FACTORS AFFECTING PRODUCTIVITY AND HARVEST RATES OF GREAT LAKES MALLARDS

By

Howard V. Singer

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ABSTRACT

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Mallard (*Anas platyrhynchos*) populations in the Great Lake States; Michigan, Minnesota, and Wisconsin (hereafter GLS), are monitored as part of a larger population known as the Mid-continent mallard population. Regulations regarding harvest of Mid-continent mallards in the mid-1990s became more liberal than at any time in the past 50-years. Waterfowl managers of the GLS were concerned that liberalized regulations would lead to declining mallard populations throughout the GLS. Resource managers in Michigan and Wisconsin adopted regulations that were more restrictive than allowed under federal regulations for harvest of female mallards. Research has suggested that declining mallard abundance throughout the GLS could be linked to declining productivity and excessive harvest under liberalized regulations. This research suggests that productivity rates of GLS mallards have remained relatively steady from 1961-2011 despite environmental variation on the breeding grounds. I also found that kill rates during the more liberal hunting seasons were lower than during years when regulations were more restrictive, there were fewer mallards, and there were more duck hunters. Further analyses suggest regulation changes at the state level will have less of an impact on harvest rates than will regulation changes at the flyway level. My results suggest that the decline of GLS mallard abundance is likely not linked to excessive harvest or declining productivity.

This work is dedicated to a dear friend, Al Macon, who unfortunately passed away while this work was in progress. During my youth, Al used to pick me up from school and take me duck hunting. It is probably worth mentioning that Al was not a duck hunter and had never hunted ducks before taking me out; he was in his early 30s. We spent countless hours together in the marsh during my childhood, and we both got our first duck together although in different years. Al's patience with me as a youth helped me become the person I am today and as cliché as it sounds, I wouldn't be here today if it weren't for Al. Al was there when I bagged my first duck and will be with me when I bag my last duck. Thanks for all the great memories Al. You will always be missed, you were a great person.

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I would first like to thank my parents for being supportive of my hobbies as a kid even if they did not always please everyone. My mom probably still has a stash of all the duck calls she stole from me for blowing them too loudly in the house. Although my dad was not a hunter nor did he own any guns, he always encouraged me to do what made me happy and he spent quite a few days sitting in a duck marsh watching me hunt, mostly hoping that I did not shoot any ducks. Thanks also to my brother Sam and sister Becky, they both have always encouraged me to do what I love in life and have helped me throughout my life.

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And lastly, if it weren't for the ducks and waterfowl conservation, I would not be living the life I am now; filled with days in the marsh listening to whistling wings as ducks pass by.

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CHAPTER 1 THESIS INTRODUCTION

Research objectives and thesis organization

The purpose of this research is to understand how productivity and kill rates of mallards breeding from 1961-2011 in the Great Lake States (Michigan, Minnesota, and Wisconsin; hereafter GLS) are influenced by environmental factors, waterfowl hunter numbers, and regulations. This research will address the needs of both state and federal waterfowl management plans and may have important management implications for future waterfowl harvest management strategies at multiple management scales.

In this research I will: 1) estimate annual mallard productivity rates, 2) model how weather during the breeding season influences productivity rates and test for density dependence, 3) estimate annual female mallard kill rates, 4) model how hunter numbers at varying spatial scales influence kill rate and finally 5) model how regulations at varying management scales and hunter numbers impact kill rates for the GLS.

Chapter 2 will focus on estimating mallard productivity rates and modeling productivity rates over the last fifty-one years (1961-2011) and also during years when states conducted waterfowl and wetland surveys (Michigan 1992-present; Minnesota 1968-present; and Wisconsin 1973-present). Chapter 3 will focus first on estimating kill rates and second, modeling kill rates as a function of duck hunter numbers at varying spatial scales and finally modeling kill rates as a function of regulations and waterfowl hunter numbers. There may be some duplication of text in Chapters 2 and 3 as they are organized as separate manuscripts for submission to scientific journals.

CHAPTER 2 CLIMATIC FACTORS INFLUENCING MALLARD PRODUCTIVITY RATES IN THE GREAT LAKE STATES

Introduction

Changing climatic patterns, such as increased drought (Johnson et al. 2005), are likely to have irreversible, negative impacts to wetland conditions, such as permanency and productivity (Peterson et al. 1997; McCarty 2001; Hoegh-Guldberg and Bruno 2010). Wetlands throughout North America have been lost due to a variety of anthropogenic factors (e.g. loss of habitat due to roads, agricultural expansion, deforestation; Krapu 1974; Boyd 1985) and now more so, environmental factors (Dahl 1990; Prince et al. 1992). With expected increases in global temperatures (IPCC 2013), wetlands will likely continue to be lost. Johnson et al. (2005) found that under different climate change scenarios, favorable habitat for breeding waterfowl will likely shift to less productive areas of the northern prairies. Climate prediction models for the upper mid-west suggest summer temperatures and precipitation will likely increase and decrease respectively, thus exacerbating the rate of wetland loss. About 70% of wetlands in the Great Lakes Region have been lost since historical times (Snell 1987).

An important function of wetlands is as wildlife habitat and breeding waterfowl depend on wetlands for successful reproduction (Krapu and Reinecke 1992; Anteau 2012) as wetlands provide food resources for breeding, concealment from predators, and function as brood rearing habitat. It is well documented that the Prairie Pothole region (hereafter PPR) is an important area for breeding waterfowl (Boyd 1981; Krapu et al. 1983; Reynolds 1987); unlike the PPR, wetlands of the Great Lake States (Michigan, Minnesota, and Wisconsin; hereafter GLS) are more permanent and sometimes considered less productive for dabbling ducks than those of the PPR (Reynolds 1987; Kantrud et al. 1989; Euliss et al. 2004; Johnson et al. 2004; Simpson et al.

2005; Soulliere et al. 2007), although there is uncertainty about how productivity of dabbling ducks breeding in the GLS varies with weather.

A substantial loss of wetlands could cause a reduction in breeding habitat availability and quality and subsequently duck population declines (Larson 1994; Glick 2005). Annual variation in duck populations have been highly correlated with wetland abundance indices during the breeding season (Crissey 1969; Dzubin 1969; Leitch and Kaminski 1985; Johnson and Shaffer 1987; Kaminski and Gluesing 1987; Reynolds 1987; Batt et al. 1989; Bethke and Knudds 1995; Krapu et al. 1997). Furthermore, Heitmeyer and Fredrickson (1981) concluded that mallard production may also be influenced by wetland conditions on the wintering grounds, thus mallard productivity and subsequently population size may respond to wetland levels throughout the annual cycle. However, other factors may also contribute to variation in productivity rates.

Productivity rates of ducks are thought to be influenced by predation and environmental and contamination factors which could potentially decrease duckling survival and subsequently productivity rates (Talent et al. 1983; Ringleman 1992; Henny et al. 2000). Cold and wet weather following hatching is known to decrease duckling survival, potentially influencing productivity (Korschgen et al. 1996; Cox et al. 1998; Krapu et al. 2000; Pietz et al. 2003). Ducks require high quality food resources and brooding cover for successful reproduction (Sedinger 1992; Cox et al. 1998) which can be provided by certain wetlands. Wetlands with open water and flooded emergent vegetation are important for duckling survival (Weller and Spatcher 1965; Bloom et al. 2012). Wetlands throughout the GLS have been invaded by a myriad of invasive species (i.e. Purple loosestrife, (*Lythrum salicaria*); Phragmites (*Phragmites australis*); Eurasian Watermilfoil (*Myriophyllum spicatum*) over the past 30 years (Welling and Becker 1993). The ecological impact from aquatic invasive species is not well understood (Parker et al. 1999), but

invasive species may displace native species in wetlands, thus reducing breeding habitat available to waterfowl (Thompson et al. 1987) and potentially displacing breeding ducks.

Female mallards often exhibit greater philopatry than do males (Clark et al.1997; Greenwood and Harvey 1982; but see Doherty et al. 2002), but local hydrological conditions may displace birds from natal breeding grounds (Hansen and Mcknight 1964; Crissey 1969; Smith 1970; Jackson et al. 1985). Potential benefits of long-distance dispersal may outweigh costs if higher quality nesting sites are acquired (Coulton et al. 2011). This may result in higher annual emigration and immigration rates which in turn could affect local breeding population size. Immigration and emigration are thought to be contributing factors to annual breeding population size (Crissey 1969), which vary annually throughout the GLS. If density dependence influences productivity rates, then changes in immigration and emigration rates could influence productivity rates.

This research assesses the GLS mallard population which began to decline around 2001 after approximately 30-years of growth. This initial decline in abundance came at a time when Lake Michigan-Huron water levels were at a 50-year low (GLERL 2013). Predictions regarding mallard abundance suggest that with the continued loss of habitat, the GLS region could see a 19-39% decrease in duck abundance by the 2030s (Glick 2005). Given current climate change prediction models and the current decline of mallard abundance, concern of the GLS mallard population is lingering. Current hypotheses regarding the GLS mallard population decline are focused around declining productivity (Van Horn et al. 2006) and non-breeding season survival (i.e. hunting; Coluccy et al. 2008). However, Hoekman et al. (2002) found >75% of the variation in population growth for mid-continent mallards can be attributed to nest success, adult hen breeding season survival, and duckling survival which all may be influenced by predator-prey

interactions. However, our understanding of the relationship between climate and vulnerability to predation during the breeding season and resulting effects on productivity is incomplete.

I estimated long-term (1961-2011) mallard productivity rates for birds breeding in the GLS to understand how productivity rates have changed over time and have been affected by wetland habitat availability (i.e., via variation in regional hydrology), weather, and mallard abundance during the breeding season. Here, I define productivity rate as the ratio of young to adult females in the pre-hunt late summer population within each GLS. I hypothesize that indices of breeding habitat availability, temperature, and precipitation during the breeding season would be positively related to productivity rates and that density dependence on the breeding grounds could be influencing productivity rates. The quantity and quality of wetlands for breeding mallards are thought to have declined in the GLS, so I predicted that productivity rates had declined. Understanding the link, if one exists, between productivity rates and climatic factors may help managers focus habitat management at particular times of the breeding season or toward wetlands that provide habitat throughout the entire breeding season.

Study area and methodology

This study included mallards breeding in the GLS, which are managed as part of the mid-continental population of mallards (USFWS 2013). Roughly 80% of the GLS lies within the Prairie Hardwood and Boreal Hardwood Transition ecoregions except for parts of western and southern Minnesota and a small portion of southeastern Michigan and western and southern Wisconsin, which are considered Prairie Pothole and Eastern-Tallgrass Prairie ecoregions respectively (NABCI 2000). Weather patterns in this region are largely driven by strong lake effects and wetlands are more permanent than those of the PPR. Mallards in this region contributed 8-15% of the entire mid-continent mallard population (USFWS 2013).

