

**University of Minnesota
Graduate School**

This is to certify that I have examined this copy of a master's thesis by

Kevin Eric Doherty

And have found that it is complete and satisfactory in all respects, and that any and all
revisions required by the final examining committee have been made

David E. Andersen

Signature of Faculty advisor

Date

**Fall movements patterns of adult female American
woodcock (*Scolopax minor*) in the western Great
Lakes region**

A Thesis submitted to the faculty of the Graduate School of the University of
Minnesota by

Kevin Eric Doherty

In partial fulfillment of the requirements for the degree of Master of Science

December 2004

TABLE OF CONTENTS

Table of Contents.....	i
Acknowledgements.....	iii
List of Figures.....	v
List of Tables.....	vii
List of Appendixes.....	viii

CHAPTER 1

Effects of habitat and weather on the movement patterns of adult female American woodcock in the western Great Lakes region:

Abstract.....	1
Introduction.....	2
Study Area.....	4
Methods.....	5
Capture and Radio Marking.....	5
Radio Tracking.....	5
Predictor Variables.....	7
Movement Data.....	8
<i>A priori</i> Models.....	8
Data Analysis.....	11
Results.....	13
Discussion.....	15
Literature Cited.....	18

CHAPTER 2

Fixed kernel home range estimation incorporating telemetry locational error:
American woodcock (*Scolopax minor*) home range analysis using real and simulated data

Abstract.....	34
Introduction.....	35
Study Area.....	37
Methods.....	38
Capture and Radio Marking.....	38
Radio Tracking.....	38
Home Range Analysis.....	39
Influence of Sample size.....	40
Monte Carlo Home Range Simulation.....	41
Influence of Sample size using Monte Carlo Simulations.....	41
Statistical comparisons.....	42

Results.....	42
Woodcock Telemetry results.....	42
Monte Carlo Simulation results.....	43
Discussion.....	45
Literature Cited.....	48

ACKNOWLEDGMENTS:

My research is part of a large collaborative effort investigating woodcock survival, habitat use, and movement in the western Great Lakes region. First, I would like to thank 2 graduate students with whom I collaborated very closely during the field seasons and who coordinated the collection of movement data for me for 2 years on their respective study sites; Jed Meunier of the University of Wisconsin and Eileen Oppelt of Northern Michigan University. I would also like to thank their major professors and Co-PI's on the project John Bruggink of Northern Michigan University and Scott Lutz of the University of Wisconsin. Last and by no means least I would like to thank my major professor David Andersen. I would like to thank him for sharing his patience, intellect, keen editorial skills, and passion for game birds with me. This thesis would not be what it is without his mentoring. Everybody who has worked for David has said the same; you really can't get a better boss. Finally, I would like to thank him for showing me the world of pointing dogs. It's hard to beat walking through the woods with your shotgun on a cool fall day hunting woodcock and watching a bird dog work; especially if that's your lab meeting!

This project was funded by the U.S. Fish and Wildlife Service, Region 3; U.S. Geological Survey (Science Support Initiative); Wisconsin Department of Natural Resources; Minnesota Department of Natural Resources; Michigan Department of Natural Resources; the 2001 Webless Migratory Game Bird Research Program; University of Wisconsin-Madison; University of Minnesota-Twin Cities; Northern Michigan University; the Minnesota Cooperative Fish and Wildlife Research Unit; the Ruffed Grouse Society; Wisconsin Pointing Dog Association; and the North Central Wisconsin Chapter of the North American Versatile Hunting Dog Association. We thank D.G. McAuley for helping with identifying mist-netting and night-lighting sites and suggestions for techniques for handling woodcock. On the Minnesota study site, special thanks are due Dick Tuszynski, Craig Kostrzewski, Steve Piegras, Jeremy Abel, Richard "Zeke" Black, and Tim Pharis for assistance with various aspects of field work and Mike Trentholm for locating missing birds by

aerial telemetry. On the Michigan study site, we thank D.E. Beyer for the Michigan Department of Natural Resources for coordinating telemetry flights.

LIST OF FIGURES:

CHAPTER 1

Fig. 1. Location of study areas in Minnesota, Wisconsin, and Michigan where American woodcock were radio-marked during the falls of 2002 and 2003..... 23

Fig. 2. Distance between subsequent locations ($n = 1,786$) for radio-tagged female after-hatch-year American woodcock ($n = 58$) during falls of 2002 and 2003 in Minnesota, Wisconsin, and Michigan..... 24

CHAPTER 2

Fig. 1. Standardized (probability area at n / largest 95% probability area) woodcock 95% probability areas (solid line) and 50% probability areas (dashed line) using h_{lscv} and h_{er} as the smoothing parameter in a fixed kernel in relation to sample size. Location data are from after-hatch-year female woodcock ($n = 7$) in east-central Minnesota during the fall of 2003..... 51

Fig. 2. Mean and range of the coefficient of variation vs. sample size for the 50% and 95% probability areas of fixed kernels using both h_{lscv} (white diamond/dashed line) and h_{er} (black diamond/solid line), derived from telemetry data from after-hatch-year female American woodcock in east-central Minnesota in the fall of 2003. Two hundred bootstrap samples per sample size were analyzed for each of 7 woodcock..... 52

Fig. 3. Ninety-five percent CIs of bootstrapped fixed kernel means and kernel probability estimates (using h_{er} [black diamond] and h_{lscv} [white diamond]) for 95% and 50% probability areas for after-hatch-year female American woodcock in east-central Minnesota in 2003.... 53

Fig. 4. Ninety-five percent CIs of bootstrapped fixed kernel means and kernel probability estimates for 95% and 50% probability areas using h_{er} (black diamond) and h_{lscv} (white diamond) for after-hatch-year female American woodcock in east-central Minnesota in 2003. 54

Fig. 5. Mean size and 95% CIs of bootstrap mean (dashed lines) of the 95% (black diamond) and 50% (black square) probability area of fixed kernels using h_{lscv} and h_{er} as the bandwidth selection method, on a simulated woodcock home range with 1 core use area. True area is represented by dark black line. Data are from 200 bootstrap samples per sample size..... 55

Fig. 6. Coefficient of variation vs. sample size for the 95% and 50% probability areas of fixed kernels using both h_{lscv} (dashed line) and h_{er} (solid line) for simulated woodcock home ranges with; 1 core use area, 1 core use area distant from a single satellite area of infrequent use, and 2 core use areas. True area is represented by dark black line. Data are based on 200 bootstrap samples per sample size..... 56

Fig. 7. Mean size and 95% CIs of bootstrap mean (dashed lines) of the 95% (black diamond) and 50% (black square) probability area of fixed kernels using h_{lscv} and h_{er} as the bandwidth selection method, on a simulated woodcock home range with 1 core use area distant from a single satellite area of infrequent use. True area is represented by dark black line. Data are from 200 bootstrap samples per sample size.....57

Fig. 8. Mean size and 95% CIs of bootstrap mean (dashed lines) of the 95% (black diamond) and 50% (black square) probability area of fixed kernels using h_{lscv} and h_{er} as the bandwidth selection method, on a simulated woodcock home range with 2 use areas. True area is represented by dark black line. Data are from 200 bootstrap samples per sample size.....58

Fig. 9. Mean and 95% CIs of the percent of simulated home range area estimated using fixed kernels (95% probability area) with h_{er} and h_{lscv} as the bandwidth selection method in relation to varying spatial orientations. Data are from 500 Monte Carlo simulated home ranges of $n = 50$ for each polygon type and smoothing method.....59

LIST OF TABLES:

CHAPTER 1

Table 1. American woodcock movement predictor variables and covariates at locations determined via radio telemetry in 2002 and 2003, in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan.....	25
Table 2. Descriptive statistics of predictor variables and distances between subsequent locations ($n = 1,786$) of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003.....	26
Table 3. Effects of blocking on process variation explained and summary of best models ($n = 5$ of 27 <i>a priori</i> models) and means model predicting distances between subsequent daily locations of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003.....	27
Table 4. Regression coefficient estimates and associated standard errors for the distance between subsequent daily locations of after-hatch-year female American woodcock in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003. Estimates are derived from single ΔAIC_c best models ($n = 2$) using maximum likelihood methods in a mixed-effects linear model with study area and year as blocking factors.....	28
Table 5. Summary of ΔAIC_c best models ($n = 5$ of 27 <i>a priori</i> models) and means model predicting distances between subsequent daily locations for movements <500 m of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003. Year and study area are blocks in all models except the means model.....	29

LIST OF APPENDIXES:

CHAPTER 1

- Appendix 1. Summary of all *a priori* models ($n = 27$) used to evaluate the distance to subsequent daily locations ($n = 1,786$) of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003. Models in the final analysis included a blocking effect for study areas and years.....30
- Appendix 2. Plot of the ash-free dry weight of earthworm samples (g) vs. the distance traveled to subsequent daily locations ($n = 1,786$) for after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper peninsula of Michigan during the falls of 2002 and 2003..... 31
- Appendix. 3. Plot of low temperature in °C vs. the distance traveled to subsequent daily locations ($n = 1,786$) for after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003..... 32
- Appendix 4. Plot of the percent porosity of soil samples vs. the distance traveled to subsequent daily locations ($n = 1,786$) for American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the fall of 2002 and 2003.....33

Chapter 1

Effects of habitat and weather on fall movement patterns of adult female American woodcock in the western Great Lakes region

Abstract:

In 2002 and 2003, I collected movement and habitat data for 58 adult female woodcock during fall across 3 pairs of study sites in Minnesota, Wisconsin, and Michigan. Distances between subsequent daily locations were highly variable (C.V. = 2.188), and the majority (90.9%) of distances between subsequent daily locations of woodcock were <400 m, with 47.7% of distances <50 m. Habitat variables related to food, weather, and predator avoidance were used in general mixed linear models using Information-theoretic methods to assess the importance of these variables as predictors of distance between subsequent daily locations of individual woodcock. Models incorporating all movements explained 71.56% of the process variation among individual birds. Woodcock were more likely to make large movements (>500 m) and forage in new areas when environmental conditions were not favorable, such as in the case of low earthworm abundance (biomass). Large movements into new foraging areas were correlated with the interaction between soil porosity and rainfall, presumably because earthworm availability increased following precipitation. Woodcock were also more likely to make longer movements in warmer temperatures with >2/3 of movements >500 m occurring when the daily low temperature was above the median low temperature of 2.4° C. My results suggest that the primary determinants of woodcock movements during fall (prior to migration) were low local food availability and the potential for increased food availability elsewhere. Longer movements were influenced by weather conditions, and there was little evidence that predator avoidance influenced movements between subsequent days. Adult female woodcock appear to incorporate prior knowledge of previously

used areas into the decision of foraging location on a particular day, and generally return to the previous day's foraging area unless conditions become more favorable elsewhere.

Introduction:

American woodcock (*Scolopax minor*) generally make crepuscular flights from nighttime roosting fields to forage in densely wooded diurnal areas with moist soils (e.g., Krohn 1971, Whitcomb 1974). Reasons for these flights may include avoidance of mammalian predators during nighttime by roosting in large clearings and avoidance of avian predators during the day by foraging in dense stands. Woodcock return to close proximity of previous foraging areas, with the reported distance between sequential locations in fall being 129 m (located >5 times a month, during September and October [Sepik and Derleth 1993]). Movements within the same day are short relative to the distance between subsequent daily locations (median distance ~5 m [Hudgins et al. 1985], average 22.0 m \pm 1.7 SE [Godfrey 1974]). Unless woodcock are disturbed, they generally forage in the same small patch of habitat all day (D.G. McAuley U.S. Geological Survey, personal communication and field observations). Thus, selection of diurnal habitat occurs when woodcock return from nighttime roosting fields.

Factors influencing movement and habitat selection by woodcock are not well understood. Animals move for a variety of reasons and the behavior influencing movement patterns can be viewed as having costs and benefits. As such, movement behavior should be influenced by natural selection to maximize energy intake while reducing risk of predation (Krebs and Davies 1993). Optimal Foraging Theory (MacArthur and Pranka 1966) predicts that animals forage in a manner that maximizes net energy gain (Pyke 1983), although many studies have shown that animals forage differently in the presence of predators (e.g., Milinski and Heller, 1978, Heller and Milinski 1979, Krebs 1980, Lima et al. 1985). Woodcock make

daily decisions about their movements because they must simultaneously balance the need for obtaining adequate resources to meet energetic demands while minimizing predation risk. Information gained from past patch use and food encounters are likely important predictors of future foraging opportunities (Pyke 1983). Moving into unknown areas to increase potential foraging opportunities could result in no energy gain or place woodcock at an increased predation risk.

Several environmental factors could influence woodcock movement patterns. First, woodcock primarily consume invertebrates—approximately 80% by volume and frequency, and 75% of woodcock diet is earthworms (summarized by Keppie and Whiting 1994). Diet breadth may increase to include more species of invertebrates and plant matter if soil moisture is low, and earthworms are unavailable (Keppie and Whiting 1994). Second, weather conditions may directly influence movement patterns by affecting woodcock metabolic rates (i.e., increased oxygen consumption below 20 °C [Haegen et al. 1994]). Third, woodcock seem to prefer dense stands of young hardwoods as diurnal cover (e.g., Morgenweck 1977, Hudgins et al. 1985, Keppie and Whiting 1994), which may decrease predation risk from avian or mammalian predators. Fall movement may be related to the availability and distribution of habitat that offers adequate protection from predators for foraging. Finally, in a captive food trial, woodcock exhibited strong preference for soil color (brightness more than hue [Rabe et al. 1983a]), which may be a proximate cue related to prey availability.

To better understand factors affecting woodcock movement, during the fall of 2002 and 2003, I studied movements of after-hatch-year (hereafter = adult) female American woodcock prior to migration in the western Great Lakes region, and related environmental factors to observed movement patterns. Specifically, I addressed whether food availability, weather, or predator avoidance, independently or in combination, had a measurable effect on diurnal movements (the distance between subsequent daily locations) of woodcock.

Study Areas:

I captured and radio-marked woodcock on 3 pairs of study sites in the western Great Lakes region (Fig. 1). As part of a larger study of fall woodcock ecology, study sites were selected in areas with high woodcock densities, and where woodcock hunting could be controlled on 1 of each of the pairs of study sites. Study sites were under both public and private ownership.

Michigan

Woodcock were captured and monitored in the Copper Country State Forest in northern Dickinson County in the Upper Peninsula of Michigan (Fig. 1). Field work was primarily concentrated in the eastern half of the 25,728 ha Dickinson Woodcock Research Unit. Upland forest habitats were dominated by aspen (*Populus* spp.), red maple (*Acer rubrum*), and paper birch (*Betula papyrifera*). Dominant species in coniferous forests were balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*). In addition, alder (*Alnus* spp.) dominated many moist lowland areas.

Minnesota

Study sites in east-central Minnesota included portions of the 15,672 ha Mille Lacs Wildlife Management Area (MLWMA) and the adjacent 1,166 ha Four Brooks Wildlife Management Area (FBWMA, Fig. 1). Both wildlife management areas (WMA) were managed to provide hunting opportunities to the public, primarily by habitat manipulation for game species. MLWMA and FBWMA had comparable vegetative communities, which included early regenerating aspen and lowland habitats including alder (*Alnus* spp.), willow (*Salix* spp.), and burr oak (*Quercus macrocarpa*).

Wisconsin

Wisconsin study sites were within the Lincoln County Forest and Tomahawk Timberlands in north-central Wisconsin (Fig. 1). Both study areas were managed primarily for timber and recreational opportunities. Terrain in both areas was rolling with boggy wet basins. Forest cover was mostly northern mesic forests with sugar maple (*Acer saccharinum*) dominating the better-drained soils while red maple (*Acer*

rubrum) dominated the more mesic sites. Wet basins were dominated by spruce-fir (*Picea-Abies*) on wet mineral soils and spruce-tamarack (*Picea-Larix*) on wet organic soils.

Methods:

Capture and radio-marking

Beginning on 24 August 2002 and 18 August 2003 woodcock were captured in Minnesota, Wisconsin, and Michigan study sites. Capture sites were identified by observing potential roosting areas at dusk, and subsequently placing mist nets (Sheldon 1960) in areas where woodcock were observed flying to roost and by spot lighting roosting fields (Reifenburg and Kletly 1967, McAuley et al. 1993). Wing plumage characteristics were used to age and sex captured birds (Martin 1964). Bill length was used as an additional means of determining sex (Mendall and Aldous 1943). Radio transmitters were attached to woodcock using all-weather livestock-tag cement in conjunction with a single loop wire harness using the techniques of McAuley et al. (1993). Transmitters (Advanced Telemetry Systems, Inc., Isanti, MN: use of trade names does not imply endorsement by the University of Minnesota) weighing approximately 4.4 g and powered by a 1.5-volt silver-oxide battery were attached to captured woodcock. Woodcock were released at capture locations following transmitter attachment.

