EFFECTS OF HUNTING ON SURVIVAL OF AMERICAN WOODCOCK IN THE NORTHEAST

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Abstract: Numbers of American woodcock (*Scolopax minor*) males counted on the annual singing ground survey (SGS) have declined over the last 35 years at an average rate of 2.3% per year in the Eastern Region and 1.8% per year in the Central Region. Although hunting was not thought to be a cause of these declines, mortality caused by hunters can be controlled. Furthermore, there has been no research on effects of hunting mortality on woodcock populations at local and regional levels on the breeding grounds. We used radiotelemetry to determine survival rates and causes of mortality for 913 woodcock captured during fall 1997–2000 on 7 areas in Maine, New Hampshire, Pennsylvania, and Vermont, USA. Three of 7 sites were closed to hunting. For all sites and all years combined, 176 woodcock died, and 130 were censored, of which 39 were censored mortalities. Predation was the major (n = 134, 76%) cause of mortality. Mammals accounted for 56% of the predation, raptors accounted for 25%, and 19% was attributed to unknown predators. On hunted sites, 36% of the total mortality (n = 102) was caused by hunting, 63% by predation, and 1 bird starved. Kaplan-Meier survival curves did not differ between hunted and nonhunted sites among years (P = 0.46). Overall, point estimates of survival did not differ (P = 0.217) between hunted (SR = 0.636, SE = 0.04) and nonhunted sites (SR = 0.661, SE = 0.08). We modeled hazard rates from hunting and natural mortality events using program MARK. Akaike's Information Criterion supported using a model with common constant hazards from both hunting and natural causes for groups of sites. Groupings of sites for hazard rates from natural causes were not influenced by whether a site was hunted or not. Models detected no effects of woodcock age and sex (P = 0.52) on survival. Proportional hazards models comparing hunted and nonhunted sites found no effects of age and sex (P = 0.45), interactions of age, sex, capture weight, and bill length ($P \geq 0.269$). Our data suggest that current hunting regulations are not causing lower survival of woodcock.

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The American woodcock (*Scolopax minor*) is a popular game bird in much of eastern North America (U.S. Department of the Interior [USDI] 1990). During most years prior to 1990, woodcock were among the top 10 species in the migratory game harvest in the Atlantic and Mississippi Flyways. In several states (Maine, Vermont, New Hampshire, Michigan, Wisconsin) it was the most important migratory game bird in terms of total numbers harvested (USDI 1990). Woodcock harvest is managed by the U.S. Fish and Wildlife Service (USFWS) on the basis of 2 populations (i.e., management regions). The woodcock population, measured by the Singing Ground Survey (SGS) of males, has declined during the last 35 years (1968–2003) at an annual rate of 2.3% in the Eastern Region and 1.8% in the Central Region (Kelley 2003). In 1996, the breeding population index was 1.65 singing males per route in the Eastern region, which was the lowest on record since the survey began in 1968 (Kelley 2003). Major causes of the decline are purported to be degradation and loss of suitable habitat in breeding and wintering areas, caused by forest succession and changes in land use (Owen et al. 1977, Dwyer et al. 1983, Straw et al. 1994). Although hunting was not believed to have caused the decline, there was a need determine effects of harvest on this declin-

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ing population (USDI 1990). The goal of the USFWS American Woodcock Management Plan is to stop the population declines and to increase woodcock populations above current levels. Region 5 (northeastern United States) of the USFWS has the goal of increasing the woodcock population in the Eastern Region to levels recorded in 1985 by 2005 (USFWS 1996).

Regulations on woodcock harvest are set annually by the USFWS and are established, "so that harvest level is commensurate with population status" (USDI 1990:9). From 1967 to 1985, bag limits and season lengths were stable at 5 birds and 65 days. In 1985, season length and bag limits in the Eastern region were reduced to 3 birds and 45 days, in response to the population decline. Pennsylvania imposed more restrictive regulations in 1983 and 1984 reducing the season length to 14 days with a 3 bird daily bag. Despite these efforts, singing males in most states in the Eastern region continued to decline during 1986-1996, but Connecticut, New Hampshire, Pennsylvania, and West Virginia did not show significant increasing or decreasing trends (Bruggink 1996). In 1997, the USFWS Division of Migratory Bird Management (DMBM) implemented reductions in season length in the Eastern Region from 45 to 30 days and in the Central Region from 65 to 45 days. In addition, the daily bag limit in the Central region was reduced from 5 to 3 woodcock, and the season framework date was pushed forward 2–3 weeks (Federal Register 62:44233).

Under the hypothesis of compensatory mortality, hunting and nonhunting mortality are inversely related as long as hunting mortality is below some threshold (i.e., harvest level; Anderson and Burnham 1976). The threshold may be influenced by yearly variation in the size, age, and sex structure of the population and by the quantity and quality of habitat (Anderson and Burnham 1976). Estimates of the number of woodcock killed and retrieved by hunters in the United States increased from 789,000 in 1969 (Sheldon 1971) to 1,328,000 in 1977 (Owen et al. 1977) and to 2 million in the early 1980s (USDI 1990). Harvest estimates began to decline in the late 1970s and early 1980s (Straw et al. 1994), and hunter data from the Wing-collection Survey indicated that seasonal hunter success declined during the 1980s and 1990s (Bruggink 1996) as available habitat continued to decline. Because habitat quality and quantity have declined (Dessecker and McAuley 2001) with the woodcock population, numbers of woodcock harvested may now be near the threshold of additivity, where hunting mortality becomes additive to other mortality factors. Local and regional research on the effects of hunting mortality on woodcock populations was needed because causes of the woodcock decline are unknown, but hunting mortality can be controlled.

