SURVIVAL OF SANDHILL CRANE COLTS IN NORTHEASTERN ILLINOIS: THE ROLE OF AGE AND SIGNIFICANCE OF LAND COVER IN AN URBANIZED LANDSCAPE

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2011

Urbana, Illinois

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ABSTRACT

The breeding and fledging success of Sandhill Cranes (*Grus canadensis spp.*) in urban landscapes has been largely unexplored by previous research. I evaluated survival and habitat use of young Greater Sandhill Cranes (*G. c. tabida*) in northeastern Illinois, where the Eastern Population of cranes and urban sprawl have concurrently increased for several decades. Using an information-theoretic approach to evaluate fates of 85 radio-marked young (i.e. 1 to 10 week old cranes; a.k.a. colts) revealed age was the most influential factor and the age-based probability of surviving to fledge (≈10 weeks old) was 32.44%. Birds hatched before the end of May hatched from nests in significantly larger wetland complexes and survived better than those hatching after May (35.55% and 10.34%, respectively). This was likely due to experienced breeders nesting early and in larger wetland habitats. Surprisingly, colt survival was positively correlated with urban development and declined with increases in grassland/savanna or agricultural land cover. I hypothesize that cranes acclimated to humans were buffered from predation by the human-avoidance behaviors and hunting habits of common colt predators in the region. However, while I did not observe competition within broods (i.e. sibling-strife) and neither the presence of nor size of siblings significantly affected survival, sibling fates were strongly correlated with each other and the mortality of one colt reduced the probability of the other fledging by 32.94%. Overall fledging success in northeastern Illinois appeared to be lower than previously reported throughout much of the literature on colt survival. It is therefore unlikely that birds hatched and fledged in northeastern Illinois are significantly contributing to the rapid growth of the Eastern Population observed in the region. Additional research is warranted to facilitate crane conservation efforts as cranes and urban sprawl continue to overlap.

ACKNOWLEDGEMENTS

Many thanks to Brad Semel of the Illinois Department of Natural Resources and my adviser Mike Ward for their assistance in conducting this research and reviewing this thesis. I would also like to acknowledge the generosity of Sandy and David Whitmore, the Illinois Ornithological Society, the Illinois Natural History Survey, and the Illinois Department of Natural Resources for funding this research. I am also thankful for the selfless contributions of the many volunteers and property owners in Lake and McHenry Counties with whom I have had the pleasure of working with. Lastly, I would like to thank my family and friends for their support over the past several years, and in particular Mary Huinker for the time and enthusiasm she has devoted to helping me complete this project.

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CHAPTER 1

Sandhill Crane Colt Survival and Fledging Success: Background and Literature Review

INTRODUCTION

Sandhill Cranes (*Grus canadensis spp.*) are native inhabitants of the wetlands and grasslands of North America (Tacha et al. 1992). These habitats were extensively converted to agriculture following European settlement (Sampson and Knopf 1994; Dahl and Allord 1996). Market hunting compounded the effects of habitat loss, leading to sharp declines throughout nearly all major breeding populations in the contiguous 48 states (Drewien et al. 1975; Drewien and Lewis 1987; Meine and Archibald 1996). By the 1930s and 1940s, several populations had been extirpated or reduced to critically low numbers of breeding pairs (Henika 1936; Drewien and Lewis 1987; Meine and Archibald 1996). Hunting prohibition via The Migratory Bird Treaty Act of 1918 (Migratory Bird and Habitat Programs 2010) and habitat management/restoration efforts likely rescued many populations from extinction (Drewien and Lewis 1987; Meine and Archibald 1996). Despite continued agricultural conversion of habitat (Sampson and Knopf 1994; Dahl and Allord 1996), during the past 60 years many Sandhill Crane populations have increased (Lovvorn and Kirkpatrick 1982a; Meine and Archibald 1996; Su et al. 2004; Fig. 1.1). As populations have grown many states have removed the Sandhill Crane from their threatened/endangered lists (e.g. Illinois in 2009; Illinois Endangered Species Protection Board 2010) and many have or are proposing Sandhill Crane hunting seasons (e.g. hunted in 12 states and seasons proposed in Kentucky and Tennessee; Horn et al. 2010; Minnesota Department of Natural Resources 2010; Kentucky Department of Fish and Wildlife Resources 2011; Tennessee Wildlife Resource Agency 2011). Given the increase in crane numbers and their inclusion as a game species in parts of their range, Sandhill Cranes have become one of the most widely studied crane species (Meine and Archibald 1996); however, many gaps in knowledge remain. Although numerous studies have provided detailed insight into nest success (e.g. Nesbitt 1988; Littlefield 1995, 2003; Toland 1999; Austin et al. 2007; Ivey and Dugger 2008) and recruitment (e.g. Lovvorn and Kirkpatrick 1982b; Drewien et al. 1995; Littlefield 1995, 2003), there is a paucity of information on colt survival and fledging success (i.e. colt survival post-hatching to capable of flight). Additionally, the bulk of previous research has been conducted in rural/agricultural contexts and on wildlife refuges. Factors influencing colt survival in urban contexts remain largely unexplored.

Sandhill Cranes are precocial (Tacha et al. 1992), mobile, and grow rapidly (Archibald and Viess 1979 *in* Johnsgard 1983; this study unpublished data). This makes them difficult to initially locate post-hatching or track using traditional methods (i.e. risk of constriction with leg and neck bands; Desroberts 1997). Because of this, relatively little is known about this critical pre-fledged period in the lives of cranes. One method that has been used to address survival during this period is to compare nest success data (i.e. # of birds hatched) to recruitment (e.g. # number of birds fledged by September in migratory populations; Littlefield 1995, 2003). However, this method alone cannot address specific circumstances of colt mortality or influences of age, seasonal progression (i.e. temporal variation), landscape, or intrabrood (i.e. sibling) dynamics. While some studies have successfully studied age or landscape influences through routine monitoring of young hatched by marked birds or those with known nesting sites/ranges (Nesbitt 1992; Toland 1999), radio telemetry may be the most promising approach for studying colt survival and fledging success (e.g. Spalding et al. 2001).

PREVIOUS RESEARCH ON COLT SURVIVAL AND FLEDGING SUCCESS

Studies of a declining population of Greater Sandhill Cranes (*G. c. tabida*) at Malheur National Wildlife Refuge (NWR) in Oregon reported average annual nest success (49.44%), fledging success (15.61%), and recruitment of fledged birds (6.65%; Littlefield 1995, 2003; Table 1.1). Distinguishing years with predator (e.g. coyote; *Canis latrans*) management programs revealed respective increases of 35%, 84%, and 100% compared to years without predator management (Littlefield 1995, 2003; Table 1.1). Predation of colts apparently had the greatest influence on recruitment. This was strongly supported by the findings of Littlefield and Lindstedt (1992) *in* Littlefield (2003) and Ivey and Scheuering (1997; Table 1.1), where 68% and 52% of radio-marked colts at Malheur NWR were lost to predation, respectively. Where predators were consistently controlled at Modoc NWR in California, average annual fledging success was greater (45%; Table 1.1) and the population moderately increased (17 pairs in 1976 to 36 pairs in 1992; Desroberts 1997). At Malheur NWR, it was later revealed that average annual nest success during the 1990s was approximately 72.44%, reflecting an overall steady increase of 1.20% each year since 1966 (Ivey and Dugger 2008). Relative to nest success, however, low colt survival had disproportionately influenced productivity and the number of young fledged per 100 pairs decreased (Ivey and Dugger 2008; Table 1.1).

The influence of predation on recruitment in Sandhill Cranes has also been documented via nest success and recruitment studies in the Rocky Mountain Population (*G. c. tabida*; Drewien et al. 1995, Austin et al. 2007) and Eastern Population (*G. c. tabida*; Walkinshaw 1981). Studies of other subspecies including Lesser Sandhill Cranes (*G.c. canadensis*) and the non-migratory Florida (*G. c. pratensis*) and Mississippi (*G. c. pulla*) Sandhill Cranes report similar vulnerabilities (Walkinshaw 1949 *in* Johnsgard 1983, Bennett and Bennett 1990, Dwyer and Tanner 1992, Meine and Archibald 1996). Coyotes and American Mink (*Neovison vison*) are amongst the most commonly identified predators (Desroberts 1997; Ivey & Scheuering 1997; Littlefield 2003), but depredation by foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), wolves (*C. lupus*), bobcats (*Lynx rufus*), crows (*Corvus brachyrhynchos*), ravens (*C. corax*), Golden Eagles (*Aguila chrysaetos*), Red-Tailed Hawks (*Buteo jamaicensis*), and Great-Horned Owls (*Bubo virginianus*) is also well documented (Walkinshaw 1949 *in* Johnsgard 1983; Walkinshaw 1973 *in* Tacha et al. 1992; Ellis et al. 1999). High rates of predation are common for precocial young and observed in other crane species (e.g. Wattled Crane; *Bugeranus carunculatus*; and Whooping Crane; *G. americana*; Konrad 1981 *in* Johnsgard 1983; Kuyt 1981 *in* Johnsgard 1983), as well as in Galliformes (e.g., Wild Turkeys; *Meleagris gallopavo*; Eaton 1992; Spears et al. 2007), Anseriformes (Canada Geese; *Branta canadensis*; Mowbray et al. 2002), and Charadriformes (e.g. Kildeer; *Charadrius vociferus*; and Snowy Plovers; *Charadrius alexandrinus*; Powell 1992 *in* Colwell et al. 2007; Colwell et al. 2007; Jackson et al. 2000; Page et al. 2009). The literature clearly offers broad and strong support for the prominent role that predation plays in the survival of young precocial birds.

Increased survival with age is another common trait for precocial birds (Spears et al. 2005, 2007; Colwell et al. 2007). A study of Great Basin Canada Geese (*B. c. moffitti*) found survival was lowest during the first 14 days post-hatching, but increased thereafter (Eberhardt et al. 1989). Studies of Florida Sandhill Cranes found 81% of colt mortalities occurred by 21 days of age (i.e. within the first 3 weeks of a ≈10 week pre-fledging period; Drewien 1973 *in* Tacha et al. 1992; Bennett and Bennett 1990) and that survival increased with colt age (Nesbitt 1992). These same studies reported age-based estimates of fledging success of 45.95% (Bennett and Bennett 1990) and 64.90% (Nesbitt 1992; Table 1.1). As colts age and grow they become more physically capable of evading predators, especially in dense wetland habitats. Learned behavior and experience also augment the ability to avoid and evade predators. Another variable in survival is related to habitat and breeding experience. For example, the cover provided by wetland vegetation and water, which deters mammalian predators (Sargeant and Arnold 1984; Arnold et al. 1993), provides protection from predation. Moreover, breeding experience in avian species is often associated with greater fledging success and selection of higher quality habitats (Part 2001). In the predominantly wetland-nesting Sandhill Crane, experienced breeding pairs indeed select higher quality wetland habitats, return to established breeding territories and nest earlier and when conditions are favorable, and fledge more young than younger/inexperienced pairs (Drewien 1973 *in* Tacha et al. 1992; Wenner and Nesbitt 1987 *in* Tacha et al. 1992; Tacha et al. 1984 *in* Tacha et al. 1992; Nesbitt 1988, 1992; Tacha et al. 1992; Baker et al. 1995; Ivey and Dugger 2008). As breeding experience and habitat selection as well as predation vary according to landscape and habitat structure, landscape-based variations in fledging success are expected.

The mean number of fledged colts produced per nest by Florida Sandhill Cranes in developed landscapes was less than half of what was observed in natural sites (0.32 and 0.86, respectively; Toland 1999). A separate study evaluating nest success in Florida found that all flood-related nest failures occurred within a 370 m buffer around an interstate (i.e. a developed landscape; Dwyer and Tanner 1992). The correlation between urban development and altered hydrological schemes has been increasingly well documented (Wright et al. 2006) and suspected in facilitating declines of several wetland-dependent birds via alteration of habitat structure (Ward et al. 2010). Alternatively, greater nest success for Canada Geese in urbanized habitats compared to adjacent undeveloped landscapes was attributed to predator’s (i.e. coyotes) aversion to human activities (Brown 2007). Potential negative impacts on young cranes via altered hydrology and reduction in habitat connectivity through urbanization (i.e. fragmentation; Theobald et al. 1997; Wang and Moskovits 2001; McKinney 2002; Irwin and Bockstael 2007; Girvetz et al. 2008) may therefore be offset by urbanization's influence on predator composition/behavior. However, while the aforementioned research offers valuable information that may contribute to landscape-based variations in colt survival and fledging success, few studies have specifically addressed the topic in urban habitats.

