

CHANGES IN FACTORS INFLUENCING MALLARD (*ANAS PLATYRHYNCHOS*)
RECRUITMENT IN THE MISSISSIPPI FLYWAY FROM 1980-2011

by

KALE FREDERICK WETEKAMM

(Under the Direction of Michael J. Chamberlain)

ABSTRACT

Mallards (*Anas platyrhynchos*) are the most widely-studied and harvested waterfowl species in North America. Heitmeyer and Fredrickson (1981) were among the first to demonstrate a connection between wintering habitat and mallard recruitment the following year. We used an information theoretic approach to evaluate the influence of winter wetland conditions, Wetland Reserve Program (WRP) easements and rice agriculture in the Mississippi Alluvial Valley, as well as breeding population size and wetland conditions on mallard recruitment rates (immature:adult females). We were unable to confirm that wintering habitat is more important to recruitment than breeding habitat. However, habitat provided through the WRP had the greatest influence on recruitment of the winter variables considered. Of the models considered, WRP easements, breeding habitat and population size, most influenced recruitment rates ($w_i = 0.82$). Our results highlight the potential importance of quality managed moist-soil wetlands in both breeding and wintering habitats to favorable mallard recruitment rates.

INDEX WORDS: AICc, *Anas platyrhynchos*, Mallard, Mississippi Alluvial Valley, Precipitation, Recruitment, Rice, Wetland Reserve Program, Winter

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DEDICATION

This thesis is dedicated to mom, dad, Zack and Jamie, my family and friends who have raised and supported me in reaching this goal. I thank God for the opportunity to better understand and care for His creation.

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TABLE OF CONTENTS

	Page
DEDICATION	iv
ACKNOWLEDGEMENTS	v
LIST OF TABLES	viii
LIST OF FIGURES	x
1 INTRODUCTION AND LITERATURE REVIEW	1
Waterfowl Management	1
Wintering Habitat	3
Objectives	10
2 METHODS	13
Mississippi Alluvial Valley	13
Recruitment Index and Vulnerability Adjustment.....	14
Explanatory Variables.....	17
Statistical Analysis	22
Post Hoc Analysis.....	26
3 RESULTS	28
Summary of Variables Used in Models	28
Model Results	33
4 DISCUSSION	41
Management Implications.....	48

LITERATURE CITED 49

LIST OF TABLES

TABLE 1. Summary of variables influencing mallard recruitment during 1980-2011 in the Mississippi Flyway20

TABLE 2. Model comparison hypotheses predicting the most influential variables influencing mallard recruitment during 1980-2011 in the Mississippi Flyway21

TABLE 3. Model set using only variables considered by Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987) to explain mallard recruitment in the Mississippi Flyway in a pre-AHM and pre-WRP landscape, 1980-1993.....23

TABLE 4. Post-hoc hypothesis models simplified from the *a priori* GLOBAL model and addressing cross-seasonal influences with the best-ranked BREED model, to predict variables most influential to mallard recruitment in the Mississippi Flyway, 1980-201127

TABLE 5. Corrected AIC (AICc) rankings of models explaining mallard recruitment rates in the Mississippi Alluvial Valley 1980-2011. N=160, the GLOBAL model includes 6 explanatory variables34

TABLE 6. Variance structure compared between standard linear regression and mixed effects analysis for the best ranked AICc models explaining mallard recruitment in the Mississippi Flyway, 1980-201134

TABLE 7. Corrected AIC (AICc) rankings of models explaining mallard recruitment rates in the traditional Mississippi Alluvial Valley, 1980-1993. N=42, the GLOBAL model includes 4 explanatory variables35

TABLE 8. Corrected AIC (AICc) rankings of models explaining mallard recruitment rates in the traditional Mississippi Alluvial Valley 1995-2011. N=51, the GLOBAL model includes 4 explanatory variables36

TABLE 9. Corrected AIC (AICc) rankings of models explaining mallard recruitment rates in the Mississippi Alluvial Valley 1995-2011. N=87, the GLOBAL model includes 6 explanatory variables37

TABLE 10. Corrected AIC (AICc) rankings, of models, including cross-seasonal hypotheses, explaining mallard recruitment rates in the Mississippi Alluvial Valley 1980-2011. N=160, the GLOBAL model includes 6 explanatory variables.....38

LIST OF FIGURES

FIGURE 1. Map of Mississippi Alluvial Valley and 5 study regions	27
FIGURE 2. Mean raw recruitment rate, across 5 geographic regions in the MAV, graphed with mean recruitment rate following adjustment for juvenile vulnerability to harvest for mallards in the Mississippi Flyway, 1980-2011.	28
FIGURE 3. Annual mallard breeding population estimates (BPOP) and breeding pond counts (PONDS) for the Mississippi Flyway, 1980-2011. Data obtained from the USFWS Breeding Population and Habitat Survey	29
FIGURE 4. Mean departure from LTA precipitation in the MAV during Early (Oct.-Dec.) and Late (Jan.-Feb.) winter seasons 1980-2011.	30
FIGURE 5. Trends in proportion of planted rice acreage in the Mississippi Alluvial Valley, 1980-2011. Rice is measured as proportion ha of each region, for a given year.	31
FIGURE 6. Trends in Wetland Reserve Program (WRP) enrollment and mallard recruitment, 1980-2011. Smoothing curve is polynomial recruitment trend. Mallard recruitment defined as mean age ratio from hunter harvest across 5 study regions in the MAV. WRP is measured as proportionate coverage (ha) of the entire MAV area during the previous winter, scaled +1 year after restoration to allow vegetation to establish	32
FIGURE 7. Trends in proportion of each region enrolled in Wetland Reserve Program (WRP) easements, 1995-2011. WRP is measured as cumulative ha enrolled during the previous winter, scaled +1 year after restoration to allow vegetation to establish	32

FIGURE 8. Recruitment predicted by the top-ranked BREED+WRP model plotted against observed recruitment values. Recruitment values are on the \log_e scale. Model fit is shown comparing the original linear model (A) to the same model including random effects for year and region (B)40

FIGURE 9. Distribution of residual error of the top-ranked BREED+WRP model plotted against predicted recruitment values. Recruitment values are on the \log_e scale. Model fit is shown comparing the original linear model (A) to the same model including random effects for year and region (B)40

INTRODUCTION AND LITERATURE REVIEW

Estimates of the North American waterfowl population reached a record high in 2012. Among 48.6 million waterfowl, the estimated 10.6 million mallards (*Anas platyrhynchos*) were 40% above the long-term average population size of 7.62 million (USFWS 2012). The mallard is the most abundant and commonly harvested waterfowl species in the Mississippi Flyway and the United States, making them an important ecological and economic resource (Raftovich et al. 2012). The waterfowl hunting industry accounted for an estimated \$1.8 billion in 2011 (USDI 2011). Mallards have long been the most widely-studied waterfowl species in North America, and subject of the largest waterfowl banding and survey datasets available (Cowardin and Johnson 1979). The mallards' abundance and prominence in research has led the species to become the representative waterfowl species on which much waterfowl management is based (Runge et al. 2006).

Waterfowl Management

Historically, North American waterfowl are among the world's most researched and managed wildlife. The North American Waterfowl Management Plan (NAWMP), drafted in 1986, directed international scientific and organizational efforts into focused management goals for waterfowl (Williams et al. 1999). The initial objective emphasized abundant waterfowl populations for sustainable harvest. The 2012 NAWMP revision redirects the focus of NAWMP's management goals to now include management of people groups, to recognize the interaction of all variables influencing waterfowl. The newest revision lists separate objectives for enhancing waterfowl populations, wetland habitat and the human

dimensions involving waterfowl, wetlands and wildlife (NAWMP 2012). NAWMP is administered through regional habitat Joint Ventures, which are collaborations of government agencies and private organizations involved in wildlife research and management. Through its partners, NAWMP has restored 6.3 million ha (15.7 million acres) of wetlands and become a model for international wildlife conservation (NAWMP 2012). NAWMP complements the current waterfowl management strategy of adaptive harvest management.

Since 1995, migratory waterfowl in North America have been managed under an adaptive resource management decision-making process. Adaptive harvest management (AHM) of waterfowl emphasizes scientific research to make informed management decisions to achieve specified population goals (Nichols et al. 2007). The primary goal of AHM is to provide long-term, sustainable harvest of North American waterfowl. AHM uses long-term population data, such as reproduction and survival rates, to build mathematical population models and predict population parameters the following year (Johnson 2011). Harvest regulations are set based upon those parameters to ensure sustainable populations.

The current AHM framework proposes 4 hypotheses for setting harvest regulations, based on waterfowl population response to harvest and environmental conditions. The alternative hypotheses describe a weak- or strong- density-dependence, and additive or compensatory hunting mortality (Johnson 2011). The AHM approach recognizes constraints in assessing the impact of hunting regulations, and accounts for the uncertainties of environmental variation, control, observation and biological processes by incorporating uncertainty into management options (Johnson 2011). Federal implementation of AHM endorses hunting regulation frameworks that are then sent to state agencies, which set liberal,

moderate or restrictive hunting season lengths and limits. Since 1999, the weakly density-dependent, additive harvest mortality hypothesis has received the heaviest weight of influence for management decisions (Johnson 2011). Harvest regulations preceding the implementation of AHM were classified as restrictive, with most states adhering to a 3-4 bird bag-limit and 30-40 day season length. Upon the adoption of AHM, regulations have been generally liberal in the Mississippi Flyway, representative of a 5-6 bird bag-limit and a 50-60 day hunting season (Otis 2004). Since the implementation of NAWMP and AHM, both harvest and populations of continental waterfowl, and mallards specifically, have been on the rise (Raftovich et al. 2012, USFWS 2012). As most waterfowl harvested in North America are from the US, with mallards comprising the largest portion, the US harvest dominates the decision-making process. Although the harvest regulations set forth influence many species, AHM is currently based on the vast data available for mid-continent mallards (Runge et al. 2006).

Wintering Habitat

As seasonal migrants, mallards spend nearly half of their annual cycle on southern wintering grounds. More than 50% of North American mallards winter in the lower Mississippi Alluvial Valley (MAV); hence research on how the parameters of wintering habitat used by mallards, specifically in the MAV, potentially influence population recruitment is relevant and necessary (Bartonek et al. 1984). Between the months of September – March, the dynamic wetland complexes of the MAV influence food availability, accessibility, social behaviors, physiological condition, distribution, habitat use, survival and reproduction of mid-continent mallard populations (Krementz et al. 2011, 2012, Reinecke et

al. 1988, 1989). During this time mallards complete important life events of forming pair bonds and molting before spring migration to the breeding grounds (Weller 1988).

Habitat diversity is important to meet the biological needs of wintering waterfowl, which often have different requirements for individual birds at a particular time. Diverse landscapes of contiguous forested wetlands, croplands, and non-forested wetlands are desired to reduce energy expenditure in accessing resources (Allen 1986). The MAV formed through alternate sedimentation and erosion by the Mississippi River as glaciers receded northward following the last Ice Age (Bartonek et al. 1984). This process left nutrient-rich soils and a landscape of vast woodland, forested and open water wetlands, and moist soil habitat, controlled and replenished by annual flooding events. Since the early 20th century, river channelization and habitat alterations have reduced the impact of those critical floods by almost 88%, potentially reducing soil quality and vegetative species diversity (Galloway 1980). Habitat fragmentation and degradation have escalated in the MAV, leaving patchy remnants of a once vast forested, wetland landscape (Brinson and Malvarez 2002, King et al. 2006, Reinecke et al. 1989). Over 80% of the MAV is now dedicated to agriculture including rice, soybeans, corn, and cotton (Twedt et al. 1999). It is estimated that of the original 10 million ha of bottomland hardwood forests in the MAV, only 2.8 million ha remain today (King et al. 2006). Thus, waterfowl habitats in the MAV provided through managed and conservation lands are critical to wintering and migrating waterfowl.

