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Fall survival of American woodcock in the western Great Lakes region

Eileen Johnston Oppelt

FALL SURVIVAL OF AMERICAN WOODCOCK IN THE WESTERN GREAT LAKES REGION

By

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ABSTRACT

FALL SURVIVAL OF AMERICAN WOODCOCK IN THE WESTERN GREAT LAKES REGION

By

Eileen Johnston Oppelt

I estimated fall survival and determined the magnitude and sources of mortality for American woodcock (*Scolopax minor*) using radio telemetry in Michigan, Minnesota, and Wisconsin during 2001-2004. In all 3 states woodcock were radio-marked on paired study areas; one of which was open to hunting and the other of which was either closed to hunting (Michigan and Minnesota) or was relatively inaccessible to hunters (Wisconsin). I used program MARK to estimate fall survival, and to construct a set of candidate models to examine the effects of hunting and several effects of covariates (sex, age, year, state, size) on survival. Fall (10 September-8 November) survival estimates based on data pooled among years and states were 0.784 (95% CI 0.746-0.817) in the hunted areas and 0.881(95% CI 0.824-0.921) in the non-hunted areas. Hunting accounted for 48% of the 147 woodcock deaths in the hunted areas, followed by predation (32%) and various other sources of mortality (20%). The 66 woodcock deaths that occurred in the non-hunted and lightly-hunted areas were caused by predators (58%), various other sources (24%) and hunting (18%). Akaike's Information Criterion model selection indicated that fall survival varied by treatment (i.e., hunted versus non-hunted) and year. The estimate of the treatment effect was 11.6% (95% CI 0.045-0.187). Survival estimates did not vary by age, sex, bill length, or weight. The harvest rate when data were pooled among states and years was 13.0%, and the kill rate due to hunting was 14.5%.

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INTRODUCTION

The American woodcock (*Scolopax minor*) is a popular migratory game bird throughout eastern North America, particularly in the Great Lakes States, northeastern states, and in Louisiana. Although classified as a shorebird, the woodcock is adapted for upland forest habitats and prefers young, dense early successional forests (Owen et al. 1977). The woodcock has mottled plumage which allows it to blend in with surrounding vegetation and a long prehensile bill used for probing the ground for earthworms. In the United States, woodcock are managed by the U. S. Fish and Wildlife Service (USFWS) and state wildlife agencies. Woodcock are managed on the basis of 2 regions or populations, the Eastern and the Central Management regions (EMR and CMR; Fig.1) (Kelley and Rau 2005).

Woodcock populations are currently monitored with the singing-ground survey (SGS), wing collection survey (WCS), and the harvest information program (HIP) (Kelley and Rau 2005). The SGS provides annual indices of woodcock abundance and shows woodcock populations declined an average of 2.1% and 1.8% per year in the EMR and CMR, respectively, during 1968-2004 (Fig. 2) (Kelley 2004). The WCS provides indices to recruitment (number of immatures per adult female) and hunter success. Recruitment indices have been below long term averages (1.7 in EMR and 1.6 in the CMR) in both regions for most of the last 15-20 years. The current recruitment indices are 2 immature woodcock per female in the EMR and 1.5 in the CMR (Kelley and Rau 2005). The HIP provides state-specific estimates of the number of woodcock hunters and harvest. During the 2004-2005 woodcock hunting season, hunters harvested 61,500 birds in the EMR and 234,000 birds in the CMR. The USFWS uses 2 main strategies for managing migratory game birds such as woodcock (Krementz et al. 2003). One strategy is to purchase land and/or to manage land where suitable habitat occurs. The other strategy is to alter hunting regulations in response to changes in population status.

As with other migratory game birds, hunting regulations for woodcock in the United States are modified at the federal level through changes in framework dates within which states may select seasons, daily bag limits, and the length of the hunting season (Straw et al. 1994). Hunting regulations for woodcock are formally established annually, but often remain unchanged for years. From 1967 to 1984, the daily bag limit (5) and the season length (65 days) were the same in the EMR and the CMR (Table 1). The opening framework date for the hunting season was 1 September throughout this period but the closing date varied from 31 January to 28 February. In response to the population decline in the EMR, the bag limit was reduced to 3 and season length was reduced to 45 days in 1985 and the opening framework date was set at 31 January. Additional restrictions were implemented in both regions in 1997. Currently, the daily bag limit is 3 in both areas. The hunting season length is 30 days in the EMR and 45 days in the CMR (Kelley and Rau 2005). Currently, the hunting season framework is 1 October-31 January in the EMR and the Saturday closest to 22 September to 31 January in the CMR (Kelley and Rau 2005).

Current information on woodcock survival and the relationship between hunting mortality and survival are needed to understand woodcock population dynamics and to make informed management decisions. One problem woodcock managers face is that it is unclear whether there is a link between hunting regulations and population trends of woodcock (Krementz et al. 2003). Another problem is that most growth rate and annual survival rate estimates are based on data from the 1970s and 1980s (Dwyer and Nichols 1982, Krementz and Bruggink 2000, Krementz et al. 2003). Thus, recent woodcock management decisions have been based to some degree on limited and outdated survival estimates.

Annual survival rates of woodcock have been estimated using banding and recovery information (Dwyer and Nichols 1982, Krementz and Bruggink 2000, Krementz et al. 2003). However, Krementz and Bruggink (2000) found that sample sizes of banded woodcock were insufficient for estimating regional annual survival rates after the early 1980s. Krementz et al. (2003) used banding and recovery data from a long-term spring woodcock banding program, coordinated by the Michigan Department of Natural Resources, to estimate annual survival and recovery rates of woodcock in Michigan from 1978 through 1998. The authors found that survival was age-specific and that juveniles had a low survival rate (0.265). They found no differences in survival estimates before and after the hunting regulations were changed in 1997 but had only 2 years of data after the change. Band recovery data are the least biased compared to other methods (Derleth and Sepik 1990), such as radio telemetry. However, in order to make precise annual survival estimates, large samples are required, which are often difficult to obtain (Derleth and Sepik 1990).

Woodcock survival has been estimated for various periods of the year using radio telemetry. The majority of period survival studies have been conducted in the EMR. Derleth and Sepik (1990) estimated woodcock survival to be 0.923 during summer and early fall in Maine. Krementz et al. (1994) estimated survival to be 0.647 in the southern portion of EMR during the winter. Longcore et al. (1996) estimated spring survival to be

0.789 in Maine. Longcore et al. (1996) used survival estimates from the studies above to calculate a composite survival estimate of 0.471 for the 3 periods (breeding, postbreeding, and wintering). They also estimated survival to be 0.881 during spring migration and 0.853 during fall using period survival rates and annual survival from banding data (Longcore et al. 1996). More recently, McAuley et al. (2005) studied survival during the fall in 4 states in the EMR, and compared survival in areas that were open and closed to hunting. Fall survival rates were 0.636 in the areas open to hunting and 0.661 in the areas closed to hunting. In the only previous study of period survival of woodcock in the CMR, Pace (2000) estimated winter survival of woodcock in Louisiana to be 0.720

Woodcock population declines are thought to be largely due to the loss and degradation of suitable habitat (Gregg 1984, Derleth and Sepik 1990, Straw et al. 1994, Dessecker and Pursglove 2000). The effects of other factors, including predation, parasites, diseases, contaminants, and hunting, are unknown (Straw et al. 1994, Pace 2000, Robinson et al. 2001). There are many factors that interact to influence a population. Although loss of suitable habitat is thought to be the main cause of the declines of woodcock populations, other factors, such as hunting, may also be important and should not be overlooked. Of all the factors mentioned, hunting is the only factor woodcock over which managers have direct and relatively immediate control. Because most woodcock hunting mortality appears to occur during the fall (Kelley and Rau 2005), this season may be important in overall annual mortality of woodcock. However, there is essentially no information on survival of woodcock, or the importance of hunting in woodcock population dynamics in the CMR during fall. My objectives were:

(1) To document fall survival of woodcock in Michigan, Minnesota, and Wisconsin.

(2) To compare fall survival between hunted and non-hunted or lightly-hunted areas in Michigan, Minnesota, and Wisconsin.

(3) To determine the degree to which fall survival of woodcock varies by state, year, age, sex, and size.

(4) To determine the causes and magnitude of mortality in local woodcock populations during the fall.

This project was part of a cooperative effort to examine fall survival, habitat, and local movements in Western Great Lakes Region. Data were collected for each part of the study using standardized methods among all 3 states. Results of the movement and habitat studies can be found in Doherty (2004) and Meunier (2005), respectively.