Most estimates of annual survival of woodcock have been based on analyses of band recoveries (Sheldon 1956, Martin et al. 1969, Krohn et al. 1974, Dwyer and Nichols 1982, Dwyer et al. 1988, Krementz et al. 2003). These estimates are inherently imprecise because of the difficulty of banding adequate numbers of birds. Radiotelemetry has been used to determine period survival rates (PSR) for woodcock during summer and early fall (0.92; Derleth and Sepik 1990) in Maine, during winter in areas of the southern United States (0.65; Krementz et al. 1994), and in spring (0.79; Longcore et al. 1996) in Maine. No estimates of survival exist for woodcock during fall hunting and during migration. Dwyer and Nichols (1982) estimated annual survival of woodcock banded in the Eastern region to be 0.35 during 1967–1974. Based on this annual estimate and the composite estimate from the 3 telemetry studies that equaled 0.471, Longcore et al. (1996) estimated that survival during the fall hunting and migration period would have to be 0.853 if the annual survival estimate from band analyses was correct. We think it is unreasonable to believe that survival during hunting and migration is higher than during spring and winter. We used telemetry to estimate survival rates of woodcock during the fall, and we determined sources of mortality during fall on breeding areas across the range of the woodcock in the Eastern Management Region.

STUDY AREA

We selected 7 study sites in 4 states in the northeastern United States (Fig. 1). In Maine and Pennsylvania, we used hunted sites and nonhunted sites. Our study areas in Maine were the Baring Unit of Moosehorn National Wildlife Refuge (MNWR) near Calais; the Frye Mountain Wildlife Management Area (FRYEMT) in Montville, managed by the Maine Department of Inland Fisheries and Wildlife (MEDIFW); and commercial timberland owned and managed by International Paper Corporation (IP) in Township 32 MD near Milford. The Baring Unit of MNWR was 6,580 ha and had an active, long-term, habitat management program that provided a mix of different age habitats preferred by woodcock; no hunting was allowed. The 2,120-ha FRYEMT was managed by MEDIFW to provide a mix of successional habitats, openings, and wildlife clearings and was a demonstration area of habitat management for upland game that was open to hunting. The commercial timberland was managed for wood products, primarily pulpwood, and it was open to hunting. During our study, Maine had a 30-day hunting season that began 6 October with a daily bag limit of 3 woodcock.

Fig. 1. Location of study areas in Maine, New Hampshire, Vermont, and Pennsylvania, USA.

In New Hampshire, our study site was Dartmouth College's 10,630-ha Second College Grant (NHDCG) near the town of Errol. The area was a temperate hardwood forest within the watershed of Swift Diamond and Dead Diamond Rivers. The terrain was moderately to steeply sloped, except for the river basins. The area was managed primarily for high quality sawtimber, with some early successional habitat management in lowland riparian covers. The area was open to hunting, but it had gated, limited access. New Hampshire's hunting season was 30 days and opened 6 October with a 3-bird bag limit.

In Vermont, our study area was the 4,600-ha Ethan Allen Firing Range (VTEAFR), a military facility located in the towns of Bolton, Underhill, and Jericho. Habitat was a mosaic of herbaceous openings ≤125 ha, early-successional ordinance impact areas, and timber management sites. The area was primarily mature northern hardwood and oak (*Quercus* spp.) forest with ≥70 beaver (*Castor canadensis*)-created wetlands, and it was closed to hunting.

In Pennsylvania, our study sites were Erie National Wildlife Refuge (ENWR) and the adjacent State Game Land 69 (SGL69) near the town of Guys Mills. Both were closed to hunting during our study. The ENWR and SGL 69 contained 3,878 ha of wetlands and early successional forest habitat. State Game Lands 314 and 101 (SGL314/101) in the northwest corner of Pennsylvania along the Ohio border near the towns of West Springfield and Tracy were open to hunting. State Game land 314/101 totaled 3,313 ha and was managed for early-successional habitat for woodcock. During our study, Pennsylvania's hunting season was 14 days and opened 25 October with a daily bag limit of 3.

METHODS

Capture Methods

We captured woodcock using mist nets (Sheldon 1960) and nightlighting techniques on roosting fields (Reiffenberger and Kletzly 1967, McAuley et al. 1993*a*) and in ground traps in diurnal cover. We banded captured birds with U.S. Geological Survey aluminum leg bands. We weighed each bird (nearest g) with spring scales and measured bill length. We separated birds into 2 age classes: juveniles (hatching year = HY) were <1 year old; adults (after hatching year = AHY) were >1 year old. We determined age and sex of birds by wing plumage characteristics (Martin 1964, McAuley et al. 1993*a*) and bill length (Mendall and Aldous 1943).

Marking with Radio Transmitters

Radio telemetry techniques followed protocols developed at MNWR (McAuley et al. 1993*a*). Radios weighed 4–5 g with a ground-to-ground range of 0.9 km and life expectancy of ≥100 days. The transmitters we used in Pennsylvania were equipped with mortality switches, which added ~0.5 g to the package. We used livestock ID tag cement to glue transmitters to the skin on the birds' back between the wings. A single-loop wire embedded in the transmitter served as a harness around the belly (McAuley et al. 1993*a*). This attachment does not affect woodcock behavior (McAuley et al. 1993*b*) and allows reuse of radios removed from dead birds.

Monitoring

We captured all birds before the start of the hunting season, and we attempted to mark 60 woodcock at each site each year. We searched for marked birds daily and determined status (i.e., alive, dead, lost). To facilitate this, we monitored birds during crepuscular periods when birds were active and usually moved between habitats (McAuley et al. 1993*a*). If a bird did not move or was inactive during 2 crepuscular periods, we flushed it to determine its status. We examined transmitters, bird remains, and carcasses to determine cause of death. Mammalian predators usually chewed off wings and legs, ate most of the bird (including feathers), and removed the transmitter from the carcass, leaving bite marks on the antenna and harness. Some mammals buried carcasses or carried them to den sites. Raptors typically plucked the feathers and ate the meat off the bones. Occasionally they left bill marks on the antenna and harness. We necropsied carcasses of birds to detect hunting injuries. In Maine, we also x-rayed carcasses to look for embedded shot, broken bones with traces of lead, and other indications of hunting related injuries.

