Original Article

Why woodcock commute: testing the foraging-benefit and predation-risk hypotheses

Roger J. Masse,[a] Brian C. Tefft,[b] José A. Amador,[a] and Scott R. McWilliams[a]

[a]Department of Natural Resources Science, 102 Coastal Institute in Kingston, University of Rhode Island, Kingston, RI 02881, USA and [b]Rhode Island Department of Environmental Management, Division of Fish and Wildlife, 277 Great Neck Road, West Kingston, RI 02892, USA

Moving between sites is a common behavior employed by prey in order to balance trade-offs associated with acquiring resources and avoiding predators. At dusk during summer, American woodcock frequently fly from diurnal coverts in forests to nocturnal roost fields. We tested 2 hypotheses, the foraging-benefit hypothesis and predation-risk hypothesis, to determine the benefit gained by woodcock that commute. We used telemetry to identify the diurnal coverts and nocturnal roost fields used by woodcock in Rhode Island, USA, during 2 summers. At each site, we measured the availability and diversity of woodcock prey, soil properties, and mammalian predator activity. Earthworms were 3–4 times more abundant at diurnal coverts than nocturnal roost fields. The richness and diversity of woodcock foods was greater at diurnal coverts during 2011 but similar between sites during 2012. Soil moisture content was about 1.5 times greater at diurnal coverts, whereas other soil properties were similar between sites. At night, mammalian predators visited diurnal coverts more frequently than nocturnal roost fields for 73% of the woodcock we monitored during 2011. During 2012, the number of days until initial predator visit was 1.8 times greater at nocturnal roost fields. Our results provide the first empirical support for the predation-risk hypothesis. During summer, woodcock fly from diurnal coverts to nocturnal roost fields to avoid predators and not to feed.

Key words: American woodcock, commuting behavior, diurnal covert, nocturnal roost field, predation risk, predator activity, Rhode Island.

INTRODUCTION

Prey must balance the costs and benefits of acquiring resources while avoiding predators (Milinski and Heller 1978; Sih 1980; Lima 1985; Lima et al. 1985; Lima and Dill 1990). The predation-risk allocation hypothesis states that temporal variation in predation risk imposed on prey by predators often forces prey to trade-off when to feed and when to engage in antipredator behaviors during periods of dissimilar risk (Lima and Bednekoff 1999). This hypothesis, and its associated predictions, has recently been questioned on the grounds that some assumptions may be unrealistic in ecological settings, specifically the assumption that prey experience imposed schedules of risk for set periods and, thus, cannot actively manage risk (Beauchamp and Ruxton 2011). On the contrary, antipredator behaviors allow prey to actively manage risk, but prey are unable to control when and where predators occur and so decisions to adopt such behaviors are made under risk imposed by predators (Bednekoff and Lima 2011). Discriminating between these scenarios requires studies that demonstrate spatial or temporal variation in predation risk and then show how certain antipredator behavior(s) can favorably balance predation risk and the need to feed.

Active risk management via antipredator behaviors has been documented for diverse taxa including insects (Rothley et al. 1997), amphibians (Van Buskirk et al. 2002), fishes (Ferrari et al. 2010), mammals (Searle et al. 2008; Périquet et al. 2012), and birds (Tilgar et al. 2011; Huang et al. 2012). One behavior aimed at balancing the trade-off between acquiring resources and avoiding predators involves moving between sites. For instance, red-backed salamanders (*Plethodon cinereus*) exposed to simulated predation climbed higher on plants than controls and so moved further away from food-rich areas, which were on the ground (Roberts and Liebgold 2008). Similarly, shorebirds frequently fly between shallow feeding areas at low tide and safe resting areas with less food at high tide (Dias et al. 2006; Rogers et al. 2006; van Gils et al. 2006). Organisms that typically move between sites provide behavioral ecologists unique opportunities to investigate the timescales at which predation risk allocation may occur and simultaneously test hypotheses about the trade-offs between foraging and predation risk at different sites. We investigated these aspects of the behavioral ecology of the American woodcock (*Scolopax minor*), a

Address correspondence to R.J. Masse. E-mail: rjmasse@my.uri.edu.

116–279 g shorebird that inhabits forests and shrublands in eastern North America (Keppie and Whiting 1994).

American woodcock (hereafter woodcock) are a migratory species breeding primarily across the northern half of the eastern United States and adjacent southern Canada and wintering primarily across the southern and southeastern United States. Generally, woodcock return to northern breeding grounds during March and depart for southern wintering grounds during October (Keppie and Whiting 1994). Throughout the year, woodcock often commute between quite different habitats during the day and night although the reasons for this behavior can vary by season. During fall and winter, woodcock frequently fly from forests to grazed pastures, recent forest clear-cuts, or harvested agricultural fields at dusk to actively feed (Glasgow 1958; Krohn et al. 1977; Krementz 2000; Blackman et al. 2012) or roost (Connors and Doerr 1982). During spring, woodcock fly from forests to recent forest clear-cuts, maintained or abandoned meadows and fields, tree plantations, or other forest openings during the morning and evening crepuscular periods to perform courtship displays and copulate (Sheldon 1967; Dwyer et al. 1988). Male woodcock perform courtship flights over these forest openings, called singing grounds, whereas females typically nest and rear young in nearby forests (Sheldon 1967). During summer, woodcock typically spend the day feeding in moist, young, deciduous, or mixed hardwood-conifer forests (Sheldon 1967; Straw et al. 1986; Keppie and Whiting 1994; McAuley et al. 1996; Dessecker and McAuley 2001), called diurnal coverts, and then some fly to natural or maintained forest openings at dusk (Mendall and Aldous 1943; Sheldon 1961; Krohn 1971). Although these movements by woodcock during summer have been described, the benefits gained by woodcock that fly to forest openings at dusk are not clear.

Two hypotheses, the foraging-benefit hypothesis (Mendall and Aldous 1943; Sheldon 1961) and the predation-risk hypothesis (Dunford and Owen 1973), have been proposed to explain why woodcock fly to forest openings, called nocturnal roost fields, at dusk to spend the night during summer. Observations of some woodcock feeding on invertebrates (e.g., ants [Hymenoptera], moths [Lepidoptera], and beetle [Coleoptera] larvae) at nocturnal roost fields prompted early researchers to hypothesize that those birds flew to these areas to exploit novel food resources that were not available at diurnal coverts (Mendall and Aldous 1943; Sheldon 1961, 1967). Although earthworms (Haplotaxida) are favored woodcock foods, other invertebrates may account for 15–40% of the volume of food in woodcock stomachs (Sheldon 1967; Keppie and Whiting 1994). Because woodcock are opportunistic feeders (Sheldon 1967), it is likely that many of these prey items could be obtained at diurnal coverts. Moreover, no one to date has directly tested the foraging-benefit hypothesis by quantifying the availability or diversity of woodcock foods at both the diurnal coverts and nocturnal roost fields used by individuals.

