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Population Ecology

Fall Survival of American Woodcock in the Western Great Lakes Region

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ABSTRACT We estimated fall (10 Sep–8 Nov) survival rates, cause-specific mortality rates, and determined the magnitude and sources of mortality of 1,035 radio-marked American woodcock (*Scolopax minor*) in Michigan, Minnesota, and Wisconsin during 2001–2004. In all 3 states, we radio-marked woodcock on paired study areas; 1 of which was open to hunting and expected to receive moderate to high hunter use and the other of which was either closed to hunting (Michigan and Minnesota) or was relatively inaccessible to hunters (Wisconsin). We used Program MARK to estimate fall survival rates, to evaluate a set of candidate models to examine the effects of hunting and several covariates (sex, age, year, state) on survival, and to examine the relationship between survival rates and kill rates due to hunting. Hunting accounted for 70% of the 86 woodcock deaths in the hunted areas, followed by predation (20%) and various other sources of mortality (10%). Woodcock deaths that occurred in the non-hunted and lightly hunted areas ($n = 50$) were caused by predators (46%), hunting (32%), and various other sources (22%). Based on small-sample corrected Akaike's Information Criterion values, variation in fall survival of woodcock was best explained by treatment (i.e., hunted vs. non-hunted), year, and period (pre-hunting season intervals vs. hunting season intervals). The average fall survival estimate from our best model for woodcock in the non-hunted areas (0.893, 95% CI = 0.864–0.923) was greater than the average for the hunted areas (0.820, 95% CI = 0.786–0.854 [this estimate includes data from the lightly hunted area in Wisconsin]), and the average treatment effect (i.e., greater survival rates in non-hunted areas) was 0.074 (95% CI = 0.018–0.129). The kill rate due to hunting was 0.120 (95% CI = 0.090–0.151) when data were pooled among states and years. We detected a negative relationship between hunting kill rates and survival in our hunted areas, which suggests that hunting mortality was at least partially additive during fall. Our results illustrate the influence of hunting relative to other sources of mortality in Michigan, Minnesota, and Wisconsin, and indicate that managers may be able to influence fall survival rates by manipulating hunting regulations or access on public land.

KEY WORDS American woodcock, hunting, mortality, *Scolopax minor*, survival, western Great Lakes Region.

The American woodcock (*Scolopax minor*) is managed on the basis of 2 management regions or populations, the Eastern and Central (Coon et al. 1977, Cooper and Rau 2012), and the status of these populations is monitored primarily with the annual Singing-ground Survey, a roadside survey that provides an index to changes in the abundance of singing, male woodcock. Long-term declines in the number of woodcock heard on the survey have resulted in concern about the status of woodcock in both regions (Straw et al. 1994, Federal Register 62:44233, Cooper and Rau 2012).

Large-scale habitat changes have often been cited as the primary cause of the apparent declines in woodcock populations (Dwyer et al. 1983, Gregg 1984, Sauer and Bortner 1991, Straw et al. 1994, Dessecker and Pursglove 2000). However, understanding of other factors related to woodcock ecology is insufficient to evaluate their relative impact. Among these, hunting mortality merits special scrutiny. Unlike other factors, hunting mortality can be manipulated by managers relatively quickly through changes in hunting regulations. Although hunting may have little influence on game populations when hunting mortality rates are

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low or when hunting mortality is compensated for by density-dependent decreases in non-hunting mortality (Anderson and Burnham 1976, Burnham et al. 1984, Conroy and Krementz 1990, Devers et al. 2007, Sedinger et al. 2010), the relationship between woodcock population dynamics and hunting mortality is unclear. Evidence that hunting mortality is sometimes additive to non-hunting mortality has been found for various upland game species including the ruffed grouse (*Bonasa umbellus*; Small et al. 1991), northern bobwhite (*Colinus virginianus*; Williams et al. 2004), Eurasian woodcock (*Scolopax rusticola*; Duriez et al. 2005) and willow ptarmigan (*Lagopus lagopus*; Sandercock et al. 2011), and some authors have concluded that hunting mortality may be additive in local American woodcock populations (Goudy et al. 1970, Liscinksy 1972, Pace 2000). However, Krementz et al. (1994) observed no hunting mortality in woodcock monitored during winter in a 6-year study along the lower Atlantic coastal plain, and fall survival rates of radio-marked woodcock were similar among hunted and non-hunted study areas in Maine, New Hampshire, Pennsylvania, and Vermont (McAuley et al. 2005). Concern about the status of woodcock populations, combined with the fact that the role of hunting mortality in woodcock population dynamics is poorly understood (U.S. Department of the Interior 1985, Straw et al. 1994, Federal Register 62:44233), has periodically prompted the United States Fish and Wildlife Service to reduce bag limits and season lengths, and to adjust opening framework dates for woodcock in the Eastern (1985 and 1997) and Central (1997) regions (Kelley 2000).

