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Autumn Migration of Mississippi Flyway Mallards as Determined by Satellite Telemetry

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Abstract

We used satellite telemetry to study autumn migration timing, routes, stopover duration, and final destinations of mallards *Anas platyrhynchos* captured the previous spring in Arkansas from 2004 to 2007. Of those mallards that still had functioning transmitters on September 15 ($n = 55$), the average date when autumn migration began was October 23 (SE = 2.62 d; range = September 17–December 7). For those mallards that stopped for >1 d during migration, the average stopover length was 15.4 d (SE = 1.47 d). Ten mallards migrated nonstop to wintering sites. The eastern Dakotas were a heavily utilized stopover area. The total distance migrated per mallard averaged 1,407 km (SE = 89.55 km; range = 142–2,947 km). The average time spent on migration per individual between September 15 and December 15 was 27 d (SE = 2.88 d; range = 2–84 d). The state where most mallards were located on December 15 was Missouri (11) followed by Arkansas (8), while 5 mallards were still in Canada, and only 8 of 43 females and 0 of 10 males were present in Arkansas. The eastern Dakotas are a heavily utilized migration stopover for midcontinent mallards that may require more attention for migration habitat management. The reasons for so few mallards, especially male mallards, returning to Arkansas the following year deserves further research.

Keywords: *Anas platyrhynchos*; autumn migration; mallard; movements; satellite telemetry

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Introduction

The mallard *Anas platyrhynchos* is the most abundant, most sought after, and most harvested duck in North America (Drilling et al. 2002). Consequently both the Canadian Wildlife Service and U.S. Fish and Wildlife Service attempt to optimally manage mallard populations so that the mallard breeding population index exceeds 7.5 million birds (North American Waterfowl Management Plan [NAWMP]; U.S. Department of Interior

and Canadian Wildlife Service 1986). Information necessary to manage mallards covers a variety of topics, including the ecology of autumn migration. Surprisingly little research has been conducted on autumn migration of mallards as compared with other portions of the life cycle (Drilling et al. 2002).

Mallard migration studies have been based on subjective visual surveys (Bellrose et al. 1961; Bellrose 1980; Schummer et al. 2010), analyses of hunter-reported harvests and band recoveries (Green and Kremetz

2008), conventional VHF radiotelemetry (Dugger 1997), and satellite transmitters (platform transmitter terminals [PTTs]) in Japan (Yamaguchi et al. 2008). Drilling et al. (2002:6) concluded that mallards have the “most prolonged autumn migration of any duck species; generally no sharp peaks, except when sudden severe storm forces mass migration...Usually does not migrate until water freezes or food is covered with snow.” Despite these studies on autumn migration biology of mallards, many basic questions remain because the technology for answering some of these questions was, until recently, unavailable (Dugger 1997; Yamaguchi et al. 2008; Roshier and Asmus 2009).

Perceived changes in harvest in the Mississippi Flyway (Green and Krementz 2008) raised additional interest in autumn migration of mallards during the later 1990s and early 2000s. Hunters in the lower half of the Mississippi Flyway, especially in Arkansas, were concerned that the abundance of mallards during the first half of the hunting season was noticeably reduced (L.W.N., unpublished data; Green and Krementz 2008). Many hunters and biologists attributed the supposed declines to “short-stopping” (shortened waterfowl migration movements resulting from human-induced habitat changes); however, it was just as possible that any changes in migration timing could have been due to changes in distribution of mallards among wintering areas because of changes in climate and or habitat (Schummer et al. 2010; but see Nichols and Hines 1987). Green and Krementz (2008) investigated whether band recovery and harvest distributions had changed between 1980 and 2003 and concluded that there was no evidence for changes in the harvest distribution of mallards in the Mississippi Flyway. Schummer et al. (2010) examined changes in relative abundance of autumn–winter mallards and weather variables in Missouri and concluded that certain weather variables did explain changes in relative abundance of mallards. Based on these findings and expected changes in climate in the Mississippi Flyway (Schummer et al. 2010), autumn–winter mallard distributions could be changing.

In addition to having more basic information on autumn migration of mallards, this information will be integral to the North American Waterfowl Management Plan (NAWMP Assessment Steering Committee 2007) and on the ground implementation through Joint Ventures (JVs), which are partnerships established under the North American Waterfowl Management Plan to help conserve the continent’s waterfowl populations and habitats. A primary objective of NAWMP is to better understand geographic variation in bird-habitat relationships with particular emphasis on mallards from the Prairie Pothole region (NAWMP, Plan Committee 2004). Along migration routes, JV management plans have indicated that insufficient information exists on autumn migration timing to fine tune population estimates so that habitat objectives can be accurately calculated (Reinecke et al. 1989; Petrie et al. 2011). In the Upper Mississippi River and Great Lakes Region JV (UMRGLJV) planning document under the monitoring priority needs section (UMRGLJV 2007:47), it was stated that to inform

conservation design “Assess migratory stopover use (i.e., duration, number of stops, chronology) at staging and wintering areas” was needed. In this plan, the mallard was chosen as a “focal species” on which nonbreeding monitoring would be primarily based. Finally, having knowledge of the arrival date of mallards to their wintering grounds in the Lower Mississippi Valley will allow the Lower Mississippi Valley JV to better estimate the foraging requirements of ducks, with a focus on mallards, on the wintering grounds (Loesch et al. 1994).

We were also interested in sex-specific variation in mallard autumn migration because little information exists on the topic (Drilling et al. 2002). Krementz et al. (2011) found that during spring migration female mallards exhibited more annual variation in the number of stopovers made per year compared with males and females were also more likely to make longer individual migration movements compared with males. Information on migration patterns from autumn departure to arrival on wintering grounds gathered by following individual birds is fundamental to directing conservation strategies for the mallard. Ultimately, knowledge of individual variation in migration strategies can be used to model time–energy trade-offs in mallard migration (Dugger 1997; Farmer and Wiens 1999).

In response to hunter concerns in Arkansas, the Arkansas Game and Fish Commission initiated a study in 2004 in which researchers marked a sample of mallards in Arkansas with satellite transmitters to document mallard movements to and from Arkansas. Arkansas is an especially appropriate state to conduct such a study because more mallards probably winter there than in any other state and Arkansas hunters harvest more mallards than any other state (Green and Krementz 2008). Our objective was to use these mallard satellite telemetry locations to characterize migration of mallards during the autumns of 2004–2007 to 1) document the timing, length, duration, and spatial patterns of autumn migration, and 2) investigate sex- and year-specific variation in those variables. With more precise information concerning mallard autumn migration biology, managers can make more informed decisions about autumn habitat management for mallards. Such information also can facilitate development and refinement of population conservation objectives for mallards associated with North American Waterfowl Management Plan activities (NAWMP Assessment Steering Committee 2007).