Radio-tracking

In each year in early September (7 September 2002 and 8 September 2003) a sub-sample of adult female woodcock ($n = 15$; 2002, $n = 18$; 2003) were randomly selected from all adult female woodcock captured on each of the 3 study locations. Female woodcock were located once a day ≥ 5 times per week using hand-held rubberized H-antennas and portable receivers, until mortality or loss of radio contact (i.e., after observers failed to detect a signal during 3 consecutive aerial telemetry flights). Coordinates of daily locations of radio-marked woodcock were obtained from the ground within approximately 2-14 m of the true location of a woodcock with

a hand-held Global Positioning System (GPS). When determining daily locations woodcock were circled using telemetry receiving equipment to determine their exact location. Observers attempted not to flush woodcock with ~ 88% of visits resulting in no flushing. I estimated the distance of the recorded daily location to woodcock by locating a fixed transmitter using the Jennrich-Turner (Jennrich and Turner 1969) home range estimator before field work began (95% error polygon radius – GPS error = 13.68 m [outer bound]) and by the paced distances from radio-marked adult female woodcock intentionally flushed (2.2 m S.E. = 0.3, $n = 10$ [inner bound]).

I quantified habitat variables associated with recorded woodcock locations (daily use points) at a random direction from the radio-equipped woodcock to minimize bias in data collection. I estimated woody stems per 0.004 ha (40 m²) along bounded transects with the starting location of the transect corresponding to the GPS daily use point. The length of each transect was determined by the length of observers' arms spans (i.e., for an arm span 2 m wide, the observer walked 20 m to sample 0.004 ha) (Penfound and Rice 1957). To minimize error associated with pacing in dense habitats, each researcher used a rope equal in length to the specific distance that they needed to walk to sample the 0.004 ha bounded transect with outstretched arms. Starting at the daily location (2-14 m from the woodcock), observers walked perpendicular from the line between the daily location and the true location of the woodcock for ~10 m (i.e., half the distance based on a 20 m transect, 0.002 ha) before turning 90° in the direction of the woodcock and sampling the remaining 0.002 ha. The L-shaped transect was used to ensure adequate spacing between observers and woodcock and minimized observer influence on woodcock behavior, while still allowing collection of micro-habitat variables that characterized the daily use point. Transects did not cross into different cover types (i.e., if the transect orientation and distance would have crossed into a different cover type, it was reoriented in a randomly selected direction back into the original cover type).

Predictor variables

At woodcock use sites, observers measured stem density, estimated earthworm abundance, assessed soil color, and collected soil samples. Observers counted each vertical woody stem within the bounded transect that forked below breast height as an individual stem and then tallied all stems counted within the bounded transect to estimate the stem density in the habitat surrounding the woodcock daily use point (Penfound and Rice 1957). Earthworm biomass was measured within a 35 cm² (0.1225 m²) square plot at the daily use point. Any vegetation inside this 35 cm² plot was cleared to facilitate detection and removal of surfacing earthworms. Observers poured ~1.26 l (1/3 gallon) of oriental hot mustard solution onto the ground, and collected all earthworms that surfaced during a 5 minute period (Paulson and Bowers 2002). In order to compare worm samples across a large geographic area (Hale et al. 2004), I calculated ash-free dry mass for each earthworm sample. Samples were weighed to the nearest 0.0001 g.

At the same location where earthworms were sampled, soil color was quantified before pouring the hot mustard solution inside the plot. Soil color was separated into 6 categories based on the Munsiel soil color chart 7.5YR (Munsiel 2000). The classifications used were 2.5-1, 3-1, 4-1, 5-1, 6-1, 8-1, and the closest match to the soil color was recorded at the woodcock location. Approximately 1 m from the earthworm sample location, observers collected a 9.8 cm diameter by 6.8 cm deep (512.9 cm³) soil core at the surface. The soil sample was collected at a random direction from the earthworm plot. When collecting soil samples, observers made effort not to compact soils, so that bulk density was not artificially inflated (Blake and Hartge 1986). I determined the porosity of the soil samples by dividing the bulk density of the samples by the density of quartz (2.65 g/cm³) to find the amount of pore space in the soil sample (Danielson and Sutherland 1986).

Daily weather variables were also collected in each of the 3 study locations. Daily high and low temperatures in °C were recorded with automated digital thermometers located on or adjacent to study areas. Precipitation (cm) in the previous

24 hr period daily was recorded at 0900 with rain gauges located centrally at study locations.

Movement data

Distance to subsequent locations (response variable) was calculated using the animal movement extension (Hooge and Eichenlaub 1997) in Arcview 3.3 (Environmental Systems Research Institute 2002). Each individual woodcock locational data set was structured by date and transformed into a polyline file. The distance to the next subsequent point was automatically computed and stored for each individual woodcock location. We did not monitor night-time locations of woodcock, but the median distance from capture locations (roosting fields) to diurnal locations was 414 m, which is similar to the distance between adult female woodcock roosting sites and daytime foraging sites (179.5 m) observed in September and October in Maine (Sepik and Derleth 1993).

A priori models

When woodcock return from their nighttime roosting fields a choice of diurnal habitat and spatial use occurs. Therefore, I hypothesized a set of models prior to data analysis based on the assumption that favorable environmental conditions on a previous day would result in shorter distances between daily locations, because woodcock would return to exploit favorable conditions. There are advantages to returning to the same patch, such as familiarity with cover to avoid predators and knowledge of productive foraging areas, but at some point surrounding habitats would likely become more favorable when resources become depleted or when availability of resources elsewhere was higher. In addition, weather events may influence energy requirements.

I created 27 different models to evaluate the relationship between environmental variables and movement of woodcock (Appendix 1). All predictor variables were related to 3 major classes of models; food, weather, and predator

avoidance (Table 1). The distance between subsequent daily locations was the response variable in all models. Inclusion of predictor variables was based on published literature and my experience with woodcock movement in 2001, the pilot year of my study.

Food models.-- Earthworms are the primary prey of woodcock. Earthworm abundance likely varies both spatially and temporally and thus may influence observed woodcock movement patterns. Earthworm abundance may be influenced by several factors, including soil moisture (e.g., Sepik 1984, Straw et al. 1994), soil temperature (<5 °C or > 25 °C; Reynolds et al. 1977, Rabe et al. 1983*a*), and vegetation (Reynolds et al. 1977, Keppie and Whiting 1994). I hypothesized that an increase in the mass of earthworms collected at a daily use point would be correlated with a decrease in the distance to the subsequent daily location because I predicted that woodcock should return to exploit high earthworm abundance. The second variable relating to food resources was soil color. Soil colors that were darker were hypothesized to result in shorter distances between daily locations based on experimental evidence indicating that captive woodcock exhibited strong selection for dark soil colors (Rabe et al. 1983*b*). The final variable included in the food models was soil porosity. Porosity of the soil influences soil moisture, which likely influences availability of earthworms (Rabe et al. 1983*a*, Sepik 1984, Straw et al. 1994) by influencing both abundance of earthworms and soil conditions that affect foraging success by making it easier or harder for woodcock to find or extract earthworms. I did not hypothesize a directional response related to porosity of the soil, but suspected that there would be a threshold at which adequate moisture would be present to support foraging for earthworms.

Weather models.-- Previous day's precipitation was included in models because I observed large movements following rain events in 2001 in Minnesota. I included an interaction between rainfall and porosity of the soil in some models because rainfall influences soil moisture. Highly porous soils that were previously too dry for woodcock to forage successfully would likely become favorable after rain events stimulating selection, thus movements into new areas. Cold temperatures may

also affect woodcock energetic requirements or foraging abilities (Bell 1991), which I represented in models with daily low temperature. Woodcock metabolic demands increase at lower temperatures (Haegen et al. 1994), but woodcock could respond to increased metabolic demands by either increasing movement to increase foraging opportunities or decreasing movements to conserve energy.

Predator avoidance models.-- By decreasing their exposure to predators woodcock could decrease (1) handling time of prey, (2) observational vigilance for predators, and (3) inter-prey waiting time (Krebs 1980), increasing their energetic intake. Because I could not directly measure predation pressure, and because stem densities at foraging locations were not correlated with earthworm abundance (food models), I used stem density as a surrogate to predator avoidance. I hypothesized that an increase in the density of the stand would offer woodcock increased protection from predators (especially avian predators) and would decrease movement between daily locations, because they could forage with less risk of predation.

Interactions.-- Due to the observational nature of my study I limited my models to include only 3 first order interactions. First, I included the interaction between rainfall and porosity of the soil discussed previously. Second, I allowed for an interaction between earthworm abundance and low temperature because earthworms become less available ($<5\text{ }^{\circ}\text{C}$ or $>25\text{ }^{\circ}\text{C}$; Reynolds 1977, Rabe et al. 1983a) and this interaction was equally likely to stimulate or inhibit woodcock movement. Third, I allowed for an interaction between soil color and rainfall, because increased soil moisture (following rainfall) makes soil color darker.

Models were first created in each of the 3 main classes of variables with no interactions included to determine whether individual or groups of variables were strongly selected. In each suite of models, predictor variables were created alone before they were combined with other variables. After creating each class of models I combined variables from different classes of models. Finally, all 3 classes of variables were combined. I had 2 global models that contained all parameters plus first order interactions thought to be relevant to movement from field observations. After I created all 27 models, they were then combined into a single candidate model

set and allowed to compete against each other. Only models having logical mechanisms based on published literature or field observations were included in the model set, therefore, all possible combinations of parameters were not included.

Data Analysis

Habitat variables collected at a woodcock locations were associated with the distance that the woodcock moved to the subsequent location. In this manner the distance that a bird moved between subsequent diurnal locations was a function of the habitat that it occupied prior to moving. All adult female woodcock with >20 movements ($n = 58$) were included in the movement portion of the analysis. Because sequential movements can be serially-correlated and habitat characteristics estimated for the same woodcock closer in time are more likely to be correlated than measures more distant in time, I modeled the appropriate covariance structure that best represented the data in SAS PROC MIXED (Littell et al. 1996, 1998). The covariance structure is derived from variances at individual times and correlations between measures at different times on the same animal (Littell et al. 1998). Three covariance structures were tested; compound symmetry (CS) where all measures at all times have the same variance and all pairs of measures on the animal have the same correlation, “unstructured” (UN) where no assumptions regarding equal variances or correlations are made, and auto-regressive (ar1) where there is an inter-animal random effect and a correlation structure within animals that decreases with an increase in the time interval between measures (Littell et. al. 1996). SAS PROC MIXED is a generalization of a standard linear model and data are permitted to exhibit correlation and nonconstant variability (SAS 8.2 online doc.). I used the REPEATED statement in PROC MIXED to model the covariation *within* woodcock, which accounts for the violation of independence of the observations (Littell et al. 1998, Franklin et al. 2001). The RANDOM statement was used to model the variation *among* woodcock, which accounts for heterogeneity of variances from individual woodcock (Littell et al. 1998, Franklin et al. 2001). The random effects factor was the sub-sample of individual woodcock that were randomly chosen from

all radio-marked adult female woodcock captured as part of the larger survival study. All other factors in the model were fixed effects. Maximum likelihood methods were then used to fit a mixed-effects (both random and fixed effects) general linear model in SAS PROC MIXED. I used Akaike's Information Criterion (AIC_c) to rank competing models based on which models were best supported by the observed data (Akaike 1973, Burnham and Anderson 2002). AIC_c values computed in PROC MIXED were used to identify the model with the highest rank (i.e., minimum AIC_c value) and ΔAIC_c values were used to calculate the likelihood of the model given the data using the following equation from Burnham and Anderson (2002:74).

$$\ell(g_i | x) \propto \exp(-\frac{1}{2}\Delta_i) \tag{1}$$

$\ell(g_i | x)$ = the likelihood(ℓ) of the model(g_i) given the data(x).

“ \propto ” means “is proportional to”

and Δ_i is the AIC differences ($AIC_{(g_i)} - AIC_{(\text{minimum value})}$)

Likelihood estimates from equation 1 were used to calculate Akaike weights using equation 2 (Burnham and Anderson 2002:75),

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)} \tag{2}$$

which can be interpreted as the “weight of evidence in favor of model i being the actual Kullback-Leibler (K-L) best model for the situation at hand given that one of the R models must be the K-L best model of that set of models” (Burnham and Anderson 2002:75).

To assess how much variation *among* individual woodcock was explained by the best approximating models I conducted a variance-components analysis (Littell et al. 1996, Franklin et al. 2001). I used maximum likelihood covariance parameter

estimates from SAS PROC MIXED for the ΔAIC_c best models and the “means model” (constant only) to compute the amount of process variation explained:

$$\text{process variation explained} = (\sigma_{(c)} - \sigma_a) / \sigma_{(c)} \quad (3)$$

where $\sigma_{(c)}$ = the variance component estimate for constant only model

and σ_a = the variance component estimate for the *a priori* model

To test whether pooling data across 3 study areas was justified, the suite of models ($n = 27$) was calculated with study area and year as blocking factors, and I assessed whether model selection or Akaike weights changed. Although most movements between subsequent locations were short (~ 95% of movements <500 m) woodcock also made longer movements up to 3,806 m. To test the sensitivity of the relative importance of each model and the amount of process variation explained by the effects of these large movements (>500 m), the same analysis that was performed on the full data set was performed on a subset of the data that incorporated only movements that were <500 m. Results from this analysis were then compared to analyses of the full data set. I used the best approximating model to estimate and compare regression coefficients and standard errors.

Results:

The majority (90.9%) of distances between subsequent daily locations by woodcock were <400 m, with 47.7% of the movements being <50 m (Fig. 2). The distance between subsequent daily locations for adult female American woodcock were generally small with the median distance being 52.0 m, but were highly variable (C.V. = 2.9, Table 2). Mean ash-free dry earthworm mass was 0.077 g (S.D. 0.153, C.V. = 1.99). Woodcock were located in areas having porous soils with mean porosity of soil samples being 0.774 (S.D. = 0.096, C.V. = .13) and in dense stands with an average of 114.18 stems per 0.004 ha (S.D. = 76.06, C.V. = 0.66).

The combined effects of low temperatures, precipitation, earthworm biomass, porosity of the soil, and a rain*porosity interaction were the strongest predictors of

woodcock movements. Of the 27 models tested, 2 models, which were identical except for the inclusion of the rain*porosity interaction (T+R+W+P+R*P [model 1] and T+R+W+P [model 2]), had a strong combined weight of evidence ($w_i = 0.914$) that they were the best models in the analyses of the full data set (Table 3). Food and weather were the best predictors of movements. The inclusion of the rain*porosity interaction greatly increased the likelihood that model 1 was the best predictor of woodcock movements with an evidence ratio of 5.48 when compared to model 2. The covariate structure selected based on Information-theoretic methods was ar(1), which I used in all mixed modeling.

An increase in earthworm mass was negatively correlated with the distance moved to subsequent locations and an increase in temperature was positively correlated with the distance moved to subsequent locations (Table 4). Earthworm mass had a large standard error compared to its associated parameter estimates. The effects of rain was negatively correlated with movements when the rain*porosity interaction was included (model 1). An increase in porosity was associated with an increase in distance between subsequent locations. The rain*porosity interaction had the strongest positive effect on the movements of adult female woodcock.

The inclusion of study areas and year as blocking factors did not affect the relative importance of the models evaluated or substantially change Akaike weights (Table 3). The inclusion of study area and years, however, increased the amount of variation explained by environmental factors among individual woodcock movements from 21.39 to 71.56%.

The same 5 models were selected from 27 *a priori* models for movements <500 m as for all movements, however the relative importance of the top 2 models switched, decreasing the importance of the interaction between rainfall and porosity (model 1 $w_i = 0.277$, model 2 $w_i = 0.716$ [Table 5]). The same combined effects of low temperatures, precipitation, earthworm biomass, soil porosity, and a rain*porosity interaction were the strongest predictors of woodcock movements <500 m. The top 2 models combined (T+R+W+P+ R*P and T+R+W+P) had a strong combined weight of evidence ($w_i = 0.993$) that they were the best models of

movements <500 m (Table 5). Model 2 had an evidence ratio of 2.585 vs. model 1 (with interaction). In contrast to the high amount of variation explained among individual woodcock by the best model in the analysis of all movements (71.56% with years and study areas as blocks), the best model for movements <500 m explained very little of the variation among woodcock (3.86%, with years and study areas as blocks). For the best model, S.E. estimates for all parameters were larger than the associated regression coefficient estimate except for T (regression estimate 0.675, S.E. = 0.277), which still had a positive effect on movement.

