

EFFECTS OF THE ARRIVAL OF A NEW SPECIES UPON HABITAT UTILIZATION BY TWO FOREST THRUSHES IN MAINE

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WHEN the geographic range of a species expands strikingly over a short period of time, the student of populations is presented with an unusual opportunity. Such changes in status may bring new pairs of species into contact and provide insight into the roles of organism and environment in determining how potentially available habitats will be utilized by a complement of species.

Recent changes in the range of the Wood Thrush (*Hylocichla mustelina*) made such a study feasible. Since 1890 this species has become an addition to the breeding avifauna in many parts of the northeastern United States and adjacent Canada (Weaver *in* Bent, 1949). Before 1950 it was an uncommon summer resident in Maine (Palmer, 1949), the area considered in this study, but since that time it has become common through much of the state during the breeding season, judging from personal observations and from reports on file in the Portland Society of Natural History.

Preliminary information indicated that in certain cases Wood Thrushes had set up territories in areas frequented in earlier years by Hermit Thrushes (*H. guttata*) and Veeries (*H. fuscescens*). This study represents an attempt to supplement these observations and to determine what effects, if any, this incursion has had upon other forest thrushes in Maine.

METHODS

In 1965 I selected several habitats in two rather similar geographical localities of Maine and censused the three species of thrushes. In one locality Wood Thrushes were common and potentially in close contact with the other two species, and in the other one Wood Thrushes were uncommon. Most of the habitats utilized by the three species occurred in both localities, though their prevalence differed greatly in a few cases. Regularly singing birds were counted in relatively homogeneous habitats of the types listed in Tables 1 and 2. These habitats censused were sufficiently large (several hectares in size) that birds consistently singing there might be assigned to them with a high degree of probability. No attempt was made to census large areas exhaustively; rather the technique utilized was to record individuals encountered singing. In this way it was possible to obtain a representative ratio of the species of thrushes from each habitat, as far as the availability of the habitat and time made this possible. Censuses were conducted during early and mid-June, when all three species were singing regularly.

The first area, in Lisbon and Webster, Androscoggin Co., Maine, was selected within

the range where Wood Thrushes now are common summer residents. I have recorded them in this region regularly since 1952, and they have been common summer residents there since 1955.

The second area is a narrow strip of land not extending over two km from the ocean, running from the villages of Broad Cove (Bremen Twp.) to Round Pond (Bristol Twp.), Lincoln County, a distance of about 10 km. This study area lies approximately 70 km east of the first one. In 1965 Wood Thrushes were uncommon nesters in coastal Lincoln County, though they appeared to be increasing in numbers. Not until 1962 did I encounter apparent breeding birds in this area. Though Wood Thrushes in 1965 were not common in the area censused, they were conspicuously more common five km inland from the sea. A brief survey suggested that their numbers there approximated those in the Lisbon-Webster study area. Since it appeared that this species was continuing to increase in the coastal strip, an additional census was made there in 1967. At this time the areas studied in 1965 were resurveyed as closely as possible. However, due to extensive logging several of them had changed markedly, and consequently other similar areas were substituted where possible.

Hermit Thrushes and Veeries nest commonly in both localities censused. The only other species of this genus breeding in either of the areas is the Swainson's Thrush (*H. ustulata*), which frequents thick spruce forests immediately along the shore and on the islands in the Bremen-Bristol area. Though found in mixed coniferous-deciduous areas in some parts of its range (Knight, 1908; Palmer, 1949; Dilger, 1956a), Swainson's Thrushes nesting in this coastal strip showed little suggestion of such a selection. They were at no time found in contact with Wood Thrushes during the breeding season and hence are not considered further.

RESULTS

Overlap between species.—In the Lisbon-Webster area the Wood Thrush occupies regularly as wide a variety of potentially available habitats as does the Hermit Thrush and a wider set than the Veery (Table 1). On the average Wood Thrushes occupy both coniferous and deciduous areas that are moister than those used by Hermit Thrushes and drier than those used by Veeries. Hermit Thrushes in the study areas were most typically found in dry to mesic coniferous and deciduous forests, particularly in dry pine-oak situations. Veeries were most characteristic of damp deciduous forests. These areas are comparable to those in which the species were found by Dilger (1956a).