Statistical Analyses

We used the Kaplan-Meier (Kaplan and Meier 1958) product-limit procedure as modified by Pollock et al. (1989) to estimate survival rates, standard errors, and 95% confidence intervals for pooled age/sex classes and hunted and unhunted sites. Kaplan-Meier estimates were calculated using SYSTAT version 10.2.05 (SYSTAT Software 2002). Use of the Kaplan-Meier model allows for staggered entry of individuals into the model and right-censoring of data (Pollock et al. 1989). Monitoring began the day after birds were marked. We censored birds when (1) death was caused by entanglement in the harness (censored mortality); (2) the bird slipped out of the harness (bird alive); (3) the bird was lost because of radio failure or it moved off the study area (bird lost); and (4) the bird survived the study period and migrated (migrate). We also censored birds that moved off unhunted sites and were shot. We tested for differences in survival between sites and treatments with log-rank tests (Pollock et al. 1989). Although we searched for birds daily, we did not always locate each bird every day. Because 1 of the assumptions of the Kaplan Meier procedure is that birds can be located at will, we determined survival rates based on weeks as the survival periods. We located most (>90%) birds within the study areas ≥1 time each week.

We tested for relationships between survival rates and independent variables with Cox proportional hazards models (Kalbfleisch and Prentice 1980) using S-plus version 6.2 (Insightful Corporation, Seattle, Washington, USA). We used body mass at capture and bill length as covariates and woodcock age, sex, capture location, year of capture, and whether a site was hunted or not as strata and then as covariates. We developed models using the known fate approach in program MARK (White and Burnham 1999) to explore the interplay of hunting and natural mortality as well as examining the influence of age, sex, weight, and bill length on survival. We used Akaike's information Crition (AIC) to compare models for survival (Burnham and Anderson 1998). We used MARK to calculate estimates of daily survival rates for natural mortality factors and hunting and to calculate probabilities of surviving the study period for each site.

Population Assessment

Each year we monitored the number of singing male woodcock on every study area except VTEAFR. Early studies revealed that counts of singing males provide indices to woodcock populations and can be used to monitor yearly changes (Mendall and Aldous 1943, Goudy 1960, Duke 1966, and Whitcomb 1974). We followed

Table 1. Sample sizes and fates of American woodcock radiomarked at study sites in Maine, Vermont, New Hampshire, and Pennsylvania, USA, during fall 1997–2000. Birds that migrated are not included.

					Sources of mortality						
Site[a]	Year	Age	Sex	*n*	Mammal	Raptor	Unknown predator	Hunt	Deaths	Censored[b]	Lost
MNWR[c]	1997–1999	AD	F	48	1	1	4		6	9[d]	
		AD	M	21						6	1
		HY	F	34		3	2		5	8	2
		HY	M	62	2	3	3		8	14	1
IP	1997–1999	AD	F	58	4		1	6	11	7	4
		AD	M	31			1	2	3		
		HY	F	41	2	2	1	2	7	6	1
		HY	M	71	7	3	2	6	18	8	
FRYEMT	1998–1999	AD	F	23			2		2	1	3
		AD	M	23		4	1	1	6	4	1
		HY	F	24	2		1	1	4	2	3
		HY	M	35	3	2	2	2	9	2	1
NH	1998–1999	AD	F	24	2		3		5	4	3
		AD	M	26	3			3	6	2	1
		HY	F	5		1		1	2		
		HY	M	11		1		1	2	1	2
VT[c]	1998–2000	AD	F	49	10	2			12	3	2
		AD	M	7		1			1		0
		HY	F	35	5	1	1		7	4	4
		HY	M	54	13	4			17	3	3
ENWR[c]	1998–1999	AD	F	31	5	3	1[e]		9	4	3
		AD	M	30	2	1			3	9[f]	
		HY	F	27	2		2[e]		4	6	4
		HY	M	18	1		1[e]		2	2	1
		U	M	1							
SGL314	1998–1999	AD	F	41	3	1	2[g]	3	9	7	1
		AD	M	17	3			3	4	2	2
		HY	F	31	2			6	8	8	1
		HY	M	35	3	1		2	6	9	1

[a] Abbreviations: Moosehorn National Wildlife Refuge (MNWR) in Baring, Maine, USA; commercial forest land in Hancock County (IP), Maine, USA; Frye Mountain Wildlife Management Area (FRYEMT) in Montville, Maine, USA; Ethan Allen Firing Range (VT) in Jericho, Vermont, USA; Second College Grant (NH) in Errol, New Hampshire; Pennsylvania Game Commission's State Game Lands 314 and 101 (SGL314), Pennsylvania, USA; and Erie National Wildlife Refuge and State Game Land 69 (ENWR) in Guy Mills, Pennsylvania, USA.

[b] Includes birds that slipped out of the radio harness, and birds that died from entanglement in the harness, birds that moved from areas closed to hunting that were legally shot, and birds that moved off closed areas and were shot illegally.

[c] Sites closed to hunting.

[d] Includes 1 bird that moved off study area and was shot illegally before the season and 1 that moved off the area and was legally shot.

[e] Death attributed to starvation.

[f] Includes 1 bird that was shot illegally.

[g] Includes 1 bird that died from starvation.

protocols of the USFWS Singing Ground Survey (Clark 1970) and established enough routes to completely survey study areas. Moosehorn NWR had routes that have been surveyed since 1977.

RESULTS

We radiomarked 913 woodcock between 15 August and 6 October 1997–2000 (Table 1). In 1997, we attached radios to 99 birds at 2 sites in Maine (30 on MNWR; 69 on IP). In 1998, we attached radios to 355 woodcock at 7 sites in 4 states, (63 on MNWR; 67 on IP; 43 on FRYEMT; 45 on VTEAFR; 31 on NHDCG; 57 on SGL 314/101; 49 on ENWR/SGL69), and in 1999, we attached radios to 415 woodcock at these same sites (72 on MNWR; 66 on IP; 62 on FRYEMT; 56 on VTEAFR; 35 on NHDCG; 67 on SGL314/101; 58 on ENWR/SGL69). In 2000, we attached radios to 44 woodcock in Vermont only. Overall, we captured more juvenile males (n = 286) and adult females (n = 274) than juvenile females (n = 197) and adult males (n = 156).

