Assessment of Techniques to Evaluate American Woodcock Population Response to Best
Management Practices Applied at the Demonstration-Area Scale

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Dedication

This work is dedicated to my parents, John and Beth, for their constant encouragement,
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my wings and chase my dreams. For this I am forever grateful.

Abstract

American woodcock (*Scolopax minor*; hereafter, woodcock) have experienced long-term population declines across their breeding range based on the American woodcock Singing-ground Survey. Wing-collection surveys have also indicated a decline in woodcock recruitment across their range, especially in the Central Management Region. These declines have been widely attributed to loss or alteration of young forest cover types that support woodcock reproduction across their breeding range. In response to these apparent declines in woodcock abundance and recruitment, a system of woodcock habitat demonstration areas is being developed throughout the woodcock breeding range where specific Best Management Practices (BMPs) are applied with the goal to stabilize and ultimately increase populations. Application of BMPs at a demonstration-area scale (~200–800 ha) is designed to positively influence woodcock population growth by improving habitat quality and abundance at a landscape scale. However, how woodcock vital rates are influenced by BMPs applied at a landscape scale is not fully understood, and techniques used to evaluate woodcock populations at the demonstration-area scale have not been assessed. The objectives of our research were to (1) estimate survival of adult females, nests, and juveniles using radio telemetry and assess relationships between survival and vegetation structure resulting from BMPs, life history traits, and weather, (2) directly estimate a measure of woodcock recruitment (juveniles/adult female during late summer) at a landscape scale by using survival estimates in a population model, and use direct estimates of recruitment to evaluate the

accuracy and usefulness of indirect estimates of recruitment based on less costly and effort-intensive methods (specifically mist netting and night lighting on summer roosting fields), and (3) test for effects of radio transmitters on juvenile woodcock survival.

In 2011 and 2012, we radio-marked and tracked 41 adult female and 73 juvenile woodcock, and monitored 51 broods and 48 nests. Breeding season cumulative survival for adult females was consistent between years, whereas nest and juvenile survival were related to year. Juvenile survival was also positively related to age, minimum temperature, and stem density, and negatively related to precipitation. We found no effects of radio-marking juvenile woodcock. In July of 2011 and 2012, we captured 204 woodcock using mist nets during crepuscular movements from diurnal feeding cover to roosting fields and 69 woodcock via night-lighting on roosting fields. Our recruitment estimates (juveniles/adult female) derived from our demographic model were higher in 2012 than 2011 due to higher nest and juvenile survival rates during that year, suggesting that nest and juvenile survival, and factors related to nest and juvenile survival, may be key to understanding woodcock population ecology. Our assessment of indirect methods to estimate woodcock recruitment at a landscape scale indicated that the indirect methods we considered of estimating woodcock recruitment at a landscape scale are likely not reliable proxies for estimating recruitment directly.

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Chapter 1

American Woodcock Survival Following Management at a Demonstration Area in West-central Minnesota

Overview: American woodcock (*Scolopax minor*; hereafter woodcock) Best Management Practices (BMPs) applied at a landscape scale have been proposed to increase woodcock population densities, yet little information exists regarding population vital rates following application of BMPs. We estimated survival of woodcock adult females, nests, and juveniles at a woodcock habitat-management demonstration area in west-central Minnesota during the spring and summer (23 March – 30 June) of 2011 and 2012. We radio-marked and tracked 41 adult females and 73 juveniles, and monitored 51 broods and 48 woodcock nests to determine fates. We used Kaplan-Meier survival analysis to estimate survival of females, nests, and juveniles for both 2011 and 2012. Breeding season cumulative survival for adult females from 1 April – 30 June based on Kaplan-Meier estimates was 0.694 (95% CI: 0.528 – 1.000) in 2011, and 0.761 (95% CI: 0.528 – 1.000) in 2012. Nest survival for the 25-day laying and incubation period was 0.440 (95% CI: 0.283 – 0.685) in 2011 and 0.778 (95% CI: 0.608 – 0.996) in 2012. Cumulative survival for juvenile woodcock based on Kaplan-Meier estimates for a 61-day period (1 May – 30 Jun.) was 0.330 (95% CI: 0.188 – 0.613) in 2011 and 0.576 (95% CI: 0.398 – 0.833) in 2012. We used logistic-exposure models to assess covariates hypothesized to be related to woodcock survival, including weather covariates (maximum temperature, minimum temperature, and precipitation), reproductive status (females), initiation date (nests), hatch date (juveniles), age (nests and juveniles), and vegetation characteristics (nests and juveniles) In all survival models, we included a year covariate

(females: $\beta_{2011} = -0.16$, 95% CI: -1.67 to 1.45, nests: $\beta_{2011} = -0.768$, 95% CI: -1.70 to

0.166, juveniles: $\beta_{2011} = -0.85$, 95% CI: -1.77 to 0.07) to account for between-year

variation in survival. However, our best-supported model of female survival was the null

model, suggesting female survival was constant across years, given the sample sizes and

environmental conditions we observed. Similarly, our best-supported model of nest

survival included only a year covariate, but with no statistically significant difference in

survival between 2011 and 2012. Our best-supported model of juvenile survival included

the covariates year, juvenile age ($\beta_{AGE} = 0.098$, 95% CI: 0.04 to 0.16), minimum

temperature ($\beta_{MINT} = 0.14$, 95% CI: -0.004 to 0.28), and precipitation ($\beta_{PCPT} = -0.20$,

95% CI: -0.39 to -0.01). Juvenile survival increased with age and decreased with the

amount of precipitation and had a weak positive relation with stem density ($\beta_{STEM} =$

0.0001, 95% CI: -0.000 to 0.0003). Woodcock in our study almost solely used areas

where BMPs had been applied on the landscape within the last 20 years and that had

similar vegetation structure, making it difficult to assess relationships between survival

and vegetation covariates. Our estimates of adult, nest, and juvenile woodcock survival

were generally lower than those estimated in other studies, suggesting there may be

considerable variation temporally and spatially in woodcock survival on managed areas.

Similar to recent studies of songbird full-season productivity, our results suggest that

juvenile survival from hatch to independence from adult care, and factors related to

juvenile survival may be key to understanding woodcock population ecology.

INTRODUCTION

American woodcock (*Scolopax minor*; hereafter woodcock) have experienced significant long-term population declines in the Eastern and Central Management Regions (0.8 % per year) since American Woodcock Singing-ground Surveys (SGS) were first implemented in the mid-1960s (Cooper and Rau 2012). These apparent declines in population are coupled with declines in woodcock recruitment across their range (indexed through juvenile/adult female ratios derived from wing-collection surveys; Cooper and Rau 2012). Extensive loss or alteration of habitat critical to woodcock reproduction has been suggested as the main cause of these declines (Dwyer et al. 1988, Gregg 1984, Sauer and Bortner 1991, Kelley et al. 2008). Kelley et al. (2008) proposed stabilizing and ultimately increasing woodcock populations by increasing woodcock density on portions of the primary breeding range to that observed during the 1970s. As part of that effort, a system of woodcock habitat demonstration areas are being developed throughout the primary woodcock breeding range where specific Best Management Practices (BMPs) are applied (Wildlife Management Institute 2010). These areas are meant to demonstrate management practices to increase the amount of and to improve existing habitat to encourage increases in woodcock breeding population density and size.

Application of BMPs at a demonstration-area scale (~200–800 ha) is designed to positively influence woodcock population growth by improving habitat quality and

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abundance at a landscape scale. Best Management Practices create or maintain young

forest cover through clear-cutting, timber harvest, shearing of brush and small trees, and

prescribed burning (Wildlife Management Institute 2009). Best Management Practices

are applied at specific sites within the larger landscape, but when applied at multiple

locations at the demonstration-area scale, they create a juxtaposed mosaic of young forest

cover of different age classes that provides breeding, nesting, brood-rearing, and diurnal

feeding habitat for woodcock. Woodcock are known to respond numerically to

vegetation management (Dwyer et al. 1988, McAuley et al. 1996); therefore, it is

assumed that increasing the amount of young forest cover at the demonstration-area scale

will increase woodcock population size. However, how woodcock vital rates are

influenced by BMPs applied at a landscape scale is not fully understood, although there

are some woodcock survival estimates in the eastern portion of the woodcock breeding

range where BMPs have been applied (Dwyer et al. 1988; McAuley et al. 1996, 2010;

Longcore et al. 2000). These studies were completed prior to the establishment of

demonstration areas, making it difficult to relate survival rates with application of BMPs

at the demonstration-area scale.

Our objectives were to (1) estimate adult female, nest, and juvenile survival of

woodcock at a demonstration-area scale, and (2) assess relationships between survival

and vegetation structure (e.g., stem density, distance to edge, and basal area) resulting

from BMPs, life history traits (e.g., date of nest initiation, number of nesting attempts,

and female reproductive status), and weather (e.g., precipitation, maximum temperature,

and minimum temperature). We expected that woodcock survival would be related to

BMPs applied at a demonstration-area scale, and survival would be related to characteristics of cover types, life history, and weather, based on both previous literature (e.g., Dwyer et al. 1988) and the assumptions inherent in managing landscapes for woodcock.

STUDY AREA

We conducted our study on Tamarac National Wildlife Refuge (NWR) located near Rochert, Minnesota, USA (47.0 N, -95.7 E). Tamarac NWR lies in the glacial lake country of west-central Minnesota in Becker County and encompasses 17,296 ha dominated by forested cover types, intermingled with lakes, rivers, marshes, shrub swamps, and tallgrass prairie. Tamarac NWR is located in the transition zone between coniferous forest, northern hardwood forest, and tallgrass prairie. Sixty percent of the refuge is forested; the dominant tree species are aspen (*Populus* spp.), jack pine (*Pinus banksiana*), red pine (*P. resinosa*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red oak (*Quercus rubra*), white oak (*Q. alba*), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*). A substantial portion of the refuge is managed for early successional forest, primarily through timber harvest and prescribed fire, to provide breeding, nesting, and brood-rearing habitat for woodcock, Golden-winged warblers (*Vermivora chrysoptera*), and other migratory birds that utilize young forests.

METHODS

Capture and Radio Telemetry

We equipped adult female and juvenile woodcock with radio transmitters in the landscape at Tamarac NWR in 2011 and 2012 where BMPs had been applied. In March − June of 2011 and 2012, we used mist nets to capture woodcock during dusk (approximately 1900 to 2300 CDT) when woodcock leave diurnal areas to roost or feed (Sheldon 1971). We determined sex of all woodcock captured based on plumage characteristics (Martin 1964) and radio-marked adult female woodcock using a glue-on backpack-style harness that was ≤3% of their total mass (~4.8 g, model A5410, Advanced Telemetry Systems, Isanti, MN; McAuley et al. 1993*a*, 1993*b*). We relocated radio-marked female woodcock from the time that we released them through late June or early July of each year to estimate survival during the breeding, nesting, and brood-rearing periods, and for the beginning of the period following independence from a brood and prior to migration. We relocated radio-marked female woodcock 5-7 days per week throughout the breeding season (April – June) and into the beginning of the pre-migration season (July – October). We lost radio contact with some females when they traveled long distances, out of the range of our receiving equipment and monitoring protocol. We continued searching for these females throughout our field season and if we did not relocate them, we classified these females as "lost." When we relocated an adult female radio-marked woodcock, we assessed its status (i.e., alive or dead) and assigned it to one

of four categories related to reproduction: pre-nesting, incubating, brood-rearing, or pre-migration. If a radio-marked woodcock was dead when relocated, we assessed the cause of death, and if possible, assigned the cause of death as either mammalian or avian predation using methods described by McAuley (2005). Pre-nesting included the time from capture until egg laying and also the period between nest or brood loss and renesting. If a female renested following a failed nesting or brood-rearing attempt, we categorized her as pre-nesting between loss of eggs or young and initiation of another nesting attempt. Incubation was the period between the beginning of egg laying and either loss of the nest or hatch. Brood rearing was the period from hatch to the loss of all juveniles in the brood or fledging (15 days post-hatch). Pre-migration was the period from the end of breeding activity (i.e., date of fledge or loss of a brood or nest without a re-nesting attempt) until the last known fate of the female.

We found woodcock nests using trained pointing dogs (McAuley et al. 1993*a*) and via radio telemetry of incubating radio-marked adult females. We visited each nest at 2-3 day intervals and assessed the status of the nest as active, depredated, abandoned, or successful. If the female was not present at the nest or flushed during our visit, we floated any eggs present in ambient-temperature water to estimate nest age and initiation date (Ammann 1974). We considered nests to be active when the adult female was engaged in egg-laying or incubation, or if a female was incubating at a subsequent visit. We categorized nests as depredated if eggs were broken or absent prior to the estimated hatch date. We categorized nests as abandoned if the female was not observed incubating for two consecutive visits. We categorized nests as successful if there was evidence that

one or more eggs hatched (i.e., eggshells in or close to the nest bowl and with a longitudinal split).

To estimate survival of juvenile woodcock, we assessed the status of juveniles in broods of radio-marked adult females and also radio-marked a sample of juveniles within broods of radio-marked adult females. We used trained pointing dogs to find additional broods of unmarked adult female woodcock (Mendall 1938; Ammann 1974, 1977) and captured and radio-marked juveniles in those broods. We custom fit a micro-transmitter (BD-2NC or BD-2C, Holohil Systems Ltd., Carp, ON and custom transmitters made by Blackburn Transmitters, Nacogdoches, TX) with a whip antenna to captured juvenile woodcock by means of an elastic collar. All transmitter packages were ≤3% of a bird's mass (BD-2NC transmitters weighed approximately 0.6 g, BD-2C transmitters weighed approximately 1.6 g, and Blackburn transmitters weighed approximately 0.4 g).We attached transmitters to juvenile woodcock with an elastic collar that expanded as the juvenile woodcock grew. We positioned transmitters at the base of a juvenile woodcock's neck with the transmitter antenna lying down the juvenile's back. Transmitter lifespan was approximately 21 days (17-30 day range) for BD-2NC transmitters, 63 days (49-77 day range) for BD-2C transmitters, and 28 days (24-32 day range) for Blackburn transmitters.

We radio-marked 1-4 juveniles per brood and monitored both marked and unmarked individuals within a brood after locating radio-marked juveniles. We located broods 4-7 days per week by tracking either the adult female or juvenile(s). We assessed status (alive or dead) of juveniles and counted both marked and unmarked juveniles to

document brood size. We counted the number of individuals in the brood by tracking a radio-marked bird(s) to a distance of approximately 5 m and then encircling the brood until we were certain we detected and counted all brood members. Beginning approximately 15 days after hatching, entire broods often flushed upon our approach, affording us the opportunity to accurately determine brood size. Beyond 15 days post-hatch, the probability of detecting all members of the brood diminished as individuals from broods became more dispersed until we no longer considered them associated with one another. Because we were not able to accurately determine the fate of unmarked juveniles after the brood separated (~24 days old), we right censored unmarked juveniles at 24 days old, which was the earliest we observed brood separation.

Survival Model Covariates

For monitored females, nests, and juveniles we used covariates for year, weather (i.e., maximum temperature, minimum temperature, and precipitation) and attributes of individuals (e.g., juvenile age) to create a set of *a priori* models of survival (Table 1). We used vegetation structure covariates (i.e., stem density, basal area, and distance to nearest edge) in *a priori* models of nest survival and in a *post hoc* analysis of juvenile survival (see below). We considered covariates based on published literature and hypothesized relationships with woodcock survival.

Sepik et al. (2000) reported that weather early in the breeding season impacted woodcock recruitment, which is determined by survival of adult females, nests, and juveniles. We obtained daily weather data from a standard 20.3-cm diameter precipitation gauge and digital temperature logger (Nimbus Digital Thermometer, Sensor

Instruments Co., Inc.) at Tamarac NWR during 2011 and 2012. Precipitation and

temperature data were recorded approximately 6 to 8 km southeast of where we

monitored woodcock.   If precipitation and temperature data from Tamarac NWR were

not available, we used weather data from the nearest National Weather Service station in

Detroit Lakes, Minnesota (approximately 22 km southeast of Tamarac NWR). We used

the sum of precipitation (cm) for each day in the interval between observations to

calculate total interval precipitation (PCPT). We used the recorded maximum (MAXT)

and minimum (MINT) temperatures (°C) during each interval between observations in

models of survival of woodcock females, nests, and juveniles (Table 1).   We included

year (YEAR, 2011 or 2012) as a class variable in our models to account for between-year

variation in survival because survival of females, nests, and juveniles can vary between

years (Gregg 1984, Longcore et al. 2000, McAuley et al. 2010).

