DIVERGENT PREY SELECTION IN TWO SPECIES OF WATERTHRUSHES (*SEIURUS*)

ROBERT J. CRAIG

Quinebaug Valley Community College, Danielson, Connecticut 06239 USA

ABSTRACT.—I studied Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes during an exceptionally dry spring to determine if environmental stress elicited interspecific competition. Previously, I had found little evidence for competition between these species despite wide overlap in foraging methods, use of foraging microhabitats, and characteristics of breeding habitat. I observed breeding adults forage by placing them in a portable flight cage located in natural habitat, and concurrently gathered data on the influence of waterthrush foraging on aquatic invertebrate prey and prey abundance. The species selected different prey. Louisiana Waterthrushes fed predominantly on Trichoptera larvae and on larger average prey than did Northern Waterthrushes, which fed predominantly on Diptera larvae. The species had similar foraging methods and attack rates, indicating that, unlike many Parulinae, their principal foraging differences were in prey selection rather than in means of locating prey. Experiments with foraging exclosures gave no clear evidence that waterthrushes affected prey biomass or composition. There was no significant relation between territory size vs. prey biomass and water cover. No interspecific aggression was observed, and territories overlapped widely, indicating that interference competition did not occur. Divergence in prey selection implies exploitive competition, but invertebrate and habitat data indicate that prey were not limiting, thus making competition for prey unnecessary. Therefore, from these data I cannot eliminate the alternative hypothesis that observed differences between the species may only reflect independent specialization. *Received 4 April 1986, accepted 29 September 1986.*

INCREASINGLY, the role of interspecific competition in shaping the ecology of avian species has been questioned. Ecological patterns traditionally interpreted in terms of competition may have alternative explanations (e.g. Confer and Knapp 1981, Jehl and Parkes 1983), and therefore the importance of autecology and behavioral limitations in influencing patterns has been assessed more carefully (e.g. Rotenberry 1980, Emlen 1981). Moreover, Wiens (1977) asserted that in variable environments competition plays an important ecological and evolutionary role only during periods of environmental stress when resources are limiting. In supporting this view, Mountainspring and Scott (1985) found evidence for only intermittent competition in Hawaiian bird communities. Similarly, Robinson (1981) found increased aggression between two vireo species (*Vireo*: Vireonidae) only when population density increased and, presumably, resources became limiting.

I studied resource use by Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes to determine whether interspecific competition occurs between the two species. Both are closely associated with wooded wetlands, and from spring arrival (mid-April) to the end of incubation (late May) about 80% of foraging occurs in water (Craig 1984, 1985). Previously, I found that they overlap widely in foraging methods, use of foraging microhabitats, and characteristics of their breeding habitat, but they are not interspecifically territorial. When precipitation in December 1984 to May 1985 was 14 cm below average, one of the driest winter-spring seasons on record (NOAA 1985), there was a particularly strong potential for resource limitation. I expected that if exploitive competition occurs, I would observe divergence in resource use, and if interference competition occurs, it would produce interspecific aggression and spatial divergence (see Maurer 1984).

STUDY AREA AND METHODS

I studied waterthrushes at Yale Forest, Ashford, Tolland Co., Connecticut. The habitat was described by Craig (1985). Briefly, it consists of a ravine, Boston Hollow, vegetated by mixed hardwood-hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*) forest with sections of stream and swamp along its base. In 1985 much of the area was noticeably drier than I had observed it since 1978; normally rushing springbrooks in the vicinity were nearly dry.

Early in the breeding season foraging overlap is greatest, foraging in water predominates, and available prey are largely limited to water. I gathered foraging and prey data in aquatic habitats from mid-April to the end of May, the period when competition seemed most likely to occur. However, I continued to make qualitative observations throughout the breeding season.

