

ECOLOGICAL OVERLAP AND THE PROBLEM OF COMPETITION AND SYMPATRY IN THE WESTERN AND HAMMOND'S FLYCATCHERS

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In western North America, Hammond's Flycatcher (*Empidonax hammondi*) and the Western Flycatcher (*E. difficilis*) are sympatric north of México. *E. difficilis* breeds on south into Honduras where *E. hammondi* is absent (AOU 1957). Both species may be found in local sympatry in habitat within their common ranges. When one species is abundant, the other is usually rare or absent (Johnson 1966a, pers. comm.). Both species have very similar body size, general appearance, and foraging behavior. These similarities led Johnson to conclude that *E. hammondi* and *E. difficilis* are "ecological equivalents" and occupy very similar niches. Consequently, Johnson speculated that competition between these two species is very likely when they come into contact.

In the mountains of southern Colorado, we found *E. hammondi* breeding in aspen as well as in coniferous forest at the lower elevational limit of its range which is about 2438–3048 m (8000–10,000 ft), depending on local habitats. In this same elevational zone, we frequently found *E. difficilis hellmayri* breeding in coniferous forest along streams. Local coexistence of these two species occurred in a mosaic of habitat types produced by the physical ruggedness of the area. It was not immediately clear whether this coexistence was allowed by interdigitation and mixing of vegetation from adjacent habitats or through character displacement which reduced competition for some limiting resources.

In the same mountainous region, a third flycatcher, the Western Wood Pewee (*Contopus sordidulus*), was found breeding in aspen forest. We located overlapping breeding territories between this species and *E. hammondi* in specific habitat situations discussed fully below. While *C. sordidulus* is larger than *E. hammondi* (the former species is about 4 g or 40% heavier), giving the possibility that competitive interactions are significantly reduced, an interesting situation existed in that *E. hammondi* could be studied in contact

with individuals of either *C. sordidulus* or *E. d. hellmayri*.

The main purpose of the present study was to examine habitat selection, foraging microhabitat, and foods in relation to competition and coexistence in the very similar *E. hammondi* and *E. d. hellmayri* on the eastern edge of their range. We have also considered the interactions of *E. hammondi* and *C. sordidulus*, but primarily as they relate to the problems of competition and coexistence for the two *Empidonax* flycatchers. In the discussion following, *E. d. hellmayri* is denoted as simply *E. difficilis*. Johnson (pers. comm.) has pointed out to us that *E. hammondi* may behave differently toward *E. d. difficilis* along the Pacific Coast. Therefore, our results are not necessarily typical for interactions between *E. hammondi* and *E. d. difficilis*.

STUDY AREA

The study was conducted in the summers of 1965–66 on the eastern side of the Wet Mountains of southern Colorado in the San Isabel National Forest. The site is located in T.23S., R.69W. in parts of Sec. 8, 9, 16, and 17 at an elevation of 2900 m (9500 ft). Because the area varies in steepness of slope and aspect from place to place, especially in the eastern half, several distinct types of vegetation are present. A series of east-west-oriented ridges in the eastern half of the area produces north-facing slopes which have conditions favorable for growth of spruce-fir forest typically found at higher elevations (Costello 1954). The north slope forest is somewhat atypical in that lodgepole pine (*Pinus contorta latifolia*) and aspen (*Populus tremuloides*) are the major species of trees. Douglas fir (*Pseudotsuga menziesii*) and Engelmann spruce (*Picea engelmannii*) occur here, but less frequently (table 1). The understory in this habitat generally consists of a ground cover of decaying conifer needles, an occasional ground juniper (*Juniperus communis*), and kinnikinnick (*Arctostaphylos uva-ursi*).

The western portion of the study area is nearly level, sloping gently to the north, and has large stands of aspen interspersed with an occasional grassy meadow. This vegetation is also typical of the mid- to lower portions of south-facing slopes. The habitat is much more open than north slope forest, having about one-half the number of trees per hectare (table 1). An understory of grasses, other herbs, and forbs flourishes. The extent of this habitat is about 165 ha, a little more than half of the area studied. It is referred to beyond as "aspen habitat."

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TABLE 1. The number of trees per hectare in three habitats on the study area.

Habitat location	Area (ha)	Trees	Trees/ha	% Comp.	Average dbh ^a (cm)
North slopes	34	Aspen	320	23	15.0
		Douglas fir	247	18	22.5
		Engelmann spruce	247	18	22.4
		White fir	68	5	17.5
		Lodgepole pine	490	36	21.3
		TOTAL	1372	100	
Mid-south slopes ^b and level areas (Aspen)	165	Aspen	510	99	23.1
		Ponderosa pine	4	1	56.4
		TOTAL	514	100	
Valley bottom ^c and lower south slopes (Aspen-conifer)	57	Aspen	81	15	24.4
		Douglas fir	330	59	25.1
		Engelmann spruce	123	22	25.9
		White fir	22	4	21.3
		TOTAL	556	100	

^a Diameter breast high.^b Habitats where Hammond's and Western flycatchers occurred.^c Habitats where Hammond's Flycatcher and Western Wood Peewee occurred.