To estimate population age ratios, I used samples of mallards harvested in the GLS and collected as part of the United States Fish and Wildlife Service (USFWS) Parts Collection Survey from 1961-2011. Estimates of harvest by age/sex cohorts was derived from data collected during Mississippi Flyway "wing bees" and provided by USFWS Harvest Surveys Section personnel; I restricted the analyses to birds taken during September 1-October 31 as these months represent a period when harvest is largely comprised of local breeding birds and large scale migrations have not begun into the Great Lakes region (Jessen 1970; Krementz et al 2013). Furthermore, T. Arnold and C. de Sobrino (unpub data) found that 75, 57, and 80 percent of annual mallard harvest in Michigan, Minnesota, and Wisconsin, respectively is comprised of local breeding mallards, which lends support to the assumption that harvested mallards in September and October are primarily local breeding birds.

First, I estimated direct recovery rates for each state/age class (DRR) defined as, the proportion of the banded sample that was shot and reported (Shot) during the hunting season immediately following banding, $DRR_{ijk} = \frac{Shot_{ijk}}{Band_{ijk}}$; where $Band_{ijk}$ is the number of banded mallards in a year $_i$ in age class $_j$ of sex $_k$. I then adjusted DRR estimates for reporting rates to estimate harvest rate (HR) by the equation, $HR_i = \frac{DRR_i}{RR_i}$; where RR_i is the annual reporting rate as estimated from reward band studies (Nichols et al. 1991). I adopted reporting rates used by Arnold (T. Arnold, unpub data; 38% 1961-1995 and 77% 1996-2011). Band reporting rates increased in \sim 1996 when implementation of "toll-free" bands was adopted, allowing hunters to report harvested birds via telephone where previously birds could only be reported via USPS mail service (Royle and Garretson 2005). I then estimated cohort specific fall abundance as, $\widehat{N}_i = \frac{\widehat{H}_i}{HR_i}$, where \widehat{H}_i is the harvest of cohort $_i$ estimated from the parts collection survey data and

 \widehat{HR}_i is the harvest rate of cohort $_i$. Juvenile game birds are likely more vulnerable to harvest than are adults so I adjusted harvest age ratios for differential harvest vulnerability of age cohorts using ratios of direct recovery rates (March and Hunt 1978; Reynolds 1987; Zimmerman et al. 2010). Finally, to estimate productivity rates, I used $\widehat{PR} = \frac{N_{jf+jm}}{N_{af}}$, where N_{jf+jm} is the estimate of juvenile female and male abundance, respectively divided by the estimate of adult female abundance. Sample size of band recovery data in some year/states was small, so I used a 5-yr moving average of direct recovery rates to adjust harvest age ratios (Zimmerman et al. 2010).

I used the Mixed Models Procedure (PROC MIXED) in SAS (SAS Institute 2004) to model response of productivity rate to temperature, precipitation, wetland hydrological conditions, and mallard abundance. I excluded one and two years of data from WI and MI respectively as these were extreme outliers (SAS Institute 2004). I used Palmer Hydrological Drought Indices (hereafter PHDI; NCDC 2012) or wetland abundance estimates from spring aerial waterfowl surveys for each state (hereafter POND) as measures of breeding habitat availability. POND estimates were not available for the entire 1961-2011 time series because state waterfowl surveys began later (MI 1992, MN 1968, and WI 1973). I tested for the effects of precipitation and temperature on productivity rates by including average June and July temperature (hereafter JUNET and JULYT respectively) and average June and July precipitation (hereafter JUNEP AND JULYP respectively). These climatic variables represent a time period post-hatch, when duckling survival is quite variable, thus potentially influencing productivity rates. Density dependence in productivity is one of the current parameters used to evaluate mallard population dynamics under the Adaptive Harvest Management protocol (USFWS 2013). To test for the effects of density dependence, I included annual mallard abundance estimates

from each state (hereafter MALL). The POND variable provided a metric to assess available breeding habitat which is thought to be a limiting factor to reproduction (USFWS 2013).

However, POND was not available across the 51-year study and both MN and WI do not survey the entire state. Thus, I used a 3-month average (April-June) PHDI to index breeding habitat conditions during peak settling and nesting (Bellrose 1976). The PHDI is a drought index that is used to assess long-term moisture supply (NCDC 2012). Other researchers have found high positive correlation between Lake Michigan-Huron water levels in year t-1 and current year mallard abundance estimates (D. Luukkonen unpub data). To evaluate potential time lag effects, I considered a one-year lag effect of PHDI and POND (PHDI_LAG and POND_LAG, respectively). All predictor variables were treated as continuous and standardized with a mean of zero and standard deviation of one.

The global model for the first set of candidate models (hereafter PHDI models) included the variables: PHDI, PHDI_LAG, JUNET, JULYT, JUNEP, JULYP and an intercept term and the global model for the second set of candidate models (hereafter POND models) included the precipitation and temperature variables in addition to POND, POND_LAG, and MALL and an intercept term.

The *a priori* model sets included only main-effects and consisted of 8 models for the PHDI data set and 9 models for the POND data set (Table 1).

Table 1. Candidate models used to model productivity rates for both the (a) PHDI and (b) POND data sets. In the POND data set I was interested in the effects of density dependence on productivity and thus have included the covariate MALL in all models.

a. PHDI

PHDI+PHDI LAG+JUNET+JULYT+JUNEP+JULYP

PHDI+PHDI LAG+JUNET+JULYT

PHDI+PHDI LAG+JUNEP+JULYP

JUNET+JULYT+JUNEP+JULYP

PHDI+PHDI_LAG

JUNET+JULYT

JUNEP+JULYP

INTERCEPT ONLY

b. POND

POND + POND LAG + JUNET + JULYT + JUNEP + JULYP + MALL

 $POND + POND_LAG + JUNET + JULYT + MALL$

POND + POND LAG + JUNEP + JULYP + MALL

JUNET + JULYT + JUNEP + JULYP + MALL

POND + POND LAG + MALL

JUNET + JULYT + MALL

JUNEP + JULYP +MALL

MALL

INTERCEPT ONLY

I compared models using Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) and reported model-averaged parameter estimates ($\hat{\beta}$) and unconditional standard error (\pm SE). This approach allowed us to make inference from a set of

models instead of one model and is thought to be more useful for predictive modeling (Burnham and Anderson 2002; Arnold 2010).

I used a Chi-square goodness-of-fit test, $\hat{c} = \frac{x^2}{af}$, where x^2 is the chi-square test statistic and df is the estimable parameters from the global model plus one for the estimation of \hat{c} (PHDI global model and POND global model = 7 and 8 parameters, respectively) to check for overdispersion in the data. I used a one-fold cross validation approach to assess model fit by withholding 33% (n=17) of the data in the PHDI model set. I did not withhold data for the POND data set as the number of observations was insufficient. I then assessed model fit by fitting a linear regression model of the test and training data from the cross-validation test and evaluate model fit using the r^2 for each of the GLS.

Results

Productivity rate estimates

Mean mallard productivity rates were 2.9, 2.8, and 3.1 young/adult hen for MI, MN and WI respectively (95% CI: ± 0.35 , ± 0.27 , and ± 0.48 young/adult hen; Figure 1). Annual productivity rates ranged from 1.3-7.7, 0.7-4.0, and 1.0-9.8 young/adult hen for MI, MN, and WI, respectively (Figure 2).

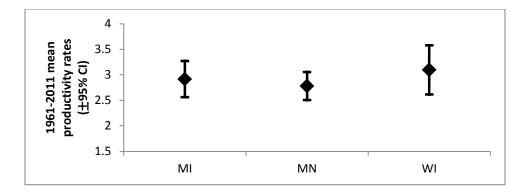
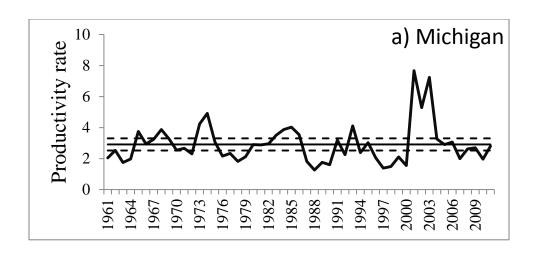
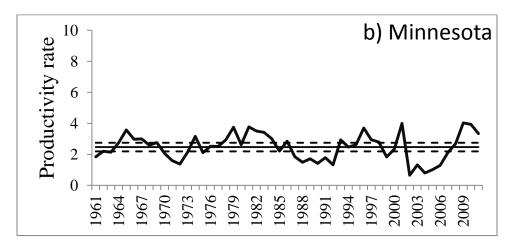


Figure 1. Mean productivity rates for mallards in the 3 GLS (\pm 95% CI) 1961-2011.





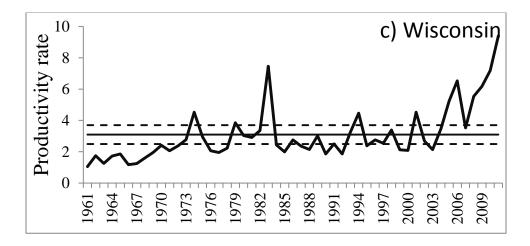


Figure 2. Annual productivity rates for mallards in the 3 GLS: (a) Michigan; (b) Minnesota; and (c)Wisconsin with long-term average (solid horizontal line) and 95% CI (dashed horizontal lines).

PHDI model results

None of the productivity models accounted for more than ~55% of the model weight based on AIC $_c$ (Table 2).