Discussion:

The distance between subsequent fall daily locations for adult female American woodcock in Minnesota, Wisconsin, and Michigan were generally small (median distance = 52.0 m), indicating that woodcock returned to the vicinity of the previous day's foraging area. Of the 27 *a priori* models I constructed, hypothesized to relate to food, weather, and predator avoidance, the same 5 models related to food and weather were selected, regardless of study site (3 states), replication (2 years), or the distance of movements considered (all movements, or movements <500 m).

In contrast to the high amount of variation explained among individual woodcock for all movements (71.56%), the best models explained only ~ 3.8% of the process variation among birds for movements <500 m. There are several plausible explanations for differences in predictive power at different scales of movements. First, the effect size could be too small in relation to the high variability in movements <500 m (C.V. = 2.2) to effectively predict movements. Second, predictor variables also exhibited high variability, thus creating large standard errors for parameter estimates. Third, if woodcock were selecting habitat on different scales for shorter vs. farther movements, and movements <500 m were based on features that varied at a small spatial scale (i.e., smaller than the distance between the woodcock and where we sampled habitat variables), then our study design would have low power to detect these effects. The distance that we kept from woodcock in order to minimize impacts on behavior could have led to the quantification of habitat at the

patch level instead of the micro-habitat characteristics of the use point, reflected in the high predictive power of models of movements when woodcock changed patches. Finally, variables that were quantified may not represent factors affecting shorter movements of adult female woodcock.

When all movement data were included in analyses, my models explained a high proportion (71.56%) of the process variation among woodcock and model parameter estimates coincided with my *a priori* hypotheses about adult female woodcock movements. Parameter estimates from the best approximating models and scatter plots (Appendix 2) indicated that increasing earthworm biomass was related to decreased movement distances. From the stand point of optimal foraging, specifically the marginal value theorem (MacArthur and Pranka 1966, Charnov 1976), it is likely that the woodcock returned to forage in areas with high earthworm mass until conditions become more favorable in other areas. Woodcock were more likely to make large movements (>500 m) and forage in new areas when earthworm mass at the previous day's foraging site was low.

Other constraints such as predator avoidance may also influence habitat selection, but stand density was not a strong predictor of movement distance in my analyses at any scale of movement. I used stem density as a surrogate of predator avoidance and other factors related to predator avoidance that were not measured could also influence woodcock habitat selection, such as the effectiveness of their cryptic plumage against different backgrounds. While soil color was strongly selected in feeding trials of American woodcock (Rabe et al. 1983a), my results did not indicate that woodcock movement was related to soil color.

Decreasing daily low temperature was negatively correlated with movement distances, with >2/3 of movements >500 m occurring when the daily low temperature was above the median low temperature of 2.4 °C (Appendix 3). This suggests that woodcock make fewer large movements to conserve energy when decreasing temperatures increase metabolic demands. Conservation of energy has been documented during a drought in Maine, where woodcock ceased to make flights to nocturnal roosting areas in conditions of low food availability (Sepik et al. 1983).

Results of laboratory studies of bumble bee and dark-eyed junco (*Junco hyemalis*) foraging (Cartar and Dill 1990, Caraco et al. 1990) suggested that animals may minimize unpredictability and prefer less risky foraging opportunities even if risky foraging is more profitable. However, when dark-eyed juncos were exposed to stress from decreasing low temperatures their response was to adopt a more risky foraging behavior. My results suggest that woodcock do not exhibit the same response to decreasing temperatures, perhaps because when soil temperatures are below 5 °C earthworms become less active (Reynolds et al. 1977, Rabe et al. 1983a), and presumably less available to woodcock.

Soil porosity had a positive relationship to the distance moved between subsequent daily locations; approximately 2/3 of movements >500 m occurred when porosity values were greater than the median porosity value of 0.770 (Appendix 4). The positive relationship of soil porosity was linked to the interaction between rain and porosity, suggesting woodcock responded to this interaction by making large movements into new foraging areas that were previously too dry to adequately provide them with their primary food source, earthworms. The combination of rain and porosity interacting together exhibited the greatest positive relationship to movement than any of the predictive variables. The positive relationship of porosity on movements was decreased by more than 50% in model 2 compared to when the interaction between R*P was included in model 1. The importance of the rain and porosity interaction to movements >500 m is further supported by the fact that the relative importance of model 1 (with the R*P interaction term) was greatly decreased when movements >500 m were not included in analyses ($w_i = 0.277$). Finally, this was consistent with field observations where woodcock made large movements into previously unused areas after precipitation events.

My interpretation of the way woodcock move and where they choose to be from day to day is that unless some environment stimuli occurs making conditions more favorable elsewhere, adult female woodcock will return to the previous day's foraging area. In this study, woodcock were more likely to make large movements (>500 m) and risk foraging in new areas when environmental conditions were not

favorable, such as in the case of low earthworm biomass, or when metabolic demands decreased at higher temperatures. The strong influence of the interaction of soil porosity and rain also suggests that habitat use is influenced by prevailing conditions that affect habitat quality at a particular time. Assessing movement behavior in woodcock allowed insight into why birds moved and how they used habitat, providing assessment of habitat selection beyond determination of preference alone. Adult female woodcock appeared to incorporate prior knowledge of previously used areas into the decision of where they will forage on a particular day.

Literature cited:

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B.N. Petrov and F. Csaki, eds. Second International Symposium on Information Theory. Budapest, Akademiai Kiado.
- Bell, W.J. 1991. Searching behavior: the behavioral ecology of finding resources. Chapman and Hall. New York, New York, USA.
- Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference. Springer-Verlag, New York, New York, USA.
- Blake, R.E. and K.H. Hartge. 1986. Bulk density. Pages 363-375 in A. Klute, ed. Soil Science Society of America Handbook Series 5. Soil Society of America, Madison, Wisconsin, USA.
- Caraco, T., W.U. Backenhorn, G.M. Gregory, J.A. Newman, G.M. Recer, and S.M. Zwicker. 1990. Risk-sensitivity: ambient temperature affects foraging choice. *Animal Behavior* 39:338-345.
- Cartar, R.V. and L.M. Dill. 1990. Why are bumblebees risk-sensitive foragers? *Behavior Ecology and Sociobiology* 26:121-127.
- Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9:129-136.
- Danielson, R.E. and P.L. Sutherland. 1986. Porosity. Pages 443-445 in A. Klute, ed. Soil Science Society of America Handbook Series 5. Soil Society of America, Madison, Wisconsin, USA.

- Environmental System Research Institute. 2002. 380 New York Street,
Redlands, CA 92373-8100.
- Godfry, G.A. 1974. Behavior and ecology of American woodcock on the breeding
range in Minnesota. Dissertation, University of Minnesota, Minneapolis,
Minnesota, USA.
- Franklin, A.B., T.M. Shenk, D.R. Anderson, and K.P. Burnham. 2001. Statistical
model selection; an alternative to null hypothesis testing. Pages 75-90 *in* T.M.
Shenk and A.B. Franklin eds. Modeling in natural resource management. Island
Press Washington D.C. USA.
- Haegen, W.M., R.B. Owen Jr., and W.B. Krohn. 1994. Metabolic rate of American
woodcock. *Wilson Bulletin* 106:338-343.
- Hale, C. M., L. E. Frelich, and P. B. Reich. 2004. Allometric equations for estimation
of ash-free dry mass from length measurements for selected European earthworm
species (Lumbricidae) in the western Great Lakes region. *American Midland
Naturalist* 151:179-185.
- Heller, R. and M. Milinski. 1979. Optimal foraging of sticklebacks of swarming
prey. *Animal Behavior* 27:1127-1141.
- Hooge, P.E. and B. Eichenlaub. 1997. Animal movement extension to Arcview:
Version 2.0. Alaska Biological Science Center, U.S. Geological Survey,
Anchorage, Alaska, USA.
- Hudgins, J.E., G.L. Storm, and J.S. Wakely. 1985. Local movements and diurnal-
habitat selection of male American woodcock in Pennsylvania. *Journal of
Wildlife Management* 49:614-619.
- Jennrich, R.I. and F. B. Turner. 1969. Measurement of non-circular home range.
Journal of Theoretical Biology 22:227-237.
- Keppie, D.M. and R.M. Whiting, Jr. 1994. American woodcock *Scolopax minor*.
The Birds of North America. 100:1-27. American Ornithologists' Union and
Academy of Natural Sciences of Philadelphia, USA.
- Krebs, J.R. 1980. Optimal foraging, predation risk and territory defense. *Ardea*
80:83-90.

- and N.B. Davies. 1993. An introduction to behavioral ecology. Blackwell Science Ltd. Malden, Massachusetts, USA
- Krohn, W.B. 1971. Some patterns of woodcock activities on Maine summer fields. *Wilson Bulletin*. 83: 396-407
- Lima, S., T.J. Valone, and T. Caraco. 1985. Foraging efficiency-predation risk tradeoff in the grey squirrel. *Animal Behavior* 33:155-165.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina, USA.
- , P.R. Henry, and C.B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science* 76:1216-1231.
- Martin, F.W. 1964. Woodcock age and sex determination from wings. *Journal of Wildlife Management* 28:287-293.
- MacArthur, R.H. and E.R. Pranka. 1966. On optimal use of a patch environment. *American Naturalist* 100:603-609.
- McAuley, D. G., J.R. Longcore, and G.F. Sepik. 1993. Techniques for research into woodcocks: experiences and recommendations. Pages 5-11 *in* J.R. Longcore and G.F. Sepik, eds. Proceedings of the eighth woodcock symposium. Biological Report 16, U.S. Fish Wildlife Service, Washington D.C., USA.
- Mendal, H.L. and C.M. Aldous. 1943. The ecology and management of the American woodcock. Maine Cooperative Wildlife Research Unit, University of Maine, Orono. Maine USA.
- Milinski, M. and R. Heller. 1978. Influence of a predator on the optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus*). *Nature* 275:642-644.
- Morgenweck, R.O. 1977. Diurnal high use areas of hatching-year female American woodcock. Pages 155-160 *in* D.M. Keppie and R.B. Owen, Jr. eds. Proceedings of the sixth woodcock symposium. New Brunswick Department of Natural Resources, Fredericton, New Brunswick, Canada.
- Munsell® Color. 2000. Munsell Soil Color Charts. GretagMacbeth, New Windsor, New York.
- Paulson, L.A. and M.A. Bowers. 2002. A test of the 'hot' mustard extraction method of sampling earthworms. *Soil Biology and Biochemistry* 34:549-552.

- Penfound, W.T. and E.L. Rice. 1957. An evaluation of the arms length rectangle method in forest sampling. *Ecology* 38:660-661.
- Pyke, G.H. 1983. Animal movements: an optimal foraging approach. Pages 7-31 *in* I.R. Swingland and P.J. Greenwood, eds *The ecology of animal movement*. Clarendon Press, Oxford, UK.
- Rabe, D.L., H.H. Prince, and E.D. Goodman. 1983*a*. The effects of weather on the bioenergetics of breeding American woodcock. *Journal of Wildlife Management* 47:762-771.
- , -----, and D.L. Beaver. 1983*b*. Feeding-site selection and foraging strategies of American woodcock. *Auk* 100:711-716.
- Reifenberger, J.C. and R.C. Kletzy. 1967. Woodcock nightlighting techniques and equipment. Pp 33-35 *in* W.H. Goudy, compiler. *Woodcock research and management, 1966*. U.S. Bureau of Sport Fisheries and Wildlife, Special Scientific Report- wildlife 101. 40pp.
- Reynolds, J.W., W.B Krohn, and G.A. Jordan. 1977. Earthworm populations as related to woodcock habitat usage in central Maine. Pages 135-146 *in* D.M. Keppie and R.B. Owen Jr., eds. *Proceedings of the sixth woodcock symposium*. New Brunswick Department of Natural Resources, Fredericton, New Brunswick, Canada.
- SAS online documentation version 8.2. SAS publishing, SAS Institute Inc. Cary, North Carolina, USA.
- Sepik, G.F. 1984. Population ecology of woodcock in Wisconsin. Wisconsin Department of Natural Resources. Technical Bulletin 144. Pages 1-51.
- and E.L. Derelth. 1993. Habitat use, home range size, and patterns of moves of the American woodcock in Maine. Pages 41-49 *in* J.R. Longcore and G.F. Sepik, eds. *Proceedings of the eighth woodcock symposium*. Biological Report 16, U.S. Fish Wildlife Service, Washington D.C. USA.
- , R.B. Owen, and T.J. Dwyer. 1983. The effects of a drought on a local woodcock population. *Transactions of the Northeast Section of The Wildlife Society* 40:1-8.
- Sheldon, W.G. 1960. A method of mist netting woodcock in summer. *Bird-banding* 31:130-135.

Straw, J.A. Jr., D.G. Krementz, M.W. Olinde, G.F. Sepik. 1994. American Woodcock. Pages 97-114 *in* T. Tacha and C. Braun, eds. Migratory, shore, and upland gamebird management in North America. International Association of Fish and Wildlife Agencies.

Whitcomb, D.A. 1974. Characteristics of an insular woodcock population. Michigan Department of Natural Resources Wildlife Division Report 2720.

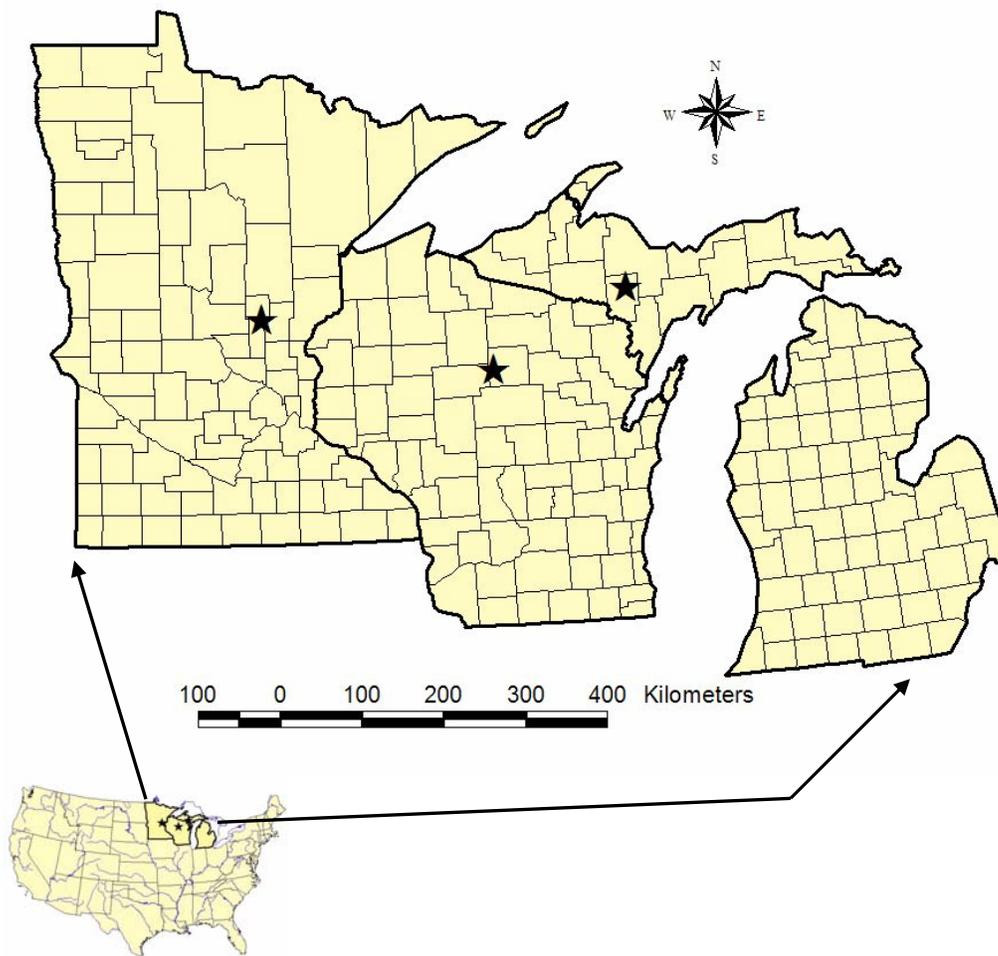


Fig. 1. Location of study areas in Minnesota, Wisconsin, and Michigan where American woodcock were radio-marked during the falls of 2002 and 2003.