A third habitat that is less well defined occurs in valley bottoms. It results from the intermixing of vegetation of south and north slopes (table 1) and the addition of certain species of vegetation such as willow in the understory. All valleys have streams or springs running in them and, therefore, support the richest understory in terms of number of species and total growth of any of the habitats. About 57 ha of this type of vegetation (referred to as "aspen-conifer habitat" below) occur on the study area.

Upper south slopes and ridge tops are the site of a fourth, more xeric, habitat because of good drainage and exposure to the sun. The vegetation found here is the uppermost extension of ponderosa pine (*Pinus ponderosa*) forests typical of lower elevations (Costello 1954). The understory is sparse, consisting mostly of short grasses. In some places scrub oak (*Quercus gambellii*) replaces ponderosa pine as the major plant species. Approximately 47 ha of the study area are of this type of habitat.

METHODS

Vegetational features and their extent on the study area were determined by direct observation and from maps and aerial photographs. In habitats occupied by flycatchers, quantitative information on density, average size, and percent composition of tree species was obtained by use of the point-centered quarter method of Cottam and Curtis (1956).

The breeding density of each species of flycatcher was determined by mapping territories of marked pairs in areas where foraging behavior and other activities were regularly monitored. The spot-map technique of Williams (1936) was used to census flycatchers in habitats where intensive work was not being conducted.

It is well known that the species of *Empidonax* flycatchers are difficult to identify in the field. Anticipating this, we obtained information on breeding behavior (habitat choice and nest placement), vocalizations (as analyzed by sonagram), morphology (length, depth, and width of bill; size and shape of wings and tail), and coloration.

Preliminary observations on the choice of micro-habitat for feeding suggested that different vertical strata of the forest were being used by each species.

Use of strata was quantified by estimating the height of feeding in relation to tree height. The forest profile was arbitrarily divided into 3-m intervals. The level where a flycatcher fed was estimated visually with a maximum error of about 1 m at lower levels and about 2 m near average tree top height (21 m). Six trees spaced appropriately as reference points in each of three areas were marked with red flagging at 3-m intervals for checking the accuracy of feeding height estimates. The amount of time spent foraging in a level was recorded with a stop watch. Birds obviously not hunting were not included, nor were birds which made no foraging flights after 5 min of apparent hunting behavior (i.e., peering and/or tracking nearby flying insects with the head).

The diet of each species was determined by collecting birds with a shotgun and examining the contents of the stomachs. Collecting was done off the study area in comparable habitats in 1965 and on the area itself in 1966. The procedure was to record feeding behavior, noting height of feeding and number of flights, for at least 10 min for each bird prior to collecting. Once in hand, digestion was inhibited by forcing 75% alcohol down the throat. Within a few hours after being collected, the birds were weighed and the stomachs removed and stored in 75% alcohol. Body weights were not corrected for the additional weight of alcohol. This degree of refinement was not deemed necessary considering the variations in body weight caused by collecting birds with a shotgun. Analysis of the stomach contents consisted of keying insects that were essentially whole to the level of family and measuring the body length (frons to tip of abdomen). Fragmented insects were taken to the level of order in nearly all cases, and many times also to family. When it could be done accurately, these insects were reconstructed (i.e., whole body parts, such as thorax, head, and abdomen reassembled) and body length estimated. This process was assisted by direct comparison with similar insects captured on the study area.

Methods of sampling insects were designed to determine the relative abundance and taxonomic composition of adult, flying insects that were potential food for flycatchers. All three habitats, represented by six sampling stations, were sampled in the summer of 1965; two habitats, the ones in which flycatchers oc-

curred, were sampled at three stations in 1966. Lower levels (0–3 m) were sampled with a sweep net, each sample consisting of 30 full sweeps of the net on foliage at each of three levels: ground level, 1.5 m, and 3 m above the ground. Upper levels (4–17 m) were sampled by suspending a smaller, modified version of a Malaise trap (Townes 1962) in open spaces adjacent to foliage.

RESULTS

SELECTION OF HABITAT

The extent of aspen habitat suitable for *E. hammondii*, approximately 35 ha, was estimated from the areas where nesting pairs were found. *C. sordidulus* was found nesting throughout the 167 ha of aspen habitat, but was most concentrated in taller aspen stands. The densities of *E. hammondii* and *C. sordidulus* were calculated at 4.7 and 2.5 birds/10 ha, respectively, in 1965 and 1.4 and 0.3/10 ha in 1966 in aspen habitat. The number of pairs of these species studied which had overlapping territories was six for *E. hammondii* and five for *C. sordidulus* in three separate locations.