Subsequent research found that little, or no, feeding occurred by woodcock at nocturnal roost fields during summer (Krohn 1970). Furthermore, nocturnal roost fields used by woodcock during summer typically are not conducive to feeding because the soils at these sites tend to be dry, hard, and lacking in potential prey items (Sheldon 1961; Krohn 1970; Wishart and Bider 1976). After flying to nocturnal roost fields, woodcock are usually inactive throughout the night during summer (Dunford and Owen 1973; Owen and Morgan 1975; Wishart and Bider 1977), so these areas likely provide some benefit other than feeding opportunities. Dunford and Owen (1973) suggested that woodcock flew from diurnal coverts to nocturnal roost fields during summer because these areas provided safer refuge from predators. Although it is generally accepted (Williamson 2010), no one to date has directly tested the predation-risk hypothesis.

Our objective was to simultaneously test the foraging-benefit and predation-risk hypotheses for woodcock that fly between diurnal coverts and nocturnal roost fields during summer to determine the benefit afforded to individuals engaging in this behavior. Specifically, we compared the availability and diversity of woodcock foods, soil properties, and mammalian predator activity at both the diurnal coverts and nocturnal roost fields used by individually marked woodcock. The foraging-benefit hypothesis predicts greater availability and diversity of soil macrofauna at woodcock nocturnal roost fields than diurnal coverts. The predation-risk hypothesis predicts greater mammalian predator activity during the night at woodcock diurnal coverts than nocturnal roost fields.

MATERIALS AND METHODS

We conducted this field study within and around 3 state wildlife management areas—Arcadia, Big River, and Great Swamp—in central and southern Rhode Island, USA. Arcadia (41°35′10″N, 71°43′20″W) is approximately 62 km² predominantly comprised of mixed (35%), deciduous (35%), and coniferous forest (26%), with roughly 88% of the management area consisting of upland habitat; Big River (41°37′0″N, 71°36′60″W) is approximately 33 km² mainly comprised of coniferous (46%), mixed (34%), and deciduous forest (8%), with nearly 84% of the management area consisting of upland habitat; Great Swamp (41°27′15″N, 71°35′19″W) is approximately 15 km² chiefly comprised of deciduous (61%), mixed (18%), and coniferous forest (8%), with only about 31% of the management area consisting of upland habitat. Red maple (*Acer rubrum*) swamps are the dominant wetland type at Great Swamp. Common trees and shrubs at all sites include red maple, oaks (*Quercus* spp.), eastern white pine (*Pinus strobus*), pitch pine (*Pinus rigida*), blueberries (*Vaccinium* spp.), and pepperbush (*Clethra alnifolia*).

At each management area, a variety of maintained forest openings including recent forest clear-cuts, herbaceous meadows, and agricultural fields are managed to improve woodcock habitat. In 1995, a series of 2–5 ha clear-cuts were made at Great Swamp to provide forest openings and create young forest habitat. Additional habitat management occurred at that site during 2007 and 2012. Similar management practices were initiated at Arcadia and Big River during 1996 and 2006, respectively, and have continued sporadically since then.

Woodcock movements and data collection

We used mist nets to catch adult woodcock on singing grounds, where males perform courtship flights and copulate with females (Sheldon 1967), during April–June 2011 and 2012 as part of a separate study investigating the distribution, habitat use, and survival of woodcock in the region (IACUC protocol AN10-02-017). We attached an Advanced Telemetry Systems Model A5400, 2-stage transmitter to each bird using all-weather cattle tag cement and a wire belly band (≤4 g; McAuley et al. 1993). We marked 98 adult woodcock between 2011 ($n = 54$; 50 males and 4 females) and 2012 ($n = 44$; 42 males and 2 females). Females were underrepresented in our sample because of the difficulty associated with catching them in mist nets during spring (McAuley et al. 1993). During 2011, 6 woodcock died, 4 slipped their

transmitters, and 20 left the study sites and could not be relocated prior to the start of field experiments. During 2012, 6 woodcock died, 4 slipped their transmitters, and 10 left the study sites and could not be relocated prior to the start of field experiments. All of the 48 remaining woodcock (2011: 15 after second year [ASY] and 9 second year [SY] males; 2012: 10 ASY and 13 SY males and 1 ASY female) flew from diurnal coverts to nocturnal roost fields on some nights.

For this study, we monitored the daytime and nighttime locations of radio-marked woodcock 1–3 times per week from 1 July to 20 August each year. We tracked each individual on foot using a 3-element antenna and used a GPS to determine exact locations once each day (0600–1900 h EST) and once each night (2030–0240 h). The location of each bird was determined by slowly moving in the direction of the radio signal while reducing the gain of the receiver until the receiver began giving an audible signal without the use of the antenna or headphones. We quantified the accuracy of this technique by placing 5 transmitters on the ground, approaching each transmitter from each cardinal direction, and then measuring the distance to the transmitter once the receiver first started giving an audible signal without the antenna or headphones. On average, we were 17.7 ± 8.3 m from transmitters using this technique. Because we were interested in determining which variables cause woodcock to fly between diurnal coverts and nocturnal roost fields, we identified the location of the diurnal covert and nocturnal roost field used during a 6-day period for each bird included in this study. This paired design allowed us to directly compare the foraging benefit and predation risk associated with each bird's diurnal covert and nocturnal roost field.

