in late April and concluded on early July of each year, and occurred from 8:00 to 14:00 CST during favorable weather conditions (Gloutney et al.

1993). Nests were defined as bowls or scrapes consisting of ≥ 1 egg. Flushed birds were identified visually, and species designation was confirmed using characteristics of eggs, down, and breast feathers found in the bowl. Nests were marked with a bamboo garden stake (1-1.3m tall, 0.5 to 1cm diameter) 4 meters in a random cardinal direction from the bowl. Date found, species, number of eggs, stage of incubation (Weller 1956), and nest-site-specific visual obstruction reading (Robel et al. 1970) were recorded for each nest. Universal Transverse Mercator (UTM) coordinates were determined for each nest site and used to aid in relocation. Nest initiation date was calculated for each nest by backdating the sum of incubation stage and number of eggs (assuming an egg-laying rate of 1 egg per day) from the date found. Dominant nest site vegetation within 10 m of the nest was assigned as being crop stubble, upland grass, upland forbs, low shrub, tall shrub or trees. Nests were revisited every 8-10 days until fate was determined.

Fate was recorded as successful if ≥ 1 egg hatched. Shell membranes and small egg fragments present in the bowl were used as evidence of hatch. Nests abandoned due to investigator disturbance were excluded from nest success analyses. Nests found incidentally were included in the sample. Unsuccessful nest remains were investigated to determine cause of nest loss. Depredated nests were examined for evidence to confirm predator species (Sargeant et al. 1998). Information collected included number of eggs remaining, location of egg shells in relation to the bowl, number and size of holes in shells, number of crushed egg, dug or scratched areas within 2 m of the nest, and any sign of predator presence (feces, tracks, hairs or feathers). Information was used to classify predators to mammalian and avian classes.

Nest exposure was calculated using Mayfield's 50% method (Mayfield 1965, Johnson 1979). Nest exposure was determined as the total days the nest was exposed to losses, from date found to date terminated. When a nest failed between visits, the mid-point of the interval was used as the termination date.

5.4.1 Statistical Analysis

Factors that could influence daily survival rates of nests were considered. Habitat factors included year of study, duck species, landscape, study site replicate nested within landscape, nest initiation date, nest concealment score (i.e., Robel et al. 1970), nest site

vegetation class, and selected interactions of these variables. Data were organized so each nest represented a binomial trial, where the outcome is success or failure, and the corresponding covariate attributes. The success/trials syntax was used to model daily survival, where the event is success and trials is the number of exposure days (Hazler 2004). Logistic regression (SAS Instit. 2009, PROC Logistic) was used with binomial distribution, a logit link function and a default scale parameter to model the effects of various covariate effects on nest survival. Goodness of fit was determined for all models by calculating variance inflation factors. The variance inflation factor (\hat{c}) obtained from the global model was used in all subsequent models to adjust for overdispersion and calculate QAIC_c values. Using backwards elimination, the least predictive covariate based on likelihood ratio and chi-squared was removed from the model and the resulting model was reexamined. This process continued until no further elimination of covariates was possible. Models were ranked using QAIC_c (Burnham and Anderson 2002). Model weights (w_i), parameter estimates (β) and standard error (SE) values are presented.

The global model for all species combined incorporated effects of landscape (LAND), year (YEAR), species (SPEC), replicate nested within landscape REP(LAND), nest initiation date (NESTIN), nest concealment index (i.e., mean Robel pole score, or RM), nest site vegetation (NESTSV), landscape by year, year by nest initiation date, year by nest concealment index, nest initiation date by nest concealment index, landscape by species, and year by species interactions.

The global model for each species incorporated effects of landscape (LAND), year (YEAR), replicate nested within landscape REP(LAND), nest initiation date (NESTIN), nest concealment index (i.e., mean Robel pole score; RM), nest site vegetation (NESTSV), and four interaction effects (landscape by year, year by nest initiation date, year by nest concealment index, nest initiation date by nest concealment index).

Daily survival rates were calculated from parameters estimated by the best approximating model and used to determine nest survival estimates (Hazler 2004). Daily survival rates were converted to nesting success rates by assuming a 32-35 day exposure period, depending on species (Klett et al. 1986).

5.5 Results

Overall, 1400 duck nests were found. Nest numbers increased each year from 2004 to 2006, with the five most abundant species in order of occurrence being northern shoveler (hereafter, shoveler), blue-wing teal, gadwall, pintail, and mallard (Table 5.1). Most nests of all species were destroyed by predators, except in 2006 when a majority of nests hatched. Predators included birds (American crow (*Corvus brachyrhynchos*), magpie (*Pica pica*) and gulls (*Larus spp.*) and mammals (badger (*Taxidea taxus*), skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*) and coyote (*Canis latrans*) based on evidence observed at destroyed nests (Sargeant et al. 1998). Weather-related losses were mainly attributed to snowfall events early in the spring, and flooding later in the season, particularly in 2005. Human-caused losses increased in 2005 and 2006 when compared to 2004, but were proportional to number of nests found. Human-caused nest loss was due to investigator damage during nest searching, as well as abandonment, particularly in newly initiated nests. Other losses were attributed mainly to cattle trampling.

5.5.1 All Ducks

Initial analysis of nest survival was conducted on all duck species combined. The best approximating model ($w_i = 0.969$) that described variation in nest survival incorporated effects of covariates for year, replicate nested within landscape, species, year, nest initiation date and mean Robel score (Table 5.2). Due to the species effect in the best model, data were analyzed by species.

Table 5.1. Annual numbers and fates of duck nests on the Milk River Ridge, Alberta, 2004-2006.

Species ^b	Successful Nests			Depredated Nests			Weather-related			Human-caused			Other Loss ^a			Total Nests		
	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006	2004	2005	2006
NOPI	12	35	60	25	36	41	3	2	0	3	9	12	1	2	2	44	84	115
NSHO	8	46	75	34	45	77	0	3	0	9	20	19	3	4	1	54	118	172
MALL	10	13	43	16	21	40	0	1	0	6	3	12	1	0	0	33	38	95
LESC	0	3	9	3	6	7	0	0	2	0	3	1	0	1	0	3	13	19
AGWT	1	1	4	6	1	1	0	1	0	0	1	0	0	0	0	7	4	5
GADW	22	44	53	29	52	32	0	1	0	2	8	6	1	3	1	54	108	92
BWTE	23	34	41	42	59	36	0	4	0	2	6	5	0	2	1	67	105	83
AMWI	8	7	23	4	8	28	0	1	0	1	1	4	0	1	1	13	18	56
Totals	84	183	308	159	228	262	3	13	2	23	51	59	6	13	6	275	488	637

^aOther losses attributed to cattle trampling.

^b NOPI=Pintail, NSHO=Shoveler, MALL=Mallard, LESC=Lesser Scaup, AGWT=Green Winged Teal, GADW=Gadwall. BWTE=Blue-Winged Teal, AMWI=American Wigeon

Table 5.2 Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), species (SPEC), year (YEAR), nest initiation date (NESTIN), Robel score (RM), nest site vegetation (NESTSV), and selected interaction effects on all duck nest survival rates on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAICc	Δ_i	w_i
LAND, REP(LAND), SPEC, YEAR, NESTIN, RM	14	2199.29	378.79	0.00	0.970
LAND, REP(LAND), SPEC, YEAR, NESTIN, RM, YEAR*LAND	18	2197.35	386.47	7.68	0.021
LAND, REP(LAND), SPEC, YEAR, NESTIN, RM, NESTSV, YEAR*LAND	19	2197.34	388.46	9.68	0.008
LAND, REP(LAND), SPEC, YEAR, NESTIN, RM, NESTSV, YEAR*LAND, NESTIN*YEAR	21	2194.26	391.95	13.16	0.001
LAND, REP(LAND), SPEC, YEAR, NESTIN, RM, NESTSV, YEAR*LAND, NESTIN*YEAR, NESTIN*RM	22	2193.57	393.83	15.04	0.001

Variance inflation factor derived from global model $\hat{c}=1.3494$, k=number of parameters, -2logL=-2 log likelihood value, QAICc=corrected quasi Akaike's information criterion, Δ_i =QAIC_c difference, w_i =model weight

5.5.2 Northern Pintails

The best-approximating model that described variation in nest survival in pintails included the covariate for year (Table 5.3). The intercept term for this model was $\beta = -3.03 \pm 0.18$, and nest success estimates (95% confidence interval) were 6.9% (1.1-12.8%) in 2004, 16.3% (5.4-27.3%) in 2005, and 22.2% (12.0-32.3%) in 2006. Nest survival rates did not differ between 2005 and 2006 ($\beta = -0.19 \pm 0.25$), but were higher in 2006 than in 2004 ($\beta = -0.59 \pm 0.28$). However, the second best model which contained the covariate for landscape received similar support (Intercept $\beta = -3.12 \pm 0.20$). Nest success estimates (95% confidence intervals) were 25.1% (13.2-37.0%) for grassland, 14.4% (4.1-24.6%) for ecotone, and 9.1% (1.6- 16.5%) for agriculture. Overall, pintail nest survival was 2-4 times higher in grassland compared to agriculture ($\beta = -0.57 \pm 0.28$), depending on the year (Table 5.4), but comparable to survival in the ecotone ($\beta = -0.35 \pm 0.26$). The model containing the covariates landscape and year received limited support. Due to interest in illustrating patterns of nest survival in relation to landscape composition over the breeding season, daily nest survival was related to nest initiation date in each landscape, and portrayed with respect to the seasonal pattern of nest initiations. Daily nest survival decreased with nest initiation date in all landscapes based on the model containing landscape and nest initiation (Figure 5.1).