STUDY AREAS

This research was conducted in study areas in Michigan, Minnesota, and Wisconsin. The areas were chosen with the help of the Department of Natural Resources in each state. Study areas were located in areas where woodcock hunting was known to be popular and where habitat conditions appeared to be suitable for capturing adequate samples of woodcock. All states had paired areas, 1 of which was open to hunting and the other of which was either closed to hunting (Michigan and Minnesota) or was relatively inaccessible to hunters (Wisconsin).

Michigan

The study areas in Michigan were in the Copper Country State Forest in northern Dickinson County (Fig. 3). The Dickinson Woodcock Research Unit (hereafter referred to as the “non-hunted area”) was an area of about 25,728 ha that was closed to woodcock hunting by the Michigan Natural Resources Commission for the purposes of this study. Field work was primarily concentrated in the eastern half of this area, which included the Gene’s Pond Study Area, the site of previous long-term woodcock research under the direction of W. L. Robinson (Northern Michigan University, emeritus). The “hunted area” did not have clear boundaries but consisted of 2 main capture sites located 0.8 and 2.7 km north of the non-hunted area.

Vegetation was similar in both areas and included aspen (*Populus* spp.), red maple (*Acer rubrum*), and paper birch (*Betula papyrifera*). Dominant species found in coniferous forests were balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*). There were very moist areas that contained extensive amounts of alder (*Alnus rugosa*).

Minnesota

The study areas in Minnesota included the 15,673 ha Mille Lacs Wildlife Management Area (hereafter referred to as the "hunted area") and the 1,163 ha Four Brooks Wildlife Management Area (hereafter referred to as the "non-hunted area"); both were located in Mille Lacs County. Prior to my study, hunting had not been permitted in the non-hunted area but it was opened to hunting during the final year of the study (2004). Both of the sites had comparable vegetative communities including aspen and lowland habitats (alder, willow (*Salix* spp.), and bur oak (*Quercus macrocarpa*)).

Wisconsin

The study areas in Wisconsin were located in Lincoln County. Lincoln County Forest (hereafter referred to as the "hunted area") was about 29,000 ha in size and the Tomahawk Timberland Forest (hereafter referred to as the "lightly-hunted area") was about 1,685 ha. Although the lightly-hunted area was not closed to hunting, it was located 3 km from the nearest road and was accessible only on foot. I hoped that because of the limited access, this site would effectively serve as a non-hunted area. Both sites were comprised mainly of mesic forests. Species such as sugar maple (*Acer saccharum*) and red maple were dominant in the well-drained and mesic sites while spruce (*Picea* spp.) and fir (*Abies balsamea*) were dominant on the moist soils.

METHODS

Capture and Banding Woodcock

The study was initiated in Minnesota in 2001, and in Michigan and Wisconsin in 2002. The study ended in all 3 states in 2004. Field crews consisted of 4 - 6 people in each state, each year. From mid-August to the end of September, field crews captured woodcock using mist nets and night lighting (Sheldon 1960, McAuley et al. 1993). The goal was to put transmitters on 60 woodcock in each of the study areas (i.e. 120 per state) during each year of the study. Mist nets were opened at sunset just before woodcock began crepuscular movements. On overcast nights, night lighting was used. Woodcock were disoriented using a high powered spotlight, which caused them to land (Reiffenberger and Kletzly 1967), after which they were captured with a handheld net. A number 3 USFWS leg band was put on each captured bird, and weight, bill length, wing chord, and tarsus length were measured. Age and sex were determined using plumage characteristics (Martin 1964). A transmitter (Advanced Telemetry Systems, Inc. model A2480) with a thermister mortality switch, weighing about 4.5g, was attached to all woodcock $\geq$ 140 g. Birds < 140g were not fitted with transmitters because the transmitter would have been have exceeded 3% of bird's body weight, the maximum allowed by our bird banding permit. Transmitters were attached using livestock tag cement and a wire harness that was connected by crimping a connector sleeve onto the adjoining wires (McAuley et al. 1993).

Monitoring

Signals of all radio-marked woodcock were searched for $\geq$ 5 days per week to assess their status (i.e., alive or dead). Missing woodcock were searched for from an airplane about weekly, as weather and aircraft schedules allowed. Woodcock located during aerial searches were subsequently tracked on the ground to check the status of the bird.

Survival Analyses

Due to possible short-term behavioral or survival effects that may have resulted from capture and adjusting to the transmitter, woodcock were not considered part of the sample until 3-days after they were captured (Krementz et al. 1994, Krementz and Berdeen 1997). Birds that died or disappeared during this time were not included in the survival analyses. After 3-days, I censored woodcock when they slipped out of their harness, or died due to entanglement in the harness. Woodcock that could not be located were assumed to have moved off the study area and were censored after the last day they were known to be in the area. Birds that were not located on the ground for > 2 weeks but were subsequently found dead were censored the day after they were last located on the ground alive.

The 60-day fall period was defined based on when each study area had at least 1 bird in the sample in all years (i.e. on 10 September all sites had at least 1 bird alive after the 3-day adjustment period). An exception was the non-hunted area in Michigan in 2003. Due to dry conditions during late August and early September, and because truck traffic associated with a logging operation disrupted an important capture site, the first bird active in this area was on 17 September. Thus, survival was estimated for a 56-day period (17 September – 4 November) for that site in 2003.

I used the nest survival model in Program MARK (White and Burnham 1999) to estimate fall survival (10 September – 8 November), and to construct a set of candidate models to examine the effects of hunting and the effects of covariates (sex, age, size, year, state) on survival. Bill length and weight were used as indices of structural size. In most recent woodcock survival studies (e.g. Krementz and Berdeen 1997, Longcore et al 2000), survival was estimated using the Kaplan-Meier method (Kaplan and Meier 1958), as modified by Pollock et al. (1989). I chose to use Program MARK instead because preliminary analyses indicated that the fully-time-dependent model (i.e., the one analogous to the Kaplan-Meier model) often was not the best model, and because MARK facilitated an information-theoretic approach to addressing questions about the effects of hunting and covariates. I used the nest survival model rather than the known fates model of MARK because our data were somewhat "ragged" due to slightly different schedules of field crews in the 3 states (White and Burnham 1999).

I began with two generic models: (1) S(.) (constant survival during the fall period) and (2) S(t) (time-dependent survival). Because there was virtually no support for the model with time-dependent survival during the fall period, all subsequent models were run assuming constant survival. Model selection was based on ΔAIC values. Models with ΔAIC (Akaike Information Criterion) values ≤ 2 have substantial support and were considered the best models (Burnham and Anderson 2002). I evaluated the significance of variables in the best model based on whether the 95% confidence intervals (CI) for the β values included zero. Survival estimates were calculated for hunted and non/lightly-hunted areas by state and year, by state with data pooled among years, and overall with data pooled among states and years. When calculating the overall survival estimates in hunted and non-hunted areas with data pooled among states and years, the lightly-hunted area in Wisconsin was included as a hunted area.

In order to directly compare the period survival rates (PSRs) from my study with those from other studies, I standardized the periods by raising the daily survival rates from my study to the appropriate power to match the period from the other study.

Causes of Mortality

When transmitters were in mortality mode, field crews homed in on the signal. When the bird or transmitter was found, conditions of the carcass and other relevant factors were recorded and the cause of death was noted when possible. Necropsies were conducted by T. Cooley, a pathologist with the Michigan Department of Natural Resources, on all woodcock for which the cause of death was not apparent.

Hunting Mortality.-- Kill rates (the proportion of woodcock shot by hunters) were estimated by censoring all natural deaths. I examined the relationship between point estimates of fall survival and point estimates of kill rates in hunted areas using linear regression (SPSS version 13.0, SPSS Inc., Chicago, Illinois, USA). I estimated harvest rates (the proportion of woodcock shot and retrieved by hunters) in the hunted areas by censoring natural deaths and un-retrieved kills (Pollock et al. 1989). I calculated the crippling loss rate by subtracting the harvest rate from the kill rate.

RESULTS

During 2001-2004, 1,310 woodcock were captured from mid-August through September in Michigan, Minnesota, and Wisconsin. Transmitters were attached to 1,171 of these woodcock (Table 2). Numbers of woodcock radio-tagged in hunted and non-hunted areas were similar among all study areas. An exception was the low number of woodcock captured in the non-hunted area in Michigan in 2003 due to very dry conditions during late August and early September, and because truck traffic associated with a new logging operation disrupted an important capture site. The total number of radio-tagged woodcock used in the fall season survival estimates was 1,037. One hundred and thirty-four woodcock were censored from survival analyses (Table 3). The majority of these woodcock died or disappeared before the fall season (10 September – 8 November) began. Woodcock that were censored during the fall season died or disappeared within the 3-day adjustment period. Four birds that were not located on the ground or during aerial searches for weeks but were later found dead were censored the last day they were known to be alive.

