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MALLARD NESTING ECOLOGY IN THE GREAT LAKES

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MALLARD NESTING ECOLOGY IN THE GREAT LAKES

By

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B.S. Humboldt State University, Arcata, California 2001

Thesis

presented in partial fulfillment of the requirements
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Mallard Nesting Ecology in the Great Lakes States

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  Understanding how habitat features influence vital rates that drive population growth is fundamental for delivery of effective conservation programs. Past decisions in management of Great Lakes mallard (*Anas platyrynchos*) populations were based largely on paradigms established in the mid-continent because regional data were lacking. Recent sensitivity analyses from the Great Lakes Mallard Study show that population growth (i.e., λ) is most sensitive to changes in nest success (16%) and duckling survival (32%).

  In spring of 2001 to 2003, as part of the Great Lakes Mallard Study, 536 mallards were radio-marked at nine sites in four states (Michigan, Ohio, Wisconsin, and Indiana). I tested a set of *a priori* candidate models to evaluate the relative influence of habitat variables on survival rate of mallard nests (DSR) at local and landscape-level scales (2 m and 2-, 5-, and 10-km radii from nest). Nest success (0.156 ± 1.420) varied regionally from a low of 0.101 in Wisconsin to a high of 0.247 in Michigan, and was higher in forested landscapes (21.7 - 24.7%) than in agricultural environments (10.1 – 16.5%). Mallard nest survival was higher for older females than for second-year birds, and probability of hatching increased with nest age. Concealment within 2 m of a nest increased nest DSR, and amount of tillage agriculture within 5-km of a nest was inversely related to survival.

  Models that combined variables at multiple spatial scales explained nest DSR better than any combination of variables that were measured at a single spatial scale. Mallard populations in the Great Lakes states are likely to expand further as forested lands are cleared for agricultural production, and mallards begin to pioneer newly created habitats. Because nest success and duckling survival are the most influential vital rates, we recommend that managers conserve and restore wetlands to increase brood survival in higher forested landscapes where small inclusions of agricultural tillage provide habitat without affecting nest success.

DEDICATION

I dedicate my thesis to Warren Eckhardt, my Grandfather who instilled values and perseverance in me at a young age. He taught me to think critically, ask questions, and to always consider the other side of the story without hasty reaction. Most of all, he taught me self-worth and convinced me that it is truly possible to follow your dreams and reach seemingly impossible goals.

ACKNOWLEDGEMENTS

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Chapter 1

INTRODUCTION

Populations of breeding mallards (*Anas platyrhynchos*) have expanded into and are now increasing in the eastern United States (Ankney et al. 1987, Merendino and Ankney 1994). Recently, populations have increased to ~1 million birds from early estimates of about 100,000 individuals in the 1970s (Trost 1984, Sheaffer and Malecki 1996). The waterfowl hunting community in the Great Lakes, southeast US, and some southern states desire stable or increasing mallard populations because estimates of harvest derivation demonstrate that these areas depend on mallards produced in the Great Lakes banding reference area for local harvest. For example, harvest derivation analyses show that 22 - 81% of mallards harvested in the Great Lakes were produced locally in the states of Michigan, Wisconsin, Illinois, Indiana, and Ohio (herein MI, WI, IL, IN, OH) (Zuwerink 2001; Table 1).

Understanding how habitat features influence vital rates that drive population growth is fundamental for delivery of effective conservation programs. Past management decisions for mallard populations in the Great Lakes region were based largely on paradigms established in the mid-continent because regional data were lacking (Johnson et al. 1987). Sensitivity analyses of the life cycle of mid-continent mallards show that 91% of variation in population growth (i.e., λ) is explained by processes that occur on the breeding grounds. For example, mid-continent mallard population growth is most sensitive to changes in nest success (43%), adult female survival (19%) and duckling survival (14%) (Hoekman et al. 2002). Conservation programs in the mid-continent

strive to conserve large blocks of grassland habitat to increase nest success by minimizing predation (Stephens et al. 2005).

Mallard populations in the eastern United States are more stable than those that evolved with drought and deluge cycles that are so characteristic of boom-bust populations in the mid-continent (Sheaffer 1998). Regional differences were expected, and recent sensitivity analyses from the Great Lakes Mallard Study (2000 - 2004) show that growth of these populations depends more on duckling survival (32%) and less on nest success (16%) than those in the mid-continent (Coluccy et al. 2008; Figure 1). This does not mean that nest success is unimportant; instead, conservation actions will need to address a larger suite of contributors to vital rates in the Great Lakes region than in the mid-continent to benefit mallard populations (Coluccy et al. 2008). Strategies to conserve mallard populations in the eastern United States are evolving (Sheaffer and Malecki 1996, Sheaffer 1998) as new information becomes available (Losito and Baldassarre 1995, Losito et al. 1995, Coluccy et al. 2008), and the same opportunity became available for conservation programs in the Great Lakes region.

In 2000, Ducks Unlimited, Incorporated, initiated the Great Lakes Mallard Study to 1) identify factors that limit mallard population growth, 2) evaluate ways to increase vital rates that drive population growth, and 3) incorporate those findings into a spatially-explicit decision support system to identify and prioritize conservation opportunities.

My role as one of three M.S. students involved in this project was to 1) quantify nest success as a vital rate of interest for subsequent use in sensitivity analyses, 2) evaluate whether local factors at the nest site influence daily survival rate, 3) assess whether landscape factors at multiple scales influence survival rate, and 4) identify the

best combination of variables at one or more scales that can best explain duck nest success in the Great Lakes region.

In this chapter, I introduce this project and provide context for my applied research. In chapter 2, I use a maximum likelihood approach to quantify nest success of breeding female mallards at nine sites in the Great Lakes region. Estimates represent the first of their kind for this region of the country. I also model the effects of nest age, hen age, Julian date, observer effects, and year to better understand factors that may explain sources of variation in daily nest survival. Throughout the rest of the thesis, I refer to these as "nuisance variables" or "nuisance effects" because, although important, inferences from these relationships cannot be used directly in management. I use "nuisance variables" in subsequent analyses to control for these sources of variation in daily survival rates of nests. In Chapter 3, I evaluate a set of *a priori* competing models to identify local and landscape models that influence daily survival rate of nests. Lastly, I discuss implications of these findings relative to management of breeding mallards in the Great Lakes region.

Table 1. Percent mallard harvest derived by major banding reference areas for the Great Lake states (Zuwerink 2001). Region 14 data show the percent of mallards harvested in Great Lake states that were also produced in that region. Reference areas 3-6 and 12-13 represent the mid-continent.

State	Major Reference Area						
	3	4	5	6	12	13	14
Michigan	0	0.5	0.9	1.2	0.2	6.1	57.4
Wisconsin	0	0.6	1.5	1.3	0.4	4.5	80.5
Ohio	0.1	0.8	2.5	1.5	0.0	5.6	22.0
Illinois	0	5.2	9.0	6.9	2.4	24.4	28.6
Indiana	0.2	1.0	3.1	2.4	0.7	13.5	29.7

Figure 1. Proportion of variation in population growth explained by variation in each vital rate in a sensitivity analysis of female mallards breeding in the Great Lakes region. Population growth was most sensitive to changes in non-breeding survival (36%), duckling survival (32%) and nest success (16%) (Coluccy et al. 2008).
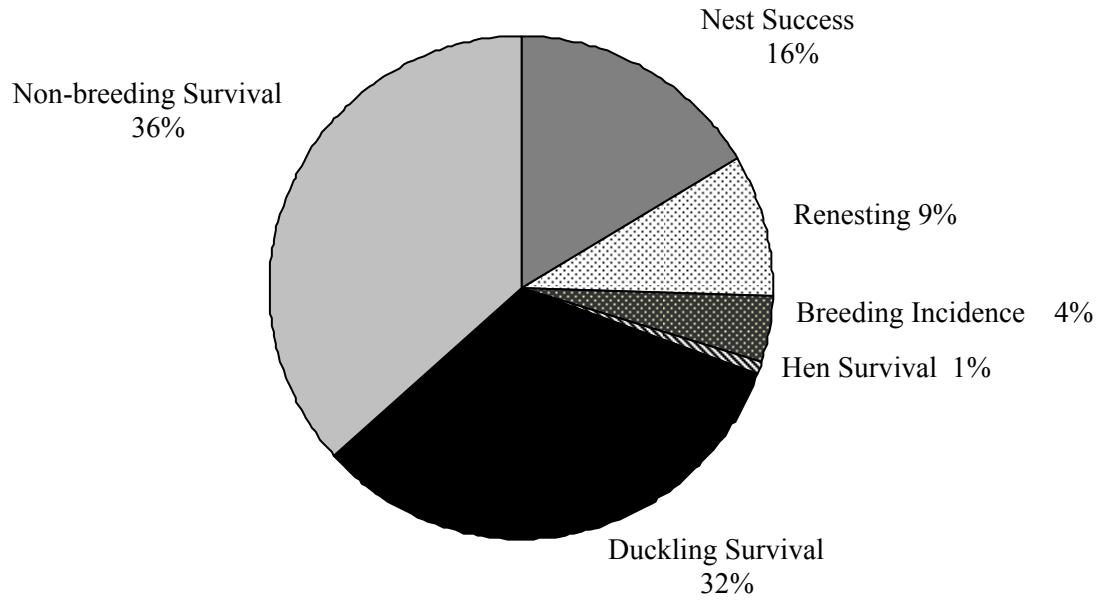
Chapter 2