Foraging.—To observe foraging I constructed a portable 3.5 $m^2 \times 2$ m tall flight cage of 1.3-cm mesh crop netting on a modified aluminum tent frame. After mist netting a breeding adult, I erected the flight cage in the birds' territory over typical feeding habitat, which included water, mossy hummocks, mud, leaf packets, and shrubs, and observed foraging from a blind about 1 m away. I recorded on tape the duration of each foraging episode, number of predation attempts (attacks), foraging method used (i.e. pick, leaf pull, hawk, hover; see Craig 1984), prey size, and, when possible, prey identity. I limited observations on each bird to 90 min to minimize interference with breeding activities and to limit alteration in type of prey available. About 45 min elapsed from the time of capture to placing a bird in the flight cage, which provided some uniformity in hunger state among the birds studied.

Despite variation in behavior among individuals, I pooled data in analyses of foraging behavior, assuming that data sets were thus more representative of the population present. This seemed reasonable because I studied 50% of the breeders in Boston Hollow. However, subsets of the data were tested to assess individual variation. For analysis of attack rate and picking frequency I used data from observation periods with a minimum length of 30 s to obtain a measure of variation in behavior (Robinson and Holmes 1982). Because nearly all attacks were by either picking or leaf pulling, I did not analyze separately data on relative proportions of other foraging methods.

I believe this method of studying diet is preferable to analyses of stomach contents (e.g. Robinson and Holmes 1982) because it provides data not only on prey size and type but also on foraging methods. Moreover, it circumvents bias that is due to differential digestability of prey, and eliminates the danger of bird mortality caused by administration of emetics (Zach and Falls 1976).

To calculate overlap in foraging methods and prey selection I used the equation:

$$\text{overlap} = 1 - 0.5 \sum |p_{x_i} - p_{y_i}|,$$

where p_x and p_y are the frequencies of resource use of species x and y in category i (Schoener 1970). The index varies from 0, no overlap, to 1, complete overlap. To obtain a relative measure of prey preference, I used the method of Johnson (1980), which involves ranking the frequency of resource use and resource abundance and computing the difference in ranks. The values obtained indicate preference relative to other prey items present, with the highest negative values being most preferred and the highest positive values being most avoided.

Prey abundance.—I sampled invertebrates in the swampy upstream half (2 ha) of Boston Hollow, an area normally used by both waterthrush species. Doing so minimized effects of downstream invertebrate drift (Hynes 1970) because the wetland originates in this area and has little stream flow. On 16–17 April I sampled 10 swamp pools to determine the composition of invertebrate populations at the time of waterthrush arrival. At this time I also anchored 1 $m^2 \times 15$ cm high wire screening exclosures (1.5-mm mesh) 8 cm into the substrate of 10 pools. Exclosures eliminated all vertebrate predators except dusky salamanders (*Desmognathus fuscus*), which are also waterthrush prey. However, waterthrushes were probably the only important vertebrate predators on aquatic organisms; small mammals and frogs in the habitat take primarily terrestrial and flying prey, no fish are present, and there are no other important avian predators. On 21–22 May I sampled invertebrates in the 10 exclosures and also those at 10 different uncovered swamp pools.

To sample, I pressed a 0.5-m^2 wooden frame 5 cm into the pool substrate, removed with a flat metal scoop the top 3 cm of bottom debris, and then swept the water column (generally <4 cm deep) 10 times with 1.5-mm mesh wire net to remove any remaining organisms. At 2 sites I repeated the sampling procedure to assess the completeness of invertebrate removal. Once collected, I rinsed mud from the samples through a 1.5-mm mesh screen and froze the remaining debris and organisms. Later, I sorted organisms from debris, identified and measured them, and weighed each sample after drying to constant mass at 60°C. I resorted 2 samples to assess completeness of removal.

Territoriality and habitat.—I color-banded and measured 13 of 18 breeding adults present, mapped territories, and observed over 26 days for intra- and interspecific aggression. To assess separately the importance of amount of feeding habitat present, I further analyzed data on water cover and prey biomass collected from 1978 to 1980 using methods described by Craig (1984, 1985).