Historical waterfowl research focused primarily on understanding dynamics of breeding habitats in the Prairie Pothole Region of the US and Canada (Weller 1988, Anderson and Batt 1983). However, when breeding conditions are poor (dry), winter wetlands may have a more significant influence on recruitment in mallards, as shown in

northern pintails (*Anas acuta*; Devries et al. 2008, Raveling and Heitmeyer 1989). In the late 1970s, researchers began to recognize and investigate the importance of winter habitat conditions in the waterfowl lifecycle (Heitmeyer and Fredrickson 1981, Fredrickson and Drobney 1979). Cross-seasonal, or carry-over, effects have been documented for a number of waterfowl species, linking the quality of winter conditions to breeding performance (Sedinger et al. 2011, Alisauskas 2002, Sheaffer 1998, Raveling and Heitmeyer 1989). The USFWS now recognizes the potential for landscape attributes other than breeding pond numbers to influence and predict fall age ratios in its AHM plan (AHM Working Group 1999).

Heitmeyer and Fredrickson (1981) were the first to show that habitats outside the breeding grounds had a significant influence on mallard recruitment. Wetlands that host migrating waterfowl in winter serve as important sites for feeding, roosting, courtship, and pairing while preparing waterfowl for the return flight to the breeding grounds (Davis 2007, Heitmeyer 1985). Dugger (1997) showed that later-molting females initiated spring migration later than earlier-molting females. As molt is energetically inefficient (Heitmeyer 1988), superior winter nutrition positions earlier-molting females to claim quality nesting habitat and food resources on the breeding grounds (Devries et al. 2008, Dugger 1997).

Mallards rely partially on endogenous reserves for laying, but must acquire half of proteins needed for egg laying on the breeding grounds (Fredrickson and Reid 1988b). Endogenous lipid reserves are more important for breeding, as hens arriving with adequate lipid reserves can immediately begin protein acquisition for egg laying and mobilize lipid reserves during laying and incubation (Fredrickson and Reid 1988b, Krapu 1981). Lipid reserves are also positively correlated with clutch size (Krapu 1981). Therefore, females that

arrive on the breeding grounds in better physiological condition exhibit higher breeding propensity, larger clutch size, and earlier nest initiation than those that arrive in poorer condition (Devries et al. 2008, Krapu 1981).

Despite the benefits of quality wintering habitat outlined above, the relationship between winter habitat and consecutive reproduction has not been widely investigated since Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987). Many characteristics influence the quality of winter wetland habitat available to waterfowl, including duration and depth of flooded wetlands, food abundance and accessibility, density and distribution of vegetative cover, hunting and predation (Davis et al. 2011, Davis 2007).

Water conditions for wintering waterfowl in the MAV are primarily influenced by winter rainfall in tributary basins (Reinecke et al. 1989). Historically, rain and backwater flooding naturally filled MAV wetlands, but since intensive flood control began in the 1920s, flooding regimes have been altered. Winter rainfall is known to create conditions that attract waterfowl, and can increase potential habitat up to ten-fold after heavy rain events (Reinecke et al. 1988, Heitmeyer 1985, Nichols et al. 1983). Heitmeyer and Fredrickson (1981) provided evidence that winter wetland quality, measured by winter precipitation, explained more variation in mallard recruitment than breeding ground wetland indices over the 18 years they studied. The late winter period (Jan.-Feb.) had the most significant influence. Between the 1969-1970 and 1979-1980 seasons, favorable mallard age ratios ($AR > 1.0$) were most correlated with the combined abundance and quality of winter wetlands and July ponds in the breeding grounds. Despite this significance to recruitment, the US Fish and Wildlife Service discontinued the July pond survey in 2004 due to budget constraints and correlation among May and July pond numbers (Kaminski and Gluesing 1987, USWFS 2012).

Nichols et al. (1983) showed that the proportion of mallards wintering in the MAV increased in years of above-average winter precipitation. Precipitation and runoff in wet years can increase the accessibility and availability of grains to waterfowl (Ringelman 1990). Kaminski and Gluesing (1987) found the amount of winter precipitation in the MAV combined with breeding population size and breeding ground wetland conditions to explain 58% of the variation in mallard recruitment rates. Population size had a greater influence on recruitment when the preceding winter was considered wet. Winter precipitation has also been associated with winter body weight through increased or decreased forage opportunity in wet and dry years, respectively (Delnicke and Reinecke 1986). Mallards consume more rice in wetter years, but forage more on energy- and protein-inefficient soybeans in drier years (Ringelman 1990, Delnicke and Reinecke 1986). In response to flooding events, mallards increase forage time, lipid intake and body mass, feed more on red oak acorns and surpass daily existence energy consumption (Heitmeyer 2006). Along with rice, acorns are resistant to decomposition when flooded, and thus remain available as forage even in wet years, synergistically increasing the quality of winter habitat (Leach 2006, Fredrickson and Reid 1988a).

In duck species that have been examined, density-dependent reproduction is most evident at the continental scale. Continental age ratios decline as population size increases, after controlling for environmental variation (Runge et al 2006, Runge and Boomer 2005, Conroy et al. 2002, Johnson et al. 1997). Kaminski and Gluesing (1987) demonstrated an inverse correlation between recruitment and breeding population size, indicating that population size may be a more important regulator of mallard recruitment rate than wetland habitat condition. This supports the widely-accepted theory that mallard recruitment rates

may be at least weakly-density dependent (AHM Working Group 1999). This correlation was only significant during wet years, again highlighting the importance of winter precipitation to recruitment.

Agricultural rice fields in the MAV provide ideal habitat for wintering dabbling ducks. Rice paddies are flooded after harvest to enhance soil nutrients, decompose rice straw and discourage weed growth (Stafford et al. 2006). This practice simultaneously increases flooded land available to waterfowl in winter months, benefitting both farmers and wildlife (Manley et al. 2005, Bird et al. 2000). Waste grain left over after harvest serves as a high-energy food source that resists decomposition when flooded. Arkansas leads the nation in total acreage planted for rice production with 526,091 ha (1.3 million ac), followed by Louisiana with 162,683 ha (402,000 ac), Missouri with 72,843 ha (180,000 ac) and Mississippi with 52,609 ha (130,000 ac; USDA 2012). These MAV states accounted for 78% of total planted rice acreage in the United States in 2012 (USDA 2012).

Flooding rice fields for wintering waterfowl poses reciprocal benefits to farmers, as flooding substantially increases rice straw decomposition and minimizes the need for autumn tilling (Manley et al. 2005, Bird et al. 2000). MAV rice farmers may also harvest a second, ratoon crop, grown from the stubble of the main crop harvest (Blanche et al. 2012). Ratoon crops are flooded later into winter and most of the crop remains for waterfowl consumption, enhancing habitat quality for wintering waterfowl. Compared to natural grains, rice is more resistant to decomposition when flooded and provides more metabolizable energy (Fredrickson and Reid 1988a). However, recent improvements in harvest efficiency have resulted in increasingly less waste grain remaining for waterfowl consumption (Stafford et al. 2006).

The landscape of the MAV has been highly altered in the 20th century by flood control, drainage, and agricultural expansion, resulting in a landscape of fragmented wetlands and agriculture (Reinecke et al. 1988, 1989). Deforestation and channelization of rivers has altered the hydrology and topography of the MAV, reducing or degrading the land available for wildlife use as well as impeding or negating the natural regeneration of wetland systems (King et al. 2006). The MAV now exists as a fragmented landscape of a once vast expanse of wetlands, marshes and bottomland hardwood forests, increasingly altered by expanding urban development and agriculture.

The rate of wetland loss and degradation in the MAV increased exponentially from 1930-1980 (Forsythe and Gard 1980). At the time of Heitmeyer and Fredrickson's (1981) study, an estimated 1.3 million acres (0.52 million ha) of wetlands in the MAV had been lost between 1970 and 1980. The rate of inland wetland losses has slowed in the past 20 years with more stringent regulations, like the Farm Bill's Wetland Conservation (Swampbuster) provision, and creation of the Conservation Reserve and Wetland Reserve Programs cost-share easement programs. In 1985, the Conservation Reserve Program (CRP) was established to restore privately-owned marginal farmland into vegetative cover. As of 2007, over 12.9 million ha (32 million acres) had been made available to waterfowl through CRP (USDA 2009). Compared with a pre-CRP landscape, mallard recruitment rate from 1992-1997 improved by 38% with the cover provided by CRP lands on the breeding grounds (Reynolds et al. 2001). The largest impact on mallards from CRP is seen on the breeding grounds, but it is also important as a staging site for spring-migrating waterfowl (O'neil et al. 2008). During recent years, enrollment in CRP has been declining; the program lost over 3 million acres from 2007 to 2013 through expiration and attrition (NRCS 2013).

The Wetland Reserve Program (WRP) which followed in 1990, incentivized private landowners enrolling in habitat-restoration easements to “restore wetland habitat on marginal croplands with the purpose of protecting and enhancing habitat for migratory birds and other wildlife” (US Congress 1990). While CRP was created to restore degraded agricultural land, the primary focus of WRP was restoring habitat for wildlife. WRP now dominates private easement holdings in the MAV. In 2006, roughly 33,200 ha of open-water wetlands had been restored through WRP, providing an estimated 3,465 duck use days per most-soil ha (King et al. 2006). By 2012, over 1,050,000 ha (2.6 million acres) had been restored nationally through the WRP, nearly 300,000 ha of which are in the MAV (NRCS 2013). Mature, WRP restored sites provide forested wetland habitat, which is used by mallards for foraging and roosting (Davis et al. 2011). As mallards spend nearly 60% or more of their time on these activities (Jorde 1981), this habitat is beneficial to successful wintering. Increasing the land available to waterfowl for nesting and wintering activities is mutually beneficial to many other wildlife species as well (King et al. 2006, Twedt et al. 2002, Reynolds et al. 2001). Management of CRP and wildlife-designated WRP contracts require flooding of impoundments. This flooding has potential to provide landscape-level improvements in habitat for mallards. Along with other flooded habitats containing quality foraging resources, such as rice in agricultural fields, these lands may reduce annual variability of suitable mallard habitat, regardless of annual precipitation.

Objectives

Recognizing the importance of winter habitat to the annual cycle of migrating mallards, our objective was to identify which factors were most influential to mallard recruitment the following year, especially in the wintering habitat of the MAV. Identifying

such important habitat parameters can help direct conservation and management efforts designed to ensure sustainable populations of waterfowl. This research will provide information to inform waterfowl resource managers and complement existing NAWMP and AHM goals and Federal and private conservation strategies.

We investigated how conditions in the MAV influenced mallard recruitment in the fall harvest during the period 1980-2011. We reassessed the previous findings of Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987) considering current environmental conditions and an extended dataset. We sought to expand upon prior studies in regards to model assessment and evaluation through the use of an information theoretic approach to model inference. Many changes have occurred in the MAV landscape since the preceding studies [(see Kaminski and Gluesing (1987) and Heitmeyer and Fredrickson (1981)], most notably in the creation of WRP conservation easements and in agricultural practices that improve efficiency of rice harvest (King et al. 2006, Manley et al. 2004). To complement prior research, we investigated the effects of winter wetland conditions, conservation lands, rice agriculture, breeding wetland conditions, and breeding population size on mallard recruitment the following year.