NEST SURVIVAL IN GREAT LAKES MALLARDS

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Abstract: Understanding how habitat features influence vital rates that drive population growth is fundamental for delivery of effective conservation programs. Recent sensitivity analyses from the Great Lakes Mallard Study show that population growth (i.e., λ) during the breeding season is most sensitive to changes in duckling survival (32%) and nest success (16%). In spring 2001 - 2003, as part of the Great Lakes Mallard Study, 536 female mallards were radio-marked at nine sites in four states (Michigan, Ohio, Wisconsin, and Indiana). I estimated nest success from >11,000 daily survival intervals and used a generalized non-linear mixed modeling approach to evaluate effects of nest age, hen age, Julian date, observer, and year on nest survival. Most mallard nests were located in grassland (65%), wetland (25%) and hayland (12%) habitat types. Average nest success (0.156) varied regionally from a low of 0.101 in Wisconsin to a high of 0.247 in Michigan. Duck nest survival was higher for after-second-year females than for younger birds, and probability of a nest hatching increased with nest age.

Introduction

Understanding the relationship among habitat features and vital rates that may drive population growth is fundamental for delivery of effective conservation programs. Past habitat conservation or management decisions in the Great Lakes region were based largely on paradigms established in the mid-continent where conservation strategies strive to conserve large blocks of grassland habitat to increase nest success by minimizing predation (Stephens et al. 2005). New research in the Great Lakes region shows that conservation paradigms adopted from the mid-continent need to be revisited because population growth in the Great Lakes depend more on duckling survival (32%) and less on nest success (16%) than those in the mid-continent (Coluccy et al. 2008). Differences were expected because composition and structure of the landscape in the Great Lakes differs greatly from prairie habitats in the mid-continent. Unlike habitats in the mid-continent, the Great Lakes states are a diverse mosaic of forested habitats interspersed with agricultural tillage, and most areas contain considerably less grassland and more urban encroachment than is characteristic of landscapes farther west.

The recent eastern expansion of breeding mallard populations to more forested habitats necessitates additional research to identify ways to increase vital rates that drive population growth so that managers effectively evaluate current conservation opportunities. In this chapter, I specifically evaluate the effects of nest age, Julian date, observer effects, and year to better understand factors that may explain sources of variation in daily nest survival. I also model the effects of female age on daily survival rates of individual nests. The age/experience hypothesis proposes that past experience makes older females more successful at nesting (Krapu and Doty 1979, Curio 1983). If

supported, then older females should exhibit a higher rate of nest survival than first year breeders. I use findings from my nuisance models in subsequent analyses to control for sources of variation explained in daily survival rates as we evaluate potential relationships between habitat variables and nest success.

Study Area

To capture spatial variability, study sites were selected based on land-use activities representative of the Great Lakes region. Land cover classification with 30-m resolution was obtained from the United States Geological Survey (USGS) National Land Cover Data (USGS 2003). Using ERDAS IMAGINE 8.4 GIS software, a land cover map of the region was created by attributing each 30 x 30-m grid cell with the amount of dairy pasture, cash crop, and deciduous forest within a 2 x 2-km area. Cells were then categorized into eight groups based upon the reclassified values. Eight rather than nine combinations of land use were selected because no landscapes contained high amounts of cash crop and deciduous forest (Table 1). Within that continuum, study sites were chosen in the four land-use categories that represented the majority of the landscape (Table 2). Potential study sites were identified as large areas of one continuous cover classification. In categories where more than one potential site existed, one was chosen that contained a sufficient wetland density to support breeding waterfowl. Logistical concerns such as road networks and field housing availability were also considered in site selection.

Nine study sites were selected, three new sites each year, throughout the Great Lakes Region from 2001 - 2003 (Figure 1). In 2001, sites were located near Port Clinton, Ohio, Riverdale, Michigan, and Ripon, Wisconsin (hereafter referred to as OH01, MI01,

3

and WI01). In 2002, sites were located near Angola, Indiana, Battle Creek, Michigan, and Shiocton, Wisconsin (MI02, IN02, and WI02). The final three study sites in 2003 were located near Warren, Ohio, Big Rapids, Michigan, and New Richmond, Wisconsin (OH03, MI03, and WI03; Figure 1).

Methods

Capture and Marking

Approximately 60 female mallards from each site prior to nesting were trapped using conventional decoy-hen traps (Sharp and Lokemoen 1987) in late March and early April. Females were banded with standard USFWS leg bands and 25-g transmitters were abdominally implanted (Advanced Telemetry Systems, Isanti, Minnesota) according to surgical procedures outlined by Korschgen et al. (1984). Radio-marked females were held for one hour after surgery and released at the trap site. Males that were captured with females were banded and released with the female to minimize disruption of pair bonds.

Tracking and Nest Monitoring

Radio-marked females were located one to six times a day using truck-mounted null-array systems (Kenward 1987). Females were located between 0600 - 1300 hr to coincide with the hours laying females are most likely to be on nests (Coulter and Miller 1968, Gloutney et al. 1993). Estimated UTM locations for females were determined via triangulation using LOCATE II software (Pacer, Truro, Nova Scotia). Females triangulated to the same position for three consecutive days were tracked using hand-held antennas to determine the approximate nest location. Nest sites were visited to count

eggs and estimate nest age in the afternoon when females were absent. Nests were

visited at 18 days of incubation to estimate size of a full clutch and to estimate hatch date.

Habitat type was recorded in the immediate vicinity of the nest (2-m radius). Habitat

types were grassland, hayland (i.e., plowed and seeded for forage production), planted

cover, cropland, woodland (woody plants $\geq$6 m in height), scrubland (shrubs <6 m tall),

or wetland (Cowardin et al. 1979).

Statistical Analyses

I modeled daily survival rate (DSR) of nests and compiled a list of competing *a

priori* models. I used generalized non-linear mixed modeling (Proc NLMIXED, SAS

Institute Inc. 2002) because this procedure can relate DSR to continuous and categorical

covariates. I used a logit link function to constrain nest DSR between zero and one and

to appropriately model the relationship between DSR and covariates that change over

time and those that remain constant over the life of the nest (Dinsmore et al. 2002,

Stephens 2003). I calculated nest success as the product of each daily survival rate for

the 35-day nesting period (Stephens 2003). The Delta method was used to calculate

standard errors (SE) for DSR and nest success values (Seber 1982).

I ranked candidate models using Akaike's Information Criterion corrected for

small sample sizes (AIC$_c$; Anderson et al. 2000, Burnham and Anderson 2002). For each

model, I calculated the AIC$_c$ score, the difference in AIC$_c$ from that of the AIC "best"

model (ΔAIC$_i$), and the Akaike weight (w_i) for each model (Burnham and Anderson

2002). The ΔAIC$_i$ measures the likelihood of models relative to the model with the

lowest AIC$_c$ score. The model with the lowest AIC$_c$ score is considered the "best"

approximating model, and models within 2 points of the AIC "best" model is considered

when making inferences. The Akaike weight (w_i) was used to assess the weight of evidence in favor of model i, given the set of models considered (Burnham and Anderson 2002).