The role of brood dynamics (i.e. interactions between siblings) in fledging success has been more thoroughly explored by previous research. In a study of Whooping Cranes, 44% of larger colts fledged while only 11% of smaller colts fledged (Bergeson et al. 2001). During the same study aggressive interactions between pairs of colts were observed and post-mortality recoveries of the smaller siblings revealed trauma to the head, beak, and eyes (Bergeson et al. 2001). Similar behavior has been reported in Siberian Cranes (*G. leucogeranus*; Flint and Sorokin 1981 *in* Johnsgard 1983) and is considered common for pairs of Sandhill Crane colts (Drewien 1973 *in* Tacha et al. 1992; Miller 1973; Walkinshaw 1981). The general consensus of most publications suggests either abandonment of the second egg (≤ 2 eggs per clutch; Walkinshaw 1973 *in* Tacha et al. 1992; Nesbitt 1988) or colt soon after the first hatches, or a dominance-hierarchy and strife between siblings due to a dichotomy in size, often leads to the mortality of the second hatching or subordinate colt. This behavior may be correlated with the availability of food (Quale 1976 *in* Tacha et al. 1992) or may be a consequence of innate behavior (Miller 1973). In contrast, aggression between siblings was rare during an eight year study of Florida Sandhill Cranes (Layne 1982). Moreover, a review of brood sizes in Drewien et al. (1995) reveals that broods of two fledged colts are not uncommon, suggesting that sibling-strife-related mortalities may not unilaterally influence fledging success in broods of two. The apparent contrast between studies evaluating brood dynamics indicates that both the causes of sibling-strife and the influence of competition between siblings on fledging success remain to be clearly defined.

A great deal of research has been published on Sandhill Crane nest success, recruitment, brood dynamics, and general population parameters via annual counts at staging and stopover sites (i.e. growth of Eastern Population; Lovvorn and Kirkpatrick 1982a; Meine and Archibald 1996; Su et al. 2004; Fig. 1.1). On the other hand, little is known about the ≈70 day period between hatching and fledging (Walkinshaw 1949 *in* Johnsgard 1983) when Sandhill Cranes are most vulnerable to mortality. As this stage of life largely influences recruitment rates it is critical that this gap in knowledge be addressed. Moreover, previous work has generally been limited to studying populations within the contexts of rural/agricultural landscapes or wildlife refuges. The future of the species as sprawling urban development reshapes landscapes at the regional and national levels is unknown (McDonald et al. 2008; Alig et al. 2010).

SANDHILL CRANES IN NORTHEASTERN ILLINOIS

Northeastern Illinois lies within the historical breeding range of the Eastern Population of Greater Sandhill Cranes (Meine & Archibald 1996). The conversion of wetland and grassland habitats (Sampson and Knopf 1994; Dahl and Allord 1996), together with large-scale market hunting (Drewien et al. 1975; Drewien and Lewis 1987; Meine and Archibald 1996), led to the extirpation of breeding cranes from the state between 1876 and 1890 (Ridgeway 1895 *in* Littlefield 1981, Walkinshaw 1949 *in* Johnsgard 1983). The Eastern Population was ultimately reduced to a few dozen breeding pairs in Wisconsin and Michigan by the 1930s (Henika 1936). As in many crane populations at the time, these small remnants were able to persist until hunting prohibition and habitat conservation became more wide spread (Drewien and Lewis 1987; Meine and Archibald 1996). Adaptability to agricultural landscapes also played a role. Cranberry reservoirs and wetland fragments adjacent to agricultural fields provided refuge and served as nesting grounds (Henika 1939; Walkinshaw & Wing 1955) while the immodest consumption of agricultural products broadly sustained the subsequent growth of crane populations in general (Guthery 1976 *in* Johnsgard 1983; Krapu et al. 2004). Remnants of the Eastern Population in Wisconsin thereby rebounded and nesting in northeastern Illinois had resumed by 1979 (Greenberg 1980).

In the Eastern Population, high rates of colt survival (96.60%; Walkinshaw 1981) and average recruitment (12%; Drewien et al. 1995; Table 1.1) together with the expansion of the crane population from south-central Wisconsin described in Su et al. (2004) articulate the species' return to Illinois. However, south-central Wisconsin's predominantly rural/agricultural contexts (Reese et al. 2002; Rhemtulla et al. 2007) are dissimilar to northeastern Illinois' rapidly urbanizing landscape. From 1972 to 1997, urban land cover in northeastern Illinois increased nearly 50% (≈ 111,000 ha) while agricultural landscapes decreased by 37% and natural cover decreased by 21% (i.e. sum of: forests, shrublands, savannas/prairies, and wetlands; Wang and Moskovits 2001). This urban/suburban sprawl and corresponding alteration of habitat and habitat structure is considered a proximal cause of general declines in several wetland-dependent species in the region, including the Common Moorhen (*Gallinula chloropus*), American Coot (*Fulica americana*), Black Tern (*Chlidonias niger*), Sora (*Porzana carolina*), and Least Bittern (*Ixobrychus exilis*; Ward et al. 2010). At the same time, Sandhill Cranes in northeastern Illinois increased at an average annual rate of more than 30% (Northeastern Illinois Wetland Bird Surveys *in* Ward et al. 2010). Considering that cranes are a wetland-dependent species whose abundance in Wisconsin and coastal wetlands around the Great Lakes has been negatively correlated with human disturbance and urban development (Su 2003; Howe et al. 2007), their rapid increase in northeastern Illinois was unexpected. Moreover, previous research on Sandhill Cranes breeding in developed and natural landscapes in Florida concluded that the former may represent reproductive sink habitat (Toland 1999). Without additional data on cranes in northeastern Illinois, however, inferences regarding the growth of the crane population and viability of the region's habitats in supporting it could not be made with certainty.

In light of predicted national and global trends in urbanization (McDonald et al. 2008; Alig et al. 2010), opportunities to investigate the dynamics of crane populations in urban contexts should be pursued and integrated into crane and habitat research and conservation. Additionally, while the strong influence of colt survival and fledging success on recruitment and population growth is apparent in previous research (e.g. Littlefield 1995, 2003; Ivey and Dugger 2008), this stage in the species' life-history remains largely uncharacterized. This thesis specifically addresses colt survival and fledging success for Greater Sandhill Cranes hatched in the urbanized landscape of northeastern Illinois.

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TABLES

Published Data on Nest Success, Colt Survival, and Recruitment									
Species	Location	Years	Average Annual Nest Success	Average Annual Colt Survival	Overall Colt Survival	Recruitment	# Young Fledged per 100 Pairs	Population Status	Source
Greater Sandhill Crane (*G. c. tabida*)	Malheur National Wildlife Refuge, Oregon	1970-1989	49.44%	15.61%	-	6.65%	14.41	Declining	(Littlefield 1995; 2003)
		1970-1971, 1982-1983, 1986-1989	42.89%	11.43%	-	5.05%	10.86		
		1972-1982, 1945-1985	57.86%	20.99%	-	10.11%	19.73		
		1991-1995	-	17.13%	18.70%	-	-	-	(Ivey and Scheuering 1997)
		1990-1998	72.44%	-	-	-	7.5	-	(Ivey and Dugger 2008)
	Modoc National Wildlife Refuge, California	1990, 1992	-	45.00%	45.83%	-	-	Increasing	(Desroberts 1997)
	Michigan	-	69.70 to 78.92%	-	96.60%	-	-		(Walkinshaw 1981)
	Total Eastern Population	-	-	-	-	12.00% average	-		(Drewien et al. 1995)
Florida Sandhill Crane (*G. c. pratensis*)	Okefenokee Swamp, Georgia	1985-1988	56.50%	46.66%	45.95%	9.40%	-	Stable (SAN *in* Tacha et al. 1992)	(Bennett and Bennett 1990)
	Northcentral Florida	1977-1987	-	-	64.90%	-	-		(Nesbitt 1992)

Table 1.1: Previously published data on nest success, colt survival, and recruitment. Average annual nest success and colt survival reflect averages for previously published annual data. Overall colt survival reflects the total number of colts surviving over the course of a multi-year study. Data for Malheur NWR published by Littlefield (1995, 2003) in the top row is followed by years in which predators were not managed at Malheur NWR (red) and years with active predator management (blue). Colt survival in all studies except those highlighted in yellow was either estimated based on the number of birds known to hatch or number of birds in the sample relative to the number of birds known to fledge; or, survival through time. Estimates derived from these methods are comparable. That is, the product of survival estimates for study intervals based on the number of birds surviving an interval / the number of birds alive at the beginning of the interval generate the same estimates as the total number of birds hatching / the total number of birds fledging (i.e. a single interval). Colt survival highlighted in yellow was estimated according to age (e.g. in 10-day intervals beginning one day after hatching; Nesbitt 1992) and is not comparable to the other estimates in the table. However, in this northeastern Illinois study I tested models evaluating survival as a function of age, which are comparable to estimates highlighted in yellow, as well as models where survival varied as a function of time, which are comparable to the bulk of previous research and the remaining estimates listed above.

FIGURES

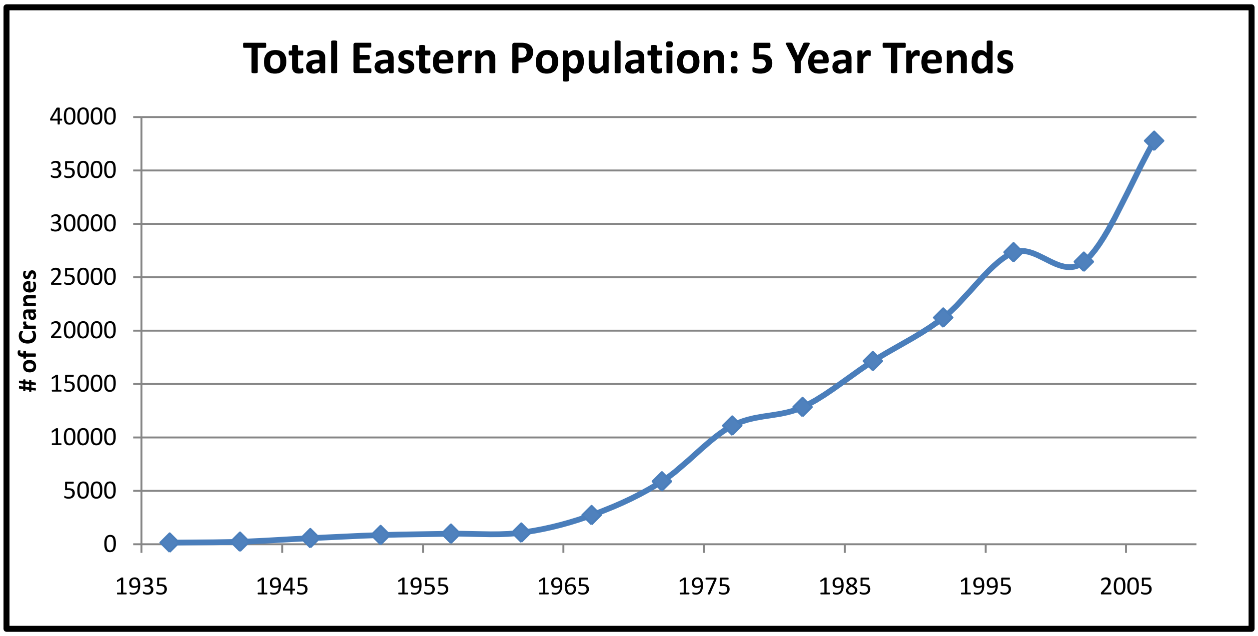

Figure 1.1: Growth of the Eastern Population of Greater Sandhill Cranes since the population's low in the 1930s (Henika 1936; Meine and Archibald 1996); each point represents the median of five year intervals beginning in 1935 and marks the average for population numbers published for the respective five year interval**s**. For example, the first point (1937) is the average of population numbers reported from 1935 to 1939. Data derived from Drewien et al. (1975), Hoffman (1977) *in* Lovvorn and Kirkpatrick (1982a), Walkinshaw (1981), Littlefield (1981), Lovvorn and Kirkpatrick (1982a), Johnsgard (1983), L. E. Schumann (unpublished Data) *in* Tacha et al. (1992), Urbanek (1994) *in* Meine and Archibald (1996), Meine and Archibald (1996), U.S. Fish and Wildlife Service (unpublished Data) *in* Horn et al. (2010).