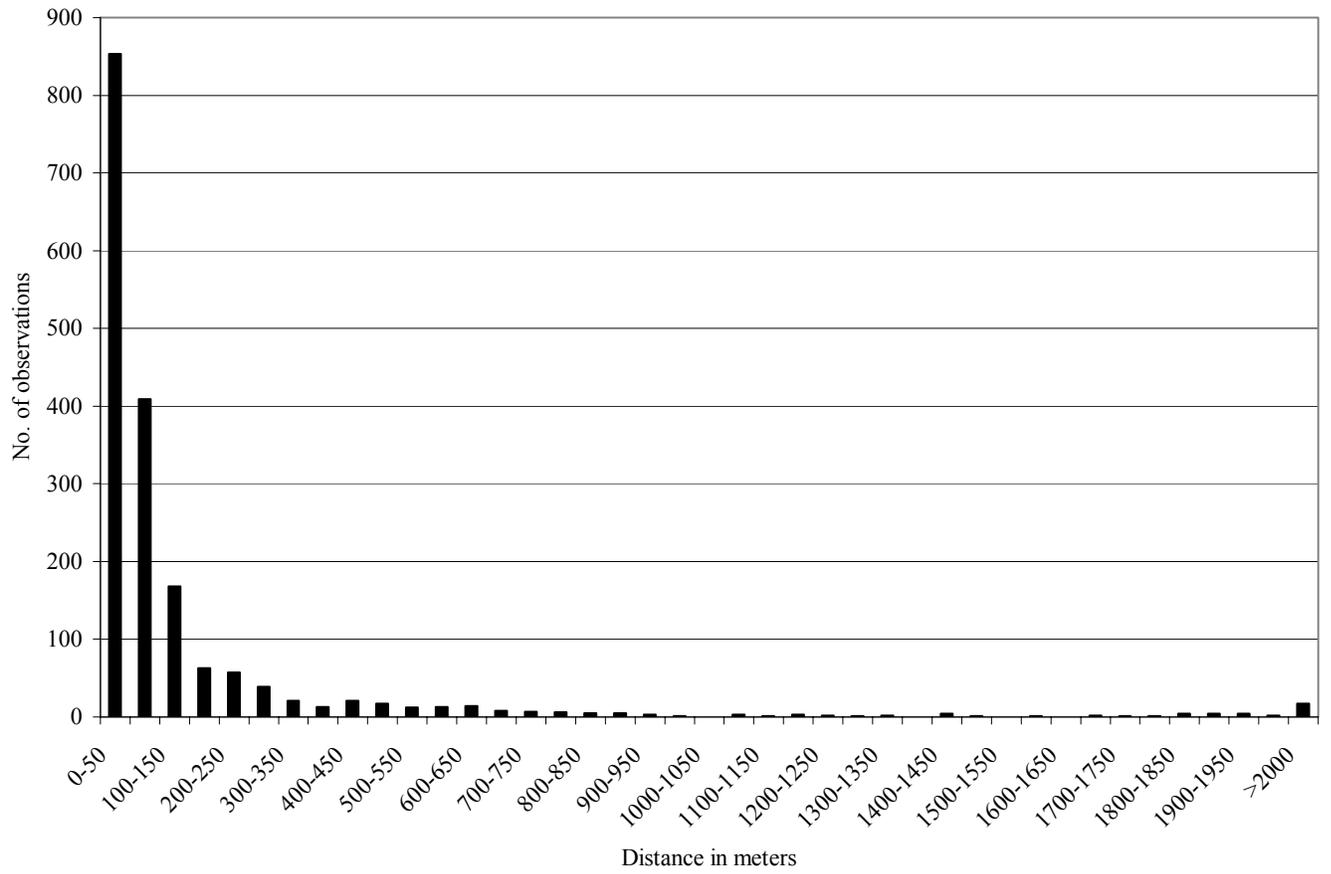


Fig. 2. Distance between subsequent locations ($n = 1,786$) for radio-tagged female after-hatch-year American woodcock ($n = 58$) during falls of 2002 and 2003 in Minnesota, Wisconsin, and Michigan.

Table 1. American woodcock movement predictor variables and covariates at locations determined via radio telemetry in 2002 and 2003, in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan.

Parameter	Symbol	Model Class
Daily low temperature (°C)	T	Weather
Daily precipitation (cm)	R	Weather
Soil color	C	Food
Ash-free earthworm dry mass	W	Food
Porosity of soil	P	Food
No. stems per 0.004 ha	S	predator avoidance

Table 2. Descriptive statistics of predictor variables and distances between subsequent locations ($n = 1,786$) of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003.

	Low Temp (°C)	Precipitation (cm)	Ash-free dry mass (g)	Porosity of soil (%)	Stems per 0.004 ha	Distance (m)
Minimum	-9.3	0.00	0.000	0.47	0.0	0.6
Maximum	17.5	21.30	1.915	1.00	457.0	3806.7
Median	2.4	0.00	0.020	0.77	100.0	52.0
Mean	3.2	0.48	0.077	0.77	114.9	156.6
Std. Error	0.1	0.04	0.004	0.01	1.8	8.1
Std. Dev.	5.9	1.78	0.153	0.10	76.1	342.6
C.V.	1.8	3.73	1.994	0.13	0.7	2.9

Table 3. Effects of blocking on process variation explained and summary of best models ($n = 5$ of 27 *a priori* models) and means model predicting distances between subsequent daily locations of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003.

Blocking	Model ^a	k	AIC _C	ΔAIC _C	$\hat{L}(g_i \mathbf{x})$	w _i	σ ^b	$(\sigma_{(.)} - \sigma_a) / \sigma_{(.)}$
area,year	T,R,W,P,R*P	8	18638.6	0	1.000	0.773	1321.550	71.561
areas,year	T,R,W,P	7	18642.0	3.4	0.183	0.141	1437.850	69.058
areas,year	T,R,C,W,P,T*W,R*P	10	18643.0	4.4	0.111	0.086	1347.130	71.010
areas,year	W,P	5	19423.1	784.5	0.000	0.000	2229.590	52.020
areas,year	P	4	20419.5	1780.9	0.000	0.000	3008.490	35.258
none	(.) means model	1					4646.910	0.000
areas	T,R,W,P,R*P	7	18637.2	0	1.000	0.774	3369.250	27.495
areas	T,R,W,P	6	18640.5	3.3	0.192	0.149	3456.130	25.625
areas	T,R,C,W,P,T*W,R*P	9	18641.8	4.6	0.100	0.078	1802.910	61.202
areas	W,P	4	19422.4	785.2	0.000	0.000	3735.420	19.615
areas	P	3	20418.2	1781	0.000	0.000	4164.280	10.386
none	(.)	1					4646.910	0.000
none	T,R,W,P,R*P	6	18634.2	0	1.000	0.753	3652.770	21.394
none	T,R,W,P	5	18637.0	2.8	0.247	0.186	3717.870	19.993
none	T,R,C,W,P,T*W,R*P	8	18639.2	5	0.082	0.062	2236.850	51.864
none	W,P	3	19419.1	784.9	0.000	0.000	3936.600	15.286
none	P	2	20414.6	1780.4	0.000	0.000	4315.970	7.122
none	(.)	1					4646.910	0.000

^a W = worms, P = porosity, T = low temp, R = rain in cm³, (.) = constant only

^b σ = covariance parameter estimate

Table 4. Regression coefficient estimates and associated standard errors for the distance between subsequent daily locations of after-hatch-year female American woodcock in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003. Estimates are derived from single ΔAIC_c best models ($n = 2$) using maximum likelihood methods in a mixed-effects linear model with study area and year as blocking factors.

Model	ΔAIC_c	w_i	Predictor variables ^a	Regression coefficient estimate	S.E.
1	0.0	0.77	T	6.91	2.09
			R	-96.70	43.74
			W	-69.89	68.43
			P	70.08	112.60
			R*P	143.87	61.61
2	3.4	0.14	T	7.08	2.09
			R	4.52	5.86
			W	-65.41	68.55
			P	140.70	108.73

^a T = low temp (°C), R = precipitation (cm), W = worm mass(g), P = porosity (%)

Table 5. Summary of ΔAIC_C best models ($n = 5$ of 27 *a priori* models) and means model predicting distances between subsequent daily locations for movements <500 m of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003. Year and study area are blocks in all models except the means model.

Model ^a	k	AIC_C	ΔAIC_C	$\hat{L}(g_i \mathbf{x})$	w_i	σ^b	$(\sigma_{(.)}-\sigma_a)/\sigma_{(.)}$
T,R,W,P	8	14053.3	0.0	1.000	0.716	622.11	3.860
T,R,W,P,R*P	7	14055.2	1.9	0.387	0.277	622.23	3.841
T,R,C,W,P,T*W,R*P	10	14062.7	9.4	0.009	0.007	594.71	8.095
W,P	5	14587.1	533.8	0.000	0.000	618.09	4.487
P	4	15405.0	1351.7	0.000	0.000	590.92	8.680
(.) means model	1					647.09	0.000

^a W = worms, P = porosity, T = low temp, R = rain in cm³, (.) = constant only

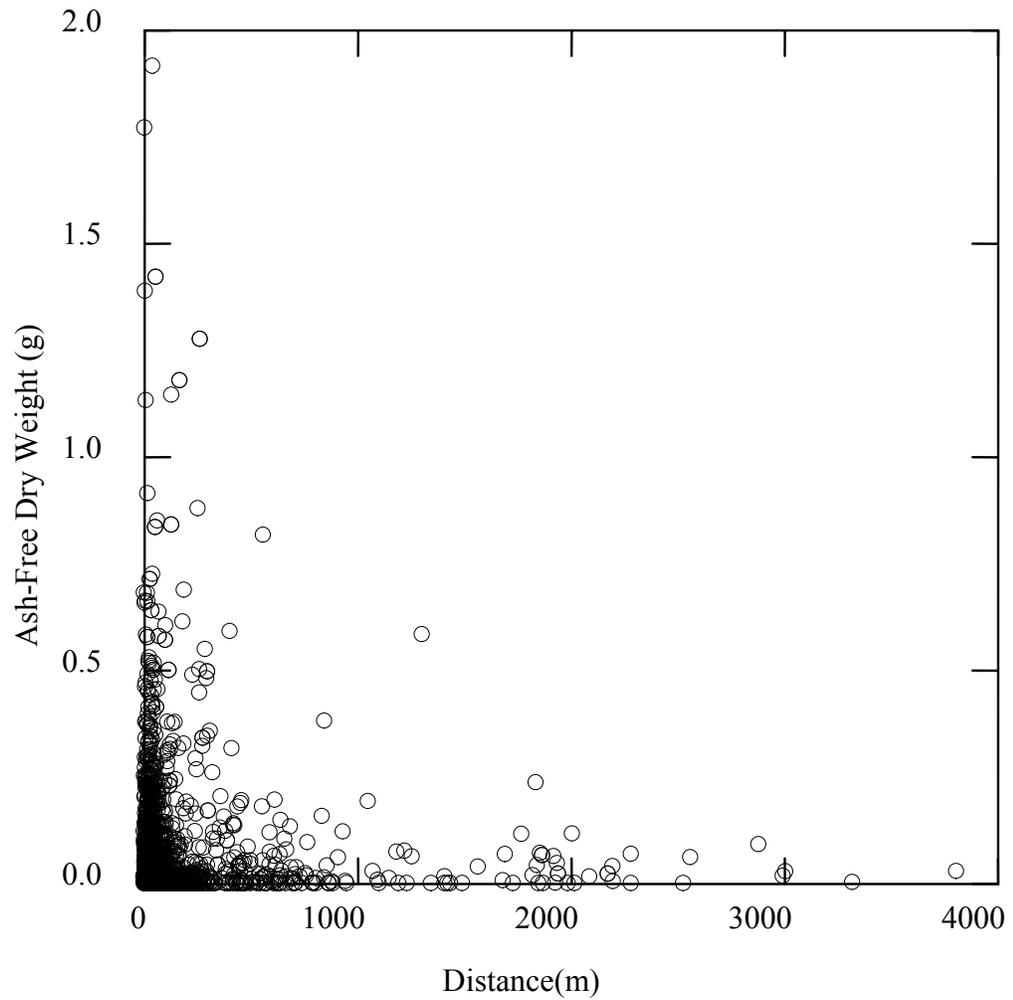
^b σ = covariance parameter estimate

Appendix 1. Summary of all *a priori* models ($n = 27$) used to evaluate the distance to subsequent daily locations ($n = 1,786$) of after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003. Models in the final analysis included a blocking effect for study areas and years.

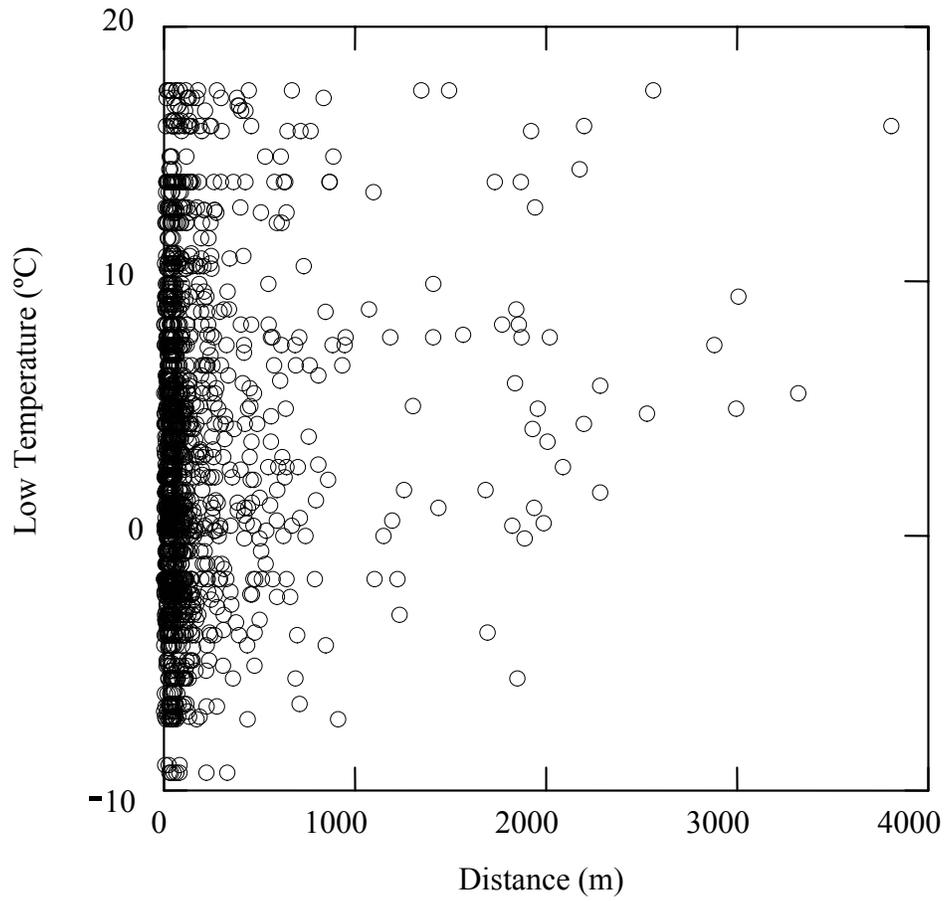
Model Class	Parameters ^a	k	ΔAIC_C
Weather	T	2	5855.4
Weather	R	2	5660.3
Weather	T,R	3	5604.5
Food	C	2	6696.6
Food	W	2	5411.3
Food	P	2	1780.9
Food	W,C	3	5413.3
Food	W,P	3	784.5
Predation	S	2	6616.8
Weather + Food	T,R,W,C	5	4375.8
Weather + Food	T,R,W,P	5	3.4
Weather + Food + Interaction	T,R,W,C,T*W,R*C	7	4380.1
Weather + Food + Interaction	T,R,W,P,R*P	6	0.0
Interaction	T*W, R*C	3	4396.9
Weather + Predation	T,R,S	4	5524.7
Weather + Predation	T,S	3	5580.9
Weather + Predation	R,S	3	6617.1
Predation + Food	S,C	3	5345.3
Predation + Food	W,S	3	5347.5
Predation + Food	W,S,C	4	4308.9
Weather + Predation + Food	T,R,W,S,C	6	4306.8
Weather + Predation + Food	T,P,W,S	5	4368.7
Weather + Predation + Food	R,W,S,C	5	4559.3
Weather + Predation + Food	T,W,S	4	4559.3
Weather + Predation + Food	R,W,S	4	4366.4
Global	T,R,C,W,P,T*W,R*P	8	4.4
Global	T,R,C,W,S,T*W	7	4310.9

^a T = daily low temp, R = rain in cm, C = soil color, W = worms, P = porosity, S = stems per 0.004 ha