RESULTS

Foraging.—I gathered data on 4 of 6 Louisiana Waterthrush and 5 of 12 Northern Waterthrush breeders present in Boston Hollow.

TABLE 1. Selection of principal invertebrate prey taxa as a percentage of total prey. Observed captures are in parentheses.

	Seiurus motacilla	*Seiurus noveboracensis*
Diptera	20.3 (13)	54.7 (66)
Trichoptera	40.7 (24)	11.0 (13)
Ephemeroptera	13.6 (8)	13.6 (16)
Oligochaeta	13.6 (8)	5.1 (6)
Isopoda	3.4 (2)	4.2 (5)
Total captures	59	118

Louisiana Waterthrushes (59 total prey) ate Trichoptera larvae significantly more often than did Northern Waterthrushes (118 total prey, adjusted $\chi^2 = 22.6$, $P < 0.01$; Table 1). In contrast, Northern Waterthrushes preyed on Diptera larvae (mostly Chironomidae) significantly more often than did Louisiana Waterthrushes (adjusted $\chi^2 = 17.1$, $P < 0.01$). Overlap in selection of the 5 most common prey groups (Table 1) that include 91.5% of Louisiana Waterthrush prey and 88.1% of Northern Waterthrush prey was 0.59. In comparisons of 3 males of each species I found significant differences between individuals in use of Trichoptera (Louisiana Waterthrush: $\chi^2 = 8.3$, 2 df, $P < 0.05$; Northern Waterthrush: $\chi^2 = 12.4$, 2 df, $P < 0.01$) and Diptera (Louisiana Waterthrush: $\chi^2 = 16.5$; Northern Waterthrush: $\chi^2 = 25.1$; both 2 df, $P < 0.01$). I could not separate the effects of flight-cage placement from those of individual preferences.

I considered other prey too infrequently selected for trends to be analyzed meaningfully; larger samples are necessary to compensate for the heterogeneous distribution of invertebrates. Because I could not identify some prey in small size classes, my findings are also biased in favor of larger taxa.

Other prey types eaten included Odonata (dragonfly) nymphs, Dytiscidae larvae, Tipulidae larvae, and diplopods by Louisiana Waterthrushes, and *Desmognathus*, Lepidoptera (moth) adults, Sialidae nymphs, Tipulidae larvae, Formicidae adults, diplopods, chilopods, and gastropods by Northern Waterthrushes. In addition, both species chased but did not catch flying adult Ephemeroptera and Diptera. Only 7 of 177 identifiable prey were nonaquatic.

TABLE 2. Percentage use of foraging methods by two waterthrush species. Observed foraging episodes are in parentheses.

	Seiurus motacilla	*Seiurus noveboracensis*
Pick	50.5 (435)	53.4 (945)
Leaf pull	48.7 (419)	45.9 (812)
Hawk/hover	0.8 (7)	0.7 (12)
Total	861	1,779

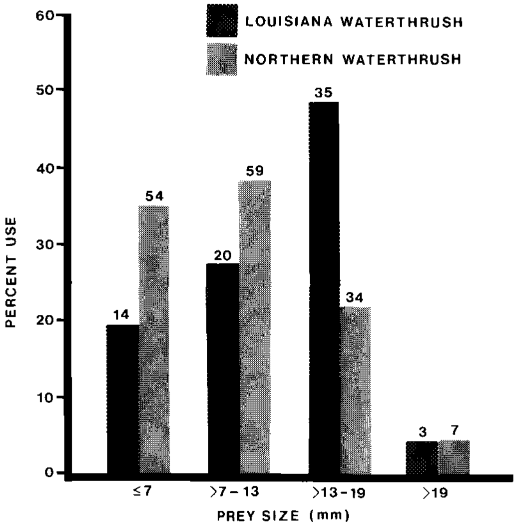

Fig. 1. Selection of prey sizes. Sample sizes are given at the top of each bar.