I evaluated 48 candidate models comprising all combinations of nest age, female age, Julian date, observer effects, and year. Female age was estimated by removing the greater secondary covert from the right wing. Five observers estimated age by visual inspection and by comparing each feather to a reference collection of feathers collected from wild mallards of known age (R. Clark, Canadian Wildlife Service, unpublished data). Results from observers were compared and if age was agreed upon the feather was classified as either an after-second-year (ASY) or second-year (SY) age class. Feathers for which observers could not agree upon were eliminated from the sample. Based upon these results, a 57:43 SY:ASY age ratio was estimated (Coluccy et al. 2008).

I tested for observer effects because human presence during routine nest visits could bias DSR (Rotella et al. 2000). The addition of this effect allowed DSR to vary on days that active nests were visited. I included time-varying covariates such as nest age and Julian date into models (Dinsmore et al. 2002) even though limited knowledge did not allow us to hypothesize how they might influence DSR.

Results

I analyzed 11,160 daily survival intervals (from 563 nests) from 536 radio-marked female mallards across nine sites in 2001 - 2003. Most nests were recorded in grassland (40%), wetland (20%) and hayland (12%) habitat types (Table 3). One hundred forty-three nests were successful, 340 were predated, 34 abandoned, 27 destroyed during hay

cutting, eight flooded, one was not viable, and 10 were lost from unknown causes. Nest

success (0.156 ± 1.420) varied regionally from a low of 0.101 in agricultural landscapes

in Wisconsin to a high of 0.247 in forested landscapes in Michigan (Table 2). Average

nest success was higher in forested landscapes (21.7 - 24.7%) and lower in agricultural

landscapes (10.1 - 16.5%) (Table 2).

The AIC best model contained female age and nest age (w_i = 0.401) (Table 4).

Nests of ASY females had higher DSR than SY females and survival rates increased

significantly with nest age (Figure 2). The second and third ranked models were within 2

AIC_c units of the top model but were less than half as likely to be the best model (Table

4). Covariates from the AIC best model also increased the ranking of the second and

third best models (Table 4). The random y-intercept model containing no covariates

received little support and was greater than 114 AIC_c units (w_i = 0.0) from the AIC best

model.

Discussion

Habitat type at the nest was highest in grassland, hayland and wetland, a finding

consistent with other studies in eastern North America (Losito and Baldassarre 1995,

Hoekman et al. 2006). Unlike the mid-continent where contiguous blocks of grassland

are abundant, mallards in the Great Lakes region nested in small remnant patches of

grass, and of the 47% of nests in grassland, only 7% were located in grassland blocks

intentionally planted as nesting cover. Other nests were located in grassy strips,

fencerows and other idle patches interspersed within other habitat types.

Similar to observations in the Great Lakes, mallards in southern Ontario nested more often in wetland habitats where grasslands were lacking (Hoekman et al. 2006). Nest site habitat type in the Great Lakes is also similar to that of the American black duck (*Anas rubripes*) in the northeast United States (Belanger et al. 1998, Maisonneuve et al. 2006), and may be a contributing factor in hybridization between the species (Conroy et al. 2002). Mallards nested less in hayland in the Great Lakes than in southern Ontario (Hoekman et al. 2006). However, 27 of 69 nests in the Great Lakes were destroyed by hay cutting, and nest loss may have been higher in hayland if precipitation events had not delayed cutting in 2002 and 2003. McMaster et al. (2005) in southern Saskatchewan reported that delayed cutting allowed 25% of nests to remain past the average cutting date.

Estimates of nest success in the Great Lakes region were similar to those in other studies in eastern North America (Dwyer and Baldassarre 1993, Losito et al. 1995), lower than those of a previous study in the Great Lakes (Gates 1965) and higher than recent estimates in southern Ontario (Hoekman et al. 2006). Estimates in the Great Lakes were similar to those in the mid-continent (Stephens et al. 2005) despite major differences in habitat composition between regions.

I found support for the age/experience hypothesis (Figure 3) because variability in nest success was in part explained by a positive relationship between female age and DSR, a finding that is consistent for mallard populations in prairie ecosystems (Stephens et al. 2005). When compared to SY birds, ASY females typically exhibit a higher reproductive effort, arrive on the breeding grounds earlier, in better condition, and select sites that minimize nest loss (Johnson et al 1992). In chapter 3, I extend analyses to

identify habitat features at local and landscape scales that influence nest DSR while holding the known effect of female age constant.

Positive correlations between nest age and DSR in the Great Lakes and in southern Ontario suggest that variability in nest success may be related to habitat composition at landscape rather than local scales (Hoekman et al. 2006). In mid-continent populations, nest success is typically low in fragmented landscapes because predators efficiently search small and isolated patches of remaining habitat (Klett et al. 1988, Clark and Nudds 1991, Greenwood et al. 1995, Dahl et al. 1999). I exercise caution in this strict interpretation because research on composition and movements of predators in forested ecosystems is lacking, and because mallard densities in the Great Lakes region are probably too low compared to those in the mid-continent (Klett and Johnson 1982, Greenwood et al. 1995) to be thought of as a major prey base of most predator populations.

Management Implications

These findings highlight the importance of considering female age when computing variation in λ because non-breeding survival is the most important factor in population growth in the Great Lakes region (Coluccy et al. 2008). Knowledge of age ratios and changes in λ over time may serve as a monitoring tool to better understand overall health and trend of the mallard population in the Great Lakes region. High nest success in ASY females (this study), sensitivity to survival outside the breeding season (Coluccy et al. 2008), and a high harvest derivation in the Great Lakes (Zuwerink 2001) provide the opportunity to explore the influence of harvest on population dynamics

through adaptive harvest management. Effects of female age and nest age have few

direct implications in habitat planning, so in chapter 3, I hold constant those known

sources of variation to identify habitat features at local and landscape scales that

influence nest DSR.

Table 1. Classification of primary land-use for the Great Lake region and associated proportion (%) within those categories. Study Area below denotes the state and year in which the estimate of nest success is derived (i.e., MI01 = Michigan in 2001, and OH = Ohio, WI = Wisconsin, IN = Indiana).

Land Use Category	Proportion of Region	Study Area
Low Forest - High Agriculture	28.4%	WI01, OH01, MI01, WI02
Intermediate Forest - High Agriculture	14.7%	IN02, WI03
Intermediate Forest - Intermediate Agriculture	12.0%	MI02, OH03
High Forest - Intermediate Agriculture	8.3%	MI03
High Forest - Low Agriculture	7.0%	
Intermediate Forest - Low Agriculture	6.0%	
Low Forest - Intermediate Agriculture	2.0%	
Low Forest - Low Agriculture	urban	
High Forest - High Agriculture	n/a	

Table 2. Nest success and summary statistics for nesting female mallards at nine sites in the Great Lake region from 2001 - 2003. Study Area below denotes the state and year in which the estimate of nest success is derived (i.e., MI01 = Michigan in 2001, and OH = Ohio, WI = Wisconsin, IN = Indiana). Regional land use category represents the primary land use corresponding to total area for the Great Lake states.

Regional Land Use Category	Study Area	Number of Nests	Nest Success (%)	SE (%)	Earliest Nest Initiation	Latest Nest Initiation
High Forest - Intermediate Agriculture	MI03	57	24.1	5.49	30 March	10 June
Intermediate Forest - Intermediate Agriculture	OH03	52	24.1	5.97	15 March	10 June
Intermediate Forest - Intermediate Agriculture	MI02	56	21.7	5.25	4 April	14 June
Low Forest - High Agriculture	OH01	69	16.5	4.13	31 March	30 June
Low Forest - High Agriculture	WI01	58	14.8	4.36	11 April	30 June
Low Forest - High Agriculture	WI02	68	13.5	3.82	24 April	01 July
Low Forest - High Agriculture	MI01	69	11.3	3.46	7 April	14 June
Intermediate Forest - High Agriculture	IN02	73	10.7	2.99	30 March	23 June
Intermediate Forest - High Agriculture	WI03	57	10.1	3.41	18 April	29 June
	Overall	*559*	*15.6*	*1.42*	*15 March*	*01 July*

Table 3. Habitat type (2-m radius around nest) of mallard nests in the Great Lakes region, 2001-2003. Proportion of nests by year is shown within dominant habitat types.