Data from the Harvest Information Program suggest that most woodcock hunting mortality occurs in breeding ground states (Cooper and Rau 2012). Woodcock survival rates have been documented with radiotelemetry during various periods of the year (e.g., Derleth and Sepik 1990; Krementz et al. 1994; Longcore et al. 1996, 2000) but only McAuley et al. (2005) examined survival in a hunted population during fall, and their study was conducted in the Eastern Region. Thus, information on survival during fall is lacking for the Central Region. Hunting regulations are more liberal, hunters spend more days afield, and more woodcock are harvested in the Central Region than in the Eastern Region (Cooper and Rau 2012). For example, during the 2011–2012 hunting season, about 3 times as many woodcock were harvested in Michigan, Minnesota, and Wisconsin combined (total land area = 494,975 km^2) than in Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, Virginia, and West Virginia combined (total land area = 615,529 km^2). Thus, woodcock in the Central Region may experience greater hunting pressure than those in the Eastern Region, and other factors that influence population dynamics may vary between the 2 regions. Therefore, we initiated a study in the Central Region in 2001 (Minnesota) and 2002 (Michigan and Wisconsin) similar to that of McAuley et al. (2005) in the Eastern Region. We addressed the hypothesis that hunting mortality reduces fall survival of woodcock in the Central Region. We predicted that fall survival rates would be greater in our non-hunted study areas than in our hunted study areas, and a negative relationship would exist between hunting mortality rates and fall survival rates.

Our objectives were to 1) determine causes and magnitude of mortality in local woodcock populations during fall; 2) compare fall survival rates of woodcock in hunted and non-hunted or lightly hunted areas in Michigan, Minnesota, and Wisconsin; 3) determine whether fall survival and kill rates varied by age, sex, year, and state; and 4) examine the relationship between fall survival rates and hunting mortality rates in hunted areas.

STUDY AREAS

We chose study areas in Michigan, Minnesota, and Wisconsin with a history of moderate to high hunting pressure and extensive woodcock habitat where conditions appeared to be suitable for capturing adequate samples of woodcock (Fig. 1). All states had paired areas, 1 open to public hunting and another that was either closed to hunting (Michigan and Minnesota) or was relatively inaccessible to hunters (Wisconsin). Study areas among the 3 states were comprised of comparable forest types and at similar latitudes.

Study areas in Michigan were in the Copper Country State Forest in Dickinson County (Fig. 1). The non-hunted area (approx. 25,728 ha) was closed to woodcock hunting by the Michigan Natural Resources Commission during our study. We selected this area because its boundaries were obvious (roads) and easy to describe to hunters, criteria that Michigan Department of Natural Resources personnel strongly recommended. We worked primarily in the eastern half of this area. The hunted area was directly north of the non-hunted area; it did not have distinct boundaries but included 2 primary capture sites located 0.8 km and 2.7 km north of the non-hunted area.

The hunted area in Minnesota was the 15,673-ha Mille Lacs Wildlife Management Area. The non-hunted area was the 1,163-ha Four Brooks Wildlife Management Area, which the Minnesota Department of Natural Resources acquired in 2000 and opened to the public (except for woodcock hunting) in 2001. During the final year of our study (2004), this area was opened to woodcock hunting. Prior to 2000, this area was held privately and we presume woodcock hunting pressure was low or non-existent. Both areas were located in Mille Lacs County.

Study areas in Wisconsin were located in Lincoln County. The hunted area (approx. 29,000 ha) was in Lincoln County Forest. The lightly hunted area was in the 1,685-ha Tomahawk Timberland Forest. Although the lightly hunted area was not closed to public hunting, it was located 3 km from the nearest road and was accessible only on foot. Because of this limited access, we expected hunting pressure to be low and that this site would effectively serve as a non-hunted area.

METHODS

Capture and Radiotelemetry

Our goal during 2001–2003 in Minnesota and 2002–2004 in Michigan and Wisconsin was to put transmitters on 60