Study Area

Our study area included anywhere mallard satellite locations occurred (Figure 1), which consisted of the midcontinent region of North America. We captured mallards on 14 public and private managed seasonal wetlands in Arkansas: nine sites in the Mississippi Alluvial Valley portion of Arkansas (“Delta”) where the land use was predominantly row crops; three sites in the Arkansas River Valley west of Little Rock where the land use was predominantly pasturelands with some row crops; and

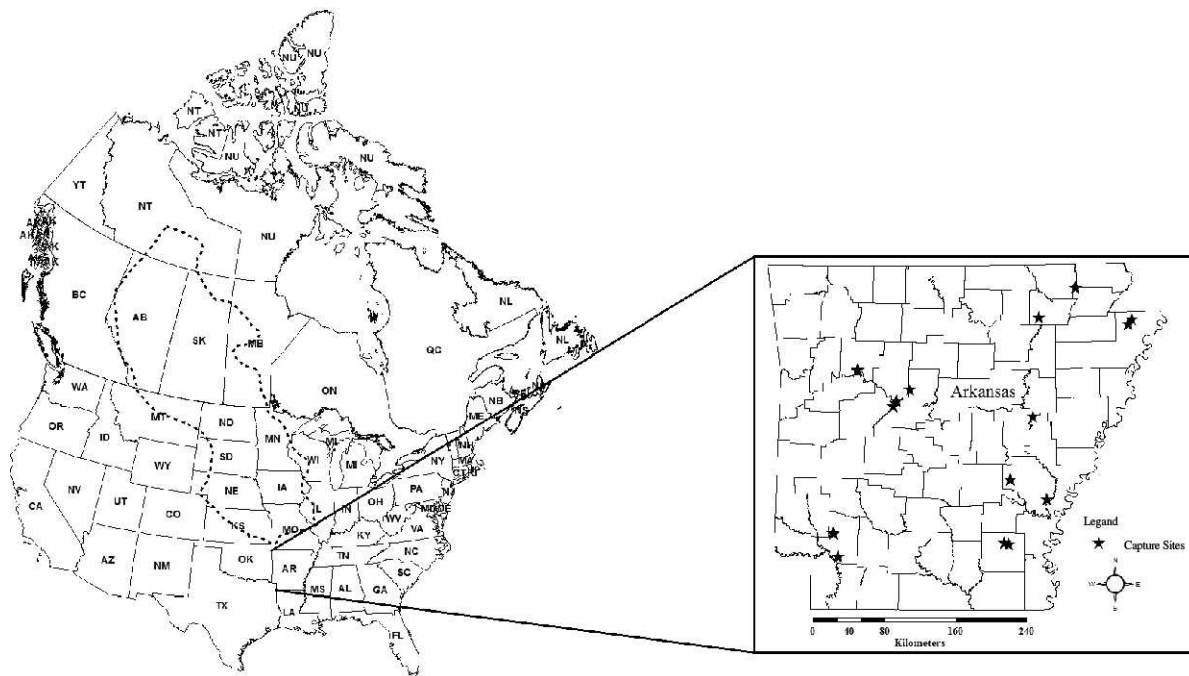


Figure 1. Locations where mallards *Anas platyrhynchos* were captured and marked with satellite transmitters in Arkansas 2004–2007. The large polygon across midcontinent North America (outlined region [dashed line] represents the Prairie Pothole Region) encompasses 95% of all satellite-marked mallard locations between September 15 and December 15, 2004–2007.

two sites in the West Gulf Coastal Plain near Texarkana, Arkansas, where the land use was predominantly pasturelands and forestlands (Natural Resources Conservation Service 2007; Figure 1). Band recovery analyses suggested that the Prairie Pothole Region (PPR; Mann 1974) was the source for most mallards that wintered in Arkansas (Munro and Kimball 1982).

For the 11 states north of Arkansas through which mallards migrated, temperature and precipitation ranks (National Climatic Data Center 2011) during the autumn months (September–November) over the study period ranged from below normal to much above normal temperatures and near normal precipitation (Table 1). Temperature ranks were mostly above normal in all years except 2006 when they were below normal. Precipitation ranks were near normal in all years. Therefore, we characterized our study years relative to 1895–2011 as 2004 being warmer and normal precipitation, 2005 as much warmer and normal precipitation, 2006 as colder

and normal precipitation, and 2007 as warmer and normal precipitation.

Methods

We captured mallards (46:134 male [M] : female [F]) at the following times: 1) February and March 2004; 2) February 2005; 3) January, February, March, November, and December 2006; and 4) January and February 2007. We attracted mallards to baited stations and captured birds using rocket nets or swim-in traps. We attached a federal leg band to each captured mallard and in 2007 only we recorded the body mass (g) of each captured mallard. We attached PTTs to both sexes of mallards during 2004–2006 and only females in 2007. We used two types of PTTs from Microwave Telemetry, Inc. (Columbia, MD), battery or solar powered. In 2004 and 2005 all PTTs were battery powered, while in 2006 and 2007 we used both battery- and solar-powered PTTs.

Table 1. Temperature and precipitation ranks for September–November 2004–2007 in 11 states that marked mallards *Anas platyrhynchos* migrated through during the autumn. States included Illinois, Indiana, Iowa, Kansas, Minnesota, Missouri, Montana, Nebraska, North Dakota, South Dakota, and Wisconsin.

Year	Temperature rank ^a	Precipitation rank
2004	Above normal (7), ^b much above normal (4)	Near normal (5), above normal (4), much above normal (2)
2005	Above normal (3), much above normal (8)	Below normal (1), near normal (6), above normal (3), much above normal (1)
2006	Below normal (10), near normal (1)	Below normal (1), near normal (6), above normal (2), much above normal (2)
2007	Above normal (8), much above normal (3)	Below normal (3), near normal (6), above normal (1), much above normal (1)

^a Ranks are based on a 117-y period (1895–2011) with much below normal falling into the bottom 12 periods, below normal falling into the next 39 periods, near normal falling into the middle 39 periods, above normal falling into the 39 higher periods, much above normal falling into the top 12 periods, and record falling into the highest ever recorded (National Climatic Data Center 2011).

^b Number of states out of 11 states with that rank for that year.

Duty cycles for PTTs varied across the study period. In 2004–2006, the duty cycle was 6 h on : 48 h off while in 2007 two duty cycles were used: 1) 10 h on : 24 h off, and 2) each unit came on at 0800, 1200, 1600, and 2000 hours. With the exception of the 2007 PTT that operated four times each day, all units were only active during the diurnal period. The units, with harness and protective neoprene pad, weighed about 22–35 g. For all mallards captured in 2007, the PTT weighed about 2% of average body mass at capture ($\bar{x} = 1,098$ g, $SE = 9.84$), which was under the 3% of body mass recommended guidelines for transmitter mass by the U.S. Geological Survey Bird Banding Laboratory (<http://www.pwrc.usgs.gov/BBL/>). We assume that the PTTs were of a similar percentage of body mass in the other years. We attached each PTT dorsally between the wings by fashioning a harness of 0.38-cm-wide (sold as 3/16 inch) Teflon ribbon (Bally Ribbon, Bally, PA). The completed harness included fore and aft body loops connected with a 1-cm length of ribbon over the keel and was based on the design used by Petrie et al. (1996) and Malecki et al. (2001; Krementz et al. 2011, figure 2). We held marked birds so they could have time to adjust to the harness and released them diurnally at the site of capture within 24 h after capture. We observed that released birds had preened their harness and PTT underneath their feathers. Doing so reduced the drag of the transmitter thereby decreasing the negative effects of increased drag on migration range and energy reserves (Pennycuik et al. 2011); note that the antenna was projecting upwards and backwards at 45°.