We measured vegetation characteristics at a subset of woodcock brood locations

and at all nest locations. We included stem density (STEM), basal area (BAS), and

distance to edge (EDGE) as covariates in models of nest and juvenile survival.

Woodcock frequent young forest cover types in the spring during nesting and brood

rearing and prefer areas of high stem density and low basal area (Sepik and Dwyer 1982,

McAuley et al. 1996, Dessecker and McAuley 2001), which may impact survival of

juveniles by affecting their ability to avoid predation or adverse environmental

conditions, and survival of nests because increased woody cover likely decreases

predation. We predicted that female, nest, and juvenile survival would have a positive

relationship with stem density and a negative relationship with basal area. We measured

vegetation structure using plot-based methods modified from McAuley et al. (1996),

centering plots 0.4 ha in area (11.3-m radius) at nests and brood locations. We counted

the number of trees in five size classes adapted from James and Shugart (1970) based on

diameter at breast height (DBH) (7.6 - 15.2 cm, 15.3 - 22.9 cm, 23.0 - 38.1 cm, 38.2 -

53.3, and > 53.3 cm), and estimated basal area (m^2/ha, McAuley et al. 1996) by assigning

each tree in each size class the average DBH for that size class using the formula from

Avery and Burkhart (2002):

$$\text{Basal Area} = 0.00007854 \times \text{DBH}^2,$$

We then summed basal area for all trees in the plot to estimate basal area for the plot.

To estimate stem density (stems/ha, McAuley et al. 1996), we established four belt

transects beginning at the central point of the plot, 3 m in width and 20 m in length (0.006

ha), in one random azimuth in each quadrant (NE, SE, SW, NW). On each transect we

counted the number of woody stems <7.6 cm DBH and >1 m tall within the transect area

and pooled the stem counts for the four transects to estimate stem density for the plot.

We hypothesized that distance to an edge would have a positive relationship with

nest and juvenile woodcock survival. We defined edges as distinct changes in height of

forest vegetation that were either anthropogenic (i.e., roads, trails, or forest clearcuts) or

natural (i.e., forest openings or wetland edges). We measured distance to edge by

visually interpreting changes in forest vegetation height using 1-m resolution aerial

photographs (2010 photos) in ArcMap 10.0 (ESRI 2011. ArcGIS Desktop: Release 10,

Environmental Systems Research Institute, Redlands, CA).

We hypothesized that reproductive status and time spent with a brood would be related to female woodcock survival (Table 1). Because reproductive status influences the behavior and energetic requirements of female woodcock (Rabe et al. 1983), we modeled survival including four categories of reproductive status (REPRO: pre-nesting, incubating, brood rearing, and pre-migration). We hypothesized that females would have lower survival during incubation and brood rearing due to increased likelihood of depredation (Longcore et al. 2000), which has been observed for other terrestrial ground nesting birds (e.g., Arnold et al. 2012) and higher energetic requirements (Rabe et al. 1983). High energetic requirements during brood rearing also may lead to decreased survival during the brood-rearing period (Rabe et al. 1983). Therefore, we included a covariate indicating whether females were with broods (BROOD) in our models of adult female survival. We could not clearly define period lengths for each reproductive status because these periods varied with each individual; therefore, we used Mayfield's method (Mayfield 1961, Johnson 1979) to directly assess the relationship between female survival and reproductive status.

We included age and hatch date in our models of juvenile survival and hypothesized that juvenile survival increased asymptotically with age; therefore, we hypothesized that juvenile age would have a positive relationship with survival and included it as a continuous variable (JAGE) in our survival models. We calculated juvenile age by knowing the hatch date of juveniles or estimating age at capture based on bill measurements (Ammann 1982, Sepik 1994). Because intervals between relocations of individual broods were short we used the age of a juvenile at the midpoint of the

interval in our survival models. We estimated Julian hatch date (HD) by either

monitoring nests of radio-marked females or by aging juveniles at the time of capture and

deriving HD based on juvenile age. Juveniles that hatch earlier may be exposed to more

extreme environmental conditions but also may be from females in the best condition

(Blums et al. 2005). Because we monitored nests of radio-marked females every 2-3

days, we generally were able to estimate HD within one day.

We hypothesized that nest initiation date (INIT) would be related to woodcock

nest survival. Earlier nest initiation has been associated with higher nest survival for

several species (e.g., Newlon and Saab 2011) and we hypothesized that nests initiated

earlier had higher survival than nests initiated later. Woodcock are known to readily

renest; however, only one re-nest per female has ever been observed in a single breeding

season (McAuley et al. 1990, personal observation). Woodcock generally renest

following a failed nest or if they lose a brood <11 days old (McAuley et al. 1990). We

were unable to assess whether most nests in this study were first nests or renesting

attempts; therefore, we could not include nesting attempt as an additional covariate in our

analysis. We estimated nest initiation date by floating eggs in ambient temperature water

(Ammann 1974) at nest discovery, or by monitoring nests until hatch and back dating 25

days.

For our survival analyses where we were missing covariate data, we used the

mean covariate value for that year if < 5% of the data were missing (i.e., if initiation date

was not known for a nest, we used the average nest initiation date for all nests for which

we knew the nest initiation date that year). If ≥ 5% of the data were missing we excluded

all observations with missing covariate data from analysis.

A Priori Model Development

We used logistic-exposure survival models (Shaffer 2004) to evaluate

relationship(s) between weather and individual characteristics and female, nest, and

juvenile survival. We also used logistic-exposure models to assess the relationship(s)

between vegetation characteristics and survival of nests and juveniles. We developed *a*

priori models to evaluate factors related to adult female, nest, and juvenile survival that

incorporated covariates related to hypotheses about effects of weather and individual

characteristics.   We incorporated covariates relating vegetation structure in our set of *a*

priori models of nest survival and in a *post hoc* analysis of juvenile survival. We

evaluated models using a stepwise approach in an information-theoretic framework

(Burnham and Anderson 2002). We started with an initial model incorporating YEAR

for each survival model of females, nests, and juveniles to assess survival differences

between 2011 and 2012 and to account for reported differences in woodcock survival

between years (Gregg 1984, Longcore et al. 2000, McAuley et al. 2010). During each

step of our modeling process subsequent to the initial model, we added covariates to the

best-supported model from the previous step individually and in all combinations and

ranked models based on Akaike's Information Criterion adjusted for small sample size

(AIC_c) to identify the best-supported model among all candidate models. We defined our

best-supported model as the model with the lowest AIC_c ($\Delta AIC_c = 0$) and competing

models as any models with $\Delta AIC_c \leq 2$. We considered covariates uninformative if they did not reduce overall AIC_c when added to the best-supported model from the previous step (Arnold 2010). We did not consider models containing the uninformative covariates to be competitive with our best-supported model, and excluded them from subsequent analyses.

Female survival model development.—We added reproductive status of the female (REPR) to the initial model (the model including only YEAR) for our first step of modeling female survival. We only considered the covariates NEST and BROOD if REPR was an informative variable (i.e., reduced overall AIC_c when compared with the initial model) in our best-supported model because both NEST and BROOD were correlated with the reproductive stage of the female (REPR).

We then added weather covariates (PCPT, MINT, and MAXT) to our best-supported model from the previous step to assess the relationship between weather and female survival. We used the best-supported model to assess the relationships between daily survival and covariates included in that model by entering multiple values representing the range of observed values for that variable while holding the other model variables constant at their mean values.

Nest survival model development.—We first modeled nest survival including only YEAR, and then added INIT and NAGE as nest-specific covariates to the initial model (the model including only YEAR). We then added weather covariates to the best-supported model considering YEAR, INIT, and NAGE to evaluate the relationship between weather and survival of woodcock nests. Finally, to our best-supported model

that incorporated YEAR, nest specific covariates, and weather covariates we added

STEM, BAS, and EDGE to evaluate the relationship between nest survival and

vegetation characteristics. We used the ESTIMATE statement in SAS 9.3 (SAS Institute

Inc., North Carolina, USA) to assess the relationship(s) between daily survival and

individual covariates in the best-supported model by entering multiple values

representing the range of observed values for that covariate while holding the other

model variables constant at their mean values.

Juvenile survival model development.—Survival of individual juveniles may not

be independent from survival of other individuals of the same brood (Chouinard and

Arnold 2007, Amundson and Arnold 2010). Therefore, we evaluated whether survival

was independent among individual juveniles within broods and whether radio

transmitters affected survival of juveniles, and found no evidence to suggest non-

independence in survival among brood mates (Chapter 3). We therefore treated

individual juveniles as independent samples in subsequent survival analyses.

We added JAGE, HD, and the interaction between HD and YEAR to the initial

model including only YEAR for the second step of our stepwise approach to modeling

juvenile survival to account for the effects of age and hatch date. We included the

interaction between HD and YEAR in models of juvenile survival because annual

changes in temperature and precipitation affect the timing of woodcock breeding

(Murphy and Thompson 1993).   Next, we added weather covariates (MAXT, MINT, and

PCPT) to the best-supported survival model considering YEAR, JAGE, and HD from the

previous step to account for relationships between weather conditions and survival of

juvenile woodcock.   We used the best-supported model to assess the relationships

between daily survival and the covariates included in the model by entering multiple

values representing the range of observed values for that covariate in the model while

holding other model variables constant at their mean values.

Finally, to evaluate additional relationships between vegetation characteristics and

juvenile survival, we conducted *post hoc* analyses by considering STEM, BAS, and

EDGE as covariates in models of juvenile survival. We assessed these covariates in *post*

hoc analyses because only a subset of juvenile locations had associated vegetation

characteristic data. To the best-supported model from our *a priori* analysis, we added

STEM, BAS, and EDGE singularly and in all possible combinations. We used the best-

supported model from our *post hoc* analysis to assess the relationships between daily

survival and covariates included in the model by entering multiple values representing the

range of observed values for that covariate in the model while holding the other model

variables constant at their mean values.

Survival Estimates.—We used the Kaplan-Meier method with staggered entry

(Pollock et al. 1989) using the KMsurv package in Program R (version 2.15.2, R Core

Team, 2012) to estimate survival of adult females, nests, and juveniles. We estimated

survival of adult females, nests, and juveniles separately for 2011 and 2012. We used

Kaplan-Meier procedures to estimate survival during the biological period defined by the

data for 2011 (1 April – 29 June) and 2012 (11 April – 30 June), and then calculated daily

survival rate (DSR) estimates from these period survival rate (PSR) estimates. We

extrapolated the DSR estimates over the same period length for 2011 and 2012 to directly

compare survival between years. For female woodcock we estimated survival for a 91-day period (1 April – 30 June). We estimated nest survival using a 25-day period that included four days for egg laying and 21 days for incubation.   We estimated juvenile survival for a 61-day period (1 May- 30 June).

We recorded the number of days from when we deployed transmitters on females and juveniles to more accurately censor individuals if radio transmitters failed prematurely. We assumed radios failed if they performed irregularly and there was no other indication an individual had died. We also assumed radios failed if they were nearing the end of their expected battery life and we subsequently received no additional signals from transmitters. We right-censored individuals in both of these circumstances, assuming the individual survived until transmitter failure (Korschgen et al. 1996).

RESULTS

Vegetation Characteristics

Nest vegetation characteristics.—We measured vegetation characteristics (stem density, basal area, and distance to edge) at 45 nest locations (Table 2).   Nests in 2011 and 2012 had similar stem densities; however, nests in 2011 had greater basal area and were farther from edges than nests in 2012 (Table 2).

Brood-rearing vegetation characteristics.—We measured vegetation characteristics (stem density, basal area, and distance to edge) at 121woodcock brood locations (2011: $n = 66$, 2012: $n = 43$) representing 45 juvenile woodcock (2011: $n = 22$, 2012: $n = 23$) from 14 broods (2011: $n = 8$, 2012: $n = 6$).   Stem density and basal area at juvenile woodcock locations were higher in 2012 than in 2011 (Table 2). Woodcock brood locations were closer to edges in 2012 than in 2011 (Table 2).

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Survival

Female survival.—From 9 April to 1 June 2011 and 22 March to 24 May 2012 we captured and radio-marked 41 adult female woodcock (2011: $n = 23$, 2012: $n = 18$). We excluded 3 (~7%) radio-marked adult female woodcock in 2011 from survival analysis that we were unable to relocate following radio marking (likely due to transmitter failure or migration). Of the remaining 38 female woodcock, we right censored one female that became entrapped in its radio telemetry harness in 2012.

In 2011 and 2012, we observed 692 intervals and 2,149 exposure days of radio-marked adult female woodcock. Intervals averaged 3.1 days between relocations and ranged from 1 day to 40 days (although intervals were generally short, 1 female left the search area and later returned and was relocated alive after 40 days). Seven of 38 (~18%) adult females were killed by predators during our study (2011: $n = 4$, 2012: $n = 3$). Mammalian predation was the highest source of mortality ($n = 4$), with the remainder attributed to raptors ($n = 3$). Mortalities of female woodcock occurred during pre-nesting ($n = 2$), nesting ($n = 2$), brood-rearing ($n = 1$), and pre-migration periods ($n = 2$). Apparent survival of females was nearly constant across reproductive stages (pre-nesting = 0.909, nesting = 0.913, brood rearing = 0.957, and pre-migration = 0.935). Daily survival based on Mayfield's method (Mayfield 1961, Johnson 1979) also was nearly constant across reproductive stages [pre-nesting = 0.995 (95% CI: 0.987 – 1.00), nesting = 0.996 (95% CI: 0.990 – 1.00), brood-rearing = 0.996 (95% CI: 0.989 – 1.00), and pre-migration = 0.998 (95% CI: 0.995 – 1.00)].

Our best-supported model of adult female woodcock survival was the null model (Table 3), suggesting that female survival was relatively constant between 2011 and 2012

and over the conditions we observed during our study. Although we constructed our base

model to include YEAR to account for differences in survival between 2011 and 2012;

survival was similar between years ($\beta_{2011}= -0.16$, 95% CI: -1.67 to 1.45) and a null

model that excluded year effects had a lower AIC_c (Table 3). No other covariates were

related to survival of adult females. Models that included MINT, MAXT, and PCPT were

within two AIC_c units of our top model (Table 3); however, we considered these

covariates to be uninformative because they did not reduce AIC_c relative to the simpler,

higher-ranked model (Arnold 2010). Because there was no evidence to suggest that

REPR was related to female woodcock survival (Table 3), we did not assess the

relationship(s) between female survival and NEST and BROOD in *post hoc* analyses.

Breeding season cumulative survival for adult females from 1 April – 30 June

based on Kaplan-Meier estimates was 0.694 (95% CI: 0.528 – 1.000) in 2011, and 0.761

(95% CI: 0.528 – 1.000) in 2012 (Table 4).

Nest survival.—We monitored 52 woodcock nests (2011: $n = 26$, 2012: $n = 26$)

from 4 May to 11 June 2011 and from 9 April to 9 June 2012. We censored four nests

from our analysis (one in 2011 and three in 2012). Of the 45 nests we included in our

analyses, eggs failed to hatch in 21 (~47%) and were either predated (71%) or abandoned

by the female (29%).   .

Our best-supported model of nest survival included only YEAR, with no

difference in survival between 2011 and 2012 ($\beta_{2011}= -0.768$, 95% CI: -1.70 to 0.166,

Table 5). Addition of other covariates did not result in competitive models (Table 5).

Cumulative survival for a 25-day laying and incubation period for nests based on Kaplan-Meier estimates was 0.440 (95% CI: 0.283 – 0.685) in 2011 and 0.778 (95% CI: 0.608 – 0.996) in 2012 (Table 4).

Juvenile survival.—From 16 May to 29 June 2011 and 20 April to 16 June 2012 we radio-marked 73 (2011: $n = 22$, 2012: $n = 51$) juvenile American woodcock from 51 broods (2011: $n = 16$, 2012: $n = 35$). We assigned fates of 134 juvenile woodcock (2011: $n = 63$, 2012: $n = 71$), including fates from 49 marked and 85 unmarked juveniles from 47 broods (2011: $n = 23$, 2012: $n = 24$), resulting in an effective sample size of 859 observation intervals. We excluded data from 24 marked juvenile woodcock due to uncertainty regarding transmitter failure (i.e., we did not know if the transmitter failed or if the juvenile was depredated). Cumulative survival for juvenile woodcock based on Kaplan-Meier estimates for a 61-day period (1 May – 30 June) was 0.330 (95% CI: 0.188 – 0.613) in 2011 and 0.576 (95% CI: 0.398 – 0.833) in 2012 (Table 4).

