Renesting by American Woodcocks (*Scolopax minor*) in Maine

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The American Woodcock (*Scolopax minor*) is one of the earliest ground-nesting birds in the northeastern United States. In Maine, nesting begins in early April when temperatures can drop below freezing and significant snowfall can accumulate. Nests are usually in open woods, where eggs are laid on the ground in a shallow depression (Pettingill 1936, Mendall and Aldous 1943, Sheldon 1967). Peak hatching occurs in early May (Dwyer et al. 1982), when temperatures are cool and precipitation is common. Woodcock chicks are dependent on the female for most of their food for at least seven days after hatching (Gregg 1984). During cool, wet weather, chicks require constant brooding by females; prolonged periods of inclement weather may lead to substantial mortality of chicks (Dwyer et al. 1988).

This reproductive strategy led Pettingill (1936), Mendall and Aldous (1943), and Sheldon (1967) to speculate that renesting by American Woodcock is common, although they could not document this behavior. Renesting would seem necessary to maintain adequate recruitment because American Woodcock clutches are small (3–4 eggs), nest success is 50–67% (Mendall and Aldous 1943, Gregg 1984), and chick survival is 59% (Dwyer et al. 1988). Renesting after loss of a clutch has been documented for other shorebirds, including the Eurasian Woodcock (*Scolopax rusticola;* Hirons and Owen 1982), plovers (*Charadrius* spp.; Warriner et al. 1986), Spotted Sandpipers (*Actitis macularia;* Lank et al. 1985, Oring and Lank 1986), Killdeer (*Charadrius vociferus;* Brunton 1988), and Red-necked Phalaropes (*Phalaropus lobatus;* Reynolds 1987). Some shorebird species are polyandrous (Schamel and Tracy 1977, Lank et al. 1985, Oring 1985, Reynolds 1987), and a few species are double-brooded (Brunton 1988). Only circumstantial evidence of late-nesting birds (Ammann 1967, Parris 1983) and prolonged brood seasons (Rabe 1979) suggest that woodcocks will renest. We present the first definitive records of renesting by American Woodcocks during a single nesting season.

We conducted this study on the 6,850-ha Baring unit of Moosehorn National Wildlife Refuge (NWR) near Calais, Maine, on the New Brunswick border. Dwyer et al. (1988) described the study area in detail. Female woodcocks were captured in mist nets on courting areas. Females on nests and those with broods were located by a pointing dog and captured with hand nets (Ammann 1977). All nesting females and females with broods ≤5 days old were radio-marked. Females were aged by wing-plumage characteristics (Martin 1964) and classified as 1 year old (SY) or ≥2 years old (ASY). We weighed each bird at the time of capture and attached a 3.5–4 g transmitter to its back by livestock-tag cement and a single-loop wire harness (Derleth 1986). We located birds daily from vehicles or on foot with portable receivers and hand-held antennas. Lost birds were located from light, fixed-wing aircraft with antennas attached to the struts (Gilmer et al. 1981). We flew transects 3.2 km apart across the study area and ≤16 km beyond its borders. Transmitter signals were detectable ≤0.8 km from the ground and ≤3.2 km from the aircraft.

The incubation stage for a clutch was determined by the methods of Ammann (1974) and Westerskov (1950). We examined nests while females were absent during crepuscular recesses. We determined chick age by bill length (Ammann 1974, 1982). Dates of egg laying were determined by back-dating clutches, assuming an egg-laying rate of 1 egg/day and that the 21-day incubation period started when the last egg was laid (Mendall and Aldous 1943). *Renesting interval* is defined as the number of days from loss of nest or brood to the time the first egg of the second clutch is laid. When the original nest site was known, we measured the distance between original nests and renests. For females caught with broods, we measured the distance between original capture locations and renests because most broods ≤5 days old do not move far from nest sites (U.S.F.W.S. unpubl.).

During 1987–1988 we captured and attached transmitters to 58 female woodcocks (22 SY and 9 ASY in 1987, and 11 SY and 16 ASY in 1988). Four females (2 SY and 2 ASY) in 1987 and 8 females (7 ASY and 1 SY) in 1988 laid two clutches of eggs (Table 1). Five females renested after either they abandoned nests or predators destroyed nests. Seven females renested after losing all the chicks in their brood. One SY female that lost a brood was found dead 3 weeks later <2 m from a nest that contained 1 egg, which suggests she had renested. For all females relocated after losing nests or broods, only one (which had lost a brood) did not renest.

