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THE SIGNIFICANCE OF RODING BY WOODCOCK *SCOLOPAX RUSTICOLA*: AN ALTERNATIVE EXPLANATION BASED ON OBSERVATIONS OF MARKED BIRDS

Roding is a display or advertisement flight in which the male Woodcock *Scolopax rusticola* travels above the woodland canopy calling repeatedly. Although roding occurs at dusk and dawn throughout the long breeding season (in Britain, late February to July), its biological meaning is not well understood and published information on the nature of the pair bond among Woodcock is inconclusive (see Shorten 1974: 39).

Tester & Watson (1973) concluded, from plotting the positions of interactions between roding birds and supposed outer flight paths of presumed different (but unmarked) birds, that roding flights defined the boundaries of the breeding ranges of individual males. They therefore interpreted roding flights as displays defining territories, as previously suggested by Warwick & van Someren (1936). This explanation is generally accepted.

On the other hand, both Steinfatt (1938) and Nemetschek (1977) have thought that roding served chiefly to find females ready to mate, and Hirons (1977), working on an area where some individuals were distinguished by voice, found that their roding grounds overlapped. The present paper reports observations of Woodcock fitted with radio-transmitters and confirms that roding areas are not exclusive. It appears that the real purpose of the male Woodcock's roding behaviour is to find or attract females with which to mate.

METHODS

The study was carried out in a 171 ha mainly deciduous wood in northeast Derbyshire (Whitwell Wood) 3 March–8 July 1978. This report is based mainly on the information gained from radio-tagging 10 male and two female Woodcock. A bantam decoy was used to catch roding males. By this technique (adapted from that described by Martinel & Chantrel 1977), when a roding male comes within sight of the observer in a hide the bantam is tossed out. Providing it is reasonably dark, roding birds react by flying straight towards the bantam and are caught in mist nets set around the hide. Fourteen roding males were caught and ringed, of which one was also fitted with a patagial tag Morgenweck & Marshall 1977) and ten were equipped with radio-transmitters with

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eighth-wave whip antennae, weighing between 3·5 and 8 g and having a life of 2–2·5 months. In seven cases the transmitters were strapped to the backs of the birds with an elastic harness passing around the breast, but on three birds harnesses of a different design were used consisting of thin latex saddles with wing holes cut out (Godfrey 1970). The latter harness proved unsatisfactory, because the rubber perished within three weeks and as a result the birds lost their transmitters. Two breeding females were also fitted with transmitters of the same configuration mounted on the elastic harness. Neither method of transmitter attachment appeared to interfere with the birds' normal behaviour. Woodcocks fitted with transmitters have roded, mated and laid eggs.

The receiving equipment used was a portable receiver (Type LA-12, AVM Instrument Company, Champaign, Illinois) operated with either a hand-held three-element unidirectional Yagi antenna, or a six-element Yagi mounted at the top of a 60-ft (18 m) tree. This equipment gave a maximum range of about 2 km when a bird was roding and a minimum of less than 300 m if it was on the ground in thick cover. Each transmitter emitted a pulsed signal of different wavelength within the 173 MHz waveband, thus allowing individual recognition of the radio-marked birds.

The roding areas of different radio-tagged males were determined by accumulating through the season all observations of marked birds passing overhead. Observations were made throughout the wood, mainly at the intersections of rides which allowed the longest view of roding birds. Even so, they could seldom be observed for more than a few seconds at a time from such places. Accordingly, additional direct observations of radio-tagged birds were made from the tops of trees and other vantage points. At high light intensities the flight paths of roding birds could be plotted accurately over considerable distances by reference to known landmarks. However, even when light levels were too low to see the roding bird some information on the extent of roding grounds could still be obtained by gauging the strength and direction of the radio-signals alone. Because the patagial tag fitted to one male was impossible to see from below, relatively few observations of this bird were made. Nonetheless they are included here for comparison with the observations of the radio-tagged birds.

All observations were plotted on maps (scale 1: 10 560) of the study area. Diurnal locations were determined by triangulation, usually at ranges below 50 m, as described by Godfrey (1967). The precision of fixes was checked regularly by flushing birds and should be within a quadrat of 0·025 acres (0·01 ha) according to Brander (1967).