CHAPTER 2

Sandhill Crane Colt Survival and Fledging Success in Northeastern Illinois: The Role of Age and Significance of Land Cover in an Urbanized Landscape

INTRODUCTION

Sandhill Cranes (*Grus canadensis spp.*) have experienced a rapid recovery after hunting and habitat loss nearly extirpated the species from most of eastern North America (Henika 1936; Stone 1937 *in* Littlefield 1981; Walkinshaw 1949 *in* Johnsgard 1983; Littlefield 1981; Johnsgard 1983; Drewien and Lewis 1987; Meine and Archibald 1996; Melvin 2002). The Eastern Population (EP) of Greater Sandhill Cranes (*G. c. tabida*) increased from a few dozen breeding pairs in Wisconsin and Michigan during the 1930s (Henika 1936) to over 30,000 birds throughout the Great Lakes States by the turn of the century (Meine and Archibald 1996; Horn at al. 2010). In Illinois, breeding pairs from the EP had been extirpated during the late 1800s (Ridgeway 1895 *in* Littlefield 1981, Walkinshaw 1949 *in* Johnsgard 1983) and remained absent until 1979, when a single breeding pair was confirmed nesting in northeastern Illinois (Greenberg 1980). However, from 1980 to 2005, the rate at which Sandhill Cranes increased in northeastern Illinois (33.3% per year; Northeastern Illinois Wetland Bird Surveys *in* Ward et al. 2010) exceeded concurrent rates of increase observed in Wisconsin or the general EP (6.9% and 8.0% per year, respectively; Sauer et al. 2005). The comparatively rapid rate of increase in northeastern Illinois was unexpected for several reasons.

First, since the 1970s urban land cover in northeastern Illinois has increased (≈50%; Wang and Moskovits 2001) and, in turn, urban runoff has increasingly altered the hydrology and habitat structure of extant wetlands in the region (Wright et al. 2006; Ward et al. 2010). Several wetland-dependent species have consequently experienced significant declines (e.g. Least

Bittern; *Ixobrychus exilis*; and Black Tern; *Chlidonias niger*; Ward et al. 2010). Additionally, negative correlations have been observed between urban development and both breeding and non-breeding densities of Sandhill Cranes in Wisconsin (Su 2003) and coastal wetlands around the Great Lakes (Howe et al. 2007). The immigration of the wetland-dependent Sandhill Crane to the urbanized landscape of northeastern Illinois was therefore unexpected. However, as a philopatric species (Baker et al. 1995; International Crane Foundation *in* Su et al. 2004), high rates of fledging success (i.e. survival of young; a.k.a. colts; from post hatching to capable of flight) in northeastern Illinois combined with immigration from an expanding population in Wisconsin (Su et al. 2004) could potentially explained the observed increase of cranes in Illinois. The primary objective of this study was therefore to evaluate the survival and fledging success of Sandhill Crane colts hatched in northeastern Illinois.

The ≈10 week period between hatching and fledging (Walkinshaw 1949 *in* Johnsgard 1983) is perhaps the least well characterized of Sandhill Cranes' life-history. However, high rates of predation and age-based survival are common for precocial species and have been well documented in studies of Galliformes (e.g., Wild Turkeys; *Meleagris gallopavo*; Eaton 1992; Spears et al. 2007), Anseriformes (Canada Geese; *Branta canadensis*; Mowbray et al. 2002), and Charadriformes (e.g. Kildeer; *Charadrius vociferus*; and Snowy Plovers; *Charadrius alexandrinus*; Powell 1992 *in* Colwell et al. 2007; Colwell et al. 2007; Jackson et al. 2000; Page et al. 2009). While predation also appears to be the most common cause of mortality for Sandhill Crane colts (Littlefield and Lindstedt 1992 *in* Littlefield 2003; Littlefield 1995a, 2003; Desroberts 1997; Ivey and Scheureing 1997), the role of age has yet to be empirically confirmed – although, it is certainly an expected trait of the species. To test for the significance of age in colt survival I compared age-based models of survival, in which survival varied as a function of colt age, against temporally-based models, in which survival varied as a function of time.

The number of colts fledged per nest by Sandhill Cranes (*G. c. pratensis*) breeding in natural landscapes (0.86) compared to developed landscapes (0.32; Toland 1999) observed during one study in Florida suggests landscape as well as predation and age may influence colt survival. This study of Florida Sandhill Cranes, however, appears to compose the bulk of published research that explicitly evaluates Sandhill Crane reproductive success in urban landscapes relative to rural/natural habitats. In addition to landscape-based survival, variations in reproductive success within and between breeding seasons have also been observed. For example, annual fluctuations in weather and water levels as well as predator and prey abundance during previous studies resulted in shifts of observed predation- and flood-related nest failure and colt mortality (Austin et al. 2007; Ivey and Scheuering 1997; Ivey and Dugger 2008). Furthermore, increased breeding experience has been correlated with early nesting, selection of larger wetland habitats, and greater nesting and fledging success (Drewien 1973 *in* Tacha et al. 1992; Johnsgard 1983; Nesbitt 1988, 1992; Ivey and Dugger 2008). However, in urban landscapes, the roles of breeding experience in habitat selection and fledging success, potential influences of annual variations in weather and urban runoff, and landscape-based colt survival remain largely unresolved.

In light of predicted national and global trends in urbanization (McDonald et al. 2008; Alig et al. 2010) opportunities to investigate the dynamics of crane populations in urban contexts should be pursued and integrated into crane and habitat research and conservation. After evaluating the role of age in colt survival, I tested the hypothesis that greater fledging success in urban habitats relative to non-urban habitats was a significant factor in the concurrent increase of both cranes and urban development in northeastern Illinois. I then evaluated colt survival between years of the study (i.e. 2008, 2009, or 2010) and used hatch dates to approximate the influence of breeding experience on fledging success in an urbanized landscape. I also estimated colt survival relative to brood status (i.e. whether or not a colt was one of a pair) and the influence of sibling size within broods, two factors which have traditionally been considered influential in colt survival (Drewien 1973 *in* Tacha et al. 1992; Miller 1973; Walkinshaw 1981; Layne 1982; Bergeson et al. 2001), as well as the influence of sibling fates within broods, a topic that has curiously been unexplored by previous research.

METHODS

Study Area and Surveys

The primary study area was in Lake and McHenry Counties in northeastern Illinois (Fig. 2.1). Breeding Sandhill Cranes within this region were located via aerial surveys during the first week of May to coincide with peak hatching (Tacha et al. 1992). Additional breeding birds were located via unison and guard calls during early morning surveys, as well as through coordinated third-party reports (e.g. International Crane Foundation annual crane count).

Capturing and Tracking Cranes

Young cranes were captured a minimum of 48 hours post-hatching. This ensured that young birds were homeothermic (Baldwin 1977 *in* Tacha et al. 1992) and strong and mobile enough to tolerate capture, handling, and the additional mass of the transmitter backpack (≤ 5% mass of bird; similar to methods of Ivey and Scheuring 1997). Captures involved discrete monitoring until opportune moments when colts could be pursued on foot and captured by hand.

Once captured, colts were placed into a cloth bag to reduce capture-related stress. I also used cloth hoods when handling larger older birds. I recorded the date, time, and GPS coordinates of capture as well as colt mass (measured via spring scale), hock-hallux and hock-long toe length (via flexible measuring tape), and apparent physical condition (e.g. presence of deformities, injuries, and/or parasites). A ≈1.5 g single-stage transmitter (JDJC Corporation Sparrow Systems, Fisher, Illinois, USA) was attached to colts during the 2008 and 2009 seasons and used for colts less than 150 g in 2010. During 2010, 6 g two-stage RI-2C transmitters (Holohil Systems, Carp Ontario, Canada) were used on birds larger than 150 g. I prepared transmitters for attachment by sewing them to the center of fabric squares (approximately 7 X 7cm) that approximated the plumage color of colts. Total mass for these transmitter backpacks ranged from 3 to 7.5 g (depending on transmitter type). In the field, transmitter backpacks were trimmed to an appropriate size for captured colts and waterproof, non-toxic, quick-drying eyelash adhesive was applied in sufficient quantity to coat the entire fabric surface. The transmitter backpack was then affixed to the bird's mid-dorsal region. Gentle restraint was required to prevent the wings from contacting uncured adhesive. This procedure was similar to that used by Spalding et al. (2001) and successfully maintained inconspicuous transmitter attachment without retention of moisture or significant irritation to the skin.

I monitored radio-tagged birds at least twice per week. Status of each bird (i.e. dead or alive) was determined via radio-telemetry and visually confirmed when possible. For each occasion, I recorded the date, time, GPS coordinates, and observed activities (e.g. foraging or preening). Mortality was typically evident based on the condition of recovered transmitter backpacks (e.g. the lack of or presence of apparent blood, tissue, and/or significant mechanical damage). When possible, I collected and froze carcasses or partial remains. Issues related to transmitter failure, damage, and/or submersion were generally resolved by monitoring the behaviors and routines (or deviations from them) exhibited by the respective mated pair of adult birds.

Initial captures (radio-tagging) and recaptures, when colts were banded and blood was samples were collected in cooperation with the International Crane Foundation, rarely exceeded 15 minutes. All (i.e. 100%) of the captured colts successfully rejoined their parents post-release. Post-reunion, transmitter backpacks were universally ignored by colts, siblings, and adult birds. Transmitter backpack attachment was not reinforced during final recaptures. This facilitated detachment and transmitter recovery before batteries failed and/or birds ventured well beyond transmitters' range. By approximately 13 weeks of age (3 weeks post-fledging) most transmitters had fallen off of colts and were recovered.

Survival Analysis

I used the staggered-entry method to generate the input file for Program MARK (version 6.0). Colts were censored after their 10th week of life to prevent estimated fledging success from being influenced by survival data for fledged birds. Individuals were divided into 10 cohorts, those that hatched before May 7th composed the first cohort. Subsequent cohorts were comprised of birds with estimated hatch dates of May 8-14th, May 15-21st, May 22-28th, May 29-June 4th, June 5-11th, June 12-18th, June 19-25th, June 26-July 2nd, and July 3-9th. Based on a known-fate model I estimated apparent survival (ϕ) for age-based survival (e.g. survival during the fifth week of life was that same regardless of cohort) and temporally-based survival (survival during the fifth week of the season was the same regardless of colt age). The better supported model (i.e. age-based survival) was subsequently used to evaluate a number of covariates.

Covariates included year of the study (2008, 2009, or 2010), hatching before or after the end of May (i.e. hatch date), whether or not colts had a sibling, sibling size when last captured (larger of pair, smaller of pair, or same size per mass), whether their sibling died, and surrounding land cover. Land cover was categorized as agricultural, grassland/savanna, wooded, wetland, urban, or open water (based on satellite photos from 1999 and 2000 and defined in GIS Layer Source 2003; land cover was updated using personal observations). ESRI ®ArcGIS (ArcMap and ArcCatalog) was used to draw buffers with 1,500 m radii around nest sites. These buffers reflected the wide range of average home ranges previously reported in territorial adult cranes (approximately 132 to 447 ha, equivalent to buffers with approximately 360 and 1,200 m radii; Walkinshaw 1973 *in* Johnsgard 1983, Nesbitt and Williams 1990) plus 370 m to account for a previously reported distance of urban hydrological influence on breeding success in Sandhill Cranes (Dwyer and Tanner 1992). Third party reports, historical nesting records (Semel unpublished data), and available nesting habitats were used in approximating nest sites when they could not be confirmed.

Akaike's Information Criterion (AICc, adjusted for sample size) was used to evaluate a suite of 36 candidate models (White and Burnham 1999, Burnham and Anderson 2002). These models tested distinct hypothesis including the influence of year (e.g. fluctuations in precipitation and temperature), hatch date (i.e. an approximation of breeding experience), individual land covers, and sibling status on fledging success. Models including interactions between hatch date and land cover were used to approximate the interaction between breeding experience and habitat selection, while an additional model evaluated potential annual variations interacting with breeding experience (e.g. experienced breeders are less likely to nest when water levels are low; Nesbitt 1992). To further explore the interaction between breeding experience and habitat selection I separately used a two-tailed t-test to compare the average percentage of each land cover for birds hatching before the end of May to average land cover for those that hatched after May. Remaining known-fate models evaluated interactions between year and land cover (e.g. to test for interactions between annual changes urban runoff or crop rotation and colt survival) or year and sibling status (e.g. to test for interactions between the availability of food between years and sibling-strife; Quale 1976 *in* Tacha et al. 1992). The apparent survival estimates were retrieved from model averaging and evidence ratios were used to determine the relative importance of each variable in colt survival (Burnham and Anderson 2002).

RESULTS

I captured a total of 85 colts (8 in 2008, 39 in 2009, and 38 in 2010; Table 2.2). Fates of 5 were unknown in 2009 and the fate of 1 was unknown in 2010. Of these 79 cranes with known fates, 40 (51%) survived to independence and 39 (49%) died (Table 2.2). Of the individuals that died, 20 were depredated, 2 died of human-related activities, and 17 died of unknown causes (Table 2.2). Note that the age of colts when first captured ranged from 48 hours to > 9 weeks of age, and therefore the number of birds fledged (40) relative to the number of birds with known fates (79) by no means suggests that the probability of survival from hatching to fledging was 51%.