E. difficilis breeds in aspen-conifer habitat in the study area. It was observed at densities of 6.9 birds/10 ha in 1965 and 1.2 birds/10 ha in 1966. *E. hammondii* also occurs in this habitat and was about half the density of *E. difficilis* in 1965 (2.8 birds/10 ha) and slightly more abundant than *E. difficilis* in 1966 (1.4 birds/10 ha). This is typical habitat for *E. hammondii* according to other workers (Johnson 1963; Davis 1954) and personal experience.

No overlap in breeding territories occurred between *C. sordidulus* and *E. difficilis*. This is seen as a result of their breeding in different habitats. In areas where aspen occurs along stream courses, three *C. sordidulus* pairs had, at most, contacting territories with *E. difficilis*. Occasional aggressive behavior by each species toward the other may be indicative of some form of interspecific territoriality, but this was not established positively in this study. However, *E. hammondii* holds completely overlapping territories with *E. difficilis* in aspen-conifer habitat. Only two instances of aggressive interaction were observed in the first summer between seven overlapping pairs of these species and that was on 8 and 11 June during the time of territory establishment. No interactions were seen in the second summer, possibly due to lower numbers of both flycatchers. However, intraspecific aggressive interactions were numerous in all three species in both years.

While a concentrated effort was not made to follow nesting success, information on survival of young was recorded for seven nests of *E.*

hammondii and for six of *E. difficilis*. Four of the seven nests of *E. hammondii* were located in the territories of *E. difficilis* in aspen-conifer habitat. Only one nest fledged young and only two of the original four survived beyond the first week out of the nest. This represented only 13% of the original 15 young hatched. None of the remaining three nests in aspen habitat fledged young (two in 1965, one in 1966 on edge of aspen-conifer habitat). *E. difficilis* had considerably better success. Of nests on territories, one nest of three young was destroyed by predators, three nests fledged four young each, and one nest, one young; two other nests fledged three of five young and two of four young, respectively. Thus, of 28 nestlings, 18 or 64% survived the first week out of the nest.

The aspen habitat on the south slopes and in the western portion of the study area is used by *C. sordidulus* and also to some extent by *E. hammondii* for feeding and nesting. The distribution of *C. sordidulus* and *E. hammondii* in this habitat is not uniform. *E. hammondii* is usually found with *C. sordidulus* (i.e., possessing overlapping territories) only in tall and well-shaded aspen forest, whereas the latter occurs in shorter and more open forest as well. It is not typical for *E. hammondii* to occur in aspen forest at lower latitudes, as reported by other workers (e.g., Johnson 1963; Manuwal 1970), but Bent (1942) and Johnson (1966a) indicate that occasionally this species will nest there in low abundance.

MECHANISMS OF PREY SELECTION

Partitioning of food resources in response to competition between the two coexisting members of each species-pair of flycatchers, assuming that food is in limited supply, could be accomplished either by their foraging in different microhabitats and selecting the same prey, or by their capturing different kinds and/or sizes of insects in the same microhabitat (MacArthur 1958; see also MacArthur and Pianka 1966). Schoener (1965) has shown theoretically that sympatric, congeneric, or confamilial species of nearly the same body weight or bill length feeding on abundant food, as appears to be the usual case for small insectivorous birds, would be likely to subdivide food by feeding on similar-sized prey in different microhabitats. When differences in body and bill size are larger, it is probable that coexistence in the same microhabitat is achieved through selection of different sizes of prey. Schoener (1965) compared the ratios of character difference, defined as the ratio of bill lengths of the larger to the smaller spe-

TABLE 2. The ratios (R) of larger to smaller dimensions of the bill and body weights of each species of flycatcher. For a full explanation see text.

Species pair	N	Culmen \bar{x} (mm)	R	Body wt. \bar{x} (g)	R	Bill depth \bar{x} (mm)	R	Bill width \bar{x} (mm)	R
<i>Empidonax difficilis</i>	23	8.4		12.1		3.6		5.7	
			1.11		1.12		1.09		1.29
<i>Empidonax hammondii</i>	14	7.2		10.8		3.3		4.4	
			1.29		1.29		1.03		1.41
<i>Contopus sordidulus</i>	69	9.3		14.0		3.4		6.2	

cies, of groups of species in several families of insectivorous birds, and he was able to define a zone of transition from small to large ratios, at approximately 1.14, above which it becomes feasible for two species to partition food by size rather than microhabitat. Schoener's formulation assumed that body size is correlated with the size of prey taken, and that this assumption would likewise hold for bill size. Recently, Hespeneide (1971a) confirmed Schoener's assumption by demonstrating a strong correlation between size of insect prey and both body size and bill size of their avian predators, although the former is more strongly correlated of the two in several families of birds, including Tyrannidae, of which the birds studied here are members.