My radio-marked sample of woodcock was comprised of juvenile males (32%), adult females (26%), juvenile females (24%), and adult males (19%) (Table 4). In each state, the smallest numbers of woodcock captured were adult males (Table 5) while the number captured of other sex-age classes varied among states.

Survival Analyses

Point estimates of survival were higher in the non-hunted or lightly-hunted areas than in hunted areas, although the confidence intervals overlapped considerably (Table 6). Fall season survival estimates with data pooled among years were similar in

Michigan and Minnesota in both the hunted and non-hunted areas (Table 7). Survival estimates in Wisconsin were somewhat lower. When data were pooled among states and years (2001-2004), the survival estimates were higher in the non-hunted areas (0.881, 95% CI 0.824-0.921) than in the hunted areas (0.784, 95% CI 0.746-0.817). There were no differences between survival estimates of adult woodcock (0.819, 95% CI 0.771-0.857) and juvenile woodcock (0.801, 95% CI 0.758-0.838), or between male (0.817, 95% CI 0.772-0.855) and female (0.801, 95% CI 0.755-0.839) woodcock. Only 1 of my candidate models, $S_{treatment,year}$, had a ΔAIC value ≤ 2 (Table 8). Thus my data provided considerable support (Akaike weight = 0.749) for variation in survival due to treatment and year (Table 9). The estimate of the treatment effect was 11.6% (95% CI 0.045-0.187). I found essentially no support for models that did not include treatment, year, or both treatment and year. Particularly noteworthy is the lack of support for models that included sex and age. Similarly, there was virtually no evidence of a relationship between survival and indices to structural size (bill length and weight).

Causes of Mortality

During 2001-2004, 213 woodcock died from hunting, predation, or other causes. Hunting was the largest single source of mortality in the hunted areas (Table 10). Out of 147 deaths in the hunted areas, 71 birds were shot (48%), 47 birds were killed by predators (32%), and 29 birds died from other causes (20%). In the non-hunted or lightly-hunted areas, predation was the primary source of mortality. Out of 66 deaths in the non-hunted or lightly-hunted areas, 38 birds were killed by predators (58%), 16 birds (24%) died from other causes, and 12 birds (18%) were shot. Necropsies indicated that 12 woodcock were shot by hunters but not retrieved. Two of these birds were killed before the hunting season, 1 in Michigan and 1 in Minnesota. The other 10 were killed during the season in the lightly-hunted area in Wisconsin.

Mammals accounted for 23% of the predation in both hunted and non-hunted areas while raptors accounted for about 17%. The primary mammalian predators were weasels (*Mustela* spp.) and mink (*Mustela vison*). Although we were unable to identify specific avian predators, several species in the Great Lakes Region are known to prey on woodcock, including Cooper's hawks (*Accipiter cooperii*), northern goshawks (*Accipiter gentiles*), sharp-shinned hawks (*Accipiter striatus*), barred owls (*Strix varia*), and great horned owls (*Bubo virginianus*) (McAuley et al. 2005).

The overall kill rate in Michigan (19.9%) was higher than in Minnesota (12.8%) and Wisconsin (13.1%) but there was more variation in Minnesota and Wisconsin (Table 11). There was little difference between harvest rates and kill rates (Table 12). The overall kill rate, when data were pooled among years and states, was 14.5% (95% CI 11.7-18.0), whereas the harvest rate was 13.0% (95% CI 10.3-16.3). There was a significant negative relationship ($F_{1,9} = 17.478$, $P = 0.003$) between kill rates and survival rates in hunted areas (Fig. 4).

The candidate model $S_{year,\ sex}$ had the most support in the data (Table 13). Although the effect of sex was not statistically significant (the confidence intervals for β included 0), the point estimates of kill rates were higher for females than for males in all years (Table 14).

DISCUSSION

The major influences on woodcock survival during fall were treatment (i.e. hunted versus non-hunted areas) and year. Survival estimates varied over years and were generally higher in non-hunted areas than in hunted areas. With data pooled among years and states, woodcock survival was 11.6% higher in non-hunted areas (0.881) than in the hunted areas (0.784). In contrast to my results, McAuley et al. (2005) found no significant difference in fall survival between hunted and non-hunted areas in the EMR, where hunting regulations are more restrictive. The period survival rates (PSR) in the hunted and non-hunted areas in my study (0.691 and 0.826, respectively; extended to match the 91-day period in the EMR) were higher than the PSRs (0.636 and 0.661) reported by McAuley et al. (2005), especially in the non-hunted areas. Hunting was the largest single source of mortality (48.0%) in the hunted areas in my study. In contrast, McAuley et al. (2005) found that predation was the primary source of mortality (63.0%) in the hunted areas and only 36% of the deaths were due to hunting. These results suggest that hunting is a more important source of mortality for woodcock in the CMR than in the EMR. This may be due to the more liberal regulations in the CMR, greater hunting pressure, or a combination of these or other factors. In contrast, natural mortality, particularly predation, exerts more of an influence in the EMR where survival even in the non-hunted areas was lower than survival in my hunted areas.

Survival was lowest and the kill rate was highest in 2003 but the reasons for the inter-year this variation are unclear. In general, the amount of precipitation varied more among years and states (Fig. 5) than temperature (Fig. 6) from 2002 to 2004. These 2 variables may influence woodcock activity. Doherty (2004) found that woodcock made larger local movements (> 500m) to forage in new areas when there were poorer environmental conditions (i.e. low earthworm abundance) and warmer temperatures. He also found that earthworm abundance was correlated with rainfall and soil porosity. During the drier conditions, woodcock may have been concentrated in lowland areas or not flush as easily when disturbed. These actions may make them more vulnerable to predators or hunters. Hunting pressure in our study areas may have varied among years for unknown reasons.

Standardized fall survival estimates over a 77-day period for female woodcock in my study (0.752) were similar to the estimate (0.720) reported by Pace (2000) in Louisiana during 1 December-15 February (Table 15). He reported that hunting caused 19% of the known deaths. Pace (2000) also estimated winter survival (0.840) over a 45-day period (24 December-7 February) which was higher than the survival estimate (0.720) reported by Krementz and Berdeen (1997) in Georgia from 25 December-7 February. My fall survival estimates (0.833) over a 45-day period were also higher than those reported by Krementz and Berdeen (1997). Forty percent of the deaths in the Georgia study were caused by hunting. The daily survival estimates of Krementz and Berdeen (1997) were similar to those of Krementz et al. (1994). Krementz et al. (1994) found no mortalities were caused by hunting 15 December to 15 February along the Atlantic Coast (Georgia, South Carolina, and Virginia). Woodcock hunting is not as popular in most southern states as it is in the Great Lakes states, which may explain the lack of hunting mortality (Krementz et al. 1994). Krementz et al (1994) and Krementz and Berdeen (1997) concluded that winter was a period of low survival. Previous studies in the EMR have found summer woodcock survival estimates to be higher than during other parts of the year. Standardized fall survival estimates from my study were the same or higher than the estimates reported by Derleth and Sepik (1990) except during the 15 June-17 July period. The PSRs estimated during that period were higher than those in my study.

I found no sex or age-related differences in woodcock survival. Similarly, no sex or age-related variation has been found in most telemetry-based studies of woodcock survival (Krementz et al. 1994, Longcore et al. 1996, Krementz and Berdeen 1997, Longcore et al. 2000, McAuley et al. 2005) during various parts of the year. An exception was Derleth and Sepik (1990), who found that summer-fall survival estimates were age-specific. Adults tended to have higher summer survival rates (0.890-0.920) than juveniles (0.640-0.680). The authors attributed the differences in survival to different predation rates, possibly caused by age-related differences in mobility.

Analyses based on banding data have provided evidence that annual survival of female woodcock is greater than that of males in the EMR (Dwyer and Nichols 1982), and that annual survival rate of adults is greater than that of juveniles (Dwyer and Nichols 1982, Krementz and Bruggink 2000, Krementz et al 2003). Krementz et al. (2003) analyzed Michigan banding and recovery data from 1978-1998 and reported annual survival rates of adult and juvenile woodcock to be 0.490 and 0.265, respectively. Olinde et al. (2000) used direct band recoveries during the winter in Louisiana and reported that juveniles were 2.5 times more likely to be shot than adult woodcock. My results indicate that the lower survival estimates of juveniles found by Krementz et al. (2003) were not accounted for by differential vulnerability to hunting during the fall season. Although I found no evidence of sex-related differences in overall survival, I did find weak evidence that hunting mortality is higher for females. This suggests sex-specific differences in the balance between hunting mortality and natural mortality.

