Foraging location quality as a predictor of fidelity to a diurnal site for adult female American woodcock Scolopax minor

Authors: Doherty, Kevin E., Andersen, David E., Meunier, Jed, Oppelt, Eileen, Lutz, R. Scott, et al.

Source: Wildlife Biology, 16(4) : 379-388

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/09-100

Wildl. Biol. 16: 379-388 (2010)
DOI: 10.2981/09-100

www.wildlifebiology.com

Original article

Foraging location quality as a predictor of fidelity to a diurnal site for adult female American woodcock *Scolopax minor*

Kevin E. Doherty, David E. Andersen, Jed Meunier, Eileen Oppelt, R. Scott Lutz & John G. Bruggink

Quality of recently used foraging areas is likely an important predictor of fidelity to specific locations in the future. We monitored movement and habitat use of 58 adult female American woodcock *Scolopax minor* at three study areas in Minnesota, Wisconsin and Michigan, USA, during autumn 2002 and 2003, to assess the relationship between foraging habitat use decisions and environmental conditions at previously used foraging locations. We assessed whether habitat variables which related to food and weather were related to distance between locations on subsequent days of individual woodcock that choose diurnal foraging locations when they return from night-time roosting locations. We predicted that woodcock would return to foraging locations used on the previous day (i.e. shorter distances between daily foraging locations) when environmental conditions on the prior day were favourable. Woodcock generally made short (i.e. 48% < 50 m and 91% < 400 m) between-day movements, but also occasionally (~ 7%) abandoned prior foraging areas. The primary determinants of woodcock movements during autumn (prior to migration) were low local food availability and potential for increased food availability elsewhere. The quality of foraging locations was an important predictor of future foraging habitat use for woodcock, consistent with the hypothesis that woodcock movement behaviour balances the risks associated with movement with the potential benefits of increased energy intake in new foraging areas.

Key words: American woodcock, fidelity, foraging, habitat quality, movement, Scolopax minor

Kevin E. Doherty, Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108, USA - e-mail: kevin_doherty@fws.gov*
David E. Andersen, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108, USA - e-mail: dea@umn.edu
Jed Meunier & R. Scott Lutz, University of Wisconsin, Department of Wildlife Ecology, 226 Russell Labs, 1630 Linden Drive, Madison, Wisconsin 53711, USA - e-mail addresses: jedmeunier@hotmail.com (Jed Meunier); rslute@facstaff.wisc.edu (R. Scott Lutz)
Eileen Oppelt & John G. Bruggink, Department of Biology, Northern Michigan University, 1401 Presque Isle Avenue, Marquette, Michigan 49855, USA - e-mail addresses: eileenoppelt@yahoo.com (Eileen Oppelt); jbruggin@nmu.edu (John G. Bruggink)

**Present address: United States Fish & Wildlife Service, North Dakota 58503, USA*

Corresponding author: Kevin E. Doherty

Received 12 November 2009, accepted 11 October 2010

Associate Editor: Ilse Storch

Movement behaviour is influenced by natural selection to optimize energy intake while minimizing exposure to factors that reduce survival (e.g. predation; Krebs & Davies 1993). Moving from familiar into unknown areas to increase potential foraging opportunities could result in no energy gain or increased predation risk. Environmental cues, including food availability and ease of resource extraction, learned from a history of foraging are likely important predictors of future foraging opportunities (Pyke 1983) and influence choices associated with habitat use.

American woodcock *Scolopax minor* (hereafter woodcock) choose diurnal foraging habitat each morning as they depart from the night-time roosting fields to forage in densely wooded diurnal areas with moist soils (e.g. Krohn 1971, Morgenweck 1978). Favourable experiences may result in short between-day movement distances of diurnal locations if woodcock respond to recent environmental conditions when choosing diurnal foraging locations. Furthermore, woodcock movements within the same day are extremely short (i.e. 5 m median; Hudgins et al. 1985, and 22 m on average; Godfrey 1974) compared to between-day movements (129 m on average; Sepik & Derleth 1993), which makes between-day movement distance a useful measure of daily choice of foraging habitat. Several environmental cues learned from a history of foraging could influence whether woodcock return to the previous day's foraging location. First, 75% of the biomass of woodcock diet is earthworms (summarized by Keppie & Whiting 1994), and invertebrate availability may influence the movement patterns. Woodcock are also believed to exhibit strong preference for soil colour (Rabe et al. 1983b), which may be a proximate cue related to prey availability. Furthermore, weather conditions (e.g. maximum and minimum daily temperatures and precipitation) may directly influence movement patterns by increasing or decreasing the energetic expense associated with movement and the availability of earthworms. Woodcock metabolic rates increase sharply below 20°C, which increases the risk of unprofitable foraging decisions (Vander Haegen et al. 1994).