We have calculated ratios of character difference for bill dimensions and body weight for the two species-pairs in this study (table 2) following Schoener's method. The prediction can be made that *E. difficilis* and *E. hammondii* will feed in different microhabitats on the same size of insect prey when they occur together because the ratio of bill length is small (1.11). Further, the large ratio for bill length of *C. sordidulus* and *E. hammondii* (1.29) indicates they will feed on different sized insects and may, therefore, occur in the same microhabitat. The same predictions are reached when ratios are calculated for body weights (table 2). However, the shape (i.e., length, depth, and width) of the bill may be equally important in determining differences in food selection (Bowman 1961; and Root 1967). For the other dimensions of bill depth and width, we find small ratios for depth, even between *C. sordidulus* and *E. hammondii*, and large ratios for width (table 2), requiring re-examination of predictions.

Root (1967) suggests that the dorso-ventrally compressed bill of flycatchers is an adaptation to aerial capture of prey, and, therefore, bill depth may be the dimension of the trophic appendage most sensitive to the selection of

prey size. From table 2, it can be seen that bill length and bill width increase more rapidly in relation to body weight of the flycatcher than does bill depth. This suggests that with an increase in body size, bill depth becomes less important in prey capture relative to length or width. Or, stated in a different way, the relatively greater depth of the small bill (*E. hammondii*) may indicate the need for strength to hold the prey after it is captured. As for width, the large magnitude of the ratio for bill width in both species-pairs can be interpreted to mean that each species will select different sized prey and will, therefore, be able to co-utilize microhabitats for foraging.

SELECTION OF FORAGING MICROHABITAT

Attention to foraging heights of members of each species-pair reveals that, in aspen-conifer habitat, *E. hammondii* feeds most often in a zone from 6-12 m high, which corresponds to middle canopy portions of taller conifer and aspen trees, and *E. difficilis* feeds mostly from ground level to 9 m (fig. 1). There is some indication that the female in both species feeds lower than the male, but we do not have sufficient data to show this statistically. The frequency of feeding in all levels by *E. hammondii* and *E. difficilis* is significantly different ($\chi^2 = 37.57$, $P < 0.005$, G-test, Sokal and Rohlf 1969) (fig. 1). Contrarily, *C. sordidulus* and *E. hammondii* in aspen habitat (fig. 2) completely overlap in use of microhabitat for feeding. All levels of the habitat are used with equal frequency by both flycatchers ($\chi^2 = 8.92$, $P > 0.10$). The heights where the greatest amount of feeding was done correspond to the mid-foliage portion of trees and the air space immediately below (3-12 m). Thus, predictions of microhabitat selection for the flycatchers studied here based on the ratios of bill length and body weight are confirmed by these data.

Although no quantitative data are available for comparison, accounts in the literature sug-

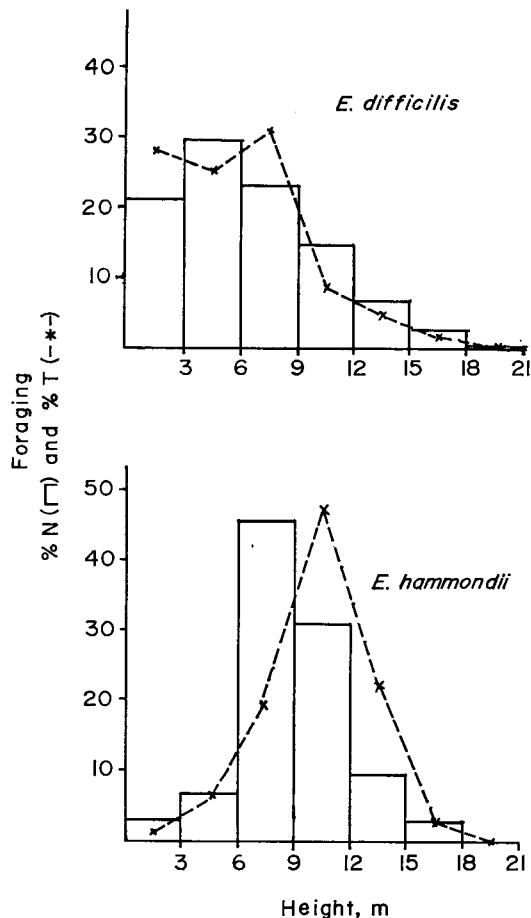


FIGURE 1. Percent foraging frequency and time in relation to height for *E. difficilis* (N = 144, Time = 406.2 min) and *E. hammondii* (N = 61, Time = 83.7 min) in aspen-conifer habitat.

gest that selection of microhabitat for feeding is similar for these species in several other localities (Hespenheide 1964 for *C. sordidulus*; Bent 1942; Davis 1954; Davis et al., 1963 for *E. difficilis* and *E. hammondii*). It may be noted here that *E. hammondii* fed with nearly equal frequency in the same levels in aspen-conifer and aspen habitats (compare *E. hammondii* in figs. 1 and 2, $\chi^2 = 6.97$, $P > 0.25$). Thus, differences in nesting habitat are not accompanied by changes in foraging level for this species.