Considerable overlap of certain pairs of species was noted in the Lisbon-Webster region (Table 1), which in each case involved the Wood Thrush and another species. Hermit Thrushes and Veeries did not occupy any habitat in nearly equal numbers. Only in the mixed coniferous-deciduous forests with red maple and/or alder and mixed deciduous forests with red maple and/or alder were both Hermit Thrushes and Veeries regularly found. Even these data should not be interpreted to indicate that they utilized the two habitats similarly, since these habitats encompass a wider variety of conditions than most of the others in Tables 1 and 2. Within

TABLE 1
NESTING HABITATS OF THRUSHES IN LISBON-WEBSTER IN 1965

Habitat	Hermit Thrush	Wood Thrush	Veery
Red oak (<i>Quercus rubra</i>)	11	0	0
Red oak-white pine (<i>Pinus strobus</i>)	7	0	0
Cutover coniferous forest	6	0	0
Mixed coniferous forest	3	2	0
Old white pine (9 m or over)	9	1	0
Young white pine (under 9 m)	9	4	0
Mixed coniferous-deciduous forest with no red maple (<i>Acer rubrum</i>) or alder (<i>Alnus rugosa</i>)	8	4	0
Mixed coniferous-deciduous forest with red maple and/or alder	10	6	3
Young white pine-alder	1	7	1
Mixed deciduous forest with no red maple or alder	8	3	0
Mixed deciduous forest with red maple and/or alder	10	3	3
Red maple	0	13	8
Alder-red maple	0	5	4
Alder	0	0	15
TOTAL	82	48	34

the two habitats under consideration a tendency usually appeared for the three species to sort out, with Hermit Thrushes in the driest situations, Wood Thrushes in the most mesic, and Veeries in the wettest. No overlap was noted in the driest habitats between Hermit Thrushes and Wood Thrushes (red oak and dry oak-pine) or in the wettest habitat between Veeries and Wood Thrushes (alders). Thus, the Hermit Thrush and Veery enjoyed exclusive use of certain areas. Wood Thrushes were not found in any habitats to the exclusion of the two other species, though they did occupy young white pine-alder areas nearly to the exclusion of the other species.

Data upon Hermit Thrushes and Veeries from the Bremen-Bristol area in 1965 and 1967 reveal relatively few differences in the areas utilized by Hermit Thrushes and Veeries (Table 2). What overlap occurred between the two species was again in the mixed coniferous-deciduous forest with red maple and/or alder and in the mixed deciduous forest with red maple and/or alder. Again the species appeared largely to utilize different parts of the two last-mentioned habitats. The increase in numbers of the Wood Thrush in the Bremen-Bristol area is perhaps significant, however. Num-

TABLE 2
NESTING HABITATS OF THRUSHES IN BREMEN-BRISTOL IN 1965, 1967*

Habitat	Hermit Thrush	Wood Thrush	Veery
Red oak	9,9	0,0	2,0
Red oak-white pine	26,8	0,0	1,0
Red spruce (<i>Picea rubens</i>)	6,11	0,0	0,0
Cutover coniferous forest	6,8	0,1	0,0
Old white pine (9 m and over)	8,9	2,2	0,0
Young white pine (under 9 m)	3,2	0,2	0,0
Mixed coniferous-deciduous forest with no red maple or alder	3,9	0,0	1,1
Mixed coniferous-deciduous forest with red maple and/or alder	19,19	1,3	5,10
Mixed deciduous forest with no red maple or alder	14,5	0,0	0,1
Mixed deciduous forest with red maple and/or alder	4,5	0,1	8,7
Red maple	0,0	1,0	26,15
Alder-red maple	0,0	1,2	6,3
Alder	0,0	0,1	9,9
TOTAL	98,85	5,12	58,46

* Figures preceding commas refer to data from 1965; those following commas refer to 1967.

bers of Wood Thrushes were still too low in 1967 to reveal in great detail particular affinities of this species to any specific habitats, but those in which this species was noted correspond with those from the Lisbon-Webster census, suggesting that this species is colonizing areas that on the average are more mesic than those utilized either by Hermit Thrushes or Veeries.