We collected soil macrofauna at the nocturnal roost field and diurnal covert of each woodcock by digging five 900 cm^2 soil pits to 10 cm deep. We flushed each woodcock once at its nocturnal roost field from 8 to 20 August 2011 and from 9 July to 7 August 2012 and centered the first soil pit on the flush point. Four additional soil pits were located 5 m in each cardinal direction from the flush point to provide an overall average density of soil macrofauna at each site. We stored soil pit contents in plastic bags that were tied shut, returned early the following morning, and then collected all soil macrofauna by hand sorting similar to the study by Dangerfield (1997) except we sorted pit contents over white plastic bags. On subsequent days, we flushed each woodcock once at its diurnal covert and collected potential prey in the same manner but immediately hand sorted soil pit contents after digging. We counted all soil macrofauna and identified individuals to Order except centipedes (Chilopoda) and millipedes (Diplopoda). Because earthworms are the dominant prey of woodcock (Sheldon 1967), we also weighed fresh and freeze-dried earthworm samples from each site. We tested the foraging-benefit hypothesis using 38 of the available radio-marked woodcock (2011: 9 ASY and 8 SY males; 2012: 8 ASY and 12 SY males and 1 ASY female) because we had complete information on food abundance at both their diurnal coverts and nocturnal roost fields.

We collected a 10-cm-deep soil core from the flush point and 2 randomly chosen soil pits at each diurnal covert and nocturnal roost field to determine soil moisture content and soil pH during 2011 and these variables along with soil organic matter content during 2012. We measured soil moisture content gravimetrically by drying to a constant weight at 105 °C. We measured soil pH using a 1:5 soil/water (mass/vol) ratio (Hendershot et al. 1993) with a glass pH electrode and a pH meter (model UB-10; Denver Instruments). We measured soil organic matter content using the loss-on-ignition method via combustion of oven-dry (105 °C) soil in a furnace at 550 °C for 4 h. We expressed soil moisture content and soil organic matter content as percent by weight.

We quantified mammalian predator activity at the diurnal covert and nocturnal roost field of each woodcock in 2 ways. First, during 2011, we established baited track stations (Linhart and Knowlton 1975; Gompper et al. 2006) at each site and monitored them for evidence of mammalian predator activity for 10 nights each from 2 to 30 September. We expanded the soil pit at each flush point to 1 m^2 by loosening and smoothing the soil and baited each station with 0.25 can of albacore tuna (*Thunnus alalunga*). We prepared track stations during the late afternoon and checked them for evidence of mammalian predator activity (e.g., tracks, dig marks, or missing bait) early the following morning. For each site, we recorded the total number of nights (out of 10) that any mammalian predator visited and, when possible, predator identity. Second, during 2012, we established bait stations at each site in the same manner and monitored them constantly for up to 14 days using camera traps (Gompper et al. 2006) from 6 to 31 August. We baited each station with 0.25 can of albacore tuna and a single northern bobwhite (*Colinus virginianus*) carcass and replenished bait after 7 days as necessary. For each site, we recorded the number of days until initial predator visit along with predator identity. During both years, we delayed the start of predator monitoring at these sites until after all soil macrofauna were collected (2011: average = 19 days, range = 12–24 days; 2012: average = 17 days, range = 1–31 days) in order to minimize the influence of these activities on predator behavior and ensure that all sites were monitored for predator activity during a similar time period within each year. Because several woodcock might roost in the same forest opening at night (Sheldon 1967), we randomly selected 1 woodcock from forest openings where >1 radio-tagged bird was present to include in our sample. This reduced our sample size but was necessary to ensure independence between pairs of observations. We tested the predation-risk hypothesis using 23 of the 38 woodcock (2011: 6 ASY and 5 SY males; 2012: 4 ASY and 8 SY males) included in the test of the foraging-benefit hypothesis because these individuals satisfied our independence criteria and we had complete information on mammalian predator activity at both their diurnal coverts and nocturnal roost fields.

We acknowledge that raptors are also important predators of woodcock. Great horned owls (*Bubo virginianus*) and barred owls (*Strix varia*) may occasionally kill woodcock in forest openings at night during spring and summer (Derleth and Sepik 1990; Longcore et al. 1996), but mammalian predators, particularly weasels (*Mustela* spp.) and raccoons (*Procyon lotor*), pose a more serious threat at diurnal coverts (Longcore et al. 2000; McAuley et al. 2005).

Statistical analysis

We calculated the population density of each potential prey item at each diurnal covert and nocturnal roost field used by each woodcock. Because woodcock might not consume all macrofauna found in the soil, we also calculated the cumulative density of known woodcock foods (Keppie and Whiting 1994) at each site. We estimated the richness of soil macrofauna at each site by counting the number of unique taxonomic groups and estimated diversity by calculating the Shannon index, H′, (Magurran 2004) and then converting to diversity (Jost 2006). We used either paired *t*-tests or Wilcoxon signed-rank tests (Ott and Longnecker 2010) to compare population densities of potential prey, cumulative densities

of known prey, richness, and diversity depending on the normality of paired differences. We assessed normality using a combination of histograms, boxplots, or normal probability plots. We also used paired *t*-tests or Wilcoxon signed-rank tests to compare earthworm weight, soil moisture content, soil pH, and soil organic matter content. We tested for a difference in the number of nights that baited track stations were visited by any mammalian predator during 2011 using log-linear regression assuming a Poisson distribution (Gardner et al. 1995; Agresti 2007; Pedan 2011). We used a mixed effects model (PROC GLIMMIX, SAS Version 9.2; SAS Institute Inc 2008.) and included bird identity as a random effect to account for the paired nature of our data. Finally, we used a paired *t*-test to compare the number of days until initial predator visit at each site during 2012. Unless otherwise stated, we used Program R (Version 2.10.1) to conduct these analyses. We considered a significance level of $\alpha = 0.05$ for all tests.

RESULTS

Woodcock flew on average 1200.9 ± 594.2 m (range: 402–2236 m) in 2011 (17 males; 1 observation per bird) and on average 873.9 ± 543.8 m (range: 85–2133 m) in 2012 (20 males and 1 female; 1 observation per bird) between sample locations at diurnal coverts and nocturnal roost fields.