Table 2. Performance of models used to explain variation in productivity rates for the PHDI (34 randomly selected years) and POND (1968-2011, 1973-2011, and 1991-2011 for MN, WI, and MI respectively) data sets for each state (a) Michigan; (b) Minnesota; and (c)Wisconsin. The number of model parameters (K) with all models including an intercept, Akaike's information criterion adjusted for small sample size (AIC_c), AIC_c compared with the best model (Δ AIC_c), and the likelihood of each model in a set (Akaike weight, W_i) are reported.

a) Michigan				
PHDI model set	K	AIC_c	ΔAIC_c	\mathbf{W}_{i}
PHDI + PHDI_LAG + JUNET+JULYT	6	89.8	0	0.55
PHDI+PHDI_LAG	4	92.3	2.5	0.16
PHDI+PHDI_LAG+JUNET+JULYT+JUNEP+JULYP	8	92.8	3	0.12
JUNET+JULYT	4	93.9	4.1	0.07
INTERCEPT ONLY	2	95.3	5.5	0.04
PHDI+PHDI_LAG+JUNEP+JULYP	6	95.5	5.7	0.03
JUNET+JULYT+JUNEP+JULYP	6	96	6.2	0.02
JUNEP+JULYP	4	98.1	8.3	0.01
POND model set	K	AIC_c	ΔAIC_c	W_{i}
JUNET+JULYT+MALL	4	50.5	0	0.22
POND+POND_LAG+JUNET+JULYT+MALL	7	51.1	0.6	0.16
POND+POND_LAG+JUNET+JULYT+JUNEP+				
JULYP+MALL	9	51.5	1	0.13
MALL	3	51.6	1.1	0.12
INTERCEPT ONLY	2	52.1	1.6	0.10
JUNET+MALL+JULYT+JUNEP+JULYP	7	52.1	1.6	0.10
POND+POND_LAG+MALL	5	52.4	1.9	0.08
JUNEP+JULYP+MALL	5	53.5	3	0.05
POND+POND_LAG+JUNEP+JULYP+MALL	7	53.6	3.1	0.05

Table 2 (cont'd)

b) Minnesota				
PHDI model set	K	AIC_c	ΔAIC_c	W_{i}
PHDI+PHDI_LAG	4	90.2	0	0.37
PHDI+PHDI_LAG+JUNEP+JULYP	6	90.4	0.2	0.33
INTERCEPT ONLY	2	92.8	2.6	0.10
PHDI+PHDI_LAG+JUNET+JULYT	6	93.4	3.2	0.07
PHDI+PHDI_LAG+JUNET+JULYT+JUNEP+JULYP	8	93.9	3.7	0.06
JUNEP+JULYP	4	95.1	4.9	0.03
JUNET+JULYT	4	95.5	5.3	0.03
JUNET+JULYT+JUNEP+JULYP	6	97.9	7.7	0.01
POND model set	K	AICc	ΔAIC_c	W_i
POND model set INTERCEPT ONLY	K 2	AIC _c 119	ΔAIC_c	W _i 0.31
INTERCEPT ONLY	2	119	0	0.31
INTERCEPT ONLY POND+POND_LAG+MALL	2 5	119 119.4	0 0.4	0.31 0.26
INTERCEPT ONLY POND+POND_LAG+MALL MALL	2 5 3	119 119.4 120.6	0 0.4 1.6	0.31 0.26 0.14
INTERCEPT ONLY POND+POND_LAG+MALL MALL JUNET+JULYT+MALL	2 5 3 5	119 119.4 120.6 121.2	0 0.4 1.6 2.2	0.31 0.26 0.14 0.10
INTERCEPT ONLY POND+POND_LAG+MALL MALL JUNET+JULYT+MALL POND+POND_LAG+JUNET+JULYT+MALL	2 5 3 5 7	119 119.4 120.6 121.2 121.4	0 0.4 1.6 2.2 2.4	0.31 0.26 0.14 0.10 0.09
INTERCEPT ONLY POND+POND_LAG+MALL MALL JUNET+JULYT+MALL POND+POND_LAG+JUNET+JULYT+MALL POND+POND_LAG+JUNEP+JULYP+MALL	2 5 3 5 7 7	119 119.4 120.6 121.2 121.4 123.2	0 0.4 1.6 2.2 2.4 4.2	0.31 0.26 0.14 0.10 0.09 0.04
INTERCEPT ONLY POND+POND_LAG+MALL MALL JUNET+JULYT+MALL POND+POND_LAG+JUNET+JULYT+MALL POND+POND_LAG+JUNEP+JULYP+MALL JUNEP+JULYP+MALL	2 5 3 5 7 7 5	119 119.4 120.6 121.2 121.4 123.2 124.2	0 0.4 1.6 2.2 2.4 4.2 5.2	0.31 0.26 0.14 0.10 0.09 0.04 0.02

Table 2 (cont'd)

$\frac{\Delta AIC_c}{0}$	$\mathbf{W}_{\mathbf{i}}$
0	
	0.27
0.9	0.17
1.3	0.14
1.8	0.11
2	0.10
2.3	0.08
2.5	0.08
3	0.06
	2.3 2.5

POND model set	K	AIC_c	ΔAIC_c	W_i
INTERCEPT ONLY	2	141.8	0	0.23
JUNET+JULYT+MALL	4	142.6	0.8	0.16
MALL	3	142.7	0.9	0.15
POND+POND_LAG+MALL	5	143.2	1.4	0.12
POND+POND_LAG+JUNET+JULYT+MALL	7	143.6	1.8	0.09
JUNET+JULYT+JUNEP+JULYP+MALL	7	144	2.2	0.08
JUNEP+JULYP+MALL	5	144.2	2.4	0.07
POND+POND_LAG+JUNEP+JULYP+MALL	7	144.7	2.9	0.05
POND+POND_LAG+JUNET+JULYT+JUNEP+				
JULYP+MALL	9	144.8	3	0.05

Model averaged parameter estimates (Figure 3) showed that PHDI was positively related to productivity rates and was the most influential predictor variable explaining variation in productivity rates for all states, however 95% CI overlapped zero in WI. JULYT was positively related to productivity rates in all 3 states with the greatest effect seen in MI and WI. Productivity rates were weakly related to PHDI_LAG, JUNET, JUNEP, and JULYP with 95% CI broadly overlapping zero. Chi-squared goodness-of-fit tests suggested that generally the data were not overdispersed in MI or MN, but were overdispersed in WI ($\hat{c} = 1.03, 1.18, \text{ and } 3.59 \text{ for the global model from the PHDI data set for MI, MN, and WI, respectively and <math>\hat{c} = 0.38, 1.47,$ and 2.93 for the global model from the POND model set for MI, MN, and WI, respectively;

Burnham and Anderson 2002). However, the data were underdispersed in the POND data set for Michigan ($\hat{c}=0.38$). Cross-validation results suggest that the top ranking model based on AIC_c explained about 10% of the variation of productivity rates for mallards in Michigan.

Productivity rates in Minnesota and Wisconsin did not respond well to the top models ($R^2 \le 0.1$).

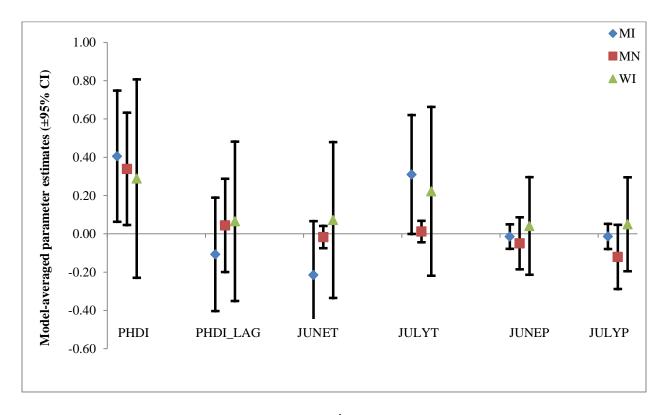


Figure 3. Model-averaged parameter estimates $(\hat{\beta})$ and 95% CI from standardized predictor variables across all models for the PHDI model set. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

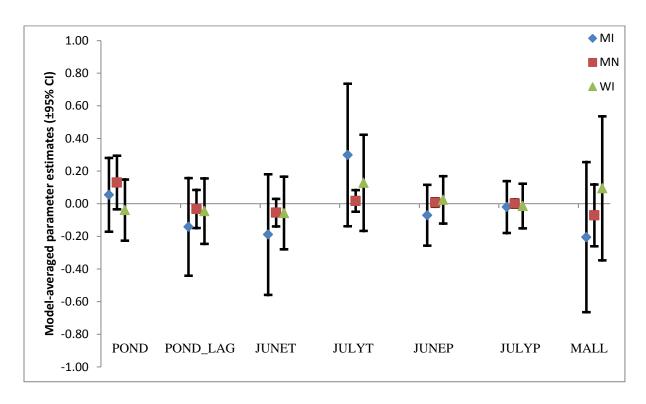


Figure 4. Model-averaged parameter estimates ($\hat{\beta}$) and 95% CI from standardized predictor variables across all models for the POND model set.

POND model results

No model accounted for more than \sim 31% of the model weight based on AIC_c (Table 2). Model averaged parameter estimates overlapped zero suggesting large uncertainty evaluating the effects of the variables on productivity rates (Figure 4).

Similar to the PHDI model set, temperature explained more of the variation in productivity rates than did precipitation, but 95% CI overlapped zero for all variables. The JULYT variable explained more variation than the other variables and was positive for all states, but CI overlapped zero. There appears to be some evidence for a density dependence effect on

productivity rates as observed by a slightly negative estimate for the MALL covariate in Michigan and Minnesota, but again 95% CI overlapped zero.

Discussion

My results suggest that annual variation in productivity rates is most influenced by wetland hydrologic conditions, as indexed by the PHDI variable, more so than temperature, precipitation, and mallard abundance during the breeding season. Hydrology is an important component of wetlands that likely reflects habitat availability for mallards during settling, pairing, and brood rearing. Mallard nest survival in the aspen parklands has been linked to the amount of herbaceous vegetation on study areas and total precipitation for the 12 months prior to nesting; also, nesting effort was positively related to wetland inundation in July and duckling survival was positively related to the proportion of seasonal wetlands holding water in July (Howerter et al. 2014). Others have found similar positive relationships between mallard abundance and pond counts which might result from more birds settling to breed or greater return of birds breeding or produced in previous years when landscapes are wet (Stoudt 1969; Krapu et al. 1983; Kaminski and Prince 1984; Leitch and Kaminski 1985; Johnson and Grier 1988); however, the estimate of ponds in the POND model set explained less variation in productivity than did the PHDI variable. Crissey (1969) found that mallard abundance in a given year was correlated with July pond counts from the previous year and attributed this to increased reproduction. Although I did not directly look at July pond counts, I found that July temperature was positively related to productivity rates. My estimate of ponds did not cover the entire time series and may not be a reliable indicator of breeding habitat availability as this data does not classify wetlands as potential breeding habitat (i.e. sheet water in fields) and this variable may

too coarsely index changes in hydrology to be a useful predictor of productivity. Many wetlands of the GLS are permanent or semi-permanent lakes, ponds, and rivers and since these typically would not become dry, the count of ponds in the GLS may not capture variation in habitat available for breeding mallards.