Table 5.3 Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), nest initiation date (NESTIN), Robel score (RM), nest site vegetation (NESTSV), and selected interaction effects on pintail nest survival rates on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAICc	Δ_i	w_i
YEAR	3	697.78	117.16	0.00	0.463
LAND	3	698.12	117.21	0.05	0.451
LAND, YEAR	5	693.59	120.55	3.39	0.084
LAND, REP(LAND), YEAR	11	682.90	130.98	13.82	0.001
LAND, REP(LAND), YEAR, NESTIN	12	680.89	132.68	15.52	0.000
LAND, REP(LAND), YEAR, NESTIN, YEAR*NESTIN	14	674.46	135.71	18.55	0.000
LAND, REP(LAND), YEAR, NESTIN, RM, NESTSV, LAND*YEAR, YEAR*NESTIN, YEAR*RM, NESTIN*RM	23	799.328	171.24	54.09	0.000

Variance inflation factor derived from global model $\hat{c}=1.1969$, k =number of parameters, $-2\log L=-2 \log$ likelihood value, $QAICc$ =corrected quasi Akaike's information criterion, Δ_i = $QAIC_c$ difference, w_i =model weight

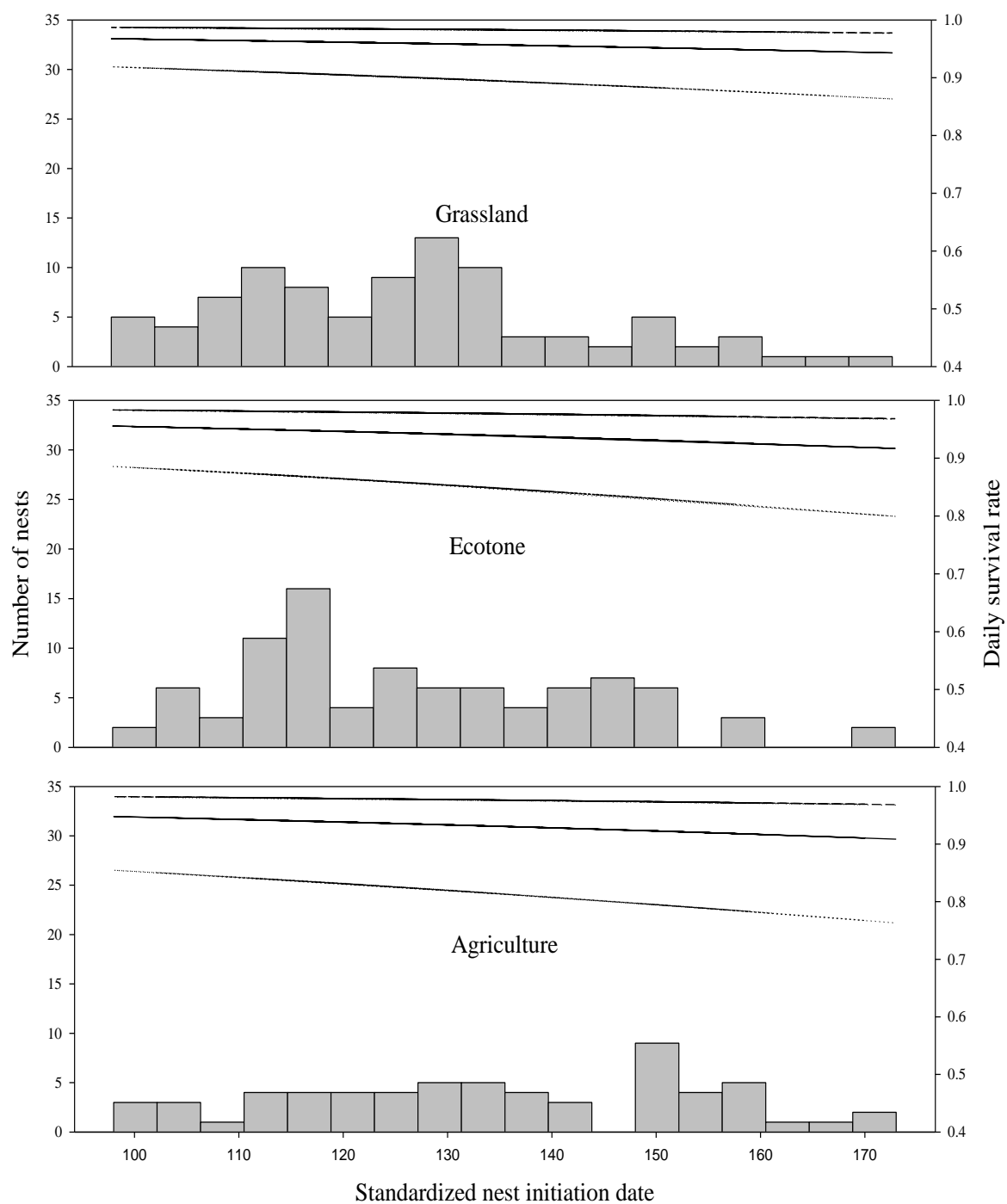


Figure 5.1 Relationships between standardized nest initiation date (number of nests initiated is shown in shaded bars) and daily nest survival (solid lines) with 95% CL (dotted lines) for pintails nesting on grassland, ecotone and agricultural landscapes on the Milk River Ridge, Alberta 2004-2006.

Table 5.4. Annual Mayfield nest success estimates (% , with 95% confidence interval) for pintails in Agriculture, Ecotone and Grassland landscapes, 2004-2006, Milk River Ridge, Alberta.

Year	Agriculture	Ecotone	Grassland
2004	2.7 (0.2-12.3)	6.2 (1.1-18.5)	12.6 (3.8-27.0)
2005	8.8 (1.5-24.6)	15.4 (4.6-32.5)	25.0 (11.1-41.8)
2006	12.8 (4.0-27.4)	20.8 (8.3-37.2)	31.1 (15.7-48.8)

5.5.3 Northern Shovelers

The best-approximating model describing nest survival variation in shovelers included the covariate for year (Table 5.5). The intercept term for this model was $\beta = -3.34 \pm 0.15$, and the nest success estimates (95% confidence interval) were 5.0% (0.7-9.4%) in 2004, 21.9% (9.0-34.8%) in 2005, and 30.6% (20.1-41.1%) in 2006. Shoveler nest survival was much higher in 2006 than 2004 ($\beta = -0.95 \pm 0.27$), but not 2005 ($\beta = -0.25 \pm 0.24$). The next best model included the covariate for landscape (Intercept $\beta = -3.27 \pm 0.21$) and received less support, but no difference in nest survival was observed in grassland compared to ecotone ($\beta = -0.41 \pm 0.28$) and agriculture ($\beta = -0.13 \pm 0.26$). Nest success estimates were (95% confidence intervals) were 28.1% (14.8-41.4%) for grassland, 15.1% (3.8-26.4%) for ecotone, and 23.8% (9.3- 38.2%) for agriculture. The model containing landscape and year covariates also received less support. Daily nest survival decreased with nest initiation date in all landscapes based on the model containing landscape and nest initiation (Figure 5.2). Nest survival estimates were structured to highlight trends by year and landscape (Table 5.6). As anticipated on the basis of results above, no difference in nest survival was observed across landscapes in any year.