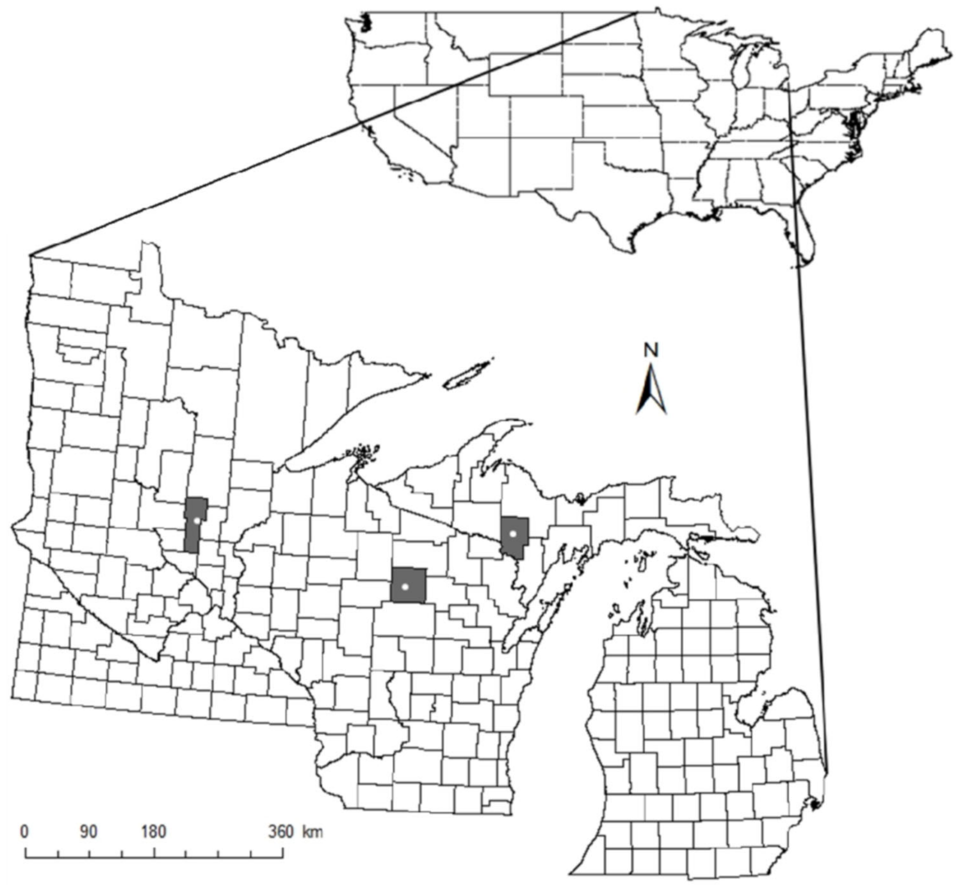

Figure 1. Locations of American woodcock study areas (white dots) in Mille Lacs County, Minnesota; Lincoln County, Wisconsin; and Dickinson County, Michigan, 2001–2004.

woodcock in each study area (120 in each state) during each year of the study. In Minnesota in 2004, our goal was to put transmitters on 90 woodcock in the Four Brooks Wildlife Management Area, which was opened to hunting in 2004, and 30 woodcock in Mille Lacs Wildlife Management Area. From mid-August to the end of September in 2001 (Minnesota) and 2002–2004 (Michigan, Minnesota, and Wisconsin) on each pair of study areas, we captured woodcock using mist nets (Sheldon 1960, McAuley et al. 1993) and night lighting (Rieffenberger and Kletzly 1967). We weighed each captured woodcock and recorded its bill length, wing chord, and tarsus length. We determined sex and age using plumage characteristics (Martin 1964). We marked each woodcock with a number 3 United States Geological Survey leg band, and attached an approximately 4.5-g transmitter with a thermister mortality switch to all woodcock that weighed $\geq$140 g (Advanced Telemetry Systems, Inc., Isanti, MN; model A2480; use of trade names does not imply endorsement by the U.S. Federal Government, Northern Michigan University, the University of Minnesota, or the University of Wisconsin-Madison). We attached transmitters using livestock tag cement and a wire harness following the methods of McAuley et al. (1993). Our study was approved by the Institutional Animal Care and Use Committees of Northern Michigan University (protocol Bruggink 1), the University of Minnesota (protocol 0309A51828), and the University of Wisconsin-Madison (protocol A00861).

We searched for signals of all radio-marked woodcock $\geq$5 days/week to assess their status (i.e., alive or dead). We conducted aerial searches for woodcock we were unable to locate from the ground approximately weekly, as weather and aircraft schedules allowed, and subsequently confirmed locations on the ground to assess their status.

Because of possible short-term behavioral or survival effects that may have resulted from capture and adjusting to the transmitter, we left censored all birds that died or disappeared within 3 days after they were captured (Krementz et al. 1994, Krementz and Berdeen 1997). We right censored woodcock that appeared to have shed their transmitters (i.e., no signs of mortality) or were found dead with their bills caught in the transmitter harness. We considered woodcock that we were unable to locate from the ground or air to have moved off the study area and right censored them after the last day they were known to be in the area. We right censored birds that were not located on the ground for >2 weeks, but were subsequently found dead, on the day after they were last located on the ground alive. We right censored woodcock that we were temporarily unable to locate during the period that they were missing and entered them back into the sample on the date they reappeared.

We defined a 60-day fall period over which we estimated kill rates and survival rates based on when each study area had at least 1 bird in the sample in all years (i.e., on 10 Sep, all areas had at least 1 bird alive after the 3-day adjustment period) with the exception of the non-hunted area in Michigan in 2003 where, because of dry conditions and logistical constraints, the first bird included in our sample was on 17 September. Therefore, we estimated the kill rate and survival rate for a 53-day period (17 Sep–8 Nov) for the non-hunted area in Michigan in 2003.

When a transmitter's signal indicated mortality, we located and recovered the transmitter from the ground. When we found the bird or transmitter, we attempted to determine the cause of death based upon the condition of the carcass and other relevant signs, although we recognize that the activity of scavengers and other factors make assigning a source of mortality with certainty difficult (Bumann and Stauffer 2002). We classified mortality events as mammalian predation when woodcock carcasses were cached, typically with the heads missing or detached and sometimes with tooth marks on the transmitters. We classified mortality events as avian predation when the feathers were plucked and the breast meat was consumed, sometimes with bill marks on the transmitters, antennas, or harnesses. T. Cooley (Michigan Department of Natural Resources) conducted all necropsies on all woodcock for which we were not able to determine the cause of death. Necropsies included a gross examination (external and internal) of all organ systems, and an X-ray to check for the presence of shotgun shot and bone fractures.

