

## TERRITORIALITY, DISPLAY, AND CERTAIN ECOLOGICAL RELATIONS OF THE AMERICAN WOODCOCK<sup>1</sup>

BY FRANK A. PITELKA

FOLLOWING the appearance of Pettingill's monograph (1936) on the American Woodcock (*Philohela minor*) attention was drawn to our limited evidence for territoriality in that species (Linsdale, 1936). Recently, however, Norris, Beule, and Studholme (1940) and Studholme and Norris (1942) have published limited observations which touch on the problem of territoriality. With the same problem in mind, in the early spring of 1939, I undertook to study a small concentration of Woodcocks on a semi-wooded plot north of Crystal Lake Park, Urbana, Champaign County, Illinois.

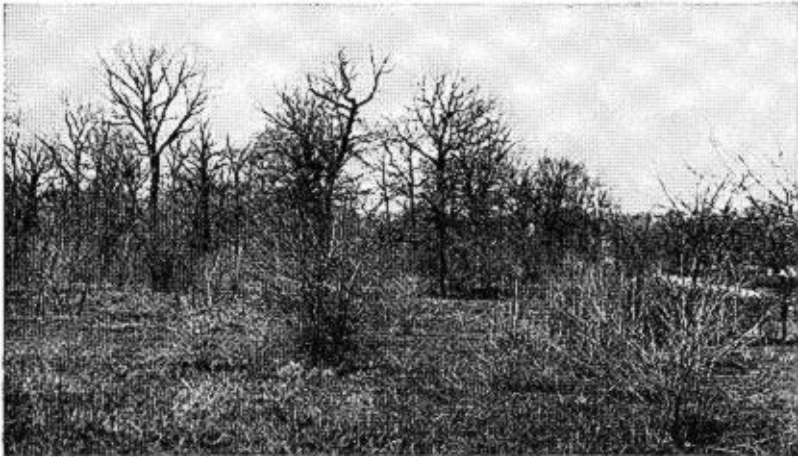


Figure 1. Habitat of the Woodcock. Photograph taken facing west near upper end of north-south road in territory C (Figures 3 and 5); east-west road is seen in right background. All of the open area seen in this photograph constituted part of male C's display territory; his feeding area was located in the woodland seen in left background.

The area of study, approximately 45 acres in extent, is illustrated in Figures 1 to 3. The open portions of this area were used by Woodcocks as "singing-fields" for their crepuscular displays. During the day, Woodcocks were confined largely to the wooded and more densely vegetated portions within the northern half of the area. The patch of relatively dense deciduous woodland (Figure 1) contained white oak (*Quercus alba*), red oak (*Q. rubra*), ash (*Fraxinus* sp.), shagbark

<sup>1</sup> Contribution from the Zoological Laboratory of the University of Illinois.

hickory (*Carya ovata*), and elm (*Ulmus americana*). Thickets to the southeast of the main wooded area contained large hawthorn shrubs (*Crataegus* sp.), honey locust (*Gleditsia triacanthos*), and young elms. Additional hawthorns, elms, and a few sycamores (*Platanus occidentalis*) were scattered over the open area partially encircled by the old stream bed or "ox-bow" (Figure 3), which was bordered largely by willows (*Salix* sp.). The ground cover of this open area consisted only of matted dead vegetation (largely grasses); the leaf-littered floor of the wooded area was overlain with the usual stratum of small shrubs. Within a haw thicket and woods of the northern half of the study area, there were small shallow pools, the edges of which were frequented by the Woodcocks. Several recent studies of the American Woodcock include data of interest on habitat preferences (Aldous, 1938; Merovka, 1939; Studholme and Norris, 1942).



Figure 2. Westward view across display territories of males B and A, showing "open" portions of study area, as indicated in Figure 3.

Observations extended from early March to mid-April and totalled approximately 40 hours. The Woodcock was first recorded on the study area on March 5, when a single bird was flushed by J. Murray Speirs. Crepuscular calling and singing of the males was noted from March 9, when at least two performing males were present, through April 3. It is possible, since no observations were made between March 5 and 9, that calling and singing began prior to March 9. Following April 3, no Woodcocks were detected on the area, and apparently none remained to breed that season. Observations included 10 full evening performances and one morning performance (Table 1).

TABLE 1  
SUMMARIZATION OF CALLING AND SINGING PERIODS

Date	Birds Studied <sup>1</sup>	Calling Periods	Pre-display Calling	Singing Periods	Post-display Calling	No. of Singing Birds	No. of Calling Birds
Mar. 9		(Flight displays)					2
10	B	(Flight displays)	15 min.	6:20-6:50 P. M. 30 min.	0 min.	2	5
13	A	6:05-6:50 P. M. 45 min.	33	6:13-6:40	2	4	6
14	A, B	5:40-6:42	—	None	—	3	5
17	A, B	6:13-6:24	14	6:23-6:46	5	0	3
20	A, B	6:09-6:51	12	6:26-6:54	4	3	6
21	A	6:14-6:58	44	6:18-6:51	1	7	7+
	C	6:11-6:52	7	6:24-6:56 P. M. 32	4	—	8
22	C	6:09-7:00 P. M. 51	15	4:58-5:26 A. M. 28	0	5	5+ <sup>2</sup>
24	C	4:45-5:26 A. M. 41	13	6:34-7:00 P. M. 26	6	3	4
27	A, B	6:30-7:06 P. M. 36	4	6:36-6:58	1	3	3 <sup>3</sup>
28	A, B	6:33-6:59	3	6:43-6:57 P. M. 14	4	2	3
31	B	6:39-7:01	4	None	—	—	—
	A	6:50-6:59	9	None	—	—	—
Apr. 3	A, B	6:36-6:54 P. M. 18	—	—	—	0	2

<sup>1</sup> In this column are listed the males, as designated in the text, to which particular attention was paid on different dates.

<sup>2</sup> Following this morning singing period, a systematic survey disclosed the presence of at least 12 Woodcocks.

<sup>3</sup> An additional individual was found on the feeding area of male A just before calling began.

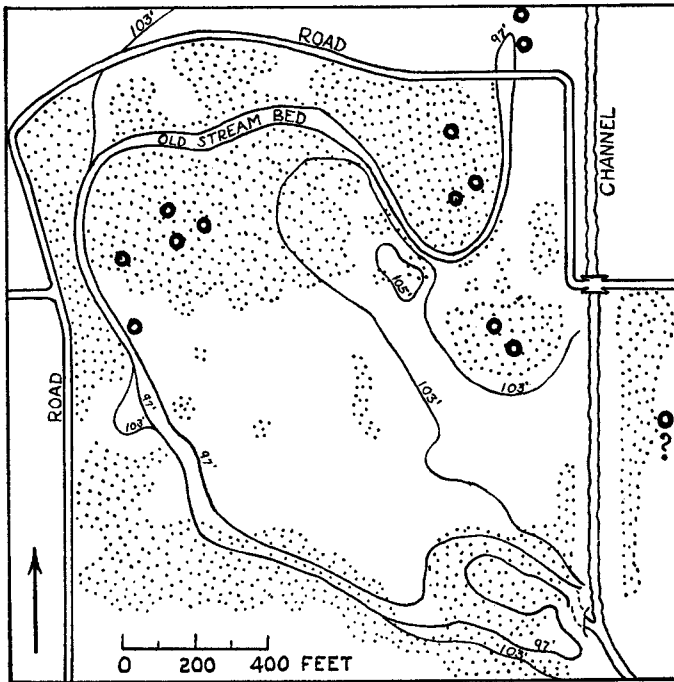


Figure 3. Map of study area. Dotted portions represent areas covered with woodland or relatively tall and dense thickets; clear portions represent areas covered with grasses, forbs, and numerous scattered shrubs, and a few small trees. Small dark circles indicate distribution of Woodcocks over feeding areas following the morning display period of March 24.