Table 5.5 Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), nest initiation date (NESTIN), Robel score (RM), nest site vegetation (NESTSV), and selected interaction effects on shoveler nest survival rates on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAICc	Δ_i	w_i
YEAR	3	788.87	131.76	0.00	0.612
LAND	3	797.57	133.24	1.48	0.293
LAND, YEAR	5	787.44	135.52	3.76	0.093
LAND, REP(LAND), YEAR	11	777.36	145.81	14.05	0.001
LAND, REP(LAND), YEAR, RM	12	767.82	146.15	14.39	0.001
LAND, REP(LAND), YEAR, NESTIN, RM	13	757.51	146.34	14.57	0.000
LAND, REP(LAND), YEAR, NESTIN, RM, NESTSV, LAND*YEAR, YEAR*NESTIN, YEAR*RM, NESTIN*RM	23	1051.141	210.48	78.71	0.000

Variance inflation factor derived from global model $\hat{c}=1.3926$, k=number of parameters, -2logL=-2 log likelihood value, QAIC_c=corrected quasi-Akaike's information criterion, Δ_i =QAIC_c difference, w_i =model weight

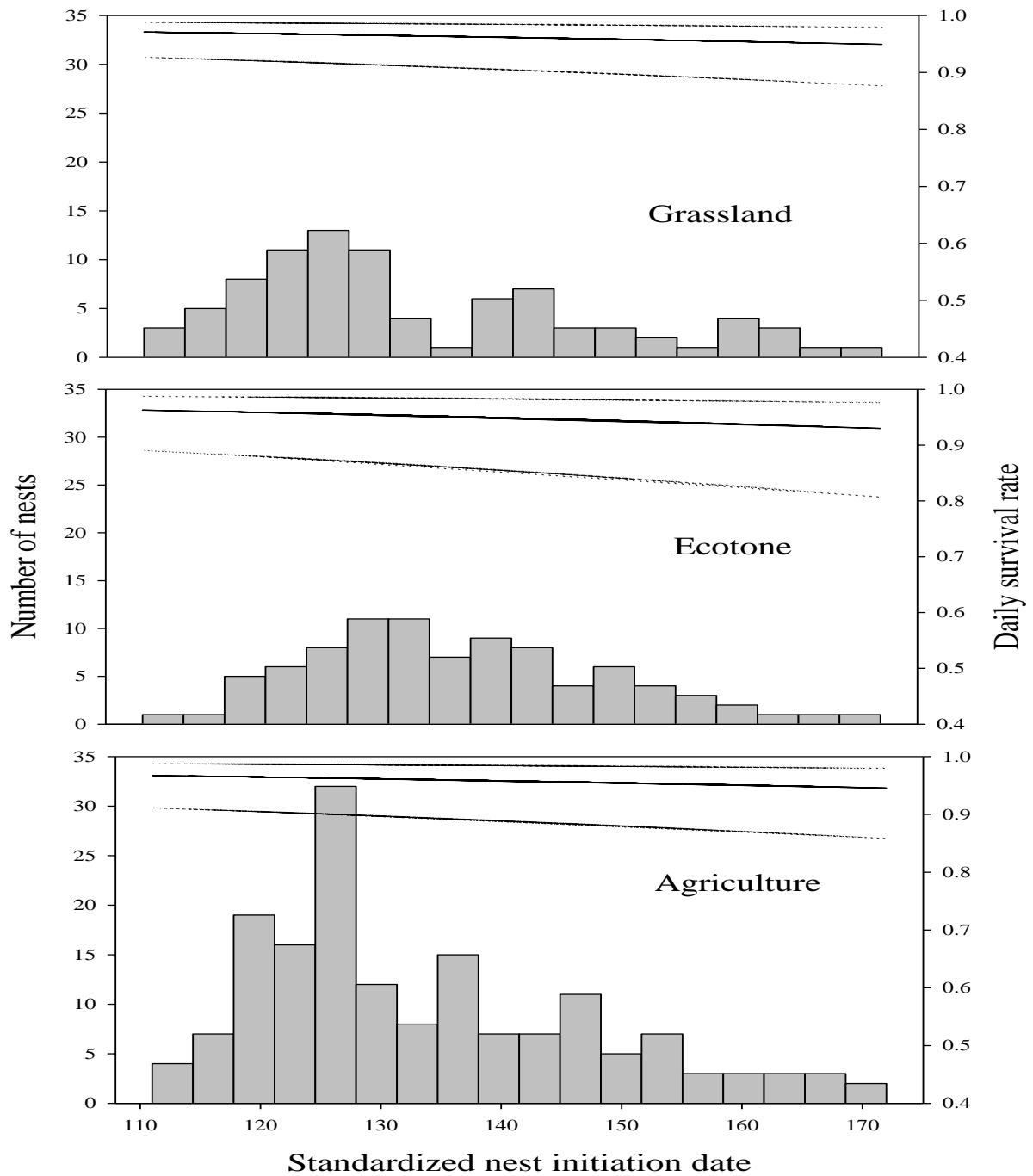


Figure 5.2 Relationships between standardized nest initiation date (number of nests initiated is shown in shaded bars) and daily nest survival (solid lines) with 95% CL (dotted lines) for shovelers nesting on grassland, ecotone and agricultural landscapes on the Milk River Ridge, Alberta 2004-2006.

Table 5.6. Annual Mayfield nest success estimates (% , with 95% confidence interval) for northern shovelers in Agriculture, Ecotone and Grassland landscapes, 2004-2006, Milk River Ridge, Alberta.

Year	Agriculture	Ecotone	Grassland
2004	4.2 (0.6-14.9)	3.4 (0.2-14.4)	8.3 (1.9-21.1)
2005	21.0 (7.4-39.5)	18.9 (5.4-38.9)	29.6 (14.2-46.9)
2006	28.5 (13.4-45.8)	26.1 (11.6-43.4)	37.6 (20.7-54.5)

5.5.4 Mallards

The best-approximating model describing variation in nest survival for mallards included year effects (Table 5.7). The intercept for this model was $\beta = -3.04 \pm 0.22$, and the nest success estimates (95% confidence interval) were 9.3% (0.7-17.9%) in 2004, 8.0% (0.6-15.5%) in 2005, and 19.4% (8.1-30.7%) in 2006. Mallard nest survival did not differ between 2004 and either 2005 or 2006. Additional support was obtained for a model containing landscape effects (Intercept $\beta = -3.08 \pm 0.32$), but no difference in nest survival was obtained in grassland compared to ecotone ($\beta = -0.60 \pm 0.47$) and agriculture ($\beta = -0.22 \pm 0.39$). Nest success estimates were (95% confidence intervals) were 20.8% (5.3-36.4%) for grassland, 6.0% (0.1-12.0%) for ecotone, and 14.4% (1.7-27.0%) for agriculture. Daily nest survival decreased with nest initiation date in all landscapes based on the model containing landscape and nest initiation effects (Figure 5.3). The model containing the covariates for year and landscape also received limited support. Nest survival estimates by year and landscape were calculated to identify any difference by year and landscape (Table 5.8). No difference in nest survival was observed across landscapes for any of the years of the study based on this model.

Table 5.7 Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), nest initiation date (NESTIN), Robel score (RM), nest site vegetation (NESTSV), and selected interaction effects on mallard nest survival rates on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAICc	Δ_i	w_i
YEAR	3	335.13	57.83	0.00	0.478
LAND	3	335.28	57.86	0.03	0.471
LAND, YEAR	5	334.02	61.62	3.79	0.072
LAND, REP(LAND), YEAR	11	329.36	72.71	14.88	0.000
LAND, REP(LAND), YEAR, NESTSV	12	328.74	74.59	16.76	0.000
LAND, REP(LAND), YEAR, RM, NESTSV	13	326.91	76.22	18.39	0.000
LAND, REP(LAND), YEAR, NESTIN, RM, NESTSV, LAND*YEAR, YEAR*NESTIN, YEAR*RM, NESTIN*RM	24	469.389	122.82	64.99	0.000

Variance inflation factor derived from global model $\hat{c}=1.4556$, k=number of parameters, -2logL=-2 log likelihood value, QAIC_c=corrected quasi Akaike's information criterion, Δ_i =QAIC_c difference, w_i =model weight