Although renesting was never documented, delayed hatching peaks that followed spring snowstorms provided circumstantial evidence that woodcocks renest (Mendall and Aldous 1943). As reported in Ammann (1967), T. Prawdzik (Michigan Dep. Nat. Resour.) noted unusually late nesting by woodcocks in 1966 after a snowstorm that occurred in the early part of the hatching season, suggesting that females had lost broods and renested. Rabe (1979) collected a female woodcock in Michigan, accompanying a brood >20 days of age. Her reproductive tract contained

TABLE 1. Status of female American Woodcocks that lost original nests or broods during the breeding season at Moosehorn National Wildlife Refuge, Maine, 1987–1988. SY is 1 year old; ASY is ≥2-year-old bird.

Year	No. of females	Died	Radio failed	Not relocated	No. renesting/ no. relocated
			Lost nests[a]		
1987	8	1 (SY)	1 (SY)	5 (4ASY)	1/1 (ASY)
1988	7	1 (ASY)	1 (SY)	1 (SY)	4/4 (3ASY)
			Lost broods[a]		
1987	5	0	0	2 (SY)	3/3 (1ASY)
1988	10	1 (SY)	1 (SY)	2 (ASY)	5/6 (4ASY)[b]

[a] All hatching dates were before 1 June.
[b] Includes one bird found dead and suspected of renesting but not confirmed.

enlarged follicles, which suggests she may have been recycling to lay a second clutch. Ammann (1970) attempted to document renesting by taking chicks from woodcock females marked with wing tags. He then searched intensively for the marked hens for several weeks, but none were relocated. If renesting distances in our study are typical, it is understandable why investigators without radiotelemetry have been unable to document renesting.

Females that abandoned nests or had nests destroyed traveled farther to renest ($\bar{x} \pm SD = 6.7 \pm 6.5$ km, $n = 5$, range = 0.9–15.5 km) ($t = -2.08$, df = 4, $P = 0.10$) than females that lost broods (0.6 ± 0.4 km, $n = 7$, range = 0.2–1.1 km) (Table 2). In 1988 the four females that renested after nests were destroyed moved an average of 8.1 km. Average distance moved may have been greater than this because during both years there were 13 other females (6 ASY and 7 SY) that lost nests ($n = 8$) or broods ($n = 5$) that we could not relocate (Table 1). Also, transmitter range in 1987 was poor and relocation of lost birds was difficult. Because of other constraints, we limited our search to the area within 16 km of the study area. Regardless of distances that relocated females ($n = 14$) moved from the original site, most ($n = 13$) renested. We believe that the lost birds renested >20 km from their original nests, which would increase the mean distance traveled to renest.

Homing and fidelity to nesting areas by female woodcocks have been mentioned by several authors. Mendall and Aldous (1943) and Gregg (1984) observed unmarked females on active nests near destroyed nests and presumed these to be the same females renesting within "the original territory" (Mendall and Aldous 1943: 104). Dwyer et al. (1982) captured six banded females with broods in two of four years in the same areas. Of five other returning hens that had been banded as chicks on their study area, two were caught with broods within 5 m of where they were captured the previous year. We support the findings of Dwyer et al. (1982) but not Mendall and Aldous (1943) and Gregg (1984).

Woodcocks that lost broods renested nearer to their original nesting areas than those that lost nests. Nesting-area fidelity was influenced more by successfully hatching a nest than by successfully rearing a brood. Movement to new nesting sites after nest predation was documented for several passerine species (see Jackson et al. 1988). All woodcocks, however, renested in an entirely different block of woods and usually in a different habitat type (U.S.F.W.S. unpubl.). Females that renest far from their original nesting site may still maintain a long-term fidelity to the original nesting site. In 1987, one female that left the study area after she lost her brood was captured later that summer in a modified shorebird trap 2.5 km from the original nest site and again on a roosting field 7.5 km from the nest site. Site fidelity may be especially high for ASY birds that may have successfully raised a brood in previous years.

Clutch size of renests averaged 3.0 eggs ($n = 10$) (Table 2). Females that lost nests laid an average of 3.2 eggs whereas those that lost broods averaged 2.8. The difference was not significant ($t = -0.942$, df = 8, $P = 0.37$). The mean number of eggs laid in the second clutch ($\bar{x} \pm SD = 3.0 \pm 0.67$) was significantly less (paired t-test, $t = 3.21$, $P = 0.01$) than mean brood or clutch size ($\bar{x} = 3.80 \pm 0.42$) of the first attempt. Of 12 renests, 6 were successful (hatched ≥1 egg). Hatch rate for successful nests was 95% (19 of 20 eggs). We were able to determine egg fertility for only one abandoned nest, which contained two infertile eggs.

Nest success (50%) and hatching success (95%) of original nests and renests were similar to that reported by Mendall and Aldous (1943) and Gregg (1984), and they were consistent with data for other ground nesters (Ricklefs 1969). Given a 50% nest success and a high probability of renesting, the proportion of nesting females that hatch clutches may approach 75% of the nesting population in any given season.