Weather data (Figure 4) were provided by the University of Illinois Meteorological Station through the kindness of H. P. Etlar. Supplementary field measurements of temperature were made with an ordinary mercury thermometer. Data on light intensities were obtained with an illumination meter (Model 603, Weston Electrical Instrument Corp., Newark, New Jersey). For the loan of field equipment, I am indebted to S. C. Kendeigh and V. E. Shelford, and to the Department of Zoology, University of Illinois.

Acknowledgement is made gratefully to Mrs. Margaret M. Nice, S. C. Kendeigh, J. T. Nichols, and especially to O. S. Pettingill, Jr., for critical reading of the manuscript. I wish also to thank Mr. and Mrs. J. Murray Speirs for their field notes on the Woodcock, also recorded at Urbana; J. T. Nichols for records of song-flights and nesting of the Woodcock on Long Island; and C. T. Black for excerpts from the manuscript notes of I. E. Hess, formerly of Philo, Illinois.

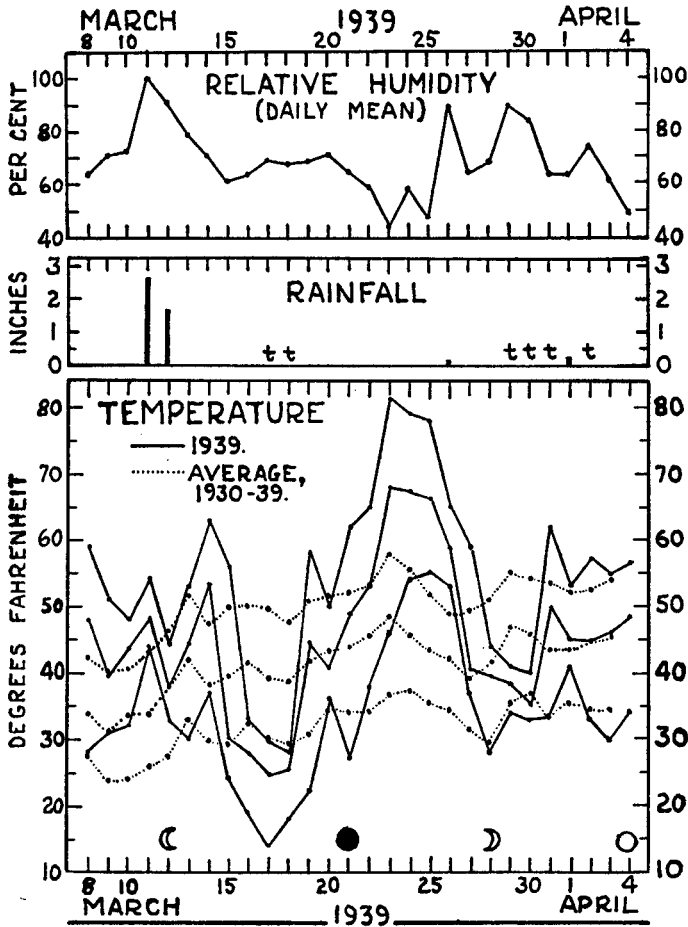


Figure 4. Weather data for the period of observation. In the graph of temperature data, daily values include minima, means, and maxima. In the graph of rainfall, *t* = trace. Moon phases are shown in the lower part of the figure.

THE PROBLEM OF TERRITORIALISM

In the American Woodcock, habitat and spatial relations are relatively complex. Within the period and geographic range of breeding, the male confines himself to a feeding area (usually wooded—the “diurnal territory” described by Pettingill, 1936:280) except for excursions to an adjoining display ground (= open-country territory or the singing-field) during crepuscular or nocturnal periods. Feeding areas may be temporary, largely because of weather factors, and they undoubtedly shift with the advance of the spring and summer seasons.

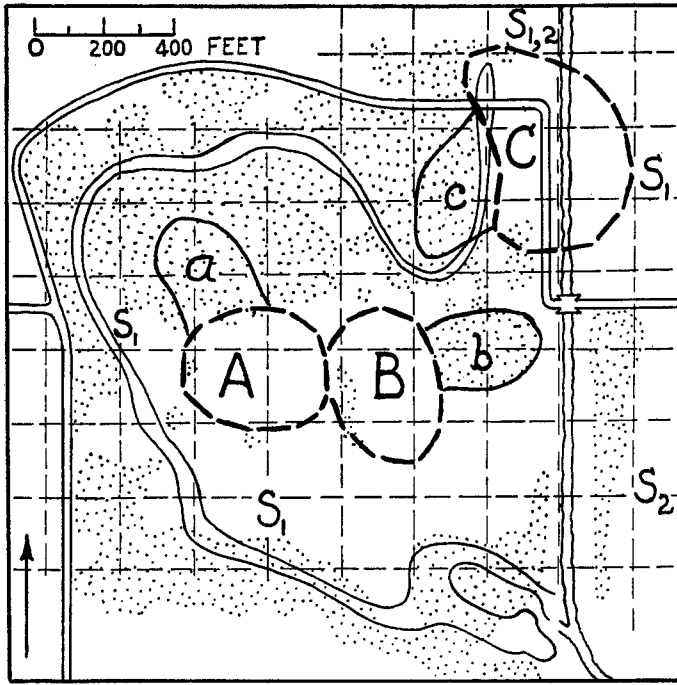


Figure 5. Open-country display territories (A, B, C) and adjoining feeding areas (a, b, c) of three male Woodcocks. Distribution of additional singing males is shown for March 21 (S<sub>1</sub>) and 24 (S<sub>2</sub>).

Following mating, the female occupies an area within which the nest is placed. This she leaves periodically to feed at sites at variable distance from the nest. The female performs all nesting duties, and, except for mating, the two sexes apparently remain independent of each other.

The question now remains, does the male or female display territoriality within one or more parts of the breeding habitat occupied by the species? Various aspects of this question are considered below, but to simplify the discussion, it may be stated at the outset that only the display sites of the male Woodcock are known to be defended, and only these areas will be termed territories.<sup>2</sup>

My observations were made largely on three males (A, B, and C) which remained established on fairly definite feeding and display grounds throughout the period of study. The display territories and feeding areas of these males are shown in Figure 5. The territorial boundaries shown are based on (1) location of calling posts on the

<sup>2</sup> The term territory, as used here, will refer to any defended area. This follows recent usage by Nice (1941:441) and other investigators.

ground, (2) spatial extent of the display flights, and (3) territorial claims as evidenced by threat behavior and chases. These points are all discussed in the following sections. The feeding areas were determined by repeated observations of individuals within the limits shown, and of the emergence of each of the males A, B, and C, from his respective feeding area prior to display. Whereas these birds were not marked, all evidence drawn from their behavior leads me to conclude that the same birds held the same territories throughout the period of occupancy.

During the four-week observation period, there were, besides females, at least five additional displaying males on the study area. The latter were present for only one to three days. In Figure 5, locations of singing males other than A, B, and C are shown for March 21 ( $S_1$ ) and March 24 ( $S_2$ ). It was not feasible to census the study area repeatedly, but such data as are available indicate that numbers of individuals increased to March 21, when there were between 10 and 15 Woodcocks present. On March 22, Speirs estimated that there were 14 in the area. On March 24, following a morning singing period, a systematic census count revealed at least 12 Woodcocks (Figure 3), although only 5 of these had performed (Figure 5).