Nichols et al. (1983) recovered a greater proportion of hatch year mallards in the MAV during years of low population size. Therefore, we included breeding population size with the knowledge of a density-dependent reproductive response by mallards (AHM Working Group 1999, Kaminski and Gluesing 1987). Because of the potential trade-off in the importance of breeding and wintering habitats during wet and dry years on nesting and production, we included breeding wetland conditions, indexed by number of May ponds in the breeding grounds (Devries et al. 2008, Raveling and Heitmeyer 1989). Winter

precipitation, as an index to winter wetland condition, was considered based on the findings of Kaminski and Gluesing (1987), Nichols et al. (1983) and Heitmeyer and Fredrickson (1981). In the face of historic, current, and projected inland and coastal wetland loss, qualifying the significance of winter wetland conditions to continental mallard populations is critical. Mallard recruitment benefited from CRP easements on the breeding grounds (Reynolds et al. 2001), but the effect of the high concentration of WRP acreage in the MAV has yet been investigated relative to potential influences on mallard recruitment. For this reason, we considered WRP acreage based on the benefits to waterfowl outlined by King et al. (2006). We also included winter rice acreage informed by the habitat and forage benefits to waterfowl outlined by Stafford et al. (2006) and Manley et al. (2004).

We predicted that mallard recruitment would fluctuate positively with quality of wetlands on the breeding and wintering grounds, availability of WRP acreage, and planted area of rice agriculture. Because mallard recruitment is density dependent, recruitment rates (immatures:adults) were expected to be regulated by a larger breeding population size. We predicted that rice and WRP would positively influence mallard recruitment rates.

METHODS

Mississippi Alluvial Valley

The lower Mississippi Alluvial Valley (MAV) is comprised of southern areas of Illinois and Missouri, Arkansas, Louisiana and western Mississippi. Some land included in our study falls outside the traditional MAV boundary (western Louisiana and Arkansas, southwest Missouri and southern Illinois). These areas are dominated by deciduous and evergreen forests and pasture land (NASS 2013).

We divided the MAV into 5 study regions to best manage data and account for local environmental and landscape variability (Figure 1). Study regions included area surrounding the MAV to the north (NMAV – 105,847 ha) and to the west (WEST – 121,992 ha), as well as the traditional expanses in the northern alluvial valley, (NVAL – 36,466 ha), the central alluvial valley (CVAL – 44,225 ha) and the southern alluvial valley (SVAL – 35,070 ha). We delineated these regions to represent areas within the MAV based on traditional boundaries of geology and topography, band and harvest returns of mallards, and mallard density (Green and Krementz 2008, Reinecke et al. 1989, Allen 1986,). Specifically, we chose to expand our definition of the MAV north and west of the traditional boundary to include southern Illinois, and western Louisiana and Arkansas, based on density distribution maps from Green and Krementz (2008). Although the authors found no statistical difference in favor of a northern-latitudinal shift of mallard distribution over their study period (1980-2003), historical maps did show relative changes in mallard density and occurrence (Green and Krementz 2008).

Due to the length of our study period, we chose to encompass all areas in the MAV that are currently and were historically densely-populated by wintering mallards. We made this decision in recognition that wintering waterfowl select habitats on a landscape-wide scale, and the number of birds present at specific locations will vary year-to-year based on local conditions. Waterfowl will bypass previously used, but currently unsuitable habitat and move to the most favorable conditions, an adaptation described as flexible homing (Bellrose and Compton 1970). Flexible homing further warrants the analysis of areas adjacent to the MAV. Geography and quantity of band returns guided the decision of boundaries for the western and northern study regions, which are expansions of the traditional definition of the MAV.

Recruitment Index and Vulnerability Adjustment

Recruitment is regarded as the best indicator of annual change in waterfowl population size (Martin et al. 1979). We defined recruitment as the ratio of immatures to adult females harvested from the population. We defined immatures as hatch year birds (HY) and adults as any bird aged as after hatch year (AHY). We chose this index to remain consistent with prior research that informed our study (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987). Therefore:

$$AR_{i,j} = HY_{i,j} / AHY_{i,j}$$

Where AR = age ratio for year i in region j , HY = hatch year birds (immatures) reported in year i from region j and AHY = after hatch year (adults) harvested in year i from region j .

Wing receipts used to calculate harvest age ratio were obtained from the USFWS Wingbee Parts Collection Survey (Raftovich 2013).

Unlike the studies of Kaminski and Gluesing (1987) and Heitmeyer and Fredrickson (1981), we chose to adjust age ratios for possible bias from juvenile vulnerability to harvest. We adjusted for juvenile vulnerability to harvest following the methods of Sheaffer (1998) and Runge and Boomer (2005). We used direct recovery rate estimates of mallards encountered during hunting season in the US to calculate the vulnerability of juveniles to harvest relative to adults. First, we calculated direct recovery as the total number of pre-season bands released in Strata 26-40 (July-September) and recovered in each study region during that same hunting season (September-January; Runge and Boomer 2005, Heitmeyer and Fredrickson 1981). We calculated direct recovery rates (f) and corresponding variance in year i for each of two age classes (a , hatch-year (HY) and after hatch-year (AHY)), in each region (j) according to Runge and Boomer (2005):

$$f_{i,j,a} = m_{i,j,a} / R_{i,a}$$

$$Var(f_{i,j,a}) = f_{i,j,a} (1 - f_{i,j,a}) / R_{i,a}$$

where, $m_{i,j,a}$ = direct recoveries during year i from region j of individual females of age class a , and $R_{i,a}$ = total number of females banded and released in year i of age class a from Strata 26-40 in the Mississippi Flyway.

We also accounted for changes in harvest regulations over the study period. In the Mississippi Flyway prior to 1995, harvest regulations were classified as restrictive, but have been considered liberal since (Otis 2004). To incorporate this shift in regulation and, subsequently, harvest pressure, into the recruitment index, we grouped the harvest vulnerability adjustment factor into 2 periods, prior to and following the implementation of AHM in 1995. For each region, we estimated an adjustment factor relative to harvest

regulation (*h*) for recoveries during restrictive regulations (*r*, 1980-1994) and liberal regulations (*l*, 1995-2012). We calculated vulnerability of the juvenile age class to harvest as:

$$V_{h,j,HY} = f_{i,j,HY} / f_{i,j,AHY}$$

$$Var(V_{h,j,HY}) = \frac{Var(f_{i,j,HY})}{f_{i,j,AHY}^2} + \frac{f_{i,j,HY}^2}{f_{i,j,AHY}^4} (Var f_{i,j,AHY})$$

We calculated annual, region-specific adjusted age ratios (i.e., the recruitment index $Y_{i,j}$) as the raw age ratio, per year and region ($AR_{i,j}$), divided by the juvenile vulnerability to harvest ($V_{h,j,HY}$):

$$1980-1994 (r): Y_{i,j} = AR_{i,j} / V_{r,j,HY}$$

$$1995-2011 (l): Y_{i,j} = AR_{i,j} / V_{l,j,HY}$$

We recognize potential pitfalls in using banding data to infer distribution, as banding data are influenced by hunting season-lengths, timing of migration, and hunter effort (Nichols et al. 1983, Green and Krementz 2008). White et al. (2013) concluded that variation in reporting rates did not cause major bias in survival estimates of waterfowl, therefore we assumed reporting probability was constant among age classes and years. We assumed that relative vulnerability of adults and juveniles to recovery was constant within the 2 time periods and within regions, but that vulnerability differed among regions due to hunting pressure and activity. We obtained banding data through the USFWS Division of Migratory Bird Management GameBird CD, current as of June 1, 2013.

Explanatory Variables

We obtained the breeding population estimates (BPOP) and breeding pond counts (PONDS) from the USFWS Breeding Population and Habitat Survey for Strata 26-40, the primary breeding ground for Mississippi Flyway mallards. These estimates served as indices to breeding population and habitat conditions, respectively (Table 1). The annual population estimate and pond count was the same for all regions within a single year

Winter rainfall acts as an accurate reference to wetland conditions in the MAV (Reinecke et al. 1989). Following Heitmeyer and Fredrickson (1981), we measured departure from long-term average precipitation (LTA) as an index to winter wetland conditions (Table 1). We divided the winter season into an early (EARLY; Oct.-Dec) and late (LATE; Jan.-Feb) period to better measure the significance of early and late winter wetland conditions to recruitment in following years (Heitmeyer and Fredrickson 1981). Data from the US Historical Climatology Network (USHCN) weather stations in each region was combined to calculate a single mean precipitation during the EARLY and LATE periods, and a LTA for each region (beginning with the first year of available data per weather station). We classified winters as wet or dry if they were ± 1 SD from the LTA, respectively.

We used total planted rice area as an index to flooded rice acreage (Table 1). We recognize that summer planted rice does not translate directly to flooded winter rice fields that would provide foraging habitat for mallards. However, with increased attention given to flooding post-harvest rice fields for waterfowl and an increase in planted rice area since 1980, we assumed that a greater proportion of winter rice fields would be flooded each year. We acquired total planted rice area by county from the National Agricultural Statistics Service (NASS) Quick Stats database (Quick Stats 2013). NASS crop acreage estimates are

based upon the NASS June Agricultural Survey (Boryan et al. 2011). Each county was coded within an administrative agricultural district, which we used to assign counties to their respective study region. Some data values had no county label, but only an agricultural district assigned to them. When exclusive to a single study region, we used the agricultural district code to assign these additional data to the appropriate region. Some districts were split by 2 regions; for these comparatively small parcels we either dismissed the data or assigned it to a region based on which region covered most of the agricultural district. This method produced a single, annual value for planted rice area in each study region.

The proportion of Wetland Reserve Program (WRP) hectares to total area in each region served as an index to WRP (Table 1). Geographic county area was compiled from NASS Quick Stats 2007 Census data. Spatial data from Ducks Unlimited (DU) and the National Conservation Easement Database (NCED) were partitioned by year and region to assess annual WRP area in the MAV. We used ArcMap 10 to assign each easement to the appropriate region. We chose to use GIS Acres rather than the Reported Area within the spatial database, as we believed it to be a more accurate measure of the existing WRP on the landscape. The DU dataset included some easements not listed in the NCED data. We isolated and added these additional easements to the final dataset to calculate the fullest availability of WRP for wintering mallards. We determined the date when easements potentially became available for use by mallards using the closing date accompanying the spatial data layer from which WRP area was extrapolated. Closing date was the day the land was signed over into federal easement. Some easements did not include a closing date (CVAL, n=1; SVAL, n=5). In an effort to include this remaining area in the WRP acreage, we divided the area of these remaining tracts of land by the total number of easements in the

region, then added the quotient to each annual area estimate. This method increased annual area incrementally, allowing minute annual changes to each easement while resulting in the cumulative representation of WRP area on the landscape that wintering waterfowl actually encountered.

Because actual use of WRP easements by waterfowl is unpredictable, and time until full restoration is variable for each easement, we assumed that the easement was functional and available to waterfowl one year after the closing date. Closing date was the only holistic, concrete information available for WRP in all states, and therefore the only measurement available to designate easements chronologically. We recognize that at the time of closing, hydrology and vegetative structure may not be fully restored to a state that is exploitable by waterfowl. Restored wetlands may require 3-4 years until full restoration, and up to 10 years to reach maturity (Twedt et al. 2002). We analyzed WRP as the cumulative hectares available during the previous winter season (e.g., easements dated March 1994 – Feb. 1995 were used against 1996's recruitment). This method allowed a consistent one-year period to approximate the time required for restored land to establish, assuming managers meet NRCS protocol of beginning restoration practices within one year of the easement recording (NRCS WRP 2010 §514.42 A.3).

We recognize that WRP use is not exclusive to waterfowl of a certain locale and adjacent easements outside of the study area have potential to influence wildlife and provide habitat for waterfowl wintering nearby (Bellrose and Compton 1970). However, we only selected easements that fell within the boundary of our study sites so that measurements were consistently calculated among regions.