Causes of Mortality

On the 4 sites with hunting 102 birds died. Hunters killed 38 birds (37% of the mortality). Predation was the largest source of mortality: mammalian predation 33%, raptors 15%, and un-

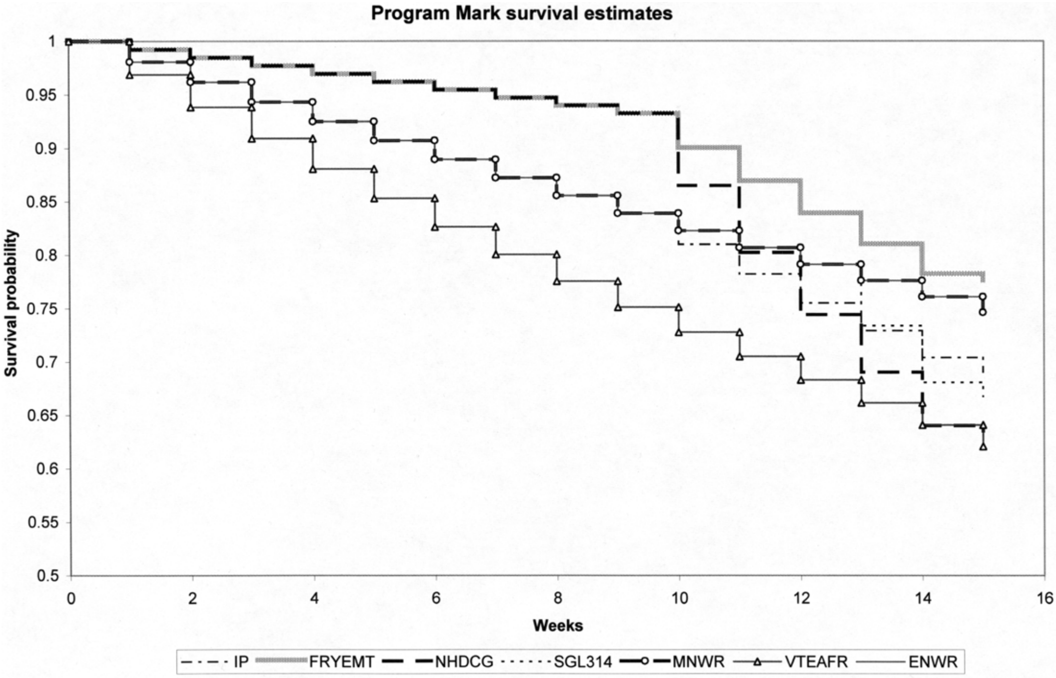

Fig. 2. Period survival curves for American woodcock radiomarked at Moosehorn National Wildlife Refuge (MNWR), ME; forest land in Hancock County (IP), Maine; Frye Mountain Wildlife Management Area (FRYEMT), Maine; Ethan Allen Firing Range (VTEAFR), Vermont; Second College Grant (NHDCG), New Hampshire; Pennsylvania Game Commission's State Game Lands 314 and 101 (SGL314/101), Pennsylvania; and Erie National Wildlife Refuge and State Game Land 69 (ENWR/SGL69), Pennsylvania, during fall 1997–2000. Estimates were calculated using program MARK using weeks as survival periods.

known predators 15%. One bird starved. No radiomarked birds were shot in NH during 1998, but 5 were shot in 1999. On the IP site 6 birds were shot in 1997, 9 in 1998, and only 1 in 1999. On the state wildlife management area WMA in Maine only 2 birds were shot each year, but on the WMA in Pennsylvania 5 were shot in 1998 and 7 in 1999. In 1997, 2 of 6 hunting mortalities at the IP site were unretrieved kills, and in 1998, 1of 9 hunting mortalities on the same site was an unretrieved cripple. In Pennsylvania, 1 bird was shot and not retrieved during the season.

Over all sites and years combined, 176 woodcock died and 130 were censored, of which 39 were censored mortalities. Predators killed 134 woodcock (76%; Table 1). Mammalian predators, primarily weasels (*Mustela* spp.; Maine, New Hampshire, Vermont) and raccoons (*Procyon lotor*; Pennsylvania), accounted for most (56%) of the predation. Raptors accounted for 25% of the predation, and unknown predators accounted for 19%. Pennsylvania was near drought conditions during August and September 1998 (National Oceanic and Atmospheric Administration http://lwf.ncdc.noaa.gov/oa/ncdc.html), which likely affected earthworm availability (Sepik et al. 1983), and at least 5 birds died of starvation. In Maine, 2 birds moved off sites closed to hunting and were legally shot (censored mortalities), and 1 moved off a closed site and was shot illegally before the season (censored mortality). In Pennsylvania, 1 woodcock was illegally shot after the season on a site closed to hunting.

Survival Analyses

We used a survival period from 1 September through the end of November. Estimates of survival did not differ among study sites (Fig. 2). Survival did not differ among age and sex groups (Table 2; Likelihood Ratio Test [LRT] = 2.28, 3 df, P = 0.517). Kaplan-Meier survival curves did not differ between hunted and nonhunted sites among years (χ^2 = 5.7, 6 df, P = 0.459). Using pooled data, point estimates of survival rate (SR) did not differ (χ^2 = 1.5, 1 df, P = 0.217) between hunted sites (SR = 0.636, SE = 0.044) and sites not open to hunting (SR = 0.661, SE = 0.083; Table 3; Fig. 3). Proportional hazards models detected no effects of woodcock age and sex (R^2 = 0.002, LRT = 2.28, 3 df, P = 0.517) on survival. With propor-

Table 2. Pooled survival of American woodcock age and sex groups radiomarked at MNWR[a], IP[b], FRYEMT[c], VTEAFR[d], NHDCG[e], SGL314/101[f], and ENWR/SGL69[g] during fall 1997–2000. Estimates are point estimates calculated using Kaplan-Meier survival procedures for a 10-week survival period (1 Sep–9 Nov).

	n	Survival rate	SE	Lower CI	Upper CI
AHY F	274	0.702	0.045	0.619	0.796
AHY M	156	0.717	0.074	0.585	0.878
HY F	197	0.706	0.050	0.614	0.812
HY M	286	0.664	0.045	0.580	0.759

[a] Moosehorn National Wildlife Refuge in Baring, Maine, USA.
[b] Commercial forest land in Hancock County, Maine, USA.
[c] Frye Mountain Wildlife Management Area in Montville, Maine, USA.
[d] Ethan Allen Firing Range in Jericho, Vermont, USA.
[e] Second College Grant (NHDCG) in Errol, New Hampshire, USA.
[f] Pennsylvania Game Commission's State Game Lands 314 and 101 near West Springfield and Tracey, Pennsylvania, USA.
[g] Erie National Wildlife Refuge and State Game Land 69 in Guy Mills, Pennsylvania, USA.

tional hazards models comparing hunted and unhunted sites, we found no effects of age and sex (R^2 = 0.007, LRT = 6.83, 7 df, *P* = 0.447), or interactions of age, sex, capture weight, and bill length (LRTs = 4.21–8.78, 7 df, *P*'s = 0.269–0.755).