RESULTS

The radio-tagged males did not maintain exclusive territories either for roding or for feeding. The areas over which seven of the marked birds were observed to rode overlapped considerably, and ranged from 43 ha (for the wing-tagged bird) to 132 ha in size (Fig. 1 and Table 1), much larger than the 6·02–12·75 ha estimates by Tester & Watson (1973). Furthermore, these areas are minimum estimates; the birds may have roded unrecorded outside the ranges plotted. On the other hand some birds did not fly over the whole of the area shaded in Figure 1 every evening. For example, on some days birds *O* and *R* roded only over the group of outlying woods 2 km northwest of Whitwell (see Fig. 1), on other evenings only over Whitwell Wood itself, and on others over both woodland areas on the same evening.

Less information was obtained for the other four radio-tagged males but these too roded over the same general area, as did an unknown number of unmarked birds. Other evidence against roding males being territorial was provided by many observations of more than one marked bird roding along the same flight paths on the same evening, sometimes less than a minute apart. There were also several evenings when more than one roding male was caught at the same bantam decoy while others flew uncaptured overhead.

Daytime locations of the roding birds are plotted in Figure 1. Again these provide no evidence for territoriality. During the breeding season male Woodcock spent much of the day feeding solitarily within the wood and marked birds were often recorded in the same area, sometimes less than 30 m apart.

On several occasions during the breeding season four of the radio-tagged males stopped roding for periods ranging from one to at least 11 days (Table 1). In every instance the marked male was found to be accompanying a second bird, and both would fly off together if flushed. The birds would then be found together every day, usually in the same small area to which they returned if flushed. On two occasions nests were subsequently found in this same area after the male had begun roding again; the second bird

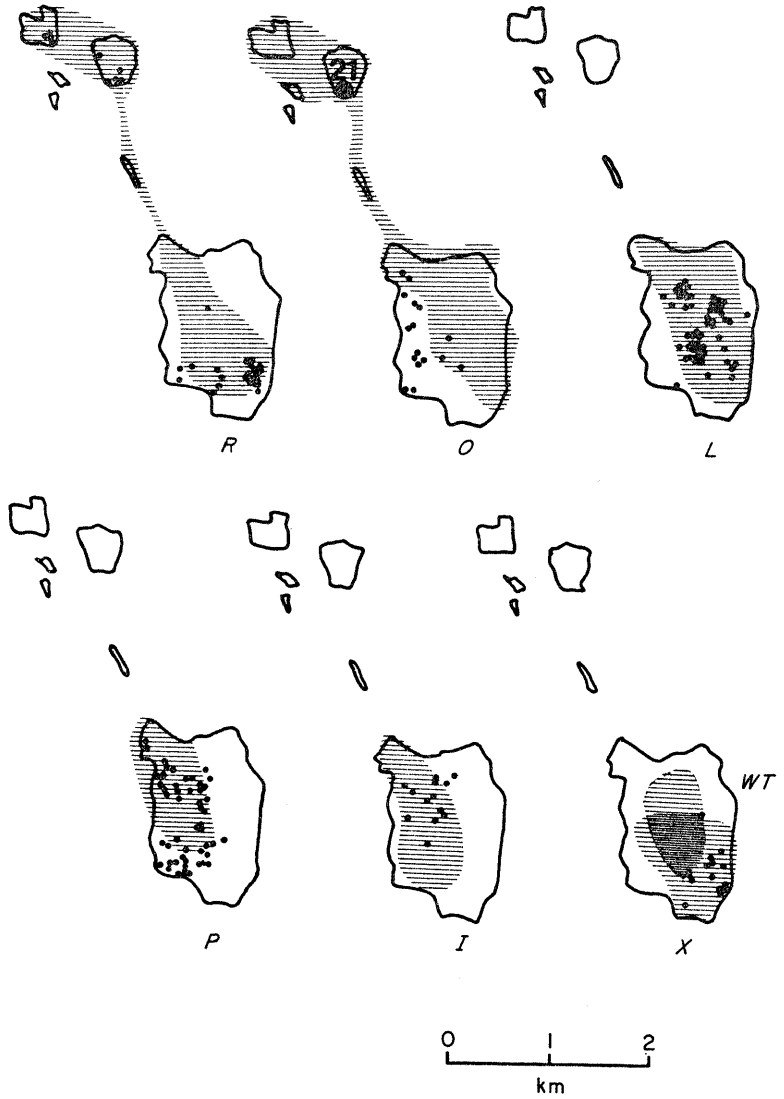

FIGURE 1. Roding grounds (shaded) and diurnal locations (filled circles) of seven individually marked male Woodcock (code letters as in Table 1) at Whitwell Wood and nearby copses March–July 1978. Diurnal locations are the first fixes obtained each day. Bird *WT* was not radio-tagged but was identified while roding by a patagial tag; there were no diurnal observations of this bird.