#### CALL NOTES

##### 1. *The Peent Note and Crepuscular Calling Periods.*

The harsh, loud, nasal note given repeatedly by the male on the display territory has been expressed verbally in numerous ways (Pettingill, 1936:292). *Peent* is one of the more acceptable renditions and is used throughout the following discussions. Apparently both sexes may call on the display territory of one male, although calls of birds other than the occupant male are given only intermittently and briefly (see also Brewster, 1937:168). In some instances the *peents* of several birds on one territory may sound similar, but in several instances, it was possible to distinguish *peents* lower pitched than those of the performing males. Pettingill (1936:294) has suggested that the lower-pitched calls may be those of females, and a difference in the quality of calls between the two sexes has also been suggested in the European Woodcock (*Scolopax rusticola*) by Pay (see Steinfatt, 1938:389).

On March 28 and 31, males A and B both called a few times from their respective feeding areas before flying to their display territories. Pettingill (1936:282, 296) and Brewster (1937:170) also cite instances when calling began on feeding areas. Generally, however, calling began almost immediately after arrival on the display territory. One bird began the calling, others followed, and calling continued up to the first flight song; thereafter periods of calling alternated with song. During the preliminary period, all individuals exhibited an acceleration of calling, probably synchronized with the approach of darkness. The number of

calls given per minute prior to the first song ranged usually from 6 to 20 (Figure 6). For male A, however, the maximum rate, recorded just before the first song, was 26 calls per minute. If no interruption occurred, it maintained this rate between songs during the height of the display period. In this respect, male A differed from the other birds, with whom the rate of calling was lower, as a rule, between songs than before the first song. Pettingill (1936:294) records a maximum of 27 calls per minute between flight songs.

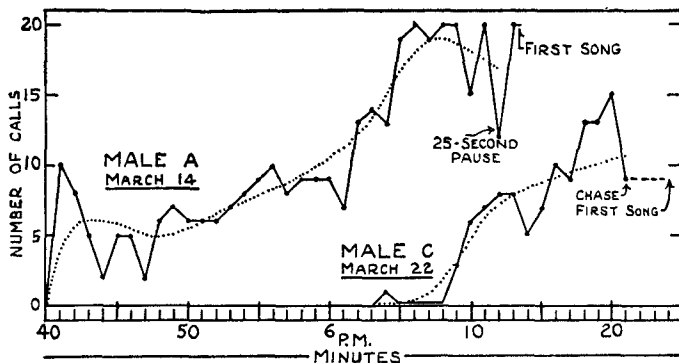


Figure 6. Two examples of preliminary calling periods of the male Woodcock, showing acceleration of calling prior to display.

A preliminary calling period may be illustrated by a record of calls given by six birds scattered over the open area south of the woods on the evening of March 13. From 6:05 to 6:10, bird 1 called alone, giving four calls. From 6:10 to 6:15, 23 calls were given by bird 1, and 17 by bird 2; bird 3 called once. From 6:15 to 6:20, 34 calls were given by bird 1, 27 by bird 2, and 15 by bird 3. Birds 4 and 5 each gave four calls during this five minutes, and bird 6, three. The first song began at 6:20.

Neighboring males A and B consistently called more frequently during territorial occupation than male C, whose "neighbor troubles" were only intermittent. This type of competition is also seen in the observations of Norris *et al.* (1940:14) who, by imitating the *peent* note, stimulated established males to call more vigorously and to attempt assault on the "intruder."

The lengths of calling periods (including the singing periods from the beginning of the first song within an evening's performance through the last song) are summarized in Table 1. Calling periods are equivalent to total time spent on the display territory. During this time, the *peent* note is given continually, except for interruptions by flight display.

Given the suitable habitat, the chief factors which enter into the variation among calling periods of established birds are light intensity,



weather (especially temperature), and psychological stimulation exerted among neighboring individuals. Other factors affecting calling (and display as well) are not to be overlooked: the presence of females may influence calling and display; and the strength of the sexual urge in relation to particular time of the breeding cycle would be reflected in the length of calling and display periods (Studholme and Norris, 1942:233). During the early part of the breeding season, the complex of environmental and physiological factors which influence migratory movements may be superimposed on the previously mentioned factors, and birds seemingly established in suitable habitat may depart after subsidence of territorial calling and display (see below).

*Light intensity.*—Light measurements were taken on display grounds. The receptor piece of the illumination meter was placed on clear ground six feet away from the recorder and directed toward the zenith. During evening and morning observation periods, readings were taken every five minutes (Figure 7). Measurements were also taken with the receptor piece six feet above the ground and directed toward the sunset, but because of certain irregularities in the data, these were discarded. Moreover, the bird on the ground is obviously affected more directly by light of the zenith.

TABLE 2  
RECORDS OF LIGHT INTENSITY AND TEMPERATURE AT THE BEGINNING OF  
CREPUSCULAR CALLING

Date	Beginning of Calling	Light Intensity (Foot-candles)	Temperature (U. of I. Sta.)	Field Temperature
March 20	6:09 P. M.	17	38°F.	
21	6:14	11	53	
22	6:09	28	56	
27	6:30	2	37	36.5°F.
28	6:33	1.5	38	37.0
31	6:39	2.3	52	51.3

The amount of illumination at the beginning of calling on the display territory showed an appreciable variation (Figure 7 and Table 2). On March 22, calling began at 28 foot-candles, whereas on March 28, it began at 1.5 foot-candles. The average of six records is 10.3. Pettengill (1936:297) reports only one measurement, of two foot-candles, obtained with an exposure meter directed toward the sunset.

The possibility that the start of calling might be related in part to temperature does not appear to be supported by the available (admittedly limited) data (Table 2). The beginning of the calling periods may be determined by the time of departure from the feeding area, and therefore by the light intensity at the site of departure. Since such areas are visibly shaded by even leafless winter vegetation, the features of the particular site which the bird occupies would affect the onset

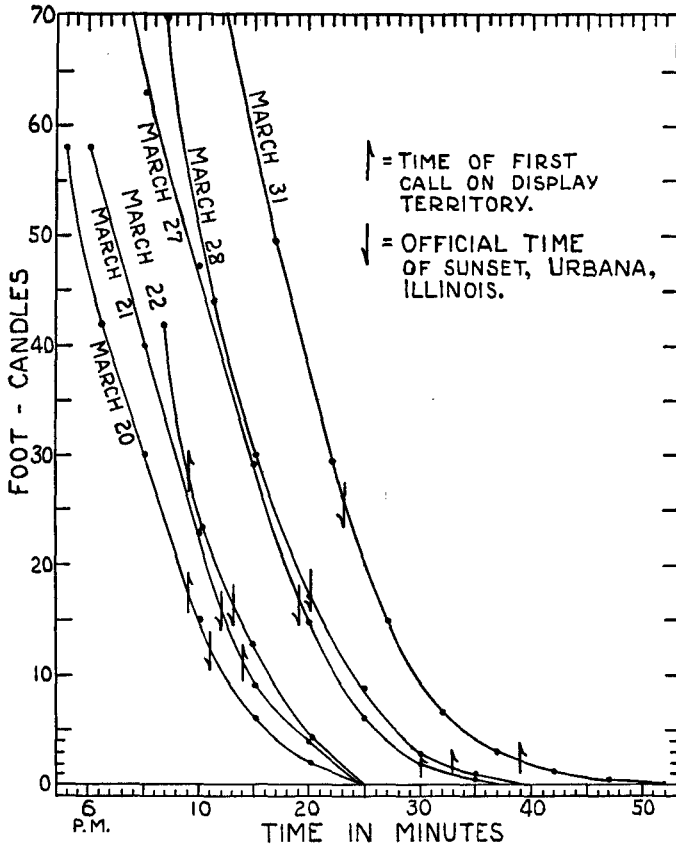


Figure 7. The time of first evening call in relation to light intensity. Each line represents declining light values during one evening. A symbol on each line indicates time of first call on the display territory in relation to light intensity at that moment. Light readings (taken every five minutes) are shown by points along the lines. (See also Table 3.)

of calling. It was observed, in fact, that Male C, whose feeding area was at the eastern end of the forested area and therefore less lighted in the evening, consistently appeared on his display territory before males A or B on theirs. Accurate arrival times for all males are available for three evenings:

	A	B	C
March 21	6:14	6:14+	6:11 P.M.
March 27	6:30	6:30+	6:23
March 28	6:28	6:30	6:24

The rate of calling and the time calling begins are both affected in any one bird by the activity of neighboring birds. Calling begun by

one bird stimulated others to leave their feeding areas to take up positions on singing fields. Calling was sustained at higher rates (20 to 26 calls per minute) during periods on March 20, 21, and 22, when Woodcocks were apparently most numerous on the study area (Table 1). On each of these evenings, calling also started relatively earlier.