Table 3. Period estimates of survival rates (SR), standard errors, and 95% confidence intervals for pooled sample of American woodcock radiomarked at sites that were hunted (IP[a], FRYEMT[b], NHDCG[c], SGL314/101[d]) and sites not hunted (MNWR[e], VTEAFR[f], ENWR/SGL69[g]) during fall 1997–2000.

	n	Survival rate	SE	Lower CI	Upper CI
Hunt	496	0.636	0.044	0.555	0.729
No hunt	417	0.661	0.083	0.517	0.844

[a] Commercial forest land in Hancock County, Maine, USA.
[b] Frye Mountain Wildlife Management Area in Montville, Maine, USA.
[c] Second College Grant (NHDCG) in Errol, New Hampshire, USA.
[d] Pennsylvania Game Commission's State Game Lands 314 and 101 near West Springfield and Tracey, Pennsylvania, USA.
[e] Moosehorn National Wildlife Refuge in Baring, Maine, USA.
[f] Ethan Allen Firing Range in Jericho, Vermont, USA.
[g] Erie National Wildlife Refuge and State Game Land 69 in Guy Mills, Pennsylvania, USA.

Analyses Using Program MARK

Using the known fate approach, we estimated the overdispersion parameter, $\hat{c}$, to be 1.70, and all AIC values were adjusted and reported as $QAIC_c$ values. Because there were 7 sites, we developed models based on 7 groups. We ran 4 generic, predefined models: (1) S(.) (constant survival over-

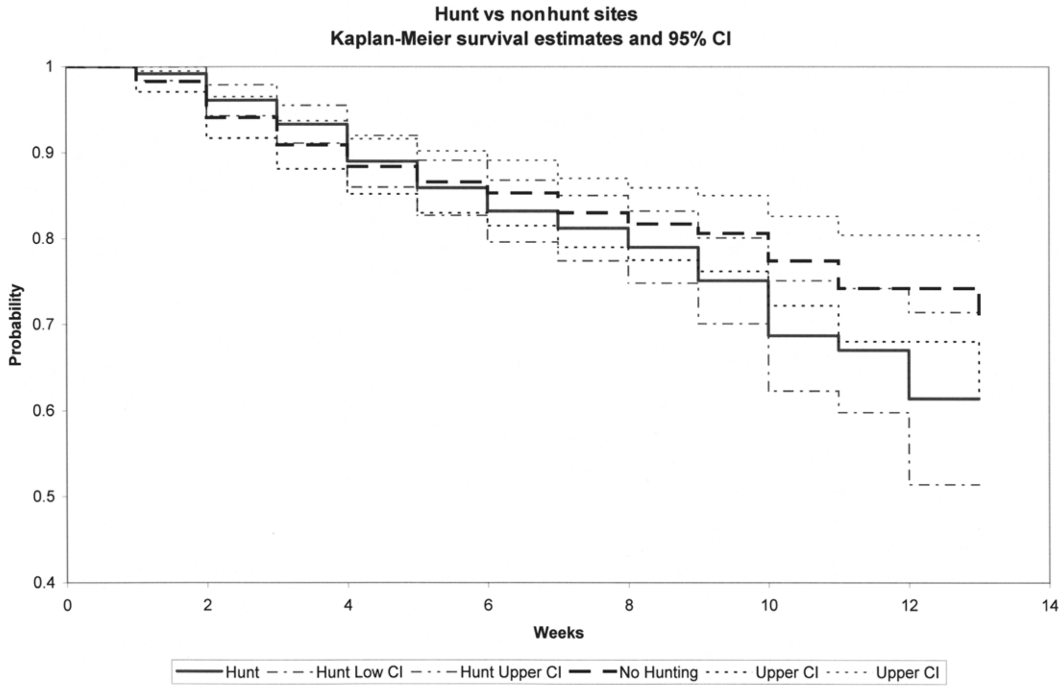

Fig. 3. Product–moment survival estimates for 496 American woodcock radiomarked at sites that were hunted (forest land in Hancock County, Maine; Frye Mt. Wildlife Management Area, Maine; Second College Grant, New Hampshire; and Pennsylvania Game Commission's State Game Lands 314 and 101) and 417 woodcock at sites that were not hunted (Moosehorn NWR, Maine; Ethan Allen Firing Range, Vermont; and Erie NWR and State Game Land 69, Pennsylvania) during fall 1997–2000. Estimates are calculated with Kaplan-Meier Survival procedures using weeks as survival periods.

Table 4. Akaike's Information Criterion ($QAIC_c$) ranking 4 generic, predefined models developed using program MARK to estimate survival rates for radiomarked American woodcock (n = 906) marked at study sites[a] in Maine, Vermont, New Hampshire, and Pennsylvania, USA, during fall 1997–2000. Model selection based on a $\hat{c}$ = 1.700.

Model	$QAIC_c$	Delta $QAIC_c$	No. parameters
{S(.) constant survival overall}	930.769	0.000	1.000
{S(g) survival constant over time, unique to each site}	935.814	5.045	7.000
{S(t) time-dependent survival, does not vary across sites}	938.142	7.373	12.000
{S(g*t) survival time and site dependent}	969.302	38.533	64.000

[a] Moosehorn National Wildlife Refuge in Baring, Maine, commercial forest land in Hancock County, Maine, Frye Mountain Wildlife Management Area in Montville, Maine, Ethan Allen Firing Range in Jericho, Vermont, Second College Grant in Errol, New Hampshire, Pennsylvania Game Commission's State Game Lands 314 and 101 near West Springfield and Tracey, Pennsylvania, and Erie National Wildlife Refuge and State Game Land 69 in Guy Mills, Pennsylvania.

all), (2) S(g) (survival constant over time, unique to each site), (3) S(t) (time-dependent survival, that does not vary across sites), and (4) S(g*t) (survival is time and site dependent) (Table 4). These results indicate support for an overall constant hazard rate or for site specific hazard rates. There was little or no support for time-dependent hazard rates. We added covariates sex (M/F), age (adult/juvenile), weight, and bill length to the site specific hazard rate models to determine whether they improved the fit. The $QAIC_c$ values from the covariate models were all >938.5 (the $QAIC_c$ value of S[.] model), and they were a poorer fit than the time-dependent hazard rate model.