Mean renesting interval for all females was 8.7 ± 2.4 days (9.2 in 1987 and 8.5 in 1988). Initial nests had been incubated 5–20 days (Table 2) at the time they were abandoned or destroyed. Renesting intervals for females losing nests (Table 2; $\bar{x} = 7.8 \pm 2.3$ days, range = 5–11 days, $n = 5$) and losing broods (Table 2; $\bar{x} =$

TABLE 2. Renesting by female American Woodcocks after loss of original nest or loss of entire brood at Moosehorn National Wildlife Refuge, Maine, 1987–1988. SY is 1 year old; ASY is ≥2 years old.

Bird no.	Age	Mass at capture (g)	Date of loss	Days incubated or brood age	Renest interval (days)	Distance moved (km)	Renest clutch size
			Lost nests				
4.844	ASY	197[a]	20 Apr 1987	5	5	0.63	4
4.920	SY	213[b]	29 Apr 1988	18	9	7.05	3
4.700	ASY	224[a]	27 Apr 1988	7	7	1.22	3
4.810	ASY	192[b]	24 Apr 1988	15	11	2.59	2
4.888	ASY	237[a]	27 Apr 1988	20	7	9.66	4
			Lost broods				
5.146	SY	185[c]	6 May 1987	4	14	0.41	3
5.398	SY	185[c]	14 May 1987	10	9	0.23	3
5.289	ASY	176[c]	5 May 1987	9	9	0.71	2
4.750	ASY	195[b]	2 May 1988	6	6	0.55	3
4.840	ASY	189[c]	4 May 1988	7	9	0.15	3
4.940[d]	ASY	214[b]	17 May 1988	1	10	0.50	—
4.660[d]	ASY	174[b]	11 May 1988	11	9	0.16	—

[a] Obtained on date of nest loss (abandoned).
[b] Obtained >3 days before the date of loss.
[c] Obtained ≤3 days before date of loss.
[d] Renest clutch size unknown (nest destroyed before it could be examined).

9.4 ± 2.4 days, range = 6–14 days, $n = 7$) were not statistically different ($t = -1.91$, $P = 0.26$).

The renesting intervals (5–14 days) for woodcocks are similar to those reported for other shorebirds (7 days for Red-necked Phalaropes [Reynolds 1987] and Snowy Plovers [Warriner et al. 1986]; 4 days for Spotted Sandpipers [Lank et al. 1985]). Hirons and Owen (1982) reported that two European Woodcocks renested after losing a brood and started the second clutch in 12 days.

Age was not clearly related to renesting probability, as 9 of 9 ASY and 4 of 5 SY females that lost nests or broods, and that were relocated, renested. We found no relationship between number of days eggs were incubated ($r = 0.56$, $P = 0.33$) or age of chicks at time of loss ($r = -0.35$, $P = 0.44$) and length of renesting interval. Although one woodcock that lost a brood renested within 6 days, another that lost a nest after 15 days of incubation required 11 days to renest (Table 2). We are unable to make meaningful comparisons between female mass and renesting interval because we did not know the masses of most hens at the time nests and broods were lost.

Our data document conclusively that woodcocks renest and that renesting is the norm. Even females that lose broods ≤11 days have a high probability of renesting, although they generally nest in a different block of woods. Renestings seem to have a probability of hatching similar to the original nests, but clutches average ca. 1 egg fewer. Considering both initial and renesting efforts, nesting success of American Woodcocks might approach 75% in any given year.

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Egg Size and Parental Quality Influence Nestling Growth in the Shag

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Within any avian population, egg size can vary considerably. For most species, this is due primarily to differences in egg size among clutches laid by different females (e.g. Ojanen et al. 1979, Grant 1982, Bancroft 1984, Greig-Smith et al. 1988), but egg size within individual clutches may also vary (see Slagsvold et al. 1984, and references therein). Nestlings hatched from large eggs grow faster (Schifferli 1973, Williams 1980), achieve higher fledgling mass (Howe 1976; but see Greig-Smith et al. 1988), or have higher survival rates (e.g. Davis 1975, Howe 1976, Thomas 1983; but see O'Connor 1979, Moss et al. 1981, Bancroft 1984) than those hatched from small eggs. Within clutches, large eggs may also be less vulnerable to predation (Montevecchi 1976, Verbeek 1988). Because previous studies of nestling growth and survival have been descriptive, it cannot be concluded that there is a specific effect of egg size. For several species, the age (e.g. Coulson et al. 1969, Nisbet 1978, Thomas 1983; but see Davis 1975, Ojanen et al. 1979), and body mass (DeSteven 1978) or condition (Murphy 1986) of the female have a positive correlation with egg size. Similarly, reproductive success, expressed as the number of offspring fledged successfully, generally