Little information exists on kill rates, harvest rates, and crippling loss rates for woodcock. Kill rates in my study ranged from 6.7% to 11.8% among years. Harvest rates of woodcock in my study ranged from 6.7 to 10.4%. There was 1.5% crippling loss rate. Although not directly comparable with my results, Nauertz (1997) and Robinson et al. (2000) estimated local harvest rates by leg banding woodcock from March through October and conducting interviews and bag checks during the fall in Dickinson County, Michigan in the same area used for the Michigan study area in my study. Local harvest rates were estimated by dividing the number of banded birds shot by the number of birds banded. Nauertz (1997) estimated 8.6% of the population was harvested locally per year. Robinson et al. (2001) reported local harvest rates ranging from 9 to 17 % over a 7-year period and a mean of 14.9% for 1994-2000. Using similar techniques in Marquette County, Michigan, Froiland (1998) estimated an 8.2% local harvest rate during 1996-1997. This rate corresponded closely with Nauertz's (1997) 8.6% local harvest rate from 1993-1994.

Pursglove (1975) estimated that crippling loss for woodcock may be as high as 17%, and information provided by participants in the USFWS Wing-collection Survey indicate a crippling loss rate of about 6% (J. G. Bruggink, Office of Migratory Bird Management, USFWS, unpublished data). Thus, the low crippling loss rate of radio-marked woodcock that I observed was somewhat surprising.

According to the compensatory mortality hypothesis, there is no relationship between survival and kill rates, below some threshold value, because increases in the kill rate are compensated for by density-dependent decreases in natural mortality (Anderson and Burnham 1976, Conroy and Krementz 1990). The negative relationship I observed between kill rates and fall survival suggests that hunting mortality was at least partially additive to other sources of mortality during the fall (Fig. 4). However, it is important to note that compensation for hunting mortality could occur at some other point in the annual cycle.

An important consideration when interpreting my results, and those of similar studies, is the degree to which the hunted areas were representative of woodcock habitat as a whole. Unfortunately, this is difficult to assess. Because my study areas were located in areas where woodcock hunting was popular, my results may represent something close to a worst case scenario for woodcock in terms of hunting-related mortality. However, wing receipts from the USFWS wing-collection survey suggest that all of the study areas were located in counties where woodcock hunting is popular (Fig.7), and that many other counties in the 3 states are similarly popular. Thus, my results may be fairly representative of large portions of the woodcock's range, at least where woodcock habitat is relatively accessible.

Finally, it is worth noting the implications of violations of the assumption that woodcock that could not be located had moved off the study area or successfully migrated. Censoring such birds is not a problem, unless the reason that they could not be located is because they actually were dead. Of particular concern is the possibility of non-reporting of kills by hunters, whether intentional or through oversight, which would result in overestimates of survival and underestimates of kill rates. Although I believe hunters were generally very cooperative, 1 hunter in Michigan, who shot some of our radio-marked birds in 2002 and 2003, expressed concern over what my findings might show and hinted that he might not report any additional woodcock that he shot. There also was a case in Michigan where the transmitter from a long-missing bird suddenly reappeared and upon examination, it appeared that the wire harness had been cut.

MANAGEMENT IMPLICATIONS

We now have information on fall survival of woodcock and a better understanding of the importance of hunting relative to other sources of mortality in the CMR. Hunting was the primary source of woodcock mortality in our hunted areas and overall survival was 11.6% higher in non-hunted areas than in hunted areas. Despite more liberal hunting regulations in the CMR and the impact of hunting that I observed, survival estimates from my study were higher than those reported for the EMR by McAuley et al. (2005). These results should be useful to biologists and administrators involved with making decisions about woodcock harvest management.

An important question remaining is what these survival and kill rate estimates mean in terms of woodcock population dynamics. This question cannot be fully answered without additional information, such as the population growth rate and the degree to which hunting mortality is additive, which is unavailable. However, unless hunting mortality is completely compensatory, which seems unlikely (Conroy and Krementz 1990, Sinclair and Pech 1996), it will reduce the population growth rate to some extent. Thus, whether hunting mortality results in slower growth, stability or negative growth depends on where the population growth rate is relative to stability in the absence of hunting mortality.

I think more research is needed on woodcock survival during other parts of the year in the CMR. Estimating survival during various times of year will allow for annual survival to be estimated in this region. Annual survival estimates in the CMR would be useful in woodcock management and would assist managers in making appropriate adjustments to regulations.

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Table 1. Changes in bag limits and hunting season lengths for American woodcock in the Central and Eastern regions, 1967-2005 (Kelley and Rau 2005).

	Central Management Region		Eastern Management Region	
Years	Bag limit	Season length (days)	Bag limit	Season length (days)
1967-1984	5	60	5	60
1985-1996	5	60	3	45
1997-2005	3	45	3	30

Table 2. Number of radio-marked American woodcock in hunted and non-hunted or lightly-hunted areas in Michigan, Minnesota, and Wisconsin 2001-2004.

	Michigan		Minnesota		Wisconsin	
Year	Hunted	Non-hunted	Hunted	Non-hunted	Hunted	Lightly-hunted
2001	--	--	31	44	--	--
2002	65	56	67	69	71	48
2003	59	16	66	75	70	52
2004	63	52	33	97[a]	70	67
Total	187	124	197	285	211	167

[a]Opened to woodcock hunting in 2004

Table 3. Radio-marked American woodcock omitted from survival analyses because their fate occurred before the fall season (10 September-8 November) or because they died during the 3-day adjustment period in Michigan, Minnesota, and Wisconsin, 2001-2004.

Fate	Fate occurred before fall season	Fate occurred during adjustment period
Shot	0	6
Mammal predation	19	8
Avian predation	9	7
Unknown mortality	10	2
Trauma	0	1
Pulmonary congestion	0	2
Research-related deaths	21	11
Departed study area	6	5
Slipped transmitter	12	3
Bad radio	1	0
Enter/left sample same day	0	4
Canine	1	2
Miscellaneous[a]	0	4
Total	79	55

[a]Woodcock died after 3-day adjustment period but were not located until weeks later during aerial searches

Table 4. Year-specific sex-age composition of radio-marked American woodcock in Michigan, Minnesota, and Wisconsin, 2001-2004.

	Female		Male		
Year	Adult	Juvenile	Adult	Juvenile	Unknown
2001[a]	11	29	7	28	0
2002	103	90	72	110	1
2003	88	78	67	105	0
2004	99	80	71	131	1
Total	301	277	217	374	2

[a] Minnesota only

Table 5. State-specific sex-age composition of radio-marked American woodcock in Michigan Minnesota and Wisconsin during 2001-2004.

State	Female		Male		Unknown
	Adult	Juvenile	Adult	Juvenile	
Michigan	98	62	58	92	1
Minnesota	126	120	108	127	1
Wisconsin	77	95	51	155	0

Table 6. Fall season survival estimates of radio-marked American woodcock in hunted and non-hunted or lightly-hunted areas in Michigan, Minnesota, and Wisconsin, 2001-2004.

		Hunted			Non-hunted[a]		
State	Year	n[b]	Survival	95% CI	n	Survival	95% CI
Michigan	2002	61	0.830	0.640-0.926	51	0.850	0.649-0.941
	2003	52	0.809	0.641-0.904	17	0.886	0.427-0.983
	2004	61	0.719	0.566-0.825	46	0.874	0.698-0.951
Minnesota	2001	29	0.933	0.614-0.990	39	0.960	0.746-0.994
	2002	62	0.723	0.565-0.832	52	0.911	0.779-0.965
	2003	60	0.673	0.506-0.795	60	0.826	0.670-0.913
	2004	111	0.833	0.735-0.898	N/A[c]	N/A	N/A
Wisconsin	2002	64	0.799	0.638-0.894	47	0.874	0.658-0.957
	2003	58	0.591	0.418-0.728	49	0.754	0.581-0.863
	2004	61	0.818	0.670-0.905	59	0.844	0.686-0.927

[a]Lightly-hunted in Wisconsin
[b]The number of birds that provided any useable data during the 60-day fall season
[c]Opened to woodcock hunting in 2004

Table 7. Fall season survival estimates of radio-marked American woodcock in hunted and non-hunted or lightly-hunted areas in Michigan, Minnesota, and Wisconsin. Estimates are based on data pooled among years (2001-2004 in Minnesota, 2002-2004 in Michigan and Wisconsin).