Our best-supported model of juvenile woodcock survival included YEAR, JAGE, MINT, and PCPT (Table 6). In our best-supported model, 95% confidence intervals around coefficient estimates for YEAR ($\beta_{2011}= -0.85$, 95% CI: -1.77 to 0.07) and MINT ($\beta_{MINT} = 0.14$, 95% CI: -0.004 to 0.28) included zero, indicating no statistically significant relationship with survival of juvenile woodcock (Table 6). JAGE ($\beta_{AGE} = 0.098$, 95% CI: 0.04 to 0.16) was positively associated with juvenile survival and PCPT ($\beta_{PCPT} = -0.20$, 95% CI: -0.39 to -0.01) was negatively associated with juvenile woodcock survival. Daily survival of juvenile woodcock decreased approximately 0.007

for each additional cm of precipitation. Juvenile daily survival increased approximately 0.002 for each additional day of age up to 15 days old.

We considered covariates related to vegetation structure in our *post hoc* analysis of juvenile survival. STEM was the only covariate related to vegetation characteristics to decrease AIC_c when added to our best-supported model based on our stepwise *a priori* analysis (Table 7). STEM had a significant positive relationship with juvenile woodcock survival ($\beta_{STEM} = 0.0001$, 95% CI: 0.000 to 0.0003). Juvenile daily survival increased with stem density, resulting in a 0.006 increase in survival for every additional 10,000 stems/ha.

DISCUSSION

Understanding the influence of BMPs applied at a demonstration-area scale on woodcock vital rates can help elucidate how the application of BMPs at this scale may affect local population growth. Although female, juvenile, and nest survival have been estimated previously for woodcock, these estimates are limited to the eastern portion of their breeding range (e.g., Wiley and Causey 1987, Derleth and Sepik 1990, Krementz and Berdeen 1997, Longcore et al. 2000) and estimates are not available at the demonstration-area scale.

Our estimates of survival of females and nests were lower than those reported in other studies (Table 4; Mendall and Aldous 1943, Gregg 1984, Derleth and Sepik 1990, McAuley et al. 1996, Longcore et al. 2000) and our estimates of juvenile survival were similar to (Gregg 1984, Wiley and Causey 1987) or higher than survival rate estimates reported in other studies (Table 4; Dwyer et al. 1988, McAuley et al. 2010). These

previous studies also were carried out in areas where management for woodcock was applied. Woodcock are known to respond to vegetation management and select managed areas to breed, nest, and rear broods (Dwyer et al. 1988, McAuley et al. 1996). Woodcock are also known to select for a narrow range of habitat conditions (McAuley et al. 1996). We did not observe any evidence of relationships between survival of females and nests and vegetation characteristics; however, we did observe a slight positive relationship between juvenile survival and stem density. We likely had difficulty detecting relationships between survival and vegetation characteristics created by application of BMPs because female woodcock selected for similar cover types for diurnal cover, nesting, and brood rearing.

Female Survival

No covariates we included in our analysis were associated with female woodcock survival suggesting that female survival did not differ between years, with reproductive status, or as a function of the environmental conditions we observed. In contrast, Longcore et al. (2000) reported that survival of female woodcock breeding in Maine varied among years during the four-year course of their study on area that was managed for woodcock. Longcore et al. (2000) estimated mean female survival during the breeding season (1 April to 15 June) to be 0.810 for second-year females (females known to be in the second calendar year of life), and 0.815 for after-second-year females (females known to be in their third or later calendar year of life) in a similar radio-telemetry study in Maine. Derleth and Sepik (1990) reported post-breeding season (15 June – 20 October) survival of adult females ranged from 0.88 to 0.90. Our breeding-

season survival estimates generally were lower than those reported by Longcore et al. (2000) for the same 76-day period (1 April to 15 June), and lower than their four-year mean of 0.826, suggesting that females in the western portion of the breeding range of woodcock may survive at lower rates during the breeding season. However, some breeding-season survival estimates for years reported by Longcore et al. (2000) were similar to our estimates (Table 4), suggesting that adult female woodcock survival may be variable among breeding seasons.

Inter-year variation in survival has been observed in woodcock in both the breeding season and during fall (Longcore et al. 2000, Bruggink et al. 2013). Longcore et al. (2000) attributed inter-year differences in survival to one year with lower female survival due to an extended period of nesting. However, we observed no relationship between reproductive status of females and survival, which suggests females may not be more vulnerable during nesting as speculated by Longcore et al. (2000) and reported for other ground-nesting species (e.g., Brasher et al. 2006). Female woodcock may be vulnerable to predation at a similar rate independent of their reproductive status due to their cryptic nature and relatively high mobility (Derleth and Sepik 1990).

Temperature and precipitation conditions varied considerably throughout our study; however, we did not observe a relationship between female survival and minimum or maximum temperatures or precipitation. Longcore et al. (2000) found no relation between survival and minimum temperature in the spring. Females also may delay or reduce energetically costly behaviors (breeding and nesting) in spring if weather conditions are adverse or food availability is low, allowing for high survival of females

during the spring (Rabe et al. 1983, Longcore et al. 2000). Females likely are able to withstand consistent temperatures below freezing because of their relatively large body size and associated increased thermoregulatory ability to conserve heat (Mendall and Aldous 1943, Longcore et al. 2000).

We did not assess the relationship between adult female survival and vegetation characteristics during the breeding season because our vegetation data were recorded only when females were associated with a nest or brood. Because few radio-marked female woodcock in our study died, our estimates of breeding-season survival were relatively high for both years, which constrained our ability to assess relationships between habitat characteristics and adult female survival. However, at less-fine categories [e.g., hardwoods, conifers, and alder (*Alnus* spp.)] of forest cover types in Maine, Longcore et al. (2000) detected survival differences between cover types used by female woodcock.

Nest Survival

We found no relationships between year, initiation date, weather, or vegetation characteristics and survival of woodcock nests. Considerable differences can occur in nest-site selection when females return to breeding areas in spring and snow depth likely influences availability of nest sites (Sepik et al. 1989, McAuley et al. 1990). Spring phenology was much earlier in 2011 than 2012 on our study site, and snow depths in 2011 were substantially higher than in 2012 early in the nesting period. If nest-site selection is dependent on early spring snow depths, vegetation characteristics around nest sites are likely to vary between years. Our results indicated nest-site selection differed

between years at our study site. Basal area was higher around nesting sites in 2012, perhaps because lower snow depth that year made areas farther from edges and with more mature trees available for nesting. Although distance to edge may have been farther in 2011 than 2012, this was likely an artifact of our sample of females. In 2011 we captured a higher proportion of females prior to nesting than we did in 2012.   In 2012 we captured more females when they were already associated with a nest that we found by searching along edges with dogs, perhaps biasing our sample in that year to nests closer to edges. We found no difference in stem densities between years, which suggests that woodcock select for high stem densities independent of other nesting vegetation characteristics.

We also suspect that difference in snow depth between 2011 and 2012 affected the timing of nesting; the mean initiation date in 2011 was 3 May (SE = 2.3 days) and in 2012 was 19 April (SE = 3.6 days). Roboski and Causey (1981) and Dwyer et al. (1988) also found nest initiation dates to differ between years and suggested local weather conditions as the cause.   In Missouri, Murphy and Thompson (1993) observed nest initiation peak when male displaying activity was highest, which also could be delayed if unfavorable weather conditions are present. Therefore, female woodcock likely are taking advantage of favorable weather conditions to nest, as suggested by Whiting (2006).

Woodcock select for nest sites with relatively low basal area and high stem density (McAuley et al. 1996). Stem density around nests in our study was similar to that in Maine (McAuley et al. 1996, also based on radio telemetry), where stem densities were high ($\bar{x}$ = 13,919 stems/ha, SE = 1,688). Nest sites we found in 2011 had similar basal area as nest sites in Maine ($\bar{x}$ = 9.5 m^2/ha, SE = 1.0, McAuley et al. 1996); however, nest

sites we found in 2012 had higher basal area than those in 2011 and than those reported by McAuley et al. (1996) in Maine. Our 2012 estimate of basal area surrounding nest sites is the highest reported to date (McAuley et al. 1996), which may have been due to the unseasonably early spring. Under the conditions we observed in 2012, woodcock may have selected more mature forest cover types for nesting than previously thought if those areas had less snow and therefore afforded more available nest sites. Murphy and Thompson (1993) measured stem densities, basal area, and distance from field in a study of woodcock nest sites in Missouri; their average stem density and distance to field were considerably lower than our average stem density and distance to edge, but their estimates of basal area were similar to ours. The difference in these measurements could be due to a bias in their study because they only searched along edges to locate nests (Murphy and Thompson 1993).

Similar to results reported by McAuley et al. (1996), we found no differences in vegetation characteristics around nest sites between nests that failed and nests where eggs hatched. Across their breeding range, woodcock select nest sites with high stem density (McAuley et al. 1996), and we similarly observed high stem density at both failed and successful nests.

Our apparent nest survival for both years combined (0.56) was similar to the apparent survival of 0.59 reported by McAuley et al. (1996), 0.62 reported by Mendall and Aldous (1943), and 0.26 – 0.51 reported by Gregg (1984) using Mayfield's method (Mayfield 1961). Although we found no evidence that inclement weather or nest initiation date was related to nest survival, a late-season snow storm occurred on 7-8 May

2011 and resulted in many nests being abandoned, suggesting extreme weather events may cause lower nest survival in woodcock. A later nest initiation date in 2011 also may have affected nest survival; however, we may have been unable to detect these relationships because we included year as a covariate in our analysis and year may be correlated with other covariates.

Juvenile Survival

Total interval precipitation (PCPT) was the only covariate that showed a significant relationship with juvenile woodcock survival. Precipitation, especially high precipitation within an interval, was negatively related to juvenile woodcock survival. Sheldon (1971) and Owen (1977) suggested that periods of adverse weather (i.e., precipitation) can cause significant mortality in juvenile woodcock. Dwyer et al. (1988) reported finding a significant negative relationship between precipitation and juvenile production; this relationship also has been suggested in other precocial birds (e.g., Pietz et al. 2003, Brundey et al. 2013). Rabe et al. (1983) suggested that due to growth requirements of juvenile woodcock, weather-related stress has the greatest potential to limit survival of juveniles during the brood-rearing period.

Although juvenile age (JAGE) and minimum temperatures (MINT) did not exhibit a significant relationship with survival in our best-supported model, in previous steps in our modeling of juvenile survival, JAGE was positively related to survival, suggesting that survival increased with juvenile age. As juveniles age, they are better able to thermoregulate (Rabe et al. 1983) and may therefore better survive periods of inclement weather, and they also are better able to escape predators as they gain the

ability to fly. This is contrary to what Wiley and Causey (1987) estimated in Alabama, where juvenile woodcock had higher survival prior to fledge (<15 days), and were most vulnerable between fledge and brood break-up (15 to 32 days). However, they also suggested that this may have been due to their research methods, which may have negatively influenced juvenile survival (in contrast, we found no evidence for an effect of transmitters on survival, Chapter 3). In contrast to our results, Wiley and Causey (1987) reported no apparent effects of weather on juvenile woodcock survival. Similar to our results, McAuley et al. (2010) also found a positive relationship between juvenile survival and minimum temperature in Maine. Juvenile woodcock in northern parts of the breeding range (e.g., Minnesota and Maine) may be more likely to be physiologically stressed from exposure to cold and wet weather than juveniles in southern portions of their breeding range (e.g., Alabama). However, it was difficult for us to determine proximate cause of death of many radio-marked juveniles (e.g., predation versus exposure and subsequent consumption by a predator); therefore, it was not apparent whether or how predation and weather may have interacted to affect juvenile woodcock survival in our study.   We also were unable to determine the cause of death of unmarked juvenile woodcock.

Previous studies of woodcock survival were concentrated in the eastern portion of the woodcock breeding range on landscapes where young forest cover was an emphasis of management, and in general, published estimates of survival are higher than our estimates. Adult female survival was constant between years and under the environmental conditions experienced in our study, but nest and juvenile survival differed

between years, suggesting that nest and juvenile survival may be driving local population growth at the demonstration-area scale.   Similar to recent studies of songbird full-season productivity (Streby and Andersen 2011), our results suggest that juvenile survival from hatch to independence from adult care, and factors related to juvenile survival may be key to understanding American woodcock population ecology.

Table 1. Covariates used in logistic-exposure analysis of survival of American woodcock females, juveniles, and nests at Tamarac National Wildlife Refuge, Minnesota in 2011 and 2012, symbol, model(s) in which each covariate was included, and explanation of relationship between covariate and survival.

Covariate	Symbol	Model(s)
Basal area	BAS	Nest and Juvenile

Woodcock choose areas with relatively low basal area (Sepik and Dwyer 1982, McAuley et al. 1996, Dessecker and McAuley 2001). Areas with greater basal area provide a greater number of perches for raptors and therefore we hypothesize basal area to have a negative relationship with juvenile and nest survival.

Distance to edge	EDGE	Nest and Juvenile

It is a common assertion that edges provide travel corridors for mammalian, avian, and reptilian predators although empirical evidence is lacking or contradicting (Chalfoun et al. 2002, Lariviére 2003). However, nest survival of ground nesting birds has been shown to decrease around edges (Manolis et al. 2002). We hypothesized that survival of nests would be positively related to distance to an edge (Gregg 1984, Manolis et al. 2002) and made the same hypothesis for juvenile woodcock (Gregg 1984).

Hatch date	HD	Juvenile

Juveniles that hatch earlier are more likely to be from the females in the best condition (Blums et al. 2005); therefore we hypothesized that hatch date is negatively associated with juvenile survival.

Initiation date	INIT	Nest

Nests initiated earlier in the season experience higher survival than nests initiated later for many species (Newlon and Saab 2011); therefore, we hypothesized nest initiation date to have a negative relationship with nest survival.

Juvenile age	JAGE	Juvenile

Survival likely asymptotically increases with age of the juvenile because they are better able to thermoregulate as they age (Rabe et al. 1983) and likely most vulnerable to predation soon after leaving the nest (Streby and Andersen 2013); therefore, we hypothesized a positive relationship with age and juvenile survival.

Maximum temperature	MAXT	Female, Nest, and Juvenile

We predicted that maximum temperature would be positively related to

survival of females in the spring and was likely positively related to survival of nests and juveniles, especially early after egg laying or hatching. During the breeding season, energetic demands are high for female woodcock (Rabe et al. 1983), especially during egg laying, incubation, and brood rearing. Higher maximum temperatures likely increase survival of females during incubation and brood rearing (Rabe et al. 1983, Longcore et al. 2000). Females are also more active at higher ambient air temperatures (Vander Haegen 1992) and females will brood juveniles when temperatures are low (McAuley et al. 2010); therefore, at higher temperatures females likely spend more of their time foraging and are more capable of meeting their own energetic requirements and those of juveniles in their brood because females will feed juveniles for the first 7 days after hatch (Gregg 1984, Vander Haegen 1992).

Minimum temperature   MINT   Female, Nest, and Juvenile

We predicted female, nest, and juvenile survival would have a positive relationship with minimum temperature. Lower minimum temperatures likely decrease survival of adult females by decreasing earthworm availability in the spring (Vander Haegen et al. 1993) when energetic requirements are the highest during the breeding season (Rabe et al. 1983). Nests are likely to experience low temperatures and other adverse weather conditions in the spring (Dwyer et al. 1988) and may fail either because associated females have lower survival or females abandon nests due to high energetic demands. Juveniles may be less likely to survive at lower minimum temperatures because they lack the ability to thermoregulate (Sheldon 1971, Owen 1977, Rabe et al. 1983, McAuley et al. 2010).

Nest age   NAGE   Nest   .

Survival asymptotically increases with nest age, therefore we hypothesized that nest age has a positive relationship with nest survival

Precipitation   PCPT   Female, Nest, and Juvenile

Precipitation hinders the ability of woodcock to thermoregulate (Rabe et al. 1983) and has been negatively related to juvenile woodcock survival (Dwyer et al. 1988); therefore, we hypothesized that precipitation is negatively associated with female and juvenile survival. High amounts of precipitation also can cause nests to flood in low lying areas or females to abandon nests and thus decrease nest survival. We hypothesized precipitation to have a negative relationship with nest survival.