	Grassland	Wetland	Hayland	Scrubland	Planted Cover	Cropland	Woodland	Other
2001	58	51	12	24	21	0	2	2
2002	92	44	25	19	12	4	3	1
2003	81	52	32	12	6	5	0	5
TOTAL	231	147	69	55	39	9	5	8
% total nests	*40%*	*25%*	*12%*	*10%*	*7%*	*2%*	*1%*	*1%*

Table 4. Competing model set used to explain variation in daily survival rate of mallard nests in the Great Lakes region, 2001 - 2003. Presented are number of model parameters (k), Akaike's Information Criteria (AIC$_c$) adjusted for small sample size, ΔAIC$_c$ values, and AIC$_c$ weights (w_i) for each model in order of increasing ΔAIC$_c$ units, starting with the best approximating model.

Model	k	AIC$_c$	ΔAIC$_c$	w_i
S{female age+nest age}	4	3132.2	0.0	0.401
S{female age}	3	3133.6	1.4	0.199
S{female age+nest age+julian date}	5	3134.0	1.8	0.163
S{female age+nest age+year}	5	3136.3	4.1	0.052
S{female age+year}	4	3137.6	5.4	0.027
S{female age+nest age+julian date+year}	5	3138.0	5.8	0.022
S{female age+julian date+year}	4	3138.1	5.9	0.021
S{nest age}	2	3138.8	6.6	0.015
S{nest age+julian date}	3	3139.5	7.3	0.010
S{julian date}	2	3140.1	7.9	0.008
S{female age+nest age+observer effects}	5	3140.7	13.9	0.005
NULL	1	3246.5	114.3	<0.001

Figure 1. Locations of nine study sites in four states in the Great Lakes region. In Wisconsin, sites were located near the towns of Ripon in 2001, Shiocton in 2002 and New Richmond in 2003. In Michigan, sites were near Riverdale in 2001, Battle Creek in 2002 and Big Rapids in 2003. Study sites in Ohio were located near Port Clinton (2001) and Warren (2003) and nearby in Angola, Indiana in 2002.

Figure 2. Average daily nest survival (DSR) for after-second-year (ASY) and second-year (SY) female mallards during the 35-day nesting period. The DSR was positively related to age of the nest. The DSR increased with nest age for ASY and SY females. The DSR for ASY was higher than that of SY females.
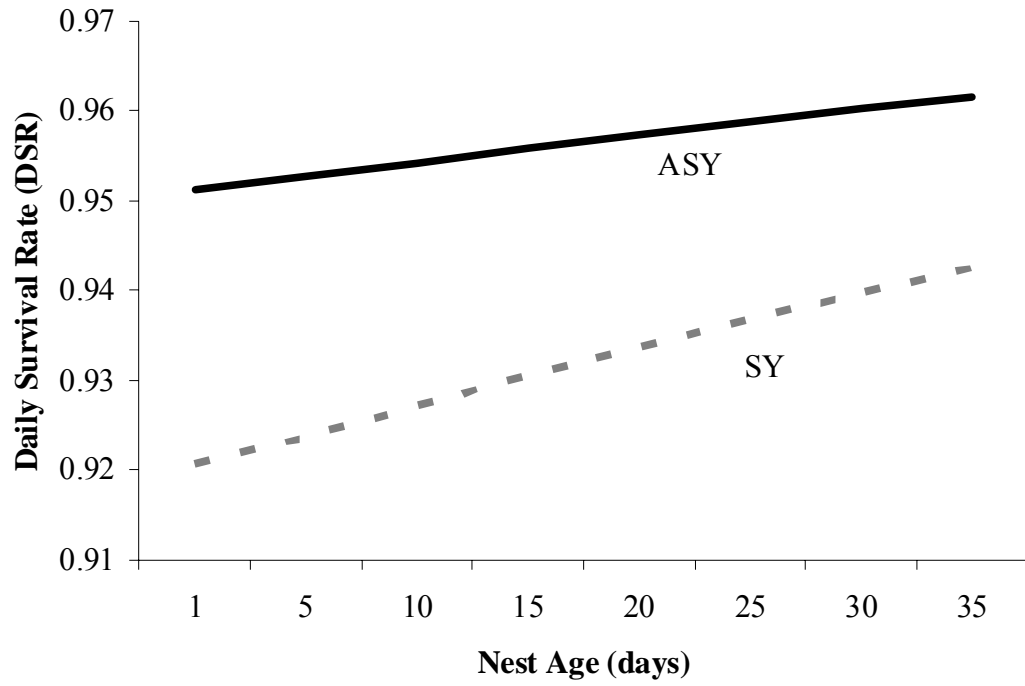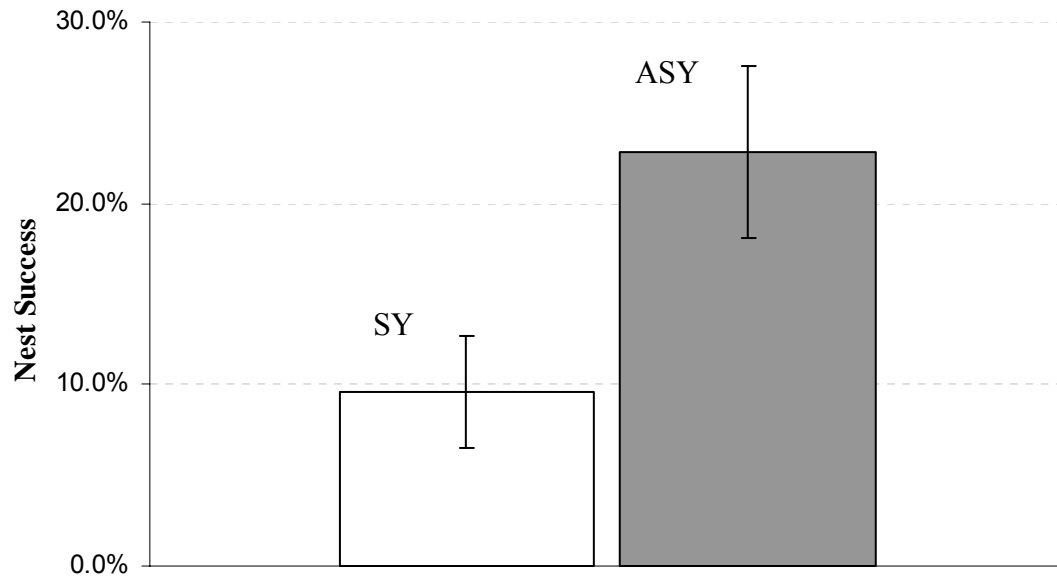
Figure 3. Estimated nest success for after-second-year (ASY) and second-year (SY) female mallards in the Great Lakes region, 2001 - 2003. ASY females exhibited overall higher nest success (22.8% ± 4.7) than SY females (9.6% ± 3.1).

Chapter 3

DUCK NEST SUCCESS IN THE GREAT LAKES REGION: EFFECTS OF HABITAT AT MULTIPLE SCALES

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Abstract: Understanding the relationship among habitat features and vital rates that drive population growth is fundamental for delivery of effective conservation programs. Past decisions in management of Great Lakes mallard (*Anas platyrynchos*) populations were based largely on paradigms established in the mid-continent because regional data were lacking. Recent sensitivity analyses from the Great Lakes Mallard Study show that population growth (λ) is most sensitive to changes in nest success (16%) and duckling survival (32%). In spring 2001 - 2003, as part of the Great Lakes Mallard Study, 536 female mallards were trapped and radio-marked at nine sites in four states (Michigan, Ohio, Wisconsin, and Indiana). I tested a set of *a priori* candidate models to evaluate the relative influence of habitat variables on survival rate of mallard nests (DSR) at local and landscape scales (2-m and 2, 5, and 10-km radii from nest). Nest success (0.156 ± 1.420) varied regionally from a low of 0.101 in Wisconsin to a high of 0.247 in Michigan, and was higher in more forested landscapes (21.7 - 24.7%) than in primarily agricultural landscapes (10.1 – 16.5%). Concealment within 2 m of a nest increased DSR, and amount of tillage agriculture within 5-km of a nest was inversely related to survival. Models that combined variables at multiple spatial scales explained DSR better than any combination of variables that were measured at a single spatial scale. Mallard populations in the Great Lakes states are likely to expand further as forested lands are cleared for agricultural production, and mallards begin to pioneer newly created habitats. Because nest success and duckling survival are the most influential vital rates, I recommend that managers conserve and restore wetlands to increase brood survival in higher forested landscapes where small inclusions of agricultural tillage provide habitat without affecting nest success.