Our objective was to test the hypothesis that woodcock movement and choice of diurnal foraging habitat is affected by environmental cues. To test this hypothesis, we monitored movements of after-hatch-year (hereafter adult) female woodcock prior to migration in the western Great Lakes region, USA, and we tested *a priori* predictions that woodcock would return to foraging locations used on the previous day, when environmental conditions on the previous day were favourable. We restricted our analyses to the adult female portion of the population because the woodcock is a species of conservation concern due to long-term declines in population indices and because the woodcock has a promiscuous mating system making individual male contributions to population growth low. We assessed empirical support for hypotheses related to between-day movements in a competing model-selection framework (Burnham & Anderson 2002).

Material and methods

Study areas

We captured and radio-marked woodcock on three study areas (east-central Minnesota, north-central Wisconsin and the Upper Peninsula of Michigan, USA) in the western Great Lakes region during late summer and early autumn 2002 and 2003. We selected study areas with high woodcock densities and in which vegetation and land management practices were similar. Our study area 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). Vegetation communities in our Minnesota study area included early regenerating aspen *Populus tremuloides* and *P. grandidentata* and lowland habitats dominated by alder *Alnus* spp., willow *Salix* spp., and bur oak *Quercus macrocarpa*. Our north-central Wisconsin study area was within the Lincoln County Forest and Tomahawk Timberlands industrial forest and was characterized by rolling terrain with boggy wet basins. Northern mesic forests comprised most forest cover with sugar maple *Acer saccharum* dominating the better-drained soils and red maple *Acer rubrum* dominating 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. Our Michigan study area was in the Copper County State Forest in Dickinson County in Michigan's Upper Peninsula and we primarily concentrated field work in the eastern half of the 25,728-ha Dickinson Woodcock Research Unit. Upland forest habitats were dominated by aspen, red maple and paper birch *Betula papyrifera*. Dominant species in coniferous forests were balsam fir *Abies balsamea* and black spruce *P. mariana*. In addition, alder dominated many moist lowland areas. Woodcock hunting was allowed on a portion of each of our study areas (see Andersen et al., in press, for a description of hunting pressure on a portion of the Minnesota study area subsequent to this movement study).

Capture and radio-marking

We captured woodcock in the Minnesota, Wisconsin and Michigan study areas beginning on 24

August 2002 and 18 August 2003. We identified capture sites by observing potential roosting areas at dusk, and subsequently placed mist nets (Sheldon 1960) in areas where woodcock were observed flying to roost and spot-lighted roosting fields (Rieffenberger & Kletzly1967, McAuley et al. 1993). We used wing plumage characteristics to classify age (hatch year, 'HY'; and after hatch year 'AHY' or 'adult') and gender (male or female) of captured birds (Martin 1964) and bill length as an additional means of determining gender (Mendall & Aldous 1943). We attached radio-transmitters weighing approximately 4.4 g ($<$ 3% of body weight) to woodcock using all-weather livestock tag cement in conjunction with a single-loop wire harness using the techniques of McAuley et al. (1993). We released woodcock at capture locations following transmitter attachment.

Radio-tracking

We randomly selected a subsample (N = 15 in each of the study areas in 2002 and N = 18 in each of the study areas in 2003) of adult female woodcock from all radio-marked adult female woodcock in each study area in each year in early September (7 September 2002 and 8 September 2003). We relocated woodcock from the ground once per day (during daylight hours) 5-7 times/week using hand-held antennas and portable receivers by searching for signals from roads and determining direction(s) to the source of the signal from $\geq$ 1 receiving location(s). We then estimated a general location for the source of the signal, and walked to that general location by homing on the signal. We determined estimated locations of woodcock without flushing them using a hand-held Global Position System (GPS) unit (Garmin GPS 76, Garmin International, Olathe, Kansas; use of trade names does not imply endorsement by the U.S. Geological Survey) and walking around the source of the signal. If we were unable to locate woodcock on the ground for multiple days, we located them via fixed-wing aircraft approximately weekly, using standard aerial-telemetry methods. Once woodcock were located from the air, we located them subsequently from the ground to obtain precise locations and measure foraging-location variables. We monitored woodcock until mortality occurred or until woodcock migrated from our study areas (median departure date was in early November with 95% of woodcock leaving our study areas by mid-November; Meunier et al. 2008), which we defined as occurring after the last date that we detected a woodcock's radio signal followed by failure to detect a signal during three consecutive aerial telemetry flights. We searched from the air out to approximately 10 km from a woodcock's last known location.

We obtained ~ 88% of locations without flushing woodcock, thus minimizing our influence on their movements. However, because we did not flush woodcock, our estimated woodcock locations were influenced by several sources of error, including error in estimating locations based on our telemetry procedures, and error associated with deriving GPS coordinates. We estimated the distance between estimated and true woodcock locations by repeatedly (N = 50) locating a transmitter placed in woodcock habitat, following our field monitoring protocol in a blind trial to bound these errors. We then used the Jennrich-Turner home-range estimator (Jennrich & Turner 1969) to estimate the 95% error ellipse radius of these points (28.6 m), which represented the distance from estimated to true woodcock locations plus GPS error. We also recorded 50 GPS locations of the same fixed transmitter and again used the Jennrich-Turner home-range estimator to derive the radius of the 95% error ellipse associated with deriving GPS coordinates to account for GPS error. The radius of the 95% error polygon for our estimate of transmitter locations was 13.68 m when we removed GPS error, which represented the maximum distance between estimated and true woodcock locations. Finally, to estimate minimum distance between estimated and true woodcock locations, we intentionally flushed 10 adult female woodcock and paced the distance from the location of the observer when the bird flushed to the location from where the bird flushed (0 = 2.2 m, SE = 0.3). Woodcock were between two and 14 m from the estimated locations where we measured foraging-location variables, based on these estimates.