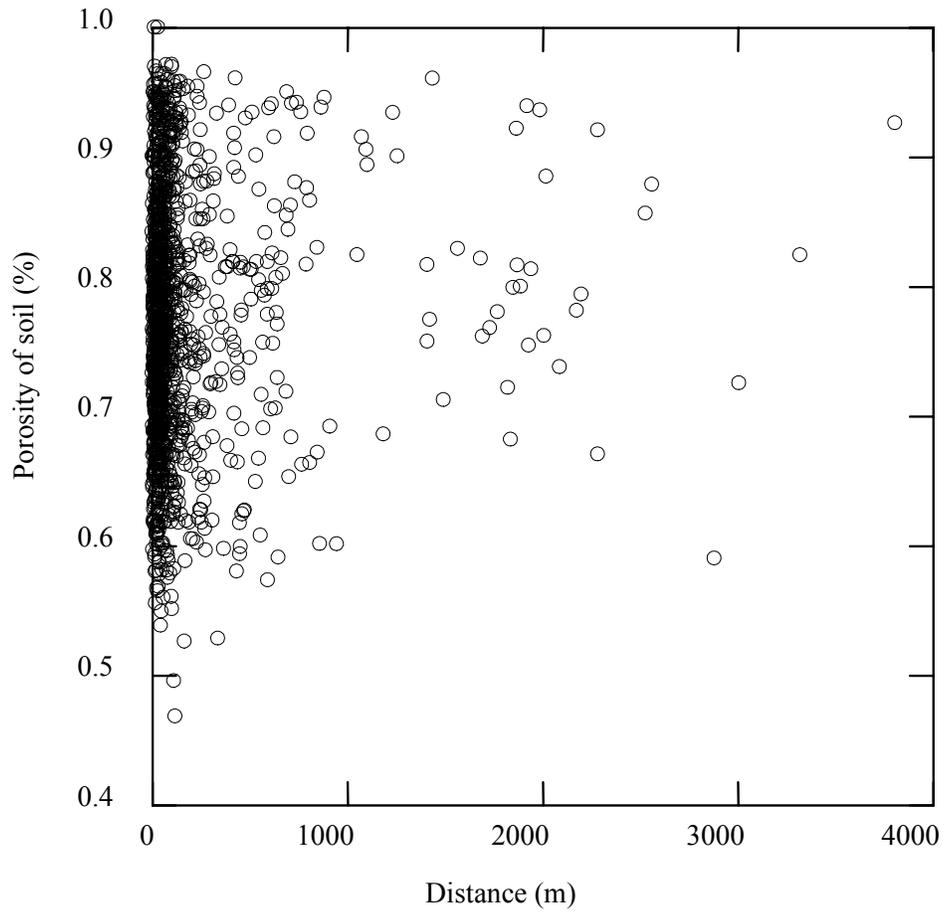
Appendix 2. Plot of the ash-free dry weight of earthworm samples (g) vs. the distance traveled to subsequent daily locations ($n = 1,786$) for after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper peninsula of Michigan during the falls of 2002 and 2003.



Appendix. 3. Plot of low temperature in °C vs. the distance traveled to subsequent daily locations ($n = 1,786$) for after-hatch-year female American woodcock ($n = 58$) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the falls of 2002 and 2003.



Appendix 4. Plot of the percent porosity of soil samples vs. the distance traveled to subsequent daily locations (n = 1,786) for after-hatch-year female American woodcock (n = 58) in central Minnesota, central Wisconsin, and the Upper Peninsula of Michigan during the fall of 2002 and 2003.



Chapter 2

Fixed kernel home range estimation incorporating telemetry location error: American woodcock (*Scolopax minor*) home range analysis using real and simulated data

Abstract:

Bandwidth selection in fixed kernel home range estimation can influence interpretation of results, especially when data are over-smoothed. Currently, the accepted method of bandwidth selection is least square cross validation, which results in unbiased use area estimates, but may also result in large areas of unused habitat being included. An alternative to least squares cross validation may be using error associated with telemetry locations, which represents the resolution at which data are collected. To evaluate using telemetry error in fixed kernel home range estimation, I analyzed American woodcock (*Scolopax minor*) home ranges derived from telemetry data using fixed kernels with two different bandwidth selection methods coupled with bootstrap re-sampling and Monte Carlo simulations. The method of using 95% circular error probability from data points as the smoothing parameter (h_{er}) was compared to least squares cross validation (h_{lscv}) as an automated bandwidth selection method. I tested each bandwidth selection method's sensitivity to sample size, non-continuous use of space, and impacts of outliers to the 95% and 50% probability areas. Using h_{lscv} resulted in a low coefficient of variation (C.V. ~ 0.11) and comparable area estimates at low sample sizes ($n > 30$) if the home ranges were continuous, had no outliers, and had a single core area. In simulations with a sample size of 50, the presence of 1 outlier area with 2 locations, or having 2 core areas separated in space significantly biased probability areas upward when using h_{lscv} as the smoothing

method in a fixed kernel. Using h_{er} resulted in a low C.V. (~ 0.11) and comparable area estimates for the 95% probability areas at low sample sizes ($n > 30$), regardless of the presence of outliers or non-continuous spatial use. Home range estimates using h_{er} were consistent with published home range estimates for after-hatch-year female woodcock during the fall, and outperformed h_{lscv} at moderate sample sizes ($n = 30-50$) in Monte Carlo simulations. I conclude that h_{er} is a viable alternative to h_{lscv} as an automated, non-arbitrary, selection of bandwidth, especially in cases with modest sample sizes, outliers, or non-continuous spatial use. Using h_{er} as the smoothing parameter for fixed kernel estimation represented the finest resolution (smoothing) home range estimate supported by field data.

Introduction:

Since the inception of the concept of home range (Burt 1943), there have been many methods proposed to quantify the area in which an animal moves during its normal activities. These include non-statistical models such as the minimum convex polygon (MCP [Mohr 1947]), bivariate normal statistical models (Jennrich and Turner 1969), grid methods such as harmonic mean (Dixon and Chapman 1980), and a non-parametric probabilistic kernel estimator (Worton 1989). Kernel estimation has long been used in the field of statistics (Silverman 1986) and the fixed kernel is now widely regarded as the preferred method for home range estimation in the ecological literature (e.g., Seaman and Powell 1996, Kernohan et al. 2001).

Kernels are distribution free, free of assumptions except independence among data points (Silverman 1986), and have performed well in simulation studies (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999). However, the choice of a smoothing parameter is widely regarded as the most important factor in the performance of kernel estimation (e.g., Silverman 1986, Worton 1995, Kernohan et al. 2001). Insufficient smoothing results in density estimates that are too rough and contain spurious features that are artifacts of the sampling process, while over smoothing results in loss of important features (Jones et al. 1996). Using least-

squares cross validation (h_{lscv}) (Silverman 1986) in a fixed kernel is widely used as the default bandwidth choice for smoothing and is the current recommendation in the ecological literature (Seaman and Powell 1996).

Unfortunately, there is a large bias vs. variance trade off in the selection of bandwidth in the use of kernels (Silverman 1986) with h_{lscv} being an extreme case resulting in non-biased estimates with high variability (Jones et al. 1996, Park and Marron 1990, Hansten et al. 1997). Kernels have also been shown to overestimate the 95% probability area in simulation studies and Worton (1995) applied correction factors to h_{lscv} to control for this overestimation. Kernels do not have a variance and therefore do not permit sample size calculations in experimental design or measures of precision of estimated areas (White and Garrott 1990). Seaman et al. (1999) performed a simulation study to address this issue and recommended a minimum of 30 points, with 95% probability areas generally reaching an asymptote at around 50 points. To date however, there are no studies that address sample size issues using real field data coupled with bootstrap re-sampling and Monte Carlo simulations. Herein, I use telemetry data from American woodcock (*Scolopax minor*) to assess kernel estimation of home range size.

American woodcock make crepuscular flights from nighttime roosting fields to densely wooded diurnal areas with moist soils. Distance between observed subsequent daily locations in past studies are relatively far (129 m [Sepik and Derleth 1993], $122.81 \text{ m} \pm 12.81 \text{ SE}$ [Andersen et al. 2003]) compared to movements within the same day (median distance $\sim 5 \text{ m}$ [Hudgins et al. 1985], average $22.0 \text{ m} \pm 1.7 \text{ SE}$ [Godfrey 1974]). Unless woodcock are disturbed, they generally remain in the same small patch of habitat all day (D. G. McAuley, U.S. Geological Survey, personal communication and field observations). Woodcock are generally located in the same stand each day, but some woodcock have >1 area of concentrated use separated by a substantial distance by areas of non-use. Because the smoothing parameter in h_{lscv} is estimated from the distance to all points from each particular grid intersection, large distance between use areas leads to oversmoothing. In our study, many woodcock

also made large pre-migratory movements before returning to their core area and subsequently migrating for the winter (Andersen et al. 2003). These long-distance movements also could bias the smoothing parameter derived using h_{lscv} leading to an oversmoothed home range estimate that yields little biologically useful information. Other wildlife researchers have recognized this problem in the past and Naef-Daenzer (1993) modified the kernel function so that it only calculated densities for points below 1 SD from the grid intersection.

To assess estimation of woodcock diurnal home ranges from daily locations during the fall, I (1) estimated sample size effects on the performance of fixed kernel estimation on a real data set using bootstrap re-sampling, (2) assessed the effects of non-continuous spatial use on kernel home range estimation, and (3) compared the use of 95% circular area probability (precision of my daily location points as the smoothing factor [h_{er}]) vs. h_{lscv} in a fixed kernel. I conducted a simulation study in Arcview 3.3 (Environmental Systems Research Institute 2002) with the animal movements extension (Hooge and Eichenlaub 1997) to facilitate a direct comparison with known home range areas exhibiting the same patterns as our radio-marked sample of woodcock.

Study Area:

Woodcock telemetry data were collected on parts of the 15,672 ha Mille Lacs Wildlife Management Area (MLWMA) and the adjacent 1,166 ha Four Brooks Wildlife Management Area (FBWMA) in east-central Minnesota. Both WMAs are managed to provide hunting opportunities to the public, primarily by habitat manipulation for game species. Upland bird hunting (including hunting for woodcock) was allowed on MLWMA, and the recently acquired FBWMA was closed to woodcock hunting (not other game bird hunting) during the three-year study period 2001-2003. Data used in this analysis are from the 2003 field season. MLWMA is in close geographic proximity to FBWMA and they have comparable vegetative communities, which include early regenerating aspen (*Populus* spp.) and lowland

habitats including alder (*Alnus* spp.), willow (*Salix* spp.), and burr oak (*Quercus macrocarpa*).

Methods:

Capture and radio-marking

I began capturing woodcock on 20 August 2003 in both the MLWMA and the adjacent FBWMA. Woodcock were captured at night-roosting fields by means of mist netting (Sheldon 1960) and by spot lighting roosting fields (Reifenburg and Kletzy 1967, McAuley et al. 1993). Wing plumage characteristics were used to age and sex captured birds (Martin 1964) and we used bill length as an additional means of determining sex (Mendal and Aldous 1943). Captured woodcock were radio marked using all-weather livestock tag cement in conjunction with a single-loop wire harness using the techniques of McAuley et al. (1993). Transmitters (Advanced Telemetry Systems, Inc.; use of trade names does not imply endorsement by the University of Minnesota) weighing approximately 4.4 g were attached to captured woodcock. Woodcock were released at capture locations following transmitter attachment.

Radio-tracking

On 6 September 2003, 18 after-hatch-year (hereafter = adult) female woodcock were randomly selected from all adult female woodcock radio-tagged as a part of a larger cooperative study of woodcock survival (specifically hunting mortality) and habitat ecology in the western Great Lakes region. Woodcock were located once a day ≥ 5 times per week using hand-held rubberized H-antennas and portable receivers, until mortality or loss of radio contact. Precise locations of radio-marked woodcock were obtained by hiking to individual woodcock and recording their daily location with a Global Positioning System (GPS). We did not intentionally flush woodcock and target birds were circled by the observer to triangulate their location, using the strength and direction of the radio signal to assess the distance of

observers to the bird. To estimate the precision of woodcock locations (error = GPS error + distance to woodcock), a transmitter was placed in aspen seedling sapling habitat (diameter breast height < 7.5 cm), the dominant cover type used by woodcock. Observers obtained multiple estimated locations ($n = 45$) of the transmitter (“simulated woodcock”) using the equipment that was assigned to them for the duration of the study in a non-blind trial. The Jennrich-Turner bivariate normal home range estimator (Jennrich and Turner 1969) was used to calculate the radius of the 95% circular error probability, because circular compass error and GPS error are bivariate normally distributed. The distance between observers and target woodcock was ~ 2-14 m, based on distance estimates from transmitters using the Jennrich-Turner home range estimator on a “simulated woodcock” (95% error polygon radius – GPS error = 13.7 m [outer bound]) and by the paced distances from AHY female woodcock intentionally flushed by researchers (2.2 m, S.E. = 0.3, $n = 10$ [inner bound]). Random compass bearing were used to determine the azimuth of the observer to the woodcock for daily use points. This was done to randomize the directional error of the daily use points and removed observer bias in placement of use points.

Home Range Analysis:

Only woodcock with ≥ 26 locations ($n = 12$) were included in home range analyses. Four woodcock ($n = 26-27$ locations) exhibited a large spatial distribution of locations compared to the other 8 woodcock and were graphed separately for scaling purposes. One woodcock (bird 1323, $n = 27$ locations) was grouped with the 7 woodcock with ≥ 30 points because it only used one area with no major outlying points and had similar home range size estimates. Woodcock with ≥ 30 points ($n = 7$) were included in the sample size bootstrap analysis.

Estimated locations of each woodcock were buffered using the radius of the 95% circular error probability (28.6 m) in Arcview. Boundaries of the polygons that buffered the individual points were not dissolved into a single polygon (i.e., there is

an individual polygon for each GPS location). In this manner I created a polygon surrounding each woodcock use point that represented the boundary of the error distribution for each individual point. This was done to incorporate the variation in the distance to the woodcock and GPS error into the home range estimate. A bivariate normal distribution estimated from the standard deviations of the x and y coordinates of individual buffer polygon was used to generate one hundred random points into each of the buffered polygons, simulating the error distribution of the observed woodcock locations. Bootstrap replicates ($n = 500$) were drawn from each individual's simulated error distribution with replacement. The number of points in each individual's bootstrap replicate was determined from the number of observed locations collected in the field for a particular bird. For each woodcock, 500 home range estimates were made using both the 95% circular error probability from data points as the smoothing parameter (h_{er}) and least squares cross validation (h_{lscv}) as the automated bandwidth selection method for the fixed kernel. These estimates were used to simulate the variance of home range estimates used to produce CIs around the kernel point estimate (point estimate = home range size using the original data collected in field).

Influence of Sample Size

A second bootstrap analysis was conducted for each woodcock with ≥ 30 locations ($n = 7$) to assess the influence of sample size on kernel home range size using h_{lscv} and h_{er} . Points were drawn with replacement from original woodcock data starting at a sample size of 10 and increased in increments of 5 until the original sample size for the woodcock was reached with 200 replicates at each sample size. To assess how home range size was related to sample size, I plotted the means of the bootstrap samples against sample size after standardizing across birds by dividing each woodcock mean area by the maximum area for each bird. The standard deviation from the bootstrapped sample for each sample size was used to calculate the coefficient of variation (CV) for each bird, which I then plotted against sample size to assess the relationship between precision and sample size.

Monte Carlo Home Range Simulation

To assess the influence of spatial orientation and outliers on fixed kernel estimates using h_{lscv} and h_{er} , I simulated 3 patterns of spatial use based on patterns exhibited by radio-marked woodcock; 1 core use area, 1 core use area with 1 small satellite area (30 m radius) ~750 m distant from the core area, and 2 core use areas (~250 m apart).

Fifty random points from a uniform distribution were placed inside the polygon(s) for each of the 3 spatial use patterns. Each of the points was buffered with a 30 m radius (simulated error of woodcock points). Individual buffer polygon boundaries were dissolved to create a single known size, shape, and spatially oriented woodcock home range for each of the 3 home range orientations simulated. To create simulated woodcock location data, 50 points from a uniform distribution were randomly distributed into each of the 3 home range types, so that ≥ 1 point fell in the outlying buffer polygon, if the home range had one, with a total of 500 replications each. The 500 replicates of $n = 50$ (simulated woodcock data set) were used to calculate fixed kernel home range estimates using both h_{lscv} and h_{er} as the bandwidth selection method. These replicate home range estimates were used to simulate the variance of home range size. These variances were then used to create 95% CIs around the bootstrap means to assess the influence of spatial orientation and outliers on fixed kernels using h_{lscv} and h_{er} .

Influence of Sample Size Using Monte Carlo Simulation

For each of the 3 home range configurations tested, a single simulated “woodcock” locational data set was randomly selected and bootstrapped. Procedures used to create bootstrap samples from the simulated data were the same as the real woodcock data. Points were drawn with replacement starting at a sample size of 10 and increased in increments of 5 until a sample size of 50 was reached with 200 replicates at each sample size. The 200 replicates were used to calculate the bootstrap

mean and 95% CIs (based on a Z-distribution) at each sample size (10-50). The bootstrap mean and 95% CIs were then plotted at each sample size to examine how simulated location data were influenced by sample size.