Analyses

We used nest survival models in Program MARK (White and Burnham 1999, Dinsmore et al. 2002) to estimate survival rates, to investigate the influence of covariates (age, sex, year, state) on survival rates, and to examine the relationship between survival rates and kill rates in hunted areas. We used an information-theoretic approach and selected the best models using Akaike's Information Criterion adjusted for small sample size (AIC_c), AIC_c differences (ΔAIC_c), and AIC_c weights (w_i) to evaluate support among competing models relative to the best-supported model (Burnham and Anderson 2002). We considered variables in the best-supported models to be informative if the 95% confidence intervals for the β values excluded 0.

We estimated fall survival rates of woodcock in hunted and non- or lightly hunted areas by state and year. Because a relatively high number of woodcock were shot in the lightly hunted area in Wisconsin, we treated it as a hunted area in subsequent survival analyses. To investigate the influence of experimental treatment (hunted or non-hunted) and covariates (age, sex, year, state) on fall survival rates of woodcock, we began with 2 general models with which we constrained survival rates to be constant among treatment, years, ages, and sexes. With 1 model, we held the daily survival rate constant throughout the fall period (i.e., the null model). We used the other model to address the hypothesis that fall survival would have within-year temporal variation because the first 10–15 days (depending on the year) of our 60-day fall period preceded the woodcock hunting season (Cooper and Rau 2012). We constrained daily survival rates to be constant within the first 2 weekly intervals (i.e., approx. the pre-hunting season period) and within the remaining 7 weekly intervals (the final interval was only 3 days long) during the hunting season but allowed survival rates to vary between the 2 periods. We fit 13 additional a priori models to evaluate the influence of treatment, year, sex, age, and state.

Because the effect of treatment on survival rates was a major focus of our study, we produced overall estimates of survival rates in hunted and non-hunted areas by averaging survival rates (S) among years from our best model by treatment. Furthermore, we estimated the effect size ($\hat{\theta}$) of treatment by year as the difference between $S_{\text{non-hunted}}$ and S_{hunted}, with associated variance:

$$\hat{\text{var}}(\hat{\theta}) = \hat{\text{var}}(S_{\text{non-hunted}}) + \hat{\text{var}}(S_{\text{hunted}}) - 2\text{cov}(S_{\text{non-hunted}}, S_{\text{hunted}})$$

and 95% confidence intervals calculated as (Mood et al. 1974, Doherty et al. 2002):

$$\hat{\theta} \pm 1.96\sqrt{\hat{\text{var}}(\hat{\theta})}$$

With equal survival rates in non-hunted and hunted areas, the expected difference between $S_{\text{non-hunted}}$ and $S_{\text{hunted}} = 0$, and the 95% confidence interval around the estimate should include 0. In contrast, if survival rates are greater in the non-hunted areas, the difference will be >0 and the entire 95% confidence interval should be above 0. We calculated confidence intervals associated with average survival rates and the average effect size using the delta method (Powell 2007).

We estimated cause-specific mortality estimates and tested for the influence of covariates on cause-specific mortality using the survival package (Therneau 2012) in R 2.14.1 (R Development Core Team 2011). We attributed each mortality event in areas where hunting occurred (including the lightly hunted area in Wisconsin) to 1 of 2 causes, hunting or non-hunting, and used the non-parametric cumulative incidence function estimator (Heisey and Patterson 2006) to estimate fall kill rates (the proportion of radio-marked woodcock shot by hunters), and non-hunting mortality rates. We estimated harvest rates (the proportion of radio-marked woodcock shot and retrieved by hunters) similarly by recoding un-retrieved kills as non-hunting mortality events. We calculated the un-retrieved kill rate as 1 − (harvest rate/kill rate). We tested for influence of the covariates sex, age, state, and year on the 2 cause-specific mortality rates using the Cox proportional hazard model stratified by cause of death (Heisey and Patterson 2006).

In theory, hunting mortality can be completely additive to other sources of mortality, completely compensated for by reductions in non-hunting mortality up to some threshold point at which it becomes additive, or more likely partially compensated for by reductions in non-hunting mortality (Anderson and Burnham 1976, Burnham et al. 1984, Conroy and Krementz 1990, Sinclair and Pech 1996). When additive, hunting mortality results in an inverse relationship between survival rates and kill rates. We examined evidence for such a relationship during fall in our hunted areas by building an additive mortality model in which we constrained study area-year-specific fall survival estimates to be a linear function of corresponding point estimates of hunting kill rates. We evaluated this model against a model in which we constrained fall survival rate estimates to be constant (i.e., no relationship between kill rates and fall survival rates), and a model in which we allowed fall survival rates to vary (i.e., among study area-year differences not related to kill rates). To examine whether compensation occurred during fall, we compared non-hunting mortality rates between hunted and non-hunted areas. Similar estimates of non-hunting mortality in hunted and non-hunted areas would suggest that hunting mortality was mostly additive during fall, whereas lesser estimates in the hunted areas would suggest that hunting mortality was being compensated for by reductions in non-hunting mortality.