SELECTION OF PREY

We have used the magnitude of ratios of character difference for bill length and body weight to predict the position of feeding microhabitat for the two species pairs and the data are consistent with expectations. However, the assumption that these ratios are also indicative of differences in the size of food selected must be tested before concluding that

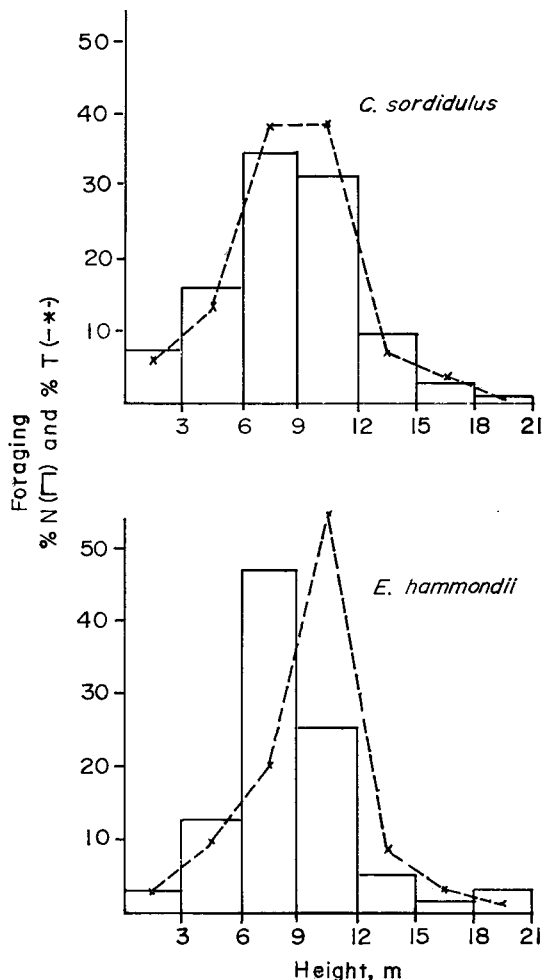


FIGURE 2. Percent foraging frequency and time in relation to height for *C. sordidulus* (N = 300, Time = 684.5 min) and *E. hammondii* (N = 55, Time = 123.9 min) in aspen habitat.

selection of feeding heights and size of foods eaten are correlated. There is room to question the prediction because, as noted earlier, the ratio of bill depth and width provides conflicting prediction of how food resources will be divided.

An estimate of preferred prey size can be made by examining insects from the diets of each species. The data are drawn from an analysis of insects found in the stomachs of 69 *C. sordidulus*, 23 *E. difficilis*, and 14 *E. hammondii*. Nearly all (10) of the individuals of the latter species were collected in aspen-conifer habitat. Comparison of the diets of *E. hammondii* with *C. sordidulus* was made assuming that size selection of insects does not vary for the former species between the two habitats.

Frequency histograms of numbers of insects in each body-length class (fig. 3a) show curves

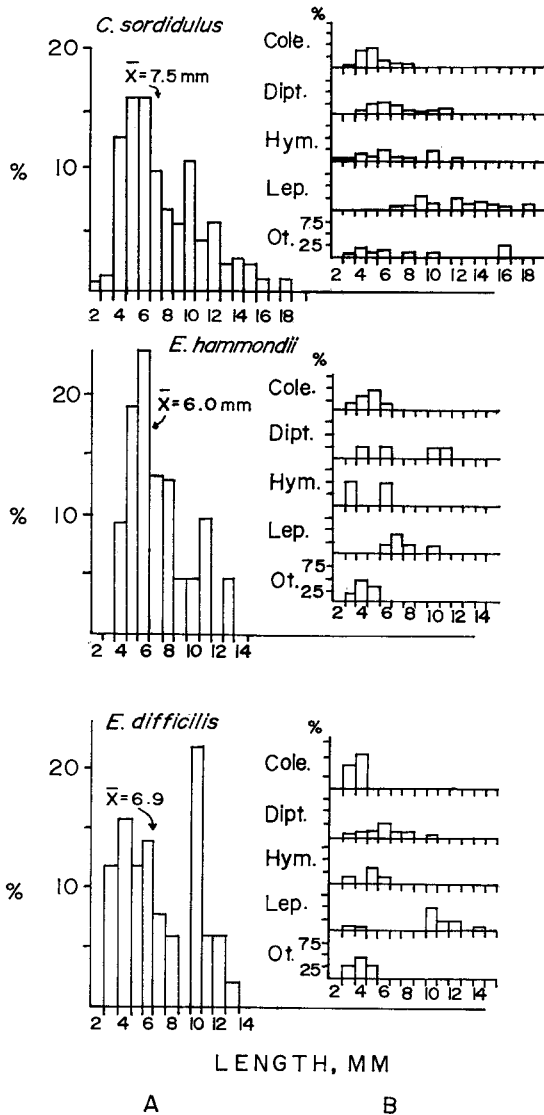


FIGURE 3. Frequency distributions for insect lengths in the diets of flycatchers. Numbers of insects are: *C. sordidulus*—152, *E. difficilis*—52, *E. hammondii*—23. Inset is the frequency distribution for length within each insect order in the diet. Abbreviations: Cole. = Coleoptera, Dipt. = Diptera, Hym. = Hymenoptera, Lep. = Lepidoptera, and Ot. = Other Orders (mostly Hemiptera Homoptera, and Neuroptera).