Cold and wet weather, especially for ducklings < 10 days old, is expected to negatively affect survival (Mendenhall and Milne 1985; Krapu et al. 2006; Bloom et al. 2012). I did not observe any significant effects of precipitation on productivity rates but I did observe effects of temperature on productivity rates for Michigan and Wisconsin. However, productivity rates in Minnesota were affected minimally by June or July temperature. Mallard duckling survival in the aspen parklands was negatively related to the number of days in June and July when minimum air temperature dropped below 10°C (Howerter et al. 2014). If a brood rearing season was on the average wetter and colder and duckling survival was lower, productivity rates could be affected. Extreme temperatures have been shown to influence thermoregulation in one-dayold mallard ducklings (Koskimies and Lahti 1964) and ducklings are more vulnerable to temperature extremes as thermal regulation is incomplete during the first ten days post-hatch (Orthmeyer and Ball 1990; Rotella and Ratti 1992). Although mallard ducklings are able to thermoregulate within one day after hatch, they can require brooding for up to 3 weeks (Untergasser and Hayward 1973). I studied effects of average monthly temperatures on productivity rates rather than daily extremes. It is possible that monthly averages may be high while daily extremes set record lows and vice versa, thus my methods would fail to capture these extreme events. Furthermore, I estimated productivity at the state scale and there is often a great deal of climatic variation within states. However, Jehl and Hussel (1966) did not observe any negative effects on waterfowl reproduction (i.e. observed brood counts) during a summer with a

severe three day snow storm. My productivity rate estimates were at a coarse spatial scale (i.e. individual states) and thus I could not capture climatic variation at certain areas where duck production may have been higher or lower than a states average. It is likely that weather patterns vary substantially across individual states.

Many of the model-averaged parameter estimates had 95% CI that overlapped zero, but estimates from the PHDI model set which included the entire time series were likely more robust than estimates from the POND model set. Furthermore, predation has been found to decrease hen success, however was not found to negatively impact mallard productivity in the PPR (Amundson et al. 2013). Mallards breed across a broad geographical area (Bellrose 1976), often have multiple clutches during a single breeding season (Bellrose 1976), and initiate nests over a broad temporal scale during a breeding season (Bellrose 1976), likely making them capable of overcoming extreme weather events which could impact productivity of species that may be less resilient.

Many factors that might affect mallard productivity changed over the course of the study, but productivity rates stayed relatively stable. For example, the amount of Conservation Reserve Program (CRP) acres on the landscape changed the amount of upland herbaceous cover in the GLS during the mid-1980's (Figure 5). Also, invasive wetland plant species such as purple loosestrife and phragmites became established. While some studies suggest that the decline of the GLS mallard breeding populations could be linked to a decline in productivity (Van Horn et al. 2006), my results suggest that long-term productivity rates have remained relatively stable, or increased in the case of Wisconsin, despite considerable annual variation. Although productivity rates were not significantly different among the GLS, Michigan and Wisconsin were more similar than were productivity rates in Minnesota. I suspect this is due to differences in

ecoregions amongst portions of the GLS. Portions of Minnesota that are ideal for breeding waterfowl lie within the PPR and past research has demonstrated differences among effects of climate in the ecoregions (Hokeman et al. 2005; Soulliere et al. 2007; Coluccy et al. 2008). Furthermore, variation in vital rates effecting population growth rates are different for mallards breeding in geographically diverse breeding regions (Hokeman et al. 2005; Coluccy et al. 2008; Howerter 2014).

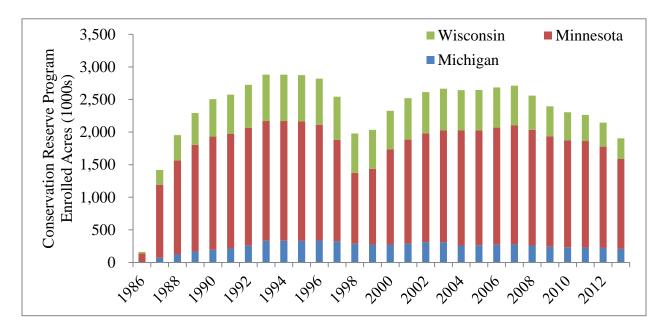


Figure 5. Acreage of land in the GLS that was enrolled in the CRP program from 1986-2013.

Coluccy et al. (2008) found that breeding season parameters such as nest success and duckling survival account for 63% of the variation in annual population growth rate. My results suggest that July temperature and breeding habitat availability effect productivity rates and this is likely due to increased nest success and duckling survival when breeding habitat is abundant and July temperatures are warmer during the brood rearing stage. However, I did not find any strong relationships with June temperature except a slight negative relationship for productivity rates in MI. June is likely the month that the majority of mallard nests hatch (Bellrose 1976) and predation rates on nests decline as the breeding season progresses (Greenwood et al. 1995).

Furthermore, natural disasters have been found to have minimal effects on nest loss in riparian bird communities (Best and Stauffer 1980). Thus, I expect that June temperature will be linked to productivity rates via decreased duckling survival. Perhaps during the month of June, nest success is high and duckling survival is high thus there appears to be a minimal effect of June temperature on productivity rates.

The importance of breeding habitat to successful waterfowl reproduction and abundance is well documented. Furthermore, annual variation in breeding habitat availability is likely greater in the PPR than the prairie and boreal hardwood transition regions (Kantrud et al. 1989, Soulliere et al. 2007), suggesting that mallard breeding abundance likely varies more on an annual basis in prairie type ecosystems than it does in the GLS. Variation in water levels across the GLS has been linked to climatic change at multiple scales (Keough et al. 1999). My results suggest that productivity rates are influenced by hydrological factors such that climatic changes could potentially negatively affect productivity rates by reducing breeding habitat availability. Recent climate change models predict areas of the upper Midwest are likely to experience dryer and hotter summers (UCS 2009), which could lead to poorer quality habitat through decreased water depth and consequently altered emergent vegetation patterns (Cowardin et al. 1988; Simpson et al. 2007).

My productivity rate estimates were higher than biologically likely for some years (i.e. productivity rates > 8 young/adult hen). Mallards typically lay a clutch of 9 eggs (Bellrose 1976) and it would be unlikely for all eggs to survive until fledging. I could not determine why this is so, but offer some speculation. Extremes in productivity rates were potentially do to: 1) an early influx of migrating mallards, and 2) a larger than normal sample of harvested mallards from a certain area (i.e. banding just prior to opening of hunting seasons on a managed waterfowl area).

Nonetheless, most of my estimates should be robust and show the importance of long-term studies (Gibbs et al. 1999) to understand variation in reproductive rates as often times there is a great deal of annual variation and trends correlating with climatic events.

Although productivity rates have remained relatively stable, future climatic changes could cause productivity rates to decrease due to reduced breeding and brood rearing habitat availability. My models suggest that productivity rates are influenced by weather patterns throughout the brood rearing and nesting periods. With the predicted increase of summer temperatures and decrease of summer precipitation (Hayhoe et al. 2009), evapotranspiration is expected to increase resulting in drying of wetlands that once could have provided ideal breeding and brood rearing habitat, leaving managers with the difficult decision of where to focus management.

Management Implications

My main findings suggest that mallard productivity rates have remained relatively stable despite varying climatic conditions and habitat alterations. The best predictor I found suggests that management for suitable nesting and brood rearing habitat should be the focus for waterfowl managers, but I caution that focus on one vital rate may influence another vital rate to either decrease or increase (Hoekeman et al. 2014). Mallards seem to have wide tolerance for nesting conditions and have been able to continue to reproduce effectively over the past 51-years despite changes in habitat and weather. However, the estimate obtained by the annual spring surveys in the GLS may not capture variation in breeding habitat availability as wetlands are more permanent than those of the prairies (Soulliere et al 2007), thus further classification of wetlands during spring surveys may help quantify breeding habitat availability.

Further studies could be conducted at smaller spatial and temporal scales so to quantify the effects of hydrological variation at different regions of the GLS and ensure management is being focused in the correct areas. However, I caution that long-term studies are needed in order to capture variation in hydrological periods and weather cycles. The potential exists for extreme variation in waterfowl productivity at certain locations, so focusing resources on areas of generally high mallard abundance may be of importance under certain climate change scenarios. Although intensive, managers in the GLS will want to consider the costs and benefits of creating or enhancing wetlands to provide water level control as a hedge against drying conditions.

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CHAPTER 3 FACTORS AFFECTING HARVEST RATES OF FEMALE MALLARDS BANDED IN THE GREAT LAKE STATES

Introduction

Wildlife management is focused around three guiding principles; managing populations, habitat and people (Giles 1978) for wildlife-related benefits such as recreational hunting, photography and wildlife viewing. Managers must focus attention on all three principles as each potentially influences the others. Furthermore, populations are managed for continued recreational opportunities for future generations of outdoor enthusiasts.

Waterfowl management is no different and mallards (*Anas platyrhynchos*) are a focal species of waterfowl management (USFWS 2013). Mallard harvest is highest among duck species taken in the Mississippi flyway (USFWS 2013) and duck hunting has substantial economic, recreational, and aesthetic value (Martin et al. 1980; Virtiska 2013). Continued management for sustaining populations of mallards and recreational opportunities is important.

Aerial surveys have been conducted since 1955 over the Prairie Pothole region (PPR) to obtain spring breeding population and pond count estimates (USFWS 2013). This area is thought to be one of the most important waterfowl breeding areas (Hochbaum 1983) and holds the most breeding ducks in North America (Pospahala et al. 1974). Furthermore, large scale banding operations were initiated in the 1950s and managers use data from recovered marked individuals to obtain robust estimates of survival and harvest rates. Furthermore, aerial surveys provide information that helps estimate population size for a myriad of species and this information helps in setting regulations for waterfowl hunting seasons.

Considerable time and money is annually devoted to setting hunting season regulation frameworks for waterfowl and this activity is a primary means of managing populations. Flyway

Councils, States, and the U.S. Fish and Wildlife Service (USFWS) set frameworks at broad regional levels (i.e. flyways; Johnson et al. 1993; Conroy et al. 2002) and the States may adopt regulations as liberal as the frameworks allow or may further restrict regulations. Waterfowl abundance is thought to be influenced by habitat availability (Crissey 1969) and harvest dynamics, thus monitoring and management of harvest and habitat should ensure continued duck abundance, recreational opportunities and subsequent hunter participation. Interest in the role of hunter harvest on waterfowl population dynamics has been a concern for decades (Nichols et al. 1995).