RESULTS

During 2001–2004, we captured 1,310 woodcock from mid-August through September in Michigan, Minnesota, and Wisconsin and attached transmitters to 1,171 woodcock. Numbers of woodcock radio-marked in hunted and non-hunted areas were similar among all study areas except for the non-hunted area in Michigan in 2003. We used data from 1,035 radio-marked woodcock to estimate fall season survival rates; we censored 140 woodcock from survival analyses. Most of these were left-censored because they died or disappeared before the fall season (10 Sep–8 Nov) began. We right-censored 4 birds that were not located on the ground or during aerial searches for an extended period but were later found dead. Woodcock in our radio-marked sample were comprised of juvenile (hatch year) males (32%), adult (after hatch year) females (26%), juvenile females (24%), and adult males (19%).

One hundred thirty-six woodcock died from hunting, predation, or other non-research related causes. Hunting was the largest single cause of mortality in the hunted areas (Table 1). Of 86 radio-marked woodcock that died in hunted areas, 60 (70%) were shot, 17 (20%) were killed by predators, and 9 (10%) died from other causes. Of 50 radio-marked woodcock that died in non-hunted or lightly hunted areas, 23 (46%) were killed by predators, 16 (32%) were shot, and 11 (22%) died from other causes. Necropsies indicated that 12 woodcock were shot by hunters and not retrieved. Two of these 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. Forty woodcock were killed by predators in the hunted and non- or lightly hunted areas combined. We attributed 20 (50%) of these deaths to mammals and 20 (50%) to raptors.

Point estimates of survival rates for woodcock in individual states and years were greater in the non-hunted or lightly hunted areas than in hunted areas, although the confidence intervals overlapped considerably (Table 2). The best-supported model ($w_i = 0.997$; Table 3) included period, treatment (hunted [including lightly hunted] vs. non-hunted), and year, and we found essentially no support ($\Delta AIC_c > 12$) for the other candidate models. As expected, weekly survival estimates were greater during the pre-hunting season period (0.990, 95% CI = 0.987–0.994) than during the hunting season (0.972, 95% CI = 0.966–0.977) in the hunted areas. Contrary to expectations, we also observed this pattern in the non-hunted areas (0.995, 95% CI = 0.992–0.997 in pre-hunting season vs. 0.984, 95% CI = 0.979–0.989 in hunting season) albeit with greater survival rates than in the hunted areas. The average fall survival estimates from our best model were 0.893 (95% CI = 0.864–0.923) for woodcock in the non-hunted areas and 0.820 (95% CI = 0.786–0.854) for woodcock in the hunted areas. The average treatment effect was 0.074 (95% CI = 0.018–0.129; Fig. 2).

We detected no influence of sex, age, state, or year on cause-specific mortality rates ($P \geq 0.13$) in our hunted areas. The overall kill rate with data pooled among sexes, ages, states, and years was 0.120 (95% CI = 0.090–0.151), whereas the harvest rate was 0.106 (95% CI = 0.077–0.136). Thus, our estimate of the un-retrieved kill rate was 0.117.

We generated 12 sets of study area and year-specific fall survival and kill rate estimates from study areas in which hunting mortality occurred (data were insufficient for

Table 1. Fate of radio-marked American woodcock in hunted and non-hunted or lightly hunted study areas in Michigan, Minnesota, and Wisconsin, 2001–2004. We assumed woodcock with unknown fates 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 ($n = 194$)	Non-hunted[b] ($n = 144$)	Hunted ($n = 166$)	Non-hunted[b,c] ($n = 216$)
Shot	1	0	15	0	25	7	19	9
Mammal predation	0	1	2	5	5	2	1	4
Avian predation	0	0	4	3	3	5	2	3
Unknown mortality	0	0	3	3	1	3	2	3
Trauma	0	0	1	0	1	0	0	2
Pulmonary congestion	0	0	0	0	0	0	1	0
Entangled in harness	0	1	4	3	1	1	1	0
Left censored	2	5	16	24	27	19	15	28
Total	3	7	45	38	63	37	41	49

[a] Only Minnesota study area.
[b] Lightly hunted in Wisconsin.
[c] Non-hunted area in Minnesota was opened to hunting in 2004.

Table 2. Fall season (10 Sep–8 Nov) survival rate 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 rate**	**95% CI**	n	**Survival rate**	**95% CI**
Michigan	2002	61	0.833	0.656–0.929	51	0.852	0.667–0.943
	2003	54	0.812	0.655–0.907	21	0.888	0.499–0.985
	2004	61	0.723	0.580–0.831	48	0.876	0.712–0.953
Minnesota	2001	29	0.935	0.653–0.991	39	0.960	0.766–0.994
	2002	62	0.727	0.579–0.838	52	0.912	0.788–0.967
	2003	60	0.678	0.522–0.802	59	0.829	0.682–0.916
	2004	30	0.849	0.622–0.950	83[c]	0.889	0.786–0.946
Wisconsin	2002	64	0.802	0.651–0.897	46	0.876	0.677–0.959
	2003	55	0.596	0.436–0.739	49	0.757	0.596–0.868
	2004	60	0.821	0.681–0.908	59	0.846	0.698–0.929

[a] Lightly hunted in Wisconsin.
[b] The number of birds in sample during the 60-day fall season.
[c] Opened to woodcock hunting in 2004.

estimating a kill rate using the non-parametric cumulative incidence function estimator for the hunted area in Minnesota in 2001). Variation in overall fall survival rate in these areas was best described by the additive mortality model ($w_i = 0.999$), which constrained study area and year-specific fall survival estimates to be a linear function of kill rate estimates (Fig. 3); we found virtually no support ($\Delta AIC_c > 12$) for the competing models (constant and variation in study area-year combinations). Estimates of non-hunting mortality in the hunted areas were less than in the non-hunted areas although confidence intervals overlapped considerably (Fig. 4).