Many of our hypotheses came directly from the previous research of Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987). They found that winter precipitation, particularly in the late winter months (Jan.-Feb.) combined with breeding ponds, heavy winter precipitation and breeding population size, were important drivers in mallard recruitment rates. Since these studies, favorable mallard habitat has increased with growth in planted rice agriculture and WRP enrollment. We developed our model set to include hypotheses from Heitmeyer and Fredrickson (1981; HF model) and Kaminski and Gluesing (1987; KG model), as well as the changes to the MAV since those studies (Table 2).

Table 1. Summary of variables influencing mallard recruitment during 1980-2011 in the Mississippi Flyway.

Type	Variable	Index	Definition
Response	AR	Recruitment	$\log_e(\text{immature:adult females in fall harvest})$
Predictor	PONDS	Breeding wetlands	May breeding pond count
Predictor	BPOP	Breeding population size	May population estimate
Predictor	EARLY	Winter wetlands	Departure from LTA, Oct.-Dec.
Predictor	LATE	Winter wetlands	Departure from LTA, Jan.-Feb.
Predictor	RICE	Rice agriculture	Proportion of total region planted
Predictor	WRP	Wetland Reserve Program	Proportion of total region in WRP

Table 2. Candidate model set for predicting the most influential variables influencing mallard recruitment during 1980-2011 in the Mississippi Flyway.

Model No.	Name	Predictor Variables^a
M1	NULL	AR ~ β_0^b
M2	GLOBAL	AR ~ BPOP + PONDS + EARLY + LATE + RICE + WRP
M3	GLOBALX	AR ~ BPOP + PONDS + EARLY + LATE + RICE + WRP + RICE:EARLY + RICE:LATE + WRP:EARLY + WRP:LATE
M4	BREED	AR ~ BPOP + PONDS
M5	WINTR	AR ~ EARLY + LATE + RICE + WRP
M6	WINTRX	AR ~ EARLY + LATE + RICE + WRP + RICE:EARLY + RICE:LATE + WRP:EARLY + WRP:LATE
M7	HF ^b	AR ~ LATE + PONDS
M8	BPOP ^c	AR ~ BPOP
M9	KG ^c	AR ~ BPOP + EARLY + LATE
M10	PRECIP	AR ~ EARLY + LATE
M11	NEW	AR ~ WRP + RICE
M12	RICE	AR ~ RICE
M13	WRP	AR ~ WRP

^a Variable descriptions: AR = recruitment index, defined as log(immature:adult females in fall harvest), BPOP = breeding population size, PONDS = breeding wetland index, by breeding pond count, EARLY = departure from LTA winter precipitation from Oct.-Dec., LATE = departure from LTA winter precipitation from Jan.-Feb., RICE = proportion of planted rice acreage in each MAV region, WRP = proportion of each MAV region enrolled in WRP easement.

^b Model derived directly from Heitmeyer and Fredrickson (1981).

^c Models derived directly from Kaminski and Gluesing (1987).

^b β_0 represents a intercept estimate of 0

Statistical Analyses

Each variable was summarized for each breeding year (*i*) and region (*j*), except for BPOP and PONDS, which were consistent for all winter regions. We tested for correlation among the explanatory variables before building the *a priori* model set using the `rcorr()` function in the `Hmisc` package in program *R* version 3.0.2 (R Core Team 2013), using a limit of $R^2 \geq 0.60$ to determine independence among the explanatory variables (Harrell and Dupont 2014). We found a slight correlation between BPOP and PONDS ($R^2 = 0.46$, $P=0.008$), but this relationship is widely known and was expected. Therefore, we elected to include both of these variables moving forward with our analyses. Otherwise, no significant correlations existed across the MAV as a whole, so we concluded that explanatory variables were sufficiently independent of one another to justify their joint inclusion in our models.

Our *a priori* model selection included 4 primary approaches. First, we sought to analyze potential factors influencing mallard recruitment throughout our entire study area from 1980-2011. Second, we wanted to re-assess hypotheses reported in Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987; Table 3). This analysis was restricted to the traditional MAV, rather than our expanded study area, included only variables used in those previous studies, and encompassed the time period prior to the development of AHM and the WRP; we assumed that both of these could influence mallard recruitment and were unavailable in those prior studies. Third, we used the same set of explanatory variables available in our second approach to determine how they influenced mallard recruitment from 1995-2011. This analysis was also restricted to the traditional MAV and encompassed the period after AHM was adopted, bag limits and season lengths became liberal, and WRP was initiated. Accounting for AHM, we recognize the potential for hunting pressures to have

influenced the underlying dataset used in our models. Fourth, we developed models also restricted to the 1995-2011 timeframe, but that included additional variables across our full study area (Figure 1). Therefore, our model selection was informed by previous literature and new landscape variables that were unavailable in previous assessments. Fixed effects included an index of winter wetland conditions (EARLY, LATE), proportion of planted rice area (RICE), proportion of WRP cover (WRP), breeding population size (BPOP), and a breeding wetland condition index (PONDS). In total, we measured 160 observations (N) over 32 years (i) and across 5 geographic regions (j). We excluded 1994 from all efforts with exception of our first approach because during this year, the first WRP land occurred along with a pre-AHM juvenile vulnerability correction factor. All subsequent observations of WRP occurred with a post-AHM adjusted age ratio, so for uniformity in our analysis of WRP's effect on age ratio, we kept the adjustment factors consistent throughout the period with WRP.

Table 3. Model set using only variables considered by Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987) to explain mallard recruitment in the Mississippi Flyway in a pre-AHM and pre-WRP landscape, 1980-1993.

Model No.	Name	Predictor Variables^a
M1	GLOBAL	AR ~ BPOP + PONDS + EARLY + LATE
M2	BREED	AR ~ BPOP + PONDS
M3	HF ^b	AR ~ LATE + PONDS
M4	BPOP ^c	AR ~ BPOP
M5	KG ^c	AR ~ BPOP + EARLY + LATE
M6	PRECIP	AR ~ EARLY + LATE

^a Variable descriptions: AR = recruitment index, defined as $\log(\text{immature}:\text{adult females in fall harvest})$, BPOP = breeding population size, PONDS = breeding wetland index, by breeding pond count, EARLY = departure from LTA winter precipitation from Oct.-Dec., LATE = departure from LTA winter precipitation from Jan.-Feb.

^b Model informed by Heitmeyer and Fredrickson (1981).

^c Models informed by Kaminski and Gluesing (1987).

We first tested hypotheses with a multiple linear regression using the linear model function (R package lme4, Bates et al. 2014) and package MASS (Venables and Ripley 2002). We used corrected Akaike Information Criterion (AICc) values to rank candidate models with the AICcmodavg R package (Mazerolle 2013, Burnham and Anderson 2008). We applied the following general linear regression model to our data:

$$Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} \dots \beta_\rho X_{ij} + \varepsilon_{ij}$$

$$\varepsilon_{ij} \sim N(0, \sigma_{ij}^2)$$

where Y_{ij} was the natural log-transformed response (dependent) variable, recruitment index; X_{ij} was the explanatory (independent) variable for each year (i) and region (j); β_ρ represented the slope parameter of the ρ^{th} variable, and ε_{ij} was the residual variance, assumed to be independent and normally distributed with a mean of 0 (Zuur et al. 2009).

When fitted response estimates (\hat{Y}_{ij}) were plotted against residual variance, an increasing horizontal spread was apparent and a histogram of the residual variance revealed non-Gaussian distribution of the dependent variable. We subsequently performed a natural log transformation of the response variable to better meet the assumption of normality.

After we assessed model output, we used a linear mixed effects model in program R to look more closely at the variation structure within the most parsimonious models. We chose the top-ranking models ($\Delta_{AIC} < 2$) to analyze with random effects of spatial variation among regions (j) and temporal variation among years (i). We used the following random intercept mixed effects model, which allowed the intercept estimate to change for each random effect, modified from Zuur et al. (2009):

$$Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} \dots \beta_\rho X_{nij} + a_i + c_j + \varepsilon_{ij}$$

$$a_i \sim N(0, \sigma_a^2), c_j \sim N(0, \sigma_c^2), \varepsilon_{ij} \sim N(0, \sigma_{ij}^2)$$

Where a_i was the random effect of year i and c_j was the random effect of region j . The global model with random and interaction effects was, therefore:

$$\begin{aligned} \log(Y_{ij}) = & + \beta_0 + \beta_1 \text{EARLY}_{ij} + \beta_2 \text{LATE}_{ij} + \beta_3 \text{WRP}_{ij} + \beta_4 \text{RICE}_{ij} + \beta_5 \text{BPOP}_{ij} + \beta_6 \text{PONDS}_{ij} + \\ & \beta_7(\text{EARLY: WRP}_{ij}) + \beta_8(\text{LATE}_{ij} \cdot \text{WRP}_{ij}) + \beta_9(\text{EARLY: RICE}_{ij}) + \\ & \beta_{10}(\text{LATE}_{ij} \cdot \text{RICE}_{ij}) + a_i + c_j + \varepsilon_{ij} \end{aligned}$$

Where, $\log(Y_{ij})$ was the natural log transformation of recruitment for year i , region j . The EARLY and LATE winter precipitation were continuous variables, whereas WRP and RICE were continuous proportion indices. Likewise, BPOP and PONDS were continuous variables. We assumed random intercepts a_i and c_j were normally distributed with mean 0, each with their own variance. The residual (ε_{ij}) was assumed to be normally distributed with mean 0 and variance σ^2 . We assumed both random terms were independent (Zuur et al. 2009). We chose to investigate interactions of RICE and WRP with variation in winter precipitation, assuming that the effect of either landscape variable may be changed in years of high or low rainfall. We set random effects for year and region as categorical variables using the `as.factor()` function in program R. A maximum likelihood framework is preferred when comparing models with the same random effects structure and differing fixed effects (R Core Team 2013, Zuur et al. 2009), therefore, we turned off the default restricted maximum likelihood (REML) function.

Post Hoc Analyses

Burnham and Anderson (2008) noted problems associated with mixing post hoc hypotheses and model selection using AICc, primarily in the context of the potential for data dredging. As detailed in our results, we found consistent support for variables on the breeding grounds being most influential to mallard recruitment rates. That being said, our original intent as detailed herein was to investigate which variables on the wintering grounds, if any, most influenced mallard recruitment. Therefore, we decided to explore which variables may function in coordination with conditions on the breeding grounds to favor mallard recruitment. Separating the variables by type, it was logical to evaluate biologic (BPOP), environmental (EARLY and LATE winter precipitation) and landscape variables (PONDS, WRP and RICE). Additionally, we had not before considered a model with only PONDS, a landscape-only model (LANDS), or only flooded wetlands (WETLAND). All other variables had been considered individually *a priori*.

We were also interested in cross-seasonal variables that may combine with our BREED model (BPOP + PONDS) to explain more variation in recruitment rates. We added each winter habitat variable (WRP, RICE, EARLY, LATE) to the BREED model to deduce which winter habitat variable may be the most influential (Table 4). If the model still ranked higher than the BREED model while accounting for the increase in the number of parameters, we assumed that the model displayed good fit.