	Hunted			Non-hunted[a]		
State	n[b]	Survival	95% CI	n	Survival	95% CI
Michigan	174	0.777	0.689-0.843	114	0.866	0.759-0.928
Minnesota	233	0.800	0.743-0.851	112	0.891	0.815-0.936
Wisconsin	183	0.742	0.655-0.811	155	0.818	0.727-0.881

[a]Lightly-hunted in Wisconsin
[b]The number of birds that provided any useable data during the 60-day fall season

Table 8. Models evaluated for variation in survival rate estimates of radio-marked American woodcock in Michigan, Minnesota, and Wisconsin, 2001-2004 during the 60-day fall season.

Model	AIC_c[a]	ΔAIC_c	AIC_c Weight	Model Likelihood	Parameters	Deviance
$S_{treatment,\ year}$	1644.160	0.000	0.748	1.000	5	1634.159
$S_{treatment,\ year,\ state}$	1648.106	3.946	0.104	0.139	7	1634.103
S_{year}	1649.184	5.024	0.061	0.081	4	1641.183
$S_{treatment,\ year,\ treatment*year}$	1649.898	5.738	0.042	0.057	8	1633.894
$S_{treatment}$	1650.652	6.491	0.029	0.039	2	1646.651
$S_{treatment,\ age,\ sex}$	1653.542	9.381	0.007	0.009	4	1645.540
$S_{treatment,\ state}$	1654.058	9.897	0.005	0.007	4	1646.057
$S_{(.)}$[b]	1657.305	13.145	0.001	0.001	1	1655.305
S_{state}	1658.546	14.386	0.001	0.001	3	1652.545
$S_{bill\ length,\ weight}$	1658.667	14.506	0.001	0.001	3	1652.666
$S_{bill\ length}$	1658.772	14.612	0.001	0.001	2	1654.772
S_{sex}	1658.988	14.828	0.000	0.001	2	1654.988
S_{age}	1659.001	14.840	0.000	0.001	2	1655.001
S_{weight}	1659.232	15.072	0.000	0.001	2	1655.232
$S_{(t)}$[c]	1669.636	25.476	0.000	0.000	59	1551.445

[a]Akaike's Information Criterion
[b]Constant survival over time
[c]Survival time dependent

Table 9. Fall season survival estimates of radio-marked American woodcock in hunted and non-hunted or lightly-hunted areas, 2001-2004 from the model $S_{treatment,\ year}$. Survival estimates are based on data pooled among states.

	Hunted			Non-hunted[a,b]		
Year	*n*[c]	Survival	95% CI	*n*	Survival	95% CI
2001[d]	29	0.930	0.746-0.982	39	0.961	0.852-0.990
2002	187	0.797	0.726-0.851	150	0.883	0.817-0.927
2003	170	0.707	0.631-0.770	126	0.828	0.736-0.890
2004	233	0.820	0.763-0.864	105	0.897	0.831-938

[a]Data from the lightly-hunted area in Wisconsin were included in the hunted sample
[b]The non-hunted area in Minnesota opened to woodcock hunting in 2004; data from 2004 were included in the hunted sample
[c]The number of birds that provided any useable data during the 60-day fall season
[d]Minnesota study area only

Table 10. Fate of radio-marked American woodcock in hunted and non-hunted or lightly-hunted study areas in Michigan, Minnesota, and Wisconsin, 2001-2004. All other woodcock were assumed to have migrated.

	2001[a]		2002		2003		2004	
Fate	Hunted (n = 31)	Non-hunted (n = 44)	Hunted (n = 203)	Non-hunted[b] (n = 173)	Hunted (n =195)	Non-hunted[b] (n = 143)	Hunted (n = 263)	Non-hunted[b,c] (n = 119)
Shot	1	0	17	0	28	9	25	3
Mammal predation	1	2	6	8	12	7	8	5
Avian predation	0	0	5	7	8	8	7	1
Unknown mortality	0	1	5	5	3	4	12	5
Trauma	0	0	1	0	1	0	2	0
Pulmonary congestion	0	0	3	1	1	0	1	0
Slipped transmitter	1	1	11	12	3	6	1	0
Censored mortality	1	1	9	11	6	6	10	5
Total	4	5	57	44	62	40	66	19

[a]Only Minnesota study area
[b]Lightly-hunted in Wisconsin
[c]Non-hunted area in Minnesota was opened to hunting

Table 11. Kill rates of radio-marked American woodcock in Michigan, Minnesota, and Wisconsin, 2001-2004.

	Michigan		Minnesota		Wisconsin	
Year	Kill rate	95% CI	Kill rate	95% CI	Kill rate	95% CI
2001	--	--	6.7	0.1-38.6	--	--
2002	13.8	5.4-32.7	21.6	11.9-37.3	3.4	0.9-12.3
2003	14.1	6.1-30.5	24.0	13.3-41.0	24.8	16.3-36.8
2004	28.1	17.5-43.4	3.8	1.3-11.4	10.1	5.2-19.1
Overall[a]	19.9	13.6-28.6	12.8	8.6-18.8	13.1	9.2-18.5

[a]Data pooled among years

Table 12. Year-specific harvest and kill rates of radio-marked American woodcock, 2001-2004. Data were pooled among states.

	Harvest rate		Kill rate	
Year	%	95% CI	%	95% CI
2001	6.7	1.0 - 38.6	6.7	1.0 - 38.6
2002	10.9	6.6 - 17.7	11.6	7.2 - 18.5
2003	19.4	13.7 - 27.0	21.9	16.0 - 29.7
2004	10.4	6.9 - 15.5	11.8	8.1 - 17.1
Overall[a]	13.0	10.3 - 16.3	14.5	11.7 - 18.0

[a]Data pooled among years

Table 13. Models evaluated for variation in kill rate estimates of radio-marked American woodcock in Michigan, Minnesota, and Wisconsin during the 60-day fall season, 2001-2004

Model	AIC_c[a]	ΔAIC_c	AIC_c Weight	Model Likelihood	Parameters	Deviance
$S_{year\ sex}$	942.820	0.000	0.290	1.000	5	932.818
S_{year}	944.500	1.678	0.126	0.432	4	936.496
$S_{year,sex,state}$	944.624	1.803	0.118	0.406	7	930.620
$S_{year,age,sex}$	944.805	1.985	0.108	0.371	6	932.802
S_{sex}	945.251	2.431	0.086	0.297	2	941.251
$S_{year,sex,state,year*state}$	945.868	3.048	0.063	0.218	9	927.862
$S_{year,state}$	946.073	3.253	0.057	0.196	6	934.070
$S_{year,age}$	946.312	3.492	0.051	0.175	5	936.310
$S_{age,sex}$	947.173	4.353	0.033	0.114	3	941.172
$S_{(.)}$[b]	947.189	4.369	0.033	0.113	1	945.189
S_{state}	948.046	5.226	0.021	0.073	3	942.045
S_{age}	948.829	6.009	0.014	0.050	2	944.828
$S_{(t)}$[c]	962.927	20.107	0.000	0.000	59	844.666

[a]Akaike's Information Criterion
[b]Constant survival over time
[c]Survival time dependent

Table 14. Sex-specific kill rates of radio-marked American woodcock in Michigan, Minnesota, and Wisconsin, 2001-2004.

	Female		Male	
Year	Kill rate (%)	95% CI	Kill rate (%)	95% CI
2001	0.080	0.012-0.449	0.051	0.001-0.318
2002	0.141	0.085-0.229	0.092	0.052-0.158
2003	0.261	0.184-0.361	0.174	0.114-0.261
2004	0.144	0.095-0.216	0.094	0.059-0.148

Table 15. Comparison of seasonal American woodcock period survival estimates using daily survival estimates from my study (2001-2004).