We tracked marked mallards until they died or were censored. We categorized a mallard as dead if it remained at the same location for more than two consecutive duty cycles assuming that the on-board activity counter in the PTT indicated no movement of the PTT during that time. If we lost complete contact with the PTT within the expected lifespan of its power source, we categorized the PTT as censored. All other PTT locations were considered to be from living birds.

We used the CLS-Argos location and data collection system (Collecte Localisation Satellites [CLS] 2008) to monitor tagged mallard movements. Calculated location classes (LCs) were categorized and labeled as 3, 2, 1, and 0, which had accuracies rated as <150 m, 150–350 m, 350–1,000 m, and >1,000 m, respectively. We favored LC categories 3, 2, or 1, and of the 200 locations that we used, some 35% of the locations fell into these classes. We note that in 2004, 94% of the LCs used were LC 0. In the other 3 y, LC 0 codes never exceeded 62%. Our most frequent class was the 0 class ($n = 132$ records) followed by class 1 ($n = 45$), class 2 ($n = 16$), and class 3 ($n = 7$). The accuracy of class 0 was not of special concern; however, because mallards moved around 1,000 km during migration (see below, Yamaguchi et al. 2008), location errors of <10 km were thus negligible. We retained at least one location per transmission period for each individual based on the rate of movement between location fixes, the angle of movement in relation to adjacent fixes, the proximity to previous and subsequent locations, the location derived from the most transmissions, and the LC value based on

exclusion rules (Kenow et al. 2002; McIntyre et al. 2008). Subsets of these locations were the bases for all data analyses.

Data analyses

The primary metrics of location and movement we analyzed were 1) departure dates after September 15, 2) distance traveled on individual migration legs and for the entire migration movement, 3) numbers of stops en route as well as the number of days when a bird remained at a single location for more than one duty cycle, 4) duration of migration (days), and 5) end migration date and final location.

Mallards have an extended autumn migration (Drilling et al. 2002), but defining autumn migration is subjective because mallards are known to continue to move throughout the winter (Nichols et al. 1983). Bellrose (1980) defined autumn migration as September 1–December 31, while Nichols et al. (1983) defined winter as beginning on December 1. We defined autumn as September 15–December 15. Some mallards continued to move after December 15, and only in the case of determining the “final” autumn movement, we continued to track them until January 1.

We defined the start of migration as the Julian Day (JD) on or after September 15 for which a location was obtained and the subsequent location was >8 km in a southerly direction. Once migration began, we categorized mallards in one of two states: 1) located at a single location for one duty cycle (hereafter termed a “single”) and had movements <8 km, or 2) remaining at a single location for more than one duty cycle (hereafter termed a “stopover”). We examined the frequency histogram of distances (km) moved within a duty cycle for five random females each year and found that >75% of movements were <8 km. Note that within an 8-km radius, multiple observations often were recorded. We randomly selected one available location with the highest LC code to base our movement data on. Following this protocol, the total number of locations we used to investigate movements was reduced from 17,379 to 636. All 636 locations were used to map mallard locations, but we could only use 136 single locations and 64 stopover locations for analyzing movements and distances moved because the LC values were not always reliable based on auxiliary information from the units (e.g., battery strength, temperature). We used ARCVIEW GIS (ESRI, Inc., Redlands, CA) to analyze and plot locations to delineate movements. Based on the best location, we calculated the distance (m) of each vector formed by two consecutive locations (hereafter termed a “leg”). Hence, the migratory journey for each individual was represented as a series of legs connecting the best locations per duty cycle. These movements represent average daily progress across the landscape, as opposed to in-flight speed. We never recorded any within-duty-cycle unidirectional migration movements which we assume was because our PTTs (with one exception) were not recording nocturnal movements. Mallards typically migrate at night (Bellrose 1980). We did record cases in which a mallard was last located north of Arkansas on September 15 and

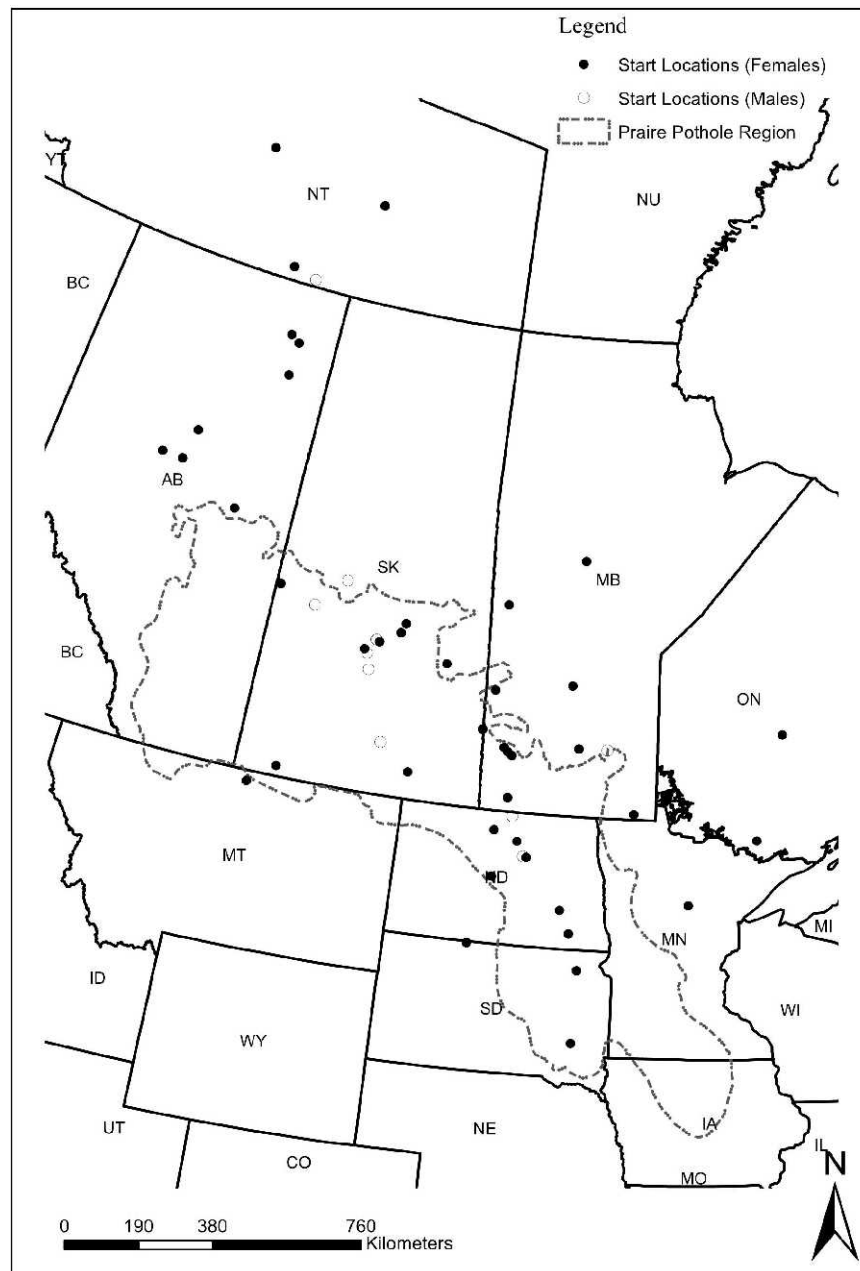


Figure 2. Locations of satellite-marked mallards *Anas platyrhynchos* on September 15, 2004–2007. The outlined region (dashed line) represents the Prairie Pothole Region.