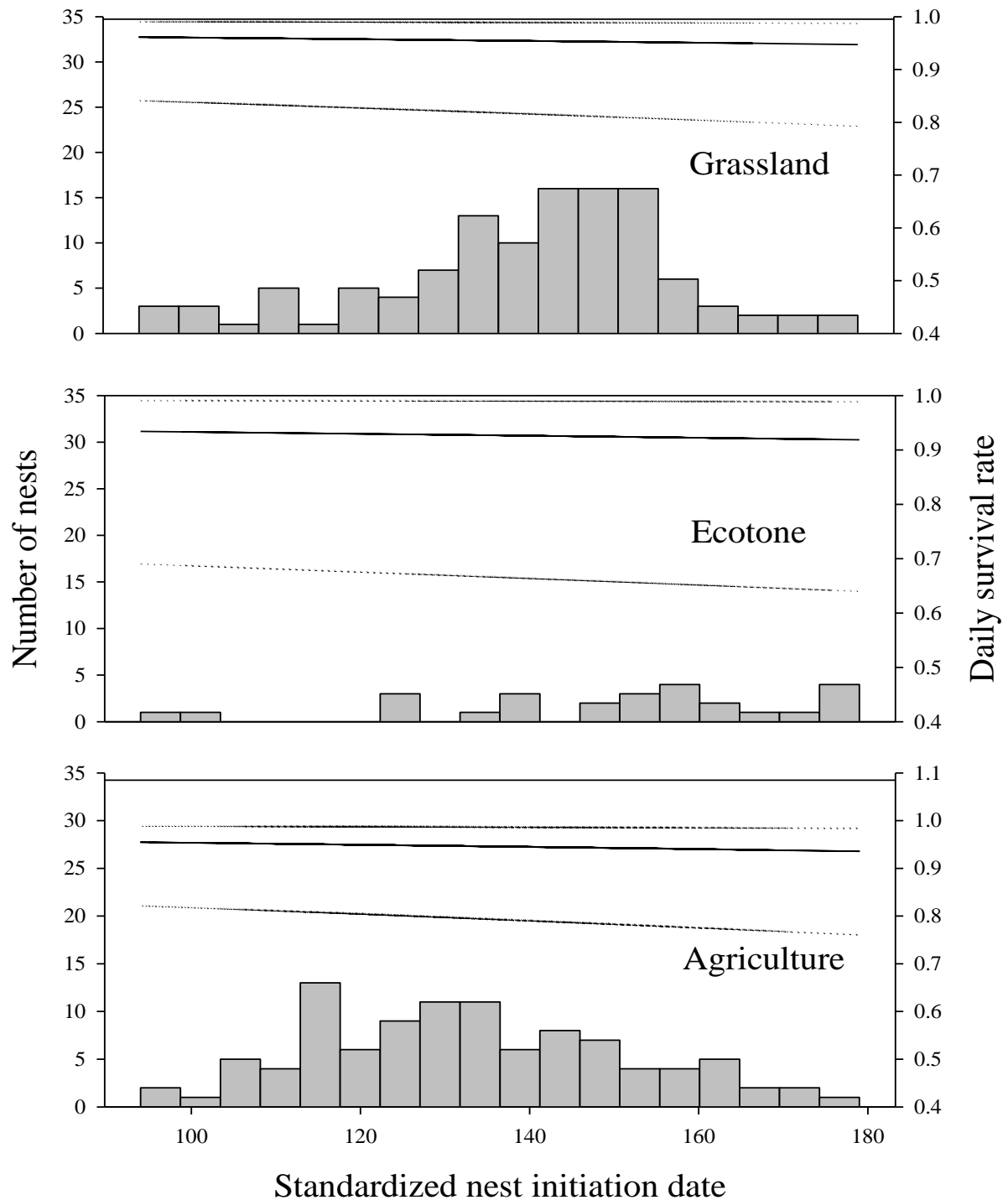


Figure 5.3 Relationships between standardized nest initiation date (number of nests initiated is shown in shaded bars) and daily nest survival (solid lines) with 95% CL (dotted lines) for mallards nesting on grassland, ecotone and agricultural landscapes on the Milk River Ridge, Alberta 2004-2006.

Table 5.8. Annual Mayfield nest success estimates (% , with 95% confidence interval) for mallards in Agriculture, Ecotone and Grassland landscapes, 2004-2006, Milk River Ridge, Alberta.

Year	Agriculture	Ecotone	Grassland
2004	11.0 (1.0-35.7)	5.3 (0.1-31.8)	16.7 (2.9-40.8)
2005	8.1 (0.5-30.7)	3.5 (0.03-27.0)	12.9 (1.8-35.9)
2006	18.4 (3.5-42.9)	10.4 (1.2-32.1)	25.4 (6.6-50.4)

5.5.5 Blue-winged teal

The best approximating model describing nest survival variation in blue-winged teal included the covariate for year (Table 5.9). The intercept for this model was $\beta = -3.51 \pm 0.22$, and nest success estimates (95% confidence interval) were 19.3% (4.7-33.8%) in 2004, 13.6% (3.1-24.1%) in 2005, and 31.8% (16.8-46.8%) in 2006. Teal nest survival tended to be higher in 2006 than in 2005 ($\beta = -0.57 \pm 0.29$), but not in 2004 ($\beta = -0.37 \pm 0.33$). Although some support existed for a model containing landscape effects (Intercept $\beta = -3.30 \pm 0.19$), no difference in survival was observed in grassland compared to ecotone ($\beta = -0.24 \pm 0.30$) and agriculture ($\beta = -0.38 \pm 0.31$). Nest success estimates (95% confidence intervals) were 27.7% (13.2-42.3%) for grassland, 19.9% (5.5-34.3%) for ecotone, and 15.5% (3.5-27.6%) for agriculture. Daily nest survival decreased with nest initiation date in all landscapes based on the landscape and nest initiation model (Figure 5.4). The model containing the covariates for year and landscape received limited support. Nest survival estimates by year and landscape were calculated to illustrate patterns, as shown for other duck species (Table 5.10). No difference in nest survival was observed across landscapes for any of the years of the study based on this model.

Table 5.9 Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), nest initiation date (NESTIN), Robel score (RM), nest site vegetation (NESTSV), and selected interaction effects on blue-winged teal nest survival rates on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAIC _c	Δ_i	w_i
YEAR	3	596.50	100.95	0.00	0.510
LAND	3	598.95	101.38	0.43	0.413
LAND, YEAR	5	595.24	104.74	3.79	0.077
LAND, REP(LAND), YEAR	11	591.40	116.10	15.15	0.000
LAND, REP(LAND), YEAR, NESTIN	12	588.83	117.65	16.70	0.000
LAND, REP(LAND), YEAR, NESTIN, NESTSV	13	587.84	119.48	18.53	0.000
LAND, REP(LAND), YEAR, NESTIN, RM, NESTSV, LAND*YEAR, YEAR*NESTIN, YEAR*RM, NESTIN*RM	24	811.732	175.03	19.38	0.000

Variance inflation factor derived from global model $\hat{c}=1.4109$, k=number of parameters, -2logL=-2 log likelihood value, QAIC_c=corrected quasi-Akaike's information criterion, Δ_i =QAIC_c difference, w_i =model weight

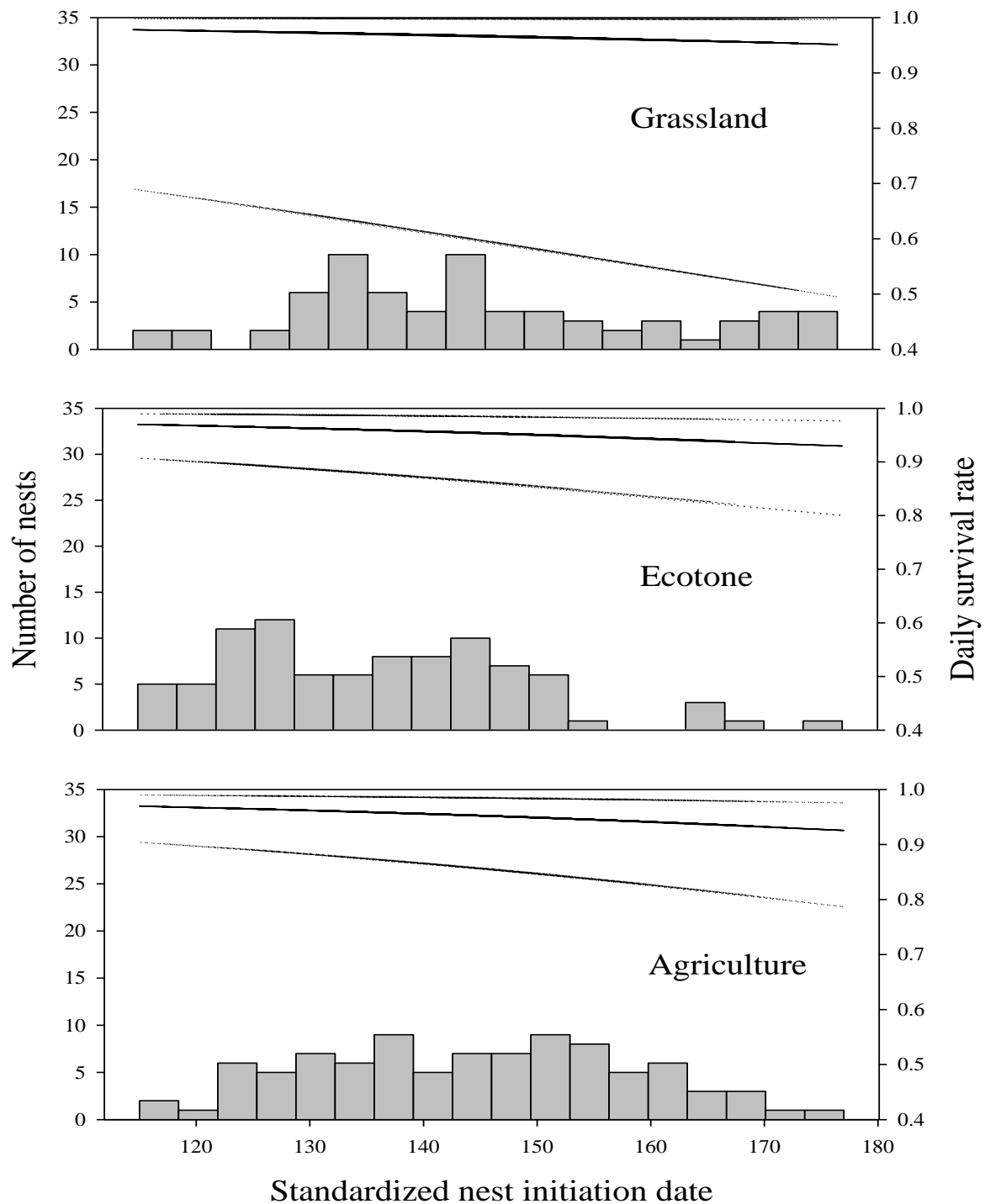


Figure 5.4 Relationships between standardized nest initiation date (number of nests initiated is shown in shaded bars) and daily nest survival (solid lines) with 95% CL (dotted lines) for blue-winged teal nesting on grassland, ecotone and agricultural landscapes on the Milk River Ridge, Alberta 2004-2006.