	My study					
Period Length	Hunted[a,b]	Non-hunted[a,c]	Survival Estimate	Hunted?	Season	Source
33-days	0.875	0.933	0.956	No	15 Jun-17 Jul	Derleth and Sepik (1990)
			0.859	No	18 Jul-19 Aug	Derleth and Sepik (1990)
31-days	0.882	0.937	0.877	No	20 Aug-19 Sept	Derleth and Sepik (1990)
			0.937	No	20 Sept-20 Oct	Derleth and Sepik (1990)
91-days	0.691	0.826	0.636	Yes	1 Sept-30 Nov	McAuley et al. (2005)
			0.661	No	1 Sept-30 Nov	McAuley et al. (2005)
77-days	0.732	0.850	0.720	Yes	1 Dec-15 Feb	Pace (2000)
45-days	0.833	0.910	0.848	Yes	24 Dec-7 Feb	Pace (2000)
			0.717	Yes	25 Dec-7 Feb	Krementz and Berdeen (1997)

[a]Survival estimates calculated by using the daily survival estimates from my study and raising them to the power of the period length the other studies
[b]Daily survival rate (pooled among states and years) in the hunted area was 0.995949
[c]Daily survival rate (pooled among states and years) in the non-hunted area was 0.997895

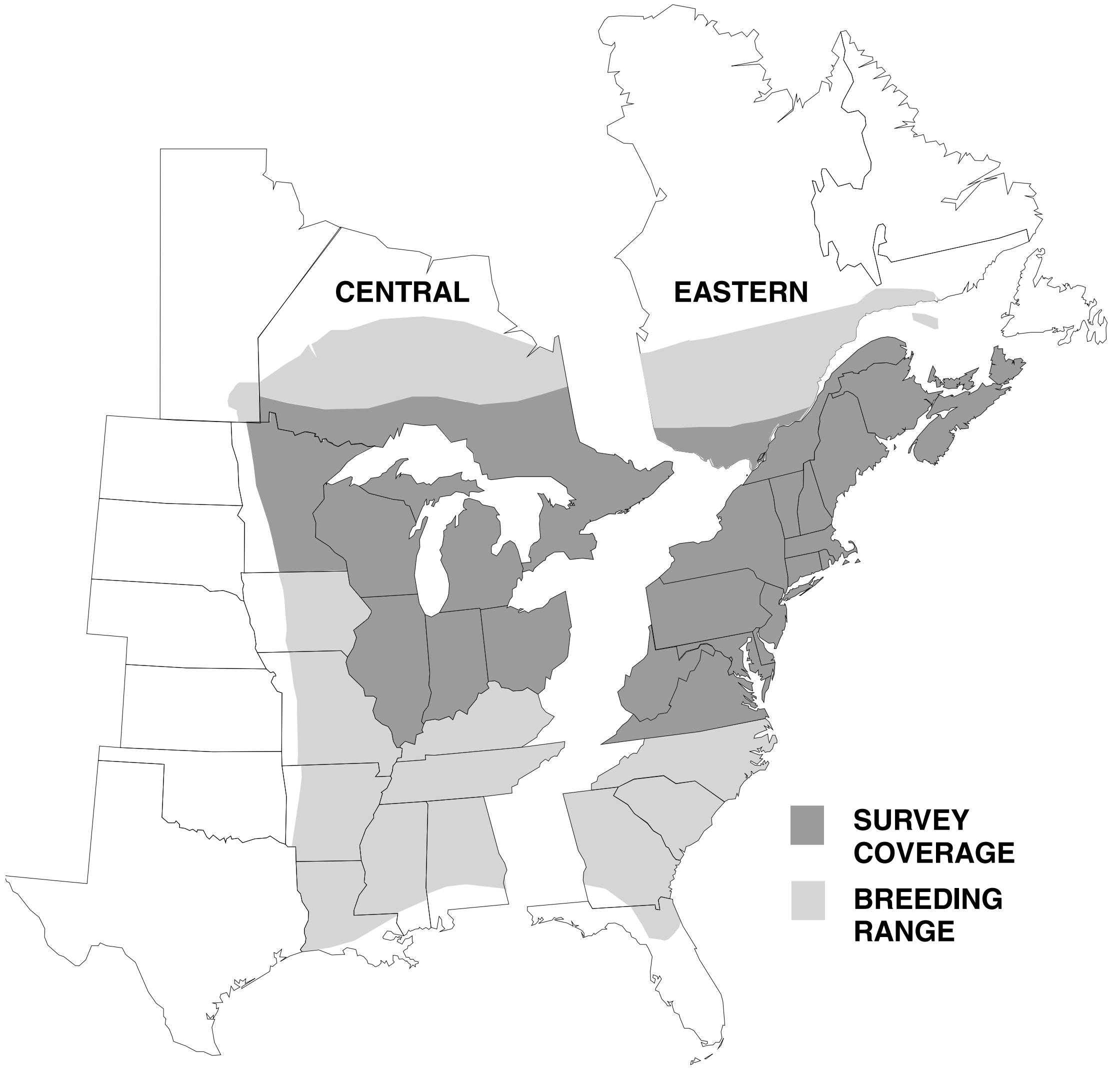
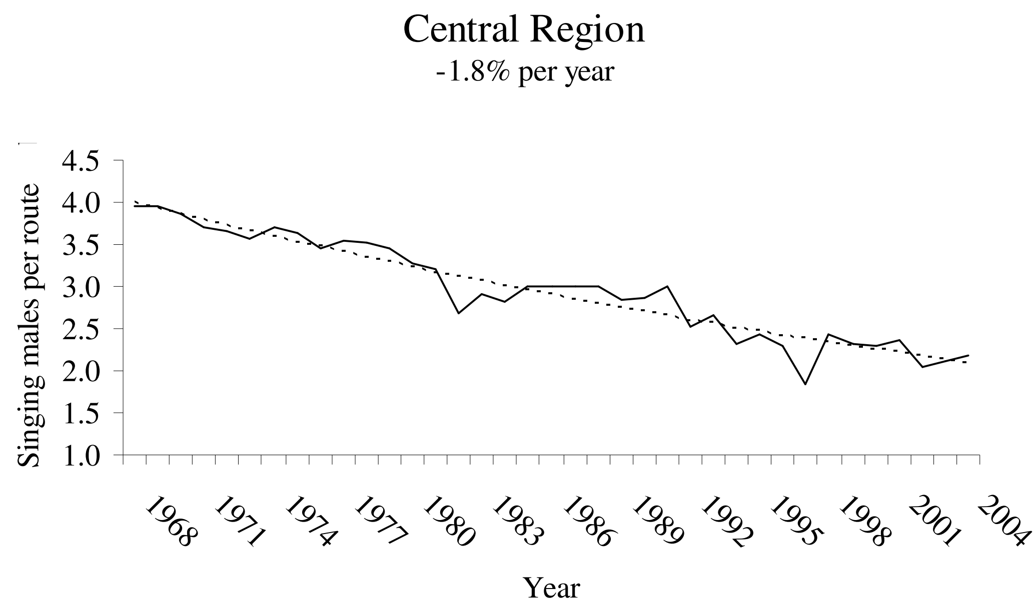


Figure 1. American woodcock breeding range, management regions, and the area covered by the Singing-ground Survey (Bruggink 1998).



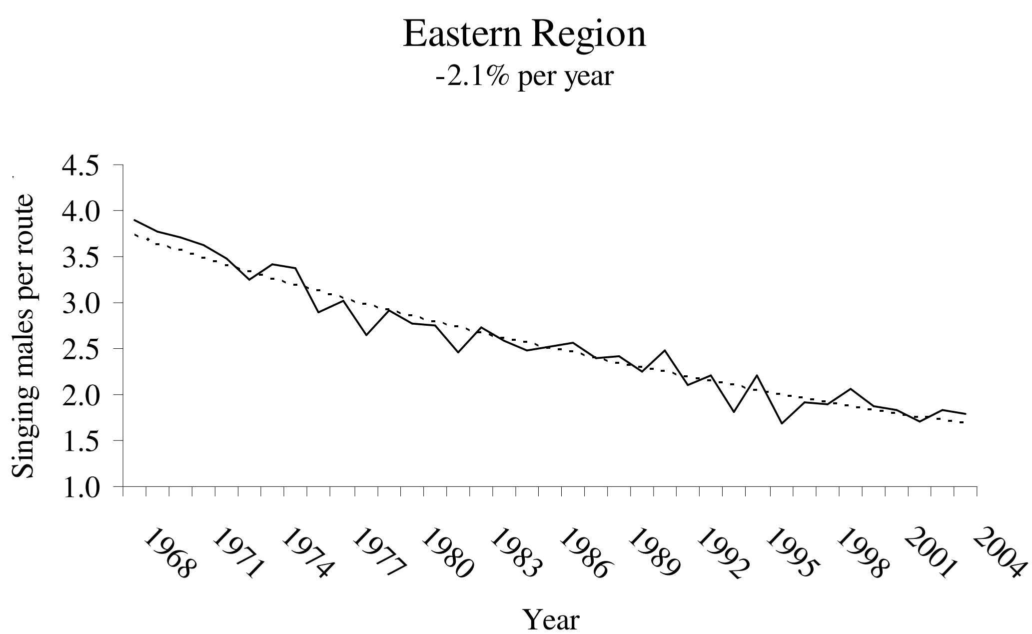


Figure 2. Long-term trends from the Singing-ground Survey for the Central and Eastern Management Regions, 1968-2004 (Kelley 2004).