was next located at its winter terminus and did not move from there before January 1. Note, however, that because of the duty cycle (up to 48 h off), these mallards could have made one or more stops between the beginning of autumn migration and their wintering location.

We used two basic approaches to analyze these data. First, we examined the effects of sex, year, and sex \times year for comparisons involving movement dates or distances moved. For these analyses, we could only use the 2004–2006 data because there were no males marked in 2007. For tests involving all years monitored, we only examined females. Using program JMP 9.0 (SAS Institute,

Inc., Cary, NC), we used a 2-way factorial analysis of variance (ANOVA) to test for main effects. If an effects test determined that a variable was significant ($\alpha = 0.10$), we then conducted a post-ANOVA comparison using a Tukey honestly significant difference (HSD) test to determine which comparisons were significantly different. We used a higher alpha level because this study was observational and not experimental. Our measure of significance for the Tukey HSD test was based on the studentized range statistic ("Q") when two or more comparisons were made and on a t -test when only a single comparison was made. We present the least square means (LSMs) for those variables. Second, we

Table 2. Number of mallards *Anas platyrhynchos* with operational satellite transmitters on September 15 in 2004–2007 categorized by transmitter duty cycle. Duty cycles are for the September–January period.

Year	Duty cycle		
	6 h on, 48 h off	10 h on, 24 h off	0800, 1200, 1600, and 2000 hours
2004	9		
2005	8		
2006	18	5	1
2007	1	13	

used likelihood ratio tests to examine main effects for comparisons involving the number of single versus stopover events during migration.

We pooled data over years and sexes to examine the spatial pattern where marked mallards concentrated on autumn migration. We used ARCVIEW GIS 9.3 (ESRI, Inc.) to query, analyze, and map autumn locations. We calculated 50% and 95% kernel density estimates for all male and female locations using fixed-kernel estimation, which assumes a random sample and independence of points (Worton 1989), and visually examined the location of 50% kernels. We used least-squares cross validation to determine smoothing factors in the fixed-kernel estimation procedure because it is less biased and performs better than other methods, especially with sample sizes >50 (Seaman and Powell 1996; Seaman et al. 1999). Kernel methods are also less sensitive to autocorrelation with the data than are other home-range estimators (Swihart and Slade 1997; de Solla et al. 1999). We used a pixel cell size of 100×100 with a 100,000-m search radius to conduct the analysis. We violated the independence of points assumption but offer that our intention here was to describe autumn concentration areas of mallards rather than predict where mallard autumn concentration areas will be in the future. We finally classified each kernel density estimate into five categories based on the Jenks (1967) natural breaks algorithm.

Results

Of the 143 mallards with transmitters that migrated out of Arkansas during spring migration, 55 PTTs were still transmitting at the beginning of autumn migration (M:F, respectively: 2004, 2:7; 2005, 3:5; 2006, 6:14; 2007, 0:18; Table 2; Table S1, *Supplemental Material*). One male from autumn 2004 was tracked again in autumn 2005, while three 2006 females were tracked again in autumn 2007. Most mallards (29) were located in the PPR when they began autumn migration (Figure 2). The most frequented state/province on September 15 was Saskatchewan ($n = 16$) with eight mallards each in Manitoba and North Dakota and six in Alberta; after this, the number of mallards in any one state/province fell quickly.

Of those mallards active on September 15, the average date of departure was October 23 (SE = 2.62 d) with a range from September 17 to December 7 (Figure 3). We

found no effect of sex ($F_{1,36} = 0.07$, $P = 0.80$), or year ($F_{2,36} = 1.66$, $P = 0.21$) on the date that a mallard began autumn migration, but there was evidence of a sex \times year interaction ($F_{2,36} = 2.83$, $P = 0.07$). On average, 2005 females initiated migration later (Tukey HSD, $Q = 3.04$, $P < 0.05$; LSM = November 11, SE = 7.16 d) than 2006 females (LSMs = October 16, SE = 4.28 d) and 2004 females (LSM = October 12, SE = 6.05). Examining only females, we found an effect of year ($F_{3,43} = 3.63$, $P = 0.02$) on initiation date with females migrating later (Tukey HSD, $Q = 2.68$, $P < 0.05$) in 2005 (LSM = November 11, SE = 8.52) than in 2004 (LSM = October 12, SE = 7.2).

The modal number of stopovers per mallard making a stopover was one ($\bar{x} = 1.47$, range = 1–3). The average length of time spent on a stopover was 15.4 d (SE = 1.47) with a range from 2 to 69 d. We found no effect of sex ($\chi^2_1 = 1.24$, $P = 0.27$), year ($\chi^2_2 = 1.36$, $P = 0.51$), or sex \times year ($\chi^2_2 = 1.50$, $P = 0.47$) on the number of mallards making single stops or stopovers. When we examined for a year effect on the number of single and stopovers made by females, we found no effect of year ($\chi^2_3 = 1.97$, $P = 0.58$). We found no effect of year ($F_{2,44} = 2.12$, $P = 0.13$), or sex \times year ($F_{2,44} = 0.72$, $P = 0.50$), but there was an effect of sex ($F_{1,44} = 3.15$, $P = 0.08$) on the average number of days while on a migration stopover. Females spent more time on migration stopovers (LSM = 20 d, SE = 2.81) than males (LSM = 13 d, SE = 2.93). When we examined the number of days on stopovers for just females, we found that the average number of days while on a migration stopover varied by year ($F_{3,63} = 3.31$, $P = 0.03$), with females stopping for a longer period (Tukey HSD, $Q = 2.64$, $P < 0.05$) in 2004 (LSM = 24 d, SE = 3.19) than in 2007 (LSM = 13 d, SE = 2.53).

The average distance traveled in one leg was 536 km (SE = 34 km) with a range of 8–2,141 km. When we examined for an effect on the leg distance, we found no effect of year ($F_{2,98} = 1.05$, $P = 0.35$), or sex \times year ($F_{2,98} = 0.60$, $P = 0.55$), but we did find an effect of sex ($F_{1,98} = 7.32$, $P = 0.008$). Females traveled on average farther per leg (LSM = 640 km, SE = 59) than did males (LSM = 377 km, SE = 77). Examining only females, we found no effect of year ($F_{3,156} = 0.41$, $P = 0.75$) on the average distance traveled per leg.