Reproductive status [a]   REPR   Female

Energetic requirements and behavior of adult females differ depending on reproductive stage (Rabe et al. 1983). High energetic costs during nesting and incubation and the females' association with the nest can make the female more vulnerable to predation (Longcore et al. 2000). Brood rearing

also can make decrease female survival due to sharing of food resources and tending to juveniles (Rabe et al. 1983). For these reasons, we hypothesized survival would be higher when females were not associated with a nest or brood.

| Stem density | STEM | Nest and Juvenile |

Woodcock select areas with high stem densities (Sepik and Dwyer 1982, McAuley et al. 1996, Dessecker and McAuley 2001) that provide thermoregulatory cover for juvenile and predatory cover for juveniles and nests. We hypothesized areas with higher stem densities have a positive association with juvenile and nest survival.

| Year [a] | YEAR | Female, Nest, and Juvenile |

Woodcock survival has been shown to differ between years (Gregg 1984, Longcore et al. 2000, McAuley et al. 2010). We included year in our analysis to account for annual variation in survival of females, juveniles and nests.

[a] Indicates a categorical variable.

Table 2. Comparisons of vegetation characteristics surrounding American woodcock nests in 2011 ($n = 22$) and 2012 ($n = 23$) and juvenile American woodcock locations in 2011 ($n = 116$) and 2012 ($n = 119$) at Tamarac National Wildlife Refuge, Rochert, Minnesota.

Vegetative characteristic	Year		$\bar{x}$ (SD)	t-statistic	df	P
Stem Density (stems/ha)						
	Nests					
		2011	12,113 (8,358)			
		2012	10,216 (4,297)	0.95	31	0.35
	Juveniles					
		2011	11,588 (5917)			
		2012	13,834 (5566)	−2.07	88	0.04
Basal Area (m^2/ha)						
	Nests					
		2011	7.7 (13.7)			
		2012	29.3 (36.9)	−2.62	28	0.01
	Juveniles					
		2011	11.9 (13.9)			
		2012	18.4 (17.3)	−2.16	80	0.03
Distance to Edge (m)						
	Nests					
		2011	45.3 (72.2)			
		2012	16.1 (23.6)	1.80	25	0.08
	Juveniles					
		2011	75.1 (86.6)			
		2012	55.6 (55.7)	2.04	195	0.02

Table 3. Stepwise model-selection results and *a priori* models of American woodcock adult female survival at Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. Survival related to year (YEAR; 2011 or 2012), reproductive status (REPR; pre-nesting, incubating, brood-rearing, or pre-migration), maximum and minimum temperature (MAXT and MINT), and precipitation (PCPT). Models were ranked according to the difference in Akaike's information criterion (ΔAIC_c) corrected for small effective sample size ($n = 2{,}091$ intervals) within steps. Akaike model weights (ω_i) and number of estimable parameters (K) are presented for each model. Null model includes only an intercept and no covariates and is presented as reference. Stepwise model development started with an initial model including only a YEAR covariate. Step two included the addition of the REPR covariate and step three included the addition of weather-related covariates.

Model step	Model	AIC_c	ΔAIC_c	ω_i	K
	Null	71.21	--	--	1
Initial model:					
	YEAR	73.15	--	--	2
Step two:					
	YEAR [a]	73.15	0.00	0.92	2
	YEAR+REPR	78.06	4.91	0.08	6
Step three:					
	YEAR [b]	73.15	0.00	0.29	2
	YEAR+MINT	73.74	0.59	0.21	3
	YEAR+PCPT	74.89	1.74	0.12	3
	YEAR+MAXT	75.11	1.96	0.11	3
	YEAR+MINT+PCPT	75.27	2.12	0.10	4
	YEAR+MAXT+MINT	75.61	2.46	0.08	4
	YEAR+MAXT+PCPT	76.64	3.49	0.05	4
	YEAR+MAXT+MINT+PCPT	77.27	4.12	0.04	5

[a] Indicates best-supported model for each step, model moved on to next step in analysis.
[b] Indicates best-supported overall model; AIC_c of top-ranked model = 73.15.

Table 4. Comparison of American woodcock survival estimates for adult females, nests, and juveniles from Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012, and American woodcock survival estimates from previous studies. Period survival rates (PSR) are estimated for the breeding season for adult females and juvenile woodcock. PSR for female woodcock was calculated for a 91-day period, for juvenile woodcock for a 61-day period, and for woodcock nests for 25-day egg-laying and incubation period..

	PSR (95% CI)	DSR (95% CI)	Year(s)	Source
Females				
	0.694[a] (0.528 – 1.000)	0.996 (0.993 – 1.000)	2011	This study
	0.761[a] (0.528 – 1.000)	0.997 (0.993 – 1.000)	2012	This study
	0.913[a] (0.833 – 1.000)	0.999 (0.998 – 1.000)	1982 – 84	Derleth and Sepik 1990
	0.761[a] (0.694 – 0.913)	0.997 (0.996 – 0.999)	1986 – 89	Longcore et al. 2000
Nests				
	0.440[a] (0.283 – 0.685)	0.968 (0.951 – 0.985)	2011	This study
	0.778[a] (0.608 – 0.996)	0.990 (0.980 –1.000)	2012	This study
	0.62[b]		1943	Mendall and Aldous 1943
	0.43[c]		1969 – 80	Gregg 1984
	0.59[b]		1986 – 89	McAuley et al. 1996
Juveniles				
	0.330[a] (0.188 – 0.613)	0.982 (0.973 – 0.992)	2011	This study
	0.576[a] (0.398 – 0.833)	0.991 (0.985 – 0.997)	2012	This study
	0.166[d] (0.073 – 0.374)	0.971 (0.958 – 0.984)	1976 – 79	Dwyer et al. 1988
	0.613[c] (0.274 – 0.885)	0.992 (0.979 – 0.998)	1984 – 85	Wiley and Causey 1987
	0.833[a] (0.693 – 1.000)	0.997 (0.994 – 1.000)	1982 – 84	Derleth and Sepik 1990

0.114[a]	0.965	1986 – 89	McAuley et al. 2010
(0.073 – 0.177)	(0.958 – 0.972)		

[a] Kaplan-Meier estimates.

[b] Apparent survival, 95% CI not available.

[c] Mayfield method used, no variation reported.

[d] Closed population mark-recapture model estimates.

Table 5: Stepwise model-selection results and *a priori* models of American woodcock nest survival at Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. Survival related to year (YEAR; 2011 or 2012), nest age (NAGE), nest initiation date (INIT), maximum and minimum temperature (MAXT and MINT), precipitation (PCPT), stem density (STEM), basal area (BAS), and distance to edge (EDGE). Models were ranked according to the difference in Akaike's information criterion (ΔAIC_c) corrected for small effective sample size ($n = 548$). Akaike model weights (ω_i) and number of estimable parameters (K) are also presented. Null model includes only an intercept and no covariates and is presented as reference. Stepwise model development started with an initial model including only a YEAR covariate. Step two included the addition of AGE and INIT covariates, step three included the addition of weather-related covariates, and step four included the addition of vegetative structure covariates..

Model step	Model	AIC_c	ΔAIC_c	ω_i	K
	Null	141.66	--	--	1
Initial model:					
	YEAR	140.95	--	--	2
Step two:					
	YEAR [a]	140.95	0.00	0.48	2
	YEAR+NAGE	142.38	1.43	0.24	3
	YEAR+INIT	142.81	1.86	0.19	3
	YEAR+NAGE+INIT	144.29	3.34	0.09	4
Step three:					
	YEAR [a]	140.95	0.00	0.27	2
	YEAR+MAXT	141.88	0.93	0.17	3
	YEAR+MAXT+MINT	142.33	1.38	0.13	4
	YEAR+MINT	142.41	1.46	0.13	3
	YEAR+PCPT	142.46	1.68	0.12	3
	YEAR+MAXT+PCPT	143.74	2.79	0.07	4

YEAR+MINT+PCPT	143.82	2.87	0.06	4
YEAR+MAXT+MINT+PCPT	144.23	3.27	0.05	5

Step four:

YEAR [b]	140.95	0.00	0.29	2
YEAR+STEM	141.48	0.53	0.22	3
YEAR+EDGE	142.86	1.91	0.11	3
YEAR+BAS	142.93	1.98	0.11	3
YEAR+STEM+EDGE	143.06	2.11	0.10	4
YEAR+STEM+BAS	143.34	2.39	0.09	4
YEAR+BAS+EDGE	144.86	3.91	0.04	4
YEAR+STEM+BAS+EDGE	144.94	3.99	0.04	5

[a] Indicates best-supported model for each step, model moved on to next step in analysis.
[b] Indicates best-supported overall model, AIC_c of top-ranked model = 140.95.

Table 6: Stepwise model-selection results and *a priori* models of juvenile American woodcock survival at Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. Survival related to year (YEAR; 2011 or 2012), juvenile age (JAGE), hatch date (HD), maximum and minimum temperature (MAXT and MINT), precipitation (PCPT), stem density (STEM), basal area (BAS), and distance to edge (EDGE). Models were ranked according to the difference in Akaike's information criterion (ΔAIC_c) corrected for small effective sample size ($n = 1,754$). Akaike model weights (ω_i) and number of estimable parameters (K) are also presented.   Null model includes only an intercept and no covariates and is presented as reference. Stepwise model development started with an initial model including only a YEAR covariate. Step two included the addition of AGE and HD covariates, and step three included the addition of weather-related covariates.

Model step	Model	AIC_c	ΔAIC_c	ω_i	K
	Null	245.59	--	--	1
Initial model:					
	YEAR	247.10	--	--	2
Step two:					
	YEAR+JAGE [a]	238.83	0.00	0.54	3
	YEAR+JAGE+HD	240.76	1.93	0.20	4
	YEAR+JAGE+HD+(HD×YEAR)	241.87	3.04	0.12	6
	YEAR+JAGE+(HD×YEAR)	241.86	3.04	0.12	5
	YEAR	247.10	8.27	0.01	2
	YEAR+HD	248.04	9.22	0.01	3
	YEAR+HD+(HD×YEAR)	248.15	9.32	0.01	5
	YEAR+(HD×YEAR)	248.15	9.32	0.01	4
Step three:					
	YEAR+JAGE+MINT+PCPT [b]	235.03	0.00	0.28	5
	YEAR+JAGE+MAXT+MINT+PCPT	235.57	0.54	0.21	6

YEAR+JAGE+MAXT+PCPT	236.22	1.19	0.15	5
YEAR+JAGE+PCPT	236.81	1.78	0.11	4
YEAR+JAGE+MINT	236.85	1.82	0.11	4
YEAR+MAXT+MAXT+MINT	238.22	3.19	0.06	5
YEAR+JAGE	238.83	3.80	0.04	3
YEAR+MAXT	239.38	4.35	0.03	4

[a] Indicates best-supported model for each step, model moved on to next step in analysis.
[b] Indicates best-supported overall model, AIC_c of top-ranked model = 235.03.

Table 7: Model-selection results from *post hoc* analysis of models assessing the relationship of juvenile American woodcock survival and habitat covariates at Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. Survival related to year (YEAR; 2011 or 2012), juvenile age (JAGE), minimum temperature (MINT), precipitation (PCPT), stem density (STEM), basal area (BAS), and distance to edge (EDGE). We assessed our best-supported model from *a priori* analysis and added all combinations of vegetation structure covariates to this best-supported model. Models were ranked according to the difference in Akaike's information criterion (ΔAIC_c) corrected for small effective sample size ($n = 420$); Akaike model weights (ω_i) and number of estimable parameters (K) are presented also.

Model	ΔAIC_c	ω_i	K
YEAR+JAGE+MINT+PCPT+STEM [a]	0.00	0.38	6
YEAR+JAGE+MINT+PCPT [b]	1.90	0.15	5
YEAR+JAGE+MINT+PCPT+STEM+BAS	1.93	0.14	7
YEAR+JAGE+MINT+PCPT+STEM+EDGE	2.06	0.13	7
YEAR+JAGE+MINT+PCPT+EDGE	3.28	0.07	6
YEAR+JAGE+MINT+PCPT+BAS	3.89	0.05	6
YEAR+JAGE+MINT+PCPT+STEM+BAS+EDGE	4.01	0.05	8
YEAR+JAGE+MINT+PCPT+EDGE+BAS	3.99	0.02	7

[a] Indicates best-supported overall model, AIC_c of top-ranked model = 91.50.
[b] Indicates the best-supported model from *a priori* analysis.

Are Indirect Estimates of American Woodcock Recruitment Useful Proxies for

Direct Estimates of Recruitment?

*Overview***:** We estimated recruitment of American woodcock (*Scolopax minor*;
hereafter, woodcock) at a habitat-management demonstration area in west-central
Minnesota directly using radio telemetry, and indirectly by capturing woodcock using
mist nets and night lighting. Indirect methods (e.g., night lighting and mist-netting) used
to estimate woodcock recruitment are more cost- and effort- efficient than direct
measures of recruitment (e.g., telemetry) and may provide comparable recruitment
estimates. In 2011 and 2012 we radio-marked and tracked 41 adult female and 73
juvenile woodcock, and monitored 51 broods and 48 nests. We used the Kaplan-Meier
with staggered entry method to estimate survival rates of females, nests, and juveniles,
and from these survival rate estimates, developed a population model to derive estimates
of woodcock recruitment for both 2011 and 2012. In July of 2011 and 2012, we used
mist nets to capture 204 woodcock during crepuscular movements from diurnal feeding
cover to roosting fields and 69 woodcock via night-lighting on roosting fields. Our
recruitment estimates (juveniles/adult female) derived from our population model were
1.13 (range: 0.59 – 1.97) in 2011 and 2.61 (range: 2.25 – 3.16) in 2012. We attribute the
higher recruitment estimate in 2012 to higher nest and juvenile survival rates during that
year. Recruitment estimates from mist-netting were 3.50 juveniles/adult female in 2011
and 2.28 in 2012, whereas recruitment estimates for night lighting were 1.46 in 2011 and

0.38 in 2012. Recruitment estimates from mist netting and night lighting varied

considerably between years, with neither method providing recruitment estimates

comparable to those derived from our population model in 2011 and 2012.

Key Words: American woodcock, BMP, female, Minnesota, recruitment, telemetry,

Scolopax minor, survival

INTRODUCTION

American woodcock (*Scolopax minor*; hereafter, woodcock) have experienced

long-term population declines across their breeding range, based on the spring American

Woodcock Singing-ground Survey (Cooper and Rau 2013). Wing-collection surveys

also have indicated a decline in woodcock recruitment across their range, especially in

the Central Management Region (Cooper and Rau 2013). These declines have been

widely attributed to loss or alteration of young forest cover types that support woodcock

reproduction across the woodcock breeding range (Gregg 1984, Dwyer et al. 1988, Sauer

and Bortner 1991, Kelly et al. 2008). In response to these apparent declines in woodcock

abundance and recruitment, a system of woodcock habitat-demonstration areas is being

developed throughout the woodcock breeding range where specific Best Management

Practices (BMPs) are applied with the goal of stabilizing and ultimately increasing

woodcock populations (Wildlife Management Institute 2010). These demonstration areas

are meant to promote young forest management on public and private lands, and increase

the abundance and distribution of young forest cover types at a landscape scale.

A measure of woodcock recruitment (juveniles/adult female) is estimated annually for the Eastern and Central Management Regions and by state through wing collection surveys (Cooper and Rau 2013). These ratios provide both short- and long-term trends for woodcock recruitment at a broad spatial scale. Estimates of recruitment at a demonstration-area scale (~200–800 ha), utilizing the same metric as wing collection surveys (juveniles/adult female), also can be used to assess whether BMPs applied at demonstration areas result in increased woodcock production. However, estimating recruitment with direct methods (e.g., telemetry) can be both expensive and require in-depth field studies that span multiple years. Indirect methods of estimating recruitment (e.g., capture via night-lighting or mist-netting during late summer, see below) may provide an alternative to directly estimating recruitment and may be more cost- and effort-efficient. Indirect methods also may provide a means of estimating changes or trends in recruitment at spatial scales relevant to management, such as those of demonstration areas. To date, however, alternatives to directly estimating woodcock recruitment at the scale of demonstration areas have not been evaluated.

Our objectives were to (1) directly estimate a measure of woodcock recruitment (juveniles/adult female during late summer) at a landscape scale by monitoring nests and radio-monitoring adult females and juveniles, and (2) use direct estimates of recruitment to evaluate the accuracy and usefulness of indirect estimates of recruitment. The indirect methods we used were less costly and effort-intensive and were based on the ratio of juveniles to adult females captured via night-lighting and mist-netting during the post-fledging period. If indirect methods of estimating recruitment are useful, we expected

resulting juvenile/adult female ratios to be similar to those from direct estimates of recruitment, or that trends in indirect estimates be similar to trends in direct estimates.