We calculated the distance between daily estimated locations on subsequent days (response variable) using the animal movement extension (Hooge & Eichenlaub 1997) in ArcView 3.3. We structured each individual woodcock locational data set by date and transformed location points for each woodcock into a segmented line file to measure the length between location points.

Foraging location variables

We quantified habitat characteristics at woodcock foraging locations in a random direction ~ 2-14 m (estimated minimum and maximum distance between estimated and true woodcock foraging locations) from radio-equipped woodcock. We measured earthworm biomass within a 35 × 35 cm square plot at the estimated woodcock location. We removed vegetation and ground litter inside this plot to facilitate collection of surfacing earthworms and poured 1.25 l of oriental hot mustard solution onto the ground and collected all earthworms that surfaced during a 5-minute period (Paulson & Bowers 2002). We calculated ash-free dry mass (to the nearest 0.0001 g) for each earthworm sample.

We quantified soil colour and soil porosity at estimated woodcock foraging locations. We separated soil colour into six categories (2.5-1, 3-1, 4-1, 5-1, 6-1 and 8-1) based on the Munsell soil colour chart 7.5YR (Munsell 2000) and recorded the closest match to soil colour. We also collected a 9.8-cm diameter by 6.8-cm deep soil core at the surface 1 m in a random direction from the estimated woodcock location to measure soil porosity. We were careful not to compact soil when collecting soil samples so as not to artificially inflate bulk density (Blake & Hartge 1986). We estimated soil porosity by dividing the bulk density of the samples by the density of quartz (2.65 g/cm^3; Danielson & Sutherland 1986).

We recorded daily high and low temperatures (°C) at stations in or adjacent to study areas with automated digital thermometers to incorporate weather variables into movement models. We located weather stations in study areas in open areas to match temperature and precipitation registration conditions at public weathers stations adjacent to our study areas. We recorded precipitation (in cm) in the previous 24-hour period daily at 09:00 with rain gauges located centrally at study sites.

Movement predictions

We created 14 models *a priori* to evaluate testable predictions of the relationship between environmental variables and movement to test the hypotheses that woodcock incorporate experience with recently used foraging locations and environmental cues into movement behaviour. We predicted that woodcock would make shorter movements between subsequent daily locations and return to previously used foraging locations when environmental conditions on the prior day were favourable, because returning to familiar cover affords incorporation of previous site-specific environmental cues related to food availability. Weather conditions may also influence energy requirements and resource availability. Therefore, we identified predictor variables that were related to two major classes of models; food and weather, based on published literature and our experience with woodcock movement in a 2001 pilot study.

Food hypotheses

We hypothesized that woodcock would return to areas with a high earthworm abundance and predicted that earthworm biomass per unit area would be negatively related to distance between subsequent daily locations. Earthworm abundance varies spatially and temporally and therefore may influence woodcock movement patterns. Earthworm abundance may be influenced by several factors, including soil moisture (e.g. Straw et al. 1994), soil temperature (a decrease in abundance at $< 5°$ or $> 25°$; Reynolds et al. 1977, Rabe et al. 1983b), and vegetation (Reynolds et al. 1977, Keppie & Whiting 1994).

We hypothesized that soil characteristics were an important predictor of food availability and thus, overall quality of foraging locations. We predicted that soil colours that were darker would be associated with shorter distances between daily locations because captive woodcock exhibited strong selection for dark soil colours in captive trials (Rabe et al. 1983a). Soil colour may serve as a cue related to food availability, as moist soils are generally darker than dry soils. Our rationale for including this variable was that not all soils are covered by litter, and we wanted to test experimental trial results in the field. The final model variable that we included, which were related to food, was soil porosity. Soil porosity influences soil moisture retention, which influences earthworm availability (Rabe et al. 1983b, Straw et al. 1994) and soil conditions that affect foraging success. We hypothesized that there would be a threshold at which moisture was sufficient to support foraging for earthworms.

Weather hypotheses

We hypothesized that precipitation would stimulate movement because we observed long movements by woodcock following rain events in 2001 in Minnesota, and therefore we included the previous day's precipitation in movement models. We included daily low temperature because low temperatures affect woodcock energetic requirements and may affect foraging abilities (Bell 1991). Woodcock metabolic demands increase at lower temperatures (Vander 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 (Cartar & Dill 1990, Caraco et al. 1990).