Key Words: Anas platyrhynchos, breeding, Great Lakes, habitat, landscape, mallard, nest success, nest survival, waterfowl.

INTRODUCTION

The critical concept of scale is recognized by nearly all ecologists (e.g., Wiens 1989, Turner et al. 2001) and understanding the relative importance of local and landscape scale variables in habitat selection is central to developing effective conservation strategies (Carroll et al. 2003, Johnson et al. 2005, Reynolds et al. 2006). Previous studies of nest site selection at local scales have increased dramatically our understanding of habitat relationships (Duebbert and Kantrud 1980, Voorhees and Cassel 1980, Kaminski and Prince 1981), but conflicting results were evident (Clark and Nudds 1991). Recent studies have shown that habitat features at multiple scales can influence duck nest success (Ball et al. 1995, Greenwood et al. 1995, Reynolds et al. 2001, Howerter 2003, Stephens et al. 2005).

Landscapes in the Great Lakes region have undergone dramatic change with increases in tillage agriculture and its associated wetland drainage, clearing of forested lands for various forms of development, and urbanization. Research in the mid-continent has demonstrated that loss of large tracts of secure nesting habitat results in shifts in predator communities that exacerbate nest loss (Sovada et al. 1995, 2000), which is the major cause of decline in breeding mallard populations (Reynolds et al. 2001, Stephens et al. 2005). Unfortunately, less is known in the Great Lakes region where estimates of nest success are sparse (Livezey 1981a,b) and research on predator dynamics as they relate to nest survival are lacking. In two Wisconsin studies, nest success was low in relatively large blocks of dense nesting cover (Livezey 1981a), whereas successful nests were in tall dense cover located far from water (Livezey 1981b).

However, dense cover may not benefit populations if birds are attracted to landscapes where composition and abundance of predators results in a high rate of nest loss (i.e., population sinks [e.g., Pulliam 1988]). Therefore, multi-scale assessments are necessary to determine if nest survival is related to local habitat conditions, composition and abundance of habitats at landscape scales, or both. A sensitivity analysis conducted as part of the Great Lakes Mallard Study demonstrated that population growth (λ) was most sensitive to changes in nest success (16%) and duckling survival (32%) (Coluccy et al. 2008). Two graduate projects were designed to identify local and landscape factors influencing habitat use during the nesting and brood rearing periods. The first graduate study found the highest rates of duckling survival in predominantly forested landscapes that contained a variety of vegetated, palustrine wetlands, and lowest rates of predicted survival in agricultural landscapes with mostly open water and riverine wetlands (Simpson et al. 2005). In this chapter, I evaluate local and landscape factors influencing nest success, the second most important vital rate during the breeding season of mallards in the Great Lakes region.

Methods

Study site selection, data collection, and statistical procedures for nest survival estimates are presented in detail in Chapter 1. Outlined here is the methodology specific to an investigation of relationships between DSR of nests and habitat covariates at multiple spatial scales.

Local and Landscape Variables

Landscape composition and land cover were quantified with a geographic information system (GIS) constructed from National Land Cover Data (30-m resolution; USGS 2003) at three spatial scales: 2- (12.5 km^2), 5- (78.5 km^2), and 10-km (314 km^2) radii from the location of each nest. Mapping was verified in landscapes where nesting occurred to ensure that the GIS depicted current patterns of land use. The proportion of grassland, hayland, tillage agriculture, scrubland and forested land were calculated with ArcMAP (ESRI 2002) to relate nest survival to composition and abundance of major land uses in the surrounding landscape (Table 1). Grassland included fields enrolled in the Conservation Reserve Program (CRP) and other perennial herbaceous cover. Hayland was predominantly alfalfa (*Medicago sativa*) or tame pasture.

The proportion of the landscape in forested and in emergent wetland types were calculated at each scale to examine the relationship between nest survival and the proportion of wetlands in the surrounding matrix within each measured scale. Lastly, EdgeGrid was used in ArcInfo 8.3 (ESRI 2002) to calculate the proportion of edge adjacent to agricultural, wetland, and grassland habitats at each scale to examine the relationship among proportion of edge and nest survival. Nests were treated as the experimental unit despite partial overlap within 2, 5, or 10-km buffers around nests because females trapped before the onset of nesting independently selected nest locations.

A visual obstruction reading (VOR) was estimated one meter from the nest and one meter in height in four cardinal directions (Hines and Mitchell 1983). Readings were obtained immediately after nest termination. An average was calculated from those four readings to assign a concealment value of 0, 1, 2, 3, or 4. A VOR value of zero was

assigned when a nest was completely unobstructed in all four directions, and a value of four was recorded when the nest was entirely concealed by vegetation.

Predictions and Statistical Analyses

I evaluated whether nest survival was related to hypothesized changes in predation that accompany the loss and fragmentation of habitats at local and landscape scales (Stephens et al. 2005). I hypothesized that habitat variables at multiple scales might be related to daily survival rate (DSR) of nests through their effects on the foraging behavior of predators and their nest-finding efficiency. Predictions in this study were based largely on knowledge of variables that influence nest survival in mallard populations in grassland habitats in the mid-continent and in the aspen parklands in Canada because no landscape-scale studies have been conducted in the Great Lakes region.

Predator foraging behavior and nest survival rates reportedly vary as a function of the proportion of the landscape that has been converted from forest land and grassland to more intensive human use (e.g., agricultural tillage) (Greenwood et al. 1995, Reynolds et al. 2001, Howerter 2003, Emery et al. 2005, Stephens et al. 2005). The amount of habitat edge also has been reported as an important factor influencing predator behavior (Phillips et al. 2003), and thus, DSR (Howerter 2003). Therefore, I predicted that nest DSR would be low where the proportion of habitat loss and natural or anthropogenic edge within measured scales is high. Predator foraging efficiency might be reduced if females placed their nests in tall dense vegetation (Livezey 1981b). Therefore, I further predicted that nest DSR would be higher in patches of vegetation that offer nest concealment. Lastly, growing evidence in species other than waterfowl suggests that both local and landscape

variables might affect the density and/or productivity of birds (e.g., Fletcher and Koford 2002). Therefore, I tested whether habitat features at single or multiple scales best predicted DSR of female mallard nests.

I modeled DSR using the same modeling approach (Proc NLMIXED, SAS Institute Inc. 2002) as described in Chapter 2. Based on the analysis in Chapter 2, I included the best nuisance model of female age and nest age as covariates to control for known sources of variation in nest survival. I also ranked candidate models using Akaike's Information Criterion (AIC$_c$; Anderson et al. 2000, Burnham and Anderson 2002) in the manner described in Chapter 2. The number of biological models I tested was large enough to encompass a range of plausible outcomes but small enough to minimize the risk of committing a Type I error (Burnham and Anderson 2002).

I tested a suite of 82 models that represented combinations of local and landscape variables hypothesized to be related to DSR, potentially through their effects on predator foraging behavior and/or their nest-finding efficiency. I first examined the role of landscape variables in DSR by testing 42 models (i.e., 14 *a priori* models x 3 scales = 42) at three spatial scales (2, 5, and 10-km radii from nests) in nine study sites. Next, I tested the relative importance of local variables on DSR by including nest concealment (i.e., VOR) and re-running the initial 42 models in six study sites. I used a reduced data set to test the importance of nest concealment because VOR measures were only collected in the last two out of three years of the study. Lastly, I used AIC to evaluate whether local or landscape scales, or both, best explained DSR of female mallard nests in the Great Lakes region. Under the AIC framework, inference on model results from 2002 and 2003 could not be evaluated in relation to model results from all

three years (Burnham and Anderson 2002) therefore all hypothesized models were evaluated again only utilizing the last two years of data to determine the influence of local habitat variables on nest survival.

Results

The best fit model based on AIC explaining nest DSR at the landscape scale was female age, nest age, and proportion of tillage agriculture at the 5-km scale (Table 2, see also Table 4). When VOR were included, the best fit model based on AIC consisted of female age, nest age, VOR at the nest site and the proportion of tillage agriculture at the 5-km scale (Table 3, see also Table 5), but received moderate support (w_i = 0.439). Proportion of tillage agriculture at the 5-km scale remained the best predictor of nest DSR at a landscape scale (Table 2), and model fit increased (13 AIC_c units lower) when the best landscape model was combined with VOR at a local scale (Table 3). In the AIC best landscape model (Table 2), estimated DSR of nests at 1, 15, and 30-days of age each decreased as proportion of tillage agriculture within 5-km of a nest increased (Figure 1). Nest success was higher for older (ASY) than younger females (SY; Figure 3 in Chapter 2), but DSR of ASY birds was inversely related to the proportion of cropland in the landscape (Figure 2). A steep and positive relationship between DSR and VOR was consistent across age classes (Figure 3).