Because some sites were open to hunting during the period of observation while others were not, we developed a series of models exploiting this feature. The models were a (1) constant hazard to describe the natural mortality and a different constant hazard to describe the mortality during the hunting season (Model 4, Table 5), (2) constant hazard for the natural mortality and site specific hazard during the hunting season for sites that had hunting (Model 3, Table 5), (3) site specific hazard for the natural mortality and a constant hazard for the hunting mortality (Model 6, Table 5), (4) site specific hazards for natural and hunting mortalities (Model 5, Table 5). Because the parameter estimates for some sites were very similar while others were not, we examined 2 additional models: (5) 3 groups of sites, each with different hazards, for the natural mortality and site specific hazards for hunting mortality (Model 2, Table 5) and (6) grouped natural and grouped hunting hazards (Model 1, Table 5).

Results of AIC supported model 1, which had common constant hazards for natural and hunting mortality for groups of sites. Groupings with common natural mortality hazards were MNMWR, ENWR, IP, and SGL314/101 (group1), VTEAFR (group 2), and NHDCG and FRYEMT (group 3). The 2 groupings that had similar hunting hazards were IP and FRYEMT and NHDCG and SGL314 (Table 5). We added covariates sex, age, weight, and bill length to these models, and they did not improve the fit.

Daily survival rates for hazards from natural mortality for model 1 were 0.969 (SE = 0.005) for VTEAFR; 0.981 (SE = 0.002) for MNWR, IP, ENWR, and SG314/101; and 0.992 (SE = 0.003) for FRYEMT and NHDCG. Daily survival rates during hunting were 0.970 (SE = 0.006) for IP, 0.956 (SE = 0.010) for FRYEMT, 0.938 (SE = 0.17) for NHDCG, and 0.912 (SE = 0.024) for SGL314/101. Group DSRs from hunting hazard were 0.970 (SE = 0.006) for IP, FRYEMT, and 0.938 (SE = 0.017) for NHDCG and SGL314/101 (Table 6). Probabilities of surviving the entire study period ranged from 0.621 for VTEAF to 0.776 for FRYEMT (Table 7). Mean and median days

Table 5. Akaike's Information Criterion ($QAIC_c$) for models developed using program MARK and used to estimate survival rates for radiomarked American woodcock (n = 906) marked at MNWR (M)[a], IP (I)[b], FRYEMT (F)[c], VTEAFR (V)[d], NHDCG (N)[e], SGL314/101 (S)[f], and ENWR/SGL69 (E)[g] during fall 1997–2000. Model selection based on a $\hat{c}$ = 1.700.

Model	$QAIC_c$	Delta $QAIC_c$	No. parameters
1. {MEIS V NF natural mortality, IF NS hunting mortality}	912.644	0.000	5.000
2. {MEIS V NF natural mortality, site specific hunting mortality}	915.297	2.650	7.000
3. {constant natural mortality, site specific hunting mortality}	919.461	6.820	5.000
4. {constant natural mortality, constant hunting mortality}	919.601	6.960	2.000
5. {site specific natural mortality, site specific hunting mortality}	921.082	8.440	11.000
6. {site specific natural mortality, constant hunting mortality}	921.213	8.570	8.000

[a] Moosehorn National Wildlife Refuge in Baring, Maine.
[b] Commercial forest land in Hancock County, Maine.
[c] Frye Mountain Wildlife Management Area in Montville, Maine.
[d] Ethan Allen Firing Range in Jericho, Vermont.
[e] Second College Grant in Errol, New Hampshire.
[f] Pennsylvania Game Commission's State Game Lands 314 and 101 near West Springfield and Tracey, Pennsylvania.
[g] Erie National Wildlife Refuge and State Game Land 69 in Guy Mills, Pennsylvania.

Table 6. Cause-specific daily survival rates (DSR), standard errors (SE), and 95% confidence interval (Lower CI, Upper CI) of American woodcock radiomarked at MNWR (M)[a], IP (I)[b], FRYEMT (F)[c], VTEAFR (V)[d], NHDCG (N)[e], SGL314/101 (S)[f], and ENWR/SGL69 (E)[g] during fall 1997–2000. Estimates derived in program MARK. Natural mortality is all nonhunting causes of mortality, including predation and starvation.

Cause	Sites	DSR	SE	Lower CI	Upper CI
Natural	M[h], E, I, S[h]	0.9807	0.0023	0.9755	0.9848
Natural	V	0.9687	0.0053	0.9565	0.9776
Natural	N[h], F[h]	0.9923	0.0031	0.9829	0.9965
Hunting	I, F	0.9655	0.0050	0.9530	0.9750
Hunting	N, S	0.9275	0.0140	0.8950	0.9510

[a] Moosehorn National Wildlife Refuge in Baring, Maine.
[b] Commercial forest land in Hancock County, Maine.
[c] Frye Mountain Wildlife Management Area in Montville, Maine.
[d] Ethan Allen Firing Range in Jericho, Vermont.
[e] Second College Grant (NHDCG) in Errol, New Hampshire.
[f] Pennsylvania Game Commission's State Game Lands 314 and 101 near West Springfield and Tracey, Pennsylvania.
[g] Erie National Wildlife Refuge and State Game Land 69 in Guy Mills, Pennsylvania.
[h] Sites open to hunting.

Table 7. Probability of surviving the duration of the study period for American woodcock radiomarked at study sites in Maine, Vermont, New Hampshire, and Pennsylvania, USA, during fall 1997–2000. Estimates were calculated using program MARK for the model with grouped natural mortality and grouped hunting mortality.