During 2011, all potential prey items found at woodcock nocturnal roost fields were also found at diurnal coverts (Table 1). Average population densities of millipedes and earthworms were about 49 times greater ($V = 78.00$, $P < 0.01$) and 3 times greater ($t_{16} = 2.14$, $P = 0.02$), respectively, at diurnal coverts, whereas the average population density of ants was about 10 times greater ($V = 5.00$, $P = 0.04$) at nocturnal roost fields. Average population densities of all other soil macrofauna were similar between sites ($P \geq 0.09$; Table 1). During 2012, cockroaches (Blattodea), centipedes, and butterfly/moth larvae were unique to nocturnal roost fields, but average population densities of these were extremely low (Table 2). The average population density of beetles was nearly 3 times greater ($V = 26.00$, $P = 0.01$) at nocturnal roost fields, whereas average population densities of earthworms and pillbugs (Isopoda) were approximately 4 times greater ($t_{20} = 2.52$, $P = 0.01$)

Table 1
Average density (no./m²) of potential prey found in the soils at the diurnal coverts and nocturnal roost fields of 17 radio-marked American woodcock males during August 2011 in Rhode Island, USA

| Taxon | Common name | Average density (no./m²) | | Test statistic | | |
		Diurnal coverts	Nocturnal roosts	V	t_{16}	P
Araneae	Spiders	0.39	0.00	6.00	—	0.15
Coleoptera	Beetles	11.63	17.12	—	0.96	0.35
Diplopoda	Millipedes	6.40	0.13	78.00	—	<0.01
Diptera	True flies	5.23	0.52	27.00	—	0.22
Haplotaxida	Earthworms	30.59	9.93	—	2.14	0.02
Hymenoptera	Ants	1.31	13.59	5.00	—	0.04
Isopoda	Pillbugs	0.78	0.00	10.00	—	0.09
Lepidoptera	Butterflies/ Moths	0.13	0.52	3.00	—	0.23
Stylommatophora	Slugs	0.52	0.00	3.00	—	0.37

Wilcoxon signed-rank test (V) or paired *t*-test (t_{16}).

Table 2
Average density (no./m²) of potential prey found in the soils at the diurnal coverts and nocturnal roost fields of 21 radio-marked American woodcock (20 males and 1 female) during July–August 2012 in Rhode Island, USA

| Taxon | Common name | Average density (no./m²) | | Test statistic | | |
		Diurnal coverts	Nocturnal roosts	V	t_{20}	P
Araneae	Spiders	0.53	0.95	18.00	—	0.33
Blattodea	Cockroaches	0.00	0.11	0.00	—	1.00
Caudata	Salamanders	0.11	0.11	1.50	—	1.00
Chilopoda	Centipedes	0.00	0.21	0.00	—	0.35
Coleoptera	Beetles	5.18	14.71	26.00	—	0.01
Dermaptera	Earwigs	0.11	0.00	1.00	—	1.00
Diplopoda	Millipedes	3.60	1.38	70.50	—	0.09
Diptera	True flies	0.42	0.74	13.50	—	0.28
Haplotaxida	Earthworms	15.66	4.23	—	2.52	0.01
Hemiptera	True bugs	0.42	0.11	12.00	—	0.23
Hymenoptera	Ants	23.70	80.84	57.00	—	0.22
Isopoda	Pillbugs	2.65	0.32	60.00	—	0.02
Lepidoptera	Butterflies/ Moths	0.00	0.11	0.00	—	1.00

Wilcoxon signed-rank test (V) or paired *t*-test (t_{20}).

and 8 times greater ($V = 60.00$, $P = 0.02$), respectively, at diurnal coverts. Average population densities of all other soil macrofauna were similar between sites ($P \geq 0.09$; Table 2). During both years, earthworm fresh weight ($P < 0.03$) and dry weight ($P < 0.03$) were greatest at diurnal coverts (Figure 1a), and the cumulative density of known woodcock foods was similar between sites ($P \geq 0.39$; Figure 1b). During 2011, we found greater richness ($t_{16} = 2.85$, $P = 0.01$) and diversity ($t_{16} = 2.30$, $P = 0.04$) of soil macrofauna at diurnal coverts, but these measures were similar between sites during 2012 ($P \geq 0.46$; Figure 1c).

Generally, radio-marked woodcock spent the day in forested wetlands, floodplain forests, or moist upland forests and flew to small forest clear-cuts, maintained or abandoned herbaceous meadows, or other idle agricultural fields to spend the night. At diurnal coverts, soil moisture content during 2011 ($41.6 \pm 25.1\%$) and 2012 ($43.3 \pm 28.5\%$) was 1.7 times greater ($t_{16} = 2.97$, $P < 0.01$) and 1.5 times greater ($t_{20} = 2.67$, $P = 0.01$), respectively, than at nocturnal roost fields. Soil pH was similar between sites during both years ($P \geq 0.22$), and we found no evidence that soil organic matter content differed between sites ($P = 0.09$).

During 2011, nocturnal mammalian predators visited baited track stations at diurnal coverts more frequently than nocturnal roost fields for about 73% (8 of 11) of the woodcock that we monitored ($F_{1,10} = 8.11$, $P = 0.02$; Figure 2). We observed raccoon, mink (*Neovison vison*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), domestic cat (*Felis catus*), striped skunk (*Mephitis mephitis*), domestic dog (*Canis familiaris*), and unidentified canid and mustelid tracks at sites used by woodcock. During 2012, the number of days until initial predator visit was approximately 1.8 times greater at nocturnal roost fields than diurnal coverts ($t_{11} = 2.02$, $P = 0.03$; Figure 3). We photographed raccoon, fisher (*Martes pennanti*), coyote, red fox, Virginia opossum (*Didelphis virginiana*), striped skunk, domestic cat, and long-tailed weasel (*Mustela frenata*) at sites used by woodcock. We also photographed 1 broad-winged hawk (*Buteo platypterus*) at a diurnal covert and 1 red-tailed hawk (*Buteo jamaicensis*) at a nocturnal roost field.
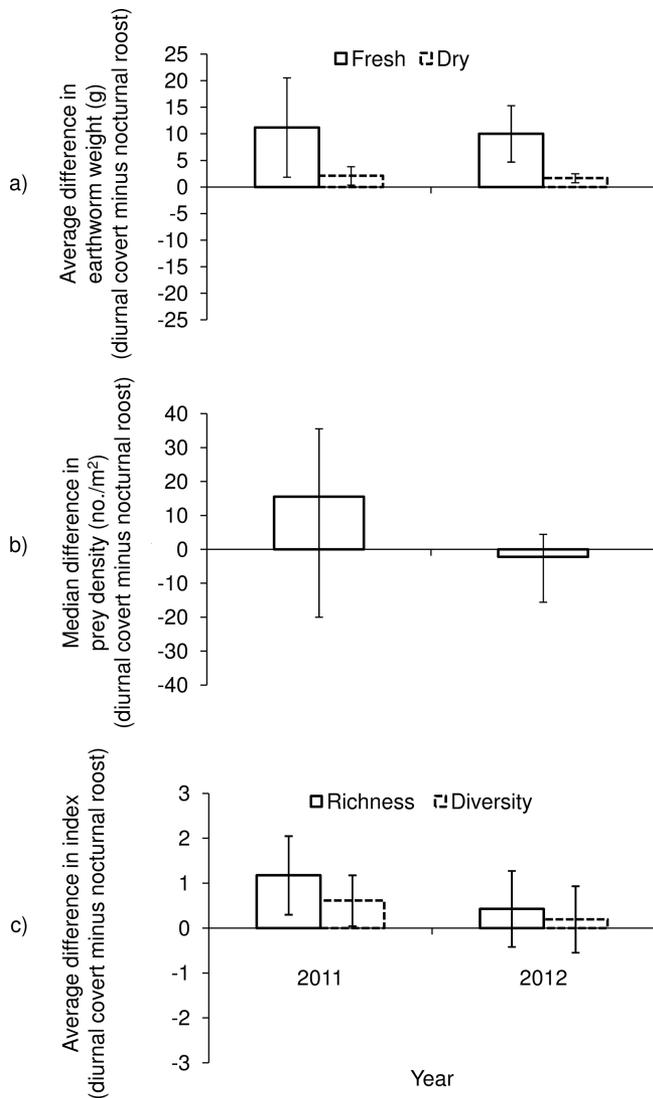
Figure 1