Waterfowl harvest management in the 1960s took a very simple approach. That is, when spring breeding habitat conditions were good and duck abundance estimates were high, hunting seasons were liberalized (i.e. long seasons and high daily limits; Babcock and Sparrowe 1989). The opposite was true when duck numbers and pond abundance were down. This approach is considered to be a "passive" approach to management (Sedinger and Herzog 2012). Over time, as populations changed, seasonal regulations waxed and waned accordingly. Then, beginning in the early 1990s, a new approach to waterfowl harvest management was introduced (Williams and Johnson 1995).

Adaptive harvest management (AHM; USFWS 1995) was adopted as a means to reduce the amount of uncertainty in; 1) population dynamics and 2) the impact of harvest when setting waterfowl regulations (Walters 1986; USFWS 2014). Furthermore, it explores the relationships between regulations, harvest, and waterfowl abundance (USFWS 2014) and is intended to reduce uncertainties about how density dependence affects mallard population dynamics. Managers use monitoring data to build models that predict population size under various population dynamic scenarios and then compare these predictions to observed population levels. Furthermore,

harvest rates are predicted annually for Mid-continent (MC) adult male mallards for three regulation packages and compared to those observed from band-recovery data. Mallards of the Great Lake States (Michigan, Minnesota, and Wisconsin; GLS) are also considered in management decisions for the MC mallard population.

Mallards of the GLS are managed under the AHM protocol as part of the MC mallard population. The GLS population has been monitored as a whole since 1991, but monitoring began in 1968 and 1973 for Minnesota and Wisconsin, respectively. During this time frame, the mallard population increased despite harvest rates exceeding 50-year highs and record numbers of waterfowl hunters (USFWS 2013; Figure 6). The population reached an all-time high in the early 2000s before declining. Other measures of population trends such as the North American Breeding Bird Survey also support the notion that mallards were on a long-term increase in the GLS since 1968 (Sauer et al 2014.) Furthermore, the GLS mallard population has been prone to very high local harvest; total GLS mallard harvest is often comprised of > 50% local mallards (75, 57, and 80% for Michigan, Minnesota, and Wisconsin respectively; T. Arnold and C. de Sobrino, unpub data).

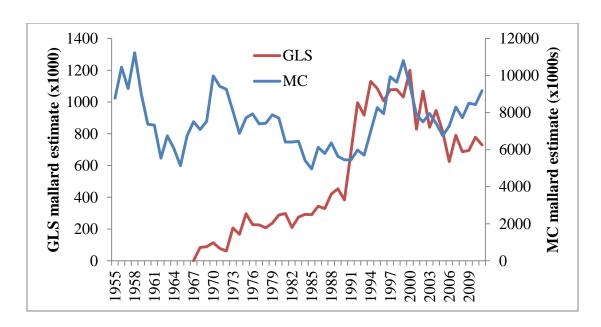


Figure 6. Mallard population estimates for the GLS (red line) and the MC (blue line; not including the GLS) from 1961-2011. Surveys began in 1968, 1973, and 1991 for Minnesota, Wisconsin, and Michigan, respectively. Michigan supports the most breeding mallards of the GLS which explains the large increase in 1991 when Michigan began surveying mallard abundance.

The apparent decline in GLS breeding mallard abundance has been attributed to non-breeding season survival (i.e. high harvest pressure under AHM; Coluccy et al. 2008) and declining productivity (Van Horn 2006. Furthermore, over the past 4 decades, hunter numbers have declined in the GLS and throughout the Mississippi Flyway. Policy makers have been concerned about recent trends for mallards and waterfowl hunters and Michigan and Wisconsin have restricted mallard limits to include only 1 hen daily since the inception of AHM while the federal framework for hen mallards has allowed 2 in the daily harvest; similarly Minnesota restricted hen mallard daily limits, but for a subset of years during AHM. Little research has been done to determine how this restriction beyond federal frameworks has influenced hen mallard harvest rates.

The goal of this research was to shed some light on how harvest regulations and hunter numbers have influenced mallard harvest rates in the GLS. In particular, have restrictive regulations that have been implemented in the GLS since the inception of AHM been effective?

The main objectives of this chapter were twofold. First, I investigated effects of hunter numbers at varying spatial scales on kill rates.

Second, I investigated impacts of regulations at varying scales (i.e. season length and daily limit) and hunter numbers on kill rates. My main interest is to understand how decisions regarding hen mallard daily limit at varying spatial scales have influenced kill rates.

Study area and methodology

This study included mallards breeding in the GLS, which are managed as part of the MC population of mallards (USFWS 2013). The majority of the GLS lies within the Prairie Hardwood and Boreal Hardwood Transition ecoregions except for parts of western and southern Minnesota and southeastern Michigan which are considered Prairie Pothole and Eastern-Tallgrass Prairie ecoregions, respectively (PPR; NABCI 2000). Weather patterns in this region are largely driven by strong lake effects and wetlands are more permanent than those of the PPR. Mallards in this region contributed 8-15% of the spring abundance of the entire MC mallard population (USFWS 2013).

Duck hunter analysis

My goal was to select the estimate of waterfowl hunter numbers from different spatial scales that was most predictive of kill rates under various management scenarios. I explored three different scales of hunter numbers to determine the most appropriate scale.

I used samples of mallards banded in the GLS and harvested throughout North America from 1961-2011 to estimate kill rates. Band and recovery data were obtained from the U.S. Geological Survey; I restricted the analysis to birds banded during "pre-season" (July-September) banding operations 1961-2011 in Michigan, Minnesota, and Wisconsin that were marked with "federal numbered band only" or "captured by spotlighting" (Add_Info codes '00' and '70' respectively), and were "normal, wild-birds" (Status '3'). I omitted birds that were banded with reward bands as reward bands are often reported at a higher rate than are standard federal leg bands (Nichols et al. 1991). Recoveries were restricted to birds that were "shot" or "found dead" (reporting codes "00" and "01", respectively) from September 1-January 31. Birds were classified into two age groups (1=hatch year and local and 2=after hatch year).

First, I estimated direct recovery rates for each state/age class (DRR) defined as, the proportion of the banded sample that was shot and reported (Shot) during the hunting season immediately following banding, $DRR_{ij} = \frac{Shot_{ij}}{Band_{ij}}$; where $Band_{ij}$ is the number of banded mallards in year $_i$ in age class $_j$. I then adjusted DRR estimates for reporting rates to estimate harvest rate (HR) by the equation, $HR_i = \frac{DRR_i}{RR_i}$; where RR_i is the annual reporting rate as estimated from reward band studies (Nichols et al. 1991). I adopted reporting rates used by Arnold (T. Arnold, unpub data; 38% 1961-1995 and 77% 1996-2011). Band reporting rates increased in ~ 1996 when implementation of "toll-free" bands was adopted, allowing hunters to report harvested birds via telephone where previously birds could only be reported via USPS mail service (Royle and Garretson 2005). Estimates of wounding loss are ~20% (Anderson and Burnham 1976) so I adjusted HR to obtain kill rate (KR). The final equation to estimate KR is; $\widehat{KR}_l = HR_i \times 1.2$.

I obtained estimates of the number of Mississippi flyway waterfowl hunters from the USFWS Federal Duck Stamp office (USFWS 2012). This report documents estimates of waterfowl hunters based on the sale of Federal Migratory Bird Hunter and Conservation Stamps (hereafter duck stamp) for each state in the Mississippi flyway. . In this analysis, I was interested in evaluating the impact of estimates of duck hunter numbers on kill rates at varying spatial scales as numbers of waterfowl hunters, more specifically duck hunters, likely influence kill rates of ducks at varying spatial scales (Conroy et al. 2005). Duck hunting regulations are set according to the AHM protocol and thus are flyway wide, therefore kill rates could be influenced by the number of duck hunters in the entire Mississippi flyway. I used the number of duck stamps sold at the flyway scale (hereafter FHUNT) as one predictor of kill rates. T. Arnold an de Sobrino (unpub data) suggest that mallard harvest in the GLS is largely (>50%) comprised of local breeding birds, so the potential for kill rates to be more closely tied to local hunter numbers exists. As an estimate of waterfowl hunters at the state scale, I used the number of duck stamps sold in each state (hereafter SHUNT). Furthermore, if mallards from one state are primarily harvested in an isolated region, I hypothesized that duck hunter numbers in a given harvest region may have the greatest impact on kill rates. To obtain an estimate for this hypothesis, I analyzed band recovery data for each of the states to find the top five harvest states/provinces for each stock of mallards (mallards banded in a state). I used data from mallards banded and recovered in the same year (direct recoveries) to select the states and provinces. The province of Ontario was one of the top 5 kill states/provinces for MI banded mallards. Since estimates of duck hunters in the Canadian provinces only date back to 1966, I decided to not consider this variable in kill rate models (Environment Canada 2014). I then ran separate analyses for all 3 states considering FHUNT and SHUNT as predictors of kill rates.

Duck hunter number estimates from duck stamp sales have some biases (K. Wilkins, USFWS, personal communication). In recent years (2000-2011) the estimates are likely not as robust because duck stamp sales from large corporations have not been tracked back to the state of sale, but rather the corporations' headquarters and also the United States Post Office reported its' duck stamp sales to regional offices which may not be contained in the state of sale (K. Wilkins personal communication). Furthermore, speculation has been made that purchasing of duck stamps by non-hunters has increased over time (K. Wilkins personal communication).

I fitted linear models in program SAS (SAS 9.3) to evaluate the effects of hunter numbers at varying spatial scales on kill rates. I ranked models using Akaike's information criterion adjusted for small sample size (AICc; Burnham and Anderson 2002). The top ranking model for each state would then allow us to select the appropriate scale to model hunter numbers in my kill rate models. All estimates of duck hunter numbers were standardized with a mean of zero and standard deviation of one. I used a Chi-square goodness-of-fit test, $\hat{c} = \frac{x^2}{df}$, where x^2 is the chi-square test statistic and df is the estimable parameters from the global model plus one for the estimation of \hat{c} to check for overdispersion in the data.