TABLE 1

The size of roding grounds and number of non-roding periods recorded for six radio-tagged (I, L, O, P, R, X) *and one wing-tagged* (WT) *male Woodcock in Whitwell Wood, Derbyshire, March–July 1978*

Identifying letter	Period observed	Size of roding ground (ha)	No. and duration of non-roding periods (days)
I	24 March–24 May	68	None
L	29 March– 7 July	126	Two (7, 8)
O	31 March–30 May	134	None
P	31 March– 7 July	61	Three [4, 2, (3)[1]]
R	17 April –17 June	120	Two (1, at least 11)
X	7 June – 7 July	66	One (5)
WT	19 March– 7 July	43	—

Note: [1] *P*'s transmitter failed on the third day.

was therefore presumed to be female. This was confirmed when a radio-marked female lost her clutch and was accompanied 36 h later by a radio-marked male. Similarly, a radio-tagged female was flushed with a second bird only 24 h after losing her brood and then on several subsequent occasions before she relaid 12 days later. Once a third bird flushed simultaneously a few metres from the other two.

There was no evidence that females were territorial. In April four clutches were found being incubated within a circle of radius 170 m, two nests being only 75 m apart. The radio-tagged female that relaid did so 300 m from her original site.

DISCUSSION

Agressive interactions occurred frequently between roding male Woodcock, as found by many previous workers (e.g., Nemetschek 1977, Janich 1977, Hirons 1977), but this obviously did not prevent several males from displaying over the same area (Fig. 1). Moreover the flight paths of individual roding males were not always consistent from one evening to the next. I conclude that roding flights do not define territory boundaries, although they may possibly deter rival males to some extent. It seems more likely that the roding display serves to attract the attention of females. The two radio-marked females flew comparatively seldom during the breeding season and the success of the bantam decoy demonstrated that roding Woodcock are interested in birds on the ground as well as in other displaying males. Nemetschek (1977) suggested that the height of the flight of displaying males was associated with visual scanning for mates, since males fly considerably lower at the end of the evening display when light intensities are low. Hoffmann (1867), Pay (1937), Steinfatt (1938) and Müller-Using (1970) all believed that the female utters an advertising call which is heard by the flying male and causes him to alight next to her; such behaviour was not recorded in Whitwell. However, if these observations are correct, initially at least, mate choice may be the prerogative of the female.

Many fundamental aspects of the Woodcock's breeding biology are not well understood (Shorten 1974) and it is not known whether females are double-brooded. However, as three of the radio-tagged males stopped roding for more than one period during the breeding season (Table 1) it is possible that they mated with more than one female, and one male certainly spent time with two different females. None of the radio-marked males incubated or cared for the young and at one nest studied only the (radio-tagged) female incubated. I conclude that the pair bond is transitory.

My interpretation of these data is that roding male Woodcock are probably successively polygynous but that, unlike other waders with polygynous mating systems, male Woodcock do not defend either an exclusive or specific area to which females are attracted and in which mating and/or nesting takes place. Instead a Woodcock displays solitarily at dusk and dawn over a wide area until he finds a receptive female. Then to ensure that he alone copulates with her he remains with the female constantly until the clutch is laid before resuming his display flights.

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HEAT LOSS FROM THE FEET OF MALLARDS *ANAS PLATYRHYNCHOS* AND ARTERIO-VENOUS HEAT EXCHANGE IN THE *RETE TIBIOTARSALE*

The feet of birds are generally naked and well vascularized and thus constitute an excellent avenue for heat dissipation. Previously it was thought that the heat produced during flight was lost primarily by evaporation from the respiratory system. However, recent experiments on Herring Gulls *Larus argentatus* have shown that most of the excessive heat is lost from the feet (Baudinette *et al.* 1976).

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