Evidence ratios between models revealed age-based survival was 120 times better supported than temporally-based survival (Table 2.3). Model-averaged estimates of age-based models revealed the overall probability of fledging was 32.44% and that survival increased as colts aged (Table 2.5; Figs. 2.2 and 2.3, respectively). However, survival over time (e.g. # of *G. c. tabita* colts fledged by September relative to # of colts known to hatch; Littlefield 1995a, 2003) is a more common method of estimating colt survival in previous research. To provide a frame of reference between studies, I also generated model averaged estimates for temporally-based survival models (14.46%; Table 2.5). While evidence ratios also revealed that the relative size of siblings within broods was the least well supported covariate in explaining colt survival (Table 2.3), significant differences based on evidence and likelihood ratios between the remaining models or between summed AICc weights for model sets were not apparent (Tables 2.3 and 2.4). Although, after colt age, the relative ranking of models (Table 2.3) together with summed AICc weights (Table 2.4) suggest that hatch date, year, sibling fate, and wetland land cover explained observed survival best.

Hatch date models revealed contrasting survival between colts hatched before the end of May (35.55%) and colts that hatched later (10.34%; Table 2.5). Survival during 2009 (46.39%) was also more than twice survival during 2008 (19.64%) or 2010 (22.04%; Table 2.5). However, relative to hatch date and year, the death of one colt in a brood appeared to have the greatest influence on survival. Specifically, mortality of one colt in a brood reduced the probability of the other colt fledging from 50.87% to 17.93% (Table 2.5). The correlation between fledging success and wetland land cover was stronger and more positively correlated than observed for other land covers (Fig. 2.4). However, urban and open water land covers were also correlated with greater fledging success, while increases in grassland/savanna, agriculture, or wooded land cover resulted in decreased probabilities of fledging (Fig. 2.4). An interaction was also apparent between hatch date and wetland land cover (Table 2.3; Fig. 2.5) and, after dropping land cover data for a single bird as an outlier, average wetland cover around nests that hatched before the end of May was significantly greater than for nests hatching later ($df = 16$, $t = 2.6$, $P < 0.02$; no overlap in 95% Confidence Intervals; Fig. 2.6). A second interaction between year and open water (Table 2.3) also appeared to influence fledging success, with survival during 2010 negatively correlated with open water while survival in 2008 and 2009 was positively correlated with increases in open water (Table 2.3; Fig. 2.7).

DISCUSSION

The results of this study confirmed the role of age in the survival of Sandhill Crane colts (Table 2.3). However, the age-based probability of fledging for colts hatched in northeastern Illinois (32.44%; Table 2.5; Fig. 2.2) was far lower than age-based survival observed in Florida Sandhill Cranes (45.95% to 64.90%; Bennett and Bennett 1990; Nesbitt 1992; Table 2.6). Temporally-based colt survival estimates (14.46% overall 14.14% average annual; Table 2.5) were also lower than previously observed at Modoc National Wildlife Refuge (NWR) in California (45% average annual; Desroberts 1997) or during the 1970s and 1980s in a declining population at Malheur NWR in Oregon (15.61% average annual; Littlefield 1995a, 2003; Table 2.6). At Malheur NWR, high rates of colt mortality via predation (52% to 68%; Littlefield and Lindstedt 1992 *in* Littlefield 2003; Ivey and Scheuering 1997) were the primary causes decline (Littlefield 1995a, 2003) and reduced productivity (Ivey and Dugger 1998; Table 2.6). I observed similar rates of predation-related colt mortality in northeastern Illinois (51%; Table 2.2).

I suspect that predation, perhaps by the same local predator that depredated the first colt, was responsible for the correlation between sibling fates. Specifically, if a colt was one of a pair and had a living sibling, the probability of fledging was 50.87% (Table 2.5). If that sibling died the probability of fledging dropped to 17.93% (Table 2.5). The high ranking and relative support for sibling fate models (Tables 2.3 and 2.4) indicates the strength of this relationship. At the same time, models evaluating the influence of sibling sizes within broods, or whether or not colts were one of a pair, were among the least well supported (Tables 2.3 and 2.4). These results contrast with much of the previous research; the general consensus of which suggests a dichotomy in sibling size, perhaps due to asynchronous hatching, frequently results in a dominance-hierarchy and inter-sibling strife leading to mortality of the smaller colt (Drewien

1973 *in* Tacha et al. 1992; Miller 1973; Walkinshaw 1981). For example, mortality of smaller colts via sibling-strife in a study of Whooping Cranes (*G. americana*) was considered a proximal cause of 44% of larger colts fledging as compared to 11% of smaller colts (Bergeson et al. 2001). Previous research has also observed sibling-strife may be influenced by annual variations in resources (e.g. the availability of food; Quale 1976 *in* Tacha et al. 1992). In my study, I observed physical conflict between siblings on only one occasion and attribute this to capture-related stress (i.e. both had just been radio-tagged and released). I also found no physical or circumstantial evidence of sibling-strife-related mortalities and there was little support for annual variations in sibling fates (Tables 2.3 and 2.4).

The interaction between wetland land cover and hatch date (Table 2.3) as well as the high ranking and summed weights of wetland and hatch date covariates (Tables 2.3 and 2.4, respectively) support prominent roles for breeding experience and wetlands in fledging success. In wetlands, the significance of natural buffers against predation (e.g. water; Sargeant and Arnold 1984; Arnold et al. 1993) in facilitating nest and fledging success is well known (Nesbitt 1988, 1992; Nesbitt and Williams 1990; Austin et al. 2007; Ivey and Dugger 2008). As these buffers are inherently augmented with increased wetland size, the factors underlying the positive correlation between fledging success and wetlands I observed in northeastern Illinois (Fig. 2.4) are apparent. Previous studies have also emphasized the role of breeding experience in fledging success. For example, experienced breeding pairs are more productive (i.e. fledge more young per year; Nesbitt 1992) and return to breeding territories earlier in the season to initiate nests (Nesbitt 1992; Ivey and Dugger 2008) and ward off conspecifics (Drewien 1973 *in* Tacha et al. 1992; Johnsgard 1983; Baker et al. 1995). Accordingly, I found that colts hatched before the end of May survived better than colts that hatched later (35.55% and 10.34%, respectively; Table

2.5). Significantly greater average wetland land cover around nests that hatched before the end of May (Fig. 2.6) also suggests that habitat selection by experienced breeders may be influenced by the quantity of wetland habitat. In turn, I hypothesize that the selection and occupation of larger wetland habitats by experienced breeding pairs early in the season relegated the younger/less experienced pairs arriving later to smaller wetlands and wetland peripheries (i.e. where their late-hatching colts were more vulnerable to predation), and that this was why fledging success for colts hatched after May was negatively correlated with larger wetland habitats (Fig. 2.5). While I was unable to conclusively support this hypothesis with the available data, the significance of breeding experience and habitat selection in avian species (Part 2001) as well as for wetlands in habitat selection and occupation by breeding Sandhill Cranes has broadly been established by previous research (Nesbitt and Williams 1990; Tacha et al. 1992; Meine and Archibald 1996; Su 2003).

On the other hand, the results of a preceding study evaluating fledging success between landscapes in Florida found that 54% fewer colts fledged per nest in developed sites compared to natural landscapes (Toland 1999). This contrasts with my observations of greater fledging success in more urbanized areas than in adjacent non-wetland habitats (Fig. 2.4). While differences in predator communities between study regions may partly explain this contrast (e.g. there are no alligators; *Alligator mississippiensis*; in northeastern Illinois), I suspect my findings were largely the result of predator behaviors and hunting habits. Common colt predators such as coyotes and raccoons (Johnsgard 1982; Littlefield 1995a, 1995b, 2003) typically avoid human activity (Prange et al. 2003; Gehrt et al. 2009). Urban coyotes also primarily rely on hunting in natural and undeveloped habitat fragments for sustenance (Gehrt et al. 2009), while common birds of prey (e.g. Red-Tailed Hawks; *Buteo jamaicensis*; and Great-Horned Owls; *Bubo* *virginianus*) typically hunt in more open landscapes with available perches (e.g. silos and telephone poles; Houston et al. 1998; Preston et al. 2009). Thus, human-avoidance behaviors and the hunting habits of predators in northeastern Illinois likely buffered cranes acclimated to urban habitats from predation while increasing predator-crane encounters in adjacent agricultural landscapes and grassland/savanna habitats (Fig. 2.4). Supporting this conclusion is the fact that all confirmed predation-related mortalities in urban landscapes during this study occurred in small isolated/undeveloped habitat fragments within the landscape or along the landscape perimeter.

Direct relationships between land covers might also explain variations in apparent landscape-based survival. For example, the positive correlation between fledging success and wetland habitat in this study echoes similar findings in Sandhill Crane nest success and productivity studies (e.g. Nesbitt 1988, 1992). At the same time, the positive correlation between fledging success and urban habitats I observed in northeastern Illinois contrasts with previously published results for a crane study in urban habitats (e.g. Toland 1999). The positive correlation between urban and wetland land covers around nest sites in northeastern Illinois (Fig. 2.4) was likely contributory in the apparent relationship between urban habitats and fledging success. I also suspect that the apparent interaction between year and open water (Table 2.3 and Fig. 2.7) was primarily due to urban runoff influencing the hydrology of adjacent landscapes. That is, urban runoff from greater precipitation during May of 2010 (124 mm, + 40 mm from average) relative to 2008 (104 mm) and 2009 (92 mm; National Environmental Satellite, Data, and Information Service 2010) perhaps forced cranes at the low points of the water shed (i.e. near open water) to wetland peripheries and upland habitats, where encounters with predators were more likely.

CONCLUSION AND FUTURE RESEARCH

Colt survival in northeastern Illinois during this study (Table 2.5) did not support a prominent role for local fledging success in the rapid increase of Sandhill Cranes in the region (Northeastern Illinois Wetland Bird Surveys *in* 33.3% per year; Ward et al. 2010). Instead, overall rates of predation (51%; Table 2.2) and fledging success (14.14%; Table 2.5) resembled observations of a study on a declining population at Malheur NWR in Oregon (Littlefield and Lindstedt 1992 *in* Littlefield 2003; Littlefield 1995a, 2003; Table 2.6). While the urbanized landscape of northeastern Illinois may not be conducive to breeding productivity in Sandhill Cranes, the concentration of wetlands in the region (approximate 130,000 ha in Lake and McHenry Counties; Suloway and Hubbell 1994) does appear to draw significant numbers of birds from the expanding EP in Wisconsin. Without this immigration, my findings suggest that Sandhill Cranes in northeastern Illinois would likely begin to decline.

The results of this study also reveal fledging success for Sandhill Cranes in northeastern Illinois is positively associated with early hatching and wetland size. I attribute these findings to experienced breeders selecting larger wetland habitats and initiating nests earlier than younger/less experienced pairs. Wetland habitats should therefore be a priority in facilitating the productivity of Sandhill Cranes breeding in northeastern Illinois. While prominent roles for wetland size and breeding experience in fledging success have been broadly established by previous research, my observations do contrast with studies where fledging success was lowest in urbanized landscapes (e.g. in Florida; Toland 1999). In northeastern Illinois, greater fledging success in urban habitats relative to adjacent non-wetland habitats (Fig. 2.4) was likely due to predators' human-avoidance behaviors and use of natural and undeveloped habitat fragments for hunting (e.g. coyotes; Gehrt et al. 2009). Overall high rates of predation and low fledging success, though, suggest predator management as well as wetland conservation/restoration may improve breeding productivity in northeastern Illinois. The effectiveness of habitat management (increased nest success) and predator management (increased colt survival) in facilitating productivity at Malheur NWR in the past (Littlefield 1995a, 1995b) supports this approach.

However, more research is needed to resolve the population dynamics of cranes in northeastern Illinois. If, for example, survival during 2009 rather than 2008 and 2010 (Table 2.5) was more representative of reproductive success in the region, then Sandhill Cranes may be able to maintain population growth or stability in similar urban habitats without significant immigration. Additional research is therefore necessary to determine the viability of northeastern Illinois' urban wetlands in supporting breeding cranes. Furthermore, several colts in this study died within three weeks post-fledgling (19.62% of birds known to fledge). One was hit by a car and three were likely predated. To what extent do urban habitats directly affect mortality rates for fledged birds and how might landscape influence learned behavior? Do cranes reared in urban landscapes spend equal amounts of time and effort scanning for predators as their rural counterparts and do they respond to predators the same way? More importantly, a 49% increase of urban land cover around Chicago corresponded with a 4% increased in the human population (1970 to 1990; Wang and Moskovits 2001) and during the first quarter of the 21st century the region's population is expected to increase 25% (Northeastern Illinois Planning Commission *in* Wang and Moskovits 2001). As urban sprawl around the Great Lakes region accelerates (Alig et al. 2010) it is possible that the breeding productivity of Sandhill Cranes in urban habitats may begin to influence overall recruitment in the EP. Future studies should aim to resolve the role of urban habitats in source-sink dynamics to facilitate proactive crane conservation and management.