Table 5.10. Annual Mayfield nest success estimates (% , with 95% confidence interval) for blue-winged teal in Agriculture, Ecotone and Grassland landscapes, 2004-2006 Milk River Ridge, Alberta.

Year	Agriculture	Ecotone	Grassland
2004	14.3 (2.8-35.2)	16.8 (5.6-37.4)	24.8 (8.0-46.5)
2005	11.0 (1.7-30.4)	13.2 (2.7-32.6)	20.4 (5.7-41.7)
2006	27.1 (9.4-48.8)	30.2 (11.4-51.9)	39.2 (18.3-59.9)

5.5.6 Gadwall

The best approximating model describing variation in nest survival for gadwall included the covariate for year (Table 5.11). The intercept term for this model was $\beta = -3.03 \pm 0.18$, and the nest success estimates (95% confidence interval) were 18.2% (3.9-32.5%) in 2004, 19.5% (5.8-33.1%) in 2005, and 35.7% (20.2-51.2%) in 2006. Gadwall nest survival did not differ between 2006 and either 2005 ($\beta = -0.47 \pm 0.29$) or 2004 ($\beta = -0.51 \pm 0.33$). Additional support occurred for the model containing landscape (Intercept $\beta = -3.03 \pm 0.18$). Estimates of nest survival based on the model revealed no difference in survival in grassland compared to ecotone ($\beta = -0.50 \pm 0.31$) and agriculture ($\beta = -0.03 \pm 0.28$). Nest success estimates were (95% confidence intervals) were 28.3% (15.9-40.7%) for grassland, 12.7% (2.3-23.1) for ecotone, and 27.1% (10.6- 43.6%) for agriculture. Daily nest survival decreased with nest initiation date in all landscapes based on the model containing landscape and nest initiation (Figure 5.5). The model containing the covariates for year and landscape (Intercept $\beta = -3.03 \pm 0.18$) also received limited support. Nest survival estimates by year and landscape indicated generally that nest survival was high, especially on grassland and agricultural sites (Table 5.12).

Table 5.11 Models used to assess the effect of landscape (LAND), replicate (landscape) (REP(LAND)), year (YEAR), nest initiation date (NESTIN), Robel score (RM), nest site vegetation (NESTSV), and selected interaction effects on gadwall nest survival rates on the Milk River Ridge, Alberta, 2004-2006.

Model	K	-2logL	QAIC _c	Δ_i	w_i
YEAR	3	596.56	96.90	0.00	0.474
LAND	3	597.38	96.99	0.09	0.452
LAND, YEAR	5	594.02	100.63	3.72	0.074
LAND, REP(LAND), YEAR	11	591.54	112.39	15.48	0.000
LAND, REP(LAND), YEAR, NESTSV	12	589.96	114.21	17.31	0.000
LAND, REP(LAND), YEAR, RM, NESTSV	13	555.96	112.20	15.30	0.000
LAND, REP(LAND), YEAR, NESTIN, RM, NESTSV, LAND*YEAR, YEAR*NESTIN, YEAR*RM, NESTIN*RM	24	733.87	153.10	56.20	0.000

Variance inflation factor derived from global model $\hat{c}=1.3455$, k =number of parameters, $-2\log L=-2 \log$ likelihood value, $QAIC_c$ =corrected quasi-Akaike's information criterion, $\Delta_i=QAIC_c$ difference, w_i =model weight

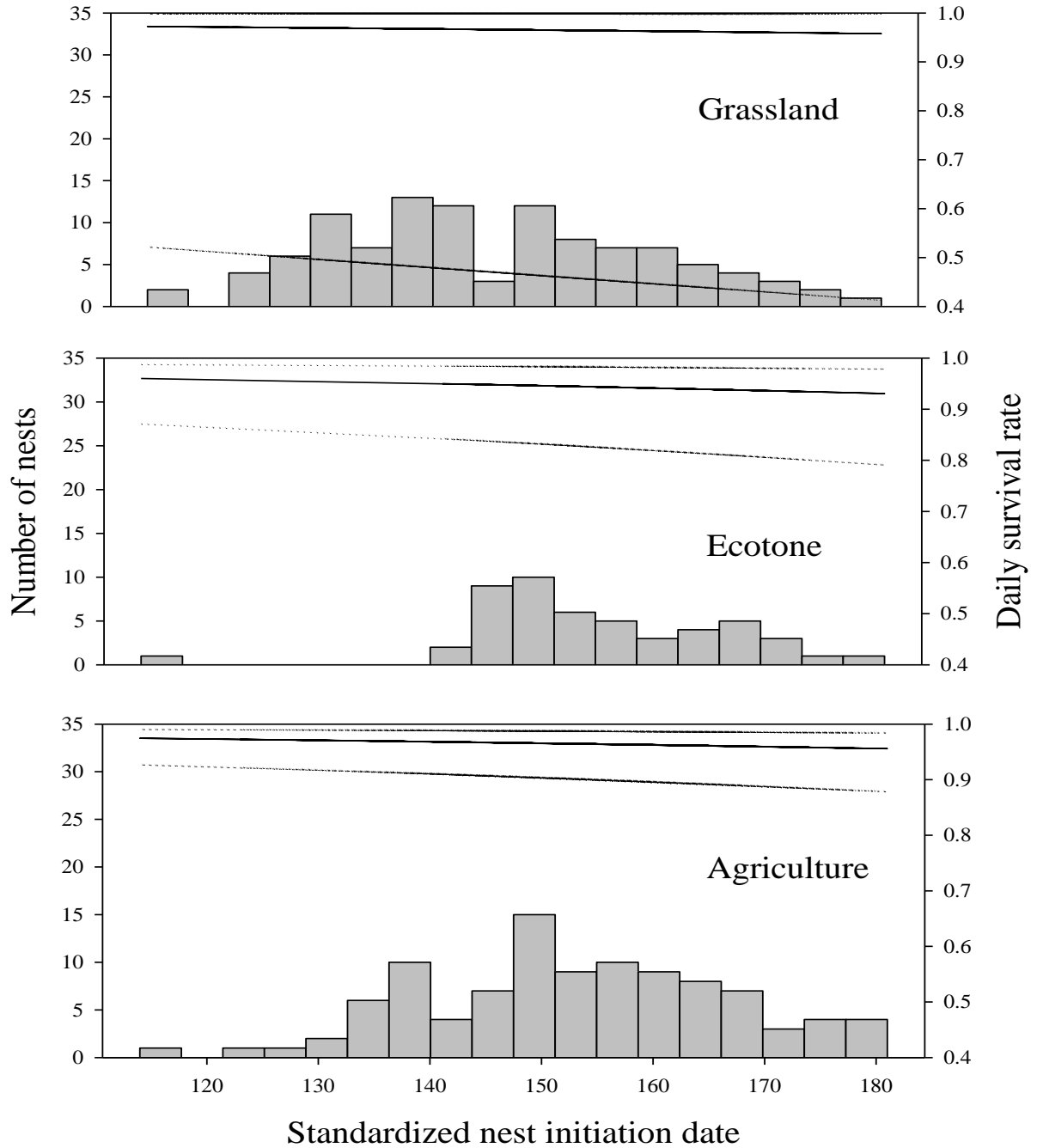


Figure 5.5 Relationships between standardized nest initiation date (number of nests initiated is shown in shaded bars) and daily nest survival (solid lines) with 95% CL (dotted lines) for gadwall nesting on grassland, ecotone and agricultural landscapes on the Milk River Ridge, Alberta 2004-2006.

Table 5.12. Annual estimates of Mayfield nest success (% , with 95% confidence interval) for gadwall in Agriculture, Ecotone and Grassland landscapes, 2004-2006, Milk River Ridge, Alberta.

Year	Agriculture	Ecotone	Grassland
2004	22.1 (7.4-41.8)	10.2 (0.3-29.0)	24.6 (9.1-44.2)
2005	23.1 (8.0-42.9)	10.9 (1.8-30.1)	25.7 (9.8-45.3)
2006	39.6 (20.4-58.4)	24.5 (9.0-44.1)	42.3 (22.8-60.7)

5.6 Discussion

Nest survival was considered from a spatial and temporal perspective to better understand some of the fine and coarse-scale drivers of nest survival rates. Although not significant in all cases, the general trend was toward higher nest survival on grassland areas for all species of ducks nesting on the Milk River Ridge, and particularly for pintails, as compared to ecotone and agricultural sites. Variables measured at finer scales (nest site vegetation and visual concealment) were unrelated to nest survival. Overall, temporal trends indicated higher survival rates in years of greater wetland abundance (2006), and these emerged as being the strongest drivers of nest survival in most species.