Kill rate analysis

I used the Mixed Models Procedure (PROC MIXED) in SAS (SAS Institute 2004) to model the response of kill rates to age class (hatch-year, and after hatch-year), season length (hereafter DAYS), daily hen mallard limit at the state level (hereafter LIMIT), and hunter numbers (hereafter SHUNT or FHUNT) at the flyway level for Minnesota and state level for

Michigan and Wisconsin. I attempted to include season opening dates and dates in which it ran, but states have different zones that open on different dates. The DAYS and LIMIT variables were categorical with DAYS divided into three categories (1- <38 days; 2- >= 38<50; 3->=50) and LIMIT into two categories for all states based on the observed daily limit and season lengths from state regulations (Table 3). States did not restrict season length beyond the federal frameworks, so DAYS was relevant only at the flyway scale. I omitted two and three years of data from Wisconsin and Minnesota respectively as they had seasons with a 4 hen mallard daily limit and there were too few years with these limits to get meaningful estimates. However, the LIMIT variable did vary temporally from the federal framework as states adopted more restrictive daily limits in many cases. Prior to 1995, there was only one year (1968) when federal regulations had multiple options regarding for the Mississippi flyway states regarding season length, daily limits and species restrictions (Martin and Carney 1977).

Waterfowl managers in the GLS have suggested that restrictions of federal regulations at the state level have little impact on kill rates (S. Cordts personal communication), but I felt obligated to mention these fine details regarding variation in season length and daily limits. Substantial variation in federal framework regulations and environmental conditions makes understanding directly how changes in season length or daily limit influence kill rates convoluted (William and Johnson 1995). Nonetheless, I modeled kill rates in response to coarse changes in regulations that are most likely to impact kill rates. Data to determine state regulations used for predictor variables was obtained from the Wisconsin Department of Natural Resources, Minnesota Department of Natural Resources, and the Michigan Department of Natural Resources.

Table 3. Number of years that a given state had various season lengths and daily hen mallard limit combinations. Season lengths were categorized as follows: 1= <38 days; 2=≥ 38 days <50 days; 3=≥50 days. The limit was the total number of hen mallards allowed per day by each state. Years with season limits of four were omitted from the analyses.

	Limit						
	1 2						
		Length					
	1	2	3	1	2	3	
Michigan	8	6	17	2	5	13	
Minnesota	8	7	9	2	5	17	
Wisconsin	8	6	17	2	5	11	

I evaluated eleven *a priori* models and an intercept only model to test for the effects of hunting regulations and hunter numbers on kill rates of GLS mallards (Table 4).

Table 4. *A priori* model set considered to predict kill rates for hen mallards in Michigan, Minnesota, and Wisconsin from 1961-2011. All models included the covariate HUNT, AGE, and an intercept. I used the standardized average of duck hunters from Michigan and Wisconsin for those states respectively and used the standardized average of flyway duck hunters for Minnesota.

KILL RATE MODELS
AGE + HUNT + LIMIT
AGE + HUNT + LIMIT + LIMIT*HUNT
HUNT + AGE*LIMIT
AGE + HUNT + DAYS + LIMIT
AGE + HUNT
AGE + HUNT + LIMIT + DAYS + LIMIT*HUNT*DAYS
AGE + HUNT + DAYS*LIMIT
AGE + HUNT + DAYS
HUNT + AGE*DAYS
AGE + HUNT + DAYS + DAYS*HUNT
HUNT + AGE*DAYS*LIMIT
INTERCEPT

All models included the estimate of duck hunter numbers that was most predictive of kill rates from the hunter numbers analysis, the AGE variable in all models as there is strong

evidence for differential harvest vulnerability between age classes (Reynolds 1987), and finally an intercept term.

I used the ESTIMATE function in SAS to predict kill rates under different harvest regulation scenarios. I made kill rate predictions using a sub-set of models containing 95% of the model weight and then reweighted these models for model-weighted prediction (Burnham and Anderson 2002). To simulate recent levels of hunter participation, I used the 2007-2011 standardized average of FHUNT for Minnesota and SHUNT for Michigan and Wisconsin. I followed Burnham and Anderson (2002) for model-weighted estimation and associated prediction variances.

During AHM years (1997-2011), Minnesota was the only state to adopt the 2-hen daily limit allowed under the federal framework while in other years (2005-2010) was more restrictive than the federal framework by allowing only 1 hen daily limit. I ran a separate set of models for AHM years in Minnesota to estimate the effects of state-specific regulation changes during AHM (Table 5). I used the best ranking model based on AIC_c and then the ESTIMATE function to predict kill rates during one hen and two hen daily limits for Minnesota banded female mallards. This would help explain the affects that an individual state can have on kill rates when further restricting harvest from the federal framework.

Table 5. *A priori* model set considered to predict the influence on kill rates for hen mallards in Minnesota from 1997-2011. Note that season length (variable DAYS) was not included due to a constant season length of 60 days from 1997-2011.

AGE + FHUNT + LIMIT + LIMIT*FHUNT

FHUNT + AGE*LIMIT

AGE + FHUNT

INTERCEPT

Results

Duck hunter analysis

Duck hunter numbers initially increased, peaked during the 1970's and then declined throughout the GLS and the Mississippi flyway during the 51-year (1961-2011) period over which I modeled effects of duck hunter numbers on mallard kill rates for the GLS (Figure 7).

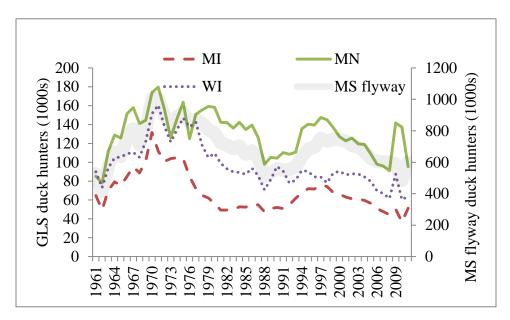


Figure 7. Federal duck stamp sales for the Great Lake States (Michigan= dashed line, Minnesota=solid, thin line, Wisconsin=dotted line) and the entire Mississippi flyway (MS flyway; thick, gray line) from 1961-2011.

Furthermore, the relationship between waterfowl hunters and MC mallard population changed in the mid-1990s after the AHM protocol was adopted (Figure 8).

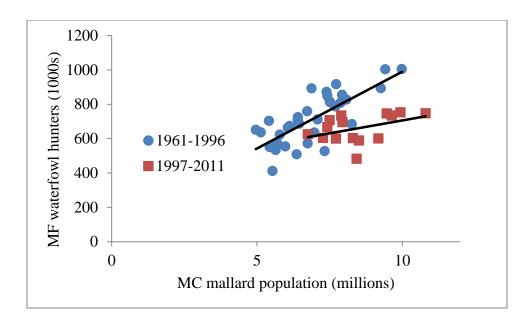


Figure 8. Relationship between the estimate of Mississippi Flyway waterfowl hunters (y-axis) and the Mid-continent mallard population (x-axis) from 1961-2011 (1961-1996 circles and 1997-2011 squares). Variation explained by the relationship, r², for 1961-1996 and 1997-2011 was 0.58 and 0.18, respectively.

I found that the number of duck hunters at the flyway and state scale was an important predictor of kill rates in Minnesota ($\hat{\beta} = 0.027$, SE 0.006) and Wisconsin ($\hat{\beta} = 0.041$, SE 0.006), respectively when added to an age and intercept model (Table 6). Although the age only model was the top ranking model in Michigan (Table 6), the second-ranked model contained the state scale waterfowl hunter number variable ($\hat{\beta} = 0.013$, SE 0.005). For evaluating models with regulation predictors (e.g. season length and hen daily limit), I included the FHUNT variable in all Minnesota models and the SHUNT variable in all Michigan and Wisconsin models.

Table 6. *A priori* models used to determine the most predictive estimate of hunter numbers at varying spatial scales to include in my kill rate analyses for (a) Michigan , (b) Minnesota, and (c) Wisconsin.

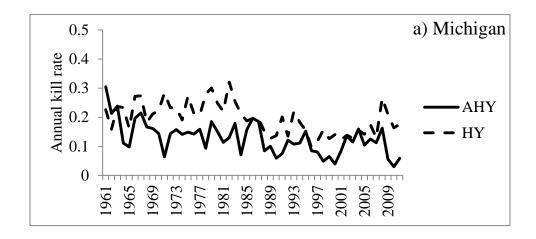
a) Michigan				
	K	AIC_c	ΔAIC_c	W_{i}
AGE	4	-287	0	0.73
AGE + SHUNT	5	-283.9	3.1	0.15
AGE + FHUNT	5	-283.4	3.6	0.12
INTERCEPT	2	-261.4	25.6	0.00

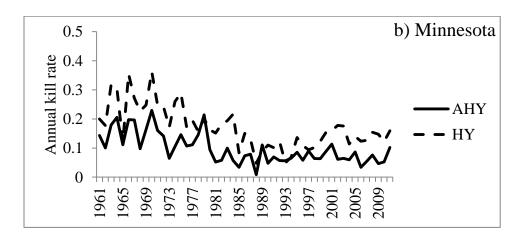
b) Minnesota				
	K	AIC_c	ΔAIC_c	W_i
AGE + FHUNT	5	-264.0	0	0.95
AGE + SHUNT	5	-257.5	6.5	0.04
AGE	4	-255.7	8.3	0.01
INTERCEPT	2	-233.0	31	0.00
c) Wisconsin				
	K	AIC_c	ΔAIC_c	W_i
AGE + SHUNT	5	-267.2	0	0.99
AGE + FHUNT	5	-254.6	12.6	0.00
AGE	4	-238.4	28.8	0.00
INTERCEPT	2	-201.2	66	0.00

Kill rate analysis

Kill rates were variable across the 51-year (1961-2011) time period for the GLS (Figure

9).





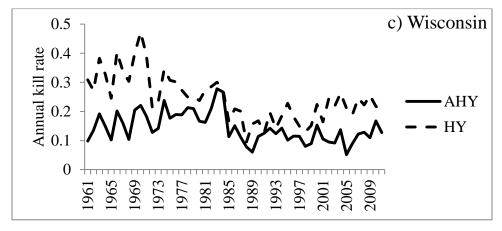


Figure 9. Kill rates for female mallards banded in Michigan (a), Minnesota (b), and Wisconsin (c) 1961-2011 (AHY=solid line and HY=dashed line).

Kill rates were generally higher among hatch year females and kill rates were higher during the 1960s and 1970s, followed by a period of restrictive regulations in the mid-1980s when they declined and then kill rates under AHM began to increase to historically intermediate levels.

Kill rates in all models were higher for hatch year birds than for after hatch year birds, thus I included AGE in all models. Kill rates in Michigan and Wisconsin were influenced more by hunter numbers and daily hen limit than by season length (Table 7). Kill rates generally increased when daily limits increased from 1 hen to 2 hens. The top ranking model for Minnesota supported an interaction term with DAYS and LIMIT while this interaction was not in the top models for the other states (Table 7).