Interactions

We limited our models to include three first-order interactions. First, we included an interaction between rainfall and soil porosity because rainfall influences soil moisture. We postulated that rainfall improved foraging condition more in porous soils than in less porous soils because highly porous soils that were previously too dry for woodcock to forage in successfully would likely become more favourable, stimulating movements into new areas. Second, we allowed for an interaction between earthworm abundance and temperature because earthworms become less available as a function of temperature; this interaction was equally likely to stimulate or inhibit woodcock movement (Cartar & Dill 1990, Caraco et al. 1990). Third, we allowed for an interaction between soil colour and rainfall, because increased soil moisture (following rainfall) results in darker soil colour.

Statistical analyses

We analyzed data from all adult female woodcock in our random subsample with > 20 between-day movements ($N = 58$). Woodcock were located between 20 and 46 times during our study with an average of 31 locations per bird. We had a balanced study with each individual woodcock accounting for only 1.0-2.5% of the cumulative locations. Because sequential locations can be serially-correlated and therefore habitat characteristics measured for the same woodcock closer in time are more likely to be correlated than measures more distant in time, we modeled the appropriate covariance structure that best represented the data in SAS PROC MIXED (Littell et al. 1996, 1998). We used the REPEATED statement in PROC MIXED to model the covariation within individual woodcock, which accounted for the violation of independence of the observations (Littell et al. 1998). We used the RANDOM statement to model the variation among woodcock, which accounted for heterogeneity of variances from individual woodcock (Littell et al. 1998). The random effects factor was the subsample of individual woodcock that was randomly chosen from all radio-marked adult female woodcock captured as part of a larger survival study. We modeled other factors as fixed effects. We used maximum likelihood methods to fit a mixed-effects (both random and fixed effects) general linear model using SAS PROC MIXED. We chose the covariate structure ar(1) using information-theoretic methods (Akaike 1973, Burnham & Anderson 2002) and used this structure in all mixed modeling.

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to rank competing models (Akaike 1973, Burnham & Anderson 2002). We used AIC_c values computed in PROC MIXED to identify the model with the highest rank (i.e. minimum AIC_c value) and ΔAIC_c values to calculate the likelihood of the model given the data. We used likelihood estimates from Burnham & Anderson (2002:74) to calculate Akaike weights (w_i), 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 & Anderson 2002:75).

We conducted a variance-components analysis (Littell et al. 1996) to assess how much variation among individual woodcock was explained by the best approximating model(s). We used maximum likelihood covariance parameter estimates from SAS PROC MIXED for the ΔAIC_c best model(s) and the intercept-only model to compute the amount of process variation explained by our foraging location habitat variables:

$$\text{process variation explained} = (\sigma_{(.)} - \sigma_a)/\sigma_{(.)} \quad (1)$$

where $\sigma_{(.)}$ = the variance component estimate for the intercept-only model and σ_a = the variance component estimate for the ΔAIC_c best *a priori* model.

We constructed the same set of models ($N = 14$) with study area and year as blocking factors and assessed whether model selection or Akaike weights changed, to test whether pooling data across the three study areas was appropriate. We also conducted the same analysis that we performed on the full data set on a subset of the data that incorporated only local movements that were < 500 m. We arbitrarily defined local movements as movements of < 500 m between subsequent locations using the distribution of all movement distances (Fig. 1) as the basis of our definition. We did this because wood-

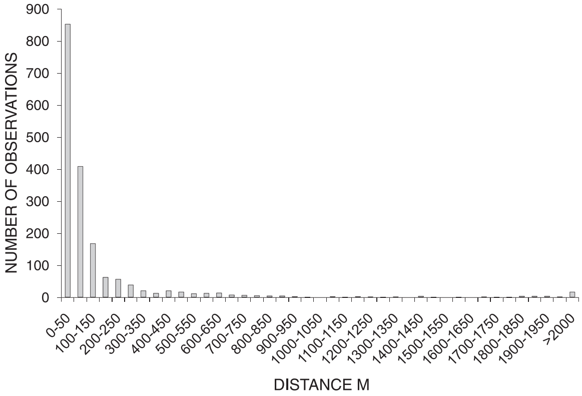

Figure. 1. Distance between subsequent-day locations ($N = 1,786$) for radio-marked female after-hatch-year American woodcock ($N = 58$) during autumn 2002 and 2003 in Minnesota, Wisconsin and Michigan, USA.

cock occasionally make relatively long between-day movements, and we wanted to test the sensitivity of the models to these relatively long movements. We compared results from this analysis to results of analyses of the full data set. We used the best approximating model to estimate and compare regression coefficients and standard errors; all other results are reported as means ± SE.

Results

We obtained > 20 estimates of between-day movements for 58 adult female American woodcock (Table 1). Woodcock were generally located on porous soils (0 porosity = 0.77 ± 0.01) that contained earthworms (0 = 0.077 ± 0.004 g ash free dry mass; see Table 1). Woodcock almost always returned to the vicinity of the previous day's foraging area, but also made longer movements and abandoned prior foraging areas 7% of the time. The majority (91%) of distances between subsequent daily locations was < 400 m, with 48% of movements < 50 m (see Fig. 1). The median distance between subsequent daily locations of adult female woodcock was 52.0 m, but was highly variable (coefficient of variation = 2.2).