Interpretation of nest survival estimates requires an appreciation for the differences in structure of the different landscapes investigated. Although not modeled explicitly in analyses, two general differences existed between landscapes. These differences included amount of perennial cover present and the amount of edge associated with each landscape block. Generally there was an inverse relationship between these two variables with the highest amount of perennial cover and lowest amount of edge in grassland and the lowest amount of perennial cover and highest amount of edge in agriculture. These factors play an important role in predator-prey dynamics, with larger, intact areas of idle perennial cover typically supporting higher duck nest survival than smaller, fragmented habitats.

Predation had the largest impact on nest survival in all landscapes and has been linked to landscape composition in the past. Increased nest survival has been tied to increased amount of perennial cover on the landscape (Reynolds et al. 2001) and decreased nest survival with increased amount of cropland (Greenwood et al. 1995). In the case of agricultural landscapes, the nest survival appears to trend lower in pintails more so than the other species investigated, but is comparable with previous works. Klett et al. (1988) observed that nest survival was 7-10% for pintails nesting in fields of planted cover within agricultural landscapes. Greenwood et al. (1995) recorded a 7% nesting success rate for pintails nesting in Prairie and Parkland regions of Canada. These works are consistent with observations in agricultural and ecotonal landscapes on the Milk River Ridge. Although my results bracket (2-13%) the findings of Klett et al. (1988) and Greenwood et al. (1995), our agricultural sites did not include planted cover which could enhance nest survival (Emery et

al. 2005). Without that enhancement, the performance of agricultural landscapes on the Milk River Ridge may be even lower than experienced elsewhere.

Pintail nest survival rates were higher in grassland landscapes when compared to ecotone and agriculture, a pattern that is consistent with studies conducted on large unbroken grassland habitat in Montana, where nest success for pintails based on observations of brood/pair ratios was 45-60% (Ball et al. 1995). High nest success has also been realized on vast Conservation Reserve Program (CRP) lands in the Dakotas (Reynolds et al. 2001). Nest survival in pintails appears to be respond positively to the amount of grassland (at large spatial scales) to a greater extent than it does in other species of dabbling ducks (Stephens et al. 2005).

How nest survival rates varied over years and landscapes differed between pintail and the other species of ducks that I investigated. Differences in nest survival between agriculture and grassland were weak or absent in shovelers, mallards, blue-winged teal, and gadwall. Specifically, these species appear to experience higher nest survival rates than pintails in agricultural landscapes. This difference may be related to species-specific nest habitat use in agriculture landscapes compared to grassland. In previous studies, shoveler, mallard, blue-winged teal, and gadwall nests were found in odd areas (shelter belts, haystacks, rock piles, gravel pits) in agricultural landscapes to a greater degree than pintails (Klett et al. 1988, Reynolds et al. 2001), resulting in higher nest survival for these species. The trend may be the same on the Milk River ridge, where shovelers, mallards, blue-winged teal and gadwall find suitable nest sites in agriculture, resulting in nest survival rates that are more comparable to those experienced in the grassland landscape.

Spatially, nest survival estimates correlate positively with overall breeding population densities of pintails and wetlands – both of which were highest in 2006 and lowest in 2004 (Huggins 2006). This may suggest that pintails have flexible habitat selection mechanisms and select nesting sites based on habitat quality. This also suggests that pintails may be selecting habitat based on some quality-based queues that result in somewhat higher nest survival rates in these landscapes.

Temporally, pintail, shoveler, and blue-teal nest survival rates increased from 2004 to 2006, while mallard and gadwall did not. This change in nest survival may have been attributed to an increase in wetland abundance observed from 2004 to 2006 (Huggins 2006)

which may disperse nesting effort over a larger area, and reduce the effect of predation. This increase in nest survival that also corresponds to increase in wetland density, contradicts current literature regarding this topic. Wetland abundance at large spatial scales has been linked to increased waterfowl numbers, but at intermediate scales (i.e., regionally), wetland abundance either does not support increased nest survival or is negatively related to nest survival (Reynolds et al. 2001, Stephens et al. 2005)

The differences I observed in nest survival rates associated with landscape and year seem to be related to species-specific nesting ecology. In the case of pintails, a grassland specialist species, selection of grassland habitat resulted in higher nest survival, a trend that was not observed (as strongly) in the other duck species. Pintails may be better able to recognize and respond appropriately to cues that guide grassland habitat selection decisions. In the case of other species, habitat cues may allow selection to occur across a wider landscape gradient. The result of this selection however does not seem to affect the nest survival rates experienced by these species. According to Fretwell-Lucas models, different habitat selection strategies emerge as a consequence of variation in habitat quality, as indexed by measurements of reproductive success and(or) survival. Assuming that nest success is a reliable measure of habitat quality; pintails settling in grassland landscapes were nesting the best quality habitat. Settlement by breeding pintails across the three landscapes (Chapter 2) suggested that grassland habitat was higher quality habitat; evidence of higher nesting success on grassland areas is consistent with this conclusion. Taken together these results suggest that the distribution of breeding pintails among the three landscapes may be driven by territorial behaviour and aligned with predictions of Fretwell and Lucas's (1970) ideal-despotic model. However, further work is needed to evaluate the mechanisms that determine spacing patterns of pintails in relation to landscape-scale gradients in habitat quality.

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CHAPTER 6 – GENERAL SUMMARY AND CONCLUSIONS

The initial motivation for this research arose from concerns for northern pintail populations in North America and, more specifically, the crucial role that large areas of remaining grasslands in southern Alberta could play in supporting productive pintail populations (i.e., local population growth rates $[\lambda] > 1$). Unlike most other prairie-nesting dabbling duck populations, the pintail population had failed to increase during periods of excellent wetland conditions, and have remained well below conservation goals. Pastures on the Milk River Ridge in southern Alberta provided large expanses of grasslands adjacent to areas of mixed land uses and intensive agriculture, and thus created an opportunity to compare how pintails (and several other duck species) used these landscapes as well as determine the reproductive consequences of settling in these areas. But, I was also motivated to learn and apply ecological theories to help expand and guide my thinking and research. Early discussions with other (waterfowl) ecologists began to catalyse my interest in framing my work within the context of classical and contemporary habitat selection and life-history theories. I hoped that my research could be used to inform future habitat conservation decisions, but I also tried to advance our understanding of some of the mechanisms underlying the trade-offs female pintails confront when choosing to breed in different habitats.

By integrating applied and theoretical aspects of pintail reproductive ecology (Figure 6.1), I attempted to provide some deeper insights into the processes that shape behavioral decisions by breeding pintails and other bird species. Conceptually, my results were expressed in terms of a life-cycle perspective, from spring arrival and settlement on breeding areas, to assessing the age and quality of nesting females, to determining timing and investment in reproduction, and finally to measuring nesting success. For many of these breeding stages, it was possible to compare the observed patterns with those predicted by habitat selection models, particularly in pintails. Below, I briefly review and integrate the main findings (Figure 6.1), and recommend future studies that could help to clarify unresolved conceptual and applied questions.

Pintail breeding cycle – integration of theory and application

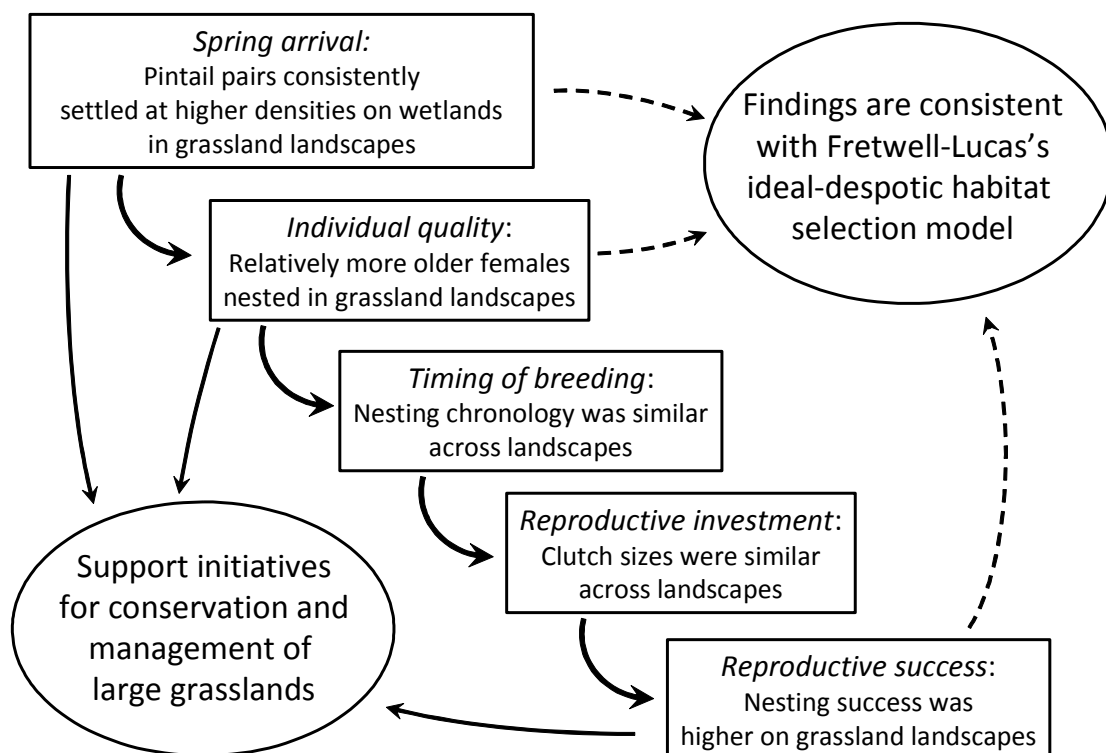


Figure 6.1. Pintail breeding cycle results as they relate to models of habitat selection, as well as applied conservation and management opportunities.