STUDY AREA

As part of a larger study of woodcock population ecology, we directly and indirectly estimated juvenile/adult female ratios in late summer in 2011 and 2012 at Tamarac National Wildlife Refuge (NWR) near Rochert, Minnesota, USA (47.0 N, -95.7 E). Tamarac NWR is a woodcock habitat demonstration area and lies in the glacial lake country of west-central Minnesota in Becker County and encompasses 17,296 ha of mostly forested lands, intermingled with lakes, rivers, marshes, shrub swamps, and tallgrass prairie. Tamarac NWR is located in the transition zone between coniferous forest, northern hardwood forest, and tallgrass prairie. Sixty percent of the refuge is forested, with dominant tree species of aspen (*Populus* spp.), jack pine (*Pinus banksiana*), red pine (*P. resinosa*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red oak (*Quercus rubra*), white oak (*Q. alba*), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*). A substantial portion of the refuge is managed for early successional forest cover for breeding, nesting, and brood-rearing habitat for woodcock, golden-winged warblers (*Vermivora chrysoptera*), and other migratory birds that utilize young forest cover types, which are maintained through timber harvest and prescribed fire.

METHODS

Data Collection

In early spring of 2011 and 2012, we used mist nets (Avinet 38-mm black

polyester nets, four pockets, 2.6 m high, 6 and 9 m wide; Avinet, Inc., Dryden, NY) to

capture woodcock during dusk (approximately 1900 to 2300 CDT) when woodcock leave

diurnal areas to roost or feed (Sheldon 1971), and equipped captured adult female

woodcock with radio transmitters. We determined sex of all woodcock captured based on

plumage characteristics (Martin 1964) and radio-marked adult female woodcock using a

glue-on backpack-style harness that was ≤3% of their total mass (4.5 g, model A5410,

Advanced Telemetry Systems, Isanti, MN; McAuley et al. 1993*a*, 1993*b*). We relocated

radio-marked female woodcock 5-7 days per week throughout the breeding season (April

– June) and into July, following the nesting period. We lost radio contact with some

females when they traveled long distances, out of the range of our receiving equipment

and monitoring protocol. We continued searching for these females throughout our field

season and if we did not relocate them, we classified these females as "lost." When we

relocated a radio-marked adult female, we assessed its status (i.e., alive or dead) and if it

was dead, assessed the cause of death. If depredated, we attempted to ascertain the

source of predation (mammalian or avain) using methods described by McAuley et al.

(2005).

We found woodcock nests using trained pointing dogs (Ammann 1977, McAuley

et al. 1993*a*) and radio telemetry of incubating radio-marked adult females. We visited

each nest on 2-3 day intervals and assessed the status of the nest as active, depredated,

abandoned, or successful. If the female was not present at the nest or flushed during our visit, we floated all eggs in ambient-temperature water to estimate nest age and initiation date (Ammann 1974). We considered nests to be active when the adult female was either laying or incubating, or if a female was incubating at a subsequent visit. We categorized nests as depredated if eggs were broken or absent prior to the estimated hatch date. We categorized nests as abandoned if the female was not observed incubating for two consecutive visits. We categorized nests as successful if ≥1egg exhibited signs of having hatched (i.e., was in or close to the nest bowl with a longitudinal split).

We assessed the status of juveniles in broods of radio-marked adult females and also radio-marked a sample of juveniles within broods of radio-marked adult females. We also used trained pointing dogs to find additional broods of unmarked adult females (Mendall 1938; Ammann 1974, 1977) and captured and radio-marked juveniles in those broods. We custom fit a collar-type micro-transmitter (BD-2NC or BD-2C, Holohil Systems Ltd., Carp, ON and custom transmitters made by Blackburn Transmitters, Nacogdoches, TX) with a whip antenna to captured juvenile woodcock. All transmitters were ≤3% of the bird's mass (BD-2NC transmitters weighed approximately 0.6 g, BD-2C transmitters weighed approximately 1.6 g, and Blackburn transmitters weighed approximately 0.4 g) and we attached transmitters to juvenile woodcock with an elastic collar designed to expand as the juvenile woodcock grew. We positioned transmitters at the base of a juvenile woodcock's neck with the transmitter antenna lying down the juvenile's back. Transmitter lifespan was approximately 21 days (17-30 day range) for

BD-2NC transmitters, 63 days (49-77 day range) for BD-2C transmitters, and 28 days (24-32 day range) for Blackburn transmitters.

We radio-marked 1-4 juveniles per brood and monitored both marked and unmarked individuals within a brood after locating radio-marked juveniles. We located broods 4-7 days per week by tracking either the adult female or juvenile(s). We assessed status (alive or dead) of juveniles and counted both marked and unmarked juveniles to document brood size and assumed juveniles were dead if previously observed but subsequently not detected. We counted the number of individuals in the brood by tracking the radio-marked bird(s) to a distance of approximately 5 m and then encircling the brood until we were certain all brood members were counted. Beginning approximately 15 days after hatching, entire broods often flushed at our approach, affording us the opportunity to determine total brood size. Beyond 15 days post-hatch, the probability of detecting all members of the brood diminished. Because we were not able to accurately determine the status of unmarked juveniles after brood breakup, we right censored unmarked juveniles at 24 days old, which was earliest we observed brood breakup.

Starting in early July each year and concluding in early August, we used mist-netting and night-lighting to captured woodcock on summer roost fields (Dwyer et al. 1988). We used mist nets to capture woodcock during dusk (approximately 1900 to 2300 CDT) when woodcock leave diurnal areas to roost or feed (Sheldon 1971). We calculated trap nights as the sum of the total number of mist nets set per night during the period in which we deployed mist nets. We also captured woodcock via night-lighting in

known woodcock roosting areas (Dwyer et al. 1988) following the period of crepuscular movement. Each night during night-lighting, we had a single person shinning a spot light (Cabela's 35-Watt HID spotlight, 3,000 lumens and Cyclops Sirius 500 spotlights, 500 lumens; Cabela's, Sydney, NE) and 1-2 people attempting to capture woodcock with long-handled nets. We assigned age (hatch year or after hatch year) and sex to all captured birds using body measurements and feather characteristics (Martin 1964, Sepik 1994).

Estimating recruitment indices from radio telemetry

We estimated survival rate of adult females, nests, and juvenile woodcock using the Kaplan-Meier with staggered entry estimator (Pollock et al. 1989) in the KMsurv package in Program R (version 2.15.2, R Core Team, 2012). We estimated survival rate of adult females, nests, and juveniles separately for 2011 and 2012 (see Chapter 1). We used these survival rate estimates to construct a model (described below) of the woodcock population in our study area, and derive juvenile/adult female ratios for late summer 2011 and 2012, which were the periods we indirectly estimated recruitment via mist-netting and night-lighting. For the purposes of our model, we estimated female woodcock survival rate for a 91-day period (1 April – 30 June). We estimated nest survival rate for a 25-day period that included four days for egg laying and 21 days for incubation and we estimated juvenile survival rate for a 61-day period (1 May- 30 June).

We recorded the number of days following transmitter deployment on females and juveniles to accurately censor individuals if radio transmitters failed prematurely. We assumed radios failed if they performed irregularly and there was no other indication an

individual had died. We also assumed radios failed if they were nearing the end of their

projected battery life and we subsequently received no additional signals from

transmitters. We right-censored individuals in both of these circumstances, assuming the

individual survived until transmitter failure (e.g., Korschgen et al. 1996).

We used Kaplan-Meier period survival estimates for females, nests, and juveniles

to construct a population model to estimate recruitment of woodcock at Tamarac NWR in

both 2011 and 2012. We applied estimates of period survival to derive the number of

female woodcock surviving the breeding season, and the number of juvenile woodcock

produced and surviving through the end of the breeding season (30 June).

In addition to estimates of survival rates, we used published estimates of renesting

rates, clutch sizes, and hatching rate to model the woodcock population on our study area.

Woodcock are known to be prolific renesters; however, only one renesting attempt per

female has ever been observed in a single breeding season (McAuley et al. 1990).

Woodcock generally renest following a failed nest or if they lose a brood <11 days old

(McAuley et al. 1990). Because we were capturing females into the nesting portion of

the breeding season and the time from nest or brood failure to renesting can be as short as

4-5 days (McAuley et al. 1990, personal observation) we were unable to assess whether

the majority of nests in our study were first nests or renesting attempts. We therefore

assumed the same survival probability for first nests and renests. McAuley et al. (1990)

reported 13 (~93%) of 14 radio-marked female woodcock renested after losing a nest or a

brood. Because of this high renesting probability, we assumed that all woodcock that lost

a first nest initiated a second nest in our population model. We applied the same survival

rate to both first nesting attempts and renests to estimate the number of nests that produced young. Clutch size of renests reported by McAuley et al. (1990) averaged three eggs per nest, whereas for first nesting attempts, clutch size is usually four eggs per nest. Both first nesting and renesting attempts have high hatching rates (~0.95; McAuley et al. 1990).

To calculate the number of juveniles produced throughout the breeding season for woodcock, we assumed all females that returned successfully bred and initiated a nest. We applied the Kaplan-Meier estimate of nest-survival rate to all nests and assumed that clutch size was four eggs in first nesting attempts (McAuley et al. 1990). For first nests that did not survive a 25-day egg-laying and incubation period, we assumed all females from these nests renested (i.e., initiated a second nest) and clutch size for renests was three eggs (McAuley et al. 1990). We applied the same Kaplan-Meier nest-survival rate estimate as we did for first nests to renesting attempts. We assumed that if the nest was successful (i.e., $\geq$1 egg hatched), hatch rate of eggs was 0.95. From these estimates of nest survival rate and hatch rate, we calculated the number of juveniles hatched for each year (based on an arbitrary starting population of 1,000 females). We then applied the Kaplan-Meier estimate of juvenile survival rate to the resulting number of juveniles to calculate the number of juveniles that were produced for 2011 and 2012, separately. We calculated a recruitment ratio by dividing the number of juveniles that were produced and survived the breeding season by the number of females that survived the breeding season. We calculated a range of possible recruitment estimates for each year by using the lower and upper bounds of the 95% confidence interval associated with our survival-rate

estimates in our population model. We compared the recruitment indices derived from

radio telemetry to those derived from age and sex composition of woodcock captured via

mist-netting and night-lighting. We also compared the recruitment estimates in our study

to those obtained from the wing-collection survey at both statewide and Central

Management Region-wide scales reported by Cooper and Rau (2012, 2013).

RESULTS

In 2011, our estimates of recruitment through early August varied considerably as

a function of capture technique. We captured 3.50 juveniles per adult female ($n = 87$) via

mist netting, and 1.46 juveniles per adult female ($n = 42$) via night-lighting (Table 1).

We captured more woodcock using mist netting than night lighting, in part because night

lighting is only effective under very specific weather conditions. We spent a total of 16

hours and 20 minutes mist netting and a total of 23 hours and 30 minutes night lighting

between 7 July and 24 July 2011. We set an average of 9.5 mist nets per night and

trapping effort for mist netting totaled 114 trap nights. Capture rate for mist netting on

summer roosting field was 5.3 woodcock captured per hour (across the average 9.5 mist

nets per night), whereas the capture rate for night lighting on roosting fields was 1.8

woodcock captured per hour.

Our summer capture results from 2012 followed a similar pattern to those from

2011, with mist netting providing higher recruitment estimates than night-lighting. We

captured 2.28 juveniles per adult female ($n = 117$) via mist netting, and 0.38 juveniles per

adult female ($n = 27$) via night-lighting (Table 1). We spent a total of 39 hours and 59

minutes mist netting and 29 hours night-lighting between 1 July and 30 July 2012,

resulting in a capture rate of 2.92 woodcock per hour mist netting and 0.93 woodcock per hour night-lighting. Trapping effort for mist netting totaled 220 trap nights with an average of 10.5 mist nets set per night.

From 9 April to 1 June 2011 and 22 March to 24 May 2012, we captured and radio-marked 41 adult female woodcock (2011: $n = 23$, 2012: $n = 18$). We excluded 3 (~7%) radio-marked adult female woodcock in 2011 from survival analysis that we were unable to relocate following radio marking (likely due to transmitter failure or migration). Of the remaining 38 female woodcock, we right censored one female that became entrapped in its radio telemetry harness in 2012. From 4 May to 11 June 2011 and from 9 April to 9 June 2012 we monitored 52 woodcock nests (2011: $n = 26$, 2012: $n = 26$). We censored four nests from our analysis (one in 2011 and three in 2012). Of the 45 nests analyzed, eggs failed to hatch in 21 (~47%) and were either depredated (71%) or abandoned by the female (29%).   From 16 May to 29 June 2011 and 20 April to 16 June 2012 we radio-marked 73 (2011: $n = 22$, 2012: $n = 51$) juvenile woodcock from 51 broods (2011: $n = 16$, 2012: $n = 35$). We assigned fates of 134 juvenile woodcock (2011: $n = 63$, 2012: $n = 71$), including fates from 49 marked and 85 unmarked juveniles from 47 broods (2011: $n = 23$, 2012: $n = 24$), resulting in an effective sample size of 859 observation intervals. We excluded data from 24 marked juvenile woodcock due to uncertainty regarding transmitter failure (i.e., we did not know if the transmitter failed or if the juvenile was depredated).

Kaplan-Meier estimates of survival rates during the breeding season for adult females from 1 April – 30 June were 0.694 (95% CI: 0.528 – 1.000) in 2011, and 0.761

(95% CI: 0.528 – 1.000) in 2012 (Table 2). Kaplan-Meier estimates of survival rates for a 25-day laying and incubation period for nests were 0.440 (95% CI: 0.283 – 0.685) in 2011 and 0.778 (95% CI: 0.608 – 0.996) in 2012 (Table 2). Kaplan-Meier estimates of survival rates for juvenile woodcock for a 61-day period (1 May – 30 June) were 0.330 (95% CI: 0.188 – 0.613) in 2011 and 0.576 (95% CI: 0.398 – 0.833) in 2012 (Table 2). Our estimate of recruitment based on survival and reproduction of females and survival of nests and juveniles was 1.13 (range: 0.59 – 1.97) juveniles per adult female in 2011 and 2.61 (range: 2.25 – 3.16) in 2012 (Table 1).

In both 2011 and 2012, recruitment estimates derived via mist netting were higher than those derived via night lighting (2.4× greater in 2011, and 6.0× greater in 2012; Table 1); however, estimates of recruitment derived from both mist netting and night lighting indicated lower recruitment in 2012 than in 2011. Compared to recruitment estimates derived from our population model, night lighting provided a more similar estimate in 2011, and mist netting provided a more similar estimate in 2012. Our population model of woodcock recruitment indicated that woodcock recruitment at Tamarac NWR was greater in 2012 than in 2011 (Table 1). Neither indirect method provided an estimate similar to that derived from our population model for both 2011 and 2012, nor did they follow the same trend as the recruitment estimates derived from our population model (Fig. 1).

DISCUSSION

The primary objective of our assessment was to evaluate whether indirect estimates of woodcock recruitment could serve as useful proxies for estimating

recruitment directly, which is both expensive and requires considerable investment of effort. Neither indirect estimate we evaluated (juvenile/adult female ratios derived from mist-netting and night-lighting) was consistently related to the recruitment estimates we derived from our population model, suggesting that neither was a useful proxy for recruitment. Furthermore, we expected our indirect estimates of recruitment to increase from 2011 to 2012 based on results from our population model. However, our indices of recruitment based on mist netting and night lighting woodcock indicated a decrease in recruitment in 2012 compared to 2011, which did not correspond with the increase in recruitment between 2011 and 2012 indicated by our population model. We therefore conclude that neither of these indirect estimates of recruitment is likely to be a useful alternative to estimating woodcock recruitment directly.

Both indirect estimates of recruitment we considered are likely related to the amount of brood-rearing cover in the landscape we studied, the amount of other suitable roosting cover, and local production of juveniles (Dunford and Owen 1973). However, biases in these estimates could result from several potential factors. First, a positive bias in indirect recruitment estimates could result from an influx of juvenile woodcock to areas with high-quality habitat in late summer, although we would expect such movement to affect ratios derived from mist netting and night lighting similarly. Recruitment estimates derived from mist netting woodcock during crepuscular hours also may be biased high (i.e., relatively higher estimated proportion of juveniles; Table 2) if adult females are relatively less likely to be captured in mist nets than juveniles. We captured a similar number of adult female woodcock ($n = 14$ mist netting and $n = 13$ night

lighting, Table 1) even though the total number of woodcock captured via mist netting was higher than that captured via night lighting, suggesting that adult females were relatively less likely to be captured than juveniles in mist nets.