Table 4. Post-hoc hypothesis models simplified from the *a priori* GLOBAL model and addressing cross-seasonal influences with the best-ranked BREED model, to predict variables most influential to mallard recruitment in the Mississippi Flyway, 1980-2011

Model no.	Name	Model Variables ^a
M14	LANDS	AR ~ PONDS + WRP + RICE
M15	WETLAND	AR ~ PONDS + EARLY + LATE
M16	PONDS	AR ~ PONDS
M17	BREED+WRP	AR ~ BPOP + PONDS + WRP
M18	BREED+RICE	AR ~ BPOP + PONDS + RICE
M19	BREED+EARLY	AR ~ BPOP + PONDS + EARLY
M20	BREED+LATE	AR ~ BPOP + PONDS + LATE

^a Variable descriptions: AR = recruitment index, defined as $\log(\text{immature}:\text{adult females in fall harvest})$, BPOP = breeding population size, PONDS = breeding wetland index, by breeding pond count, EARLY = departure from LTA winter precipitation from Oct.-Dec., LATE = departure from LTA winter precipitation from Jan.-Feb., RICE = proportion of planted rice acreage in each MAV region, WRP = proportion of each MAV region enrolled in WRP easement.

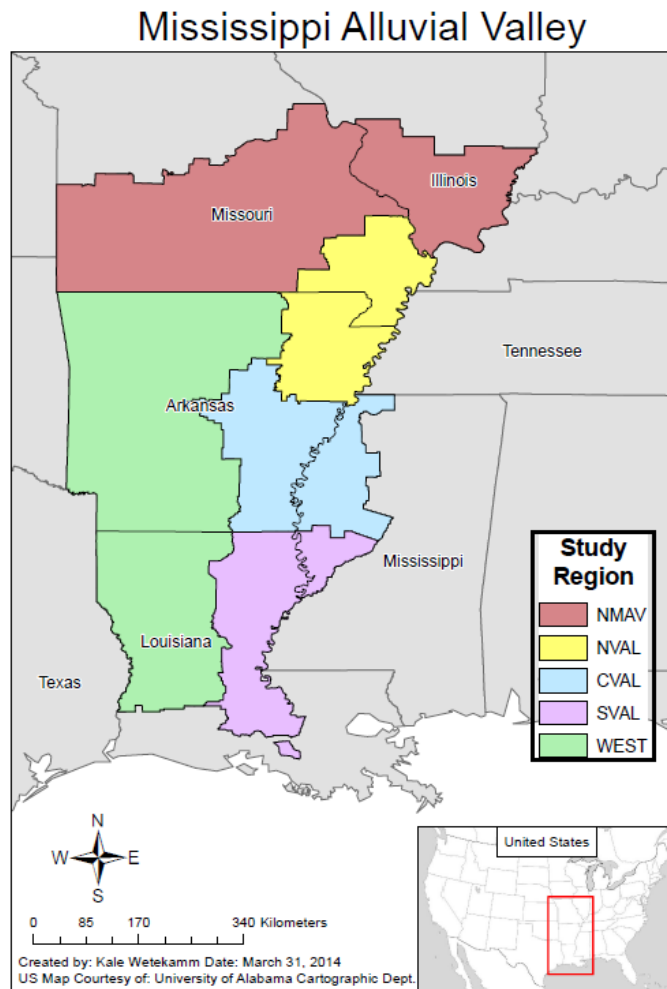


Figure 1. Map of the Mississippi Alluvial Valley and 5 study regions.

RESULTS

Summary of Variables Used in Models

Recruitment rates of mallards have been improving since the mid-1990s (Figure 2). Lowest mallard recruitment measured by the MAV harvest was 0.7487 immatures:adults in 2000, and highest recruitment was seen in 2010 (3.868 immatures:adults). From 2003-2006 ($\bar{x} = 1.809$), and 2009-2011 ($\bar{x} = 2.048$), recruitment was higher than at any point during the study.

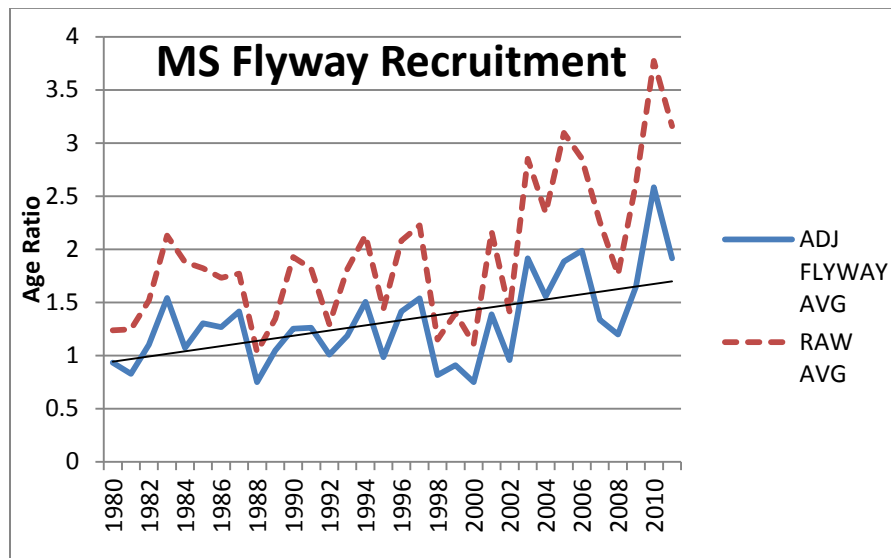


Figure 2. Mean raw recruitment rate, across 5 geographic regions in the MAV, graphed with mean recruitment rate following adjustment for juvenile vulnerability to harvest for mallards in the Mississippi Flyway, 1980-2011.

Mid-continent mallard populations (BPOP) peaked in 1998 (3.84 million \pm 0.56) and 1999 (4.07 million \pm 0.61), and were lowest in 1989 (1.78 million \pm 0.33). The BPOP in 2011 was estimated at 9.2 \pm 0.3 million, 22% above the LTA (Zimpfer et al. 2011). Breeding wetlands (PONDS) were highest in 1996 (5.00 million \pm 0.52), 1997 (5.06 million \pm 0.58), and 2007 (5.04 million \pm 0.35); PONDS were lowest in 1989 (1.44 million \pm 0.29) and 2002 (1.43 million \pm 0.79). The BPOP paralleled PONDS for most of the study period (Figure 3). Winter precipitation was highly variable across years (Figure 4). Only early precipitation displayed a relative pattern, which was higher in the 1980s, coinciding with a lower recruitment rate.

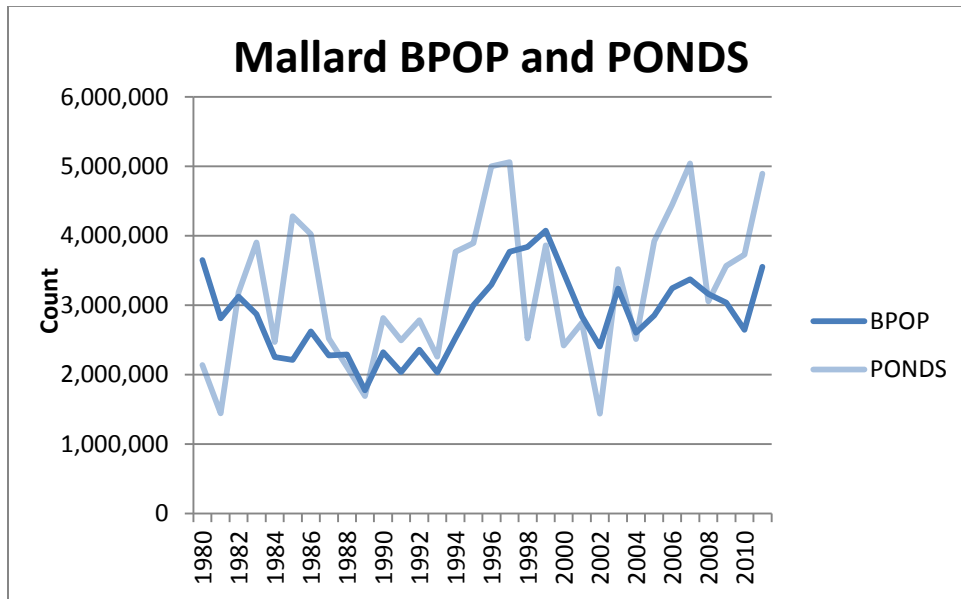


Figure 3. Annual mallard breeding population estimates (BPOP) and breeding pond counts (PONDS) for the Mississippi Flyway, 1980-2011. Data obtained from the USFWS Breeding Population and Habitat Survey

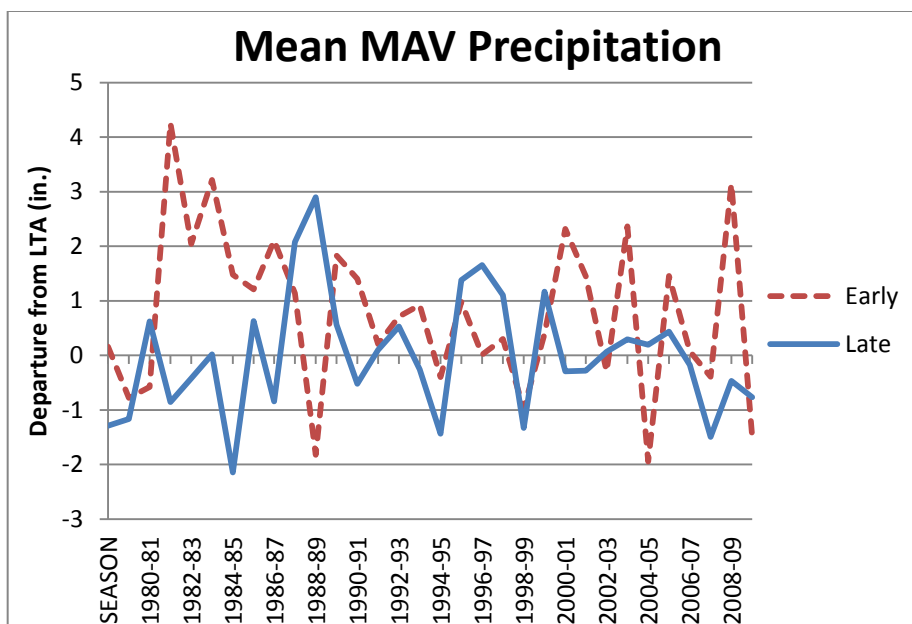


Figure 4. Mean departure from LTA precipitation in the MAV during Early (Oct.-Dec.) and Late (Jan.-Feb.) winter seasons 1980-2011.

Area of land devoted to rice harvest increased over the course of the study (Figure 5). Throughout the study period, the NVAL region contained the highest proportion and area of planted in rice of any MAV region (\bar{x} = 349,410 ha, 9.18% cover). Mean rice acreage was lowest in the SVAL (\bar{x} = 64,877 ha, 1.84% cover) and WEST regions (\bar{x} = 46,528, 0.36% cover). The year of lowest rice acreage occurred in 1983 (breeding season 1984, \bar{x} = 532,768 ha) and the highest was in 2010 (breeding season 2011, \bar{x} = 1,043,320 ha). There was no rice agriculture reported by NASS in the NMAV region.