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TABLES

Model	K	AICc	ΔAIC	*wi*
ϕ(Age, Year + Hatch Date + Wetland + (Hatch Date * Wetland))	16	258.20	0.00	0.08
ϕ(Age, Hatch Date)	12	258.39	0.19	0.08
ϕ(Age, Year + Sibling Fate)	15	258.56	0.35	0.07
ϕ(Age, Year + Hatch Date + Urban)	15	258.71	0.51	0.07
ϕ(Age, Year + Hatch Date)	14	258.76	0.56	0.06
ϕ(Age, Year + Hatch Date + Wetland)	15	258.83	0.63	0.06
ϕ(Age, Year + Hatch Date + Open Water + (Year * Open Water))	17	258.94	0.74	0.06
ϕ(Age, Year + Hatch Date + Grassland/Savanna)	15	259.12	0.92	0.05
ϕ(Age, Year)	13	259.63	1.43	0.04
ϕ(Age, Year + Hatch Date + Agriculture)	15	260.13	1.93	0.03
ϕ(Age, Year + Sibling Fate + (Year * Sibling Fate))	17	260.23	2.03	0.03
ϕ(Age, Sibling Fate)	13	260.34	2.14	0.03
ϕ(Age, Urban)	12	260.48	2.28	0.03
ϕ(Age, Wetland)	12	260.49	2.29	0.03
ϕ(Age, Year + Hatch Date + Open Water)	15	260.49	2.29	0.03
ϕ(Age, Year + Hatch Date + Wooded)	15	260.65	2.45	0.02
ϕ(Age)	11	260.81	2.61	0.02
ϕ(Age, Agriculture)	12	260.81	2.61	0.02
ϕ(Age, Year + Hatch Date + Urban + (Hatch Date * Urban))	16	260.85	2.65	0.02
ϕ(Age, Grassland/Savanna)	12	261.21	3.01	0.02
ϕ(Age, Year + Hatch Date + Grassland/Savanna + (Hatch Date * Grassland/Savanna))	16	261.27	3.07	0.02
ϕ(Age, Open Water)	12	261.36	3.16	0.02
ϕ(Age, Year + Hatch Date + Wetland + (Year * Wetland))	17	261.64	3.44	0.02
ϕ(Age, Year + Hatch Date + Agriculture + (Hatch Date * Agriculture))	16	261.87	3.67	0.01
ϕ(Age, Year + Hatch Date + Urban + (Year * Urban))	17	262.28	4.08	0.01
ϕ(Age, Year + Hatch Date + (Year * Hatch Date))	16	262.41	4.21	0.01
ϕ(Age, Year + Hatch Date + Grassland/Savanna + (Year * Grassland/Savanna))	17	262.43	4.23	0.01
ϕ(Age, Year + Hatch Date + Open Water + (Hatch Date * Open Water))	16	262.63	4.43	0.01
ϕ(Age, Year + Hatch Date + Wooded + (Hatch Date * Wooded))	16	262.76	4.56	0.01
ϕ(Age, Sibling Present)	12	262.90	4.70	0.01
ϕ(Age, Wooded)	12	262.93	4.73	0.01
ϕ(Age, Year + Hatch Date + Agriculture + (Year * Agriculture))	17	263.35	5.15	0.01
ϕ(Age, Year + Hatch Date + Wooded + (Year * Wooded))	17	263.39	5.19	0.01
ϕ(Age, Sibling Size)	14	266.52	8.32	0.00
ϕ(Temporal, Year)	18	268.00	9.80	0.00
ϕ(Temporal)	16	270.43	12.23	0.00

Table 2.1: Models evaluating apparent survival of Sandhill Crane colts from hatching week to fledging age at 10 weeks old. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AICc). K is the number of parameters in the model, ΔAIC is the difference in AICc values from the most supported model, and w_i is the model weight. In these models, ϕ is apparent survival probability; Age models evaluate survival according to colt age (in weeks); Temporal models evaluate survival according to time; Year is the year of the study; Hatch Date is whether or not the bird hatched before the end of May; Sibling Present is whether or not the colt was one of a pair or independent when first captured; Sibling Size is whether a colt with a sibling was larger, smaller, or of equal size (per mass) relative to the sibling; Sibling Fate is whether or not a colt from a pair had a sibling that died; and land covers are as listed in the models (i.e. Wetland, Grassland/Savanna, Agriculture, Urban, Wooded, or Open Water).

Colt Fates	2008	2009	2010	Total
Captured	8	39	38	85
Censored	0	5	1	6
Fledged	3	21	16	40
Mortality	5	13	21	39
Predation	4	9	7	20
Canid	1	2	2	5
Raccoon	0	1	0	1
Avian	0	3	0	3
Unknown Predator	3	3	5	11
Unknown	1	3	13	17
Observed Absent	0	0	7	7
Trauma With Unknown Cause	1	3	6	10
Human-related	0	1	1	2
Study Related	0	1	0	1
Hit By Car	0	0	1	1

Table 2.2: Sandhill Crane colt fates for each year of the study and known causes of mortality. Censored birds represent birds those with unresolved fates that were removed from the analysis prior to fledging. Note that the age of colts when first captured ranged from 48hrs to > 9 weeks, and therefore the number of birds fledged (40) relative to the number of birds with known fates (79) does not suggest that the probability of survival from hatching to fledging is 51%.

Evidence Ratios		Model #	# 34	# 35	# 36
		AICc Weights	0.00131	0.00062	0.00019
# 1	ϕ(Age, Year + Hatch Date + Wetland + (Hatch Date * Wetland))	0.08405	64.16	135.56	442.37
#2	ϕ(Age, Hatch Date)	0.07662	58.49	123.58	403.26
# 3	ϕ(Age, Year + Sibling Fate)	0.07039	53.73	113.53	370.47
# 4	ϕ(Age, Year + Hatch Date + Urban)	0.06527	49.82	105.27	343.53
# 5	ϕ(Age, Year + Hatch Date)	0.06352	48.49	102.45	334.32
# 6	ϕ(Age, Year + Hatch Date + Wetland)	0.06129	46.79	98.85	322.58
# 7	ϕ(Age, Year + Hatch Date + Open Water + (Year * Open Water))	0.05794	44.23	93.45	304.95
# 8	ϕ(Age, Year + Hatch Date + Grassland/Savanna)	0.053	40.46	85.48	278.95
# 9	ϕ(Age, Year)	0.04118	31.44	66.42	216.74
# 10	ϕ(Age, Year + Hatch Date + Agriculture)	0.03207	24.48	51.73	168.79
# 11	ϕ(Age, Year + Sibling Fate + (Year * Sibling Fate))	0.03042	23.22	49.06	160.11
# 12	ϕ(Age, Sibling Fate)	0.02881	21.99	46.47	151.63
# 13	ϕ(Age, Urban)	0.02689	20.53	43.37	141.53
# 14	ϕ(Age, Wetland)	0.0268	20.46	43.23	141.05
# 15	ϕ(Age, Year + Hatch Date + Open Water)	0.02678	20.44	43.19	140.95
# 16	ϕ(Age, Year + Hatch Date + Wooded)	0.02468	18.84	39.81	129.89
# 17	ϕ(Age)	0.02282	17.42	36.81	120.11
# 18	ϕ(Age, Agriculture)	0.02278	17.39	36.74	119.89
# 19	ϕ(Age, Year + Hatch Date + Urban + (Hatch Date * Urban))	0.02231	17.03	35.98	117.42
# 20	ϕ(Age, Grassland/Savanna)	0.01867	14.25	30.11	98.26
# 21	ϕ(Age, Year + Hatch Date + Grassland/Savanna + (Hatch Date * Grassland/Savanna))	0.01814	13.85	29.26	95.47
# 22	ϕ(Age, Open Water)	0.0173	13.21	27.90	91.05
# 23	ϕ(Age, Year + Hatch Date + Wetland + (Year * Wetland))	0.01503	11.47	24.24	79.11
# 24	ϕ(Age, Year + Hatch Date + Agriculture + (Hatch Date * Agriculture))	0.01341	10.24	21.63	70.58
# 25	ϕ(Age, Year + Hatch Date + Urban + (Year * Urban))	0.01095	8.36	17.66	57.63
# 26	ϕ(Age, Year + Hatch Date + (Year * Hatch Date))	0.01024	7.82	16.52	53.89
# 27	ϕ(Age, Year + Hatch Date + Grassland/Savanna + (Year * Grassland/Savanna))	0.01016	7.76	16.39	53.47
# 28	ϕ(Age, Year + Hatch Date + Open Water + (Hatch Date * Open Water))	0.00917	7.00	14.79	48.26
# 29	ϕ(Age, Year + Hatch Date + Wooded + (Hatch Date * Wooded))	0.00859	6.56	13.85	45.21
# 30	ϕ(Age, Sibling Present)	0.008	6.11	12.90	42.11
# 31	ϕ(Age, Wooded)	0.00791	6.04	12.76	41.63
# 32	ϕ(Age, Year + Hatch Date + Agriculture + (Year * Agriculture))	0.00639	4.88	10.31	33.63
# 33	ϕ(Age, Year + Hatch Date + Wooded + (Year * Wooded))	0.00629	4.80	10.15	33.11
# 34	ϕ(Age, Sibling Size)	0.00131	1.00	2.11	6.89
# 35	ϕ(Temporal, Year)	0.00062	-	1.00	3.26
# 36	ϕ(Temporal)	0.00019	-	-	1.00

Table 2.3: Models evaluating apparent survival of Sandhill Crane colts from hatching week to fledging age at 10 weeks old. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AICc). Values in the third column from left and second row from top right are model weights (w_i). Values to the right and below the model weights are evidence ratio. For example, model # 3 from the second column (left) was 53.73 times better supported than model # 34 (top right) (i.e. 0.0739 / 0.00131 = 53.73). Values highlighted in red represent models with relative model likelihoods of ≥ 95%. For example, model # 15 was ≥ 95% more likely in explaining observed survival relative to model # 34. Evidence ratios and model likelihoods that were not representative of ≥ 95% likelihoods were omitted from the table, but evidence ratios of interest may be calculated based on respective model weights in the third column (i.e. the model with greater weight / the model with less weight = evidence ratio between the two models). Note the higher ranking of the hatch date X wetland model (model # 1) relative to the additive model without the interaction (model # 6) and the year X open water model (model # 7) relative to model # 15.

Model Sets		Hatch Date	Year	Land Cover	Wetland	Urban	Open Water	Grassland/ Savanna	Agriculture	Wooded	Sibling Status	Sibling Fate	Sibling Present	Sibling Size
	Summed AICc Weights	0.6759	0.7413	0.6459	0.1872	0.1254	0.1112	0.1000	0.0747	0.0475	0.1389	0.1296	0.0080	0.0013
Hatch Date	0.6759	1.00	0.91	1.05	-	-	-	-	-	-	-	-	-	-
Year	0.7413	-	1.00	1.15	-	-	-	-	-	-	-	-	-	-
Land Cover	0.6459	-	-	1.00	-	-	-	-	-	-	-	-	-	-
Wetland	0.1872	-	-	-	1.00	1.49	1.68	1.87	2.51	3.94	1.35	1.44		
Urban	0.1254	-	-	-	-	1.00	1.13	1.25	1.68	2.64	0.90	0.97	-	-
Open Water	0.1112	-	-	-	-	-	1.00	1.11	1.49	2.34	0.80	0.86	-	-
Grassland/Savanna	0.1000	-	-	-	-	-	-	1.00	1.34	2.11	0.72	0.77	-	-
Agriculture	0.0747	-	-	-	-	-	-	-	1.00	1.57	0.54	0.58	-	-
Wooded	0.0475	-	-	-	-	-	-	-	-	1.00	0.34	0.37	-	-
Sibling Status	0.1389	-	-	-	-	-	-	-	-	-	1.00	1.07	-	-
Sibling Fate	0.1296	-	-	-	-	-	-	-	-	-	-	1.00	-	-
Sibling Present	0.0080	-	-	-	-	-	-	-	-	-	-	-	1.00	6.11
Sibling Size	0.0013	-	-	-	-	-	-	-	-	-	-	-	-	1.00

Table 2.4: Summed AICc weights (second column and second row) for selected model sets (based on individual model weights in the fifth column of Table 2.1). Values in the matrix represent evidence ratios between summed weights for model sets represented by an approximately equal # of individual models. For example, the summed weight for models including wetland land cover (0.1872) relative to the summed weight for wooded land cover (0.0475) reveals wetland land cover models were 3.94 times better supported than woodland land cover models in explaining observed Sandhill Crane colt survival.