DISCUSSION

The factors that influenced woodcock survival in our study areas in the western Great Lakes Region during fall were treatment (i.e., hunted [including lightly hunted] vs. non-hunted), year, and period during fall. Survival rate estimates varied among years and averaged 7% greater in non-hunted areas than in hunted areas. Hunting was the largest source of mortality (70% of deaths) in the hunted areas. In contrast, McAuley et al. (2005) found no significant difference in fall survival rates between their hunted and non-hunted study areas in the Eastern Region, where hunting regulations were more restrictive; predation was the primary source of mortality (63%) in their hunted areas and only 36% of the deaths were due to hunting. Average woodcock survival rates in our study (0.893 in non-hunted areas and 0.820 in hunted areas) were greater than those in the areas studied by McAuley et al. (2005) in the Eastern Region, which were 0.784 in non-hunted areas and 0.707 in hunted areas when their data set was truncated to closely match our shorter fall period (D. G. McAuley, U.S. Geological Survey, personal

Table 3. A priori models used to examine the influence of treatment (hunted [including lightly hunted] vs. non-hunted), year, state, age, sex, and period during fall on daily survival rate estimates of radio-marked American woodcock in Michigan, Minnesota, and Wisconsin, 2001–2004 during the 60-day fall season (10 Sep–8 Nov).

Model	AIC_c[a]	ΔAIC_c	w_i	Model likelihood	Parameters	Deviance
Period + treatment + year[b]	1,629.8	0.0	0.997	1.0	6	1,617.8
Period	1,642.2	12.4	0.002	0.0	2	1,638.2
Treatment + year	1,644.2	14.4	0.001	0.0	5	1,634.2
Treatment + year + state	1,648.1	18.3	0.000	0.0	7	1,634.1
Year	1,649.2	19.4	0.000	0.0	4	1,641.2
Treatment + year + (treatment × year)[c]	1,649.9	20.1	0.000	0.0	8	1,633.9
Treatment	1,650.7	20.9	0.000	0.0	2	1,646.7
Week[d]	1,651.8	22.1	0.000	0.0	9	1,633.8
Treatment + sex + age	1,653.5	23.8	0.000	0.0	4	1,645.5
Constant	1,657.3	27.5	0.000	0.0	1	1,655.3
State	1,658.6	28.8	0.000	0.0	3	1,652.5
Sex	1,659.0	29.2	0.000	0.0	2	1,655.0
Age	1,659.0	29.2	0.000	0.0	2	1,655.0
Time-dependent	1,669.6	39.9	0.000	0.0	59	1,551.4

[a] Akaike's Information Criterion corrected for small sample size.
[b] For models including period, survival was constrained to be constant during the first 2 weekly intervals (the pre-hunting season period), and the remaining 7 weekly intervals but allowed to vary between the 2 periods.
[c] Effect of treatment, year, and treatment by year interaction.
[d] Survival was allowed to vary among the 9 weekly intervals.

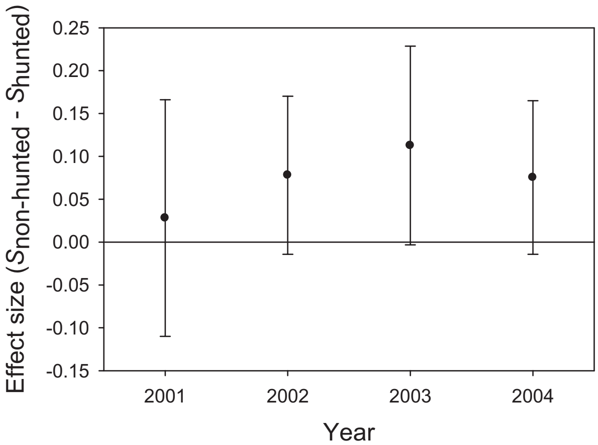

Figure 2. Effect size estimates for treatment ($S_{\text{non-hunted}} - S_{\text{hunted}}$) from the best supported model (Period + treatment + year) of fall survival of American woodcock in Michigan, Minnesota, and Wisconsin, 2001–2004. If $S_{\text{non-hunted}} - S_{\text{hunted}} = 0$, survival between non-hunted and hunted areas were not different. If $S_{\text{non-hunted}} - S_{\text{hunted}} > 0$, survival rates were greater in non-hunted areas than in hunted areas. We included data from the lightly hunted area in Wisconsin and the formerly non-hunted area in Minnesota when it was opened to woodcock hunting in 2004 in the hunted sample.