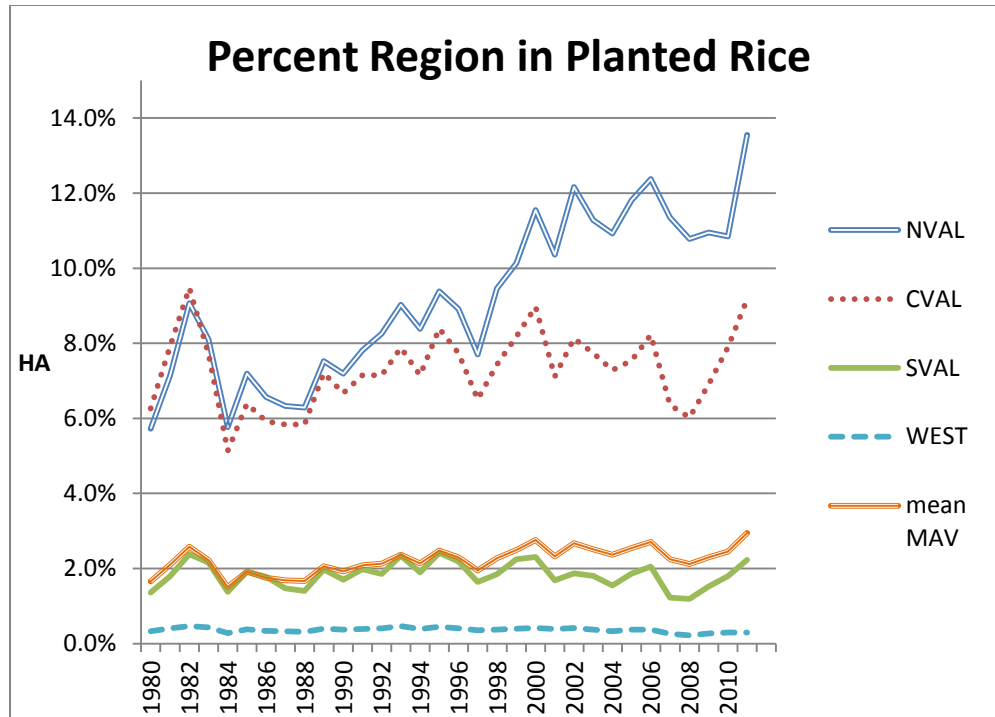


Figure 5. Trends in proportion of planted rice acreage in the Mississippi Alluvial Valley, 1980-2011. Rice is measured as proportion ha of each region, for a given year.

Prior to 1994 (in our analysis), there was no WRP in the MAV. Improvements in recruitment aligned temporally with the onset of WRP (Figure 6). WRP was implemented most rapidly and abundantly in the SVAL, where cumulative area enrolled totaled 109,757 ha (3.11% landscape) in 2012 (Figure 7). The CVAL region had the next highest enrollment, 84,353 ha (1.88% landscape) in 2012, followed by NVAL with 32,369 ha (0.85% landscape). WEST (29,463 ha, 0.23% landscape) and NMAV (20,067 ha, 0.18% landscape) had the lowest enrollment and proportions, but also constituted the largest geographic areas of all the regions.

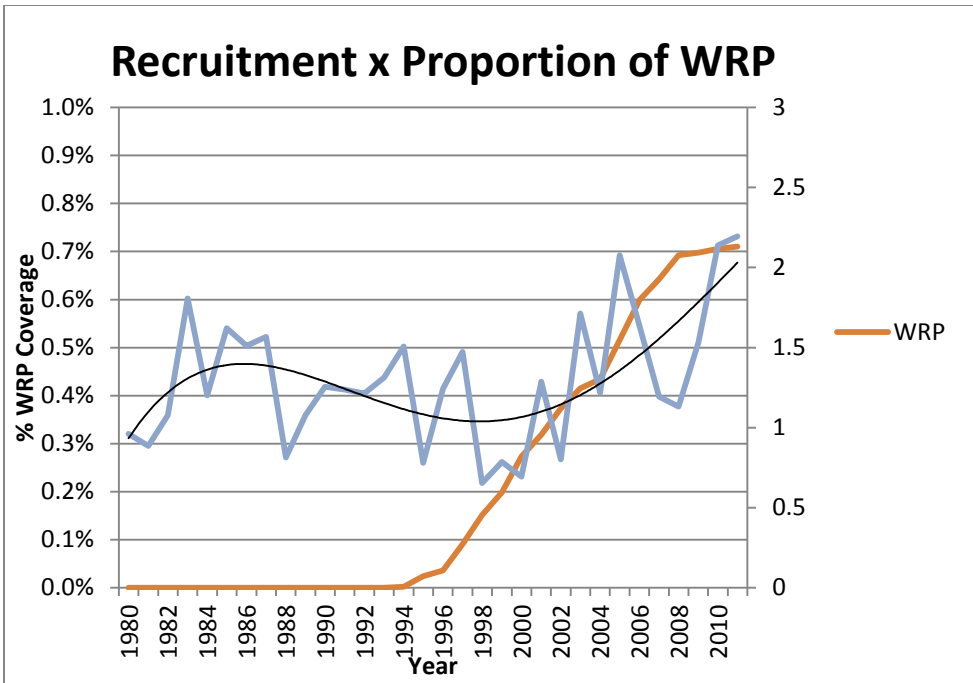


Figure 6. Trends in Wetland Reserve Program (WRP) enrollment and mallard recruitment, 1980-2011. Smoothing curve is polynomial recruitment trend. Mallard recruitment defined as mean age ratio from hunter harvest across 5 study regions in the MAV. WRP is measured as proportionate coverage (ha) of the entire MAV area during the previous winter, scaled +1 year after easement closing date to allow vegetation to establish.

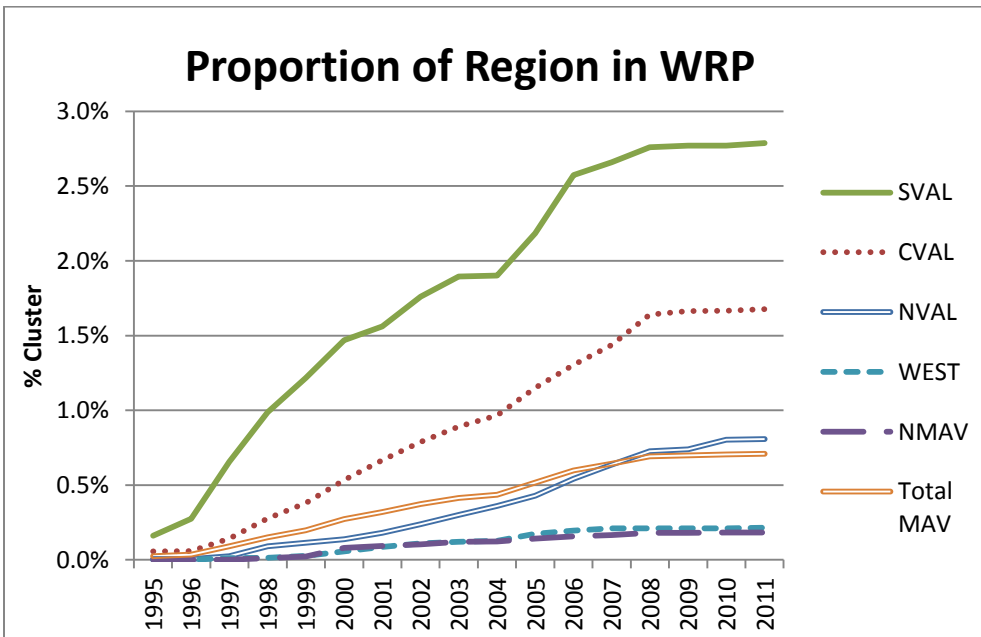


Figure 7. Trends in proportion of each region enrolled in Wetland Reserve Program (WRP) easements, 1995-2011. WRP is measured as cumulative ha enrolled during the previous winter, scaled +1 year after easement closing date to allow vegetation to establish.

Model Results

Full Study Area – Full Variable Set - 1980-2011

We initially evaluated 13 competing models focused on identifying variables most influential on mallard recruitment across our entire study area throughout the full time frame of our dataset. The most parsimonious model was the BREED model followed by the GLOBAL model (Table 5). Within the global model, we noted that only BPOP, PONDS, and WRP significantly influenced variation in recruitment. The BPOP showed a negative relationship with recruitment (as expected under density dependence), whereas PONDS positively influenced recruitment. However, the PONDS showed a more significant influence on recruitment than BPOP (PONDS: $P = 6.01e^{-07}$, $SE = 1.81e^{-08}$; BPOP: $P = 3.32e^{-04}$, $SE = 3.47e^{-07}$). The WRP estimate positively influenced recruitment ($P=0.009$).

We noted no significant support for any interactions between landscape variables and precipitation. Winter precipitation did not have a significant effect on recruitment in any of the models in which it was included, and the PRECIP model was not well supported ($\Delta_{AIC} = 28.18$, $w_i = 0.00$). Early precipitation (EARLY; Oct.-Dec.) varied inversely with recruitment in the global model, and although late precipitation (LATE; Jan.-Feb) varied positively, both variables explained little of our observed recruitment.

Table 5. Corrected AIC (AICc) rankings of models explaining mallard recruitment rates in the Mississippi Alluvial Valley 1980-2011. N=160, the GLOBAL model includes 6 explanatory variables

Model no.	Model Name	K^a	AIC _c ^b	ΔAIC_c^c	w_i
4	BREED	4	-44.30	0	0.60
2	GLOBAL	8	-43.50	0.85	0.39
3	GLOBALX	12	-36.79	7.57	0.01
7	HF	4	-32.50	11.86	0.00
13	WRP	3	-23.31	21.04	0.00
11	RICE+WRP	4	-21.30	23.05	0.00
5	WINT	6	-20.01	24.34	0.00
1	NULL	2	-17.93	26.42	0.00
8	BPOP	3	-16.73	27.63	0.00
10	PRECIP	4	-16.27	28.08	0.00
12	RICE	3	-16.10	28.25	0.00
9	KG	5	-14.44	29.92	0.00
6	WINTX	10	-12.33	32.02	0.00

^a K = the number of parameters.

^b AIC_c is Akaike's Information Criterion corrected for small sample size.

^c ΔAIC_c refers to difference in AIC_c between the given model and the most supported model.

Table 6. Variance structure compared between standard linear regression and mixed effects analysis for the best ranked AICc models explaining mallard recruitment in the Mississippi Flyway, 1980-2011.

		Linear Regression Results				Mixed Effects Variance ^b		
Period	Model	ΔAIC_c^a	w_i	$Adj R^2$	σ_e^2	σ_a^2	σ_c^2	σ_e^2
1980-2011^c	BREED	0	0.600	0.164	0.043	0.002	0.004	0.036
	GLOBAL	0.850	0.390	0.183	0.042	0.001	0.027	0.031
1980-1993^d	HF	0	0.470	0.157	0.224	0.005	0.150	0.057
	BREED	0.880	0.310	0.140	0.228	0.000	0.154	0.058
1995-2011^d	BREED	0	0.890	0.230	0.236	0.085	0.074	0.072
1995-2011^c	BREED	0	0.700	0.090	0.232	0.128	0.047	0.075
1980-2011^e	BREED+WRP	0.000	0.820	0.196	0.041	4.06e ⁻⁴	0.006	0.034

^a Top-ranked model and models within $\Delta AIC_c < 2$ of best model.

^b Includes random effect attributed to temporal (σ_a^2) and spatial (σ_c^2) variance

^c Includes *a priori* model set

^d Models only include hypotheses tested by and data used by Heitmeyer and Fredrickson (1981) or Kaminski and Gluesing (1987).

^e Includes post-hoc model set

Within the BREED model from 1980-2011, we noted low variation across regions and years, likely because the same estimate of BPOP and PONDS was applied to all regions in a given year (Table 6). Within the GLOBAL model, variation among regions was more prevalent ($\sigma_c^2 = 0.027$) than variation among years ($\sigma_a^2 = 0.001$).

Traditional MAV – Reduced Variable Set - 1980-1993

The variables in these models were selected based upon Kaminski and Gluesing (1987) and Heitmeyer and Fredrickson (1981), and our model results were consistent with their findings. The Heitmeyer and Fredrickson (HF) model was most parsimonious, suggesting that LATE and PONDS had the greatest effect on recruitment during this time period (Table 7). Likewise, model weight of the BREED model confirmed the importance of BPOP and PONDS to mallard recruitment.