skewed to the right, especially for *C. sordidulus*, indicating that longer insects were taken much less frequently than shorter ones. Hespeneide (1971a) found similar length distributions for beetles eaten by seven species of flycatchers which occur in the eastern United States. A logarithmic transformation normalized his data allowing use of conventional parametric statistics for comparing the properties of the distributions. Logarithmic transformation of our data for all insects eaten by each flycatcher also produced normal

curves, as determined by comparing measures of skewness (g_1) and kurtosis (g_2) with the expected values (zero) for the normal distribution ($P > 0.50$) in all comparisons. (See Sokal and Rohlf 1969: 117 and 171.)

The means of the log transformed data on insect lengths were compared by a *t*-test. *E. difficilis* and *E. hammondii* take insects of the same length (*E. difficilis* prey $\bar{x} = 6.4$ mm, *E. hammondii* prey $\bar{x} = 5.7$ mm, $P > 0.10$). Again, this result is the one predicted from the ratios of character difference of this species-pair, except that of bill width. Thus, in aspen-conifer forest, insects of similar length are captured in different vertical strata of the forest. *C. sordidulus* takes significantly longer insects (*C. sordidulus* prey $\bar{x} = 6.9$ mm, *E. hammondii* prey $\bar{x} = 5.7$ mm, $P < 0.025$) than *E. hammondii*. This result is also the one predicted from the ratios of character difference (except for ratio of bill depth). We can infer from these data that *C. sordidulus* and *E. hammondii* can feed from the same vertical strata of the forest without competition for food by selecting insects of different length, if we can assume that length of items selected does not differ for the latter species from aspen-conifer to aspen habitat.

We have carefully avoided the use of the word "size" when referring to our data on the selection of insect prey because it implies weight or volume. The dimension of length can be expected to indicate size of an insect only within the same taxonomic group or between distantly related taxonomic groups only when the body form is very similar (see below). The distributions of insect length constructed from insects found in the stomachs of each species of flycatcher are composites of insects almost entirely from the orders Coleoptera, Diptera (suborder Brachycera), Homoptera, Hemiptera, Hymenoptera, and Lepidoptera. It follows that selection of a particular length of insect by the flycatchers has little meaning in relation to the energy value of the food item unless the weight characteristics are known for the taxon or morphological type. Thus, a complete analysis of prey selection should include a discussion of insect weight.

Since no data on weight-length relationships within an insect order could be found in the literature, insects of the orders mentioned previously collected in the field and preserved in 75% alcohol were sorted according to order, measured to the nearest millimeter, then dried in a vacuum oven at 50°C for 24 hr, and weighed individually on a Cahn-electrobalance (Model M-10) capable of accuracy to about

TABLE 3. Regression equations and correlation coefficients for insect dry weight on body length for the most important insect orders in the diets of the flycatchers. Adult insects were used exclusively.

Insect order	N	Logarithmic equation		Correlation coefficient	
		$a \pm 0.95 \text{ CL}^a$	$b \pm 0.95 \text{ CL}$	r	P
Coleoptera	147	1.118 ± 0.173	3.148 ± 0.276	0.881	$\ll 0.01$
Diptera (Brachycera)	145	0.974 ± 0.946	2.703 ± 0.158	0.943	$\ll 0.01$
Hymenoptera	304	1.005 ± 0.771	2.648 ± 0.107	0.942	$\ll 0.01$
Lepidoptera	124	1.002 ± 0.104	2.661 ± 0.160	0.948	$\ll 0.01$

^a 95% confidence interval.

1 μg . Regressions of \log_{10} dry weight were run on \log_{10} body length as the independent variable for each insect order (table 3). Weight and length are significantly correlated ($P \ll 0.01$, all cases) within an order, as shown by the correlation coefficient, r . These equations provided a basis for estimating the dry weight of insects found in the diet which could be identified to the level of order and measured accurately.