By comparing bill to prey length in the field, I could identify 4 prey-size categories: ≤7 mm, >7-13 mm, >13-19 mm, and >19 mm. Northern Waterthrushes took a significantly lower range of prey sizes than did Louisiana Waterthrushes ($\chi^2 = 16.9$, 3 df, $P < 0.01$; Fig. 1). Overlap between the species in selection was 0.73. Moreover, Louisiana Waterthrushes had significantly longer bills (1.43 ± 0.10 cm, $n = 10$) than Northern Waterthrushes (1.29 ± 0.06 cm, $n = 20$; $t = 4.9$, $P < 0.01$). In comparisons of 3 males/species I found significant individual differences in prey-size selection by Louisiana Waterthrushes ($\chi^2 = 18.5$, 3 df, $P < 0.01$) but no significant differences between Northern Waterthrushes ($\chi^2 = 6.5$, 3 df, $P > 0.05$). Again, I could not assess the relative importance of individual preference vs. flight-cage placement in determining individual differences.

I found little difference between the species in attack rate ($t = 1.4$, 144 df, $P > 0.05$, log-transformed data; Louisiana Waterthrush: 10.1 ± 8.0 s/attack, $n = 67$; Northern Waterthrush: 9.1 ± 8.9 s/attack, $n = 79$). Analysis of

TABLE 3. Taxonomic composition of aquatic invertebrates in samples from swamp pools collected 5 weeks apart (mean no./m² ± SD).

Taxon	Sample		
	April	May control sites	May exclosure sites
Isopoda	167.4 ± 117.3	150.8 ± 82.2	83.0 ± 45.9
Plecoptera	54.2 ± 81.6	94.2 ± 121.2	43.0 ± 32.6
Ephemeroptera	24.2 ± 32.3	64.2 ± 72.9	33.3 ± 51.4
Trichoptera	50.4 ± 45.2	36.4 ± 27.3	35.8 ± 32.0
Diptera	32.6 ± 23.6	41.6 ± 36.1	80.5 ± 85.3
Coleoptera	14.0 ± 6.8	11.0 ± 6.1	3.3 ± 2.4
Megaloptera	7.2 ± 5.2	12.8 ± 14.4	12.5 ± 12.9
Gastropoda	7.8 ± 8.7	18.0 ± 12.6	2.5 ± 1.8
Oligochaeta	5.2	0.8	0.2
Odonata	0.4	0.2	0.2
Hirudinea	0.2	0.6	0.8
Desmognathus	0.4	0	0.2

variance on a randomly selected, balanced subset of data from 3 males/species, which facilitated performing F tests and eliminated possible variance because of sexual differences, confirmed the nonsignificance of interspecific differences ($F < 0.1$, 1,78 df, $P > 0.05$) and also showed no significant difference between individuals ($F = 3.1$, 4,78 df, $P > 0.05$).

In the flight cage the species used foraging methods (Table 2) in proportions similar to those of free-ranging birds in early spring (Craig 1984). Overlap in use of methods was 0.97, compared with 0.98 calculated from data collected on free-ranging birds from 1978 to 1980 (Craig 1984). The species did not differ significantly from each other in their use of the methods ($\chi^2 = 2.0$, 2 df, $P > 0.05$), and the percentage of picking for observations >30 s showed no significant interspecific difference ($t = 1.5$, 132 df, $P > 0.05$, arcsine$\sqrt{}$-transformed data; Louisiana Waterthrush: 68.4 ± 30.5%, $n = 55$; Northern Waterthrush: 64.7 ± 28.6%, $n = 77$). Analysis of variance on a subset of data from 3 males/species again showed no significant interspecific difference ($F < 0.1$, 1,30 df, $P > 0.05$) but a significant difference between individuals ($F = 12.0$, 4,30 df, $P < 0.01$). The relative importance of flight-cage placement and individual preference in determining individual differences could not be assessed.