Table 7. *A priori* models and model weights for predicting hen mallard kill rates in the GLS: (a) Michigan; (b) Minnesota; and (c) Wisconsin. Model weights, w_i, that sum to ~95% were used to model average kill rate estimates for each state. All models contained an intercept and the variable HUNT as the number of waterfowl hunters likely influences kill rates. Also, the variable AGE was in all models as research has shown that juveniles are more vulnerable to harvest than are adults.

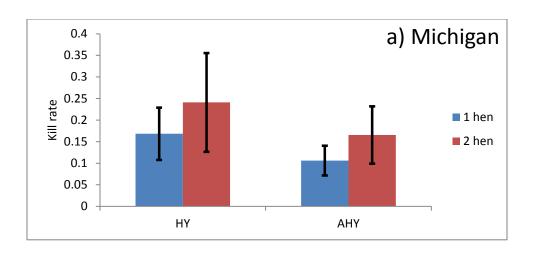
a) Michigan				
	K	AIC _c	ΔAIC_c	Wi
AGE + HUNT + LIMIT	7	-310.4	0	0.55
HUNT + AGE*LIMIT	7	-309.3	1.1	0.32
AGE + HUNT + DAYS + LIMIT	10	-307.2	3.2	0.11
AGE + HUNT + LIMIT + LIMIT*HUNT	9	-303.6	6.8	0.02
AGE + HUNT + DAYS*LIMIT	11	-302	8.4	0.01
HUNT + AGE*DAYS*LIMIT	15	-295.5	14.9	0.00
AGE + HUNT + LIMIT + DAYS + LIMIT*HUNT*DAYS	16	-286.7	23.7	0.00
AGE + HUNT	5	-283.9	26.5	0.00
AGE + HUNT + DAYS	8	-275.2	35.2	0.00
HUNT + AGE*DAYS	9	-268.6	41.8	0.00
AGE + HUNT + DAYS + DAYS*HUNT	11	-266	44.4	0.00
INTERCEPT	2	-261.4	49	0.00

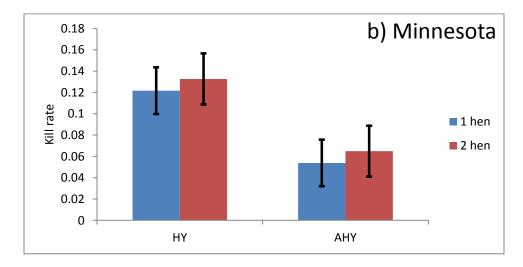
Table 7 (cont'd)

b) Minnesota				
	K	AIC _c	ΔAIC_c	W_i
AGE + HUNT + DAYS*LIMIT	11	-279.2	0	0.99
AGE + HUNT + DAYS + LIMIT	10	-269.9	9.3	0.01
AGE + HUNT + LIMIT	7	-267.2	12	0.00
AGE + HUNT	5	-263.7	15.5	0.00
HUNT + AGE*LIMIT	7	-262.8	16.4	0.00
AGE + HUNT + LIMIT + LIMIT*HUNT	9	-261.5	17.7	0.00
AGE + HUNT + DAYS	8	-258.1	21.1	0.00
HUNT + AGE*DAYS*LIMIT	15	-257.6	21.6	0.00
AGE + HUNT + LIMIT + DAYS + LIMIT*HUNT*DAYS	16	-247.9	31.3	0.00
HUNT + AGE*DAYS	9	-247.7	31.5	0.00
AGE + HUNT + DAYS + DAYS*HUNT	11	-246.3	32.9	0.00
INTERCEPT	2	-233	46.2	0.00

c) Wisconsin				
	K	AIC _c	ΔAIC_c	W_i
AGE + HUNT + LIMIT	7	-283.4	0	0.83
HUNT + AGE*LIMIT	7	-279.2	4.2	0.10
AGE + HUNT + LIMIT + LIMIT*HUNT	9	-278.3	5.1	0.06
AGE + HUNT + DAYS + LIMIT	10	-270.6	12.8	0.00
AGE + HUNT	5	-267	16.4	0.00
AGE + HUNT + LIMIT + DAYS + LIMIT*HUNT*DAYS	16	-263.3	20.1	0.00
AGE + HUNT + DAYS*LIMIT	11	-262.5	20.9	0.00
AGE + HUNT + DAYS	8	-255.1	28.3	0.00
HUNT + AGE*DAYS*LIMIT	15	-245.7	37.7	0.00
HUNT + AGE*DAYS	9	-245.4	38	0.00
AGE + HUNT + DAYS + DAYS*HUNT	11	-243.9	39.5	0.00
INTERCEPT	2	-201.2	82.2	0.00

Predicted kill rates were generally higher during years when hen mallard daily limits were 2/day, but confidence limits overlapped except in Wisconsin (Figure 10).





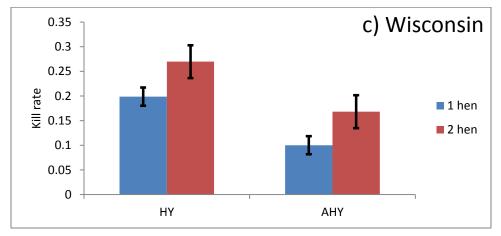


Figure 10. Model weighted predictions for: (a) Michigan, (b) Minnesota, and (c) Wisconsin female mallard kill rates from top 2 ranked models with model weighted 95% CI.

Confidence intervals for predicted kill rates for one and two hen daily limits in Minnesota during AHM (1997-2011) overlapped and the relative change in kill rates going from one to two hen daily limits as a state-imposed regulation restriction was much less than the relative change during years when the frameworks allowed the entire flyway to change daily limits (Figure 11; Table 8).

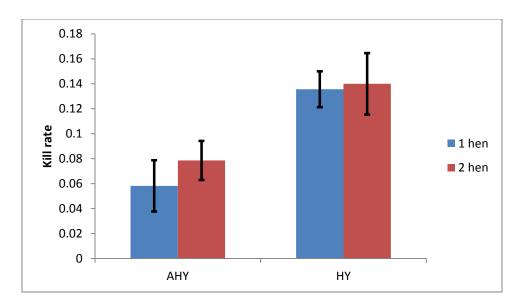


Figure 11. Mean kill rate for MN female mallards (AHY=adult and HY=juvenile) during years when MN adopted a 1-hen daily limit (2005-2010) and a 2-hen daily limit (1997-2004 and 2011) and 95% CI's.

I also found that percent change in kill rates, (KR_{pre-AHM}-KR_{AHM})/KR_{AHM}*100, during pre-AHM years (1961-1997) was greater than that during AHM years (1997-2011) for Minnesota. I then summarized the percent change in kill rates for Michigan and Wisconsin to compare those to Minnesota (Table 8). Percent increase for predicted kill rates under 2 compared to 1 hen daily in Michigan and Wisconsin was 43% and 36% for HY birds and 54% and 68% for AHY birds, respectively (Table 8). Percent increases in kill rates going from 1 to 2

hens daily were greater for AHY birds compared to HY birds in all states and time periods (Table 8).

Table 8. Percent change in model-averaged predicted kill rates when regulations change from 1-hen to 2-hens daily by state.

	Michigan		Minnesota		Wisconsin	
	HY	AHY	HY	AHY	HY	AHY
1961-1996 (MN only)			62.36	125.31		
1997-2011 (MN only)			12.23	25.43		
1961-2011	43.18	53.92	9.07	20.47	35.74	68.00

Discussion

Duck hunter analysis

Waterfowl hunter numbers have been temporally dynamic across the Mississippi flyway and so it is important to consider effects of hunter numbers when evaluating harvest regulation and kill rates. Waterfowl management policy makers have the capacity to restrict hunting licenses (e.g. South Dakota Game Fish and Parks 2014), but regulations not explicitly intended to restrict hunter numbers can also impact the number of hunters participating in migratory bird hunting seasons (Luukkonen and Frawley 2010); however, regulations have been relatively stable under AHM for 17 years and the recent declines in duck hunter numbers appear to be largely disconnected from changes in the status of waterfowl populations or harvest regulations (Vrtiska 2013). With fewer hunters, it is unlikely that liberal regulations would result in kill rates comparable to historic levels with higher hunter numbers given the same regulation regime. The average Mississippi flyway duck hunter hunts about 7.5 days out of the available 60 day season (Raftovich et al. 2014) and relatively stable effort per hunter could contribute to the weak relationship between historic season lengths and kill rates. Season lengths averaged ~39, 49, 41, 47, and 60 days during the 1960s-2000s, respectively.

My models showed that estimates of duck hunters at the state scale influence kill rates more so in states with higher harvest derivations for local birds (Michigan and Wisconsin) and estimates of total flyway duck hunters suggest the best fit for Minnesota kill rate models. This was not surprising as local mallards make up the majority of the harvest in Michigan and Wisconsin, thus local hunters may heavily influence kill rates.

Michigan and Wisconsin are unique in that harvest of locally-banded birds is higher than in Minnesota and many surrounding states (T. Arnold and C. de Sobrino unpub data). The contribution of local birds in the Wisconsin harvest increased over time (Munro and Kimball 1982; Trots 1987; R. Gatti unpub data). Zuwerink (2000) found that ~80% of Wisconsin's mallard harvest occurs from locally breeding birds. Speculation has been made for the GLS (T. Arnold personal communication; D. Luukkonen personal communication) that harvest derivation may be over-estimated as a large portion of the Hudson Bay lowlands are not included in large scale banding operations and mallard densities there have been observed as high as 62 pairs/100km² (Dennis 1974). Furthermore, the Hudson Bay Lowlands is the third largest marsh in the world (Zoltai 1973), holding potentially vast numbers of breeding mallards that enter the fall population unmarked. If a large portion of these birds migrate through or winter in Michigan or Wisconsin and are harvested but not individually marked, then contribution of local mallards to harvest derivations may be over-estimated.

Minnesota lies on the edge of the PPR and Prairie Boreal Hardwood transition zone and hunters in this state likely harvest a large number of mallards migrating from more northerly breeding areas (T. Arnold and C. de Sobrino, unpub data), thus subjecting local breeding mallards to lower harvest vulnerability locally. As with all mallards that migrate farther south, these birds may be equally prone to harvest in southern states during fall migration, but the

mixing of various mallard stocks in Minnesota during the fall, may explain why kill rates were more responsive to flyway waterfowl hunter numbers instead of state waterfowl hunter numbers.

The top ranking model in the hunter number analysis for Michigan supported the AGE + Intercept parameters and did not include an estimate of waterfowl hunter numbers. However, models containing an estimate of flyway hunters and state hunters explained ~25% of the model weight.