Age-Based Survival				Estimate	S.E.
			Overall	32.44%	6.56%
			Average Weekly	89.64%	-
Year			2008	19.64%	15.56%
			2009	46.39%	10.19%
			2010	22.04%	8.16%
			Average Annual Survival	29.36%	-
Hatch Date			Hatched Before End of May	35.55%	6.89%
			Hatched After May	10.34%	9.12%
Sibling Status			No Sibling	33.05%	9.92%
			Have Sibling	31.12%	7.21%
	Have Sibling		Larger of Sibling	36.83%	13.34%
			Smaller of Sibling	31.31%	12.39%
			Siblings Same Size	24.88%	10.20%
		Sibling Fate	Sibling Alive	50.87%	13.24%
			Sibling Died	17.93%	7.25%
Temporally-Based Survival				Estimate	S.E
			Overall	14.46%	5.81%
			Average Weekly	89.39%	-
Year			2008	6.31%	7.87%
			2009	30.37%	10.88%
			2010	5.73%	4.01%
			Average Annual Survival	14.14%	-

Table 2.5: Estimates of Sandhill Crane colt survival (standard errors in right column). Age-based estimates calculated based on colt age (i.e. from hatching to fledging at ≈10 weeks of age). Temporally-based estimates based on survival for birds in the sample from the beginning of March to the end of the third week in August (i.e. irrespective of colt age).

Published Data on Nest Success, Colt Survival, and Recruitment									
Species	Location	Years	Average Annual Nest Success	Average Annual Colt Survival	Overall Colt Survival	Recruitment	# Young Fledged per 100 Pairs	Population Status	Source
Greater Sandhill Crane (*G. c. tabida*)	Malheur National Wildlife Refuge, Oregon	1970-1989	49.44%	15.61%	-	6.65%	14.41	Declining	(Littlefield 1995; 2003)
		1970-1971, 1982-1983, 1986-1989	42.89%	11.43%	-	5.05%	10.86		
		1972-1982, 1945-1985	57.86%	20.99%	-	10.11%	19.73		
		1991-1995	-	17.13%	18.70%	-	-	-	(Ivey and Scheuering 1997)
		1990-1998	72.44%	-	-	-	7.5	-	(Ivey and Dugger 2008)
	Modoc National Wildlife Refuge, California	1990, 1992	-	45.00%	45.83%	-	-	Increasing	(Desroberts 1997)
	Michigan	-	69.70 to 78.92%	-	96.60%	-	-		(Walkinshaw 1981)
	Total Eastern Population	-	-	-	-	12.00% average	-		(Drewien et al. 1995)
Florida Sandhill Crane (*G. c. pratensis*)	Okefenokee Swamp, Georgia	1985-1988	56.50%	46.66%	45.95%	9.40%	-	Stable (SAN *in* Tacha et al. 1992)	(Bennett and Bennett 1990)
	Northcentral Florida	1977-1987	-	-	64.90%	-	-		(Nesbitt 1992)

Table 2.6: Previously published data on nest success, colt survival, and recruitment. Average annual nest success and colt survival reflect averages for previously published annual data. Overall colt survival reflects the total number of colts surviving over the course of a multi-year study. Data for Malheur NWR published by Littlefield (1995, 2003) in the top row is followed by years in which predators were not managed at Malheur NWR (red) and years with active predator management (blue). Colt survival in all studies except those highlighted in yellow was either estimated based on the number of birds known to hatch or number of birds in the sample relative to the number of birds known to fledge; or, survival through time. Estimates derived from these methods are comparable. That is, the product of survival estimates for study intervals based on the number of birds surviving an interval / the number of birds alive at the beginning of the interval generate the same estimates as the total number of birds hatching / the total number of birds fledging (i.e. a single interval). Colt survival highlighted in yellow was estimated according to age (e.g. in 10-day intervals beginning one day after hatching; Nesbitt 1992) and is not comparable to the other estimates in the table. However, in this northeastern Illinois study I tested models evaluating survival as a function of age, which are comparable to estimates highlighted in yellow, as well as models where survival varied as a function of time, which are comparable to the bulk of previous research and the remaining estimates listed above.

FIGURES

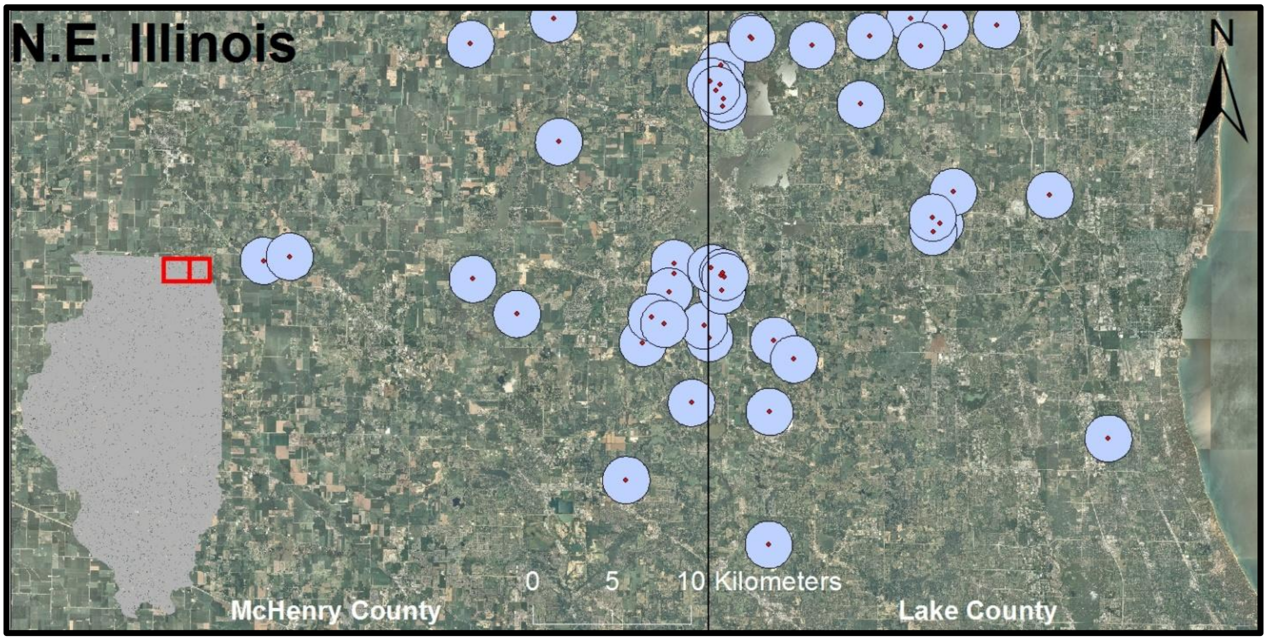


Figure 2.1: Study region in northeastern Illinois; McHenry County (left) and Lake County (right). Nest sites (red points) and 1,500 m buffers around nest sites (blue circles) used to calculate % land cover. Note that Lake Michigan is the easternmost feature and that the Wisconsin border is immediately to the north.

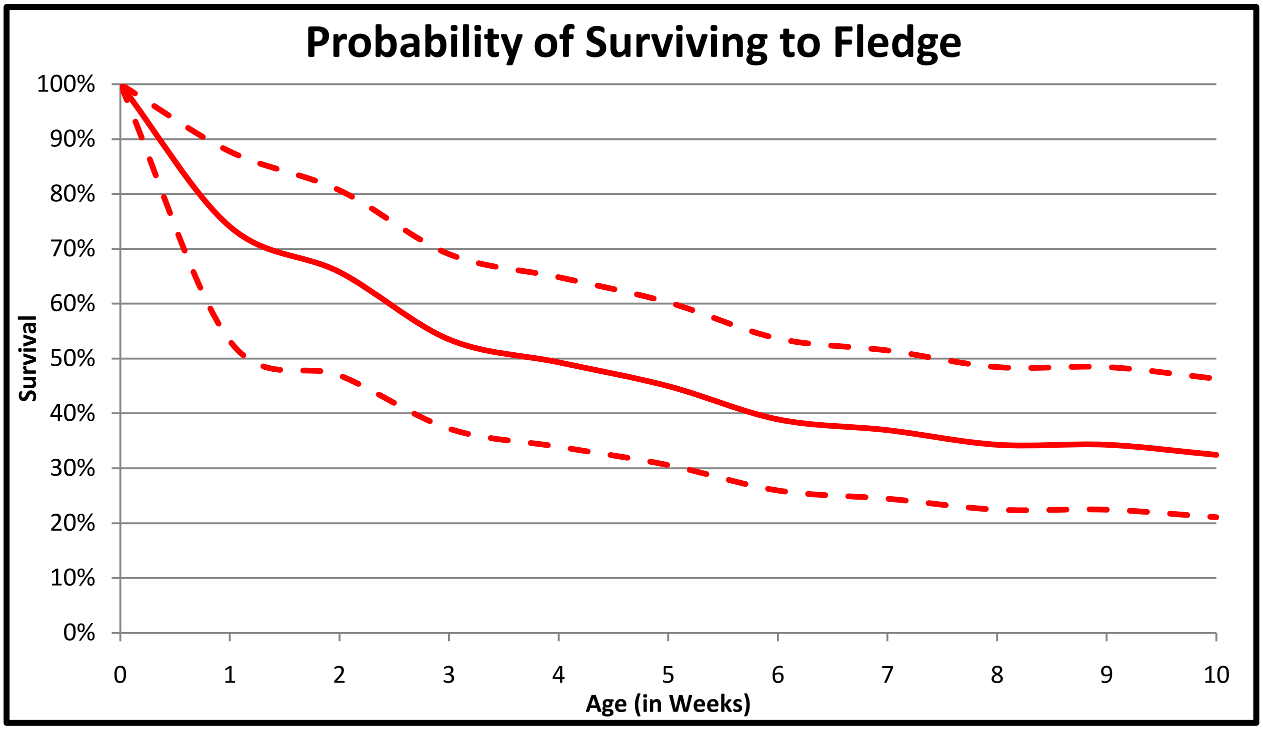


Figure 2.2: The overall probability of survival (y-axis) from hatching to the end of x-axis specified age (in weeks); hatched lines represent 95% confidence intervals. For example, the probability of survival from hatching to the end of the third week of age is approximately 53% and the probability of surviving to the end of the 10th week of age and fledging is 32.44%. Note these estimates are the products of weekly survival in Fig. 2.3.