Sites[a]	n	Survival rate	SE	Lower CI	Upper CI
MNWR[b]	165	0.746	0.027	0.690	0.795
IP	201	0.690	0.026	0.638	0.738
FRYEMT	105	0.776	0.033	0.706	0.835
NHDGC	66	0.635	0.519	0.529	0.730
VTEAFR[b]	145	0.621	0.051	0.518	0.714
SGL314/101	124	0.668	0.029	0.609	0.722
ENWR/SGL69[b]	107	0.746	0.027	0.690	0.795

[a] Abbreviations: Moosehorn National Wildlife Refuge (MNWR) in Baring, Maine; commercial forest land in Hancock County (IP), Maine; Frye Mountain Wildlife Management Area (FRYEMT) in Montville, Maine; Ethan Allen Firing Range (VTEAFR) in Jericho, Vermont; Second College Grant (NHDCG) in Errol, New Hampshire; Pennsylvania Game Commission's State Game Lands 314 and 101 (SGL314/101), Pennsylvania; and Erie National Wildlife Refuge and State Game Land 69 (ENWR/SGL69) in Guy Mills, Pennsylvania.
[b] Closed to hunting.

of survival differed ($P \leq 0.10$) among sites but were not related to hunting (Table 8).

On all sites, most radiomarked woodcock remained on the study areas throughout the hunting season. Although a few (≤4) birds left each site during the last 2 weeks of October, most birds migrated during the first 3 weeks of November. On all sites, some radiomarked birds remained on the study areas after the hunting season.

Population Assessment

We ran 33 woodcock SGS routes at MNWR during 1997–2002, 18 SGS routes on IP (1997–2002), 4 routes on FRYEMT (1998–2001), 9 routes on NHDCG (1998–2002), 10 routes on VTEAFR (2000–2002), 4 routes on SGL314/101 (1997–2002), and 11 routes on ENWR/SGL69 (1997–2002). Routes contained 1–10 stops. On all sites, numbers of males heard displaying had similar trends during the study period regardless of whether the site was hunted or not (Table 9).

DISCUSSION

The role hunting has played in the decline of the woodcock population is uncertain. We found

Table 8. Mean and Median number of days radiomarked American woodcock survived at study sites in Maine, Vermont, New Hampshire, and Pennsylvania, USA, during fall 1997–2000. Cells with the same letter are not different $P \leq 0.10$.

Capture location[a]	Mean no. of days	Median no. of days
MNWR	47.42 A	52.0 A
IP[b]	40.30 BC	41.0 BC
FYREMT[b]	51.44 AB	54.0 AB
VTEAFR	43.37 C	46.0 C
NHDCG[b]	44.08 C	40.0 C
SGL314/101[b]	37.17 C	35.5 C
ENWR/SGL69	39.19 BC	39.0 BC

[a] Abbreviations: Moosehorn National Wildlife Refuge (MNWR) in Baring, Maine; commercial forest land in Hancock County (IP), Maine; Frye Mountain Wildlife Management Area (FRYEMT) in Montville, Maine; Ethan Allen Firing Range (VTEAFR) in Jericho, Vermont; Second College Grant (NHDCG) in Errol, NH; Pennsylvania Game Commission's State Game Lands 314 and 101 (SGL314/101), PA; and Erie National Wildlife Refuge and State Game Land 69 (ENWR/SGL69) in Guy Mills, Pennsylvania.
[b] Sites open to hunting.

Table 9. Number of male woodcock heard on singing grounds surveys at study sites in Maine, Vermont, New Hampshire, and Pennsylvania, USA, during spring 1997–2002.

Sites[a]	No. of routes	1997	1998	1999	2000	2001	2002
MNWR	33	113	121	127	110	82	85
IP*	18	109	132	127	135	136	141
FRYEMT[b]	4		20	29	40	43	
NHDCG[b]	9	24	27	36	41	27	20
VTEAFR	10				27	36	38
ENWR/SGL69	11	51	63	61	76	37	43
SGL314/101[b]	4	48	66	62	80	58	56

[a] Abbreviations: Moosehorn National Wildlife Refuge (MNWR) in Baring, Maine; commercial forest land in Hancock County (IP), Maine; Frye Mountain Wildlife Management Area (FRYEMT) in Montville, Maine; Ethan Allen Firing Range (VTEAFR) in Jericho, Vermont; Second College Grant (NHDCG) in Errol, New Hampshire; Pennsylvania Game Commission's State Game Lands 314 and 101 (SGL314/101), PA; and Erie National Wildlife Refuge and State Game Land 69 (ENWR/SGL69) in Guy Mills, Pennsylvania.
[b] Sites open to hunting.

DSRs were generally lower during hunting periods than during the rest of the period, but period survival rates were similar among hunted and nonhunting sites. Two of the hunted sites (NHDCG, FRYEMT) had the highest DSR for nonhunting hazards, while the other 2 hunted sites had rates similar to nonhunted sites (Table 6). Losses to hunting seem to balance out the losses to natural mortality. Therefore, our results support the belief that hunting is not the cause of the population decline, and they indicate that harvest under the current regulations on our areas did not result in lower period survival rates of woodcock.

Except for the hunted site in Pennsylvania, predation was the major source of woodcock mortality, regardless of availability to hunters. Overall, predators caused >75% of the mortality, and on hunted sites predators accounted for 63% of total deaths. Although we were not always able to identify the species of predator, we determined that predominant mammalian predators were weasels (*Mustela* spp.), mink (*Mustela vison*), and raccoons (*Procyon lotor*). We could not determine species of raptors, but common raptors on study sites known to kill woodcock included goshawks (*Accipiter gentiles*), sharp-shinned hawks (*A. straitus*), Cooper's hawks (*A. cooperii*), barred owls (*Strix varia*), and great horned owls (*Bubo virginianus*) (Mendall and Aldous 1943, Liscinsky 1972, Longcore et al. 1996).