We documented mallards in every year (one each in 2004 and 2005, five in 2006, three in 2007) making a single migration movement between their starting point (September 15) and where they ended autumn migration (December 15); that is, between the end of one duty cycle and the beginning of the next duty cycle, the mallard migrated from its initial autumn location to its final autumn location. There was a total of 10 mallards (1 M, 9 F) making nonstop migrations. The average distance flown in a single movement was 1,075 km (SE = 213.5 km) with a range of 143–2,141 km. The dates of these movements spanned September 22–December 8 and 6 of 10 were in November.

The total distance migrated per individual mallard, after initiating autumn migration, averaged 1,407 km (SE = 89.5 km) with a range of 143–2,947 km. We found no effect of sex ($F_{1,36} = 1.32$, $P = 0.26$), year ($F_{2,36} = 1.32$, $P = 0.28$), or sex \times year ($F_{2,36} = 0.98$, $P = 0.39$) on total migration distance moved. Examining only females, we

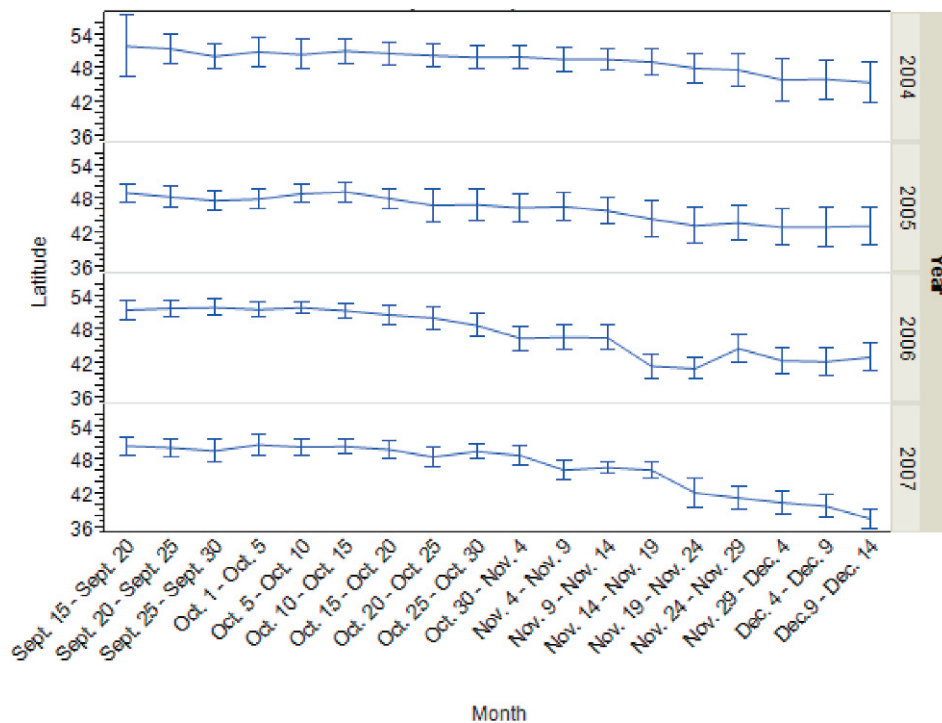


Figure 3. Average latitude (solid line) of satellite-marked mallards *Anas platyrhynchos* tracked during each 5-d segment between September 15 and December 15 by year from 2004 to 2007. Error bars represent 95% confidence interval.

found no effect of year on total distance migrated ($F_{3,43} = 0.31$, $P = 0.82$).

The average time spent on migration per individual between September 15 and December 15 was 27 d (SE = 2.88 d) with a range of 1–84 d. We found no effect of sex ($F_{1,36} = 0.28$, $P = 0.60$) or sex \times year ($F_{2,36} = 1.46$, $P = 0.25$), but we did find an effect of year ($F_{2,36} = 3.02$, $P = 0.06$) on migration duration. Although the Tukey HSD test did not detect significant differences between pairs of individual years, the migration duration point estimate for 2004 (LSM = 47 d, SE = 8.60) was almost twice as long as either 2005 (LSM = 26 d, SE = 7.83) or 2006 (LSM = 23 d, SE = 5.23). Examining only females, we found an effect of year on time spent on migration ($F_{3,43} = 3.73$, $P = 0.02$). Females in 2004 (LSM = 48 d, SE = 8.11) spent longer (Tukey HSD, $Q = 2.68$, $P < 0.05$) on migration than in either 2007 (LSM = 23 d, SE = 5.31) or 2005 (LSM = 14 d, SE = 9.59).

Over all 4 y, the distribution of mallard locations between leaving their autumn migration starting point and December 15 concentrated in a corridor running from southeastern Saskatchewan to northwestern Iowa (Figure 4). The largest concentration of observations was centered on southeastern North Dakota and northeastern South Dakota. The absence of more observations farther south of the PPR stems from mallards being killed or censored or PTT malfunctions en route.

The state where most mallards ended migration on December 15 was Missouri (11) followed by Arkansas (8); five mallards were still in Canada on December 15 (Figure 5). Five mallards continued to migrate between December 15 and 31; one from Missouri to Oklahoma, one from Missouri to Arkansas, one from Iowa to Kansas,

one from South Dakota to Missouri, and one from Wisconsin to Michigan. While females (43) ended migration equally in Missouri (8) and Arkansas (8), males (10) most often ended in Missouri (3). No males reached Arkansas by December 15. On average, mallards that reached their final destination by December 15 did so on November 19 (SE = 2.59 d) with a range of September 22–December 15. We found no effect of sex ($F_{1,36} = 0.31$, $P = 0.58$) or sex \times year ($F_{2,36} = 0.13$, $P = 0.88$), but we did find an effect of year ($F_{2,36} = 3.74$, $P = 0.04$) on end migration date. Mallards ended migration later (Tukey HSD, $Q = 2.46$, $P < 0.05$) in 2004 (LSM = December 8, SE = 6.93) than in 2006 (LSM = November 11, SE = 4.22). Examining only females, we found no effect ($F_{3,43} = 2.04$, $P = 0.12$) of year on the date when migration ended.

Since precipitation ranks were near normal each year, precipitation likely was not related to annual migration effects. We found that migration initiation was variable and not related to temperature in a consistent manner. Females started migration early in both 2004 and 2006 as compared with 2005; however, 2004 was a warmer year, 2006 was a colder year, and 2005 was a much warmer year. We found that females made longer stopovers in 2004 than in 2007, both warmer years; thus, we conclude stopover length was variable and not related to temperature. We did find that mallards ended migration later in 2004, a warmer year, than in 2006, a colder year.