Average differences in earthworm fresh and dry weight (a), median difference in the cumulative density of known prey (b), and average differences in richness and diversity of soil macrofauna (c) at the diurnal coverts and nocturnal roost fields of radio-marked American woodcock (2011: 17 males; 2012: 20 males and 1 female) during July–August in Rhode Island, USA. Positive bars indicate greater values at diurnal coverts. Negative bars indicate greater values at nocturnal roost fields. Whiskers represent 95% confidence intervals.

DISCUSSION

Our results show that the benefit afforded to woodcock that fly between diurnal coverts and nocturnal roost fields during summer is one of reduced predation risk and not novel feeding opportunities. Several lines of evidence support this conclusion. First, nearly all soil macrofauna that we found at nocturnal roost fields were also found at diurnal coverts, and the population densities of potential prey were not consistently greater at nocturnal roost fields. Second, preferred woodcock foods (i.e., earthworms) were always more abundant at diurnal coverts, the cumulative density of known woodcock foods was similar between sites, and the richness and diversity of soil macrofauna was similar or greater at diurnal coverts depending on the year. Third, 2 separate indices of
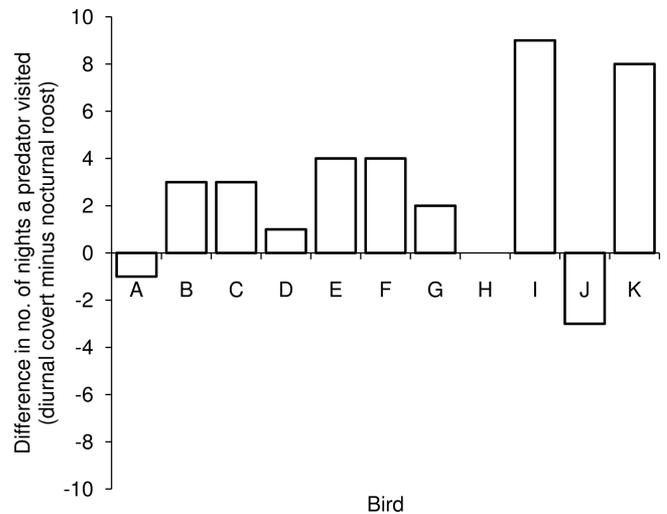

Figure 2

Difference in the number of nights that any mammalian predator visited a baited track station at the diurnal covert and nocturnal roost field for each of 11 radio-marked American woodcock males during September 2011 in Rhode Island, USA. Positive bars indicate more nights with a predator visit at diurnal coverts. Negative bars indicate more nights with a predator visit at nocturnal roost fields.
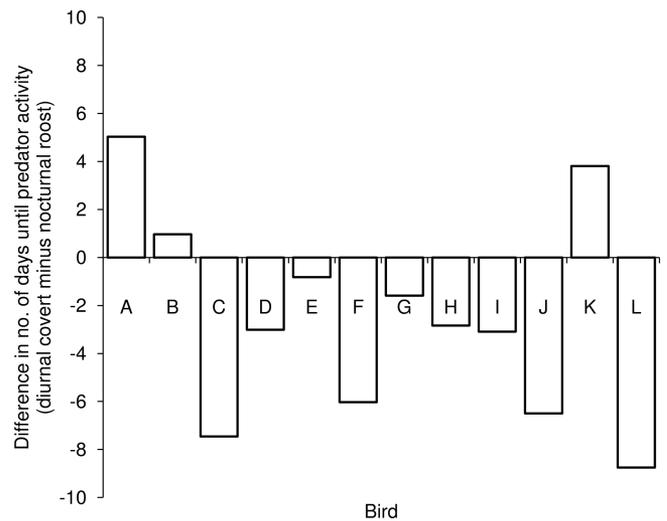

Figure 3

Difference in the number of days until initial predator visit at the diurnal covert and nocturnal roost field for each of 12 radio-marked American woodcock males during August 2012 in Rhode Island, USA. Positive bars indicate more days until initial predator visit at diurnal coverts. Negative bars indicate more days until initial predator visit at nocturnal roost fields.

predator activity suggest that nocturnal mammalian predators are more active at diurnal coverts. Taken together, this evidence provides the first empirical support for the predation-risk hypothesis and against the foraging-benefit hypothesis to explain the function of woodcock commuting between forests and fields during summer.

Why woodcock commute during summer

Previous studies have indicated that woodcock do not move to forest openings at night to feed during summer (Krohn 1970; Dunford and Owen 1973; Owen and Morgan 1975; Wishart and

Bider 1977). At a field in Maine, USA, only 1 earthworm and few other potential woodcock foods including ants, beetle larvae, and spiders (Araneae) were found in soil collected at night at 10 woodcock flush points and 20 random points (Krohn 1970). Further, the stomach contents of most birds collected from 10 fields at various times during the night contained few if any earthworms or other soil macrofauna (Krohn 1970). In contrast, earthworms were prevalent in the stomachs of birds collected immediately before or after landing in forest openings at night in Maine (Krohn 1970) and Massachusetts, USA (Sheldon 1961). This suggests that feeding occurs predominantly at diurnal coverts prior to flying to nocturnal roost fields.