The effect of cloudiness on length of calling period is seen on March 14, a dull, hazy evening, when calling began 24 minutes before sunset and continued for 32 minutes before the first song-flight (Table 3). On six more or less clear evenings (March 20-31, Table 3), calling began 4 minutes before, to 16 minutes after, sunset and continued for only 3 to 15 minutes before the first song. (See also Pettingill, 1936:297.)

TABLE 3  
BEGINNING OF CALLING AND SINGING IN RELATION TO SUNSET  
(URBANA, ILLINOIS, LATITUDE 40°N.)

Date	Time of Sunset	Beginning of Calling	Interval after Sunset <sup>1</sup>	Beginning of Singing	Interval after Sunset <sup>2</sup>	Sky Conditions
March 13	6:03 P. M.	6:05 P. M.	2 min.	6:20 P. M.	17 min.	?
14	6:04	5:40	-24	6:13	9	Cloudy
17	6:07	6:13	6	—	—	Clear
20	6:11	6:09	- 2	6:23	12	Clear
21	6:12	6:14	2	6:26	14	Clear
22	6:13	6:09	- 4	6:24	11	Clear
27	6:19	6:30	11	6:34	15	Clear
28	6:20	6:33	14	6:36	16	Partly cloudy
31	6:23	6:39	16	6:43	20	Clear
April 3	6:26	6:36	10	—	—	Clear

<sup>1</sup> Average of these 10 records is 3 minutes after sunset.

<sup>2</sup> Average of these 8 records is 14 minutes after sunset.

*Temperature.*—A correlation of length of calling periods with temperature is shown in Figure 8. Two temperature values are given for each date: value at time of calling and the day's mean. This diagram illustrates the effect of temperature *at the time* of the evening or morning calling periods. The *daily mean* temperature, shown in Figures 4 and 8, may serve as an index to the day-to-day changes, and undoubtedly the summated effect of these changes is reflected in the general physiology of the bird; that is, a Woodcock's crepuscular performance may be influenced as much by the temperature conditions of the preceding 24-hour period as by temperature at the moment of display. At least for evening periods, lengths of calling periods appear to correlate more consistently with daily mean temperatures than with temperatures during the calling periods. At best, however, these data are only suggestive.

On March 27 and 28, there was less preliminary calling, and during singing periods, performances began to be less frequent and less

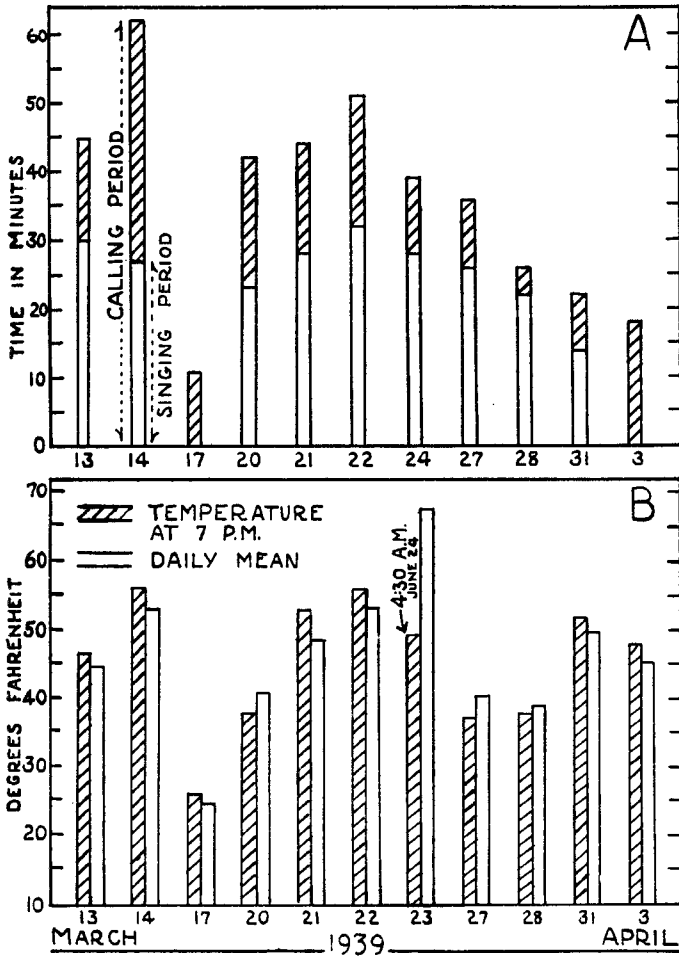


Figure 8. Correlation of daily temperature values with lengths of calling and singing periods; note that the total time designated as a calling period includes the singing period.

forceful. The data are too limited for an explanation of this subsidence of calling and display and of the ultimate disappearance of all the birds. The species is a summer resident in the region, although at present it is probably not regularly so. The weather record (Figure 4) shows unseasonably high temperature during the period March 22 to 27. Following this period, the birds apparently dispersed; on March 31, males A, B, and C were still present; on April 3, only males A and B were present, and on April 4 and thereafter, no Woodcocks were found.

During the cold evening of March 17 (temperature 26° F.), there was only a brief period of activity. No songs were given. At least three individuals called; the maximum number of calls was five within one minute, given by a single bird. Otherwise, however, no effect of temperature on *rate* of calling was detected. Of interest here is Brooks' record (1935:308) from West Virginia of a male calling and singing on April 27, 1930, when the temperature was 30° F. It remains yet for someone to determine whether the temperature thresholds for calling and singing are the same throughout the breeding season or whether these thresholds fall as the season advances (Witherby *et al.*, 1940:187).

## 2. Other Calls.

A second frequent note may be interpreted as *ka-kak-ka-k-k-k*, referred to in my subsequent discussion as a cackle. It appears to function in assault and threat, while the *peent* note appears to be one of warning, announcement, and advertisement. The cackle was heard most frequently when Woodcocks were most numerous. On several occasions the occupant of a territory was observed to give the cackle note during a preliminary, somewhat circular, flight just above the low vegetation. These flights occurred well after the calling had begun and from 3 to 10 minutes before the first song-flight. They were accompanied by a continuous whirring of the wings as heard at the onset of the song-flight. The cackle note was also given by an established male in silent flight just as it approached an intruder, whose calling had disclosed his position. All intruders were assaulted in this way. In some instances, the assault was followed by a chase, in others by a display flight, either from the site of intrusion or from the male's usual territorial position (see also Brewster, 1937:170). Also, the initial ascent in a song-flight was interrupted by slight dips marked by the cackle note (Figure 10, F). One particularly belligerent male (C) uttered this note on several occasions just as he alighted on his territory after a flight. Here, it seemed likely that the calls were evoked by the light-instruments placed close to the bird's favorite ground or by my crawling along the ground nearby. Once the cackle note was heard on A's feeding area, just prior to his flight to the display territory.