Findings support the AIC best models because the AIC second best landscape-only (Table 2) and combined models (Table 3) received slightly less support (w_i = -0.07 to -0.04) than the top models, and each contained negative relationships between nest DSR and proportion of tillage agriculture in the landscape at either 5 or 10-km scales.

Parsimony also led to accepting the top models because the addition of variables in the AIC second and third best combined and landscape-only models did not increase model fit (k > 1-2; Tables 2 and 3). Support was strong for the negative response of DSR to tillage agriculture because it was the most prevalent landscape attribute in the top eight landscape-only (Table 2) and the top three combined (Table 3) models. Few models within 2 AIC units of the best landscape-only combined models consistently contained variables other than tillage agriculture and VOR. Area of the landscape covered by wetland habitat had little influence on DSR, and hypotheses that considered potential negative effects of natural or anthropogenic edge received very little support (Tables 2 and 3).

Discussion

Findings from this study demonstrated that evaluations of habitat features that influence nest survival were best conducted at multiple spatial scales. The multi-scale analyses demonstrated that spatial context was important because females do not always choose the safest landscapes in which to nest (Martin 1993). Early studies provided conflicting evidence that nest concealment may (Schranck 1972, Voorhees and Cassel 1980, Kaminski and Prince 1981) or may not (Glover 1956, Keith 1961) increase nest success, but more recent studies recognized the importance of landscape features that influence nest success (Ball et al. 1995, Greenwood et al. 1995, Howerter 2003, Stephens et al. 2005). In the Great Lakes region, the multi-scale analysis supported that broad-scale impacts of habitat loss may largely negate the benefits of nest concealment in agricultural landscapes where predators may potentially be more efficient in finding nests

in the few remaining habitats (Figures 2 and 3). Landscape-level impacts also appear to be most pronounced in the most productive segment of the population (ASY females). I documented higher nest success in older (22.8%) than in younger less experienced females (9.6%; Figure 3 in Chapter 2), except in agricultural landscapes where declines in DSR equate to an estimated nest success rate of essentially zero (Figure 2).

Mallard populations are likely to expand further in the Great Lakes region as forest lands in the north are cleared for increasing demand of agricultural production. Unlike in the mid-continent where large grasslands are tilled for agricultural production (Greenwood et al. 1995), forest clearing in the northern Great Lakes region is a relatively slow process that initially provides openings in the forest that are readily colonized by a low density of breeding mallards. The ability of females to pioneer into these newly created habitats will be important to population growth because nest success was higher in the forestland/agricultural mosaic than predominantly agricultural landscapes (24 - 21% versus 16 - 10%; Table 2 in Chapter 2). Moreover, only 20% of the landscape in the Great Lakes region provides the types of habitats that support the highest rates of nest success (Tables 1 and 2 in Chapter 2). Additional forest clearing that exceeds 30% of the landscape likely will be detrimental to nest success. The exact mechanism is unknown, but declines in nest success that are associated with forest loss are likely related to increased rates of predation in agricultural landscapes (Howerter 2003, Stephens et al. 2005). More work is required to understand changes in the composition and abundance of predator communities that accompany land-use change in the Great Lakes region.

Facets of the study design enabled me to quantify the strong and positive influence of nest concealment on DSR. Higher rates of variability in nest concealment

were captured than most studies because females were radio-marked prior to the onset of nesting, and subsequently were tracked to their chosen nest location. This differs from the majority of studies that use a cable-chain device (Higgins et al. 1969) to find multiple nests at pre-selected sites because variation is typically lower within a few sites than across numerous individual locations on the landscape. In contrast, I found little support for negative effects of edge as relationships between these variables and nest DSR were equivocal in the Great Lakes region. Similarly, others have found that effects of edge on nest success vary due to variation in measurement of edge and by geographic region (Chalfoun et al. 2002, Howerter 2003).

Using female age and nest age to control for known sources of variation (Chapter 2) undoubtedly improved habitat models (Tables 2 and 3). As expected, nest DSR varied with nest age (Figure 1) and nest success was positively related to VOR regardless of female age (Figure 3). However, I was initially surprised to find that nest DSR of SY birds was not negatively related to the amount of agricultural tillage in the landscape (Figure 2), unlike nest DSR of ASY females. As predicted by the age/experience hypothesis (Sayler 1992), ASY females likely exerted a higher reproductive effort than SY birds in their attempt to reproduce in high-risk agricultural landscapes in the Great Lakes region. Still, further study is needed to better understand the mechanisms that influence nest DSR in different age classes of breeding female mallards.

Management Implications

Knowledge of local and landscape factors that influence nest success (this study) and duckling survival (Simpson et al. 2005), the two vital rates that influence λ (Coluccy

et al. 2008), can be used to formulate conservation programs that benefit populations. Nest success and duckling survival were both highest in landscapes with higher proportions of forest land and lowest in predominantly agricultural landscapes (this study and Simpson et al. 2005). Still, managers may want to prioritize activities that benefit duckling survival over those that increase nest success because an incremental increase in duckling survival has a greater effect on λ than an equivalent increase in nest success (Coluccy et al. 2008). I concur with Simpson et al. (2005) that maintenance and restoration of palustrine wetlands in forested landscapes is the simplest and most cost-effective means of increasing λ in mallard populations. Presently, land use patterns in the Great Lakes region make it costly and unrealistic to restore large tracts of dense nesting cover to replace grasslands that have been lost to agricultural development. Rather, I recommend planting grassland buffers around restored wetlands in across landscapes, particularly composed of a forest land/agriculture mosaic not dominated by agricultural tillage, to achieve maximum benefit to populations by increasing duckling survival and nest success in the most productive landscapes in the Great Lakes region. Providing wetlands in lower agricultural landscapes would offer more territorial sites for breeding pairs, increasing potential breeding pair densities in a landscape promoting higher nest and brood survival. Caution should be used because the threshold at which breeding densities create sink habitat is not well understood in the Great Lakes region.

Table 1. Description of local and landscape-level variables that were generated and incorporated into competing *a priori* models examining the relationship between daily survival rates (DSR) of mallard nests and habitat factors at nine study sites in the Great Lakes region from 2001 - 2003. Composition of variables were quantified at 4 spatial scales (2m, 2km, 5km, and 10km-radius) around each nest.

Variable Name	Description
km Grass	Proportion of grassland/herbaceous vegetation within the 2, 5, and 10 km radius buffer
km Hay	Proportion of hayland within the 2, 5, and 10 km radius buffer
km Agri	Proportion of row crops within the 2, 5, and 10 km radius buffer
km Scrub	Proportion of scrubland within the 2, 5, and 10 km radius buffer
km For	Proportion of deciduous/evergreen forest within the 2, 5, and 10 km radius buffer
km ForWet	Proportion of forested wetland within the 2, 5, and 10 km radius buffer
km EmrWet	Proportion of emergent wetland within the 2, 5, and 10 km radius buffer
km WetCount	The number of wetland basins within the 2, 5, and 10 km radius buffer
km AgriEdge	Proportion of habitat transitioning from agriculture to other habitat type within the 2, 5, and 10 km radius buffer
km WetEdge	Proportion of habitat transitioning from wetland to other habitat type within the 2, 5, and 10 km radius buffer
km GrassEdge	Proportion of habitat transitioning from grass to other habitat type within the 2, 5, and 10 km radius buffer

Table 2. Highest ranking landscape candidate model results ($\Delta AIC_c < 6$ and $w_i < 0.01$) for nest survival (S) across nine sites in the Great Lakes region in 2001 - 2003. The best landscape model indicated daily survival rates (DSR) were negatively related to the amount of tillage agriculture within the 5-km radius scale.