Discussion

Our results supported conclusions of Bellrose (1980) and Drilling et al. (2002) that mallards have a prolonged

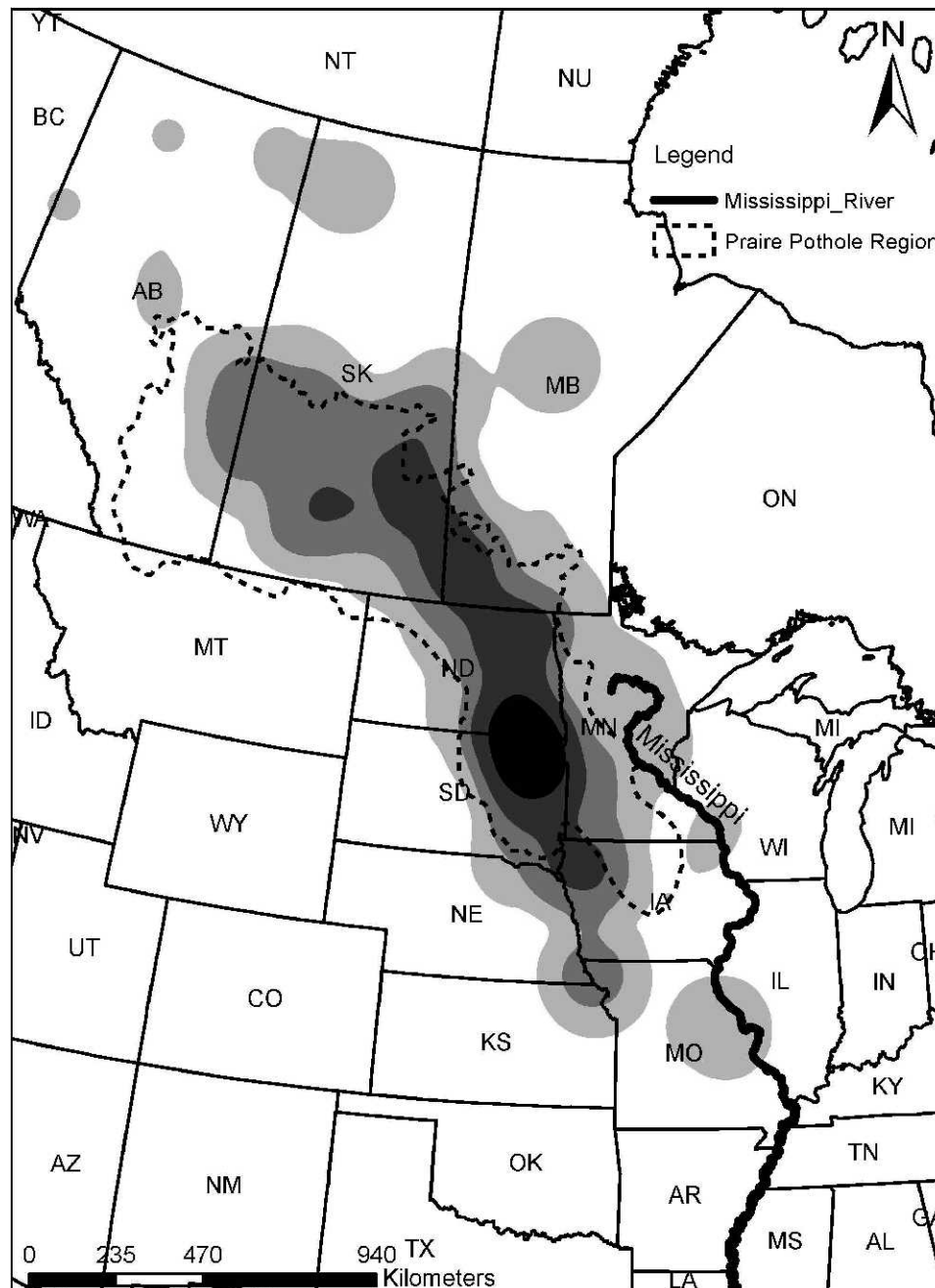


Figure 4. Kernel density estimates categorized into five abundance classes of satellite-marked mallards *Anas platyrhynchos* migrating during the autumn between September 15 and December 15, 2004–2007. Darker classes had more location records. The outlined region (dashed line) represents the Prairie Pothole Region.

autumn migration. Bellrose (1980) indicated that northern populations of mallards began migration in early September but that the first big push of mallards migrating begins in early October. Peak numbers of migrating mallards in northern populations occur in early November (Bellrose 1980). We also found that mallards began migrating from their starting locations across a large region (Northwest Territories to South Dakota) in September but our peak migration date was October 23. On average, most marked mallards began migration well before lake freeze-up in the PPR of

Canada (i.e., usually after November 15; Natural Resources Canada 2009). We found that female mallards did initiate migration earlier in 2006 (a colder than normal year); however, the earliest migration initiation was in 2004 (a warmer year). We were unable to relate migration timing to precipitation as ranks across the 4 y of our study were near normal. Contrary to the conclusion of Drilling et al. (2002) that mallard migration is driven by lake freeze-up, our data indicate that mallards began autumn migration almost a month before lake freeze-up.