However, an important difference between our study and previous ones is that our paired design allowed us to directly compare food availability at both diurnal and nocturnal sites for individuals that commuted. Because earthworms are the dominant prey of woodcock (Sheldon 1967), our findings of greater earthworm availability at diurnal coverts further support the conclusion that most feeding likely occurs at these sites. Although some woodcock have been observed feeding soon after moving to forest openings at night during summer (Sheldon 1961), this may simply represent infrequent opportunistic foraging (Sheldon 1967). Generally, woodcock were sedentary after moving to fields at night during summer in Quebec, Canada (Wishart and Bider 1977) and Maine (Dunford and Owen 1973; Owen and Morgan 1975). This contrasts with behaviors observed in forest openings at night during fall and winter in New Jersey (Krohn et al. 1977), North Carolina (Stribling and Doerr 1985), and Louisiana, USA (Glasgow 1958), where woodcock actively fed at night. The reasons for this seasonal difference in behavior are not well understood, but higher food availability at nocturnal roost fields during fall (Krohn et al. 1977) and winter (Blackman et al. 2012) may be a driving factor.

We simultaneously documented less nocturnal mammalian predator activity at nocturnal roost fields than at diurnal coverts. In addition to visiting baited track stations less frequently at night, mammalian predators took longer to find bait stations at nocturnal roost fields than diurnal coverts. In the northeastern USA, weasels and raccoons were major ground predators of woodcock (Derleth and Sepik 1990; McAuley et al. 2005). Many mammalian predators concentrate their activity along habitat edges or within wooded areas adjacent to edges and not within forest openings such as fields (Bider 1968; Gehring and Swihart 2003; Šálek et al. 2010). Thus, woodcock flying to forest openings at night during summer should be safer because these areas are less likely to be searched by potential predators. Eurasian woodcock (*Scolopax rusticola*) may experience increased predation risk in fields at night during winter (Duriez et al. 2005), whereas such predation risk in fields at night during winter is inadequately documented for American woodcock.

We acknowledge that raptors are important woodcock predators, especially during the spring courtship period when conspicuous male displays are likely to attract attention (Sheldon 1967; Longcore et al. 1996). However, it is logistically difficult to quantify the risk of depredation by raptors to woodcock during summer nights when the latter is sedentary. We attempted to accomplish this by monitoring raptor visits to caged rock pigeons (*Columba livia*) placed at diurnal coverts and nocturnal roost fields (IACUC protocol AN12-03-019) because rock pigeons are typically excellent lures for attracting raptors (Berger and Hamerstrom 1962). Surprisingly, we never documented a raptor visit at either site from 17 July to 5 August 2012 despite constant surveillance using camera traps.

Consequently, we have no reason to expect woodcock are at greater risk of raptor depredation at nocturnal roost fields where they are sedentary throughout the night. Nevertheless, additional research using alternative methods, such as call count surveys (Rogers and Dauber 1977; Fuller and Mosher 1981), to quantify raptor activity around woodcock diurnal coverts and nocturnal roost fields may be warranted.

Fully understanding the function of woodcock commuting behavior during summer is complicated by differential habitat use patterns between age–sex classes. On average, juvenile males fly to forest openings at night more often than all other age–sex classes from June to October, and males tend to fly to forest openings at night more often than females (Sepik and Derleth 1993). In contrast, female woodcock may remain at diurnal coverts or fly to different forested sites at night (Sepik and Derleth 1993). However, females frequently move to forest openings at night during July (Sepik and Derleth 1993). We were not able to determine the regularity with which female woodcock fly to forest openings at night in Rhode Island because of the difficulty associated with catching females (McAuley et al. 1993). Nonetheless, moving to forest openings at night during summer must provide some benefit to both males and females, especially during periods when this behavior is prevalent.

Testing hypotheses about the trade-offs between foraging and predation risk in ecological systems: insights provided by commuting behavior

Organisms that move between sites within each day (i.e., those that commute) provide behavioral ecologists unique opportunities to investigate the trade-offs between foraging and predation risk for individuals within a relevant ecological context. We have shown that the decision by woodcock to move from diurnal coverts to nocturnal roost fields during summer may be advantageous because woodcock can acquire resources by day and better avoid predators at night. Temporal or spatial variation in foraging benefits and predation risk should be required if prey are to use commuting behavior to best balance the trade-offs between feeding and avoiding predators (Duriez et al. 2005; Bednekoff and Lima 2011). In our case, woodcock remaining at diurnal coverts throughout the night could conserve energy compared with other birds that commute although the energy savings may be modest (e.g., corvids; Sonerud et al. 2001; Wright et al. 2003). Perhaps more importantly, woodcock remaining at diurnal coverts throughout the night could exploit preferred foods (Wishart and Bider 1977; Sepik and Derleth 1993; this study). However, our data show that predation risk during the night is elevated at diurnal coverts compared with nocturnal roost fields. During periods of high risk, prey species are expected to allocate more time to antipredator behaviors and less time to feeding, whereas feeding effort should be increased during periods of lower risk (Lima and Bednekoff 1999). Rather than remaining at diurnal coverts throughout the day and night, woodcock appear to balance the trade-off between feeding and avoiding predators by feeding at diurnal coverts during the day, a time when nocturnal mammalian predators are usually less active, and then moving to nocturnal roost fields at night.

Consistent movement by woodcock to forest openings at night during summer is influenced by the end of the breeding season, the independence of broods, and the postnuptial molt period (Sheldon 1967; Krohn 1971; Owen and Krohn 1973). Thus, during some nights, female woodcock may favor remaining at diurnal coverts,

where preferred food availability is greatest, in order to rebuild energy reserves after reproducing (Sepik and Derleth 1993). Male woodcock do not produce eggs or rear young so their decision to move to forest openings at night during summer may be less influenced by such energetically expensive events (Sepik and Derleth 1993). On the other hand, male woodcock might remain at diurnal coverts to feed during some nights to help replenish energy reserves used during spring courtship flights. Importantly, male and female woodcock may elect to remain at diurnal coverts where they can feed efficiently at night in order to meet energy demands associated with postnuptial molt (Owen and Krohn 1973) or build fat stores prior to fall migration (Sepik and Derleth 1993). Indeed, state-dependent decision making is an anticipated part of risk allocation (Beauchamp and Ruxton 2011; Bednekoff and Lima 2011) and should be expected to cause varying patterns of antipredator behavior as prey attempt to optimize their respective trade-offs between feeding and avoiding predators. For woodcock, if feeding requirements can be met during the day, and if building energy reserves is not of concern, then individuals should favor flying to nocturnal roost fields at night during summer where they are safer from predators even though foraging opportunities are more limited.