Kill rate analysis

I modeled the effects of regulations and duck hunter numbers on kill rates of female mallards banded in the GLS and recovered throughout North America from 1961-2011. The number of marked individuals in Michigan limited my ability to draw strong inference from the Michigan data set. Brownie et al. (1985) found that generally a minimum of 300 banded individuals would be required to analyze band recovery data. However, this number would vary depending on species, recovery rates, etc. Sample size for AHY females in Michigan was often <300. I ran an independent-samples t-test exploring direct recovery rates during years when bandings were <300 and years >300. 95% CI overlapped for both age classes. Thus I feel confident in my ability to draw inference from Michigan's data set, however emphasis should be made to obtain proper sample size for future research. Minnesota and Wisconsin had one year each when AHY banding were <300.

Kill rates throughout the GLS have varied greatly over the past fifty years. Kill rate is the proportion of the population harvested in a year and also takes into account the percentage of birds that are killed but not recovered by hunters. Kill rates during the 1960s and into the 1970s were at their peak (Figure 9). This came at a time when mallard populations in Minnesota and Wisconsin (Michigan was not surveyed until the 1990s) were low, duck hunter numbers were at

50-year highs and harvest regulations were moderate with regards to daily hen limits. This resulted in the highest kill rates in the past 50-years. This trend slowly declined until the mid-1980s when duck populations in the MC declined and regulations became restrictive (i.e. 1 hendaily and 30-day seasons). This resulted in declining kill rates and declining Mississippi flyway duck hunters. Furthermore, the relationship between waterfowl hunters and waterfowl populations became uncoupled (Figure 12).

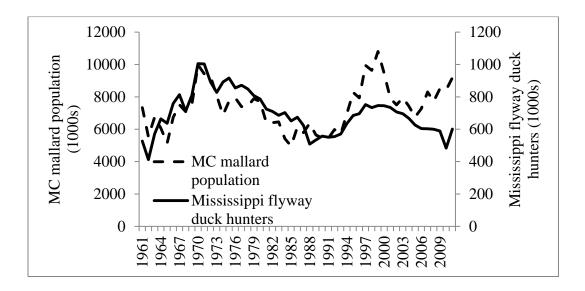
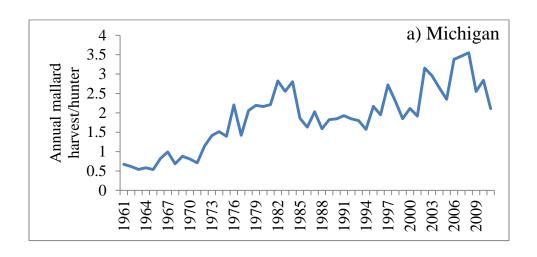
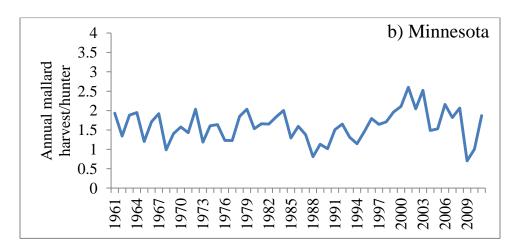


Figure 12. Relationship between the population estimate for MC mallards (not including GLS mallards) and the Mississippi flyway estimate of duck hunters as derived from the duck stamp sale from 1961-2011. Note how the trend between the two "breaks" around 1995.

Higher kill rates are expected when hunter numbers are up and populations are low. Currently we are at the opposite end of that spectrum where duck hunter numbers are down and duck populations are high with lower kill rates despite liberal season lengths and limits. The result of these recent conditions is relatively high annual mallard harvest per duck hunter in the GLS compared to historic success (Figure 13).





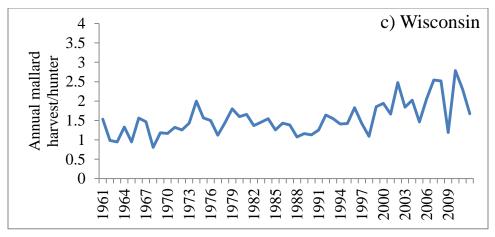


Figure 13. Annual mallard harvest per hunter as estimated from the Parts Collection Survey harvest data for both male and female and juvenile and adult mallards and the estimate of state waterfowl hunters from duck stamp sales for (a) Michigan , (b) Minnesota, and (c) Wisconsin 1961-2011.

I found that daily limit has more influence on kill rate than season length in Michigan and Wisconsin, but length was important in Minnesota. Variation of kill rates explained by season length could partially be confounded due to classification of the DAYS variable, where the majority of the third class was from AHM years when season length was longest. Nonetheless, kill rate estimates were lower under longer seasons than they were under shorter seasons. I examined models with interactions of hunter numbers and season lengths to understand if this had an impact on kill rate but these models ranked $\leq 4.0\Delta AIC_c$ from the top model. I conclude that kill rates under 60-day seasons coupled with low hunter numbers are low and likely at a sustainable level; this conclusion is supported by female mallard survival rates that have been relatively stable for most Great Lakes states (T. Arnold et al. unpub) and productivity rates that have not declined based on results of my previous chapter.

My results evaluating percent change in kill rates in response to change in daily limits suggest that percent change was smaller during AHM years than pre-AHM for Minnesota, suggesting that kill rates are more influenced by flyway wide regulation changes than they are state regulation changes. Although harvest likely varies spatially, inference can be drawn from Minnesota on the effect of more liberal daily hen limits on kill rates for mallards breeding in Michigan and Wisconsin. Hunter survey data from Minnesota generally confirm that roughly 50% of the hunters sampled are happy with the regulations pertaining to hen mallard daily limits, whether it be 2 or 1 (Fulton et al. 2002; Schroeder et al. 2012). Roughly 55% of survey respondents favored going to a 2-hen daily limit or had no opinion in Michigan (Frawley 2004). This can be viewed as trust in the DNR and more importantly use this as an opportunity to promote waterfowl hunting by making regulations more favorable to waterfowlers. My data

suggest that the influence of states adopting a more restrictive limit than that of the federal framework did not significantly impact kill rates. However, the impact from restricting, or in the case of Michigan and Wisconsin, increasing the daily limit likely will vary spatially based upon differences in harvest derivation of locally banded birds. I would hypothesize if Michigan or Wisconsin were to increase the daily limit from one to two, this would result in a larger increase in kill rate than in Minnesota, due to higher local harvest derivation, and perhaps local and regional productivity rates, but likely not as high as my predictions from models that include changes in frameworks that affect regulations in all states of the Mississippi Flyway. Other studies, Arnold et al. (2013 unpub data) found that high harvest was negatively impacting survival for Wisconsin AHY female mallards, but this occurred when kill rates were over 20% during the 1960s and 1970s. Although I did not look at the relationship between harvest and survival, it is evident that kill rates are much lower now than when they were impacting survival.

Models predicting the percent change in kill rates for the full time series suggest a slightly larger change in Michigan and Wisconsin than in Minnesota. I speculate that this could potentially be due to spatial and temporal variation in harvest of various mallard stocks of the GLS.

Modeling of kill rates as a function of regulations is not as straightforward as it seems. Complexity of the federal framework did not allow me to examine regulations at the flyway scale for all years. For example, in 1970, the framework allowed for: 1) a 45-day season with a 4 duck daily limit, where 4 may be mallard, 2) a 55-day season with a 6 duck daily limit, where 2 may be mallard, and 3) a 50 day season with a point system, where mallards were either 90 or 20 points depending on the sex. Another caveat pertains to shooting hour restrictions in Minnesota

and Wisconsin. For example, Minnesota has had opening day shooting hours start later than the rest of the year and also had four years when shooting hours ended at 4 P.M.

Mallard kill rates were at all-time highs during the 1960s when mallard populations were near record lows and hunter numbers were near record highs. Despite the high kill rates during this time, mallard populations continued to grow over the next forty years. I caution that the Minnesota example be used solely as point of reference and the change in kill rates will likely be different for Michigan and Wisconsin. I feel that if Michigan and Wisconsin adopted a 2-hen mallard daily limit, kill rates would increase, but not likely as high as kill rates observed during the 1960s-1970s.

I hope the results from this research will be used by waterfowl managers when considering adopting regulations offered by the federal framework. If nothing else, I hope this research will bring further discussion to the table for state waterfowl managers when setting season regulations.

Management Implications

This research question stemmed from concern about the GLS mallards and if regulations under AHM are sustainable. One expression of concern was the fact that the Michigan and Wisconsin DNR were being more restrictive than the federal framework in regards to hen mallard daily harvest limits. I attempted to evaluate the impact from various regulation changes from the last 51-years and gained valuable information from Minnesota over the past 6-years when they have permitted the maximum hen mallard harvest allowed by the Federal framework.

Survey data obtained from the Michigan Department of Natural Resources (Frawley 2013) suggests that ~30% of duck hunters are satisfied with the "number of ducks harvested"

and ~50% duck hunters would prefer a daily hen mallard limit greater than 1 or had no preference for daily hen mallard limit (Frawley 2004). Minnesota has found that its duck hunters are generally happy with hen mallard daily limits whether it is two or one daily (Fulton et al. 2002; Schroeder et al. 2012).

Past research such as Williams and Johnson (1995), and this research emphasize the disparity between management actions and understanding of population dynamics. Williams and Johnson (1995) noted the difficulty of understanding population dynamics when regulations "chase" populations and habitat conditions. My results are similar in the lack of certainty regarding the factors directly influencing kill rates. Regulations now are the most liberalized they have been in the past 55-years and duck populations are at their highest. Potential experimentation of altering regulations so they do not "chase" populations and habitat conditions could help us improve our knowledge of the effects of regulations on population dynamics via kill rates and survival rates (Sedinger and Herzog 2012).

My results suggest that female mallard kill rates in Michigan and Wisconsin would likely increase slightly if these states decided to adopt a 2-hen daily limit; but I speculate that mallard population abundance and future hunting success will not be affected by an increase in hen mallard daily limits. Furthermore, there has been a negative relationship between hunter numbers and mallard population estimates since the mid-1990s. Restricting hunting opportunities further than the federal framework may be unnecessary to optimize cumulative long-term harvest of mallard populations in the GLS.

As waterfowl managers, we are often the first to be aware of our direct management actions as waterfowl are the most studied game species throughout the world (Nichols and Johnson 1989). Given our knowledge of factors influencing mallard harvest rates, there appears

to be opportunities for additional sustainable mallard harvest in the GLS and current monitoring programs (e.g. waterfowl abundance estimates, band return data, etc.) are in place to provide feedback on outcomes of management experiments such as increasing the hen mallard daily limit.

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