Although data on foraging methods suggested that caged birds behaved similarly to free-ranging waterthrushes, I compared data gathered from the first 45 min of flight-cage observations with those of the last 45 min to determine if duration of observations affected results. Results were nonsignificant for prey size (Louisiana Waterthrush: $\chi^2 = 0.7$; Northern Waterthrush: $\chi^2 = 6.8$; both 3 df, $P > 0.05$), attack rate (Louisiana Waterthrush: $t = 0.3$, 35 df; Northern Waterthrush: $t = 0.7$, 64 df; both $P > 0.05$, log-transformed data) and foraging methods (Louisiana Waterthrush: $t = 0.2$, 23 df; Northern Waterthrush: $t = 0.2$, 62 df; both $P > 0.05$, arcsine$\sqrt{}$-transformed data). Results were

TABLE 4. Size distribution of invertebrate samples (mean no./m² ± SD).

Size class (mm)	Sample		
	April	May control sites	May exclosure sites
≤4	8.0 ± 5.6	4.0 ± 3.0	3.5 ± 2.6
>4–7	84.2 ± 90.4	147.2 ± 122.2	90.5 ± 77.4
>7–10	118.4 ± 76.2	170.4 ± 69.8	109.3 ± 32.1
>10–13	66.8 ± 47.5	66.2 ± 37.0	56.0 ± 24.2
>13–16	24.4 ± 17.2	25.0 ± 20.4	16.5 ± 9.4
>16–19	11.0 ± 10.2	7.4 ± 8.3	7.8 ± 6.5
>19–22	8.4 ± 10.1	8.0 ± 9.2	8.3 ± 7.2
>22	11.2 ± 10.1	13.8 ± 13.6	12.8 ± 7.0

TABLE 5. Ranking of prey selection by waterthrushes.

		Seiurus motacilla		*Seiurus noveboracensis*	
	Abundance rank[a]	Use[b]	Difference[c]	Use[b]	Difference[c]
Prey size (mm)					
≤ 7	2	3	+1	2	0
>7-13	1	2	+1	1	0
>13-19	3	1	−2	3	0
>19	4	4	0	4	0
Taxa					
Isopoda	1	5	+4	5	+4
Ephemeroptera	2.5	3.5	+1	2	−0.5
Trichoptera	2.5	1	−1.5	3	+0.5
Diptera	4	2	−2	1	−3
Oligochaeta	5	3.5	−1.5	4	−1

[a] Abundance rank in relation to other sizes or taxa, with most frequent classes receiving lowest numbers.

[b] Frequency of use in relation to other sizes or taxa.

[c] Computed by subtracting use from abundance ranks; positive values indicate relative avoidance, negative values indicate relative preference.

also nonsignificant for Louisiana Waterthrush use of Trichoptera (adjusted $\chi^2 = 2.1$, $P > 0.05$), but significant for Northern Waterthrush use of Diptera (adjusted $\chi^2 = 6.9$, $P < 0.01$). During the first 45 min 35.7% of prey were Diptera, whereas during the second 45 min 63.9% of the prey were Diptera.

Prey.—Based on averages from April and May samples taken outside exclosures, the principal aquatic invertebrates present as potential prey during the spring were isopods (*Asellus*), Ephemeroptera nymphs, Diptera (mostly Chironomidae) larvae, and Trichoptera larvae. No significant change occurred in the frequency of taxa between April and May (Table 3), nor in biomass (April: 1.46 ± 0.85 g, May control: 1.21 ± 0.51 g; $t = 0.3$, 18 df, $P > 0.05$, log-transformed data) or size frequency (Table 4). Although data were not comparable quantitatively because sampling methods differed, Culicidae larvae, Helodidae larvae, and Gastropoda (*Physa*) were much less common but Plecoptera nymphs were much more common than they were from 1978 to 1980.