Statistical Comparisons

Statistical contrasts of means were based on the overlap of 95% CIs derived from a Z-distribution. Variances used to construct S.E. were derived from either bootstrap re-sampling of woodcock field telemetry data or Monte Carlo simulated points.

Results:

Influence of Sample Size—Woodcock Telemetry Data

Mean size of woodcock home range estimates approached an asymptote using both h_{lscv} and h_{er} as the smoothing factor in a fixed kernel (Fig. 1), suggesting my sample (no. of locations ≥ 30 for $n = 7$ woodcock) was adequate to meaningfully describe home range area (Harris et al. 1990, Gese et al. 1990). Standardized 95% kernel home range estimates derived using h_{lscv} had a much wider range (1.00 - 0.53) of maximum estimated area than those derived using h_{er} (1.00 - 0.96) at $n = 40$ (Fig. 1). Standardized 50% kernel home range size estimates were consistent at low sample sizes ($n > 20$ for h_{lscv} and $n > 15$ for h_{er}). Coefficients of variation of the bootstrap resampled field data for the 50% probability area stabilized at around 35 points with h_{er} exhibiting less variation than h_{lscv} (CV = 0.29 - 0.14 vs. h_{lscv} CV = 0.43 - 0.22 [Fig. 2a]). The CV for the 95% area using h_{lscv} stabilized at around 35-40 points ranging from 0.40 - 0.11 at a sample size of 40 (Fig. 2b). The CV for the 95% area using h_{er} stabilized at around 25 observations and ranged from 0.226 - 0.115 at a sample size of 40.

Area Analysis of Woodcock Telemetry Data

Using h_{ISCV} resulted in wider 95% CIs around kernel estimates from woodcock telemetry data compared to h_{ER} for both the 95% and 50% probability areas (Fig. 3). CIs of kernel point estimates contained all of the bootstrap means in all cases but one, regardless of the bandwidth selection method used. Bird 83 had a 95% probability area bootstrap mean of 2.48 ha when using h_{ER} , which was than lower than 2.57, the lower bound of the 95% CI around the kernel point estimate. For the 95% probability area of 6 of the 8 woodcock having $n \geq 30$ locations (and using bird 1323 [$n = 27$]), CIs computed using h_{ER} and h_{ISCV} overlapped and were not statistically different. Five of the 8 birds' 50% probability areas were not statistically different as a function of bandwidth choice based on the overlap of 95% CIs.

For the 4 woodcock that were compared separately because of their smaller number of locations and larger spatial distribution among locations compared to the other 8 woodcock, there was a large difference between home-range estimates using h_{ISCV} versus h_{ER} (Fig. 4). Fifty and 95% probability area estimates using h_{ISCV} exhibited wide CIs and bootstrap area means were much larger than area estimates from the same data sets using h_{ER} . Using h_{ISCV} for these 4 woodcock produced probability area estimates that were larger and more variable compared with probability area estimates for the other 8 woodcock with $n \geq 30$ (and using bird 1323 [$n = 27$]). This was true regardless of the bandwidth selection method used to calculate the home range probability area for the first 8 birds. Results using h_{ER} were comparable with the results of the other 8 woodcock using either bandwidth selection method (Figs. 3 and 4).

Monte Carlo Simulation Results

1 Core Use Area

For simulations based on home ranges containing a single use area, 95% CI of bootstrap means contained the true area using both h_{lscv} ($n \geq 10$) and h_{er} ($n \geq 15$) (Fig. 5). The mean 95% probably area using h_{lscv} was consistently higher than that using h_{er} (8.46 ± 1.84 ha vs. 7.65 ± 1.66 ha when $n = 50$ [true area = 6.98 ha]), but size of these areas was not statistically different. Size of 95% probability areas increased as a function of sample size when using h_{er} , but not when using h_{lscv} . The CVs of size of probability areas using both smoothing parameters were similar across sample sizes (Fig. 6), with a slight decrease in CVs of 95% probability areas through $n \leq 30$.

1 Core Use Area Distant from a Single Satellite Area

Ninety-five percent CIs of the bootstrap means for the 95% probability areas contained the true area when derived from both h_{lscv} and h_{er} except at $n = 45$ for h_{er} with the 95% lower confidence limit being 0.054 ha above the true area of 7.28 ha (Fig. 7). The mean 95% probability estimate using h_{lscv} (14.48 ha \pm 7.59 at $n = 50$) was higher than when using h_{er} (8.44 ha \pm 1.76 at $n = 50$). The CV of estimates using h_{er} was unaffected by the addition of 2 outlier points in a small area 750 m distant and was similar to the CV without the outlier points (Fig. 6). The CV for probability areas using h_{lscv} increased with the addition of the 2 outlier points into the simulated area (Fig. 6).

2 Core Use Areas

For spatial use patterns with 2 core use areas, 95% probability area estimates using h_{lscv} (13.47 ± 3.50 ha) and h_{er} (8.30 ± 1.30 ha) both overestimated the true area of 5.94 ha (Fig. 8). Ninety-five percent use area estimates using h_{er} were closer to the true mean and had lower variation than estimates using h_{lscv} . The CV for 95% and 50% probability areas using h_{lscv} and h_{er} followed a similar pattern, generally decreasing at $n \leq 20-25$ and becoming more stable at $n \geq 40$ (Fig. 6).

Area Estimates from Monte Carlo Simulation

Simulated home ranges ($n = 500$) for each of the 3 spatial use patterns evaluated (1 core use area, 1 core use area and 1 small satellite area, and 2 core use areas) were over estimates of the true home range size regardless of bandwidth selection method used (Fig. 9). Simulated telemetry locations were not constrained from being placed on polygon boundaries, which partly accounted for the overestimation of home range areas. Using h_{er} as a smoothing factor resulted in the lowest home range size overestimation. The percent of true area estimated using h_{er} was not statistically different from that using h_{lscv} except when home ranges had 2 core use areas. If h_{lscv} was used to estimate home range size, the addition of 1 small satellite use area greatly increased the mean and CIs of the % of true area estimate from $145.0 \pm 30.0\%$ to $228.3 \pm 107.8\%$. Having 2 core use areas also drastically increased the percent of the true area estimated using h_{lscv} ($242.8 \pm 44.1\%$). Home range estimates using h_{er} were also affected by having 2 core use areas but the effects were much less drastic, increasing from $141.0 \pm 24.7\%$ for 1 core use area to $158.4 \pm 18.7\%$ for 2 core use areas.

Discussion:

Fixed kernel home range estimates using h_{lscv} were very sensitive to sample size, use area spatial orientation, and a few locations distinct from core use areas. Woodcock in my study that had large movements (bird 83, $n = 44$), had 2 core use areas (bird 1992, $n = 44$), or had 1 large movement before returning to their core area (bird 1192, $n = 41$) likely had home range size estimates using h_{lscv} that were considerably larger than the area birds actually used. Bird 83 had a very small core use area, but had 11 days of pre-migratory movements before returning to the original core use area prior to migration. Bird 1192 had 1 outlier point 1,260 m from the center of the core area and 7 points that were 400-500 m away from the core area. The two areas of use by bird 1992 were ~650 m apart, which likely led to overestimation of the size of use areas, based on our simulation study. These results are consistent with the results of Seaman and Powell (1996) who found that deviation from a smooth bimodal distribution resulted in a higher number of locations required

to adequately describe home range using fixed kernel estimators. For birds 83, 1192, and 1992, this appeared to be the case even though sample size—area curves approached an asymptote (Fig. 1), which suggests that sample sizes were adequate to estimate home range size (Harris et al. 1990, Gese et al. 1990).

Seaman et al. (1999) suggested a minimum of 30 points to estimate home range size using fixed kernels and h_{lscv} as the smoothing parameter. My results corroborate those results based on our re-sampling of woodcock home ranges and simulations if the home range; (1) is continuous, (2) has no outlying points, and (3) has 1 core use area. From my simulation studies with $n = 50$ locations, it was evident that spatial orientation is extremely important when calculating fixed kernels using h_{lscv} (Fig. 9). If animals exhibit non-continuous use of space or frequent “excursions”, then sample sizes > 50 would be required for h_{lscv} to adequately describe home range size, shape, and orientation. This likely explains the extremely large home-range estimates for 4 woodcock with ≤ 27 locations, which exhibited large distances between core use areas and areas visited infrequently. Hansteen et al. (1997) also questioned the reliability of bivariate estimators when the empirical utilization distribution is discontinuous or when animals use areas systematically.

The use of 95% circular error (h_{er}) as a smoothing parameter resulted in similar size of home range estimates (both 50 and 95% kernels) across a range of spatial use patterns. In simulations, home range size overestimation using h_{er} at $n = 50$ points for all 3 spatial use patterns was comparable to using h_{lscv} with 1 use area. My home range size estimates from woodcock telemetry data using h_{er} regardless of home range spatial orientation (3.68-5.71 ha 95% CI, $n = 12$) were similar to fall home range size (7 ha, using MCP) reported for adult female woodcock in Maine (Sepik and Derleth 1993). Most important, the use of h_{er} as the smoothing factor resulted in kernel estimates that were reasonable based on simulated known distributions and corresponded well with the observed use pattern in the field when applied to field telemetry locations.

Silverman (1986) stated that the appropriate choice of smoothing parameter will always be influenced by the purpose for which the density estimate is to be used.

The smoothing parameter in kernel estimation is essentially the variance of the kernel function (Silverman 1986, Seaman et al. 1998) and using the radius of the 95% circular error probability (h_{er}) as the smoothing factor approximates the finest resolution that the data can support. Smoothing factors smaller than the error associated with telemetry locations do not incorporate locational error into home range estimates. The use of h_{er} may result in either clumping, as in the case of precise telemetry points where the movement between points is greater than the radius of the 95% circular error probability, or smoothed home range estimates where telemetry points have large error in relation to movement between points. Whether this clumping or smoothing is undesirable is dependent on the biology of the species and the purpose of the study (Kernohan et al. 2001).

Spatial orientation of the home range being estimated needs to be considered when choosing a smoothing parameter for use in kernel estimation. If outliers are present or space use is non-continuous, home range estimates based on fixed kernels using h_{lscv} will over-smooth data resulting in large areas of unused habitat contained within estimated home range boundaries. Kernohan et al. (2001) concluded that bootstrap variance estimation for home range analysis is currently underutilized. Due to the wide confidence intervals associated with home ranges derived using h_{lscv} in our analysis of field and simulated data, reporting CIs along with sample sizes and method used is essential. Due to the small sample sizes typical of most ecological studies, point estimates generated from such imprecise estimators, such as kernel estimators using h_{lscv} in my study, have little utility. Having an automated band width selection method such as h_{er} or h_{lscv} is needed for comparison among studies. However, examining kernel estimates based on varying bandwidths will give much more insight into animal spatial use patterns than using a single automated bandwidth (Silverman 1986). In my study, using h_{er} as the smoothing parameter produced consistent results across spatial use patterns yielding results similar to past studies on woodcock, and performed similarly to h_{lscv} for home ranges that consisted of 1 use area. As such, h_{er} may be a viable alternative to h_{lscv} as an automated, non-arbitrary,

selection of bandwidth, especially in cases of modest sample sizes, outliers, or non-continuous spatial use.

Literature Cited:

- Andersen, D.E., J.G.Bruggink, K.E. Doherty, R.S. Lutz, J. Meunier, E. Oppelt. 2003. 2002 Field Season Summary Report. Minnesota Cooperative Fish and Wildlife Research Unit, 1980 Folwell Ave, 200 Hodson Hall, St. Paul MN, 55108
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- Dixon, K.R. and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040-1044.
- Environmental System Research Institute. 2002. 380 New York Street
Redlands, CA 92373-8100
- Gese, E.M., D.E. Andersen, and O.J. Rongstad. 1990. Determining home-range size of resident coyotes from point and sequential locations. *Journal of Wildlife Management* 54:501-506.
- Godfrey, G. A. 1974. Behavior and ecology of the American woodcock on the breeding range in Minnesota. Dissertation. University of Minnesota, St. Paul, MN 55108
- Harris, S., W.J. Cresswell, P.G. Forde, W.J. Trehwella, T. Woolard, and S. Wray. 1990. Home-range analysis using radio-tracking data- a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97-123.
- Hansteen, T. S., H.P. Andreassen, and R.A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. *Journal of Wildlife Management* 61:280-290.
- Hooge, P.E. and B. Eichenlaub. 1997. Animal movement extension to Arcview: Version 2.0. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

- Hudgins, J.E., G.L. Storm, and J.S. Wakely. 1985. Local movements and diurnal-habitat selection by male American woodcock in Pennsylvania. *Journal of Wildlife Management* 49:614-61.
- Jennrich, R.I. and F. B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* 22:227-237.
- Jones, M.C., J.S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. *Journal of the American Statistical Association* 91:401-407.
- Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125-166 *in* J.J. Millspaugh and J.M. Marzluff, eds. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- Martin, F.W. 1964. Woodcock age and sex determination from wings. *Journal of Wildlife Management* 28:287-293.
- McAuley, D. G., J.R. Longcore, and G.F. Sepik. 1993. Techniques for research into woodcocks: experiences and recommendations. *USFWS Biol. Rep. No. 16* pp. 5-11.
- Mendall, H.L. and C.M. Aldous. 1943. *The ecology and management of the American woodcock*. Maine Cooperative Wildlife Research Unit, University of Maine, Orono, Maine, USA.
- Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223-249.
- Naef-Daenzer, B. 1993. A new transmitter for small animals and enhanced methods of home-range analysis. *Journal of Wildlife Management* 57:680-689.
- Park, B.U., and J.S. Marron. 1990. Comparison of data-driven bandwidth selectors. *Journal of the American Statistical Association* 85:66-72.
- Reifenberger, J.C. and R.C. Kletzy. 1967. Woodcock nightlighting techniques and equipment. Pp 33-35 *in* W.H. Goudy, compiler. *Woodcock research and management, 1966*. U.S. Bureau of Sport Fisheries and Wildlife, Special Scientific Report- wildlife 101. 40pp.
- Seaman, D.E. and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075-2085.

- , B.Griffith, and R.A. Powell. 1998. KERNELHR : a program for estimating animal home ranges. *Wildlife Society Bulletin* 26:95-100.
- , J.J.Millspaugh, B.J. Kernohan, G.C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 54:42-45.
- Sepik G.F., and Derleth, E.L. 1993. Habitat use, home range size, and patterns of moves of the American woodcock in Maine. U.S. Fish and Wildlife Service Biological Report 16:41-49.
- Sheldon, W.G. 1960. A method of mist netting woodcock in summer. *Bird-banding*. 31:130-135.
- Silverman, B.W. 1986. Density estimation for statistics and data analysis. Chapman & Hall, London, UK.
- White, G.C., and R.A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.
- , 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-78

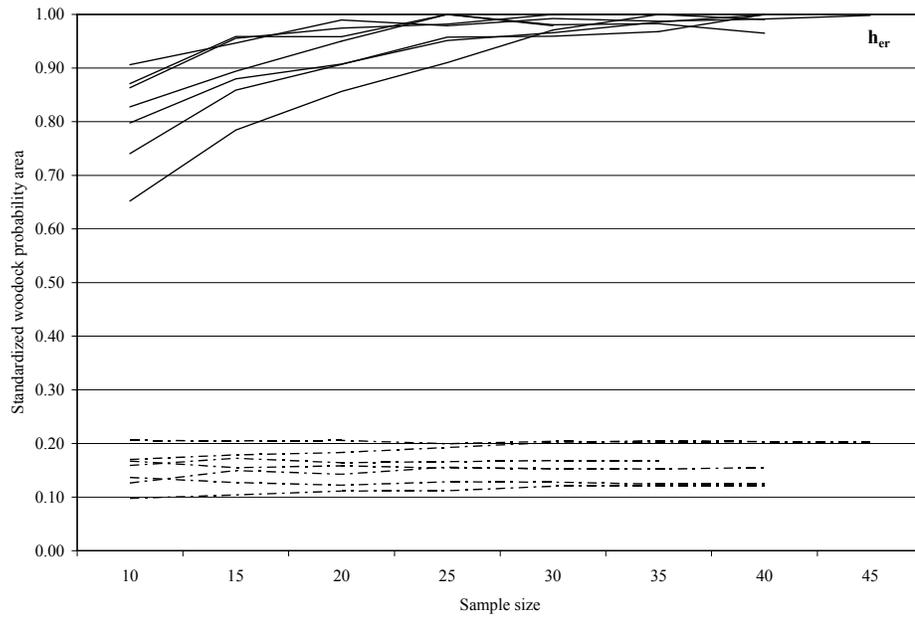
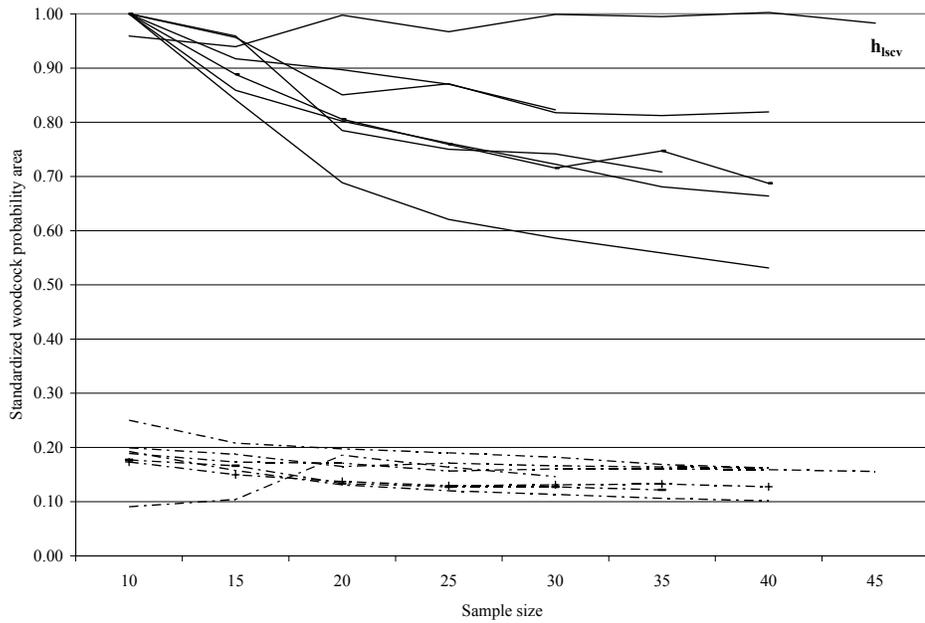


Fig. 1. Standardized (probability area at n / largest 95% probability area) woodcock 95% probability areas (solid line) and 50% probability areas (dashed line) using h_{iscv} and h_{er} as the smoothing parameter in a fixed kernel in relation to sample size. Location data are from after-hatch-year female American woodcock ($n = 7$) in east-central Minnesota during the fall of 2003.