Low temperature (T), rain (R), earthworm biomass (W), soil porosity (P), and the interaction between rain and porosity (R*P) were important predictors of woodcock movement ($w_i = 0.77$; Table 2). Inclusion of study area and year as blocking factors did not affect the relative ranking of models or substantially change Akaike weights. Including study area and year as blocking factors increased the amount of variation in movement among individual woodcock explained by environmental factors from

Table 1. Foraging location and study area characteristics for 58 after-hatch-year female American woodcock (with N > 20 estimates of distance between subsequent-day foraging locations) in Minnesota, Wisconsin and Michigan during autumn 2002 and 2003.

Study area and year[a]	Statistic	Low temp. (°C)	Precipitation (cm)	Ash-free dry mass (g)	Porosity of soil	Distance (m)
Minnesota 2002 (N = 11)	Min	-9.0	0.0	0.00	0.60	2.0
	Max	16.3	1.8	0.53	0.92	1887.9
	x̄ (SD) [b] or median	1.3	0.0	0.09 (0.11)	0.76 (0.07)	46.8
Minnesota 2003 (N = 16)	Min	-17.7	0.0	0.00	0.59	0.6
	Max	17.5	1.8	0.84	1.00	2880.4
	x̄ (SD) [b] or median	2.7	0.0	0.09 (0.12)	0.79 (0.08)	51.8
Wisconsin 2002 (N = 5)	Min	-17.7	0.0	0.00	na	4.0
	Max	16.7	2.7	1.42	na	2197.6
	x̄ (SD) [b] or median	0.6	0.1	0.11 (0.25)	na	80.9
Wisconsin 2003 (N = 14)	Min	-17.8	0.0	0.00	0.60	1.4
	Max	17.2	3.3	1.92	0.97	3806.6
	x̄ (SD) [b] or median	3.8	0.0	0.07 (0.19)	0.82 (0.07)	49.3
Michigan 2002 (N = 3)	Min	-7.2	0.0	0.00	0.59	4.2
	Max	14.4	1.7	0.84	0.95	2175.7
	x̄ (SD) [b] or median	1.1	0.0	0.10 (0.18)	0.73 (0.10)	40.7
Michigan 2003 (N = 9)	Min	-9.3	0.0	0.00	0.47	1.4
	Max	15.9	21.3	1.13	0.96	2283.1
	x̄ (SD) [b] or median	0.7	0.0	0.03 (0.08)	0.71 (0.11)	59.9

[a] N = number of adult female woodcock with > 20 locations used to calculate descriptive statistics of environmental variables and movements. Range of the number of locations per individual was 20 - 45/year.

[b] Numbers presented without (SD) are median of sample.

Table 2. Best-supported models (N = 5 of 14 *a priori* models) and intercept-only model describing the relationship of foraging location quality to the distance between subsequent-day locations of after-hatch-year female American woodcock (N = 58) in central Minnesota, central Wisconsin and the Upper Peninsula of Michigan during autumn 2002 and 2003. Study area and year were used as blocking factors in all models except the intercept-only model, which we used to assess the amount of total variation explained by the best-supported models.

Model[a]	k	ΔAIC_C	w_i	σ[c]	$(\sigma_{(.)} - \sigma_{(a)})/\sigma_{(.)}$
T,R,W,P,R*P	8	0[b]	0.77	1321.5	71.6%
T,R,W,P	7	3.4	0.14	1437.9	69.1%
T,R,C,W,P,T*W,R*P	10	4.4	0.09	1347.1	71.0%
W,P	5	784.5	0.00	2229.6	52.0%
P	4	1780.9	0.00	3008.5	35.3%
(.) intercept-only model	1			4646.9	0.0%

[a] W = earthworm biomass, P = soil porosity, T = low temperature, R = precipitation in cm , C = soil colour and (.) = constant only;
[b] The lowest AIC_c value was 18638.6;
[c] σ = covariance parameter estimate.

21 to 72% based on our variance-components analysis. Incorporating study area increased explanatory power by 6%, suggesting that movement behaviours among study areas were similar. Adding year as a blocking factor increased the process variation explained by 44%.

High earthworm biomass was related to shorter movement distances (Table 3). Woodcock that relocated to more distant foraging locations between days left areas where earthworm biomass (0.051 ± 0.008 g) was about 62% of that in foraging areas to which woodcock returned (0.079 ± 0.004 g). Increasing daily low temperatures were positively related to movement distances (see Table 3). Of movements to more distant foraging locations ⅔ occurred when the daily low temperature was above the median low temperature of 2.4°C. Soil porosity was positively related to movement to more distant foraging locations (see Table 3); approximately ⅔ of movements > 500 m occurred when porosity values were greater than the median porosity value of 0.77. Rain also stimulated woodcock movement with a ~ 2-fold increase in the amount of rain on the previous day when woodcock moved to more distant foraging locations (0.85 ± 0.22 cm rain vs 0.44 ± 0.04 cm rain). The interaction between rain and porosity had the strongest positive relationship to movement to more distant foraging locations of adult female woodcock. We found no evidence that woodcock movement was related to soil colour.