Comparison of unprotected sites with exclosures (1.00 ± 0.25 g) showed no significant difference in invertebrate biomass ($t = 0.9$, 18 df, $P > 0.05$, log-transformed data). However, isopods (Wilcoxon two-sample $T = 52$), gastropods ($T = 48$), and Coleoptera ($T = 39$, all $P > 0.05$) were significantly less common inside the exclosures than at unprotected sites. The Diptera averaged considerably more common inside the exclosure, but not significantly so (Table 3). For size classes, only the >7-10-mm size class was significantly less common inside the screen exclosures (Table 4), which was due principally to reduced numbers of isopods ($T = 51$, $P < 0.05$), the most numerous group in this class.

Analysis of resorted invertebrate samples indicated that initial sorting removed >95% of the individuals and biomass present. Resampling the same site showed that >95% of organisms and biomass were in the initial sample, and therefore biomass figures should be increased by at least 10% to obtain absolute estimates.

By averaging data from April and May control samples, I determined the abundance rank of invertebrate size classes and the 5 most frequent waterthrush prey (Table 5). Because Ephemeroptera and Trichoptera were nearly equally abundant in samples, I considered their rank to be tied. Including only the most common prey is valid in this nonparametric method because only relative preferences are determined (Johnson 1980). Comparison of use and abundance ranks showed that Louisiana Waterthrushes avoided small prey relative to large prey, most strongly preferred Diptera larvae, and strongly avoided isopods. In contrast, Northern Waterthrushes showed no preference for prey size, most strongly preferred Diptera larvae, and strongly avoided isopods.

Territory and habitat.—In 1985 2 pairs of Louisiana Waterthrushes and 6 pairs of Northern Waterthrushes inhabited Boston Hollow. This was the same as in 1984, and differed little from numbers present in 1979 (Louisiana Waterthrush: 3 pairs, Northern Waterthrush: 6 pairs) and 1980 (Louisiana Waterthrush: 3 pairs, Northern Waterthrush: 5 pairs). As in previous years, in 1985 both species exhibited intense intraspecific aggression, no interspecific aggression, and extensive territorial overlap.

Multiple regression analysis of data on prey biomass, water cover, and territory size from 8 territories per species collected from 1978 to 1980 (data reported in Craig 1984) showed no significant associations for either species (Louisiana Waterthrush: $F = 3.8$, multiple $r = 0.78$,

$P > 0.05$; Northern Waterthrush: $F = 1.5$, multiple $r = 0.60$, $P > 0.05$). Louisiana Waterthrush territories had the highest correlation with water cover ($r = -0.63$), but those of Northern Waterthrushes were most highly correlated ($r = -0.53$) with prey biomass.

DISCUSSION

The similarity in use of foraging methods between captive and free-ranging birds strongly suggests that the flight cage hardly altered foraging behavior of residents and therefore was useful in observing the details of foraging. The similarity of behavior recorded during the first and second halves of each observation period supported this view. However, predation was limited to invertebrates present in the cage. Because invertebrate distribution is heterogeneous (Hynes 1970, this study), additional investigations are required to assess the influence of invertebrate microdistribution on individual behavior. The lone significant difference for Northern Waterthrush predation on Diptera during the first and second halves of the observation period may be a reflection of this heterogeneity.

Despite this unquantified source of variance, several major differences in foraging were evident. The species preferred different prey types and different ranges of prey size. Consequently, overlap between the species in selection of prey size and type was considerably less than that previously calculated for foraging methods or selection of foraging microhabitats (Craig 1984). Differences in prey use are probably related to the prey handling capacity of the species; the larger bills of Louisiana Waterthrushes should make them more effective at handling larger prey (Hespenheide 1973) than Northern Waterthrushes. In contrast to prey use, measures of attack rate and picking frequency showed these behaviors to be highly variable and with little interspecific difference. Unlike many other species of Parulinae (e.g. MacArthur 1958) foraging differences in waterthrushes are principally in prey selection rather than in method of locating prey.