The data for the diet of each flycatcher used for construction of figure 3 were recast into frequency distributions of numbers of insects within each 0.5-mg category (fig. 4). These curves are also skewed to the right as was the case for the curves of insect length in the flycatchers' diets. A logarithmic transformation normalized these data (skewness and kurtosis parameters were not statistically different from zero, $P > 0.50$). The log mean insect weight of the diet of *C. sordidulus* (2.101 mg) is not statistically different from the log mean insect weight in the diet of *E. hammondii* (1.656 mg, t -test, $P > 0.05$). However, significance is approached and it is likely that a larger sample for *E. hammondii* would result in statistical separation of the mean insect weights in the diets of this species pair. Log mean insect weight in the diet of *E. difficilis* (1.567 mg) is lower than the log mean for *E. hammondii* but the means are not statistically different ($P > 0.80$). Thus, the trend in selection of insect length is paralleled by a similar trend in choice of insect weight, but the latter case is not as pronounced as the former. This is not surprising if one supposes that flycatchers select prey on the basis of "size." Prey length and weight are probably not chosen independently in any case.

TAXONOMIC COMPOSITION OF THE DIET

The composition of the diet at the level of family is shown for each species in table 4. The number of families identified appears to be related to the number of stomach samples

in the ratio of about one new family for two stomachs. On this basis, it is expected that the number of families of insects would not be different for samples of equal numbers of stomachs for each species of flycatcher. Selection of a wide variety of taxa as food appears to be typical for many open-air feeding birds, such as flycatchers and swallows (Hespen-

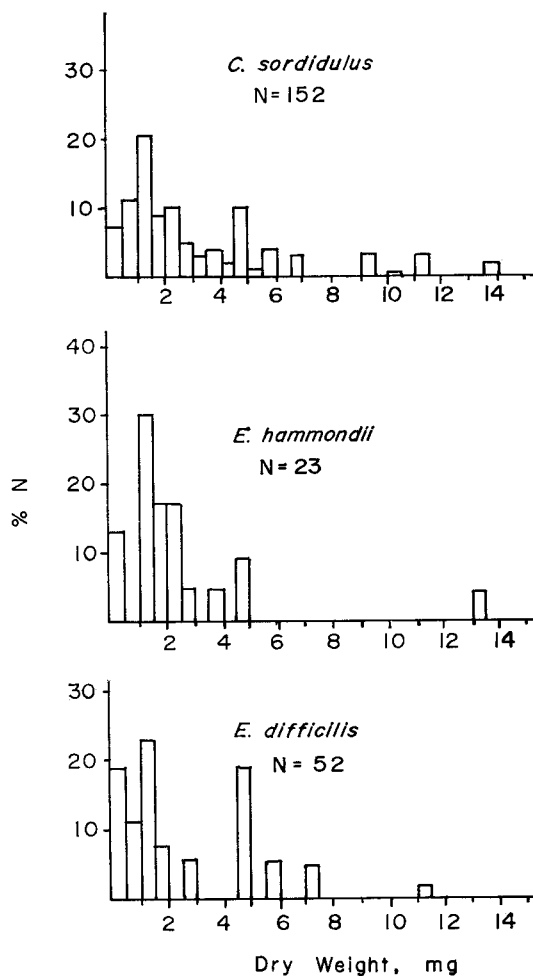


FIGURE 4. Frequency distribution of insect dry weights in the diets of each species of flycatcher. The data are grouped into 0.5-mg classes.

TABLE 4. Diets of three species of flycatchers.

Insect prey in samples		<i>Contopus sordidulus</i>		<i>Empidonax difficilis</i>		<i>Empidonax hammondi</i>	
Order	Family	N = 334 ^h	% ^a	N = 96 ^h	% ^b	N = 35 ^a	% ^b
Coleoptera		16		25		34	
	Buprestidae		8		—		—
	Cerambycidae		4		—		—
	Chrysomelidae		4		—		—
	Cleridae		—		4		—
	Curculionidae		8		8		—
	Scarabeidae		25		4		21
	Scolytidae		10		—		—
	Unidentified		41		84		79
Diptera		32		31		19	
	Calliphoridae		3		—		—
	Empididae		1		3		13
	Muscidae		4		—		—
	Rhagionidae		6		13		25
	Sarcophagidae		1		—		—
	Syrphidae		3		3		13
	Tabanidae		6		10		—
	Therevidae		1		—		—
	Tipulidae		—		—		13
	Unidentified		75		71		36
Hemiptera		4		3		—	
	Corizidae		8		—		—
	Nabidae		16		—		—
	Unidentified		76		—		—
Homoptera		2		1		3	
	Cercopidae		40		—		—
	Cicadellidae		30		—		100
	Unidentified		30		—		0
Hymenoptera		32		17		3	
	Bombidae		1		—		—
	Braconidae		2		6		100
	Cephalidae		1		—		—
	Chalcidoidea ^c		1		—		—
	Formicidae		72 ^d		37		—
	Ichneumonidae		2		8		—
	Tenthredinidae		1		—		—
	Vespidae		1		—		—
	Unidentified		19		49		0
Lepidoptera		13		22		29	
	Geometridae		9		—		9
	Nymphalidae		2		—		—
	Tortricidae		28 ^e		62 ^f		91 ^g
	Unidentified		61		38		0
Neuroptera		2		—		—	
Trichoptera		2		—		—	
Araneida		—		2		5	

^a Percent of all insects.