Table 3. Relationship of foraging location quality to the distance between daily locations of after-hatch-year female American woodcock in central Minnesota, central Wisconsin and the Upper Peninsula of Michigan during autumn 2002 and 2003. Estimates are derived from single ΔAIC_c best-supported 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	SE
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 temperature (in °C), R = precipitation (in cm), W = earthworm mass (in g), P = soil porosity (in %).

For models of woodcock movements between foraging locations of < 500 m, the best-supported models were similar to those for all movements. The rank of the top two models switched, indicating a decrease in the importance of the interaction between rainfall and porosity to shorter-distance movements between daily foraging locations. In contrast to the analysis of all movements, the best-supported model of movements < 500 m explained only 4% of the variation among woodcock. For the best-supported model, SE estimates for all parameters were larger than the associated regression coefficient estimate except for T (regression estimate 0.68 ± 0.28), which still had a positive association with movement.

Discussion

Whether woodcock returned to a foraging area or moved to more distant foraging locations in late summer and early autumn was related to conditions at their previous foraging location. Parameter estimates of the effects of environmental conditions from the best approximating models coincided with the *a priori* hypothesis that favourable environmental characteristics would result in shorter distances between daily foraging locations. Woodcock were likely to return to forage in areas with higher estimated earthworm biomass until conditions became unfavourable or became more favourable elsewhere, consistent with the optimal foraging theory, specifically the marginal value theorem (MacArthur & Pianka 1966, Charnov 1976). Woodcock were also likely to return from night-time roosting locations to a previously used foraging location when estimated earthworm biomass was high on the prior day and were more likely to move longer distances to new foraging areas when earthworm biomass was low on the prior day. When temperatures decreased, woodcock made fewer longer distance movements between foraging locations on subsequent days. Laboratory studies of bumble bee (family Apidae) and dark-eyed junco *Junco hyemalis* foraging suggested that animals minimize unpredictability and prefer less risky foraging opportunities even if risky foraging is more energetically profitable (Cartar & Dill 1990, Caraco et al. 1990). Woodcock showed this energy conservation strategy during a drought in Maine, where they ceased to make flights to nocturnal roosting areas when overall food availability was low (Sepik et al. 1983). Dark-eyed juncos, when exposed to stress from decreasing low temperatures, adopted more risky foraging behaviour. Woodcock decreased their movements when their metabolic demands increased as temperatures decreased; they did not appear to adopt a more risky foraging behaviour. Given that 75% of the biomass of a woodcock's diet is earthworms and woodcock metabolic demands are highest in cold temperatures when earthworms are less active and less available (Reynolds et al. 1977, Rabe et al. 1983b), conservation of existing fat reserves prior to migration is likely a more profitable foraging strategy than searching widely for food. Overall, foraging location fidelity appeared to be influenced by the prevailing environmental conditions at a particular time. This conclusion was also supported by the strong relationship of longer movements between foraging locations and the interaction between soil porosity and rainfall. Woodcock responded to the combination of rainfall and soil porosity by making long movements into new foraging areas that previously may have been too dry to support high earthworm availability.

Blocking by study area and year greatly increased the amount of explained process variation in between-day movement distances among woodcock. Movement patterns among study areas were similar and the relative importance of environmental factors representing habitat quality did not change between years or among study areas. However, the scale of movements between years did change. Autumn 2002 was cool and wet and woodcock generally moved shorter distances, whereas autumn 2003 was warm and dry with woodcock exhibiting longer movements following precipitation events. Blocking by year allowed us to account for different environmental conditions experienced in 2002 and 2003, which resulted in much higher precision of our movement models.

The strength of the relationship between environmental variables and movements was stronger for between-day movements to more distant foraging locations than for movements < 500 m. There are several plausible explanations for differences in the strength of these relationships at different scales of movement. First, variables that we quantified may not represent factors that affect short-distance movements between foraging locations of adult female woodcock. We observed little overlap in home ranges among woodcock in our study (K.E. Doherty, unpubl. data), suggesting that intraspecific spacing mechanisms may influence woodcock distribution, or that woodcock secure exclusive use of relatively small foraging areas. Second, the error associated with estimated woodcock locations versus the magnitude of short-distance woodcock movements may have limited our ability to detect associations between movement and environmental factors at small spatial scales. Over half of short-distance woodcock movements between foraging locations on subsequent days had overlapping error distributions. The relative imprecision of our ability to measure short between-day movements, coupled with highly variable environmental predictors, made detecting relationships at a small spatial scale difficult. Even so, the two best-supported models in the analyses of all movement distances and excluding movement distances > 500 m were the same. Our efforts to minimize impacts on woodcock movement (i.e. not flushing woodcock) may have led to habitat quantification at a spatial scale larger than that associated with short-distance movements.