Our capturing a relatively higher proportion of juvenile woodcock via mist netting also could be influenced by behavioral differences between juveniles and adults during crepuscular flights (Sheldon 1961, Dunford and Owen 1973, Owen and Morgan 1975). In previous studies of woodcock behavior in summer, adults flew later than juveniles, were $6\times$ more likely than juveniles to walk from diurnal covers to nocturnal sites, perhaps due to molt, flew shorter distances, and were less likely to take multiple flights to reach nocturnal sites (Dunford and Owen 1973, Owen and Morgan 1975). We opened mist nets prior to when woodcock began crepuscular flights and kept them open beyond when flights ceased to account for differences in flight times between juveniles and adults; therefore, differences in flight times likely do not account for bias toward juveniles in our mist-netted sample. Instead, it seems that juvenile woodcock were more likely to be captured using mist nets than adults or that juveniles disproportionately immigrated into our study area in late summer. Juveniles have been observed moving farther distances than adults, especially juvenile males (Owen and Morgan 1975, Berdeen and Krementz 1998), which could lead to an influx of juveniles in summer. However, we were unable to assess this possibility in our study.

How adult and juvenile woodcock use roosting fields also may influence biases in indirect estimates of recruitment. Although the characteristics of roosting fields used by adults and juveniles are similar (Owen and Morgan 1975, Berdeen and Krementz 1998),

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adult and juvenile woodcock may use these areas spatially and temporally differently.

Owen and Morgan (1975) reported adult woodcock remaining closer to the edge of roost

fields, whereas juveniles were generally farther from edges. Greater relative use of

roosting fields by juvenile woodcock has been observed in other studies during summer

months (Krohn 1971, Whitcomb 1972). Observations by Krohn (1971) and Whitcomb

(1972) suggested that woodcock captured in roosting fields were more likely to be

juveniles based solely on relative abundance, resulting in a positive bias in estimates of

recruitment estimates. In a study of winter roosting field use, Berdeen and Krementz

(1998) found no relationship between the use of roosting fields of radio-marked

woodcock and woodcock age and sex. Our recruitment estimates derived from night

lighting were lower than those derived from mist netting and lower than those derived

from our population model in 2012, suggesting that in our study, adult females were more

readily captured on roosting fields relative to juveniles, either because they were more

abundant or easier to capture. This result contradicts previous studies that suggested

juvenile use of roosting fields was higher in summer months (Krohn 1971, Whitcomb

1972). Adults and juveniles likely use roosting fields differently during different seasons

(Krohn 1971, Whitcomb 1972, Berdeen and Krementz 1998) and also may use roosting

fields spatially and temporally differently within the same site and season (Owen and

Morgan 1975). Without fully understanding the differences in use of roosting fields by

adults and juveniles, it is difficult to interpret the results of our study because a variety of

factors could be affecting the use of roosting fields by adults and juveniles.

In addition, because we focused our night-lighting efforts on only two roosting fields, our capture-related activities may have impacted our success capturing woodcock at these locations. Woodcock exhibit high nocturnal site fidelity (Berdeen and Krementz 1998); however, site fidelity could be affected by human disturbance (Sheldon 1961, Krohn 1971, Dunford and Owen 1973). Negative bias in recruitment estimates would result if juvenile woodcock were more likely to abandon a roosting field in response to repeated capture efforts compared with adult females. Our estimate of recruitment also could be negatively biased because adult woodcock generally roost closer to edges, and therefore have a lower likelihood of being encountered (Owen and Morgan 1975) or were less likely to be captured because they were closer to areas where they could escape.

Finally, it is possible also that our population model resulted in biased estimates of recruitment. We used values for some vital rates estimated in a previous study of woodcock reproduction and survival (e.g., hatch rate, renesting probability, and clutch size in first nests and renests; McAuley et al. 1990) because we were unable to directly estimate all of the population parameters in our model. For instance, because of the high likelihood that a female will renest, we assumed that all adult females renested following a failed first nesting attempt. Despite woodcock having a high renesting probability (McAuley et al. 1990), it is likely that not all woodcock that experience nest failure attempt to renest, which would result in a positive bias in our model-derived estimates of recruitment. Furthermore, how well estimates of vital rates derived elsewhere (e.g., McAuley et al. 1990) represent vital rates in our study population is unknown, and using

these estimates could introduce bias in our direct estimates of recruitment of unknown size and direction.

To more fully assess the utility of indirect recruitment estimates, it is likely necessary to better understand movement behavior of juveniles and adults and the relationship between woodcock movements and environmental conditions during late summer. Relatively few studies have evaluated woodcock spatial-use patterns at the landscape scale in summer following brood rearing (e.g., Dunford and Owen 1973, Owen and Morgan 1975). Movements and habitat selection of woodcock have been related to foraging quality and environmental conditions, especially moisture (Dunford and Morgan 1973, Doherty et al. 2010), with woodcock generally returning to areas with high food availability and food availability and forage quality are related to soil moisture (Doherty et al. 2010). Because woodcock also forage at night (Stribling and Doerr 1985), and it is likely that food availability is at a seasonal low in roosting fields during mid-summer due to high temperatures, adult woodcock may use roosting fields relatively less than juvenile woodcock during summer, and may use forest cover at higher rates during summer than during the remainder of the year (Berdeen and Krementz 1998).

We also note that the recruitment estimates derived from our population model provide some insight into woodcock demography and population ecology. First, our population model indicated that nest and juvenile survival were important factors determining local population growth of woodcock, as has been demonstrated for other species (Streby and Andersen 2011). Second, our estimates of recruitment suggest that the demonstration area where we conducted our study was perhaps a population source.

Compared to recruitment estimates in Minnesota derived from parts-collection surveys (1.0 juveniles/adult female in both 2011 and 2012; Cooper and Rau 2012, 2013) and the Central Management Region (1.5 in 2011 and 1.66 in 2012; Cooper and Rau 2012, 2013), recruitment estimates derived from our population model were generally higher (1.13 in 2011 and 2.61 in 2012), suggesting that current management emphasizing early successional forest cover likely has benefited woodcock at the demonstration area where we conducted our study.

However, our assessment suggests that indirect methods we considered (night lighting and mist netting) to estimate woodcock recruitment at a landscape scale likely are not reliable proxies for estimating recruitment directly. Without additional information about relative capture probabilities of adult versus juvenile woodcock, relative use of roosting areas by adult and juvenile woodcock, and landscape-level movements of woodcock during late summer and early fall it is difficult to assess the usefulness of indirect methods. It may not be practical to evaluate these factors at specific sites, as doing so would likely involve investment of resources comparable to those required to estimate recruitment directly. Therefore, we suggest that the most practical means of estimating woodcock recruitment at a landscape scale involves direct estimates of population parameters necessary to develop a population model, which requires considerable investment of resources.

Table 1. Estimates of recruitment (juveniles/adult female) derived from capturing American woodcock in summer roosting field via mist netting and night lighting, and from a population model based on direct estimates of vital rates at Tamarac National Wildlife Refuge, Rochert, Minnesota, in 2011 and 2012. Population model recruitment estimates were derived from Kaplan-Meier survival estimates of adult female, nests, and juvenile woodcock.

Capture method	Adult male	Adult female	Juvenile male	Juvenile female	Juveniles/adult female (range)
2011					
Mist netting	24	14	39	10	3.50
Night lighting	10	13	14	5	1.46
Model					1.13 (0.59 – 1.97)
2012					
Mist netting	35	25	41	16	2.28
Night lighting	9	13	2	3	0.38
Model					2.61 (2.25 – 3.16)

Table 2. American woodcock survival rate estimates for adult females, nests, and juveniles from Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. Survival rates calculated using the Kaplan-Meier method with staggered entry (Pollock et al. 1989) in the KMsurv package in Program R. Period survival rates were estimated for a breeding season for adult females and juvenile woodcock. Period survival rate for female woodcock was calculated for a 91-day period, for juvenile woodcock for a 61-day period, and for woodcock nests for a 25-day egg-laying and incubation period.

|	Year	Period survival rate (95% CI)	Daily survival rate (95% CI)
Females (91 days)			
	2011	0.694 (0.528 – 1.000)	0.996 (0.993 – 1.000)
	2012	0.761 (0.528 – 1.000)	0.997 (0.993 – 1.000)
Nests (25 days)			
	2011	0.440 (0.283 – 0.685)	0.968 (0.951 – 0.985)
	2012	0.778 (0.608 – 0.996)	0.990 (0.980 –1.000)
Juveniles (61 days)			
	2011	0.330 (0.188 – 0.613)	0.982 (0.973 – 0.992)
	2012	0.576 (0.398 – 0.833)	0.991 (0.985 – 0.997)

Figure 1: Estimates of recruitment (juveniles/adult female) derived from capturing American woodcock in summer roosting fields, via mist netting and night lighting, and from a population model at Tamarac National Wildlife Refuge, Rochert, Minnesota, in 2011 and 2012. Population model recruitment estimates were derived from Kaplan-Meier survival estimates of adult female, nests, and juvenile woodcock.
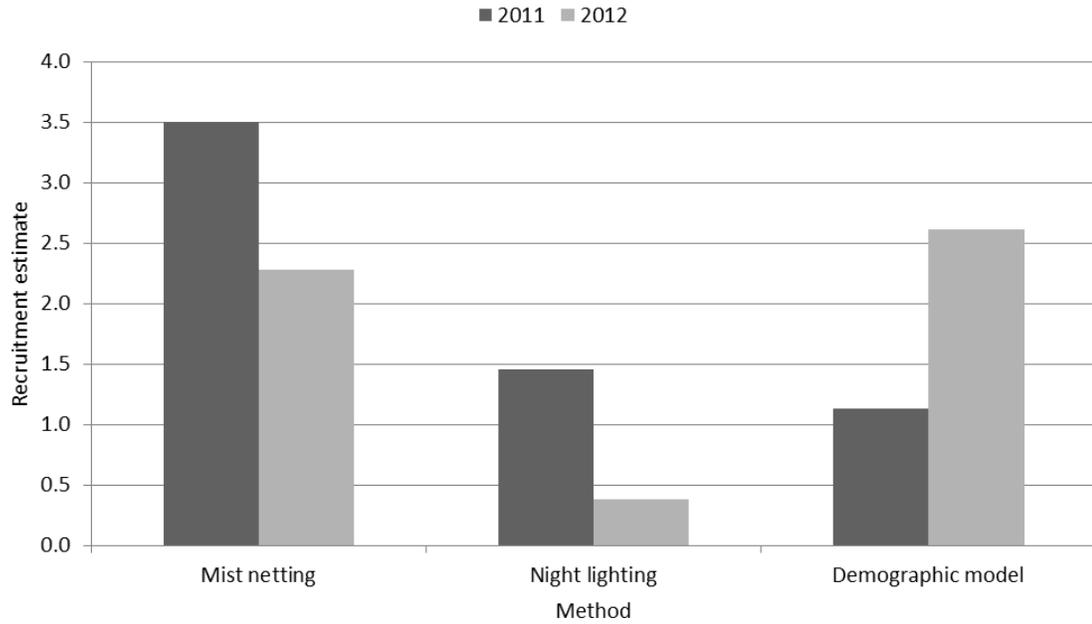
Chapter 3

Survival of Juvenile American Woodcock: Impacts of Radio-transmitters, Age, and Weather

Overview: There are few direct estimates of juvenile American woodcock (*Scolopax minor*; hereafter woodcock) survival, and no assessment of the effect of current radio telemetry techniques on juvenile survival. As part of a study of woodcock response to landscape-level habitat management in west-central Minnesota in 2011 and 2012, we radio-marked 73 juvenile woodcock and compared survival between radio-marked and non-radio-marked juvenile woodcock during the period from hatching to fledging. We compared survival of marked ($n = 58$) and unmarked ($n = 82$) juveniles with known fates and used logistic-exposure models to assess the potential impact of radio transmitters on survival. We evaluated variables related to juvenile survival including age, hatch date, maximum and minimum temperature, precipitation, and year. In addition, we visually assessed behavior of marked and unmarked juvenile woodcock to determine whether there were any obvious behavioral responses to transmitters. We tested for non-independence in survival within broods by comparing survival of all juveniles within each brood using Chi-squared goodness-of-fit tests, which suggested juveniles within the same brood could be treated as independent samples ($\chi_{44}^2 = 17.15$, $P = 0.99$). The best-supported model included the interaction of age and year and a negative effect of precipitation ($\beta = -0.76$, 85% CI: -1.08 to -0.43), but did not indicate a deleterious effect of transmitters. Cumulative survival of juvenile woodcock to 15 days

of age based on Kaplan-Meier survival estimates was 0.746 (95% CI: 0.646 – 0.862) in 2011 and 0.843 (95% CI: 0.762 – 0.933) in 2012. We attribute the difference in cumulative survival from day 1 through day 15 between years to relatively unfavorable weather conditions in 2011 (generally colder and wetter) compared with 2012. We concluded that radio-transmitters did not impact survival of juvenile American woodcock and suggest that micro-transmitters are a reliable method to study survival of juvenile woodcock, and perhaps other precocial shorebirds.

Key Words: American woodcock, brood, juvenile, logistic-exposure, Minnesota, radio telemetry, *Scolopax minor*, survival

INTRODUCTION

Radio telemetry is a common technique used to estimate survival and it is often assumed that radio- marking does not impact survival of marked individuals (Amundson and Arnold 2010). However, if attachment of radio transmitters impacts survival, estimates of vital rates resulting from radio-telemetry studies will be biased. There are few direct estimates of juvenile American woodcock (*Scolopax minor*, hereafter woodcock) survival and previous survival estimates based on telemetry (e.g., Wiley and Causey 1987) used transmitters weighing considerably more than those currently available. The impact of transmitters on survival in previous studies was not critically evaluated.

Recent advances in transmitter miniaturization and attachment methods have made radio-marking juvenile woodcock more practical. Custom-fit, expanding, collar-

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type transmitters have recently been used on woodcock (W. L. Brininger, Jr., U.S. Fish and Wildlife Service, personal communication). Micro-transmitters are significantly smaller and lighter than transmitters used to mark juvenile woodcock in previous studies (Horton and Causey 1981, Wiley and Causey 1987), and can be deployed on juveniles as early as two days after hatch. Because juvenile survival is usually lowest following hatch and asymptotically increases with age, marking younger juveniles provides a more complete assessment of daily and period survival.

As part of a larger study of woodcock population responses to habitat management in west-central Minnesota, we had the opportunity to assess factors related to juvenile woodcock survival during the period from hatch to fledging (15 days for woodcock). As part of that study, we marked 2-day-old or older juvenile woodcock with expanding-collar radio transmitters. We simultaneously radio-marked and tracked the adult female woodcock for each brood, which allowed us to locate and determine fates of unmarked juvenile woodcock. Our specific objectives were to test for effects of radio transmitters on juvenile woodcock survival and evaluate other covariates that could potentially influence survival that were related to attributes of broods and environmental conditions (weather). Based on published estimates of juvenile woodcock survival (e.g., Gregg 1984, Wiley and Causey 1987, Derleth and Sepik 1990, McAuley et al. 2010), we expected survival to increase with age and be negatively related to cold, wet spring weather.

STUDY AREA

We captured and radio-marked adult female and juvenile woodcock during April, May, and June 2011 and 2012 on the Tamarac National Wildlife Refuge (NWR) located near Rochert, Minnesota (coordinates: 47.0 North, -95.7 East). Tamarac NRW lies in the glacial lake country of northwestern Minnesota in Becker County, 97 km east of Fargo, North Dakota and encompasses 17,296 ha (42,738 acres) of forests intermingled with lakes, rivers, marshes, and shrub swamps. Tamarac NWR features a diverse vegetative community because of its location in the transition zone between the coniferous forest, northern hardwood forest, and tallgrass prairie. Sixty percent of the refuge is forested, the dominant species are aspen (*Populus* spp.), jack pine (*Pinus banksiana*), red pine (*P. resinosa*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red oak (*Quercus rubra*), white oak (*Q. alba*), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*). Timber harvest, brushland shearing, and prescribed fire programs on the refuge have sustained early successional forest cover, which is primary breeding, nesting, and brood-rearing habitat for woodcock.