Hunted sites received varying amounts of hunting effort ranging from limited access behind gated roads (NH) to unlimited access on commercial timberland and 2 state wildlife management areas (WMA). We expected losses to hunting would be highest on the 2 state wildlife management areas (FRYEMT and SGL314/101), less on the commercial timberland (IP), and least on the site with limited access (NH). Hunting mortality, however, was inconsistent and varied annually within and among sites. Among individual sites, hunting accounted for 19% (FRYEMT) – 53% (SGL314/101) of all mortality (Table 1). Although SGL314/101 had the shortest hunting season (14 days), woodcock on this site had the lowest DSR. This area, however, was stocked with pheasants (*Phasianus colchicus*), and the start of the pheasant season coincided with the woodcock season, resulting in extremely heavy hunting pressure.

In a Louisiana study (Pace 2000) hunting accounted for 19% of the mortality of radiomarked woodcock on a state WMA, and Krementz and Berdeen (1997) reported 2 of 5 mortalities caused by hunting in Georgia. Krementz et al. (1994) radiomarked wintering woodcock in Georgia, South Carolina, and Virginia and reported no hunting mortality. Period (winter) survival estimates for these studies ranged from 64% (Krementz et al. 1994) to 72% (Pace 2000), which are similar to our results. Pace (2000) studied woodcock on a heavily hunted WMA in Louisiana, which is in the Central Region and had a 65-day hunting season and a 5-bird bag limit. He reported that although hunting was not the most frequent source of mortality, it may be additive to nonhunting mortality, but he could not document this.

Overall, the number of woodcock ($n = 4$) shot and not retrieved by hunters was 10.5%, but this estimate could be low if crippled or un-retrieved killed birds were scavenged by predators before we found them. Loss of birds from crippling varied yearly and among sites. None of the telemetry studies of wintering woodcock reported any crippling losses, but Pursglove (1975) reported that crippling loss could be as high as 17%. Because woodcock occupy thick cover and they tend to sit tightly and not flush, most woodcock hunters use dogs (D. G. McAuley, U.S. Geological Survey, unpublished data), which likely reduces numbers of unretrieved kills.

Dwyer and Nichols (1982) concluded from banding and recovery data that female woodcock survived at higher rates than males, that young males had extremely low survival rates (i.e., SR = 0.202, SE = 0.048), and that no age-specific differences existed in recovery rates, although young females were recovered at a higher rate than young males. Krementz and Bruggink (2000) reanalyzed these same data but for a longer banding period and included bands from a slightly larger geographic area, and they reported that Eastern Region females survived at higher rates than males, adult males had higher recovery rates than adult females, and direct recovery rates of woodcock in the Eastern Region were lower after changes in harvest regulations in 1985, indicating a reduction in the harvest. We found no differences in vulnerability or mortality caused by hunting among the different age and sex classes. Woodcock used in banding analyses, however, were banded in spring and summer, ≥6 months before hunting seasons. Most of our woodcock were radiomarked within 1–6 weeks of the hunting season. Differential mortality, therefore, may have occurred among age and sex classes of banded samples, resulting in more males available to be shot during the hunting season. Predation was the major source of woodcock mortality in previous telemetry studies (Derleth and Sepik 1990, Krementz et al. 1994, Longcore et al. 1996, Krementz and Berdeen 1997, Pace 2000), and no large difference in survival rates among age and sex groups were reported, although power to detect differences was low in most studies. Numbers of displaying males on survey routes on our study areas showed similar trends on sites open and closed to hunting.

From banding and recovery data, Dwyer and Nichols (1982) estimated annual survival of Eastern Region woodcock as 0.35 for adult males and 0.49 for adult females, whereas Krementz and Bruggink (2000) estimated survival of adult woodcock in the Eastern Region to be 0.34 for adult males and 0.52 for adult females. Longcore et al. (1996) used period estimates of woodcock survival from telemetry studies during spring, summer, fall, and winter, and they then estimated survival during migration to derive an annual survival rate (0.47) for adult males. The fall survival estimate of 0.853 they used was from an unhunted site (MNWR; Derleth and Sepik 1990) and included the hunting and fall migration period. When we substituted our point estimate (0.70) for the fall period, the annual survival rate declined to 0.290, which is lower than previous estimates. Since 1992, the recruitment index (young/ adult female in the harvest) in the Eastern Region has been below the long-term (1963–2000) average of 1.7 (Kelley 2002) and the 1963–1985 average of 1.8 (Kelly 1986). The 2001 index of 1.4 was 18% below the long-term average (Kelley 2002). This combination of low survival and poor recruitment is a cause for concern.

Woodcock require early-successional habitats, thus loss of suitable habitat from successional change and urbanization likely contributes to their long-term population decline (Owen et al. 1977, Dwyer et al. 1983, Straw et al. 1994, Thompson and Dessecker 1997) and lower recruitment index. Populations of most bird species associated with grassland, shrub–scrub, and disturbed forest habitats have declined steeply (Hunter et al. 2001). Woodcock in the Eastern Region migrate through some of the most densely populated human areas in the country (New York/ New Jersey Metropolitan area, Baltimore, Maryland/Washington D.C. area), where habitat loss caused by urbanization has been highest. Urban land increased 53% from 1960 to1987 in the Northeast (Trani et al. 2001). In New England states, except Maine, seedling–sapling habitat makes up only 4–10% of the timberland (Trani et al. 2001). Seedling–sapling habitat within New England and the mid-Atlantic region peaked during the 1960s and declined into the 1990s (Trani et al. 2001). We believe declines in the woodcock population are related to habitat because numbers of woodcock hunters and woodcock harvest have been declining since the early 1980s (Kelley 2003) and because many species of migratory songbirds that are not hunted are also declining.

MANAGEMENT IMPLICATIONS

It is uncertain if reductions in season length and bag limits restrictions are the cause of the harvest declines or if changes in hunting attitudes and human population demographics are the reason. We believe hunting seasons and bag limits can be maintained at current levels and could be liberalized. Although hunting can be a major source of mortality on some sites, our results suggest that hunting under the current regulatory frameworks is not causing the woodcock population to decline. We are not certain how more liberal regulations may affect the population. If seasons are liberalized, we encourage research to evaluate hunting effects under the more liberal conditions. Specific research to evaluate if low recruitment is caused by contaminants, habitat fragmentation, or habitat degradation is warranted.

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