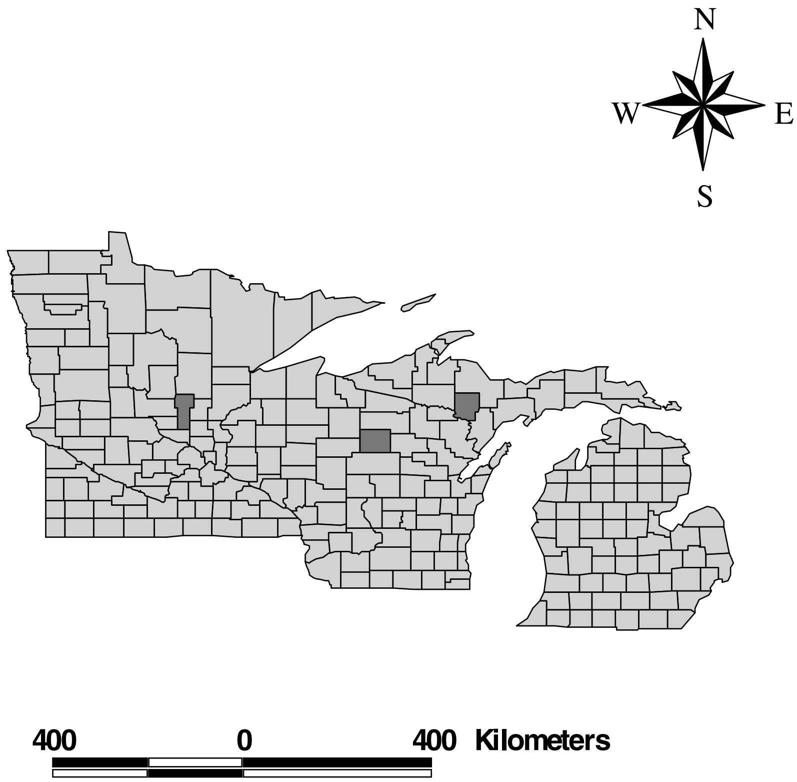


Figure 3. Locations of study areas in Michigan (Dickinson County), Minnesota (Mille Lacs County), and Wisconsin (Lincoln County), 2001-2004.

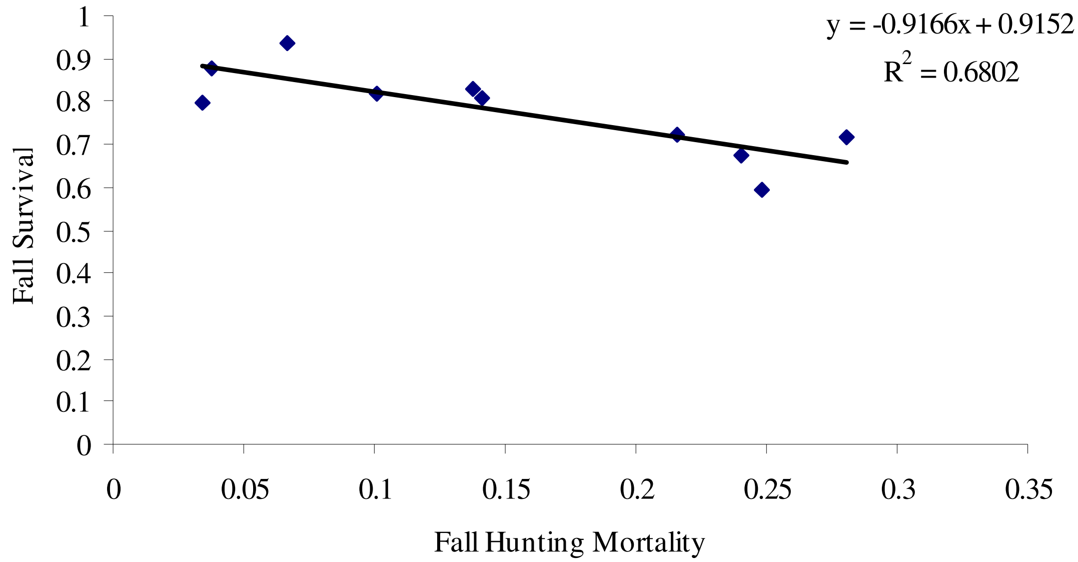


Figure 4. Relationship between survival of radio-marked American woodcock during fall (10 September – 8 November) and fall hunting mortality.

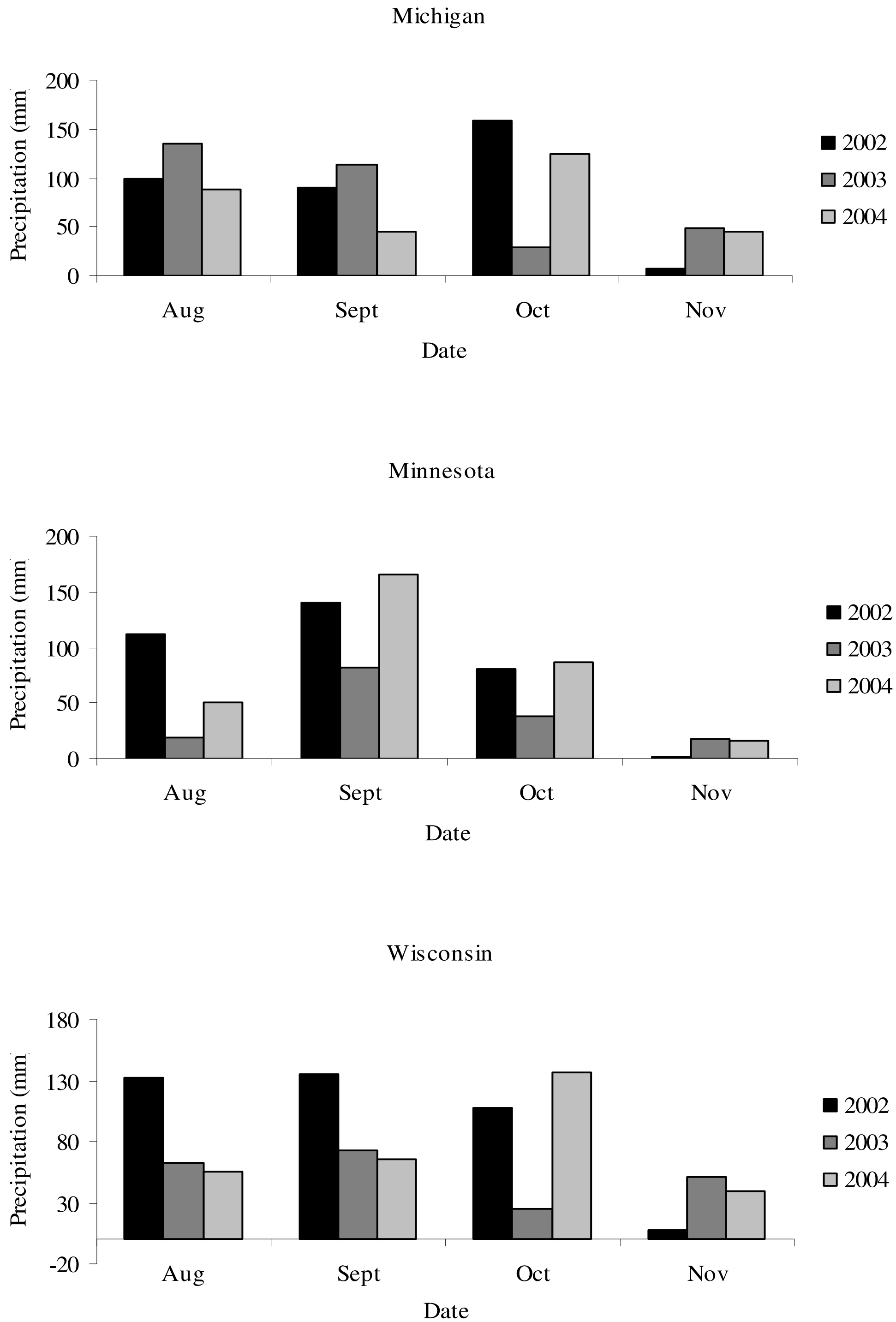


Figure 5. Average precipitation (mm) from the nearest National Oceanic and Atmospheric Administration data source to study areas in Michigan (Iron Mountain), Minnesota (Milaca) and Wisconsin (Merrill), 2001-2004 (Meunier 2005).