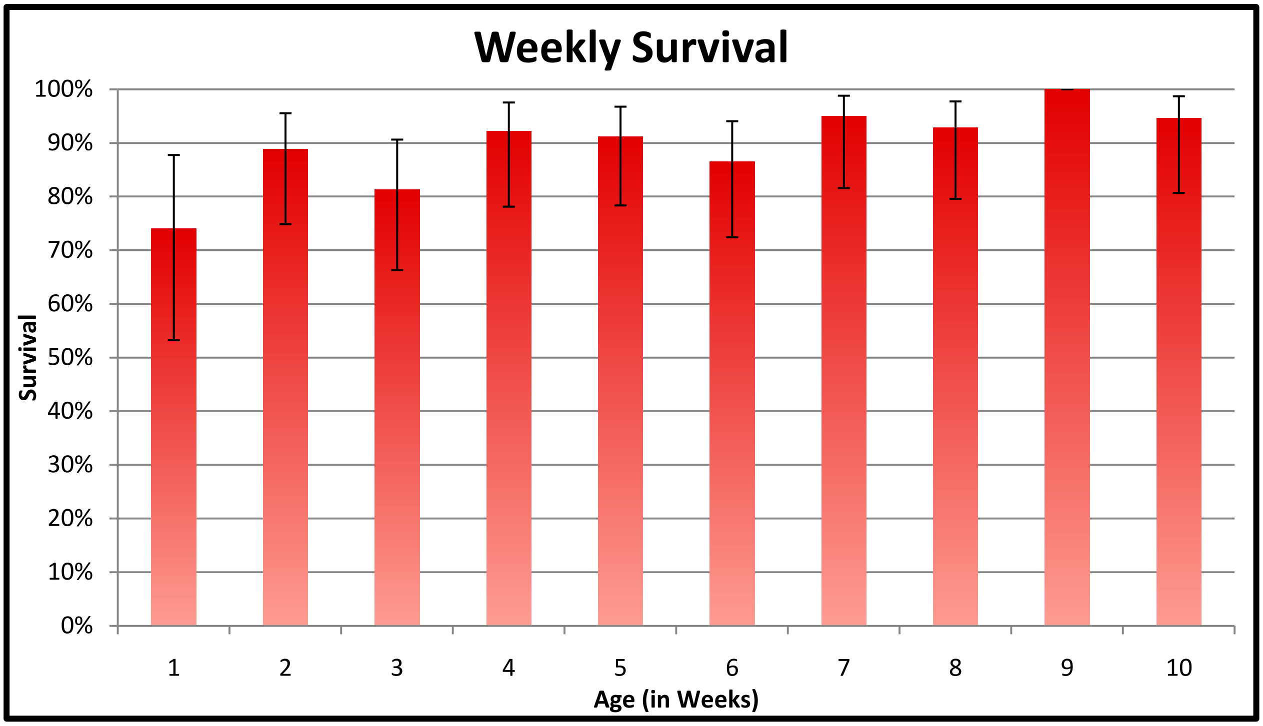
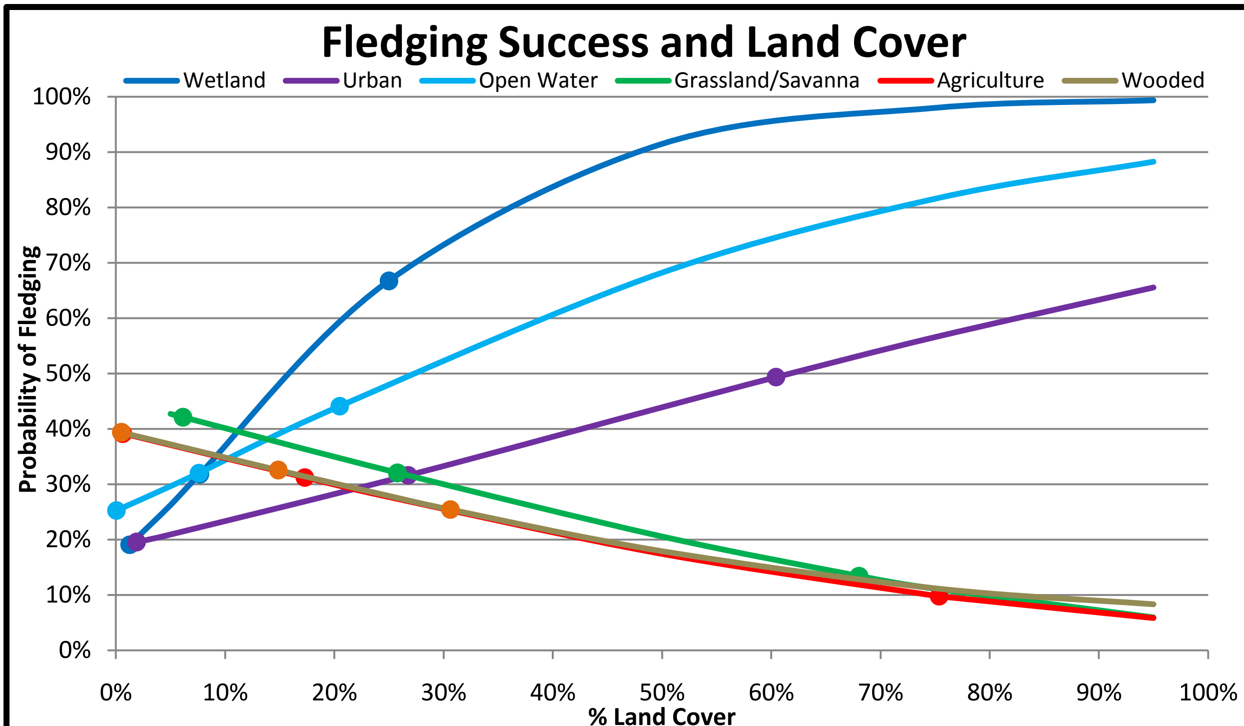


Figure 2.3: The probability of survival (y-axis) for a given week of age (x-axis); error bars represent 95% confidence intervals. Note the general trend of increased probabilities of survival with increased week of age.



Model Weights Within Land Cover	Land Cover	Colt Survival (Slope)	Wetland	Urban	Open Water	Grassland/ Savanna	Agriculture	Wooded
29%	Wetland	0.90	1	0.08 (0.01)	0.54 (0.29)	-0.23 (0.05)	-0.45 (0.20)	0.13 (0.02)
19%	Urban	0.50	0.08 (0.01)	1	0.29 (0.08)	-0.81 (0.65)	-0.47 (0.22)	0.01 (0.00)
17%	Open Water	0.69	0.54 (0.29)	0.29 (0.08)	1	-0.43 (0.18)	-0.47 (0.22)	0.00 (0.00)
15%	Grassland/Savanna	-0.43	-0.23 (0.05)	-0.81 (0.65)	-0.43 (0.18)	1	0.09 (0.01)	0.23 (0.05)
12%	Agriculture	-0.36	-0.45 (0.20)	-0.47 (0.22)	-0.47 (0.22)	0.09 (0.01)	1	-0.65 (0.43)
7%	Wooded	-0.34	0.13 (0.02)	0.01 (0.00)	0.00 (0.00)	0.23 (0.05)	-0.65 (0.43)	1

Figure 2.4: The probability of surviving to fledge (y-axis) in percentage of specified land cover within 1,500 m of nest sites (x-axis); the three points on each line represent the minimum, average, and maximum cover within this 1,500 m buffer, respectively. For example, the probability of surviving to fledge is approximately 50% when 60% of land cover within 1,500 m of nest sites is urban. Values in the first column of the matrix represent the percentage of total AICc weight of specific land covers within the land cover category (i.e. using the Total Model Weight from column 2 of Table 2.4 compared to total land cover, the relative weight of wetlands in explaining observed survival = 0.1872 / 0.6459 = 29%). Values in the third column represent the slope of linear trend lines (not shown) fit to the respective trends plotted above. Subsequent columns of the matrix represent the Pearson product moment correlation coefficient values (r-squared values in parenthesis) between land cover types within 1,500 m of nest sites.

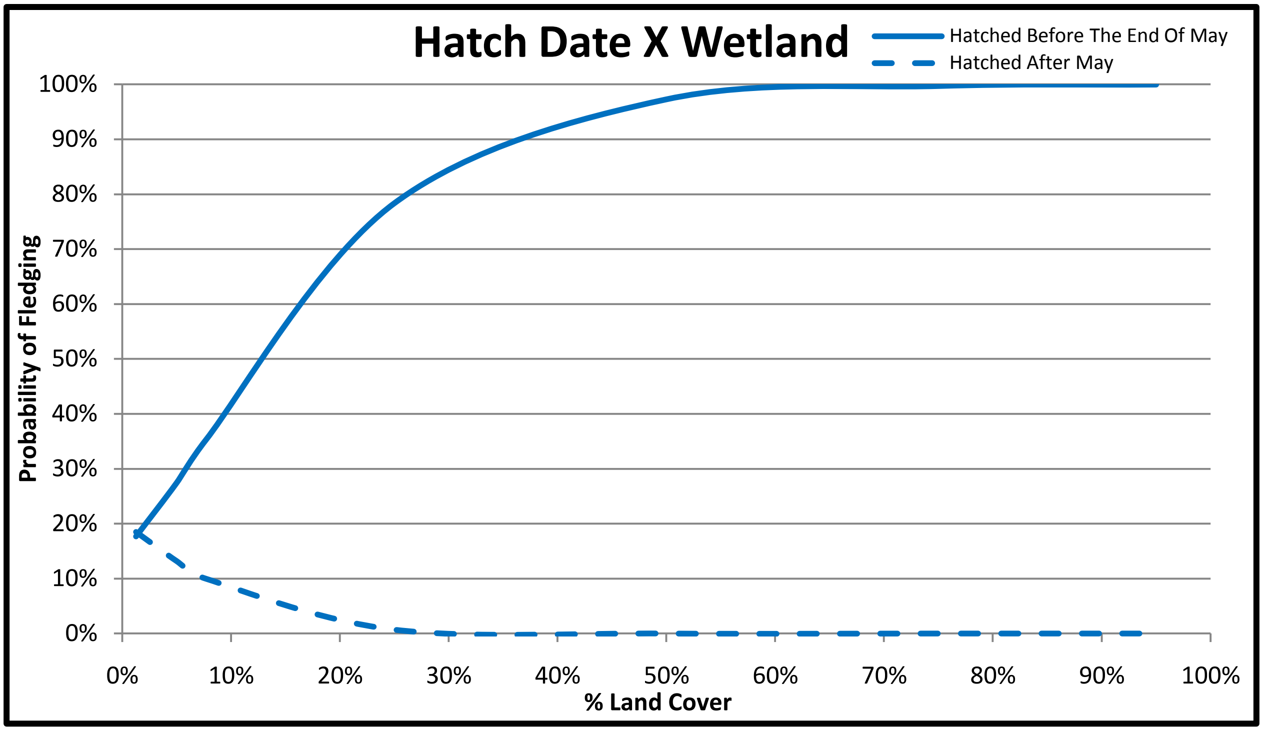


Figure 2.5: The probability of surviving to fledge (y-axis) when hatched before the end of May (solid blue line) or after May (dashed blue line) with respect to quantity of wetland land cover within 1,500 m of nest site (x-axis).

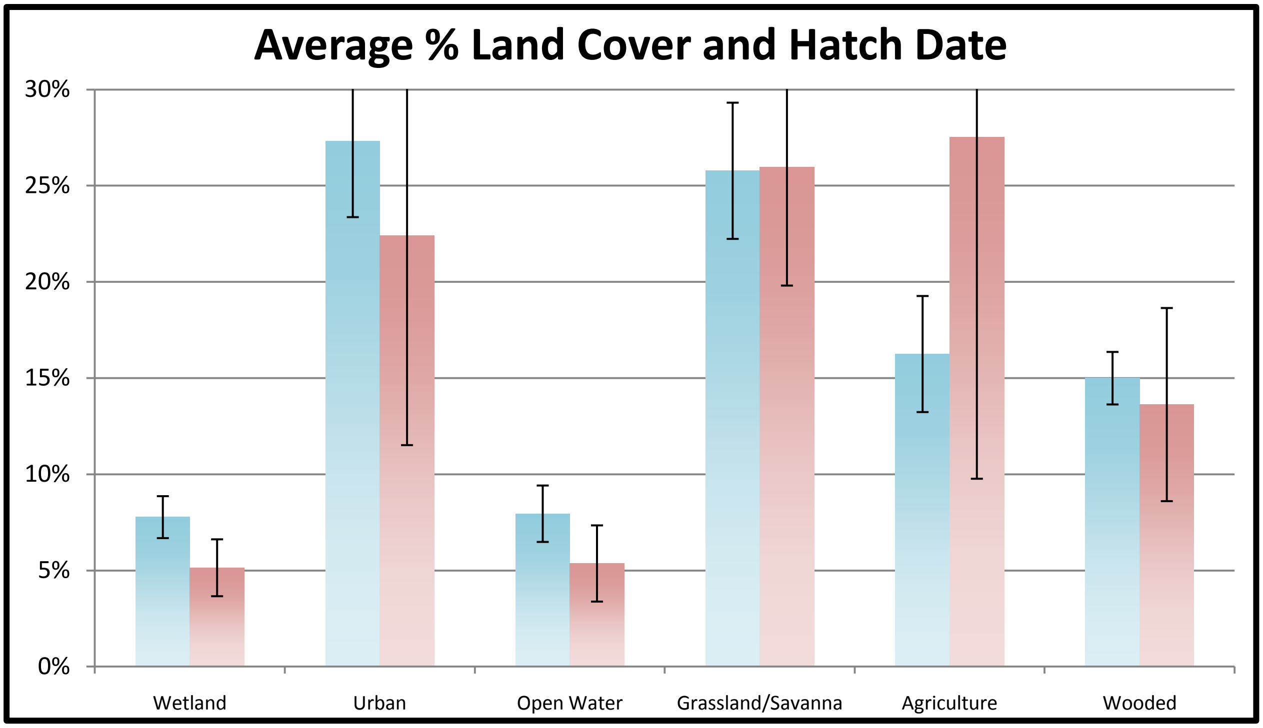


Figure 2.6: Average land cover within 1,500 m of nest sites for birds that hatched before the end of May (blue bars) and for birds that hatched after May (red bars); error bars represent 95% confidence intervals. Note that 95% confidence intervals for average wetland cover do not overlap (i.e. lower 95% C.I. for blue bar = 6.67% and upper 95% C.I. for red bar = 6.61%).