Animals living in complex environments where food availability and predation risk are variable should maximize fitness by adopting behaviors that balance trade-offs between finding food and becoming food (Lima and Bednekoff 1999; Higginson et al. 2012). Because prey allocate risk under schedules imposed by predators (Bednekoff and Lima 2011), understanding the timescale at which risk allocation occurs is an important step toward identifying behaviors employed to actively manage risk. In this study, we illustrate that woodcock experience periods of variable risk on a daily basis during summer months. Some species manage risk by increasing vigilance (Périquet et al. 2012), whereas others manage risk by moving between microhabitats where predators have limited access (Roberts and Liebgold 2008). Here, we show that some species can effectively reduce their risk of predation by moving between dissimilar habitats during the day and night. Consequently, maintaining forest openings is an important part of woodcock habitat management throughout the species summer range so that individuals have the option to fly between diurnal coverts and nocturnal roost fields where they can eat by day and stay safe by night.

REFERENCES

Agresti A. 2007. An introduction to categorical data analysis. 2nd ed. Hoboken (NJ): John Wiley and Sons.

Beauchamp G, Ruxton GD. 2011. A reassessment of the predation risk allocation hypothesis: a comment on Lima and Bednekoff. Am Nat. 177:143–146; discussion 147.

Bednekoff PA, Lima SL. 2011. Risk allocation is a general phenomenon: a reply to Beauchamp and Ruxton. Am Nat. 177:147–151.

Berger DD, Hamerstrom F. 1962. Protecting a trapping station from raptor predation. J Wildlife Manage. 26:203–206.

Bider JR. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecol Monogr. 38:269–308.

Blackman EB, Deperno CS, Heiniger RW, Krachey MJ, Moorman CE, Peterson MN. 2012. Effects of crop field characteristics on nocturnal winter use by American woodcock. J Wildlife Manage. 76:528–533.

Connors JI, Doerr PD. 1982. Woodcock use of agricultural fields in coastal North Carolina. Seventh woodcock symposium; 1980 Oct 28–30; University Park, PA. Washington (DC): US Fish and Wildlife Service. 139–147 p.

Dangerfield JM. 1997. Abundance and diversity of soil macrofauna in northern Botswana. J Trop Ecol. 13:527–538.

Derleth EL, Sepik GF. 1990. Summer-fall survival of American woodcock in Maine. J Wildlife Manage. 54:97–106.

Dessecker DR, McAuley DG. 2001. Importance of early successional habitat to ruffed grouse and American woodcock. Wildlife Soc B. 29:456–465.

Dias MP, Granadeiro JP, Lecoq M, Santos CD, Palmeirim JM. 2006. Distance to high-tide roosts constrains the use of foraging areas by dunlins: implications for the management of estuarine wetlands. Biol Conserv. 131:446–452.

Dunford RD, Owen RB Jr. 1973. Summer behavior of immature radio-equipped woodcock in central Maine. J Wildlife Manage. 37:462–469.

Duriez O, Fritz H, Binet F, Tremblay Y, Ferrand Y. 2005. Individual activity rates in wintering Eurasian woodcocks: starvation versus predation risk trade-off? Anim Behav. 69:39–49.

Dwyer TJ, Sepik GF, Derleth EL, McAuley DG. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. Washington (DC): US Fish and Wildlife Service.

Ferrari MCO, Elvidge CK, Jackson CD, Chivers DP, Brown GE. 2010. The responses of prey fish to temporal variation in predation risk: sensory habituation or risk assessment? Behav Ecol. 21:532–536.

Fuller MR, Mosher JA. 1981. Methods of detecting and counting raptors: a review. Stud Avian Biol-Ser. 6:235–246.

Gardner W, Mulvey EP, Shaw EC. 1995. Regression analyses of counts and rates: Poisson, overdispersed Poisson, and negative binomial models. Psychol Bull. 118:392–404.

Gehring TM, Swihart RK. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biol Conserv. 109:283–295.

Glasgow LL. 1958. Contributions to the knowledge of the ecology of the American woodcock, *Philohela minor*, on the wintering range in Louisiana [dissertation]. [College Station (TX)]: Texas A & M University.

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Soc B. 34:1142–1151.

Hendershot WH, Lalande H, Duquette M. 1993. Soil reaction and exchangeable acidity. In: Carter MR, editor. Soil sampling and methods for analysis. Ottawa (Canada): Canadian Society of Soil Science. p. 141–145.

Higginson AD, Fawcett TW, Trimmer PC, McNamara JM, Houston AI. 2012. Generalized optimal risk allocation: foraging and antipredator behavior in a fluctuating environment. Am Nat. 180:589–603.

Huang P, Sieving KE, St Mary CM. 2012. Heterospecific information about predation risk influences exploratory behavior. Behav Ecol. 23:463–472.

Jost L. 2006. Entropy and diversity. Oikos. 113:363–375.

Keppie DM, Whiting RM Jr. 1994. American woodcock (*Scolopax minor*). In: Poole A, editor. The birds of North America. Ithaca (NY): Cornell Lab of Ornithology. p. 100.

Krementz DG. 2000. Habitat management for wintering American woodcock in the southeastern United States. Proceedings of the ninth American woodcock symposium; 1997 Jan 26–28; Baton Rouge, LA. Laurel (MD): US Geological Survey. 50–54 p.

Krohn WB. 1970. Woodcock feeding habits as related to summer field usage in central Maine. J Wildlife Manage. 34:769–775.

Krohn WB. 1971. Some patterns of woodcock activities on Maine summer fields. Wilson Bull. 83:396–407.

Krohn WB, Rieffenberger JC, Ferrigno F. 1977. Fall migration of woodcock at Cape May, New Jersey. J Wildlife Manage. 41:104–111.

Lima SL. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia. 66:60–67.