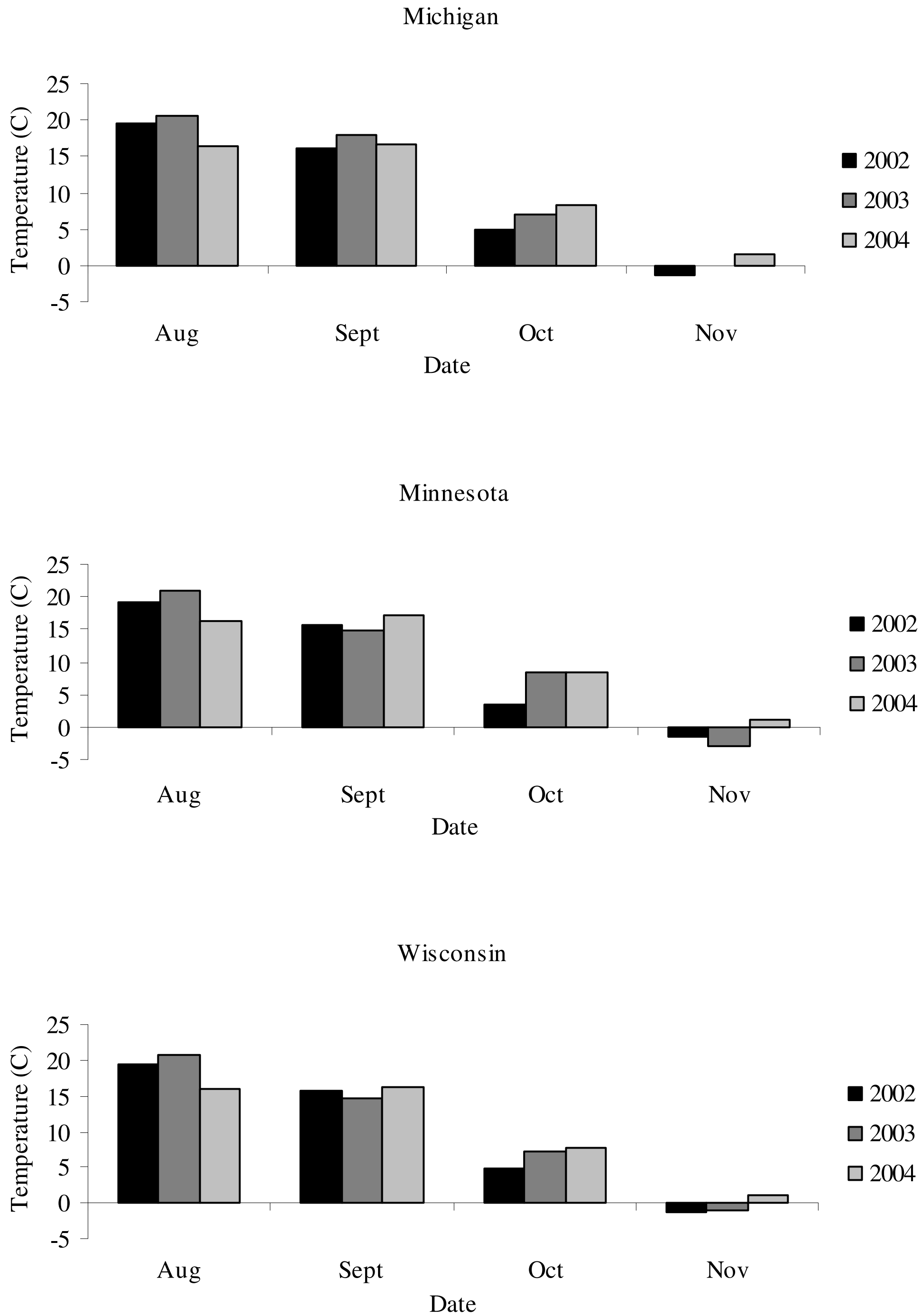


Figure 6. Average temperature (C°) from the nearest National Oceanic and Atmospheric Administration data source to study areas in Michigan (Iron Mountain), Minnesota (Milaca) and Wisconsin (Merrill), 2001-2004 (Meunier 2005).

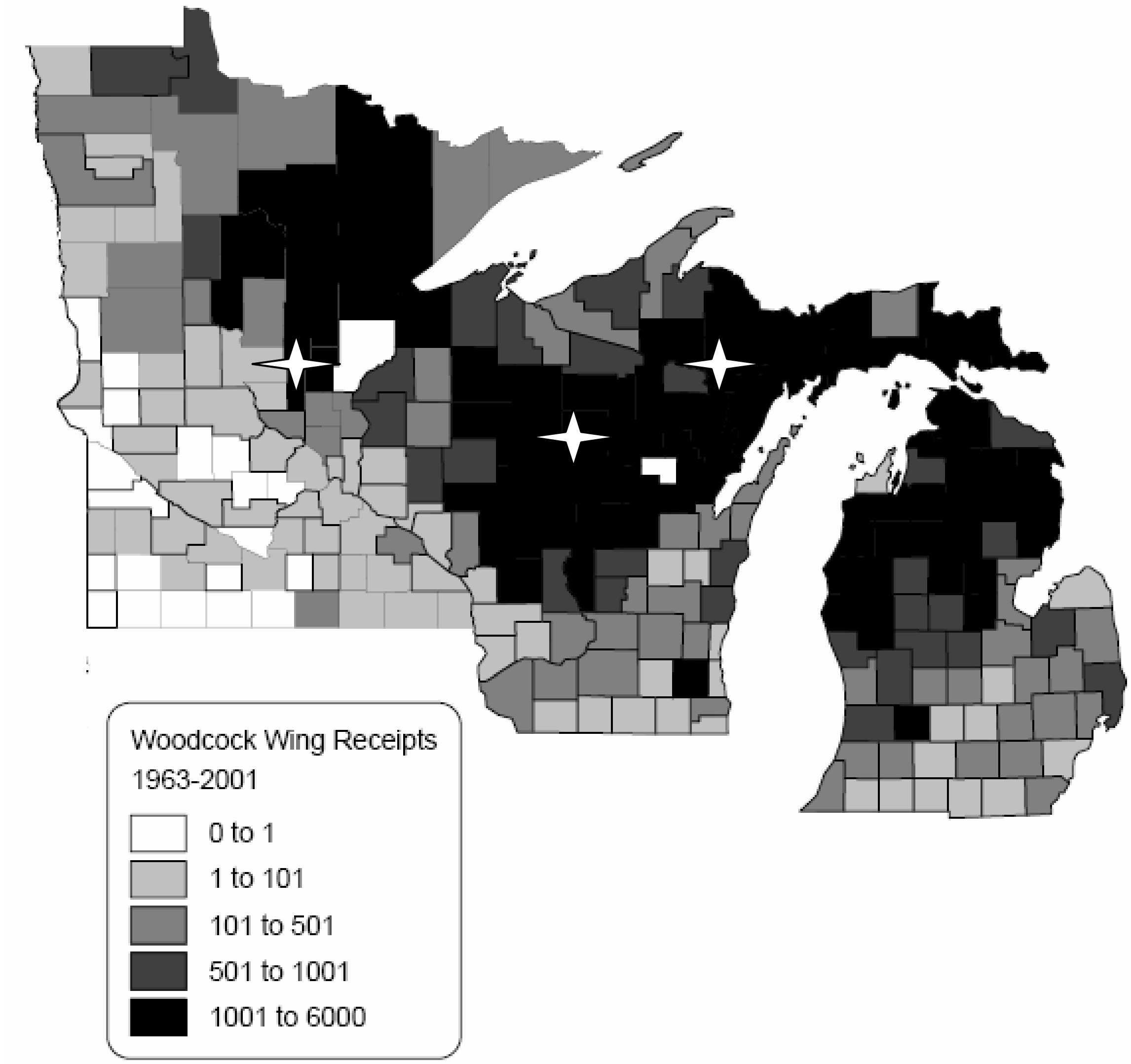


Figure 7. Woodcock Wing-collection Survey wing receipts by county from 1963 through 2001 (J. R. Kelley, Jr., Division of Migratory Bird Management, USFWS, unpublished data). Stars indicate the location of study areas.