One factor that might influence between-day movements of woodcock that we were unable to assess directly is related to predation risk. Woodcock foraging location selection could influence predation risk by providing protection from predators (especially avian predators) or by increasing predation risk if cover negatively influences predator detection. Woodcock generally forage in locations with high stem density (Morgenweck 1978; in our study, 0 = 28,725 ± 450 stems/ha (Doherty 2004)), possibly to provide protection from predators. Foraging locations with lower predation pressure could decrease observational vigilance for predators, thus reducing prey handling time. Reduced prey handling time leads to shorter interprey waiting time (Krebs 1980), which ultimately increases energetic intake by affording more time to forage. However, we observed very little variation in stem density at woodcock foraging locations, and any relationship between stem density and predation pressure is unclear, which precluded us from assessing whether between-day movements were related to predation pressure.

Quality of recently used foraging areas is likely an important predictor of fidelity to specific locations in the future. Favourable conditions (e.g. worm abundance) were associated with shorter movements and woodcock returning to previously used foraging locations, whereas less favourable conditions were associated with longer movements into previously unused areas. Woodcock also appeared to incorporate information about recent environmental conditions into decisions about movement. Woodcock were more likely to make longer movements and forage in new locations when rainfall and soil porosity combined to make foraging conditions more favourable elsewhere. Woodcock were also more likely to risk longer movements when higher temperatures decreased the metabolic risks associated with moving. Woodcock movement associated with foraging in autumn appears to balance the risks of movement with the possible benefits of increased energy intake in new foraging areas. Quantifying movement behaviour allowed us to explore how woodcock responded to changing environmental conditions, lending deeper insight into the use of habitats than simply assessing habitat selection based on used versus available locations. We suggest that this approach could be applied more broadly in studies of habitat selection to provide a means of better understanding potential mechanisms influencing selection.

Acknowledgments - our project was funded by the U.S. Fish and Wildlife Service (Region 3 Migratory Birds and 2001 Webless Migratory Game Bird Research Program), U.S. Geological Survey (Science Support Initiative and the Minnesota Cooperative Fish and Wildlife Research Unit), Wisconsin Department of Natural Resources, Minnesota Department of Natural Resources and the Michigan Department of Natural Resources. We thank all the technicians who endured hard days in the field and the staff at Mille Lacs WMA for assistance with logistics. We thank M.E. Seamans and G.S. Zimmerman, who helped with writing the SAS code, and R.J. Gutiérrez, G.L. Jones and D.M. Keppie who provided valuable comments on earlier versions of this manuscript. We thank D.G. McAuley for helping with identifying mist-netting and night-lighting sites and suggestions for techniques for handling woodcock and two anonymous reviewers for providing constructive suggestions that improved our manuscript. Finally, we thank S.D.Wilds for working to generate support and funding for this project.

References

Akaike, H. 1973: Information theory as an extension of the maximum likelihood principle. - In: Petrov, B.N. & Csaki, F. (Eds.); Second International Symposium on Information Theory. Budapest, Akademiai Kiado, pp. 267-281.

Andersen, D.E., Reiter, M.E. & Doherty, K.E. & Fulton, D.C. in press: Magnitude and spatial distribution of American woodcock hunting pressure in a central Minnesota wildlife management area. - Proceedings of the 10th American Woodcock Symposium.

Bell, W.J. 1991: Searching behavior: the behavioral ecology of finding resources. - Chapman and Hall, New York, New York, USA, pp. 358.

Blake, R.E. & Hartge, K.H. 1986: Bulk density. - In: Klute, A. (Ed.); Soil Science Society of America Handbook Series 5. Soil Society of America, Madison, Wisconsin, USA, pp. 363-375.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference. - Springer-Verlag, New York, New York, USA, pp. 488.

Caraco, T., Backenhorn, W.U., Gregory, G.M., Newman, J.A., Recer, G.M. & Zwicker, S.M. 1990: Risk-sensitivity: ambient temperature affects foraging choice. - Animal Behavior 39: 338-345.

Cartar, R.V. & Dill, L.M. 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. & Sutherland, P.L. 1986: Porosity. - In: Klute, A. (Ed.); Soil Science Society of America Handbook Series 5. Soil Society of America, Madison, Wisconsin, USA, pp. 443-445.

Doherty, K.E. 2004: Fall movement patterns of adult female American woodcock (*Scolopax minor*) in the western Great Lakes region. - M.Sc. thesis, University of Minnesota, St. Paul, Minnesota, USA, pp. 59.

Godfrey, G.A. 1974: Behavior and ecology of American woodcock on the breeding range in Minnesota. - PhD dissertation, University of Minnesota, Minneapolis, Minnesota, USA, pp. 333.

Hooge, P.E. & Eichenlaub, B. 1997: Animal movement extension to Arcview: Version 2.0. - Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA. Available at: http://alaska.usgs.gov/science/biology/spatial/gistools/index.php/ (Last accessed in February 2003).