Model	k	AIC_c	ΔAIC_c	w_i
S{female age+nest age+5km Agri}	5	3126.6	0.0	0.271
S{female age+nest age+5km Agri+5km Grass}	6	3127.9	1.3	0.204
S{female age+nest age+10km Agri+10km For}	6	3128.3	1.7	0.111
S{female age+nest age+10km Agri+10km For+10km Scrub}	7	3128.5	1.9	0.094
S{female age+nest age+10km Agri}	5	3128.6	2	0.081
S{female age+nest age+10km Agri+10km Grass}	6	3129.2	2.6	0.077
S{female age+nest age+5km Agri+5km AgriEdge}	6	3129.2	2.6	0.070
S{female age+nest age+5km Agri+5km For+5km Scrub}	7	3129.9	3.3	0.063
S{female age+nest age+5km Agri+5km For}	6	3130.4	3.8	0.063
S{female age+nest age+10km For+10km AgriEdge}	6	3130.5	3.9	0.052
S{female age+nest age+10km For+10km Scrub+10km AgriEdge}	7	3131.1	4.5	0.033
S{female age+nest age+2km Agri}	5	3131.2	4.6	0.026
S{female age+nest age+10km Agri+10km For+10km Scrub+10km AgriEdge}	8	3131.2	4.6	0.024
S{female age+nest age+5km For+5km AgriEdge}	6	3131.4	4.8	0.018
S{female age+nest age+2km For+2km Scrub+2km AgriEdge}	7	3131.5	4.9	0.017
S{female age+nest age+2km Agri+2km For+2km Scrub}	7	3131.5	4.9	0.017
S{female age+nest age+2km Agri+2km Grass}	6	3132.4	5.8	0.016
S{female age+nest age+5km EmrWet+5km ForWet+5km WetEdge}	7	3132.7	6.1	0.015
S{female age+nest age+2km Agri+2km For}	6	3132.8	6.2	0.015
S{female age+nest age+2km Agri+2km AgriEdge}	6	3132.8	6.2	0.009

Table 3. Highest ranking multiple scale candidate model results ($\Delta AIC_c < 13$ and $w_i <$ 0.001) for nest survival (S) across six sites in the Great Lakes region in 2002 - 2003. The best multiple scale model indicated daily survival rates (DSR) were positively related to nest concealment and negatively related to the amount of tillage agriculture within the 5-km radius scale.

Model	k	AIC_c	ΔAIC_c	w_i
S{female age+nest age+VOR+5km Agri}	6	1825.3	0	0.439
S{female age+nest age+VOR+10km Agri+10km For+10km Agri Edge}	8	1825.5	0.2	0.397
S{female age+nest age+VOR+5km Agri+5km For}	7	1829.4	4.1	0.057
S{female age+nest age+VOR+10km Agri+10km For}	6	1830.2	4.9	0.038
S{female age+nest age+VOR+10km For}	6	1832.3	7	0.013
S{female age+nest age+VOR}	5	1838.3	13	0.001
NULL	1	1900.9	75.6	0.000

Table 4. Beta estimates, standard errors, degrees of freedom, and 95% Confidence Limits for the best landscape model ($w_i = 0.271$) describing mallard nesting success in the Great Lakes region from 2001 - 2003.

Parameters	Estimate	Standard Error	Degrees of Freedom	Lower 95%	Upper 95%
Intercept	3.016	0.151	7745	2.719	3.313
Female age[a]	0.218	0.052	7745	0.115	0.321
Nest age[b]	0.010	0.006	7745	-0.002	0.021
5km Agri[c]	-0.914	0.331	7745	-1.563	-0.264

[a]Female age = age of nesting female categorized as second year or after-second year.

[b]Nest age = number of days a nest survives since nest initiation.

[c] 5km Agri = proportion of row crops within a 5km radius buffer around the nest.

Table 5. Beta estimates, standard errors, degrees of freedom, and 95% Confidence Limits for the best combined model ($w_i = 0.439$) describing mallard nesting success in the Great Lakes region from 2002 and 2003. Models were evaluating using a reduced data set for 2002 and 2003.

Parameters	Estimate	Standard Error	Degrees of Freedom	Lower 95%	Upper 95%
Intercept	2.647	0.531	4693	1.602	3.692
Female age[a]	0.347	0.532	4693	-0.698	1.392
Nest age[b]	0.017	0.016	4693	-0.015	0.049
5km Agri[c]	-1.986	1.189	4693	-4.320	0.349
VOR[d]	0.914	0.331	4693	0.264	1.563

[a]Female age = age of nesting female categorized as second year or after-second year.

[b]Nest age = number of days a nest survives since nest initiation.

[c]5km Agri = proportion of row crops within a 5km radius buffer around the nest.

[d]VOR = visual obstruction reading estimated in four cardinal directions 1m from the nest and averaged.