The method used in gathering data does not permit a direct comparison with Dilger's (1956a) measurements of overlap in habitats of the species concerned. However, indices of overlap (R_o) from information theory were calculated (Table 3) for the data from Lisbon-Webster and Bremen-Bristol in 1967 (Tables 1 and 2), using the equation of Horn (1966):

$$R_o = \frac{\sum (x_i + y_i) \log (x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{(X + Y) \log (X + Y) - X \log X - Y \log Y}$$

Here X and Y equal the total number of observations in the samples of habitats X and Y, respectively; x_i and y_i equal the proportion of observations made in the i^{th} habitat category in samples X and Y, respectively. These figures indicate, as Tables 1 and 2 themselves suggest, that overlap between Wood Thrushes and Hermit Thrushes and between Wood Thrushes

TABLE 3
INDICES OF OVERLAP IN NESTING HABITATS BETWEEN PAIRS OF SPECIES*

	Lisbon-Webster, 1965		Bremen-Bristol, 1967	
	Wood Thrush	Hermit Thrush	Wood Thrush	Hermit Thrush
Hermit Thrush	0.52		0.62	
Veery	0.60	0.22	0.56	0.36

* N's as in Tables 1 and 2.

and Veeries is considerably greater than between Hermit Thrushes and Veeries. Due to the small number of data on the Wood Thrush from Bremen-Bristol in 1965, a set of indices was not calculated. Because of the greatly varying sample sizes in certain habitats in the two geographic areas, it is difficult to compare directly the indices from the two localities. However, the index of overlap between Hermit Thrushes and Veeries is substantially larger in the Bremen-Bristol area, where Wood Thrushes are not common, than in the Lisbon-Webster area.

Interspecific interactions.—Since the habitats utilized by Wood Thrushes overlap broadly those of Hermit Thrushes and Veeries, considerable efforts were made to learn the basis by which the ownership of territories was determined. It soon became apparent that relatively little direct hostile interaction occurred between the Wood Thrush and the other two species. During the period when censuses were made for Tables 1 and 2 individuals were restricted to territories that upon the basis of their songs and movements appeared largely exclusive of the other species.

On 27 May 1967 the first apparent hostile interaction between a Wood Thrush and a congener was observed, with a male Wood Thrush chasing briefly a male Hermit Thrush that was singing about 25 m from it in a mixed coniferous-deciduous forest. The early date plus the absence of encounters later in the season suggested that they occurred largely at the time that Wood Thrushes arrived and set up territories, and that such early encounters might act as a major factor in demarcating territories through the season. Such a situation was noted in formation of largely exclusive territories by Yellow and Chestnut-sided Warblers (*Dendroica petechia* and *D. pensylvanica*) (Morse, 1966). As a result in 1967, 1968, and 1969 attempts were made to observe interactions in the Bremen-Bristol area in late May and early June, the time of arrival of the Wood Thrush in this region.

On 1 June 1968 two interactions between Wood Thrushes and Veeries were noted. The first took place in a wet deciduous forest along the edge of a stream. Two Catbirds (*Dumetella carolinensis*) were engaged in a protracted hostile encounter, and during the process a number of other birds were attracted to the area, including a male Wood Thrush and a male Veery. Shortly the Wood Thrush flew in the immediate direction of the Veery, which then retreated. The Wood Thrush sang for five minutes

in this location, approximately 5 m up in a small red maple tree. After being supplanted the Veery moved approximately 75 m to the west and sang for this period of time about 15 m up in a large red maple. Then the Wood Thrush flew into the tree where the Veery was situated, and the Veery immediately ceased singing, but called several times and then flew about 100 m to the northwest, where it continued singing.