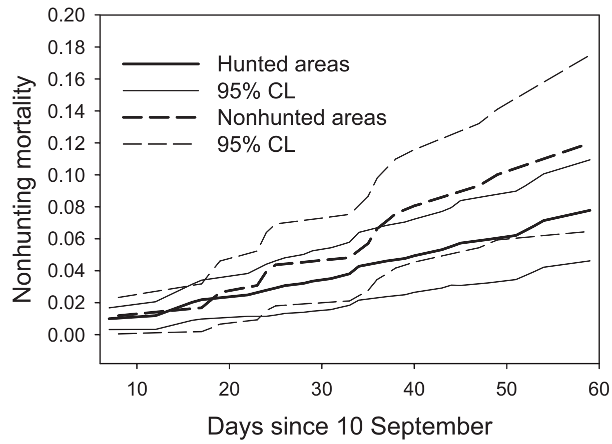

Figure 4. Cumulative non-hunting mortality rates of American woodcock, estimated using the non-parametric cumulative incidence function estimator, during fall in non-hunted and hunted areas in Michigan, Minnesota, and Wisconsin, 2001–2004.

communication). These results suggest that non-hunting mortality exerted less influence on woodcock in our study areas. Furthermore, managers may have a greater potential to influence fall survival of woodcock in the Central Region by altering hunting regulations, at least in areas where hunting pressure is comparable to that in our study areas.

We found no sex or age-related differences in woodcock survival rates during fall. 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 rate estimates were related to age. Adults tended to have greater summer survival rates (0.890–0.920) than juveniles (0.640–0.680). These authors attributed the differences in survival to different predation rates, possibly caused by age-related differences in mobility. In contrast, annual survival rate estimates based on banding and recovery data have provided evidence of regional, age-specific, and sex-specific differences in survival in woodcock (Dwyer and Nichols 1982, Krementz and Bruggink 2000, Krementz et al. 2003). Annual survival of female woodcock was greater than that of males in the Eastern Region, and annual survival of adults was greater than that of juveniles in the Eastern and Central Regions. Annual survival rate estimates of adult and juvenile woodcock were 0.490 and 0.265, respectively, in Michigan during 1978–1998 (Krementz et al. 2003). The reasons for the discrepancy between the results of most telemetry-based studies and analyses of banding data regarding sex and age-related differences in survival of woodcock are unknown.

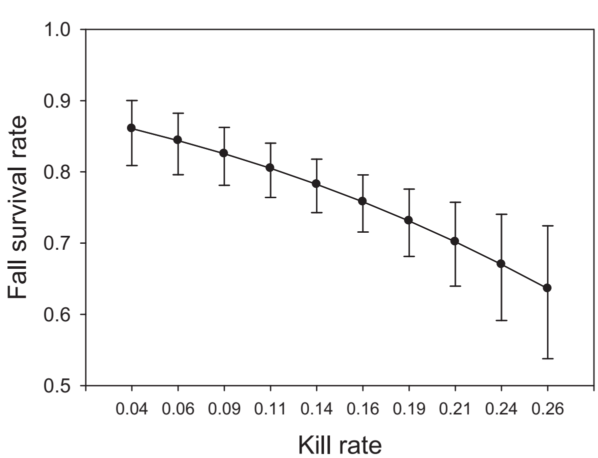

Figure 3. Model-based estimates of fall survival rates with 95% confidence intervals of American woodcock in hunted areas in Michigan, Minnesota, and Wisconsin, in relation to point estimates of hunting kill rate during 2002–2004. Average kill rate was 0.127 (range 0.034–0.264). We derived estimates from the additive mortality model with which we constrained 12 study area and year-specific survival estimates to be a linear function of kill rate estimates.

The causes of the inter-year variation in survival that we observed are unclear; although, environmental conditions varied considerably among the years we conducted our study. In general, the amount of precipitation varied more among years and states than temperature from 2002 to 2004, and these 2 variables may influence woodcock activity. Doherty et al. (2010) found that woodcock made larger local movements to forage in new areas when environmental conditions were poorer (i.e., low earthworm abundance) and temperatures were warmer. They also found that larger local movements were related to rainfall and soil porosity. During drier periods, woodcock may have been concentrated in lowland areas or not have flushed as easily when disturbed. These behaviors may influence their vulnerability to predators or hunters. Variation in hunting pressure also may have contributed to the variation in survival rates we observed among years.

Few estimates of woodcock kill rates and harvest rates are available. The kill rate during our study (0.120, 95% CI = 0.090–0.151) was within the range of pre-migration harvest estimates of 0.09–0.17 from previous work (1993–2000) in the area we used for our non-hunted area in Michigan (Nauertz 1997; W. L. Robinson, Northern Michigan University, unpublished data), and greater than the pre-migration harvest rate (0.082) in a Marquette County, Michigan study area (Froiland 1998). Hunting mortality of radio-marked wintering woodcock varied from 0.016 to 0.122 in an area with ample public hunting opportunity in Louisiana (Pace 2000). Our estimate of the un-retrieved kill rate (0.117) of radio-marked woodcock was similar to the rate of 0.105 reported by McAuley et al. (2005), and less than the estimate of 0.17 reported by Pursglove (1975), who estimated crippling loss based on records of 57 hunters in northeast Georgia. As noted by McAuley et al. (2005), if any un-retrieved killed birds were scavenged by predators before we found them and were thus misclassified as being killed by predators, our estimates of un-retrieved kill rates would be negatively biased.