Figure 1. Predicted nest survival of female mallards at nine study sites in the Great Lakes region from 2001 - 2003 in relation to the amount of tillage agriculture within a 5-km radius of the nest at day 1, day 15, and day 35 of nest age. As the amount of tillage agriculture within the 5-km buffer increases, daily survival rates (DSR) of nests decline.
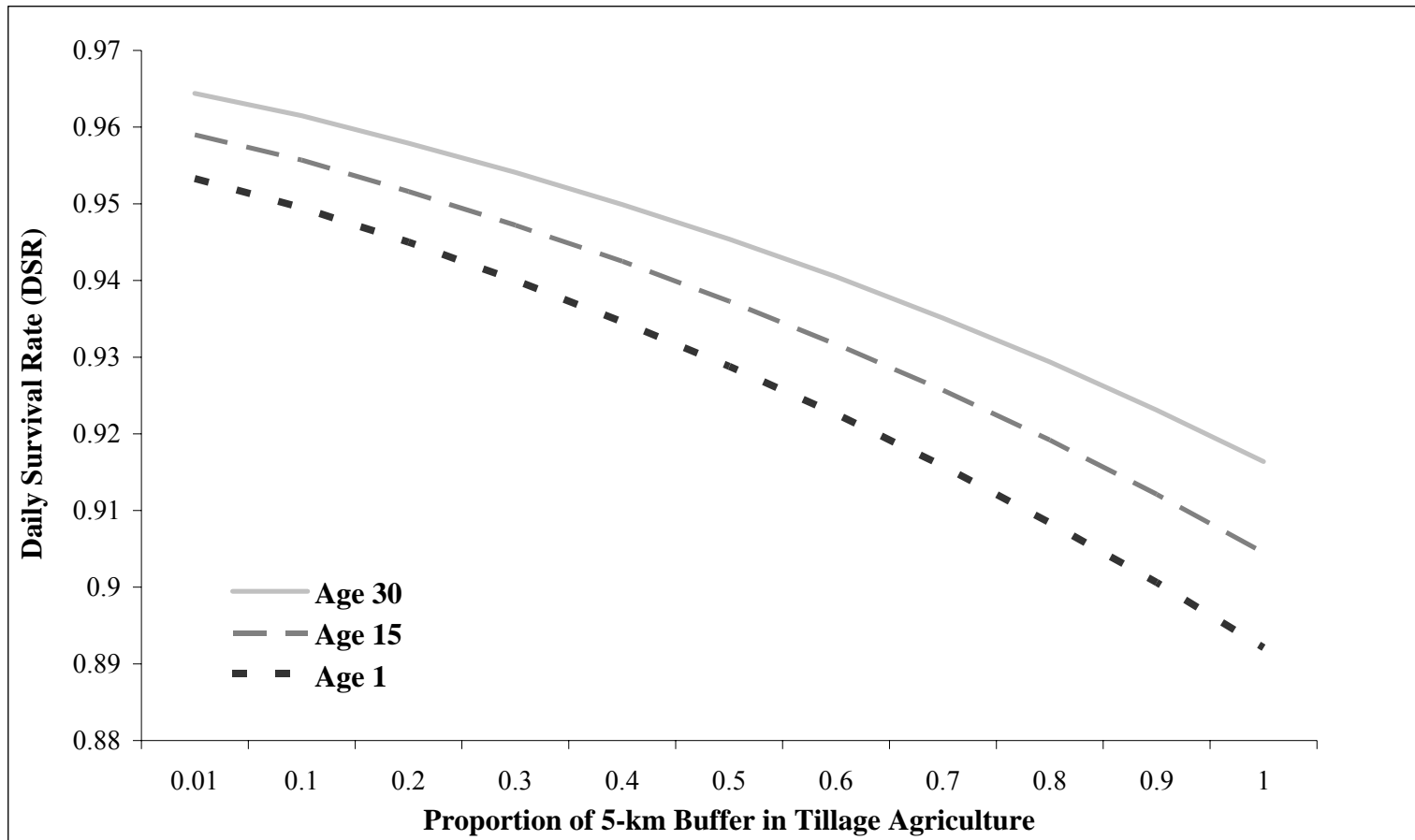
Figure 2. Predicted daily survival rates (DSR) of after-second-year (ASY) and second-year (SY) females as proportion of tillage agriculture increases within the 5-km buffer around nest at nine sites in the Great Lakes region from 2001 - 2003.
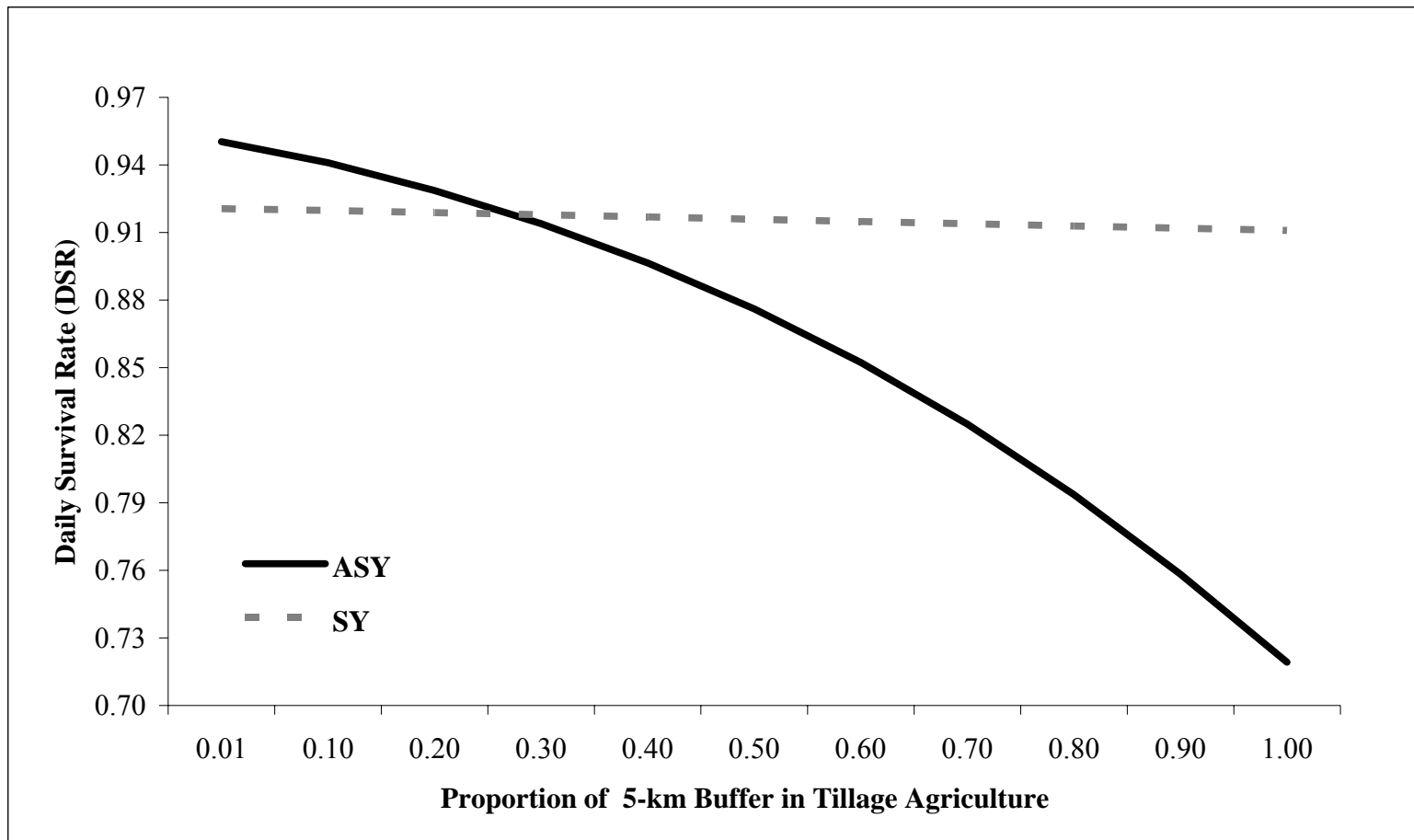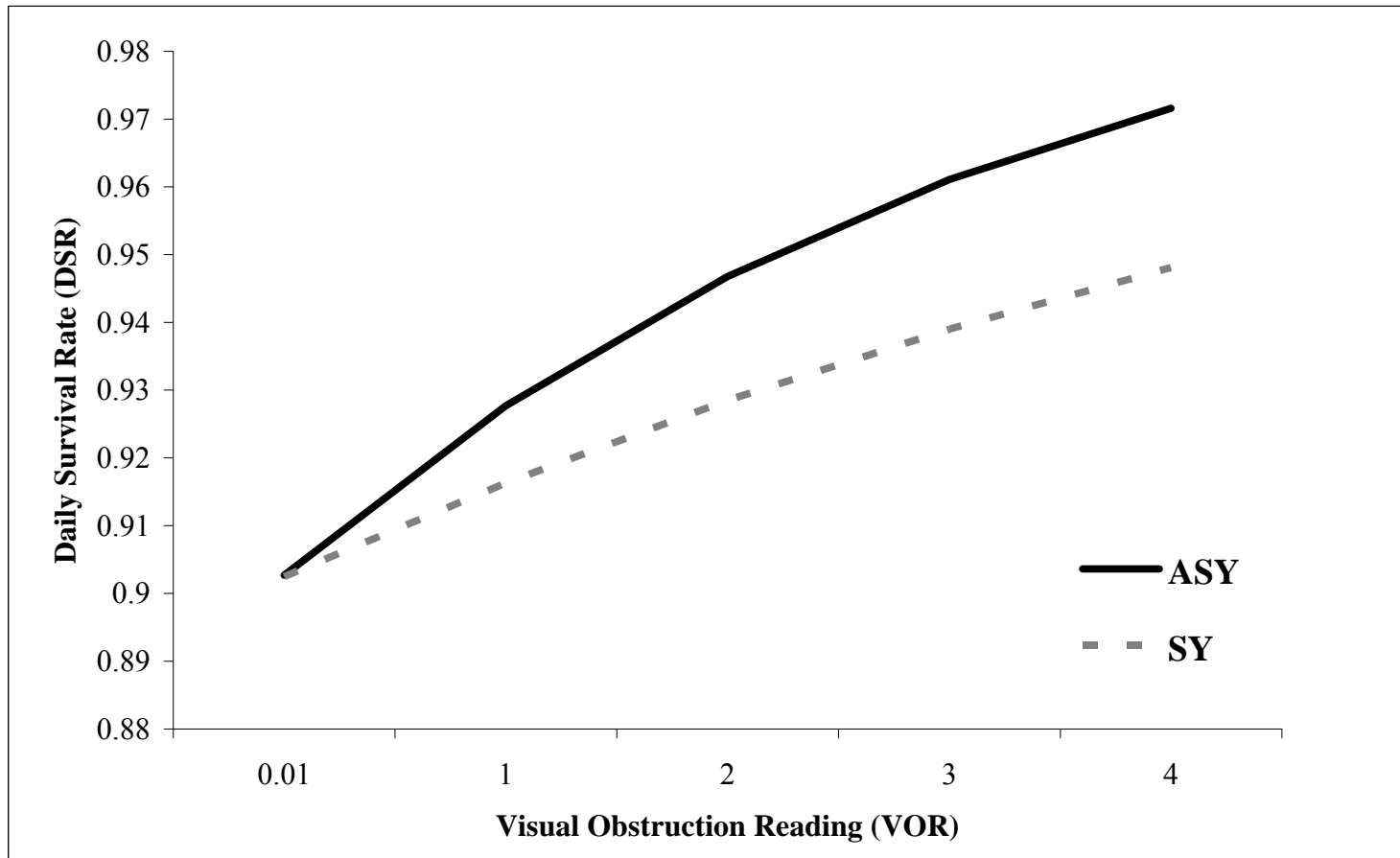
Figure 3. Predicted daily survival rates (DSR) of after-second-year (ASY) and second-year (SY) females as visual obstruction readings (VOR) around nest increase at nine sites in the Great Lakes region from 2001 - 2003. Predicted nest survival was similar for both age classes as nest concealment increased.

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