On the same day a male Wood Thrush was singing regularly in a moist mixed coniferous-deciduous forest, about 10 m up in a white pine. From here it flew about 75 m and attacked a Veery that was foraging nearby at ground level in a small open area. The Wood Thrush then sang in a small deciduous sapling immediately above where the Veery had been.

On 3 June a Veery was singing on the edge of a white pine forest and a moist deciduous area with low woody vegetation, consisting mostly of alders and willows (*Salix* sp.). A Wood Thrush, which had been singing in various perches in the pine forest at some distance (over 100 m) flew either into the pine where the Veery was singing or into the adjacent tree, and sang for two minutes. At the time that the Wood Thrush landed, the Veery flew out into the deciduous area and continued singing from there. After singing the Wood Thrush moved back into the midst of the pine forest and away from the Veery. Within 30 seconds the Veery returned to its previous position on the edge of the two habitats and commenced to sing.

On 28 May 1969 a Wood Thrush was noted singing in the driest part of a large alder thicket. A Veery then began calling about 30 m away in the wettest part of this thicket. Within 30 sec the Wood Thrush flew directly at the Veery, which immediately retreated from the area and became silent. The Wood Thrush sang in this location for two to three minutes before returning to its previous singing area. After approximately 30 minutes this Veery had moved south along a small stream about 50 m into an area adjacent to where another Wood Thrush was singing. This bird attacked the Veery and chased it repeatedly through the alders for over 45 sec, including several long flights. At one point the two birds nearly hit me as the Veery flew through this dense growth about one m above the ground, closely followed by the Wood Thrush.

Later visits to all of the areas where these encounters were noted indicated that overlap in territorial areas between species was extremely limited or nonexistent. These observations agree with the impressions of interspecific territoriality gained while making the observations reported in Tables 1 and 2. In spite of the extensive observations made on thrushes after early June upon no occasion were interspecific hostile encounters noted. Though these species are difficult to observe, the moderate number of observations made in the period of a week in late May and early June suggest that any such encounters after that time are considerably less frequent. At no time did I observe similar interactions between Hermit Thrushes and Veeries, though it was not possible to observe these species at the time of their arrival on the breeding grounds.

Territories held by different species in different years.—As indicated earlier this study was initiated because of the discovery that in two cases Wood Thrushes utilized essentially the same territories that were used the previous year by a Hermit Thrush and Veery, respectively. In 1956 in Webster a Wood Thrush used an elm (*Ulmus americana*) swamp and surrounding red maple cover that in 1955 had been the territory of a Veery.

Veeries did not nest there in 1956. Both the elms and maples in this territory averaged 15–20 m in height, and parts of the swamp remained damp through most of the summer. Since that year Wood Thrushes have utilized this plot regularly. In 1956 a pair of Wood Thrushes used a clump of white pines about 5 m in height on the edge of an old field undergoing succession, an area used by Hermit Thrushes in the previous year.

Accumulation of such data depends upon careful year-to-year censusing and mapping of territories, which had been performed for other purposes in the observations reported directly above. In 1967, two pairs of Wood Thrushes in Bremen occupied areas in young white pines that each overlapped approximately one-half of a Hermit Thrush territory of 1965. In no case was nearly direct correspondence of territories noted, as in the two cases in Webster. However, the apparent strong tendencies toward interspecific territoriality might result in such situations.