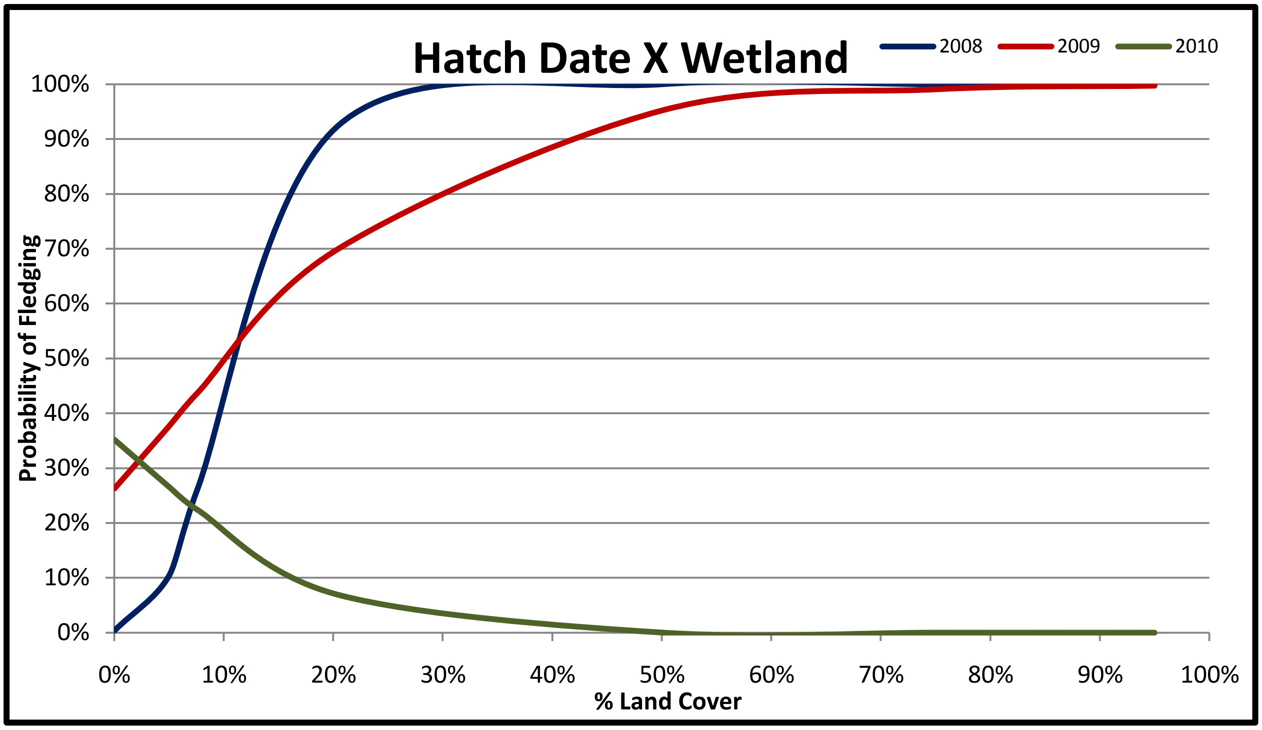


Figure 2.7: The probability of surviving to fledge (y-axis) in 2008 (blue line), 2009 (red line), and 2010 (green line) with respect to the quantity of wetland land cover within 1,500 m of nest site (x-axis).

Chapter 3

Summary

The primary objective of this study was to evaluate colt survival and fledging success of Greater Sandhill Cranes (*Grus canadensis tabida*) in northeastern Illinois. Using an information-theoretic approach (Burnham and Anderson 2002) I also explored how survival and fledging success was influenced by colt age, hatch date, year, landscape, and sibling status. Age-based models of survival were more than 120 times better supported than models where survival was a function of time. I found a strong positive correlation between fledging success and both wetland size (Fig. 3.1) and hatching before the end of May (Table 3.1). The average percentage of wetland habitat around nests hatching before the end of May was also significantly greater than the average percentage of wetland habitat around nests hatching after May ($df = 16$, $t = 2.6$, $P < 0.02$; no overlap in 95% Confidence Intervals). These findings were likely the result of experienced breeding birds selecting larger wetland habitats and initiating nests early in the breeding season.

While age-based survival was an expected result for a precocial species and prominent roles for breeding experience and wetland habitats have been broadly established by previous research, my results contrast with studies that found lower fledging success in urban landscapes (e.g. Toland 1999). In northeastern Illinois, I attribute greater fledging success in urban habitats relative to adjacent non-wetland habitats to human-avoidance behaviors and hunting habits of common colt predators (e.g. coyotes; Littlefield 1995, 2003; Gehrt et al. 2009). This trend was perhaps further influenced by the positive correlation between urban and wetland habitats, the latter of which was most strongly associated with fledging success. I also found that colt fates within a brood were tied, and that the mortality of one decreased the probability that the other

would fledge (Table 3.1). This was likely due predation (i.e. the same local predator that depredated the first colt). However, while previous studies have generally reported competition between siblings leads to mortality of smaller colts, I found no evidence of mortalities related to sibling-strife.

Sandhill Cranes in northeastern Illinois have increased in numbers rapidly for several decades (33.3% per year; Northeastern Illinois Wetland Bird Surveys *in* Ward et al. 2010). However, I observed rates of survival and fledging success (Table 3.1) that were lower than any I found in the available published literature (Table 3.2). Based on colt age, the probability of fledging (32.44%; Table 3.1) was far lower than age-based estimates for Florida Sandhill Cranes (45.95% to 64.90%; Bennett and Bennett 1990; Nesbitt 1992; Table 3.2). Using a more common method of estimating survival based on the progression of time through the breeding season instead of colt age (e.g. # of *G. c. tabita* colts fledged by September relative to # of colts known to hatch; Littlefield 1995, 2003), I found average annual survival in northeastern Illinois (14.14%; Table 3.1) was also lower than observed in a declining population (15.61%; Table 3.2). My findings suggest that fledging success has not been a significant variable in the rapid increase of Sandhill Cranes in northeastern Illinois, implicating a more prominent role for the region's concentration of wetlands (approximately 130,000 ha in Lake and McHenry Counties; Suloway and Hubbell 1994) in facilitating immigration from other states. Future studies should therefore aim to resolve the role of urban habitats in source-sink dynamics for Sandhill Cranes in the region.

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TABLES

Age-Based Survival				Estimate	S.E.
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			Have Sibling	31.12%	7.21%
	Have Sibling		Larger of Sibling	36.83%	13.34%
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		1970-1971, 1982-1983, 1986-1989	42.89%	11.43%	-	5.05%	10.86		
		1972-1982, 1945-1985	57.86%	20.99%	-	10.11%	19.73		
		1991-1995	-	17.13%	18.70%	-	-	-	(Ivey and Scheuering 1997)
		1990-1998	72.44%	-	-	-	7.5	-	(Ivey and Dugger 2008)
	Modoc National Wildlife Refuge, California	1990, 1992	-	45.00%	45.83%	-	-	Increasing	(Desroberts 1997)
	Michigan	-	69.70 to 78.92%	-	96.60%	-	-		(Walkinshaw 1981)
	Total Eastern Population	-	-	-	-	12.00% average	-		(Drewien et al. 1995)
Florida Sandhill Crane (*G. c. pratensis*)	Okefenokee Swamp, Georgia	1985-1988	56.50%	46.66%	45.95%	9.40%	-	Stable (SAN *in* Tacha et al. 1992)	(Bennett and Bennett 1990)
	Northcentral Florida	1977-1987	-	-	64.90%	-	-		(Nesbitt 1992)

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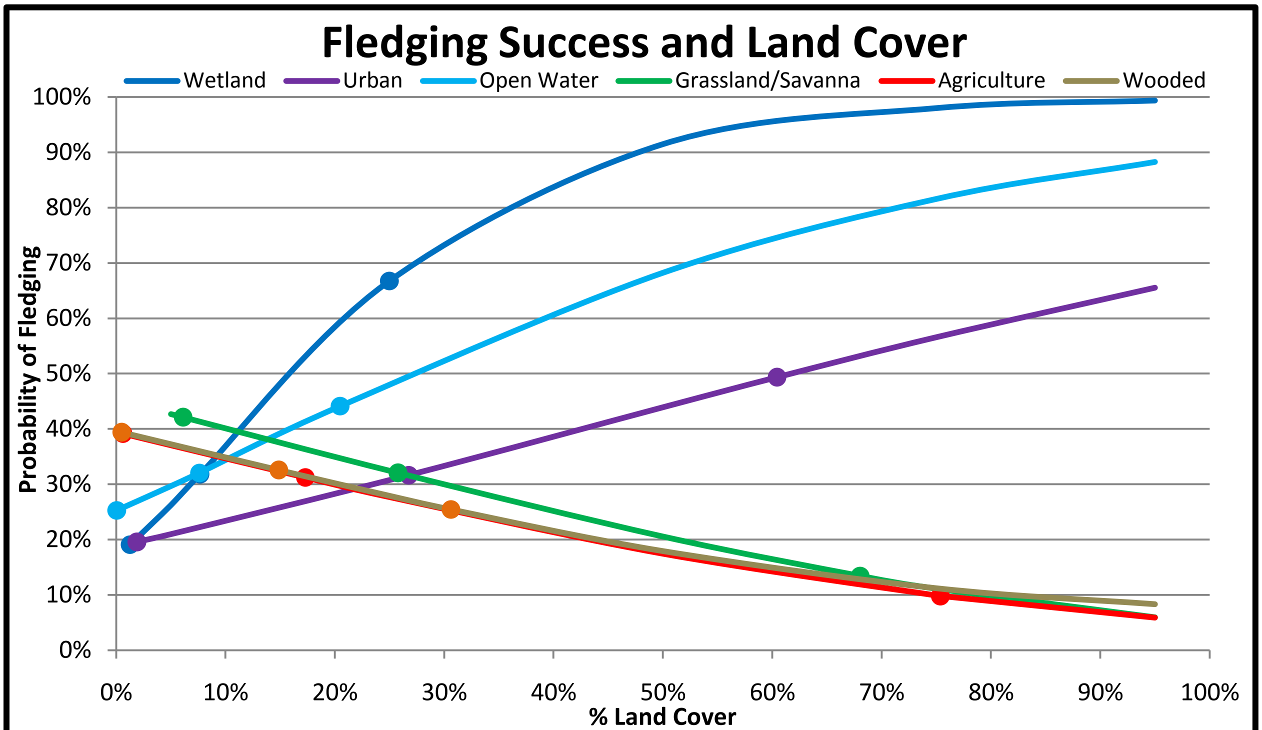
FIGURES



Model Weights Within Land Cover	Land Cover	Colt Survival (Slope)	Wetland	Urban	Open Water	Grassland/ Savanna	Agriculture	Wooded
29%	Wetland	0.90	1	0.08 (0.01)	0.54 (0.29)	-0.23 (0.05)	-0.45 (0.20)	0.13 (0.02)
19%	Urban	0.50	0.08 (0.01)	1	0.29 (0.08)	-0.81 (0.65)	-0.47 (0.22)	0.01 (0.00)
17%	Open Water	0.69	0.54 (0.29)	0.29 (0.08)	1	-0.43 (0.18)	-0.47 (0.22)	0.00 (0.00)
15%	Grassland/Savanna	-0.43	-0.23 (0.05)	-0.81 (0.65)	-0.43 (0.18)	1	0.09 (0.01)	0.23 (0.05)
12%	Agriculture	-0.36	-0.45 (0.20)	-0.47 (0.22)	-0.47 (0.22)	0.09 (0.01)	1	-0.65 (0.43)
7%	Wooded	-0.34	0.13 (0.02)	0.01 (0.00)	0.00 (0.00)	0.23 (0.05)	-0.65 (0.43)	1

Figure 3.1: The probability of surviving to fledge (y-axis) in percentage of specified land cover within 1,500 m of nest sites (x-axis); the three points on each line demark the minimum, average, and maximum cover within this 1,500 m buffer, respectively. For example, the probability of surviving to fledge is approximately 50% when 60% of land cover within 1,500 m of nest sites is urban. Values in the first column of the matrix represent the percentage of total AICc weight of specific land covers within the land cover category (i.e. using the Total Model Weight from column 2 of Table 2.4 compared to total land cover, the relative weight of wetlands in explaining observed survival = 0.1872 / 0.6459 = 29%). Values in the third column represent the slope of linear trend lines (not shown) fit to the respective trends plotted above. Subsequent columns of the matrix represent the Pearson product moment correlation coefficient values (r-squared values in parenthesis) between land cover types within 1,500 m of nest sites.