Norris *et al.* (1940:13) observed that Woodcocks flying over a singing-field were chased by the occupant male, who uttered the cackle note. Further, they observed that the *peents* of birds near a male in his singing field produced the same reaction. Pettingill (1936:268, 305) also observed that the cackle note was given when several birds were present in the vicinity of a singing-field, and he interpreted it as a note of reproof. Later, he observed two birds thought to be male and female and again heard the cackle note. He suggested that females may cackle also and referred to cackling as notes of felicitation or "talking sounds." My observations do not support that interpretation. I found that males uttered the cackle sound when assaulting any intruder and

when invading a close neighbor's territory and attempting to displace him (see below). In these and other usages described above, the note seemed clearly to function as an intimidation device. Only the territorial males produced this sound. I suspect that if not assaulted, another Woodcock present on a display territory would be a receptive female. There appear to be no published records of anyone's collecting and sexing suspected females on display territories. Trautman (1940:249) collected a suspected female in a display flight; it proved to be a male.

The third important note given during the crepuscular performance is a softer call interpreted in my notes as *ka-rurr*, recorded by Pettingill (1936:268) as *took-oo*. When the listener is only a few feet away from the bird, the note has a rolling quality evident in the first transcription; at greater distances, the note sounds softer, as in the second. In my own case, I could not hear this note at distances greater than 15 feet. The call is given one to three times between *peents*, each *took-oo* note except the last, which is followed immediately by a *peent*, being followed by a brief pause (Brewster, 1894:292; Pettingill, 1936:294). The observations of Norris *et al.* (1940:12) would indicate that the *took-oo* note is one of invitation and solicitation prior to and after copulation. They report that a male approaching a decoy, prior to treading, utters only the *took-oo* note. Brewster (1937:168) suggests that this note is also given by the female.

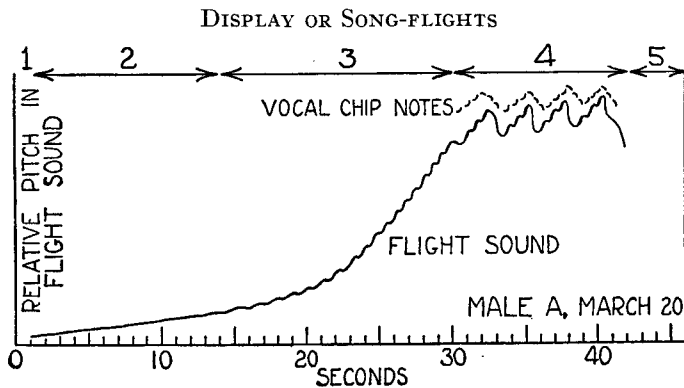


Figure 9. Pattern of sounds and time-relations observed in the song-flight of a male Woodcock. Divisions of the display, according to discussion in the text, are shown along the upper margin.

While the literature on the song-flight of the American Woodcock is extensive, most of it really states little more than that the performance is a truly phenomenal sight. Brewster (1894) and Pettingill (1936) have given us the best word pictures of the song-flight. In adding further to the literature, I am interested not only in elaborating

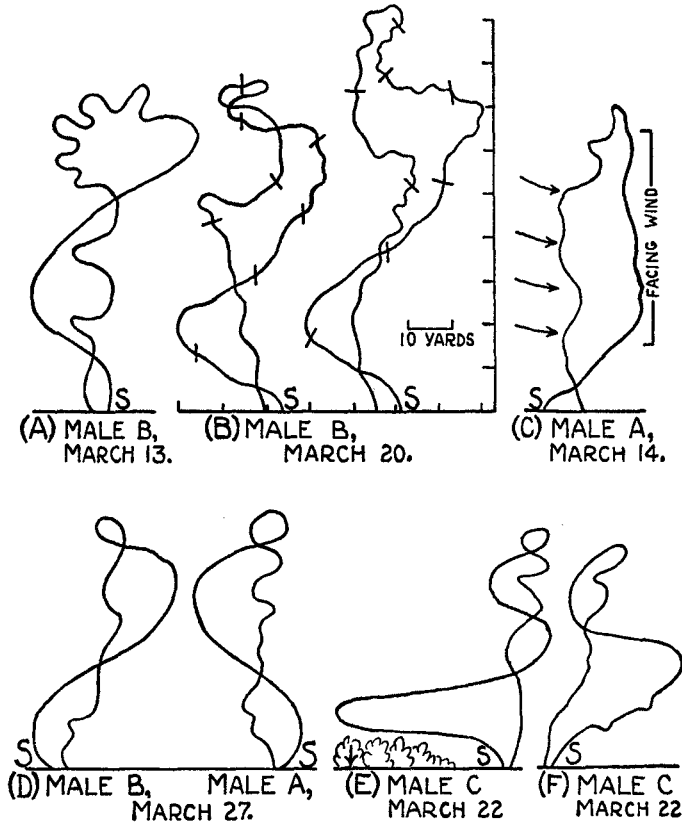


Figure 10. Courses taken by song-flights of male Woodcocks, all viewed from the side. Ascent begins at S. (A) Generalized pattern of the flight, based on a series of flights of male B. (B) Two flights of a single male with five-second intervals marked by cross-lines to show time relations. A scale is added to show approximate breadth and height of flights. (C) A flight performed in a fairly strong wind. (D) Courses of flight displays of competing neighboring males. (E) Flight of a male who began to ascend near a neighboring male (position of latter shown by small arrow). (F) Flight of a male showing dips in steady ascent during which the cackle note was given toward another male (S, Figure 5).

and amplifying certain details of the song, but also, and more importantly, in presenting a simplified and somewhat graphic picture of it in order to provide some basis for comparison with other Scolopacinae. Typical performances are illustrated in Figure 10, A and B.

The display of the Woodcock may be divided conveniently into five parts: initial silent flight, regular ascent, pulsated ascent, climax of wing and vocal sounds, and silent descent (Figure 9). (1) The start of a song-flight is silent and lasts but a few seconds. (2) The whirr of the wings is then heard with a gradual rise in the pitch as the bird

begins to climb slowly in a large regular spiral about the point of beginning; this part of the song-flight usually lasts about 15 seconds. (3) During the third part, which is the greater part of the ascent, there is a pulsation in the whirr of the wings, which becomes increasingly pronounced; at first there seems to be a distinct sound, *zzet*, alternating with each whirr of wing sound; toward the end of the main ascent, when the wing pulse is quick, these notes are obliterated. (4) At or near the peak of the ascent, the wing sounds become most distinct and are given in series of three or four, alternating with *zzet* sounds, which are again audible. This is followed by dips and irregularities in flight, during which wing sounds are reduced. Corresponding to these dips, there are series of vocal chip notes, sometimes termed "twittering" (Figure 9). The fact that the *zzet* sounds are heard during the series of chip notes suggests that they are wing sounds. This climax period in the song-flight lasts 10 to 15 seconds and may include part of the descent. (5) It is followed by a rapid and silent dive-descent to a spot near the starting point.

Exceptions to this general picture are seen in the behavior of male C, whose singing-field was enclosed in part by tall vegetation (Figures 1 and 5). He was observed to precede an ascent by a silent flight to a point about 150 feet away, where the sound of the wings was then begun (Figure 10, E). Likewise, the descent may not always be direct. Male C was observed to circle over the trees and shrubs to the west and south of his territory before alighting. Pettingill (1936:284) observed a male begin the first song-flight of an evening from his feeding area and end it on the display territory.