The ideal free distribution model proposed by Fretwell and Lucas (1970) assumes that individuals are “ideal” with full knowledge of habitat options regionally and “free” to select habitats on the basis of quality (as measured by fitness metrics, e.g., survival or reproductive rates). As density of individuals increases in habitat (A), fitness of individuals decreases due to crowding and competition for resources to the point that another habitat (B) becomes equally suitable. Thus, densities of individuals in habitats A and B would eventually reach equilibrium such that individuals occupying habitat A and B have equal fitness. Alternately, the ideal despotic distribution proposes that individuals must compete for access to high suitability habitat. Dominant individuals are better able to sequester the highest quality habitat, forcing subordinates into less suitable habitat (Petit and Petit 1996). In terms of reproductive success, the ideal despotic model predicts higher rates in preferred habitats over less preferred habitats. In this situation, observations suggest that a positive correlation exists between suitability and density, as predicted by the density-limiting territorial hypothesis (Fretwell 1970). A key assumption in both ideal free and despotic models is that at least two habitats differ in intrinsic suitability (Fretwell and Lucas 1970). Additionally, all individuals must be “ideal” and have the ability to recognize habitats of differing qualities (Petit and Petit 1996). Individuals select habitats best suited for survival and reproduction, and individuals closest to being ideal would presumably be favored via natural selection (Fretwell and Lucas 1970). Thus, populations composed of these individuals would be adapted to local conditions, or “ideal” for a specific area.

The mechanisms that produce habitat selection patterns are central to understanding differences between ideal-free and ideal-despotic models. Under the ideal-despotic distribution, individuals are forced into lower quality habitats where breeding effort and success are lower. But, anthropogenic modification to the landscape could also create unreliable cues about habitat quality such that lower quality habitats may be incorrectly perceived by breeding individuals to produce better reproductive outcomes than higher quality habitats. These areas may also provide other habitat requirements (breeding ponds, food) in greater quantity and quality thereby resulting in unexpectedly high settlement. Higgins (1977) observed a nest density of 0.07 nests/ha in tilled cropland in North Dakota which suggests that low quality habitat is selected for nesting sites. Devries et al. (2008) recorded a similar rate of 0.06 nests/ha with a nest survival estimate of 12% in spring-seeded

crops in Saskatchewan. These estimates of nest success were higher than previously recorded and may suggest that ducks are, and have been, selecting poorer quality habitats to a greater degree than expected. These poorer quality areas may be operating in a density independent fashion and offering individuals that select these habitats the benefits of population growth under density independent conditions (Murray et al. 2010). This habitat quality-nest survival tradeoff may be an example of where selection of poorer quality habitat may be adaptive for some individuals.

The contrasting landscapes studied in southern Alberta provided a habitat template that is well-suited to testing patterns and mechanism predicted by Fretwell-Lucas's models. As noted above, the research reported here focused on pintail's for two reasons. First, pintail densities are high in the vicinity of southern Alberta's Milk River Ridge, a landscape composed of habitats ranging from extensive tracts of lightly grazed, natural prairie to agricultural lands dominated by spring-seeded cropland interspersed with small areas of perennial cover. Thus, the strong gradient of land use in this region created landscapes with different habitat quality based on upland cover quality and wetland density. These prerequisite conditions allowed for testing the ideal-free and ideal-despotic models. Second, the pintail is a species of special concern and a target for enhanced research and conservation efforts (Millar and Duncan 1999). It is hypothesized that large areas of natural grasslands provide high suitability habitat (Sovada et al. 2000, Reynolds et al. 2001) whereas direct-spring-seeded cropland is among the least suitable habitats. Thus, current habitat management for pintails aims to protect and create larger areas of perennial cover either by encouraging better management of grazing lands, by converting cropland to grassland, or by promoting adoption of fall-seeded crops like winter wheat (Devries et al. 2008). From a habitat perspective, the general assumption is that intrinsic differences in landscape quality are associated with the intensity of agricultural land use. Although habitat quality had not been measured explicitly until I estimated landscape-specific nesting success for several duck species, my results imply that differences in quality can be inferred, at least generally, on the basis of "anticipated" habitat suitability characteristics particularly extent of native cover and density of wetlands in pintails.

6.1 Settlement in spring by breeding pairs

In applying the Fretwell-Lucas models to pintails, initial attention focused on settlement patterns by breeding pairs. Pintail densities on wetlands in grassland areas were higher than those in ecotone or agricultural landscapes. Overall, early spring density of pintails was consistently higher in grassland landscapes when all years were considered, and densities typically remained high in April and May each year suggesting that grassland habitat may have been filled to capacity; indeed, pair densities rose seasonally on wetlands in ecotone and agricultural landscapes. Furthermore, as regional population densities increased from 2004 to 2006, April-May pair densities in grassland changed relatively little, and most pair density increases in this period were observed on wetlands in the ecotone and agricultural areas. This pattern of settlement suggests that some pintails are opting to settle in lower pair density areas, or perhaps are being forced into less preferred habitat as regional population density increases. Finally, the strength of these local patterns was not consistent across years implying that factors such as previous breeding success (dispersal following nest failure), responses to predators (e.g., Dassow et al. 2011) or variation in wetland quality could also influence pintail habitat selection patterns.

Densities tended to be higher in grassland than other landscapes for shoveler pairs, but results for blue-winged teal and gadwall pairs were mixed and, in mallard, pair densities were actually higher in agricultural areas. Unlike pintails, seasonal changes in shoveler pair density were more consistent with nearly simultaneous and rapid wetland settlement in grassland and agricultural landscapes. These differences in settlement patterns by breeding pairs could reflect species-specific nest site preferences and upland habitat availability. Whereas pintails prefer nest sites in open grasslands, mallards are often considered to be habitat generalists, and agricultural areas might offer a greater range of nesting opportunities, including fields of dense herbaceous and shrub cover. Alternatively, intrinsic differences in adult diets or brood habitat requirements could also account for variation in habitat distribution of breeding pairs.

6.2 Measurements of female quality

It was not possible to determine the age of birds upon arrival in the spring, but many other avian studies suggest that older birds arrive on the breeding grounds before younger

birds. In previous studies of pintails and other ducks, adult females produced their first clutch earlier than yearling birds, persisted in nesting later into the season, and renested more often than yearlings when initial nests were lost (Duncan 1987a, Blums and Clark 2004, Arnold et al. 2010). More, older pintails were captured on nests in grassland than agricultural areas and, despite a tendency for earlier nest initiations on grassland areas, no significant age-related or overall differences in clutch initiation dates were detected.

A second index of female quality, body mass, did not differ among landscapes in pintail or shoveler after controlling body size or other effects. Body mass declined seasonally, a pattern reported by Duncan (1987a) and Guyn and Clark (2000). It is possible that more adults nested in 2004 when drier wetland conditions prevailed, and this may have accounted for generally larger body masses in that year. Although relatively more, older pintails nested in grassland than in agriculture landscapes, no body mass differences were detected. This lack of difference may be due to small sample size and because females were captured throughout the breeding season rather than upon arrival to the breeding grounds. It seems unlikely that a lack of landscape effects on body mass was due to trade-offs over reproductive investment, because timing of breeding and clutch sizes were similar among landscapes. Finally, it was somewhat surprising that female body mass tended to increase with incubation stage in pintail and shoveler, but perhaps nests that survived to late incubation were attended by heavier females (Gloutney and Clark 1991, Blums et al. 1997).

6.3 Timing of breeding and reproductive investment patterns

The species (pintail, shoveler, and mallard) selected to investigate habitat selection across a landscape gradient were all early to mid-season nesting waterfowl, but species-specific variation in nest initiation dates was evident. Yearly variation in habitat (wetland density) and weather conditions across the 3 years of the study may also have accounted for the variation in mean nest initiation dates.

Seasonal variation in mean nest initiation date in pintails spanned 12 days, comparable to the 7 days reported by Duncan (1987) studying pintails in Alberta from 1982-1984. The span of nest initiation dates depends upon the local temperature and water conditions, an individual pintail's physiological condition and renesting propensity (Bellrose

1980). Early season nesters such as pintails and mallards, may be restricted from earlier nesting by low temperatures and adverse weather events (Smith 1968).

