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TERRITORIAL RESPONSES TO SONG PLAYBACK IN ALLOPATRIC AND SYMPATRIC POPULATIONS OF ALDER (*EMPIDONAX ALNORUM*) AND WILLOW (*E. TRAILLII*) FLYCATCHERS

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ABSTRACT.—Previous studies have shown little response of territorial Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers to heterospecific song playback within their range of breeding overlap, suggesting the absence of interspecific territoriality. However, the same species clearly exhibit interspecific breeding territories in shared habitats in southern Ontario. Such conflicting observations may have resulted from previous studies being conducted in habitats where only one of the species was present. In an attempt to reconcile these different observations, the responses of both species to heterospecific song playback in sympatric and allopatric populations were compared near Guelph, Ontario. I hypothesized that aggressive responses to heterospecific song should occur only in shared habitats. Both species took significantly less time to approach, moved closer, and spent more time near the sound source, and more frequently elicited aggressive vocalizations in response to heterospecific song in shared habitats. The virtual absence of response by either flycatcher in allopatric populations suggests that both species learn, through coexistence, to recognize the heterospecific song as that of a potential competitor. In addition, the responses of Willow Flycatchers to both con- and heterospecific song were more aggressive than that of the Alder. Recent range expansions of the Willow Flycatcher into areas historically occupied by the Alder Flycatcher may in part be due to interspecific dominance. *Received 9 Sept. 1986, accepted 18 Mar. 1987.*

Numerous studies have shown that bird species with similar feeding ecology defend interspecific territories (Orians and Willson 1964, Cody 1969, Gorton 1977, Reed 1982), and respond aggressively to tape playbacks of heterospecific song types (Emlen et al. 1975, Gorton 1977, Reed 1982). A few investigators have observed that the aggressive response towards interspecific song types is more intense in areas where ecologically similar species occur together, but may be absent in allopatric ranges (Emlen et al. 1975, Falls 1978, Catchpole and Leisler 1986). Such observations suggest that the recognition of close competitors is dependent on prior competitive experience with heterospecific individuals (Falls and Szijj 1959, Catchpole 1978, Richards 1979, Catchpole and Leisler 1986).

The Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers are morphologically almost identical sibling species of different song types (Willow: *fitz-bew*; Alder: *fee-bee-o*) that frequently coexist in habitats within their range of breeding overlap (Zink and Fall 1981, Barlow and

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McGillivray 1983). Both species feed primarily on invertebrates, and, where they coexist, use similar foraging strategies (Barlow and McGillivray 1983). Hence, competition for food between these species, if it occurs, should be maximal in shared habitats, and selection should favor the development of interspecific territories (Orians and Willson 1964). This prediction is supported by observations made during a two-year study of the territorial behavior of the Willow Flycatcher in southern Ontario (Prescott 1986): both species vigorously excluded the other from their breeding territories. In contrast, both Stein (1958, 1963) and Barlow and McGillivray (1983) have reported that during playback experiments within the range of sympatry, both species tended not to respond agonistically to the heterospecific song. It is not clear from these studies, however, whether or not both species coexisted in all habitats where experiments were conducted, although in a few instances, Stein (1958:22, 1963:34) reported that certain males of both species responded to playback of both song types, implying occupation of shared habitat.

If prior experience with the heterospecific song is necessary for the development of interspecific territoriality, it is possible that earlier studies were completed, for the most part, in habitats containing only a single *Empidonax* species. In this study, I report the responses of Alder and Willow Flycatchers to tape playback of conspecific and heterospecific songs in both exclusive (allopatric) and shared (sympatric) habitats. I hypothesized that if the recognition of a close competitor is a learned response, then agonistic behavior directed towards the heterospecific song type, and therefore interspecific territoriality, should occur only in sympatric populations.

METHODS

Playback experiments were conducted at 8 sites within 35 km of Guelph, Ontario (43°32'N, 80°13'W), during the breeding season of 1985. Willow and Alder flycatchers occurred allopatrically in three and two habitats, respectively, and sympatrically in three habitats. Other sites in the region supported flycatcher populations, but because interspecific recognition might result from cohabitation with a heterospecific during previous breeding seasons (Emlen et al. 1975), only those habitats where the composition of flycatchers was known to be similar over two breeding seasons were chosen for investigation. Allopatric and sympatric flycatcher populations were separated by at least 3 km to minimize the possibility of contact between populations.