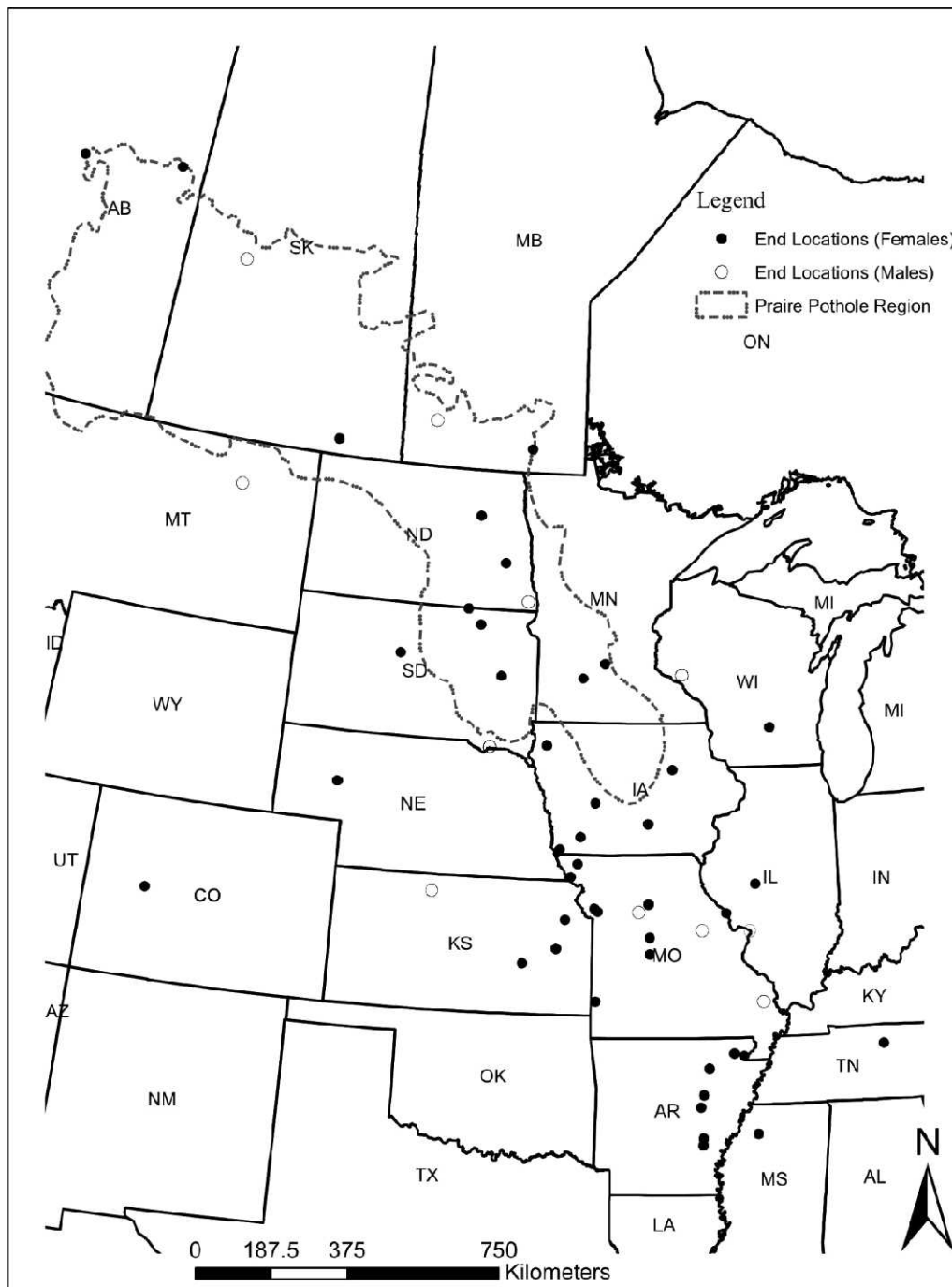


Figure 5. Locations of satellite-marked mallards *Anas platyrhynchos* on December 15, 2004–2007. The outlined region (dashed line) represents the Prairie Pothole Region.

Bellrose (1980:235) hypothesized, “that many mallards appear reluctant to migrate any farther south than necessary to obtain food.” While we did observe some mallards remaining far north (e.g., we had five mallards still present in Canada on December 15), the majority of our marked birds left the northern areas before lake freeze-up. We suspect mallards migrated before lake freeze-up because snow was already reducing food availability by covering food resources (Jorde et al. 1983). Bellrose (1980) did suggest that mallard migration did

not commence until early October and peaked in either late November or early December at intermediate migration areas. These dates are consistent with our migration initiation dates for marked mallards.

Bellrose (1980) also suggested that mallards began arriving in early October and peaked in November and December at southern winter grounds. We too found that marked mallards on average ended migration in late November (November 19), although a few birds continued to migrate into January. Late November is also the

time when the Arkansas regular duck season opens. Thus the notion held by Arkansas duck hunters that mallards are not available coincident with the opening of duck season (L.W.N., unpublished data) is not supported by our telemetry data, at least for female mallards. The general pattern of mallard migration was described by Bellrose (1980) as a "gentle slope" rather than sharp peaks in population trends as occurs in other duck species. Across our 4 y of study, we found that mallard migration was a gradual process between the third week in October and the first week in December with no sharp changes in distribution over the autumn period (Figure 3).

Bellrose (1980) suggested that food supplies determined where and when most waterfowl migrated but that the large-scale movements of waterfowl before food supplies became a limiting factor suggested that migration was programmed through the endocrine system. He further suggested that waterfowl from north temperate zones would have a stronger programmed migration pattern because those waterfowl would be exposed to limiting factors on a regular basis as compared with waterfowl in tropical or south temperate zones. Across the 4 y that we monitored mallard migration, we found a year \times sex effect on the timing of migration. The year \times sex effect was large (~ 28 d) which suggests to us that north temperate mallards are more flexible in migration departure than Bellrose (1980) had suggested. Some of this variation in migration departure may result from changing weather patterns that Schummer et al. (2010) found fine-tuned migration dates in Missouri. However Bellrose (1980) suggested that there is no simple relationship between weather factors and the initiation of migration flights. The observed variability in measured variables, such as migration timing, flight distances, and stopover duration, likely resulted from unmeasured habitat heterogeneity. However, more precise location information than available in this study would be necessary to adequately examine habitat impacts at multiple scales.

We found few sex differences in autumn migration patterns. The only substantial difference in the migration pattern between the sexes was that females remained on migration stopovers for a longer period of time (20 vs. 13 d) and that females made longer average migration movements than males (640 vs. 377 km). Eight females and zero males reached Arkansas by December 15.

The primary region used by marked mallards during autumn migration was from southeastern Saskatchewan to northwestern Iowa. Within this region, the most widely used stopover and staging area was the eastern Dakotas. Our primary region was included within the migration corridor that had the highest density of mallards in North America (Bellrose 1980) and was described by Bellrose (1980:232) as "extending from southeastern Saskatchewan to northwestern Illinois and then south to Tennessee, eastern Arkansas, and Mississippi." The preponderance of observations in the eastern Dakotas may, in part, reflect the recent changes in distribution of breeding mallards in the midcontinent region. Zuwerink (2001) and Reynolds et al. (2006) found that production of mallards in the U.S. prairies has been greater than in the Canadian prairies in

recent years, although only 12 of our 55 mallards were located in the U.S. prairies on September 15.

Robertson and Cooke (1999:22) reviewed winter philopatry in North American dabbling ducks and concluded that, "Most species of dabbling ducks do not appear to be philopatric in a general sense, except perhaps at the flyway level." Nichols and Hines (1987) reported that of the adult mallards marked during the winter in reference area 302 (Arkansas-Tennessee-Mississippi) between 1971 and 1977, some 63% ($n = 72$) of males and 58% ($n = 12$) of females were recovered in the same reference area in subsequent years. When Nichols and Hines (1987) examined winter mallard philopatry by age-sex, they found that adult males tended to return to traditional wintering areas more so than the other three age-sex classes that exhibited more temporal variation in subsequent winter distributions. Across all reference areas studied, Nichols and Hines (1987:39) concluded that "Mallards exhibit some temporal variation in wintering grounds, but that such variation is relatively small and that mallards do indeed exhibit a tendency to return to general wintering areas year after year...." In explaining the differences in age-sex winter philopatry, Nichols and Hines (1987) agreed with Hopper et al. (1978) who hypothesized that for subadult mallards, and to a lesser extent adult females, they were more likely to stray in their second year possibly because they contacted mallards using different migration routes and wintering areas. Davis and Afton (2010) marked female mallards in the lower Mississippi Alluvial Valley (LMAV) during November and December and tracked those same birds through March of the following year suggesting that once a female mallard arrived on its wintering ground, it remained there until spring migration. All of the mallards that we marked were captured in Arkansas. Most of these mallards were captured during February (73%), a time when mallards should be on their winter grounds (Dugger 1997; Drilling et al. 2002). We speculate that most of the mallards that we captured had spent at least some or all of that winter in Arkansas. If true, then the mallards we captured during February should have had some philopatry to wintering in Arkansas. None of the marked male mallards and only 8 of 43 female mallards (19%) returned to Arkansas by December 15 during subsequent autumns. Our homing rates to Arkansas were considerably lower than those reported for the LMAV by Nichols and Hines (1987). Granted, comparing our results to those of Nichols and Hines (1987) is confounded by differences in when the studies were conducted (1970s vs. 2000s), but we maintain that our results suggest that winter philopatry rates to at least the level of Arkansas and up to December 15 are low.