The link between presumed habitat quality and mean nest initiation date was not evident in this study. Early season nesters such as pintail and mallard may not require the exogenous energy to initiate clutches due to the higher amounts of endogenous energy available to them (MacCluskie and Sedinger 1999). The selection of higher quality habitat may not be required to initiate nests in pintails and mallards. Pietz et al. (2000) observed that reproductive output of early season mallards was not affected by habitat conditions, while late season nesting gadwall were correlated with habitat conditions. Using early season nesting birds may have prevented the detection of a quality difference between landscapes. If early season nesting by pintails and mallards is not affected by initial habitat quality, it may explain why selection of habitats of lower quality occurs or why there is no difference in nest initiation date between habitats of differing qualities. Advantages of early nesting include increased opportunity to renest in the event of nest loss (Arnold et al. 2010), and increased recruitment (Dawson and Clark 2000). Although insignificant, nesting birds in the grassland landscape did tend to nest earlier, and this may afford some adaptive advantage over nesting other habitats.

For all species combined, variation in clutch size is consistent with other studies (Duncan 1987, Krapu et al. 2004) and declined with nest initiation date. Annual variation in clutch size was observed for all ducks with larger clutch sizes in 2005 and especially 2006 when compared with 2004. This difference in clutch size may be a result of improved habitat conditions (food supply) across all landscapes in 2006 (Huggins 2006). Alternatively, higher nest survival in 2006 also may have contributed to larger clutch size estimates because early season nests survived longer. Nest survival was lowest in 2004, and this likely increased the number of (smaller) replacement clutches. Although only adult pintails were detected at nests in 2004, any positive age-related clutch size effects were apparently offset by those of drier conditions and lower nest survival rates.

The similarity of pintail clutch sizes among landscapes may be tied to energetic requirements. Early nesting species such as pintails may depend on more endogenous than exogenous reserves to initiate first clutches and because of this be able to select habitat independent of quality. Duncan (1987) found that pintails nesting in agricultural areas

produced larger clutches than females nesting in grasslands, and speculated that greater food availability in agricultural landscapes was responsible for this pattern; however, my results did not substantiate this hypothesis. Clutch size in shovelers and mallards followed the same trend with most variation in clutch size being explained by initiation date. Shovelers exhibited an annual effect with smaller clutches in 2004 when compared to 2005 and 2006. As in pintails, smaller average clutch size may be due to the low nest survival in 2004 and the inclusion of more renesting attempts in the calculation of mean clutch size. Mallards did not exhibit annual or landscape differences in clutch size, counter to Ball et al.'s (2002) report that clutch size of mallards nesting in artificial structures was larger in landscapes dominated by grassland as compared to cropland.

6.4 Reproductive success: temporal patterns and landscape-specific variation in nesting success

Nest survival was considered from a spatial and temporal perspective to better understand nest survival patterns in all species, but particularly in pintails. Although not significant in all cases, the general trend for all species of ducks was towards higher nest survival on the grassland landscapes as compared to ecotone and agriculture landscapes. The fine spatial scales variables (nest site vegetation and visual concealment index) did not affect nest survival. Temporally, the trend was towards higher survival rates in wetter years as compared with dryer ones.

Increased nest survival has been tied to increased amount of perennial cover on the landscape (Reynolds et al. 2001) and decreased nest survival with increased amount of cropland (Greenwood et al. 1995). In the case of agricultural landscapes, the estimates of nest survival appear to trend lower in pintails more so than the other species investigated, but are comparable with previous work. Klett et al. (1988) observed nest survival in pintails nesting in agricultural landscapes with planted cover was between 7-10%. Greenwood et al. (1995) recorded a 7% nesting success rate for pintails in Prairie and Parkland regions of Canada. These studies are consistent with nesting success rates observed in agricultural and ecotonal landscapes on the Milk River Ridge. Although the estimates observed bracket (2-13%) those of Klett et al. (1988) and Greenwood et al. (1995), my estimates may be lower on agricultural landscapes because of the absence of planted cover which tends to enhance nest

survival (Emery et al. 2005). Without that enhancement, the performance of agricultural landscapes in this region may be even lower than experienced elsewhere.

Pintail nest survival trended towards higher rates in the grassland landscapes when compared with ecotone and agriculture landscapes. The nest survival rates were also consistent with studies conducted on large unbroken grassland habitat in Montana, where nest success for pintails based on brood/pair ratio observations was 45-60% (Ball et al. 1995). High nest success has also been realized on vast Conservation Reserve Program lands in the Dakotas (Reynolds et al. 2001) where percent perennial cover is increased compared to adjacent landscapes. Nest survival in pintails appears to be respond positively to the amount of grassland (at large spatial scales) present to a greater extent than other species of dabbling ducks (Stephens et al. 2005).

Differences in nest survival arise between pintail and the other species of ducks investigated. Differences in nest survival for shovelers, mallards, blue-winged teal, and gadwall were not evident (or the trend was less pronounced) between the agriculture and grassland landscapes. In agricultural landscapes these species appear to be experiencing higher nest survival rates than pintails. This difference may be attributed to the habitat variation afforded them in agriculture landscape compared to grassland landscapes. In previous studies, shovelers, mallards, blue-winged teal, and gadwall nested in odd areas (shelter belts, haystacks, rock piles, gravel pits) in agricultural landscapes to a greater degree than pintails (Klett et al. 1988, Reynolds et al. 2001), and resulted in higher nest survival for these species. Selecting odd areas to nest, may be the same on the Milk River ridge, where shovelers, mallards, blue-winged teal and gadwall were finding suitable nest sites in the agriculture landscape. These nest sites were then producing nest survival rates comparable to the grassland landscape.

Spatially, these estimates of nest survival correlate positively with overall breeding population density of pintails in the area, and density of wetlands which was highest in 2006 and lowest in 2004 (Huggins 2006). This suggests that pintails are selecting habitat based on some quality based queues which results in somewhat higher nest survival rates.

Temporally, pintail, shoveler, and blue-teal nest survival increased from 2004 to 2006, while mallard and gadwall did not. This change in nest survival may have been attributed to increase in wetland abundance observed from 2004 to 2006 (Huggins 2006).

This increase in nest survival as it relates to increased wetland density, contradicts current literature regarding this topic. Wetland abundance at large spatial scales has been linked to increased waterfowl numbers, but at the landscape level, wetland abundance either does not support increased nest survival or is negatively related to nest survival (Reynolds et al. 2001, Stephens et al. 2005)

The differences observed in nest survival due to landscape and year may be because of the species-specific breeding biology. In the case of pintails, a grassland specialist, selection of higher quality habitat leads to higher nest survival, a trend that was not observed in the other species. The cues, on which habitat selection decisions are made, may be better interpreted by pintails, making it a species that is better suited to grassland habitats. In the case of all others, cues may allow selection to occur across a landscape gradient, as this selection does not seem to affect the nest survival rates for these species.

To better ascertain which of Fretwell and Lucas's models (ideal-free or idea-despotic) of habitat selection pertain to pintails and shovelers, settlement patterns must be linked to fitness parameters like nest success. Pintail breeding densities were consistently higher on wetlands in grassland habitat, early in the breeding season in all years, whereas density increased in ecotone and agricultural areas later in the breeding season or in years of large regional populations. Furthermore, pintails breeding in grasslands generally had higher nesting success, implying that grassland habitat is higher quality. Taken together, patterns are consistent with an ideal-despotic habitat selection model, in which older birds settle at higher densities in higher-quality habitat and force subordinate individuals (pairs) into lower quality habitats. However, this conclusion must be considered tentative, until precise spacing mechanism(s) is reliably demonstrated. The patterns of settlement and reproductive success in shovelers and mallards did not give a clear indication of which habitat selection is most applicable.

6.5 Applications and future work

Overall, an improved understanding of habitat selection patterns and reproductive consequences of those decisions provide insights for implementing effective management and conservation programs. In the case of pintails, my observations support the need to conserve large tracts of grassland habitat as these areas are preferred by nesting pintails, and

afford them higher nest survival rates, particularly in wet years when duckling survival is also expected to be higher. Additionally, habitat management that can create or increase the quality of large grassland blocks could benefit pintails.

Additional work focusing on mechanism(s) such as competition or social facilitation would improve our understanding of habitat selection by pintails and other ducks.

Examining habitat selection while considering the effect of local and regional population density would also allow a better understand of density effects on habitat selection and reproductive success. Additional work on adult female and brood survival rates would provide better evidence about the factors that influence settling decisions in pintails, and studies of individually-marked females would help in this regard. I compared grassland and cropland-dominated landscapes, but information about selection process involved in other habitats such as in landscapes dominated by fall-seeded cereal crops would also be useful. This study highlighted species-specific differences in settling patterns, reproductive potential, reproductive investment and reproductive outcomes; continued work on linking pintail vital rates with habitat selection patterns is warranted.

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