Because territorial defense in Alder and Willow flycatchers is achieved primarily through song (Stein 1958), and because these species are virtually identical in appearance, I consider here only the responses to auditory stimuli. A 150-sec tape of each song type (approx. 10 songs/min) was assembled from commercially available bird song records (Peterson 1975, National Geographic Society 1983), and played to territorial flycatchers in the field on a Sanyo model M2566 portable cassette recorder. Because territorial response to song in flycatchers varies with the time of the breeding season (Barlow and McGillivray 1983), trials were conducted only during the month of June, corresponding to the nest building and incubation periods of these species (Bent 1942, pers. obs.). A 3-in (7.6-mm) speaker was projected vertically from the approximate center of the territory under investigation (see Prescott 1986 for details on territory mapping), at a 10–12 m distance from the observer. Both song types were played to the same territory holder approximately 30 min apart, the order of presentation being determined by a coin toss. Playback began when the male was seen advertising from a prominent perch >30 m from the speaker. The tape was played to completion, during which time the following responses of the territory holder were recorded: (1) time taken by the bird to approach to within 8 m of the speaker (only if accompanied by aggressive vocalizations or displays, see below), (2) closest distance approached, (3) time spent within <3 m of the speaker, (4) number of *whit* calls, (5) number of *wee-oo* calls, (6) number of *churr* calls, and (7) presence of attacks (threat displays <0.25 m from speaker). The above vocalizations are common to both species, and represent increasing levels of agitation (Stein 1958, pers. obs.).

Individual birds were tested from 2 to 5 times during the study period. In order to prevent habituation to songs (Weeden and Falls 1959, Emlen 1972), a period of at least 5 days was allowed between playback sessions. Responses of each species to conspecific and heterospecific songs were pooled for sympatric and allopatric populations, and compared using Mann-Whitney *U*-tests (Sokal and Rohlf 1969). In addition, I compared the relative responses of Willow and Alder flycatchers to their own song with responses to the opposite pattern of song. This was done in order to test whether the response of the Willow is, in general, more intense than that of the Alder (Stein 1963).

RESULTS

Of 98 playback experiments conducted during the study period, 53 were conducted on 15 individual Willow Flycatchers (8 sympatric, 7 allopatric) and 45 on 13 Alder Flycatchers (6 sympatric, 7 allopatric). Responses to tape playback were essentially "all or nothing." Birds that did not respond either remained on their perch without vocalizing, or engaged in other activities without approaching the speaker. Birds that responded to either song type typically did so immediately. The first response of a perched bird was usually to orient towards the speaker, with an accompanying increase in the frequency of *whit* or *wee-oo* calls. Flights towards the sound source usually occurred within 10 sec of the initiation of the playback, and were followed by frequent perch changes and short flights over and around the speaker. *Churr* calls were usually only given within 4 to 5 m of the speaker, and were accompanied by agonistic body postures including crest-raising, feather-spreading, tail-pumping, and wing vibrations (see Stein 1958). Agitated birds usually moved away (>10 m) from the speaker after 60 to 90 sec, but continued to vocalize for the duration of the test.

Responses to heterospecific song type.—There were clear differences between sympatric and allopatric populations of both species in the responses to heterospecific song playback (Table 1). Both Alder and Willow

TABLE 1

RESPONSES OF ALDER AND WILLOW FLYCATCHERS (MEAN ± SE) TO HETEROSPECIFIC SONG PLAYBACK IN SYMPATRIC AND ALLOPATRIC POPULATIONS NEAR GUELPH, ONTARIO

Response	Alder response to Willow song			Willow response to Alder song			Species comparison[b]
	Sympatry (N = 24)	Allopatry (N = 21)	P[a]	Sympatry (N = 29)	Allopatry (N = 24)	P[a]	
Time to approach <8 m (sec)	19.8 ± 1.7	133.2 ± 9.2	<0.0001	19.7 ± 1.8	122.9 ± 11.1	<0.0001	>0.05
Closest distance (m)	3.3 ± 0.3	15.3 ± 1.5	<0.0001	3.7 ± 0.4	13.2 ± 1.5	<0.0001	>0.05
Number of *whits*	12.5 ± 0.8	4.1 ± 0.8	<0.0001	14.2 ± 1.0	5.2 ± 0.9	<0.0001	>0.05
Number of *wee-oos*	5.3 ± 0.6	1.5 ± 0.4	<0.0001	8.1 ± 0.7	2.2 ± 0.7	<0.0001	<0.005
Number of *churrs*	3.6 ± 0.4	0.7 ± 0.2	<0.0001	5.7 ± 0.6	1.8 ± 0.7	<0.0001	<0.05
Time spent <3 m (sec)	8.5 ± 1.6	0.0 ± 0.0	<0.0001	7.4 ± 1.6	2.6 ± 1.5	<0.05	>0.05
Number of tests with attacks	1	0	—	2	1	—	—

[a] Probability of species difference in response between sympatric and allopatric populations.
[b] Probability of species difference in sympatric populations.