We can offer two possible hypotheses for marked mallards wintering north of Arkansas the following year. First, mallards, like all migratory birds, winter in a location where the trade-off between having adequate food resources offsets the costs of extreme weather (Bellrose 1980; Dalby et al. 2013). The LMAV contains the continent's greatest concentration of wintering mallards (Bellrose 1980), suggesting that the food resources in the

LMAV must be sufficiently abundant to offset the costs of weather conditions there (but see Stafford et al. 2006). The fact that mallards did not return to the Delta the following year suggests that food resources to the north of the Delta were sufficient to offset the costs of more severe weather conditions in more northerly wintering locations. Second, mallards that winter in the Delta are exposed to high disturbance and high mortality rates from hunter harvest pressure there, and in subsequent winters, surviving mallards remain further north where harvest pressures are lower. Davis et al. (2011) found that female mallards marked with VHF transmitters in the LMAV had low winter survival rates (54% for 136 d) resulting from hunting (18%) and other nonhunting sources (34%). Davis et al. (2011) indicated that their survival rate estimates were lower than some previously estimated for the same study area, and they noted that nonhunting mortality was greater in their study than some previously estimated. In examining mallard harvest across the Mississippi Flyway, Green and Krementz (2008) found the area of highest consistent harvest was Stuttgart, Arkansas, which is near the center of the Arkansas Delta. We hypothesize that mallards surviving a winter in the Delta forgo high food availability in subsequent winters in favor of higher survival to the north of Arkansas. Alternatively, surveys of mallards in the Arkansas Delta indicate high number of mallard present in Arkansas by mid-December (aerial survey data, unpublished). As noted, however, few mallards were marked prior to February. Perhaps these “early arriving” mallards were underrepresented in our sample. Under contemporary conditions, this cohort of mallards seems to arrive in Arkansas before major weather events to the north, possibly indicating a great level of philopatry than detected in our marked sample.

Most PTT-marked mallards did not return to Arkansas to winter the following year but instead wintered to the north; this was especially true for males. Why these marked mallards are not returning to Arkansas to overwinter is an important research question that deserves investigating. It is possible that low food resource levels (Stafford et al. 2006) and/or high mortality rates in the Arkansas Delta (Davis et al. 2011) promote a phenomenon of mallards shifting wintering locations in subsequent years. Additional research on autumn migration of midcontinent mallards using PTT transmitters with GPS capabilities would be useful in exactly determining high use wetlands. Our PTT locations were usually of such low quality that habitats used could only be described in general. With more precise geographic locations, managers will be better able to focus wetland management strategies on exact wetlands of known importance.

The eastern Dakota region is a critical stopover and staging area for autumn migrating mallards. Migrating mallards need abundant food resources during their stay at these stopovers and habitats managed for food and roosting should be protected and managed. Because the eastern Dakotas are an important area for waterfowl production, federal, state, and private organizations are currently intensively and extensively managing this

region (Reynolds et al. 2006). Based on our autumn migration results, these management efforts are focused in the appropriate area although the goal of these current management efforts is to increase duck production rather than to manage for autumn migration needs. We suggest that the eastern Dakotas continue to be a focal area of wetland management not only for increased production but for autumn roosting and loafing for mallards.

We believe that the strength of this work can assist planning efforts of NAWMP partners, including JVs and Flyway Councils, by increasing our understanding of mallard migration patterns and informing conservation strategies for mallards during the autumn. Our data addressing the timing of migration, the rate of migration, stopover duration and total migration duration, and sex-specific variation in those metrics are all variables that are required to model duck-use-days (Heitmeyer 2010) and the spatial arrangement of where those use-days need to be produced along the migration route.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Fall mallard *Anas platyrhynchos* migration data. Bird number, individual mallard identification number; Gender, gender of a marked mallard; Location (C/S), “C” represents a bird that remained in a single location for more than one duty cycle, “S” represents a bird that remained in a single location for one duty cycle; First Day, the Julian Day when a bird started a southern migration after Julian Day 258 (September 15); 1st Obs. Day, the Julian Day when a bird was first observed after Julian Day 244 (September 1); Last Day, the Julian Day when a bird was last located after the First Day location; Duration (days), the sum total of days that a bird was at a particular location (zero represents a bird at a location for 1 d); Start Migration, the Julian Day that a bird first migrated southward after Julian Day 258; End of Migration, the Julian Day when a bird last made a southern migration movement up through Julian Day 349 (December 15); Migration duration, the sum total Julian Days between when a bird first began moving southward and first arrived at the final migration location; Year, calendar year; State, the province/state where a bird was last located on the last transmission day; Route_From, the Julian Day when a bird started migration after Julian Day 258 (September 15); Route_To, the Julian Day when a bird was last located after the First Day location; Route_Distances/km, the distance (km) traveled between the “From” and “To” locations; Ends, the distance (km) traveled between where a bird started and ended autumn migration.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-019.S1> (26 KB XLSX).

Reference S1. Loesch CR, Reinecke KJ, Baxter CK. 1994. Lower Mississippi Valley joint venture evaluation



plan. Vicksburg, Mississippi: North American Waterfowl Management Plan.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-019.S2>; also available at http://www.lmvjv.org/library/NAWMP/evaluation_plan.pdf (2.74 MB PDF).

Reference S2. Munro RE, Kimball CF. 1982. Population ecology of the mallard. VII. Distribution and derivation of the harvest. U.S. Fish and Wildlife Service Resource Publication 147. Washington, D.C.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-019.S3> (5.7 MB PDF).

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Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-019.S4>; also available at <http://www.fws.gov/birdhabitat/nawmp/files/nawmp2004.pdf> (2.17 MB PDF).

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Reference S6. Petrie M, Brasher MG, Soulliere GJ, Tirpak JM, Pool DB, Reker RR. 2011. Guidelines for establishing joint venture waterfowl population abundance objectives. North American Waterfowl Management Plan Science Support Team Technical Report 3-10-2011.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-019.S7>; also available at <http://www.fws.gov/birdhabitat/NAWMP/NSST/files/GuidelinesforEstablishingJVPopulationObjectives.pdf> (316 KB PDF).

Reference S7. [UMRGLRV] Upper Mississippi River and Great Lakes Region Joint Venture Implementation Plan. 2007. Fort Snelling, Minnesota: U.S. Fish and Wildlife Service.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-019.S8>; also available at <http://www.uppermissgreatlakesjv.org/docs/JV2007All-BirdPlanFinal2-11-08.pdf> (2.79 MB PDF).

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