METHODS

In early spring of 2011 and 2012, we used mist nets to capture adult woodcock during crepuscular hours (Sheldon 1955, 1960). We radio-marked adult female woodcock using a glue-on backpack-style harness (McAuley et al. 1993*a*, 1993*b*). We tracked marked female woodcock 5-7 days per week throughout the breeding, nesting, and brood-rearing periods. Upon relocating a radio-marked woodcock, we assessed its status (alive or dead) and during the brood-rearing period we counted the number of juveniles present to estimate survival of unmarked juvenile woodcock. We also radio-marked a sample of

juveniles within broods of adult females that were also radio-marked. During the brood-rearing period, we used trained pointing dogs (sensu Mendall 1938) to find additional broods that we captured and radio-marked.

We custom fit a collar-type micro-transmitter (BD-2NC or BD-2C, Holohil Systems Ltd., Carp, ON and custom transmitters made by Blackburn Transmitters, Nacogdoches, TX) with a whip antenna on captured juvenile woodcock. Transmitters were ≤3% of the bird's mass (BD-2NC transmitters weighed approximately 0.6 g, BD-2C transmitters weighed approximately 1.6 g, and the Blackburn transmitters weighed approximately 0.4 g) and the Holohil transmitters included an elastic collar designed to stretch as the juvenile woodcock grew. We attached elastic loops made from ~1-mm diameter black craft elastic to the Blackburn transmitters so they would fit the same way as the Holohil transmitters. Based upon the neck circumference of each juvenile, we custom-fit an elastic collar that we then slipped over the juvenile's head and positioned at the base of the neck with the transmitter antenna protruding down the juvenile's back. Radio lifespan of the BD-2NC radio was approximately 21 days (17-30 day range), lifespan of the BD-2C radios was approximately 63 days (49-77 day range), and lifespan of the Blackburn transmitters was approximately 28 days (24-32 day range).

We radio-marked 1-4 juveniles per brood and monitored the entire brood based on locating radio-marked juveniles. We attempted to locate broods 5-7 days per week by tracking either the adult female transmitter, juvenile transmitter(s), or both by using vehicle-mounted and hand-held Yagi (Advanced Telemetry Systems, Isanti, MN) and hand-held H-directional antennas (Telonics, Inc., Mesa, AZ) with R4000 Scientific

Receivers (Advanced Telemetry Systems, Isanti, MN). After we located a brood, we

observed each individual from a distance using binoculars to assess any negative impacts

of radio transmitters (e.g., entanglement in the elastic collar, or feather or skin wear). We

assessed status (alive or dead) of juveniles and broods and counted both marked and

unmarked juveniles to document brood size. Beginning around 15 days post-hatch, entire

broods often flushed as we approached radio-marked woodcock, affording us the

opportunity to determine brood size.   We recorded each location with a hand-held GPS

unit (Garmin GPSmap 76CSx set to coordinate system: UTM, datum: NAD83) averaged

to 100 points to achieve a minimum estimated error at each point.

Survival covariates

For each juvenile woodcock we monitored, we measured or derived covariates to

use in developing survival models (Table 1). We estimated age since hatch by either

knowing hatch date or using the equation described by Sepik (1994):

$$age = (bill\ measurement\ (mm) - 14)/2$$

to derive age based on bill measurements). We logit-transformed age since hatch to

create a continuous variable, AGE. Because intervals between relocations of individual

broods were short (usually 2-3 days), we used the age of a juvenile at the midpoint of the

interval between consecutive relocations to represent AGE for each interval observation.

We included AGE in our analysis because younger juveniles are more likely to be

negatively affected from stress related to capture and radio-marking, more vulnerable to

unfavorable weather conditions, and have higher predation risk (Wiley and Causey 1987,

Derleth and Sepik 1990). We estimated hatch date (HD; Julian date) by either

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monitoring nests of radio-marked females, or by aging juveniles upon capture and back-dating to date of hatch (HD = Julian date – age). We monitored nests of radio-marked females 5-7 times per week to estimate HD of broods. We included HD in our analyses to account for confounding effects of hatch date on survival. We hypothesized that juveniles that hatched earlier in the spring were more likely to be exposed to periods of cold weather, but may also have been from females in the best condition and with more experience nesting and rearing juveniles. Greater vegetative cover has been showed to decrease predation risk for nests in forested landscapes (Rudniky and Hunter 1993); similarly, greater vegetative cover later in the spring (e.g., forb and leaf emergence) may also be related to reduced predation risk for birds that hatch later.

We obtained daily weather data from precipitation gauges and digital temperature loggers at Tamarac NWR during 2011 and 2012. If weather data were not available for Tamarac NWR, we used weather data from the nearest National Weather Service station in Detroit Lakes, Minnesota (approximately 22 km southeast of Tamarac NWR). We used the sum of daily precipitation (cm) for each day in the interval between observations to calculate total interval precipitation (PCPT). We used the recorded maximum (MAXT) and minimum (MINT) temperatures (°C) during each interval between observations. We included year (YR) in our models of survival to account for temporal variation, and included it as a class variable in models of survival.

Survival models

We used the logistic-exposure method (Shaffer 2004) to evaluate effects of radio-transmitters on juvenile woodcock survival, and assess relationships between survival

and factors we hypothesized to be related to survival (e.g., age, temperature, etc.). We

developed a set of *a priori* models of juvenile survival during the first 15 days following

hatch (fledging occurs at 15 days post-hatch), and evaluated models using a stepwise

approach (sensu Amundson and Arnold 2010) in an information-theoretic framework

(Burnham and Anderson 2002).

A major assumption of known-fate models is survival of individuals are

independent of one another; however, entire brood mortality may result is non-

independence of survival between and among brood mates (Chouinard and Arnold 2007,

Amundson and Arnold 2010). We used Winterstein's (1992) second Chi-squared

goodness-of-fit test to evaluate intra-brood independence of juveniles with the null

hypothesis that survival rates of individuals within a brood are independent. This test

uses the entire survival sample to calculate a Mayfield (1961) period survival estimate,

which is then applied to calculate the expected number of juveniles alive at the end of a

specified period (L=15 days for our study).

We considered two base models that incorporated the linear-logistic function of

AGE and YR because survival varied between years: (1) AGE + YR, and (2) AGE $\times$ YR,

where + and $\times$ denote additive versus factorial relationships between variables. We

identified models best-supported by our data based on Akaike's Information Criteria with

a correction factor for small samples sizes (AICc; Burnham and Anderson 2002). We

defined competing models as the model with the lowest AICc value ("top model," ΔAICc

=0) and any models with ΔAICc $\leq$ 2 of the best-supported model.

After identifying the best-supported model of juvenile survival incorporating AGE and YR, we added brood-specific covariates to account for additional variation in the data. These brood-specific covariates included HD and YR × HD. We used the logit function to transform HD into a continuous variable. We included the interaction of HD and year (YR; 2011 or 2012) as a covariate in models because annual changes in temperature and precipitation affect the timing of woodcock breeding (Gregg 1984, McAuley et al. 2010). We retained these covariates in models of juvenile survival if their inclusion led to a net reduction in AICc (ΔAICc reduction of >0).

We added weather covariates to the best-fitting survival model that incorporated AGE, YR, and brood-specific covariates to account for effects of weather conditions on survival of juvenile woodcock. These covariates included PCPT, MAXT, and MINT and we treated these as continuous variables in survival models. We retained covariates in survival models if their inclusion led to a net reduction in AICc (ΔAICc reduction of > 0).

Finally, we added a covariate indicating whether juvenile woodcock were radio-marked (TRANS) to the best-supported model that incorporated AGE, YR, brood-specific, and weather covariates. Using TRANS as an additive covariate allowed us to evaluate radio-transmitter effects across all ages and years equally (Amundson and Arnold 2010). We retained TRANS in survival models if its inclusion led to a net reduction in AICc (ΔAICc reduction of > 2). We used the ESTIMATE function is SAS 9.3 (SAS Institute Inc., North Carolina, USA) to assess the relationships between daily survival rate and the covariates included in our best-supported model, by allowing the

covariate of interest to vary while holding the other model covariates constant at their mean values.

We performed a *post hoc* analysis of our best-fitting model [(YR×AGE) + PCPT] to better understand the relationship between survival and precipitation. Most intervals we used in our survival analyses contained little or no rain ($n = 300$) and only a few intervals contained high levels of precipitation (>7.5 cm, $n = 6$). This analysis allowed us to assess whether woodcock survival decreased linearly as a function of PCPT (i.e., resembling a negative linear relationship between survival and precipitation) or if there was a threshold of precipitation above which juvenile woodcock survival decreased. We assessed this relationship by removing intervals with zero precipitation and those with high precipitation (>7.5 cm) from the data and comparing our best-supported survival model [(YR×AGE) + PCPT] with all intervals (PCPT$_{all}$) and with intervals that experienced precipitation, except those with extreme precipitation events (PCPT$_{0-7.5}$). Removing the instances of zero and high precipitation allowed us to assess the effect of precipitation on survival when precipitation occurred, while avoiding rare extreme precipitation events. We used estimates of the intercept and covariates from these models to graphically represent the relationship between survival and precipitation.

Survival estimates:--We used the Kaplan-Meier method with staggered entry (Pollock et al. 1989) using the KMsurv package in Program R (version 2.15.2, R Core Team, 2012) to estimate survival of juvenile woodcock for days 1-15 post-hatch. We recorded the number of days from when transmitters were deployed on juveniles to better censor individuals if radio transmitters failed prematurely. We assumed radios failed if

they performed irregularly and there was no indication the individual had died. We also

assumed radios failed if they were nearing the end of their projected battery life and

subsequently lost signal from the radios. We right-censored individuals in both of these

circumstances, assuming the individual survived until radio failure (Korschgen et al.

1996). We assumed a juvenile died if brood counts indicated a juvenile(s) was absent

from the brood on two subsequent counts.

RESULTS

During 2011 and 2012, we radio-marked 73 (2011: $n = 22$, 2012: $n = 51$) juvenile

woodcock from 51 broods (2011: $n = 16$, 2012: $n = 35$). We knew fates of 49 marked

and 79 unmarked juveniles from 45 broods from our sample of marked juveniles and

tracking radio-marked adult females with broods, giving us an effective sample size of

1,041 observation intervals. We were unable to ascertain fates of 24 marked juveniles

due to uncertain times of radio failure and we censored these individuals from analyses.

We did not observe any negative impacts (i.e., entrapment in radio harness, or

skin or feather wear) of radio transmitters on juvenile woodcock during the course of our

study. We found no evidence of non-independence among juveniles within the same

brood ($\chi_{44}^2 = 17.15$, $P = 0.99$); therefore, we treated all individuals' fates in our sample as

independent. Our best-supported model of juvenile woodcock survival included the

interaction of AGE $\times$ YR and the additive effect of PCPT (Table 2). PCPT had a

negative relationship with juvenile survival ($\beta_{PCPT} = -0.76$, 85% CI: -1.08 to -0.43).

Although TRANS, MINT, and MAXT all appeared in survival models competitive with

our best-supported model ($\Delta AIC_c \leq 2$), these variables were uninformative as they did not

decrease the overall AIC_c by ≥ 2 when they were added as an additional covariate (Arnold 2010); therefore, we did not consider models including these covariates to be competitive with our best-supported model. There was no evidence to suggest that either TRANS or HD was related to juvenile woodcock survival (Table 2).

We calculated daily survival rates (DSR) of juvenile woodcock using our best-supported model, holding PCPT constant at the mean value ($\bar{x} = 0.19$) and allowing AGE and YR to vary across each combination of AGE and YR (Fig. 1). The effect of the AGE $\times$ YR interaction was approximately zero in 2011 ($\beta_{YR \times AGE}$ for 2011 = -0.01), but was positive in 2012 ($\beta_{YR \times AGE}$ for 2012 = 0.12). Cumulative survival of juvenile woodcock to 15 days of age based on Kaplan-Meier survival estimates was 0.746 (95% CI: 0646 – 0.862) in 2011 and 0.843 (95% CI: 0.762 – 0.933) in 2012 (Fig. 2) .

To assess the relationships between PCPT, AGE, and YR we allowed the value of the covariate of interest to vary in our best-supported model while simultaneously holding the other covariates constant at their mean values. Daily survival decreased with the amount of precipitation, resulting in an average decrease of approximately 0.01 in juvenile DSR for each additional cm of precipitation (Fig. 3). Juvenile DSR increased asymptotically with AGE, resulting in a 0.002 average increase in DSR with each additional day of age (Fig. 4).

PCPT was the only weather covariate in our best-supported survival model. However, because the distribution of PCPT across intervals was highly skewed (many zero precipitation events and few relatively high precipitation events), we evaluated both the relationship between juvenile survival and PCPT using only intervals with PCPT

below extreme levels (<7.5 cm) and between juvenile survival and PCPT when PCPT was extreme. With PCPT <7.5 cm, juvenile DSR declined an average of 0.008 per cm of precipitation ($\beta_{PCPT0<i<7.5}= -0.71$, SE = 0.46). In contrast, juvenile DSR decreased an average of 0.03 per cm of precipitation when PCPT during the interval was >7.5 cm.

DISCUSSION

Estimating survival of juvenile woodcock from hatch to fledging with radio telemetry can be biased when marking impacts survival. Radio transmitters have been attached to juvenile woodcock to estimate survival in the past (Horton and Causey 1981, Wiley and Causey 1987), but these studies assumed no negative impacts on survival resulted from attaching radio transmitters to juveniles. Neither of these studies directly assessed the possible impact of radio transmitters on survival. We found that attaching small (considerably smaller than those used in previous studies) radio transmitters using elastic harnesses to juvenile woodcock did not negatively affect survival, indicating that currently available radio transmitters can be used to estimate survival of juvenile woodcock without bias. Furthermore, our transmitter attachment methods and materials seemed to have not negatively impacted juvenile woodcock survival, in that we did not observe any obvious signs of distress, and our best-supported survival models did not include the covariate TRANS.

Of the weather and brood-specific covariates we considered, only PCPT was related to juvenile woodcock survival when we accounted for AGE and temporal variation (AGE and YR) in survival models. PCPT, especially periods of extreme precipitation, was negatively related to survival of juvenile woodcock. Precipitation

likely limits the ability of juvenile woodcock to thermoregulate and may especially impact precocial birds (e.g., Sheldon 1971, Owen 1977, Pietz et al. 2003). Sheldon (1971) and Owen (1977) suggested that periods of adverse weather (e.g., precipitation) can cause significant juvenile woodcock mortality. Rabe et al. (1983) suggested that due to growth requirements of juvenile woodcock, weather-related stress has the greatest potential to limit survival during the brood-rearing period. We did not assess a PCPT $\times$ AGE interaction in our survival models, but it is likely that the negative relationship between juvenile woodcock survival and precipitation decreases with juvenile age because older juveniles are better able to thermoregulate and have developed plumage that provides more protection from wet and cold conditions.

In our study, juvenile woodcock survival during the 15-day period from hatch to fledging was considerably higher in 2012 than in 2011. Environmental conditions in spring 2012 were generally more favorable than in 2011, as 2012 was warmer with less precipitation during the brood-rearing period. However, we attributed the majority of juvenile mortalities we observed to predation and not exposure to cold temperatures, precipitation, or a combination of these factors. We could not distinguish between mortality of marked juvenile woodcock resulting directly from predation from those resulting from exposure where the juvenile was subsequently consumed by a predator. As a consequence, we were unable to ascertain whether the apparent negative effect of precipitation on juvenile woodcock survival resulted from exposure, increased efficiency of predators in wet conditions, or perhaps different predator densities and predation pressure between years.

We note that there are potential limitations to extrapolating our conclusions beyond our study. Although we selected juvenile woodcock to equip with radio transmitters randomly within broods, our sample of broods may have been biased, as some broods in the larger population in our study area may have been more likely than others to be included in our sample due to possible biases in our efforts to find broods with pointing dogs. Pointing dogs were generally searching near edges where woodcock broods are thought to frequent, which may have biased our sample. Ideally, broods could be marked randomly from the population of woodcock. If juveniles in the broods we marked had higher or lower survival than juveniles in broods in the entire population of broods on our study area, our estimates of survival could be biased. In addition, bias in survival estimates could results from radio-marking older juveniles (closer to 15 days old), and older individuals may have a higher survival probability than juveniles marked at an earlier age. However, we minimized this potential source of bias by including the best-supported combination of AGE and YR in all of our survival models.