Males may leave the display territory immediately after descent without alighting; they may leave after alighting without calling; or they may remain on the territory for a short period (2 to 6 minutes, Table 1), during which calling continues, but subsides more or less sharply (from 14 to 2 calls per minute). Brewster (1894:297) and Pettingill (1936:300) report similar observations, although the post-display calling reported by the latter author continued for 8 to 20 minutes. On March 31, a moon-lit night, the sound of flight was heard, from the territory of male B, 8 and 10 minutes after calling ended; but during several hours' wait, no further activity was noted.

Song-flights vary in length among different individuals as well as in a single individual (Table 4). The songs generally do not exceed one minute in length. In my observations 60 seconds was maximum, in those of Pettingill (1936:291), 66 seconds. My observations on height of song-flights (Figure 10, B) agree in all essentials with those of Pettingill (1936:291).

The chief function of the display flight appears to be territorial advertisement, and, whereas the cackle note serves as a threat, the song-flight may at times function as a superlative threat behavior in



TABLE 4  
DURATION OF SONG-FLIGHTS

	Date	Number of Performances	Average Length	Extremes
Male A	March 14	11	34 sec.	29-40 sec.
	21	7	43	40-45
	27	8	40.5	37-44
	28	5	41	40-42
Male B	March 13	6	54	45-60
	27	3	46	45-48
Male C	March 22	4	52.5	50-55
	24	3	49	43-55

the face of a need for stronger offense. To cite some illustrative observations: On March 20, male A flew toward an intruder, giving the cackle note as he approached. (The lower pitched *peents* of the intruder suggested it to be a female.) A few seconds after alighting near the intruder, the male performed a flight display. On March 22, male C flew toward an intruder without alighting and returned immediately to his calling ground, where he started a song-flight. On the same date, male C flew toward the area of a neighbor to the south, giving the threat note, and then continued into a song-flight (Figure 10, E). And, finally, in beginning his ascent, male C, circling widely above the territory of a calling neighbor ( $S_1$ ), would interrupt the steady whirr of his wings with the threat note just above the other bird (Figure 10, F). Similarly, male A uttered the threat note during his ascent, as male B called from his territory (March 27).

A difference between *Philohela minor* and *Scolopax rusticola* worth noting at this time is that in details of the song-flight. The male of *Philohela minor* displays over a rather circumscribed area, separate from his feeding area. The male of *Scolopax rusticola* displays over a comparatively large area, which apparently includes his feeding sites; he seems to follow the bounds of selected territories in horizontal flight circuits, from several hundred yards to one or two miles long, over or along the edges of wooded areas, flying back and forth several times during a single crepuscular period (Warwick and van Someren, 1936: 167). A similar horizontal display flight occurs in *Scolopax saturata* (Mayr and Rand, 1937:29).

In the case of *Scolopax*, the area covered by display flights makes study of territorial relations among neighboring males rather difficult, but the flights appear to bear the same significance in territoriality as those of *Philohela*. Witherby *et al.* (1940:187) term them advertisement flights. Warwick and van Someren (1936:171) consider "roding" (as the crepuscular flights are known in Great Britain) to be largely

aggressive and to have the same territorial basis as song has in many passerines. My own opinion on comparable behavior in *Philohela* is in agreement with these views.

*"Double" Flights and Female Display.*—On March 22, Mr. and Mrs. Speirs had the good fortune to observe two Woodcocks in a peculiar flight over the territory of male B. It appears that the two birds began song-flights simultaneously, ascending about 20 feet apart. The usual whirr of wings was heard during the ascent, but instead of the gradual rise and subsequent pulsation, these two birds merely approached each other repeatedly while mounting to a height comparable with that of normal song-flights. Following this, there was a smooth descent without any chipping or twittering. I can only suggest that these were probably two males who merely chanced to start their flight simultaneously.

There is no satisfactory record for female display in the American Woodcock, and the possibility of a mating flight remains doubtful. Brooks (1935:307) describes a circular flight of two birds together; he suggests that one may have been a female, but admits that the two birds may have been males which happened to begin their flights at the same time. Bagg and Eliot (1937:208) state that "occasionally two birds perform together, facing each other, seeming to climb perpendicularly up the air, each alternately the higher; but whether these are mates, or rival males, and whether both sing, is as yet unknown." According to Zedlitz (1927:76) and Steinfatt (1938:390), the female of the European Woodcock does not display. Warwick and van Someren (1936:170) consider flights of two birds together to be those of male and female, but apparently no attempt was made to settle this point conclusively (see Zedlitz, 1927:77).

*Light.*—Whereas calling began over an appreciable range of light intensities, singing began consistently when the light fell between 1 and 0.5 foot-candles (Table 5). On the morning of March 24, both

TABLE 5  
TIME OF FIRST SONG IN RELATION TO LIGHT

Date	Time	Light Intensity
March 20	6:23 P. M.	1-0.5 foot-candles
21	6:26	0
22	6:24	1-0.5
27	6:34	1-0.5
28	6:36	1-0.5
31	6:43	1-0.5

calling and singing ceased before the light indicator rose above zero. Brewster (1894:293) observed that there was less daylight during the morning singing period as compared with the evening period.

*Temperature and Wind.*—At least from March 13 through 28 (Figure 8), length of song period, in correspondence with length of calling period, may be correlated with temperature; that is, from day to day, song periods tend to vary in length directly with variations in daily temperature (Pettingill, 1936:296). Song periods varied in length from 21 to 33 minutes (Table 6). After March 27 the dispersal mentioned earlier began, accompanied by a subsidence of singing and calling (Table 1 and Figure 8). The singing periods during this latter part of the study are therefore regarded as subnormal.

TABLE 6  
DURATION OF SINGING PERIODS AND FREQUENCY OF SONG-FLIGHTS

	Date	Time	Length of Singing Periods <sup>1</sup>	Number of Song-flights	Average Interval Between Flight Starts
Male A	March 14	6:13-6:40 P. M.	27 min.	16	1.7 min.
	20	6:23-6:46	23	10	2.3
	21	6:26-6:54	28	10	2.8
	27	6:34-7:00	26	16	1.6
	28	6:37-6:58	21	9	2.3
Male B	March 27	6:34-7:00	26	15	1.7
	28	6:36-6:58	22	9	2.4
	31	6:43-6:57	14	5	2.8
Male C	March 21	6:18-6:51 P. M.	33	12	2.7
	24	4:58-5:26 A. M.	28	11	2.5

<sup>1</sup> Measured from first to last song-flight.

Whereas length of singing periods was correlated with temperature, there was no evidence that frequency of song-flights during the singing period (Table 6) was affected by temperature. On the cold evening of March 17, no song-flights were performed. It will be recalled that no effect of temperature on rate of calling was noted except on March 17. Records of three males on various dates show that, at least within the range of available data, the variation in frequency of song-flights is slight. The low figures for March 14 and 27 may be accounted for by exceptional competitive behavior between neighboring males. Among the remaining records, song-flights were begun, on the average, once every 2.3 to 2.8 minutes—a relatively regular rate—irrespective of the length of the singing period.

Wind may have marked effect on the length and general performance of the song-flight (Pettingill, 1936:292, 293). In Figure 10, C, a song-flight performed in strong wind is diagrammed as viewed from the side. Under such conditions, the flights are shortened (see the record of male A for March 14, Table 4). Part 3 of the song-flight was shortened markedly in the face of strong wind, and lasted from 3 to 10 seconds (average 5.5 for 9 records) as against a normal 10 to 15 seconds on calm evenings.