Table 7. Corrected AIC (AICc) rankings of models explaining mallard recruitment rates in the traditional Mississippi Alluvial Valley, 1980-1993. N=42, the GLOBAL model includes 4 explanatory variables

Model no.	Model Name	K^a	AIC _c ^b	ΔAIC_c^c	w_i
3	HF	4	62.24	0.00	0.47
2	BREED	4	63.12	0.88	0.31
1	GLOBAL	6	65.26	3.02	0.10
7	NULL	2	66.76	4.52	0.05
6	PRECIP	4	67.55	5.30	0.03
4	BPOP	3	68.80	6.56	0.02
5	KG	5	69.41	7.16	0.01

^a K = the number of parameters.

^b AIC_c is Akaike's Information Criterion corrected for small sample size.

^c ΔAIC_c refers to difference in AIC_c between the given model and the most supported model.

Within the HF model, regional variance accounted for much of the random variation ($\sigma_c^2 = 0.150$) and was nearly 3 times higher than annual variance ($\sigma_a^2 = 0.005$; Table 6). Remaining residual variance in the HF model was reduced from $\sigma_e^2 = 0.224$ in the linear model to $\sigma_e^2 = 0.057$ after accounting for random effects. Among-region variation explained the most variation in the BREED model ($\sigma_c^2 = 0.154$). There was no statistical variance attributed to years ($\sigma_a^2 = 0$), and remaining residual error was $\sigma_e^2 = 0.057$.

Traditional MAV – Reduced Model Set - 1995-2011

These models were designed to simply extend the work of Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987) by evaluating data since those studies. We found that BPOP and PONDS were the most influential explanatory variables affecting mallard recruitment; the BREED model was the most parsimonious and no other models received support (Table 8). Compared to the 1980-1993 period, the HF model did not perform well.

Table 8. Corrected AIC (AICc) rankings explaining mallard recruitment rates in the traditional Mississippi Alluvial Valley 1995-2011. N=51, the GLOBAL model includes 4 explanatory variables

Model no.	Model Name	K^a	AIC _c ^b	Δ AIC _c ^c	w_i
2	BREED	4	76.90	0.00	0.89
1	GLOBAL	6	81.57	4.67	0.09
3	HF	4	84.83	7.93	0.02
7	NULL	2	88.09	11.19	0.00
4	BPOP	3	89.12	12.23	0.00
6	PRECIP	4	91.86	14.97	0.00
5	KG	5	93.72	16.82	0.00

^a K = the number of parameters.

^b AIC_c is Akaike's Information Criterion corrected for small sample size.

^c Δ AIC_c refers to difference in AIC_c between the given model and the most supported model.

During the 1995-2011 time period in the BREED model, there was slightly more variance explained among years ($\sigma_a^2 = 0.084$) than among regions ($\sigma_c^2 = 0.073$), and remaining residual variance was substantially lower when incorporating these random effects ($\sigma_\varepsilon^2 = 0.071$) than in the linear model alone ($\sigma_\varepsilon^2 = 0.236$; Table 6).

Full Study Area – Full Variable Set - 1995-2011

When considering all variables during the period after the adoption of AHM and the initiation of WRP, the BREED model was the most parsimonious with the WRP model being the only other model to receive near-notable support (Table 9). We noted nearly 3 times the annual variance ($\sigma_a^2 = 0.128$) compared to regional variance ($\sigma_c^2 = 0.047$) and substantially less residual error considering random effects ($\sigma_\varepsilon^2 = 0.0751$) than in the linear model without random effects ($\sigma_\varepsilon^2 = 0.231$; Table 6).

Table 9. Corrected AIC (AICc) rankings, explaining mallard recruitment rates in the Mississippi Alluvial Valley 1995-2011. N=87, the GLOBAL model includes 6 explanatory variables.

Model no.	Model Name	K^a	AIC _c ^b	Δ AIC _c ^c	w_i
4	BREED	4	123.71	0.00	0.70
13	WRP	3	127.66	3.95	0.10
7	HF	4	129.41	5.70	0.04
2	GLOBAL	8	129.47	5.76	0.04
11	NEW	4	129.79	6.08	0.03
8	BPOP	3	130.11	6.40	0.03
1	NULL	2	130.51	6.80	0.02
12	RICE	3	131.48	7.77	0.01
5	WINTR	6	133.12	9.41	0.01
9	KG	5	133.23	9.53	0.01
10	PRECIP	4	133.83	10.12	0.00
3	GLOBALX	12	137.16	13.46	0.00
6	WINTRX	10	142.25	18.54	0.00

^a K = the number of parameters.

^b AIC_c is Akaike's Information Criterion corrected for small sample size.

^c Δ AIC_c refers to difference in AIC_c between the given model and the most supported model.

Post Hoc Analyses – 1980-2011

Although we evaluated several simplified models from the GLOBAL model, none of them were more parsimonious than the BREED model across the full MAV. Adding models that addressed cross-seasonal effects, the BREED+WRP model (BPOP + PONDS + WRP) received the highest support of any model considered among the full study area (Table 10). Over the full study period, variance in the BREED+WRP model among regions was higher ($\sigma_c^2 = 0.006$) than among years ($\sigma_a^2 = 0.004$), but even this model did not explain all of the variation in recruitment ($\sigma_e^2 = 0.034$; Table 6).

Table 10. Corrected AIC (AICc) rankings of models, including cross-seasonal hypotheses, explaining mallard recruitment rates in the Mississippi Alluvial Valley 1980-2011. N=160, the GLOBAL model includes 6 explanatory variables.

Model no.	Model Name	K^a	AIC _c ^b	Δ AIC _c ^c	w_i
17	BREED+WRP	5	-49.47	0.00	0.82
4	BREED	4	-44.35	5.12	0.06
2	GLOBAL	8	-43.50	5.97	0.04
20	BREED+LATE	5	-42.80	6.67	0.03
18	BREED+RICE	5	-42.50	6.97	0.03
19	BREED+EARLY	5	-42.25	7.23	0.02
3	GLOBALX	12	-36.79	12.68	0.00
14	PONDS	3	-34.28	15.19	0.00
15	LANDS	5	-33.79	15.68	0.00
7	HF	4	-32.50	16.97	0.00
16	WETLAND	5	-32.41	17.06	0.00
13	WRP	3	-23.31	26.16	0.00
11	NEW	4	-21.30	28.17	0.00
5	WINT	6	-20.01	29.46	0.00
1	NULL	2	-17.93	31.54	0.00
8	BPOP	3	-16.73	32.75	0.00
10	PRECIP	4	-16.27	33.20	0.00
12	RICE	3	-16.10	33.37	0.00
9	KG	5	-14.44	35.03	0.00
6	WINTX	10	-12.33	37.14	0.00

^a K = the number of parameters.

^b AIC_c is Akaike's Information Criterion corrected for small sample size.

^c Δ AIC_c refers to difference in AIC_c between the given model and the most supported model.

Overall, accounting for random variation among years and among regions helped reduce the residual variance in every model set, but was unable to explain all of the variance in the model (Table 6). We noted higher variance among regions in all analyses that included 1980-1993, but higher annual variance in all analyses of the 1995-2011 time period. The WEST region had the highest positive regional effect, and the most negative regional effect was observed in the SVALL region. The highest positive annual effect was in 2003 and the most negative annual effect was observed in 1995. Predictive ability of models was highest in the top-ranked, BREED+WRP model ($R^2 = 0.196$). We also noted predictive ability was higher when only considering the traditional MAV, compared to our expanded MAV study area.

The BREED+WRP model achieved a tighter fit of the predicted recruitment by incorporating random effects for year and region (Figures 8 and 9). Although some variation was accounted for by regional and annual variance, some unexplained variation remained.

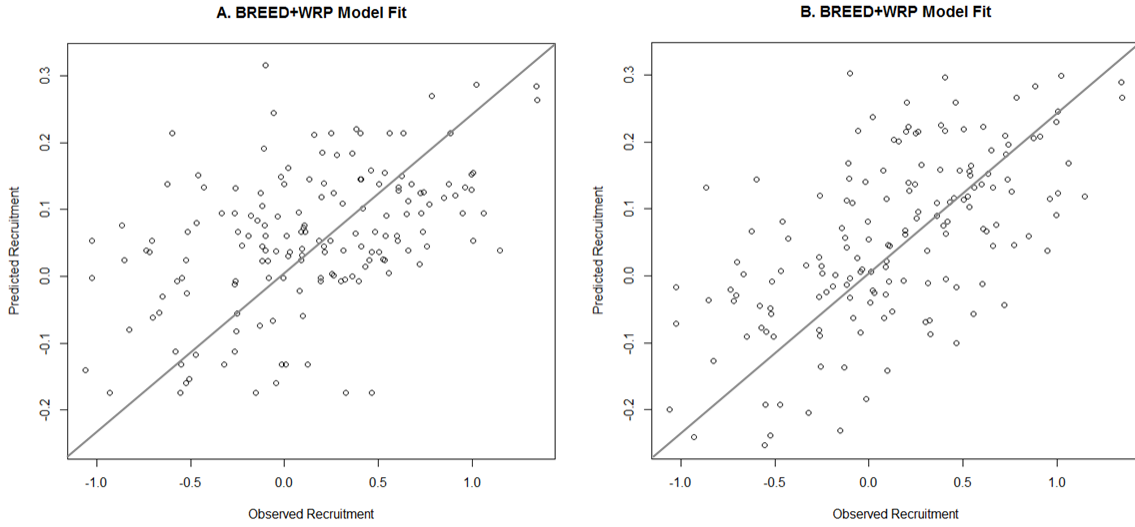


Figure 8. Recruitment predicted by the top-ranked BREED+WRP model plotted against observed recruitment values. Recruitment values are on the \log_e scale. Model fit is shown comparing the original linear model (A) to the same model including random effects for year and region (B).

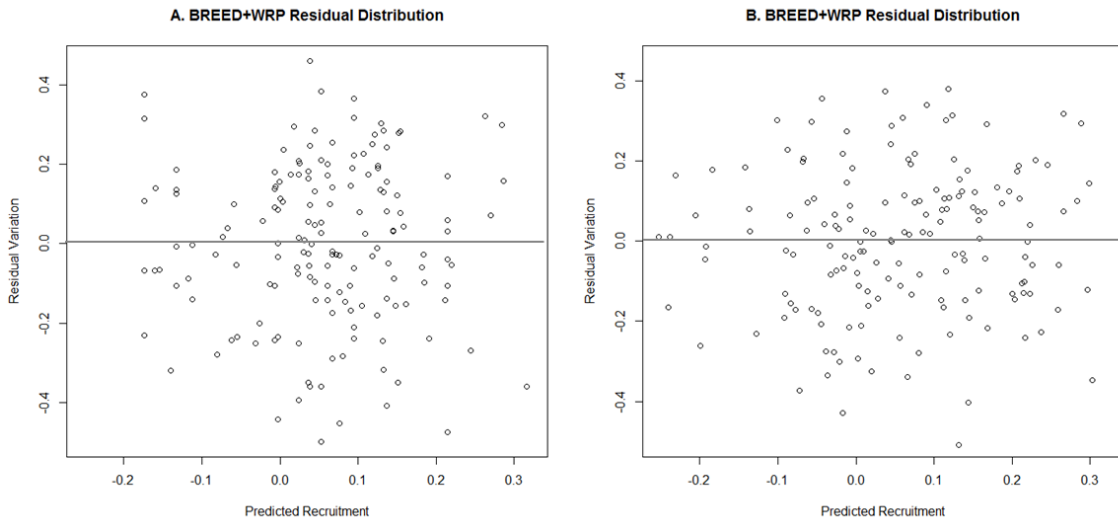


Figure 9. Distribution of residual error of the top-ranked BREED+WRP model plotted against predicted recruitment values. Recruitment values are on the \log_e scale. Model fit is shown comparing the original linear model (A) to the same model including random effects for year and region (B).