Overall, our results suggest that currently available transmitters and the attachment methods we used had little or no negative effect on survival of juvenile woodcock during the period from hatch to fledging, which we assumed was the period that juveniles are most vulnerable to mortality due to capture stress and deploying transmitters. In the future, it is likely that transmitters will continue to get smaller and therefore, the effects of deploying transmitters on juvenile birds will likely decrease as transmitters get smaller and lighter. However, we stress that researchers should test the assumption that marking individuals has no impact on their survival whenever plausible.

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Consistent with other studies of survival of juvenile woodcock (and other precocial birds), survival varied by year and age, and was negatively related to precipitation during the brood-rearing period. We suggest that employing methods similar to those we used to estimate survival and evaluate factors related to survival of juvenile woodcock (and likely other shorebirds and precocial birds) can provide unbiased estimates of survival and a better understanding of factors related to survival.

Table 1: Covariates used in logistic exposure analysis of survival of juvenile American woodcock at Tamarac National Wildlife Refuge, Minnesota in 2011 and 2012, symbol, and explanation of relationship between covariate and survival.

Covariates	Symbol	Relationship with survival
Year[a]	YR	Woodcock survival has been shown to differ between years (Gregg 1984, Longcore et al. 2000, McAuley et al. 2010). We included year in our analysis to account for temporal variation in survival of juveniles.
Age	AGE	Survival likely asymptotically increases with age of the juvenile because they are better able to thermoregulate as they age (Rabe et al. 1983) and likely most vulnerable to predation soon after leaving the nest (Streby and Andersen 2013); therefore, we hypothesized a positive relationship with age and juvenile survival.
Hatch date	HD	Juveniles that hatch earlier are more likely to be from the females in the best condition (Blums et al. 2005); therefore, we hypothesized that hatch date is negatively associated with juvenile survival. Hatch date was transformed using the logit function into a continuous variable.
Precipitation	PCPT	Precipitation hinders the ability of woodcock to thermoregulate (Rabe et al. 1983) and has been negatively related to juvenile woodcock survival (Dwyer et al. 1988) and therefore we hypothesized that precipitation is negatively associated with juvenile survival.
Maximum temperature	MAXT	We predicted that higher maximum temperatures would have a positive relationship with survival. Higher maximum temperatures likely increase survival of females during incubation and brood rearing (Rabe et al. 1983, Longcore et al. 2000). Females are also more active at higher ambient air temperatures (Vander Haegen 1992) and females will brood juveniles when temperatures are low (McAuley et al. 2010); therefore, at higher temperatures females likely spend more of their time foraging and are more capable of meeting their own energetic requirements and those of juveniles

		in their brood because females will feed juveniles for the first seven days after hatch (Gregg 1984, Vander Haegen 1992).
Minimum temperature	MINT	We predicted juvenile survival would have a positive relationship with minimum temperature. Juveniles may be less likely to survive at lower minimum temperatures because they lack the ability to thermoregulate (Sheldon 1971, Owen 1977, Rabe et al. 1983, McAuley et al. 2010).
Transmitter[a]	TRANS	Transmitters may reduce juvenile survival. We included this covariate to evaluate the effect of transmitters on juvenile woodcock survival.

[a]Indicates a categorical variable use in our models of juvenile survival

Table 2: Model-selection results from *a priori* analysis of American woodcock juvenile survival at Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. We evaluated survival related to age (AGE; 1-15 days), year (YR; 2011 or 2012), hatch date (HD; Julian date), precipitation (PCPT), maximum and minimum temperature (MAXT and MINT), and transmitters (TRANS). Models were ranked according to the difference in Akaike's information criterion (ΔAIC_c) corrected for small effective sample size ($n = 1,041$ intervals), Akaike model weights (ω_i), and number of estimable parameters (K).

Model[a]	ΔAIC_c	ω_i	K
(YR×AGE) + PCPT	0.00	0.38	4
(YR×AGE) + PCPT + MINT	1.36	0.19	5
(YR×AGE) + PCPT + TRANS	1.78	0.16	5
(YR×AGE) + PCPT + MAXT	1.91	0.15	5
(YR×AGE) + PCPT + MAXT + MINT	3.06	0.08	6
(YR×AGE)	6.97	0.01	3
(YR×AGE) + HD	7.30	0.01	4
(YR×AGE) + MINT	7.83	0.01	4
YR + AGE	8.12	0.01	3
(YR×AGE) + MAXT	8.54	0.01	4
(YR×AGE) + MAXT + MINT	8.88	0.00	5
(YR×AGE) + (YR×HD)	8.98	0.00	5

[a]AIC_c of top-ranked model = 182.01

Figure 1. Daily survival rates with associated 95% CIs of juvenile American woodcock by year (2011 or 2012) and age (1-15 days post-hatch) at Tamarac National Wildlife Refuge, Rochert, Minnesota. Daily survival rates were calculated from the best-supported survival model [(YR×AGE) + PCPT], where PCPT is held constant at the mean value ($\bar{x} = 0.19$).
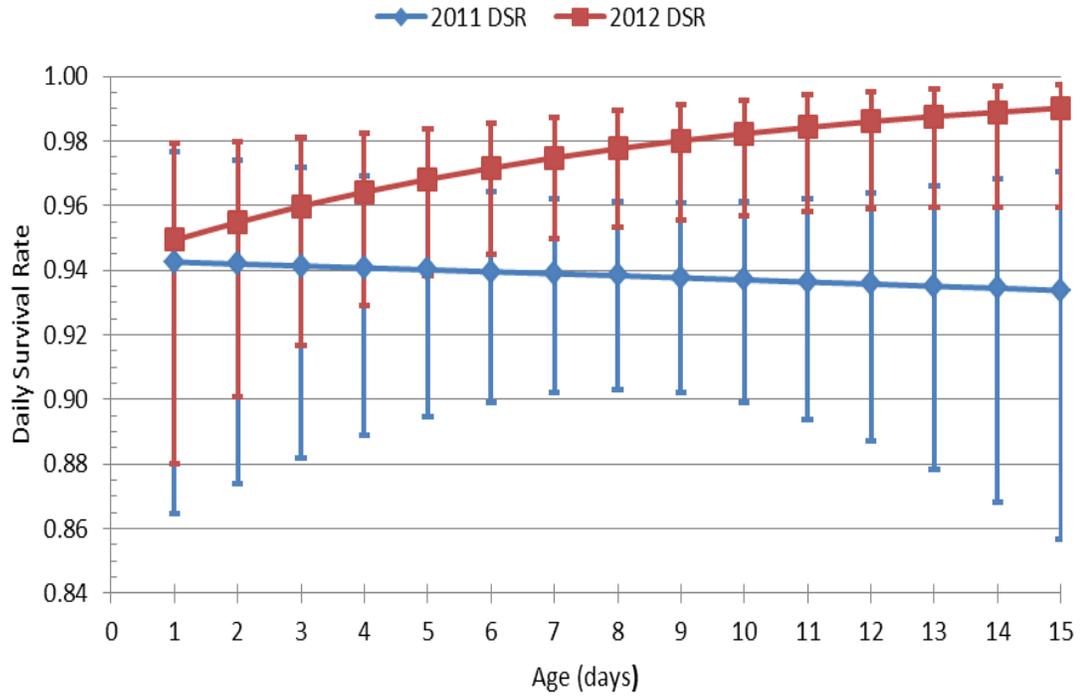
Figure 2. Cumulative survival and associated 95% CIs of juvenile American woodcock in 2011 and 2012 at Tamarac National Wildlife Refuge, Rochert, Minnesota. Cumulative survival rates were calculated using the Kaplan-Meier estimator from hatch until fledging (0 – 15 days of age).

2011 Kaplan-Meier Juvenile Survivial

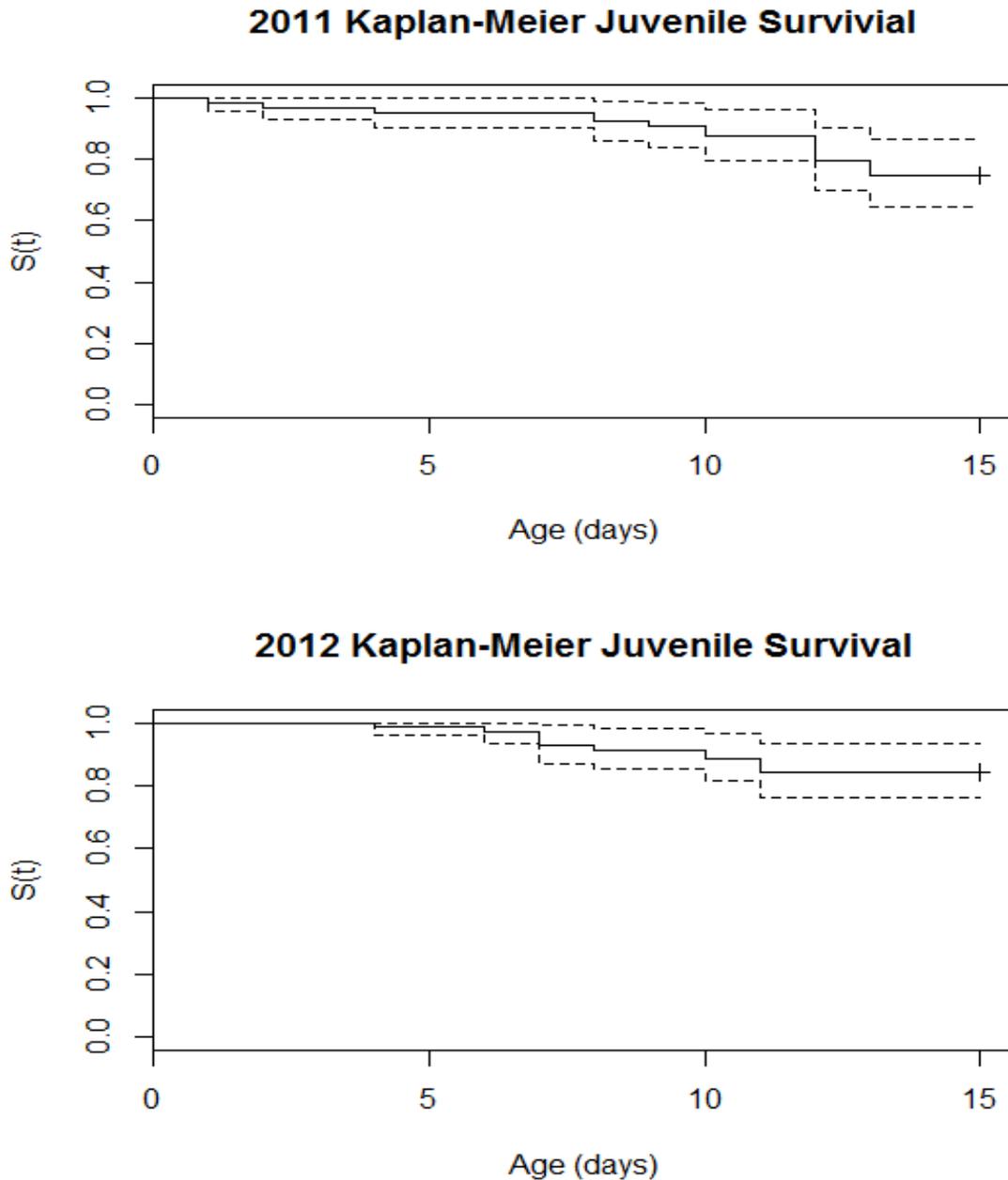**2012 Kaplan-Meier Juvenile Survival**

Figure 3. Effect of precipitation on survival of juvenile American woodcock at Tamarac National Wildlife Refuge, Rochert, Minnesota in 2011 and 2012. Daily survival rates and associated 95% CIs were calculated from the best-supported survival model [(YR×AGE) + PCPT], where PCPT was allowed to vary. Both years (2011 and 2012) are included and juvenile age was held constant at the mean value ($\bar{x} = 9.28$ days).
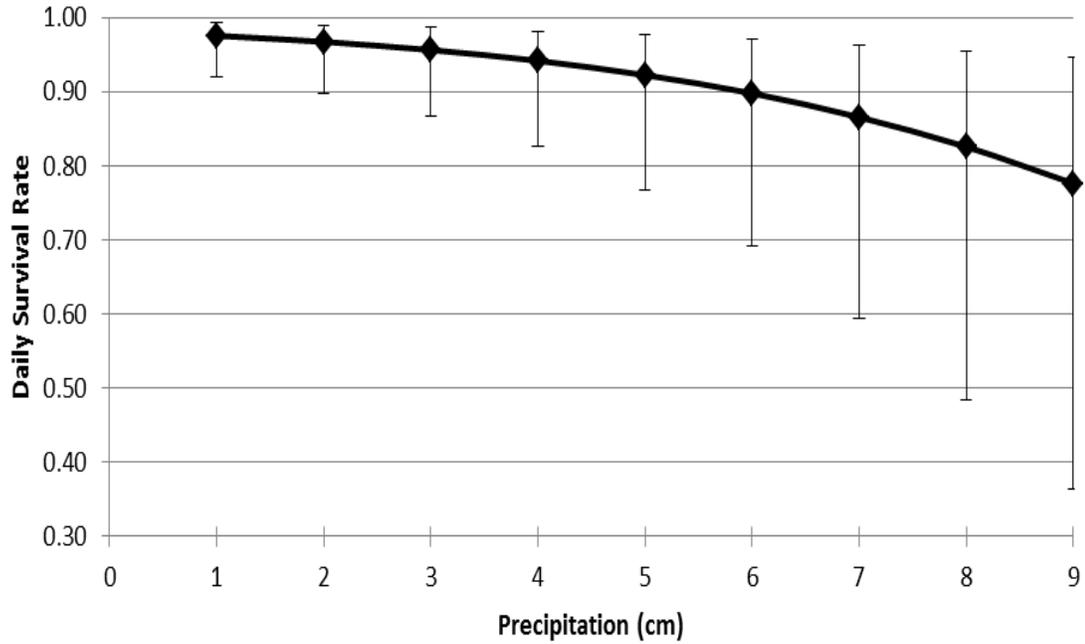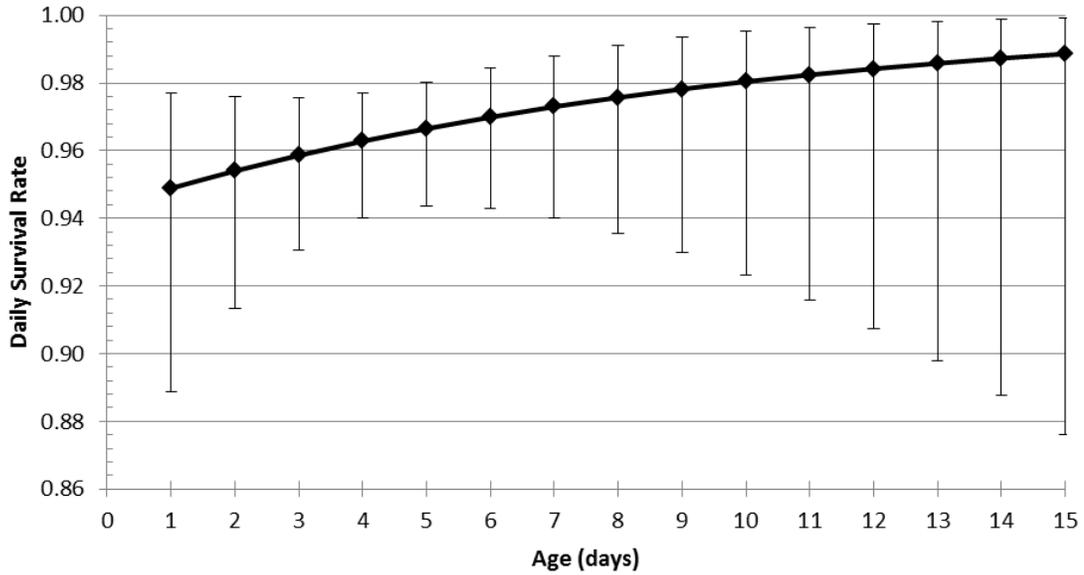
Figure 4. Effect of juvenile age on daily survival of juvenile American woodcock. Daily survival rates and associated 95% CIs calculated from the best-supported model of survival [(YR×AGE) + PCPT]. AGE was allowed to vary from 1 to 15 days post-hatch. Both years (YR: 2011 and 2012) are included and PCPT was held constant at the mean value ($\bar{x} = 0.19$ cm).

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