Lima SL, Bednekoff PA. 1999. Temporal variation in danger drives anti-predator behavior: the predation risk allocation hypothesis. Am Nat. 153:649–659.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68:619–640.

Lima SL, Valone TJ, Caraco T. 1985. Foraging-efficiency–predation-risk trade-off in the grey squirrel. Anim Behav. 33:155–165.

Linhart SB, Knowlton FF. 1975. Determining the relative abundance of coyotes by scent station lines. Wildlife Soc B. 3:119–124.

Longcore JR, McAuley DG, Sepik GF, Pendleton GW. 1996. Survival of breeding male American woodcock in Maine. Can J Zool. 74:2046–2054.

Longcore JR, McAuley DG, Sepik GF, Pendleton GW. 2000. Survival of female American woodcock breeding in Maine. Proceedings of the ninth American woodcock symposium; 1997 Jan 26–28; Baton Rouge, LA. Laurel (MD): US Geological Survey. 65–76 p.

Magurran AE. 2004. Measuring biological diversity. Malden (MA): Blackwell Publishing.

McAuley DG, Longcore JR, Clugston DA, Allen RB, Weik A, Williamson S, Dunn J, Palmer B, Evans K, Staats W, et al. 2005. Effects of hunting on survival of American woodcock in the Northeast. J Wildlife Manage. 69:1565–1577.

McAuley DG, Longcore JR, Sepik GF. 1993. Techniques for research into woodcocks: experiences and recommendations. Proceedings of the eighth American woodcock symposium; 1990 Oct 29–Nov 2; West Lafayette, IN. Washington (DC): US Fish and Wildlife Service. 5–11 p.

McAuley DG, Longcore JR, Sepik GF, Pendleton GW. 1996. Habitat characteristics of American woodcock nest sites on a managed area in Maine. J Wildlife Manage. 60:138–148.

Mendall HL, Aldous CM. 1943. The ecology and management of the American woodcock. Orono (ME): University of Maine.

Milinski M, Heller R. 1978. Influence of a predator on the optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus* L.). Nature. 275:642–644.

Ott RL, Longnecker M. 2010. An introduction to statistical methods and data analysis. 6th ed. Belmont (CA): Brooks/Cole.

Owen RB Jr, Krohn WB. 1973. Molt patterns and weight changes of the American woodcock. Wilson Bull. 85:31–41.

Owen RB Jr, Morgan JW. 1975. Summer behavior of adult radio-equipped woodcock in central Maine. J Wildlife Manage. 39:179–182.

Pedan A. 2011. Analysis of count data using the SAS system. Statistics, data analysis, and data mining [cited 2011 May 7]. Available from: http://www2.sas.com/proceedings/sugi26/p247-26.pdf.

Périquet S, Todd-Jones L, Valeix M, Stapelkamp B, Elliot N, Wijers M, Pays O, Fortin D, Madzikanda H, Fritz H, et al. 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. Behav Ecol. 23:970–976.

R Development Core Team. 2009. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing [cited 2011 May 7]. Available from: http://www.R-project.org.

Roberts AM, Liebgold EB. 2008. The effects of perceived mortality risk on habitat selection in a terrestrial salamander. Behav Ecol. 19:621–626.

Rogers DI, Piersma T, Hassell CJ. 2006. Roost availability may constrain shorebird distribution: exploring the energetic costs of roosting and disturbance around a tropical bay. Biol Conserv. 133:225–235.

Rogers DT Jr, Dauber MA. 1977. Status of the red-shouldered hawk in Alabama. ALA Birdlife. 25:19.

Rothley KD, Schmitz OJ, Cohon JL. 1997. Foraging to balance conflicting demands: novel insights from grasshoppers under predation risk. Behav Ecol. 8:551–559.

Šálek M, Kreisinger J, Sedláček F, Albrecht T. 2010. Do prey densities determine preferences of mammalian predators for habitat edges in an agricultural landscape? Landscape Urban Plan. 98:86–91.

SAS Institute Inc. 2008. SAS/STAT Version 9.2. Cary (NC): SAS Institute Inc.

Searle KR, Stokes CJ, Gordon IJ. 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. Behav Ecol. 19:475–482.

Sepik GF, Derleth EL. 1993. Habitat use, home range size, and patterns of moves of the American woodcock in Maine. Proceedings of the eighth American woodcock symposium; 1990 Oct 29–Nov 2; West Lafayette, IN. Washington (DC): US Fish and Wildlife Service. 41–49 p.

Sheldon WG. 1961. Summer crepuscular flights of American woodcock in central Massachusetts. Wilson Bull. 73:126–139.

Sheldon WG. 1967. The book of the American woodcock. Amherst (MA): University of Massachusetts.

Sih A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science. 210:1041–1043.

Sonerud GA, Smedshaug CA, Bråthen O. 2001. Ignorant hooded crows follow knowledgeable roost-mates to food: support for the information centre hypothesis. Proc Biol Sci. 268:827–831.

Straw JA Jr, Wakeley JS, Hudgins JE. 1986. A model for management of diurnal habitat for American woodcock in Pennsylvania. J Wildlife Manage. 50:378–383.

Stribling HL, Doerr PD. 1985. Nocturnal use of fields by American woodcock. J Wildlife Manage. 49:485–491.

Tilgar V, Moks K, Saag P. 2011. Predator-induced stress changes parental feeding behavior in pied flycatchers. Behav Ecol. 22:23–28.

Van Buskirk J, Müller C, Portmann A, Surbeck M. 2002. A test of the risk allocation hypothesis: tadpole responses to temporal change in predation risk. Behav Ecol. 13:526–530.

van Gils JA, Spaans B, Dekinga A, Piersma T. 2006. Foraging in a tidally structured environment by Red Knots (*Calidris canutus*): ideal, but not free. Ecology. 87:1189–1202.

Williamson SJ. 2010. American woodcock: habitat best management practices for the Northeast. Washington (DC): US Department of Agriculture.

Wishart RA, Bider JR. 1976. Habitat preferences of woodcock in southwestern Quebec. J Wildlife Manage. 40:523–531.

Wishart RA, Bider JR. 1977. Aspects of woodcock nocturnal activity in southwestern Quebec. Can Field Nat. 91:141–147.

Wright J, Stone RE, Brown N. 2003. Communal roosts as structured information centres in the raven, *Corvus corax*. J Amin Ecol. 72:1003–1014.