## TERRITORIAL BEHAVIOR

At present, only the display sites are known to be defended. It follows then that neither the feeding areas of the males nor the nesting areas of the females can be called territories. Pettingill (letter) properly points out that it would be unusual for a bird not to show evidence of territoriality in the vicinity of the nest, but no data are available. Woodcocks may be gregarious on feeding grounds in winter and in migration, but it yet remains to be determined whether or not they are gregarious in late spring and summer. Under present-day conditions of reduced abundance, there is limited opportunity to investigate these points. During day-time observations (March 24) on the study area, when at least 12 Woodcocks were found about suitable feeding areas (Figure 3), no intolerance or chasing was seen. In the literature on Scolopacinae, I have found no mention of territorial behavior on feeding or nesting areas.

*Extent of Feeding Area and Territory.*—The size of the feeding area occupied by the male Woodcock appeared to be determined largely by availability and suitability of foraging sites. The area over which a bird forages may vary to a considerable degree (Pettingill, 1936:283). The birds believed to be occupants of areas *a*, *b*, and *c* (Figure 5) were seen regularly at favored feeding sites within parts of their respective areas. The feeding areas of these birds were between 250 and 300 feet in diameter and larger than examples mentioned by Pettingill. But I attribute this to the greater extent of suitable feeding grounds in my study area. At the time of observation, scattered spring ponds and moist, soft, leaf-littered woodland floor provided excellent sites for them. Areas *a* and *c* were both surrounded by additional ground over which feeding might have occurred. I would suggest that these feeding areas were probably maximal in extent.

Calling sites on the display territory were confined to areas relatively small, and more or less circular, ranging from 50 to 75 feet in diameter. Areas of about equal extent are described by Pettingill (1936:284) and Aldous (1938:840). Depending apparently on the presence of shrubby masses over the display territory, there may be what Norris *et al.* (1940:9) term a "primary singing ground" together with one or more "auxiliary" areas. This agrees in essence with my observations of singing-grounds with scattered shrubs and without clear-cut openings, where a male might call usually from one favored site, but would move occasionally to another site as much as 75 feet away. The areas described by Norris *et al.* (average 21x37 feet) probably were small chiefly because of this vegetational factor. Brewster (1925:230; 1937:166) observed males singing and alighting at different points in fields of several acres instead of maintaining more or less definite stations.

My observations on the extent of the area covered by one song-flight differ from those of most earlier reports. Most flights, the ascents of which were more or less circular, were spread over areas of only 35- to 40-yard diameter ( $\frac{1}{3}$  acre). Certain irregular flights of male C extended over as much as  $\frac{2}{3}$  of an acre; moreover, male C consistently flew over larger areas than males A or B. He also was the most belligerent and held the largest territory. Further, the placement of the calling site in relation to large vegetational masses was such that his ascent could not be made over a circle about a beginning point, and this largely accounted for the irregularities in his song-flights (see Figure 10, E). Other factors, for instance the proximity of competing males, may influence the spatial extent, as well as the vigor, of the flight-song. Pettingill (letter) states that the total area covered by a song-flight seldom, if ever, exceeds 300 feet square (about two acres).<sup>3</sup> This figure was calculated to include flights begun or ended outside the display territory and flights performed in strong wind. Brooks (1935: 308) reports circles of as much as 400 yards in diameter. Such circles would be over  $2\frac{1}{2}$  acres in size! Brewster's estimate (1894:293) that a flight may extend over five acres likewise seems to be excessive.

However, the display flights do not always cover the same area. On different flights, males may fly in different directions so that the total area covered by all flights of one male may reach two to five acres (Figure 5). A male asserts his claims in any part of the area generally covered by his song-flights in spite of the fact that calling is usually confined to the center of the area.

*Relations of Neighboring Males.*—Several references have already been made to the territorial behavior displayed among neighboring Woodcocks; namely, (1) chasing of intruders, (2) preliminary flights over territories, and (3) warning and threat notes. In addition, chases occurred among closely neighboring birds one of whom would leave his own area, invade that of a neighbor, and chase or attempt to chase him away, indicating overlap of areas claimed by individual males. On March 21 and 22, male C chased and probably attacked at least three neighboring males (Figure 5); the third male, present only on March 22, called from the open area along the south border of C's territory, west of the road. There were numerous other instances, involving males A and B also, when fewer birds were present. Retaliatory chases were also noted. Male C assaulted and probably chased at least twice a close neighbor to the south. He was apparently successful in driving him off, for following the encounters, the south bird began a song-flight and ascended over the territory of male C, then continued to the north in a direct flight, and did not return.

Competition between males A and B was noted several times. On

<sup>3</sup> In Pettingill's monograph, the statement concerning area covered by a song-flight (1936:291) should read 300 *feet* square instead of 300 *yards* square. In a letter, he suggests that this correction be recorded here.

March 21, for instance, male A was observed to display again almost immediately after descent if male B was in display at that time. On March 27, male A displayed six times, and male B five times, within the same period of six minutes. Similarly, on March 28, males A and B gave five overlapping performances (three by male B) within a period of three minutes. Another demonstration of competitive behavior was seen in the directions of the respective ascents of males A and B, as shown in Figure 10, D, again suggesting overlap of territorial areas desired by each male. This feature of the song-flights of the two neighboring males was observed repeatedly when both were performing.

Pettingill (1936:282) observed an established bird fly over to the calling site of a second bird and there begin a song-flight. He saw no combat between one male and two others which were established within 300 yards of the first, but I found males fighting and actively competing when they were 500 feet apart (Figure 5). Aldous (1938:840) observed the shortest distance between two singing grounds to be 400 feet; this apparently refers to the boundaries, so that occupant males were probably farther apart. He makes no mention of any competitive behavior.

#### STRUTTING AND MATING

While calling, the male maintained a stiff stance with head pulled back, wings dropped, and tail spread and held vertically (see also Pettingill, 1936:294). When uttering the *peent* note he jerked his head backward. Usually, the calls were given from one position, which was then changed by a few steps. But on two occasions I saw a rhythmic strutting (by male C, March 22). Tail, wings, and head were held as described above. The bird moved stiffly along a straight line for about two feet, then turned about 120° to the left, giving a *peent* note at the end of the turn. The original direction of movement was then resumed, and at the end of another two feet, another turn was made. This performance was repeated several times.

This behavior appears to be only a manifestation of excitement during the display period. Female Woodcocks strut similarly when disturbed from the nest (Ford, 1926; Murphy, 1926), and I would regard this behavior (wings dropped, tail spread, etc.) as comparable with that seen in individuals of a variety of species when excited. It is not necessarily a courtship display—the behavior preliminary to mating may be distinctly different, as described by Norris *et al.* (1940:10). But it is possible that strutting may occur just prior to copulation: Pulchaski (see Steinfatt, 1938:410) reports a displaying male *Scolopax rusticola* that alighted near a nest which contained an incomplete clutch; the female left the nest and strutted, then crouched; copulation followed.

What can be said of the relation of mating to the display territory? The established male appears to resent all intruders and assaults them

with the cackle note. Females may visit the singing-field (Pettingill, 1936:284), but visiting birds may include males as well, both established (as competing neighbors) or unestablished (as transients or new arrivals on breeding grounds). Several authors insist on interpreting chases as occurring between male and female. The events subsequent to any territorial intrusion are determined largely by the responses of the outsider to intimidation. On several occasions, I have seen the male approach an intruder and then either display in a song-flight or chase the intruder—a chase if the latter leaves, or a display if the intruder stays his ground. Norris *et al.* (1940:10) suggest that copulation is attempted if the intruding bird remains quiet. They observed that a decoy of male proportions placed in normal standing position on a territory, if seen by the established male, was received sooner or later as a female, and copulation was attempted. Here the important point is that an intruder remaining quiet on the singing grounds of a male is accepted by him as a receptive female. Under these circumstances, the male assumed a peculiar stance, first described by Norris *et al.* With wings raised and legs stiffened, the male approached the decoy, dropping his wings occasionally and uttering only the *took-oo* notes. Treading occurred from both sides as well as from behind. Any conclusions drawn from these observations must remain tentative, however, until full data on behavior before and after natural copulation are available.