DISCUSSION

The BREED model received the most support across our full data set and study area (Table 5). We noted that PONDS appeared in every top-ranked model, regardless of time period or area, and was the most significant variable within. Similar to Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987), the HF and BREED models best explained our recruitment observations prior to establishment of WRP. We noted that factors influencing recruitment changed coinciding with the onset of WRP. Rice and winter precipitation did not have the positive influence we predicted. We also noted regional variance was higher before WRP was established and was reduced in models that included a WRP-landscape.

Across our entire study period and area, waterfowl breeding grounds in the Prairie Pothole Region consistently ranked highest in explaining observed recruitment rates in mallards. Although there is much evidence detailing the benefits of wintering habitat to subsequent mallard reproduction and recruitment, our results did not show these factors to outcompete the influence of breeding habitat conditions. This can be attributed to quality nest site selection from earlier migration, and the direct benefits gained from brood rearing habitat quality (Devries et al. 2008). Although migration readiness is a function of body condition and nutrition acquired during the late winter period (Devries et al. 2008), we did not observe this translating to a direct influence on recruitment rate. Recruitment may be most heavily influenced by predation and habitat composition in the breeding ground (Austin 2002, Cowardin et al. 1985). Quality winter habitat and subsequent improved nutrition may

help initiate migration earlier, but our findings suggest recruitment may most influenced by the direct influence of breeding ground habitat for nesting and brood rearing (and survival to fall flight). Cowardin et al. (1985) noted higher nest success in years and breeding areas with abundant wetlands. If number of young added to the fall population is a relative to the total number of young hatched, the connection between nesting success and breeding wetland availability could influence recruitment. Mallards are also known to make multiple nesting attempts in a single breeding season, and the number of nesting attempts is positively related to female body condition and nutrition (Eldridge and Krapu 1988, Cowardin et al. 1985). The effects of wintering ground may be indirect by hosting pair bonding and allowing for multiple nesting attempts following an earlier first nesting, which occurred because of nutrition acquired during winter.

Like Kaminski and Gluesing (1987), we noted density dependence in mallard recruitment. Our observations of a negative relationship between population size and recruitment were consistent with the weakly-density dependent hypothesis used in AHM models. However, we rejected Kaminski and Gluesing's conclusion that population size may be a more important regulator of mallard recruitment than habitat conditions. The observed relationship of BPOP to recruitment was less significant than that of breeding wetland ponds in the best model (BREED+WRP; $P_{BPOP}=9.23e^{-05}$, $P_{PONDS}=2.48e^{-07}$). Further, only PONDS occurred as a common variable in all of the top-ranked models. Prairie wetlands provide habitat for broods, food, and cover for protection before migration (Austin 2002). Austin (2002) observed semi-permanent pond numbers to have the most significant influence on the number of breeding pairs observed in the Prairie Potholes. Pond counts could potentially be

improved to provide a more complete picture of habitat conditions, for example, including water depths.

Because we observed different results during 1995-2011 than Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987), we understood this to be evidence of external factors, not considered in the models (Table 3), changing the relationship between the wintering environment and recruitment. We understood the implementation of the WRP and AHM to represent substantial shifts in landscape and management influences beginning in 1995. In the earliest years of the study, recruitment rates fluctuated similarly with trends in precipitation; this could explain Heitmeyer and Fredrickson's observation of LATE + PONDS best explaining recruitment. Because LATE only appeared in the best model within the traditional study area, the influence of late winter precipitation may only be influential within the traditional boundaries of the MAV. The flooded land provided through the WRP may now overshadow the role winter precipitation once played in influencing mallard recruitment.

The BREED+WRP model provided additional inference to cross-seasonal influences on recruitment. WRP was the single most influential wintering-ground variable. Though comprising a small proportion of the total MAV (Figure 7), increases in WRP coincided with overall improved recruitment (Figure 6). WRP is a consistent source of quality, flooded habitat that will exist regardless of winter rainfall. Restored wetlands are managed to provide diverse habitat and forage in time for waterfowl arrival. Reinecke et al. (1989) recognized the importance of habitat diversity to achieving habitat objectives in hosting wintering waterfowl. WRP easements, and the moist-soil habitats they contain, can be managed in a way to provide this diverse habitat on a single landscape, and attract mallards

by offering forage, cover and other needs while reducing energy expenditure to access these resources. Twedt and Nelms (1999) observed that mallard density was greater over moist soil fields than any other habitat type, including rice fields.

Lands managed through the WRP provide critical habitat for wintering waterfowl that benefits their populations across seasons. The biodiversity in these restored wetland habitats provides nutrients and lipid reserves necessary for migration and nesting advantage in the spring. This may eventually translate to improved recruitment through multiple nesting attempts and increased clutch size (Devries et al. 2008, Cowardin et al. 1985). Recent estimates of seed abundance in agricultural fields have been lower than previous estimates (Foster et al. 2010, Manley et al. 2004). The decreased availability of food resources in agricultural fields may increase the value of food resources offered by moist soil units in the WRP. Many WRP easements are still in early successional stages. It is unknown how the value of these habitats to mallards will change as stands age over time. However, our findings suggest that over our study period, the value of planted and flooded management areas for wintering waterfowl, such as through the WRP, is important for wintering mallards.

Rice did not have a significant influence on recruitment. Our observation could be explained by lower availability of waste grain in harvested fields due to advances in harvest efficiency, earlier planting and harvest dates, or irrelevance due to heterogeneous distribution of managed rice (Stafford et al. 2006, Uihlein 2000). Our findings may reflect on a larger scale those of Stafford et al. (2006), who found 325 duck use days/ha provided by rice fields, and noted a gross overestimation of duck use days (DUDs) by conservationists (previous estimate of 1,858 DUD/ha). Likewise, Greer (2009) concluded that waterfowl likely consumed most available rice grain soon after fields were flooded. Early flooding of rice

fields, either naturally through precipitation or by managers, initiates grain decomposition earlier and results in earlier depletion of the energy-rich waste grain. Rice therefore becomes less significant in the late winter season when forage focuses on accruing lipid reserves for migration and breeding (Krapu 1981). It is estimated that 79-99% of rice grain is lost between harvest and early winter to decomposition (Manley et al. 2004). Combined with gains in harvest efficiency, less grain is available for waterfowl forage. Our findings suggest that either the direct benefit of flooded rice fields to dabbling ducks may be overestimated (Stafford et al. 2006), or rice does not have the degree of influence once thought.

From 1992-1995, private landowners managed 150,000 ha of surface water, or 1.5% of the total MAV (Uihlein 2000). Uihlein (2000) observed that 88% of private lands managed for waterfowl were croplands, 63% of which was rice. Uihlein (2000) also noted heterogeneous dispersal of managed habitat, as 50% of total MAV managed private lands (70,000 ha) occurred on 2 substrata in Arkansas. Although unevenly distributed, the amount of managed private land provided exhibited little annual variation. Our results could possibly be an artifact of the distribution of flooded rice fields in the MAV; that rice fields in certain locations are providing extensive waterfowl habitat, but not all fields across the region.

It is possible that our index of planted rice area does not translate equivocally to flooded fields, or flooded fields with abundant waste grain. Uihlein (2000) noted that only 10% of harvested rice fields were managed to retain water for migrating and wintering waterbirds. Kross et al. (2008) reported that standing stubble retained the greatest abundance of rice grain, but Uihlein (2000) only found this practice implemented over 18% of rice in Arkansas, 34% in Mississippi, and 49% in Louisiana. Kross et al. (2008) found disked stubble to retain the least waste grain, and Uihlein (2000) reported over 50% of rice farmers

disked in Arkansas and Mississippi, over 80% in Missouri, and approximately 20% in Louisiana. However, Manley et al. (2004) did conclude that disked, open-flooded fields retained twice the waste grain of other postharvest treatments. Although total rice area has increased, and waterfowl use of rice fields is continually observed, the quality of forage has possibly decreased, resulting in a larger quantity of marginally beneficial land that is quickly depleted (Manley et al. 2004).

We used the best data available across our study period to quantify rice area. GIS data from the Conservation Lands Database (CLD) was limited and only available for the entire study area beginning in 2006 (CropScape 2013). NASS Rice classification is 85-95% for major crops (LMVJV Framework Report 2012). When compared to our NASS dataset, the CLD data confirmed that our NASS estimates were accurately reported, differing only by 35.96 ha on average (median difference = -6.13 ha). The CLD data layer did detect some rice grown in the NMAV region ($\bar{x} = 115.41$ ha), which was not reported in the NASS dataset. We are confident that our estimation of acreage devoted to rice agriculture was accurate, but annual and site-specific flooding was impossible to quantify over such a large area and time span.

We found that winter precipitation was a less significant factor influencing recruitment rates compared to the other variables considered. We suspected that years of heavy rainfall would enhance the effect of WRP, as flooding would increase water levels within impoundments and produce shallow flooded areas on lands beyond delineated moist-soil impoundments. The role of winter wetlands has also been more pronounced during wet years (Kaminski and Gluesing 1987, Delnicki and Reinecke 1986, Nichols et al. 1983). However, both models containing interaction effects between winter precipitation and WRP

and RICE flooded habitats performed poorly (Table 10). Despite the importance placed on winter precipitation by the results of Heitmeyer and Fredrickson (1981), it does not seem to be the primary driving factor of mallard recruitment. The significant influence attributed to LATE + PONDS by Heitmeyer and Fredrickson (1981) may have been heavily weighted by inclusion of PONDS, which was present in all of our highest ranked models and the most significant variable within. It is also likely that winter wetland conditions, as measured by precipitation, have become less significant since the introduction of WRP.

Unexplained variation remained in all models, even after random effects of year and regions were considered. We recognize that our models were not exhaustive of the factors that could influence mallard recruitment. Additional winter habitat factors to consider would include hunter effort, harvest totals, fall and winter temperature, and timing of migration. We also did not investigate the potential benefits offered through other managed conservation lands, such as Federal and state wildlife refuges, parks and forests.

Our adjustment for juvenile vulnerability, and partitioning by management regimes (restrictive harvest, 1980-1994; liberal harvest, 1995-2011), assumed a real influence of these 2 factors on recruitment rates. Further research should investigate the accuracy of these assumptions. We offer that our variable estimates are the best available, given they are scaled and estimated correctly. In an exploratory analysis, we noted higher predictive ability (R^2) in models containing only the traditional MAV area. In the 2 new regions (NMAV and WEST), we also observed the lowest proportion of rice and WRP coverage. It is possible that the inclusion of the NMAV and WEST regions negatively influenced our predictive ability, because of unpredictable factors of the landscape that contrasted geographically, hydrologically and agriculturally from the traditional MAV.

Management Implications

Based upon an annual index of recruitment, AHM coincided with improved mallard recruitment over time. Mallard recruitment rate has shown to improve since the implementation of AHM. Management efforts focusing on providing quality breeding wetland habitat and a diverse landscape of moist soil habitats in the MAV may most benefit recruitment of mid-continent mallards. Moist soil habitats and restored wetlands through the WRP appear to positively influence mallard recruitment rates, as forage quality is more diverse within moist soil fields and these lands have become more abundant. We recognize that protected moist-soil habitats sometimes do not produce the income of other land development strategies. However, the WRP provides incentives for landowners to manage moist-soil habitats, and continued enrollment in WRP may have positive influences on mallard recruitment through time.

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