TABLE 2

COMPARATIVE RESPONSES (MEAN ± SE) OF TERRITORIAL ALDER AND WILLOW FLYCATCHERS TO CONSPECIFIC SONG PLAYBACK

Response	Alder Flycatcher (N = 45)	Willow Flycatcher (N = 53)	*P*[a]
Time to approach <8 m (sec)	18.8 ± 1.0	13.0 ± 0.9	<0.0001
Closest distance (m)	3.4 ± 0.2	3.4 ± 0.3	>0.05
Number of *whits*	14.4 ± 0.8	18.7 ± 0.9	<0.01
Number of *wee-oos*	4.5 ± 0.4	10.1 ± 1.7	<0.0001
Number of *churrs*	3.4 ± 0.4	7.0 ± 0.5	<0.0001
Time spent <3 m (sec)	8.1 ± 1.6	10.9 ± 1.7	>0.05
Number of tests with attacks	1	4	—

[a] Probability of a species difference using Mann-Whitney *U*-tests.

flycatchers responded much more aggressively ($P < 0.05$) in all behavioral categories to the heterospecific song in habitats where both species were present than where only one species occurred. In general, responses by birds to the opposite song were absent in allopatric populations, although a single Alder Flycatcher did respond to the Willow song in each of the 3 trials it was involved in. Two Willow Flycatchers in allopatric areas also responded aggressively to heterospecific playback during all of the trials (N = 2 and 3) in which they were included, and one of the birds attacked the speaker. Such levels of aggressive behavior were rare, however, being observed only once in sympatric populations by Alder, and twice by Willow flycatchers in response to the opposite song form. Because of the nonindependence of the data resulting from pooling data for individual birds tested repeatedly during playback experiments, and because the responses of individuals of both species were consistent throughout the study (with respect to the presence or absence of aggressive responses), the responses to heterospecific song playback for both species were reanalyzed using a Fisher's exact test (Seigel 1956). For both species, responses were significantly more frequent in sympatric populations (Alder Flycatcher, $P < 0.005$; Willow Flycatcher, $P < 0.01$), confirming the results of the previous analysis.

A comparison of responses to heterospecific song between species (sympatric populations only) showed that Willow Flycatchers more frequently produced *wee-oo* ($P < 0.005$) and *churr* calls ($P < 0.05$) than did Alder Flycatchers. There were no significant differences with respect to the other measured behaviors ($P > 0.05$).

Responses to conspecific song type.—A comparison of responses obtained from all populations for both species (Table 2) shows that Willow Flycatchers took less time to approach within 8 m of the speaker ($P <$

0.0001), and made more frequent use of aggressive vocalizations (*whit* calls, $P < 0.01$; *wee-oo* and *churr* calls, $P < 0.0001$) than did the Alder Flycatcher. In addition, Willow Flycatchers attacked the speaker in 4 of 53 playback trials (7.5%), compared to 1 attack in 45 trials (2.2%) for Alder Flycatchers.

DISCUSSION

Aggressive responses to heterospecific song playback in these closely related flycatchers occurred more frequently in habitats where both species bred. Because the choice of habitats was designed to reflect previous experience (or inexperience) with the sibling species, it appears that the development of response to heterospecific song in Alder and Willow flycatchers represents a learned behavior (see also Emlen et al. 1975; Catchpole 1978; Falls 1978, 1982; Catchpole and Leisler 1986). The differences in response of individuals in sympatric and allopatric populations also suggest that although the songs of the two species are phonetically similar, both species are able to discriminate between their song types. Hence, interspecific aggression apparently did not occur as a result of "mistaken identity" as has been proposed for other species pairs demonstrating interspecific territoriality during the breeding season (Murray 1971, 1976, 1981). The two Willow and the single Alder flycatchers that responded to playback of heterospecific song in allopatric populations represent notable exceptions. It is unknown whether these individuals responded to the opposite song form because of an inability to distinguish it from their own song (i.e., mistaken identity), or because they recognized the "intruder" as an ecologically similar, potentially competing species. The latter could occur if these individuals had learned the other species' song by sharing habitats during previous breeding seasons (Emlen et al. 1975).