The negative relationship we observed between fall survival rates and kill rate estimates, and the lesser overall survival rates in our hunted areas suggested that hunting mortality was at least partially additive to other sources of mortality during the fall. We also found apparent evidence of partial compensation during the fall in that point estimates of non-hunting mortality were less in hunted areas than in non-hunted areas. However, we recognize that additional compensation for hunting mortality might occur at some other point in the annual cycle, or that hunting mortality may be compensated for by density-dependent increases in recruitment (Conroy and Krementz 1990). Krementz et al. (2003) and Mayhew and Luukkonen (2010) found no changes in annual survival rates of woodcock in Michigan following the implementation of more restrictive hunting regulations in 1997, and one explanation for this is that hunting mortality was largely compensated for by decreases in non-hunting mortality and possibly increases in recruitment. However, plausible alternative hypotheses are that the changes in regulations implemented in 1997 did not reduce harvest sufficiently to produce a measurable increase in survival, or that harvest rates under both sets of regulations are low enough to have little or no impact on future population size.

Interestingly, despite the lack of an apparent increase in annual survival rates, and mostly below-average recruitment since the late 1980s (Cooper and Rau 2012), rates of decline in counts of singing male woodcock on the Singing-ground Survey for the most recent 10-year periods in both management regions generally decreased after 1998 (e.g., Bruggink 1999, Kelley 2000), and no significant 10-year trends were evident from 2004 to 2012 in the Eastern Region or, with the exceptions of 2008 and 2010, in the Central Region (Cooper and Rau 2012). Whether any relationship exists between the stabilization of the number of woodcock heard on the Singing-ground Survey and the regulations changes implemented in 1997 is unknown.

McAuley et al. (2005) cited the lack of a difference between fall survival rates in their hunted and non-hunted areas as an indication that hunting was not the cause of the population decline in the Eastern Region. However, neither their nor our results are particularly well suited for addressing the causes of apparent woodcock population declines. The declines occurred over a period of about 3 decades (1970s through the 1990s) in the Eastern Region and about 2 decades in the Central Region (1980s and 1990s; Sauer and Bortner 1991, Cooper and Rau 2012). The study presented by McAuley et al. (2005) and our research were conducted subsequent to these declines and during a period with more restrictive hunting regulations. However, the fact that the woodcock population in the Eastern Region as measured by the Singing-ground Survey appears to be stabilizing suggests that under current regulations, hunting mortality is not causing woodcock populations to decline. The situation in the Central Region is less clear because of significant negative 10-year trends in 2008 and 2010.

Because our study took place in areas where woodcock hunting activity was expected to be moderate to high, our results may represent something close to a worst case scenario for woodcock in terms of hunting-related mortality. Yet even in this setting, woodcock in relatively remote locations probably faced little hunting pressure. Andersen et al. (2010) found that woodcock hunting pressure was largely restricted to highly accessible areas (along trails close to access points) in Four Brooks Wildlife Management Area. Such accessible areas may function as sink habitats where woodcock numbers are maintained by immigration from nearby inaccessible (source) areas (see Goudy et al. 1970). If so, the ratio of source to sink habitats, which is undoubtedly dynamic, may determine the degree to which hunting influences local and regional woodcock population dynamics. Because factors that reduce the source:sink ratio (e.g., succession, human activities) could increase the influence of hunting, even with constant kill rates, we encourage managers not to consider habitat changes and hunting mortality as independent phenomena.

Finally, we acknowledge the implications of violations of the assumption that woodcock that could not be located had moved off the study area or successfully migrated. Of particular concern is the possibility of non-reporting of kills by hunters, whether intentional or through oversight, because this would result in overestimates of survival rates and underestimates of kill rates. Although we suspect that the reporting rates for radio-marked woodcock killed and retrieved by hunters during our study were high, we suggest that managers consider our estimates of kill rates in our study areas as being conservative because of this potential negative bias.

MANAGEMENT IMPLICATIONS

Hunting was the largest source of woodcock mortality during fall in areas where we expected to have moderate to high hunting pressure in breeding ground states in the Central Region. Our experimental design and our analysis of the relationship between kill rates and fall survival rates indicated that hunting mortality was at least partially additive to other sources of mortality during fall. Thus, managers may be able to influence woodcock survival by further reductions in bag limits or hunting season lengths for woodcock, or manipulating access on public land. We caution, however, that the contribution of hunting mortality to annual mortality remains unclear, and that hunting mortality on the breeding grounds may be compensated for at least in part during the remainder of the year. We found no evidence that low annual survival rates of juvenile woodcock (Krementz et al. 2003, Mayhew and Luukkonen 2010) resulted from age-specific mortality during the fall. Decisions about woodcock harvest management will still have to be made with incomplete information on the overall influence of hunting on woodcock population dynamics, but our results provide a better understanding of the effect of hunting mortality that occurs in breeding ground states relative to other sources of mortality in the Central Region.

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