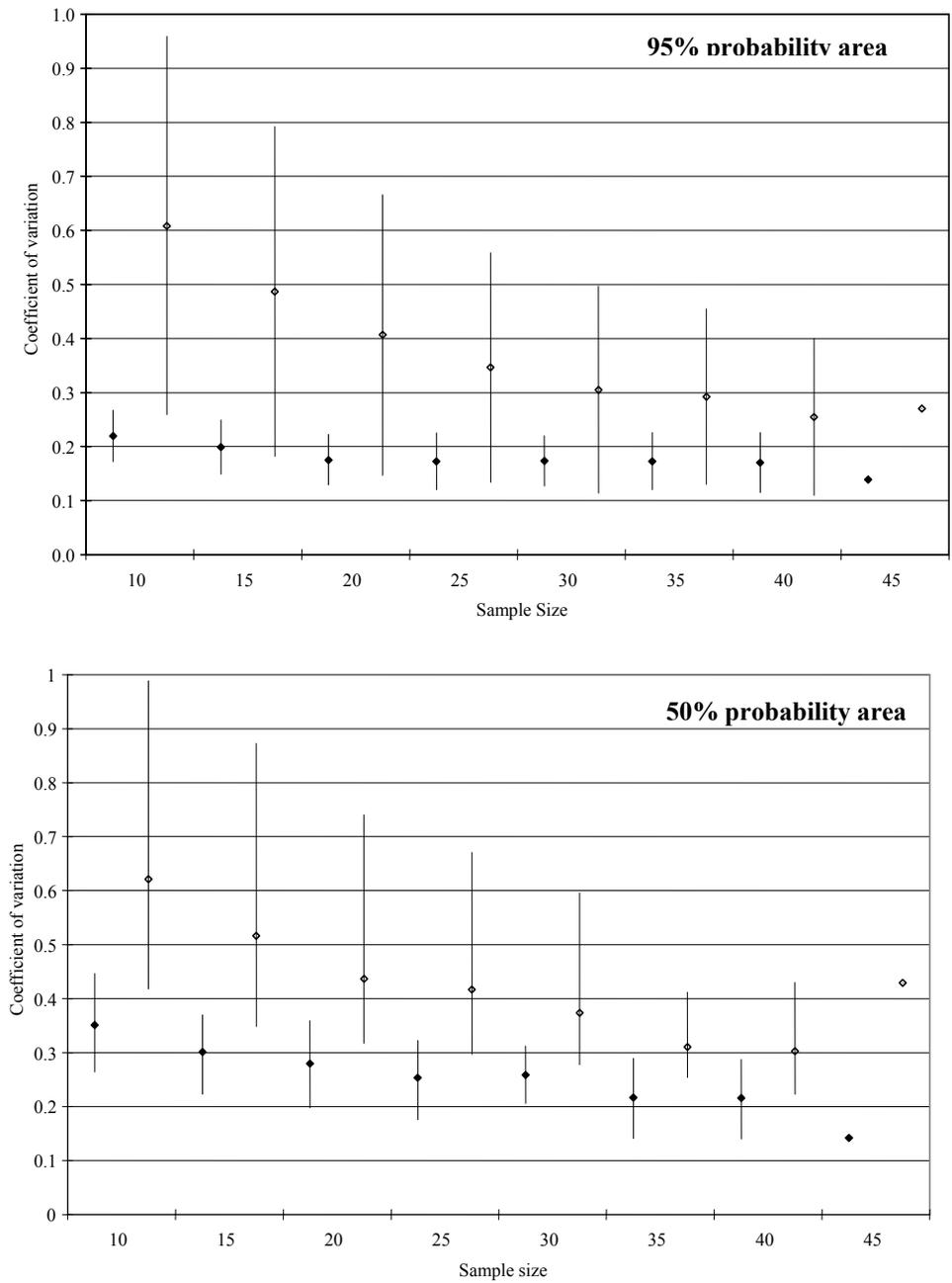


Fig. 2. Mean and range of the coefficient of variation vs. sample size for the 50% and 95% probability areas of fixed kernels using both h_{iscv} (white diamond/dashed line) and h_{er} (black diamond/solid line), derived from telemetry data from after-hatch-year female American woodcock in east-central Minnesota in the fall of 2003. Two hundred bootstrap samples per sample size were analyzed for each of 7 woodcock.

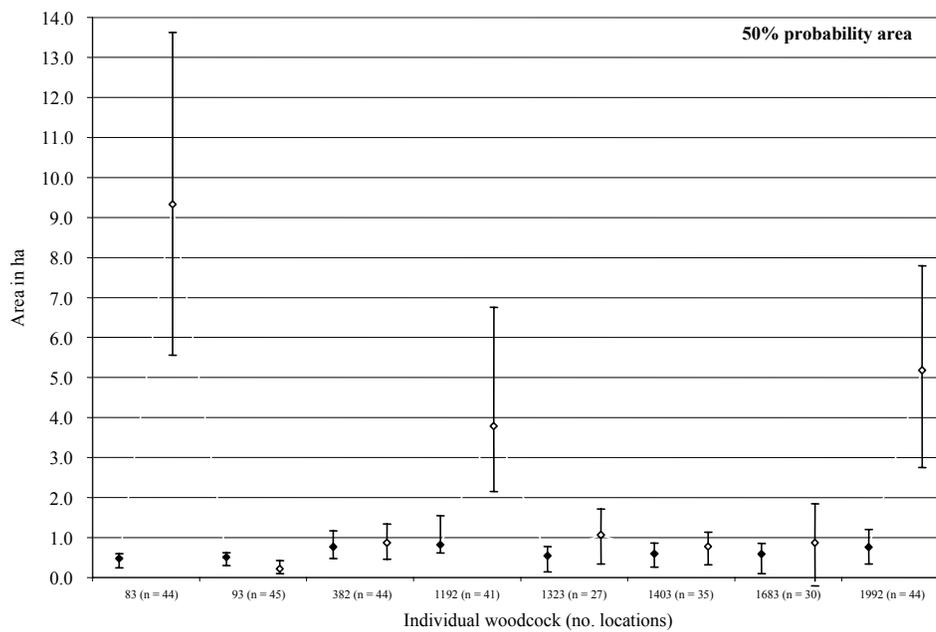
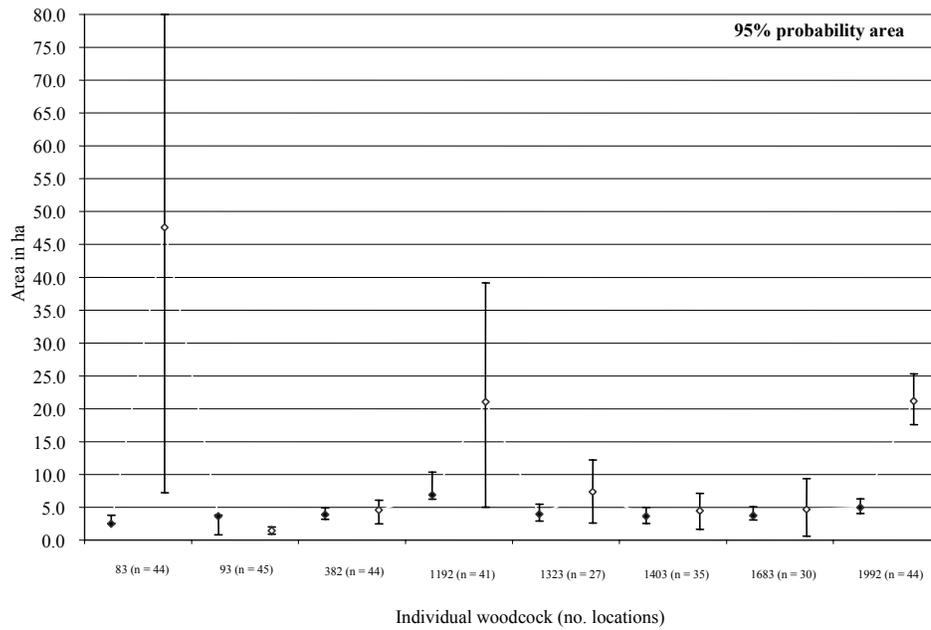


Fig. 3. Ninety-five percent CIs of bootstrapped fixed kernel means and kernel probability estimates (using h_{er} [black diamond] and h_{lscv} [white diamond]) for 95% and 50% probability areas for after-hatch-year female American woodcock in east-central Minnesota in 2003.

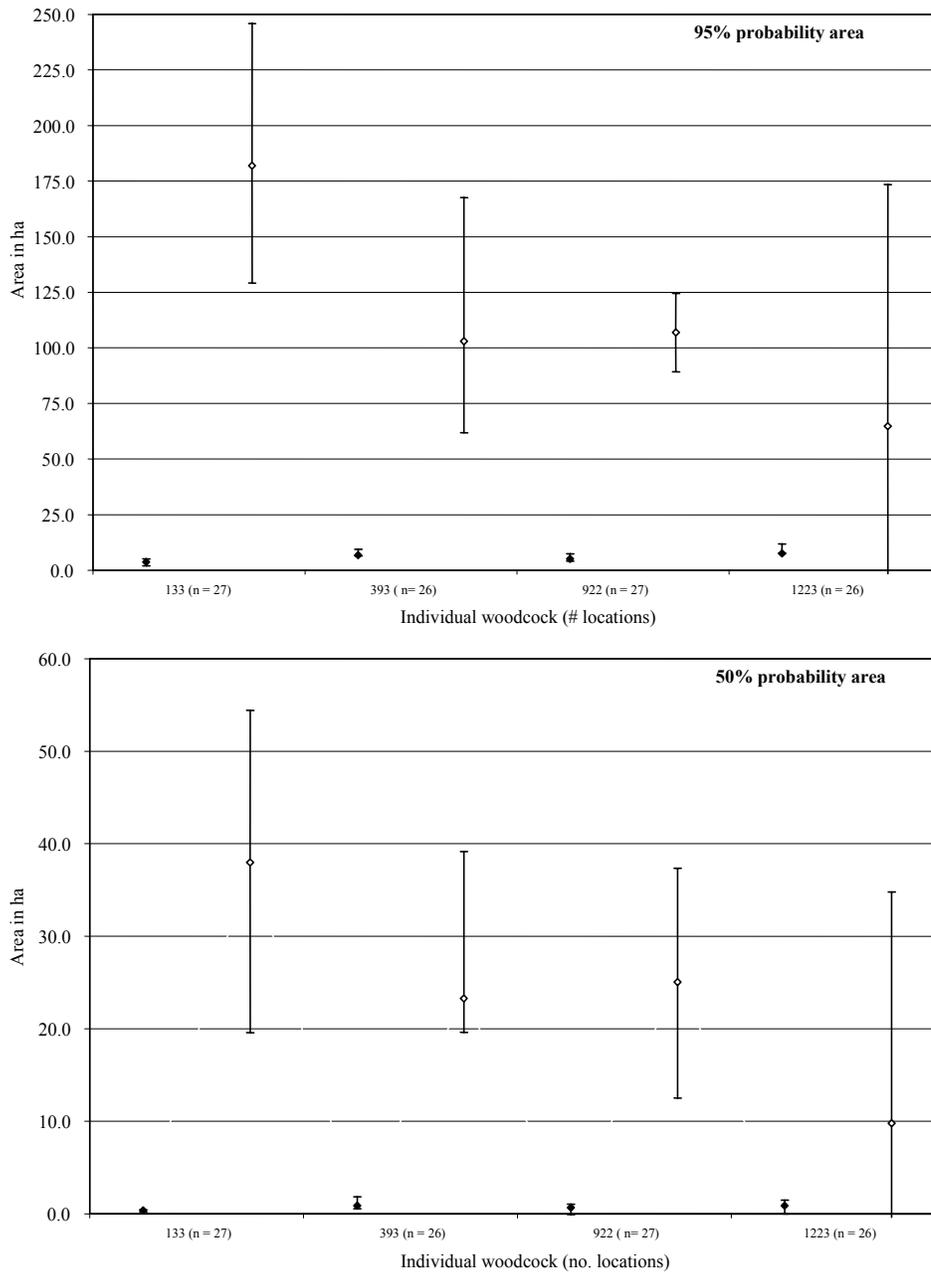


Fig. 4. Ninety-five percent CIs of bootstrapped fixed kernel means and kernel probability estimates for 95% and 50% probability areas using h_{er} (black diamond) and h_{lscv} (white diamond) for after-hatch-year female American woodcock in east-central Minnesota in 2003.