The occurrence of interspecific song recognition and aggression are contrary to the observations of both Stein (1958, 1963) and Barlow and McGillivray (1983), who found little or no response of either species to heterospecific song playback. My results suggest that previous experience with the related species through coexistence might be one explanation for the discrepancy; however, because at least some of the previous playback studies were conducted in sympatric flycatcher populations, the lack of any interspecific aggression is unexpected, and interspecific territoriality may have been absent in previously considered habitats. If competition for food has been important in the evolution of territoriality between ecologically similar species (Orians and Willson 1964, Cody 1969), long-term differences in the abundance of insect food available to different flycatcher populations may reflect the presence or absence of aggressive responses. Barlow and McGillivray (1983) suggested that the foraging behavior of Willow and Alder flycatchers was not limited by food availability in the habitats where they conducted playback experiments (also in southern Ontario). At least for Willow Flycatchers, however, food was apparently not limiting in habitats considered in the present study (Prescott 1986). Hence, differences in food abundance on a short-term basis cannot account for differences in the observed aggression between Alder and Willow flycatchers in studies conducted to date.

Methodological differences are known to affect the outcome and comparability of song-playback studies (Falls 1978, Kroodsma 1986). During the course of studies on *Empidonax* flycatchers near Guelph, it was apparent that song tapes (other than those assembled for the present study) that were recorded at too high a volume, or played back at too low or high a volume frequently failed to elicit aggressive responses, even to conspecific song. Similarly, songs from speakers placed only a short distance outside the territory under observation were often ignored by the occupant. Because of the only brief accounts of playback methodology provided in earlier studies, the extent to which such factors influenced the difference in responses observed between our studies is unclear. Nevertheless, the presence or absence of previous experience with heterospecific flycatchers remains the most plausible explanation for the results generated here, and are consistent with observations on other interspecifically territorial species pairs (Emlen et al. 1975, Catchpole 1978, Falls 1978, Catchpole and Leisler 1986).

My analyses also show that Willow Flycatchers tended to react more aggressively to both conspecific and heterospecific song playback than did Alder Flycatchers. This supports Stein's (1963) contention that the former species is behaviorally dominant to the latter. This is also supported by anecdotal field observations of aggressive encounters between these species made during 1984 and 1985. Seven aerial conflicts were recorded, all of which resulted in the Willow Flycatcher successfully expelling the Alder from the disputed area. Four of 7 such encounters were known to be the result of intrusions by Willow Flycatchers onto Alder territories, and 4 of 5 were known to have been initiated by Willow Flycatchers. In addition, three Alder Flycatcher territories were known to have been usurped by adjacent Willow Flycatchers early in the breeding season (2 in 1984, 1 in 1985). Alder Flycatchers that lost their territories in this manner apparently did not remain in the vicinity to breed. Therefore, the Willow Flycatcher may be sufficiently dominant to expel the Alder from shared habitats. Thus, the defense of interspecific territories is clearly of benefit to the Willow Flycatcher, but apparently is not to the Alder. This is in contrast to the assumptions of the mistaken identity theory of interspecific territoriality, where such interactions are considered to be nonadaptive to both participants (Murray 1971, 1976, 1981). These behavioral observations therefore reinforce the conclusion that interspecific territoriality between these flycatchers cannot be the result of misdirected intraspecific aggression.

The observed interspecific dominance of the Willow Flycatcher might have demographic implications. Stein (1963) has suggested that the Alder Flycatcher presently is contracting northward, being replaced by the northwardly expanding Willow. Recent habitat alteration associated with agricultural practices has been attributed to bringing these species into secondary contact, and may be partly responsible for the suspected range changes (Stein 1963). However, Gauthreaux (1978, 1982) has argued for the importance of intraspecific behavioral dominance in determining age and sex class distributions of certain temperate-zone birds during the nonbreeding season. The results presented here suggest that interspecific dominance might also be an important factor in the recent expansion of Willow Flycatchers into areas historically occupied by the Alder Flycatcher.

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