An observation of mating in the European Woodcock has been mentioned above. The only report of copulation in the American Woodcock is that of Shelley (Pettingill, 1936:305); this record apparently was also made on the display territory. I did not observe copulation. From our limited information, it appears that mating may occur either on display grounds or near nesting sites, but initial matings of a breeding season probably occur on the display grounds. The question arises: does one male establish a pairing bond with a female during the egg-laying period and later visit the site of the nest? Or does the occurrence of mating near the nest result from a chance discovery of a receptive female by a male moving about favorable feeding grounds?

Pettingill (1936:306) and Norris *et al.* (1940:9) consider the Woodcock to be polygamous, but the available evidence is not satisfactory. Circumstantial evidence drawn from my observations agrees with that cited by Pettingill (1936:305): more than one bird may enter the display territory and apparently remain for a time; likewise, on diurnal feeding areas, several birds may be present (Figure 3). Pair formation does not occur in the European Woodcock (Steinfatt, 1938:387), and the species is regarded as polygamous (Zedlitz, 1925:67). Zedlitz (1927:75) reports females of *Scolopax rusticola* to be polyandrous in areas where males are numerous. The studies of Steinfatt and

Zedlitz suggest that several copulations are necessary for the completion of a clutch. Considering the comparable breeding biology of *Philohela* and *Scolopax*, it is possible that these conditions obtain in *Philohela*, also. On the other hand, Aldous (1938:842) regards the species as monogamous. Certain observations by Brewster (1925:228, 229) favor this contention.

#### DISPLAY IN RELATION TO MIGRATION AND NESTING

Woodcocks did not remain to nest on the study area in 1939, and from the foregoing discussion, it is evident that American Woodcocks may, during passage northward, become established temporarily and exhibit territoriality. According to data sent to me by J. Murray Speirs, performing males were present in Champaign County in 1940 at least from March 19 to April 2, but departed; in the spring of 1941, although several observers looked for Woodcocks, none was found.

Data from other parts of the northeastern United States, presented below, show that flight displays of the Woodcock are normally given for approximately two months beyond the latest record from Champaign County. Most breeding records fall in April. There seems to be little doubt that the birds which left the study area became re-established elsewhere.

Territorial behavior, then, may not necessarily be restricted to sites where actual breeding will take place. Studholme and Norris (1942:231) report migratory movements of Woodcocks and variations in numbers of singing males during the first week of April in central Pennsylvania; after the first week, numbers were more or less stabilized, and territories were definitely established. Steinfatt (1938:384, 386) observed that males of *Scolopax rusticola* performed their crepuscular flights when stopping in the course of spring migration. It may be added that flight displays of the American Woodcock have been observed at the time of fall migration (Pettingill, 1936:303).

In east-central Illinois, as in most other parts of the state, the Woodcock generally arrives in spring during the first half of March (Pettingill, 1936:233). The earliest arrival date at Urbana is March 5. The species may be fairly common locally during migration, but as a summer resident it is uncommon. Available nesting records show that eggs are laid from late March through April (Hess, 1910:31 and 1912, MS). Nesting records from northeastern states generally range from late March through May, however, and at any particular location the breeding season may be irregular because of the relatively long time span during which nesting may take place (Brooks, 1930:249). Yet there is no satisfactory evidence that the American Woodcock generally nests more than once a year. Two nestings may take place on occasion, as suggested by records of Pettingill (1936:218), Hicks (1933:181), and Bagg and Eliot (1937:208). The European Woodcock regularly breeds twice a year (Steinfatt, 1938:390).



In east-central Illinois, display flights have been observed from March 9 through April 2. Records over a series of years, however, would probably extend this period. In northwestern Ohio, for example, records of males in flight displays extend from February 28 through May 10 (Trautman, 1940:249); in the Cayuga Lake basin, New York, from March 14 to June 2 (Pettingill, 1936:277, 297); and on Long Island, New York, from February 13 to May 28 (J. T. Nichols, letter). Bagg and Eliot (1937:208) record males in the Connecticut Valley, Massachusetts, giving crepuscular calls on February 5 and 24; dates on which flight displays were seen range from March 4 to June 7. One late date, July 17, 1933, is also given. Studholme and Norris (1942:233) found that most males ceased regular display by the middle of May, although irregular display continued until June 3. Their observations indicate that there is only one cycle of active display among the established males of an area. In the European Woodcock, there are two cycles of active flight display corresponding to the two broods per nesting season (Steinfatt, 1938:384): the "Frühlingsbalz," in East Prussia, lasts from late March through April and the "Sommerbalz" lasts from early May through most of June, or even until as late as July 12.

In making this study of the American Woodcock, I attempted primarily to investigate certain features of territorial relations left unsettled by earlier studies. Unlike Pettingill's experience (1936:283), I found evidence for (1) competition in selection and maintenance of a display territory, (2) combat, (3) overlap of territories, (4) leaving of territories to fight neighbors, and (5) increased vigor of singing among neighboring males. However, these points need to be amplified through further observation and study. My own field work was limited by lack of time. There is obviously a great deal yet to be learned about the American Woodcock, and several questions must be apparent to the reader. Among these are the problems of polygamy, pair-formation, and territoriality on areas other than display sites. Investigators may gain some idea of the data needed for the American Woodcock by reading the excellent summarization by Witherby *et al.* (1940:184) of available data on the European species.

#### SUMMARY

During the early spring of 1939, a study of territoriality, display, and certain ecological relations of the American Woodcock was undertaken at Urbana, Champaign County, Illinois. From a small concentration of migrant Woodcocks present on the semi-wooded study area from March 5 to April 3, three established males were studied. They were confined to more or less definite feeding areas and to open-country, crepuscular-display territories.

A call-note of advertisement and warning, *peent*, is given repeat-

edly on the display territory when the occupant male is not performing a song-flight. Competition among neighboring males accelerates rate of calling. Normal, day-to-day variations in temperature do not appear to affect rate of calling. But the length of the crepuscular calling period tends to correlate directly with temperature variations; that is, calling periods are longer when daily temperatures are higher. There is undoubtedly a relation between light intensity and beginning and ending of crepuscular calling, but other factors complicate this relation.

The cackle note is given by an established male in assault and threat toward other birds who invade his territory or who occupy neighboring territories.

The song-flights of the male Woodcock function chiefly in territorial advertisement but may also function in intimidation. Neighboring males may compete through more frequent performance of the song-flight. The frequency with which the song-flight is performed does not appear to be affected by temperature. First song-flights were given during evening display periods when the light intensity fell to 1.0 to 0.5 foot-candles. Length of singing period as well as length of calling period tends to vary according to day-to-day temperature fluctuations.

Only the display sites of males are known to be defended, and at present only these can be termed territories. Manifestations of territoriality among established males are seen in competitive selection and maintenance of singing-fields, combat, overlap of display territories, efforts to displace neighbors through aggression, and increased vigor of singing and calling among closely neighboring males.

Feeding areas occupied by three males were 250 to 300 feet in diameter. Calling sites ranged from 50 to 75 feet in diameter, but territorial claims are asserted over larger areas, defined in part by outer limits of display flights. Single flights may cover areas of  $\frac{1}{3}$  to  $\frac{2}{3}$  of an acre. All flights of a single male may cover a total area of two to five acres.

Both male and female Woodcocks may strut when excited. Strutting is not necessarily a courtship display preliminary to mating.

Territorial males resent all intruders and assault them with the cackle note. Events subsequent to any intrusion are determined largely by responses of the intruder to intimidation.

American Woodcocks may become temporarily established on territories during the period of spring migration.

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