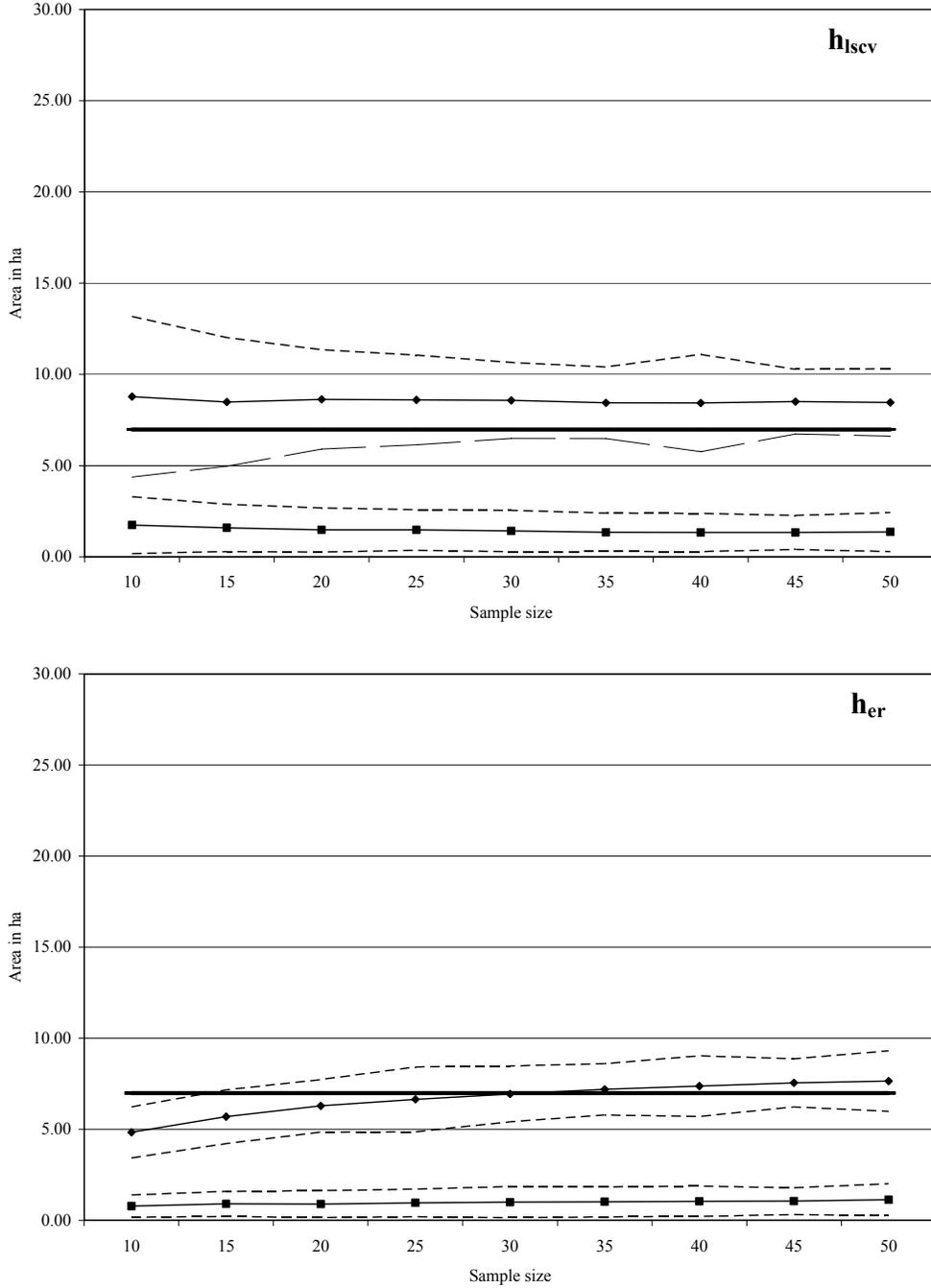


Fig. 5. Mean size and 95% CIs of bootstrap mean (dashed lines) of the 95% (black diamond) and 50% (black square) probability area of fixed kernels using h_{lscv} and h_{er} as the bandwidth selection method, on a simulated woodcock home range with 1 core use area. True area is represented by dark black line. Data are from 200 bootstrap samples per sample size.

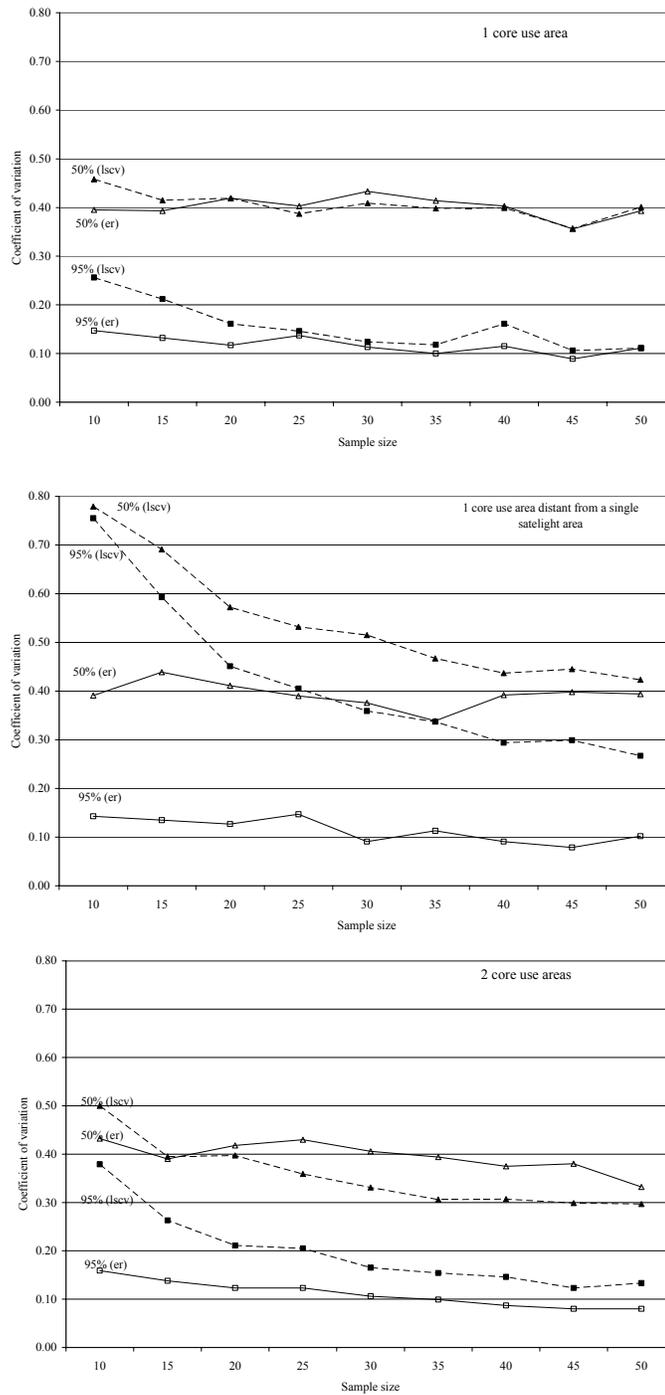


Fig. 6. Coefficient of variation vs. sample size for the 95% and 50% probability areas of fixed kernels using both h_{lscv} (dashed line) and h_{er} (solid line) for simulated woodcock home ranges with; 1 core use area, 1 core use area distant from a single satellite area of infrequent use, and 2 core use areas. True area is represented by dark black line. Data are based on 200 bootstrap samples per sample size.

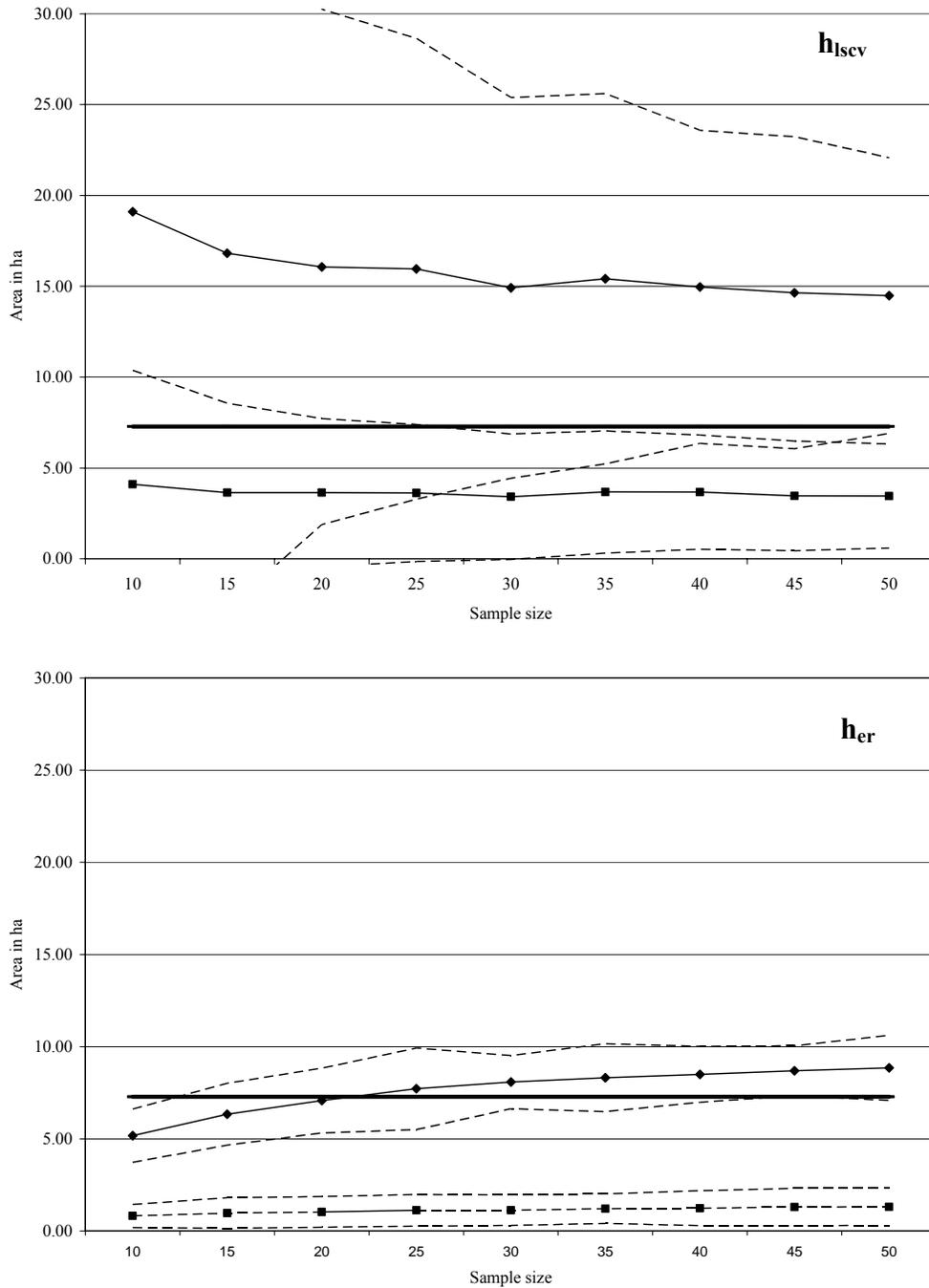


Fig. 7. Mean size and 95% CIs of bootstrap mean (dashed lines) of the 95% (black diamond) and 50% (black square) probability area of fixed kernels using h_{lscv} and h_{er} as the bandwidth selection method, on a simulated woodcock home range with 1 core use area distant from a single satellite area of infrequent use. True area is represented by dark black line. Data are from 200 bootstrap samples per sample size.

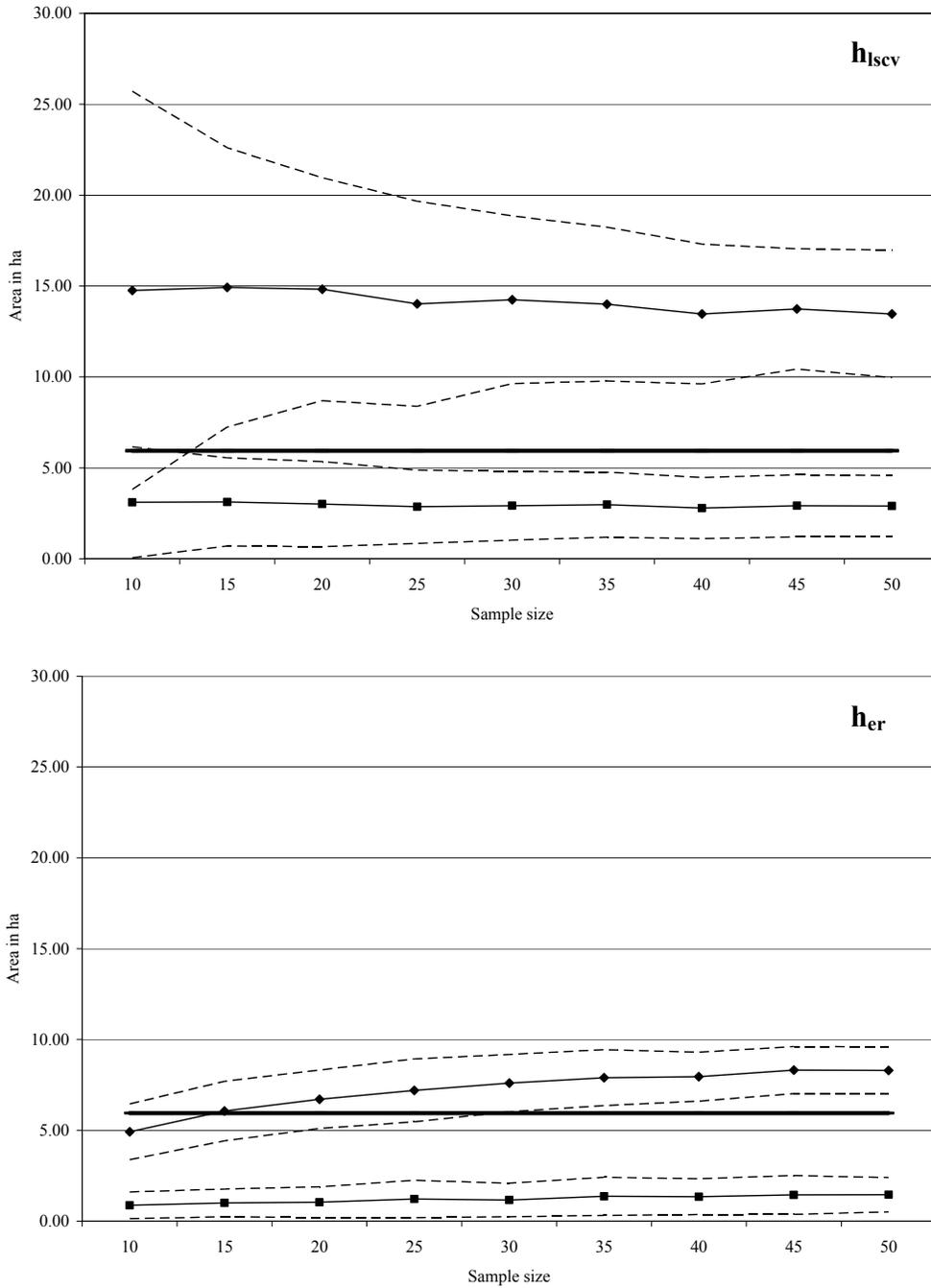


Fig. 8. Mean size and 95% CIs of bootstrap mean (dashed lines) of the 95% (black diamond) and 50% (black square) probability area of fixed kernels using h_{lscv} and h_{er} as the bandwidth selection method, on a simulated woodcock home range with 2 use areas. True area is represented by dark black line. Data are from 200 bootstrap samples per sample size.

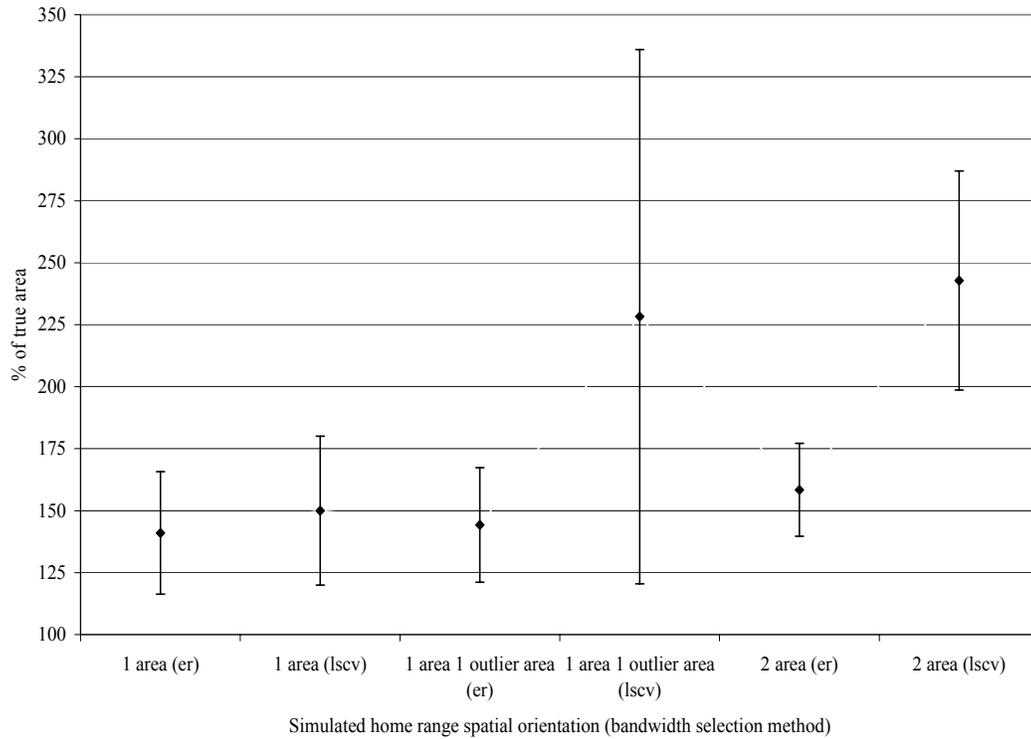


Fig. 9. Mean and 95% CIs of the percent of simulated home range area estimated using fixed kernels (95% probability area) with h_{er} and h_{lscv} as the bandwidth selection method in relation to varying spatial orientations. Data are from 500 Monte Carlo simulated home ranges of $n = 50$ for each polygon type and smoothing method.