Hudgins, J.E., Storm, G.L. & Wakely, J.S. 1985: Local movements and diurnal-habitat selection of male American woodcock in Pennsylvania. - Journal of Wildlife Management 49: 614-619.

Jennrich, R.I. & Turner, F.B. 1969: Measurement of non-circular home range. - Journal of Theoretical Biology 22: 227-237.

Keppie, D.M. & Whiting, R.M., Jr. 1994: American woodcock (*Scolopax minor)*. - The Birds of North America. American Ornithologists' Union and Academy of Natural Sciences of Philadelphia, USA, pp. 1-27.

Krebs, J.R. & Davies, N.B. 1993: An Introduction to Behavioral Ecology. - Blackwell Science Ltd. Malden, Massachusetts, USA, pp. 412.

Krohn, W.B. 1971: Some patterns of woodcock activities on Maine summer fields. - Wilson Bulletin 83: 396-407.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinge, R.D. 1996: SAS System for Mixed Models. - SAS Institute, Cary, North Carolina, USA, pp. 632.

Littell, R.C., Henry, P.R. & Ammerman, C.B. 1998: Statistical analysis of repeated measures data using SAS procedures. - Journal of Animal Science 76: 1216-1231.

MacArthur, R.H. & Pianka, E.R. 1966: On optimal use of a patch environment. - American Naturalist 100: 603-609.

Martin, F.W. 1964: Woodcock age and sex determination from wings. - Journal of Wildlife Management 28: 287-293.

McAuley, D.G., Longcore, J.R. & Sepik, G.F. 1993: Techniques for research into woodcocks: experiences and recommendations. - In: Longcore, J.R. & Sepik, G.F. (Eds.); Proceedings of the Eighth Woodcock Symposium. U.S. Fish Wildlife Service, Washington D.C., USA, Biological Report 16: 5-11.

Mendall, H.L. & Aldous, C.M. 1943: The ecology and management of the American woodcock. - Maine Cooperative Wildlife Research Unit, University of Maine, Orono. Maine, USA, pp. 201.

Meunier, J., Song, R., Lutz, R.S., Andersen, D.E., Doherty, K.E., Bruggink, J.G. & Oppelt, E. 2008: Proximate cues for a short-distance migratory species: an application of survival analysis. - Journal of Wildlife Management 72: 440-448.

Morgenweck, R.O. 1978. Crepuscular behavior of American woodcock (*Philohela minor* Gmelin) and summer and fall habitat utilization by females in northeastern Minnestoa. - PhD dissertation, University of Minnesota, St. Paul, Minnesota, USA, pp. 140.

Munsell 2000: Munsell Soil Color Charts. - GretagMacbeth, New Windsor, New York, USA pp. 9.

Paulson, L.A. & Bowers, M.A. 2002: A test of the 'hot' mustard extraction method of sampling earthworms. - Soil Biology and Biochemistry 34: 549-552.

Penfound, W.T. & Rice, E.L. 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. - In: Swingland, I.R. & Greenwood, P.J. (Eds.); The Ecology of Animal Movement. Clarendon Press, Oxford, UK, pp. 7-31.

Rabe, D.L., Prince, H.H. & Beaver, D.L. 1983a: Feeding-site selection and foraging strategies of American woodcock. - Auk 100: 711-716.

Rabe, D.L., Prince, H.H. & Goodman, E.D. 1983b: The effects of weather on the bioenergetics of breeding American woodcock. - Journal of Wildlife Management 47: 762-771.

Reynolds, J.W., Krohn, W.B. & Jordan, G.A. 1977: Earthworm populations as related to woodcock habitat usage in central Maine. - In: Keppie, D.M. & Owen, R.B., Jr. (Eds.); Proceedings of the Sixth Woodcock Symposium. New Brunswick Department of Natural Resources, Fredericton, New Brunswick, Canada, pp. 135-146.

Rieffenberger, J.C. & Kletzly, R.C. 1967: Woodcock nightlighting techniques and equipment. - In: Goudy, W.H. (compiler); Woodcock research and management, 1966. U.S. Bureau of Sport Fisheries and Wildlife, Special Scientific Report, Wildlife 101: 33-35.

Sepik, G.F. & Derleth, E.L. 1993: Habitat use, home range size, and patterns of moves of the American woodcock in Maine. - In: Longcore, J.R. & Sepik, G.F. (Eds.); Proceedings of the Eighth Woodcock Symposium. U.S. Fish Wildlife Service, Washington D.C. USA, Biological Report 16: 41-49.

Sepik, G.F., Owen, R.B. & Dwyer, T.J. 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., Krementz, D.G., Olinde, M.W. & Sepik, G.F. 1994: American woodcock. - In: Tacha, T.C. & Braun, C.E. (Eds.); Migratory, shore, and upland gamebird management in North America. International Association of Fish and Wildlife Agencies, pp. 97-114.

Vander Haegen, W.M., Owen, R.B., Jr. & Krohn, W.B. 1994: Metabolic rate of American woodcock. - Wilson Bulletin 106: 338-343.