DISCUSSION

The apparent low frequency of hostile interactions among the different species during most of the season suggests that if separation of them is not entirely by habitat selection, it is performed quite rapidly by interactions at the beginning of the season. Separation of Hermit Thrushes and Veeries may be realized largely by habitat selection at this time, but separation of Wood Thrushes from Hermit Thrushes and Veeries apparently is not effected principally by this method. The Wood Thrush is significantly larger than the other two species (Dilger, 1956*a*) and appears to be socially dominant over the two smaller species. Colquhoun (1942) found a direct correlation between size of species and dominance in a closely-related group of European titmice in Europe. If a similar situation obtains here, judging from the absence of data from later in the season initial encounters may suffice to establish territorial boundaries, even though Hermit Thrushes and Veeries have established territories by the time that Wood Thrushes appear. The somewhat greater level of overlap between Hermit Thrushes and Veeries where Wood Thrushes are uncommon (Bremen-Bristol) suggests the possibility that limited interactions may occur between these two species; however, none were noted. The lower overlap between Hermit Thrushes and Veeries where Wood Thrushes were common in Lisbon-Webster probably was caused by the Wood Thrushes occupying habitats that were marginally mesic to the former two species.

Though Dilger (1956*b*) performed experiments on species recognition in five species of *Hylocichla*, he included no information upon interspecific encounters under natural conditions. The experiments are of interest to

this paper, however, since any one of the five species would attack a model of any of the five species placed in its territory if this model were silent. When vocalizations from a speaker accompanied the model, there was no response to it or it was reduced markedly in all but conspecifics. Clearly the major discriminatory cue presented in the experiments was the vocalizations. Among the three species with which we are presently concerned, occasional Wood Thrushes in Dilger's experiments showed a low intensity response to Hermit Thrush songs, but none showed a response to "hostile" (Dilger, 1956b) calls of Hermit Thrushes. No response was shown by Wood Thrushes to either songs or "hostile" calls of Veeries.

These experiments suggest that these species are not inevitably oblivious to each other. Judging from these data a silent bird may stand a strong chance of being attacked if it enters the territory of another individual of the same or another species. The models were not tested for motion or bodily carriage, and it is possible that differences of this sort could modify the effect. Since males are not constantly singing, and females do not apparently sing, there appears to be a chance that intruders would inadvertently be treated as conspecifics, even though the probability of such a response doubtlessly would be lower than for conspecifics. In four of the five interactions noted between Wood Thrushes and Veeries, the Veery initially was not singing or uttering a "hostile" vocalization.

If overt encounters are limited, one might anticipate that vocal responses would be of importance in maintaining such relationships, at least after initial encounters. This matter was not investigated, but the presence of some interspecific responses to playbacks in Dilger's work suggests the possibility of such vocal communication. Several species of closely related wood warblers respond markedly to vocalizations of congeners (Morse, 1966, 1967).

The range extension of the Wood Thrush is a phenomenon that could potentially lower the population size of the other two species within the area concerned. However, since certain habitats do not appear to be exploited regularly by the Wood Thrush, both the Hermit Thrush and the Veery retain virtual or absolute environmental refugia, and one would predict their continuing presence in an area in which both wet lowland forest and dry upland forest exist as recognizable entities.

SUMMARY

Studies were carried out in Maine to investigate the nature of interactions existing among species of breeding thrushes following the recent addition of Wood Thrushes to the breeding fauna. Wood Thrushes (*Hylocichla mustelina*) regularly encounter two other species of forest thrushes, Hermit Thrushes (*H. guttata*) and Veeries (*H. fuscescens*). Territories of Hermit Thrushes are in mesic to dry habitats, those of

Veeries are distinctly moist ones, and those of Wood Thrushes are in areas intermediate to these two. Only limited overlap occurs between Hermit Thrushes and Veeries, and they may presently sort out largely by habitat selection. Considerable overlap in habitats utilized occurs between Wood Thrushes and both Hermit Thrushes and Veeries. Wood Thrushes maintain interspecific territories, and the boundaries appear to be demarcated by encounters with Hermit Thrushes and Veeries as soon as the socially dominant Wood Thrushes arrive on their breeding grounds in the spring. Overt encounters between Wood Thrushes and the other two species after a week are either markedly reduced in frequency or nonexistent. The presence of Wood Thrushes potentially lowers the population sizes of Hermit Thrushes and Veeries, but the latter two species nest in certain habitats that are seldom if ever exploited by the Wood Thrush. Thus, in localities containing wet, mesic, and dry forests one would predict coexistence of the three species.

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