The two species exploited the same invertebrate prey resource differently in relation to its abundance. The Louisiana Waterthrush was relatively selective compared with the Northern Waterthrush. The larger size of the Louisiana Waterthrush (Craig 1985) increases its metabolic requirements (Calder and King 1974), and likely drives its preference for larger prey. This greater selectivity may also explain the preference by Louisiana Waterthrushes for habitats with fast-moving water (Craig 1985), which contain a higher density of large invertebrates than do habitats with slow-moving water (Craig 1984).

In both species preference for prey type is probably in large part a consequence of preference for prey size. For example, average April–May data on invertebrates showed that 63.8% of Trichoptera larvae available are >13 mm and 100% of Chironomidae larvae available were ≤13 mm. However, certain prey, notably isopods, were strongly avoided regardless of size. Isopods burrow, which may make them more difficult to catch, and they also may be relatively unpalatable. Their burrowing ability also may explain why they were less common inside the exclosures. Similarly, the slow-moving, thick-bodied Trichoptera are very profitable prey (Ormerod 1985a), and thus particularly suitable for Louisiana Waterthrushes.

My findings on prey selection may provide a mechanism for coexistence by these ecologically similar species. Indeed, the findings illustrate a degree of ecological separation between the species undemonstrated previously, but for partitioning to be necessary resources must be limiting. In exclosure experiments I found that the waterthrushes appeared to have little clear effect on the biomass or composition of their prey populations. A general decline in biomass and numbers compared with control samples indicated possible negative effects of the exclosures on invertebrates, but such effects were limited principally to groups not heavily used by waterthrushes. Certainly, waterthrushes must affect invertebrate levels to some extent, evidence of which is provided by the increase (nonsignificant) of Diptera inside exclosures. However, only major influences are detectable because, as indicated by the large standard deviations in Tables 3 and 4, the distribution of invertebrates was very heterogeneous. Nevertheless, if the species reduced prey to limiting levels, such a major drop in invertebrate populations most likely would be observed.

Other studies (e.g. Holmes et al. 1979, Schneider and Harrington 1981) have shown major impacts of birds on invertebrate prey, even in experiments where prey could leave foraging exclosures (Askenmo et al. 1977). The impact disappears during peaks of invertebrate populations, however, when birds can no longer track the increase in availability (Otvos 1979). I propose that this mechanism accounts for my failure to detect appreciable impact by the waterthrushes on their prey. Even though I report that population levels of at least several prey taxa were particularly low in Boston Hollow during 1985, the high productivity of wetlands is well known (Keefe 1972). During the 5 weeks between sampling dates Culicidae matured from eggs to adults and there were major hatches of Plecoptera, Ephemeroptera, Simuliidae, and Chironomidae. Furthermore, waterthrushes also eat the foliage insects that begin to appear toward the end of the period, so it appears that the few birds present had little impact on their prey.

The weak association of prey-related factors with territory size, which should expand as prey or feeding habitat decline if they are limiting, provides additional support for the idea that neither species is limited by prey. Instead it appears that territory size is more closely related to social factors; I have observed territories of both species being halved after the arrival of new territorial males. The constant number of waterthrush pairs present over 4 years despite the dry winter and spring of 1985 further argues against close coupling of populations with prey abundance. This is in contrast to the findings of Ormerod (1985b), who found that the population density of the ecologically convergent Eurasian Dipper (*Cinclus cinclus*) was related to prey density. The Dipper is a permanent resident, however, so its populations are more likely to be closely associated with local conditions than are those of the neotropical migrant waterthrushes.

The Louisiana and Northern waterthrushes showed important differences in prey usage at Boston Hollow, although they used similar behaviors to locate prey. These differences indicate that exploitive competition can occur under certain conditions, and that it may be avoided by divergence in resource use. Evidence for prey limitation was weak, however, so there was no clear need to avoid competition. Moreover, as in earlier studies (Craig 1984, 1985), there was no indication of interference competition between the species. Based on these observations it is impossible to rule out the hypothesis that observed patterns are the product of independent evolutionary specialization, as opposed to the result of interspecific competition.

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