^b Percent of all insects within the order.

^c Superfamily.

^d *Camponotus herculeanus* (L.).

^e 2% *Choristoneura fumiferana* (Clem).

^f 100% *C. fumiferana*.

^g Larvae and pupae of *C. fumiferana*.

^h Number of insects in 69, 23, and 14 stomachs, respectively.

heide 1971a), and may even be a valid generalization for all insectivorous birds.

Even though choice of insects by the flycatchers covers a wide range of taxonomic groups, particular portions of the distribution of insect numbers in relation to length tend to be predominantly of one or two insect orders (fig. 3b). Thus, for *C. sordidulus* the smaller insects (up to about 8 mm) are mostly Coleop-

tera and Hymenoptera, larger insects (> 8 and < 12 mm) are mostly Hymenoptera and Lepidoptera, the largest insects are all Lepidoptera. The same pattern is seen for *E. difficilis*, except that Diptera represents a major block of insects from 5 to 8 mm. *E. hammondi* selects smaller Coleoptera and Hymenoptera and larger Diptera and Lepidoptera, although for this flycatcher, small sample size tends to

TABLE 5. The contribution of each insect order to the total dry weight in the diets of each species of flycatcher.

Order	<i>C. sordidulus</i> % dry wt.	<i>E. difficilis</i> % dry wt.	<i>E. hammondi</i> % dry wt.
Coleoptera	15	4	53
Diptera			
(Brachycera)	21	25	15
Hemiptera	2	—	—
Homoptera	1	—	—
Hymenoptera	14	10	2
Lepidoptera	44	61	27
Neuroptera	3	—	—
	<hr/> 100	<hr/> 100	<hr/> 100
Total dry wt., mg	499.2	137.4	53.7

oversimplify the contribution of any insect order within each length category. The results of other work on prey selection by insectivorous birds have shown similar shifts in importance of taxonomic groups in different length ranges (Root 1967; Hespeneheide 1971a).

Obviously, the contribution of any insect order to the energy balance of the flycatcher diet will depend upon the biomass of insects multiplied by the frequency of occurrence in the diet. By computing the contribution in dry weight to the total weight of the diet for each order (table 5), we find in every case the order which contributes the greatest dry weight to the diet is not the most frequently selected one. *C. sordidulus* receives 44% of its total dry weight from Lepidoptera, while this same order represents only 13% of the diet numerically (table 4). The same is true of Lepidoptera in the diet of *E. difficilis*, but for *E. hammondi*, Coleoptera is both numerically and energetically more important than Lepidoptera or any other order taken singly. A note of caution must be made here since it may be that the heavier exoskeleton of Coleoptera, which may not contribute to the energy value of the insect as food for the flycatcher but certainly to its dry weight, may be exerting more influence in the calculations than it actually does in the energy balance of the diet of *E. hammondi*. Furthermore, additional discrepancies may enter the calculations through the fact that the dry weight of the diet was estimated only from insects that could be accurately measured and identified. Many more insects could be identified to order than could be measured, and this bias could enter the calculation of the percent composition of each order in the diet. However, the proportion in each order of measured insects compared to that of identified insects did not differ greatly for each species of flycatcher

(see table 4 and fig. 3b, compare percent for each order).

DISCUSSION

MARGINAL VERSUS COMPLETE SYMPATRY

Local sympatry for *E. hammondi* and *E. difficilis* in the study area is accompanied by partial vertical separation of foraging niches and by taxonomic differences in composition of the diet. Similarly, *E. hammondi* and *C. sordidulus* take different sized prey which in turn reflect differences in the taxonomic composition of their diets. Differences in foraging microhabitat and in diet have been used by other authors as evidence for reduced competition which makes coexistence possible for closely related species [MacArthur 1958, for five species of eastern forest warblers; Crowell 1968, for two species of flycatchers (*Elaenia*) on West Indian Islands, and others]. Therefore, it is tempting to conclude that these differences alone are sufficient to allow coexistence on a local scale for *E. hammondi* and *E. difficilis* and *E. hammondi* and *C. sordidulus*.

However, the lack of sympatry between *E. hammondi* and *E. difficilis* elsewhere in their ranges, except perhaps in local areas similar to that studied here, and the rare occurrence of the former species in aspen habitat at lower latitudes (aspen forests are frequently the nesting site of these species at high latitudes) raises the question of why mechanisms promoting local coexistence have not resulted in coexistence everywhere. The ecological mechanisms demonstrated above for reducing competition are either not sufficient to allow coexistence everywhere, or perhaps the same degree of niche separation does not occur in other parts of the range.

The latter possibility cannot be ruled out because data on foraging niche and food have not been accumulated for *E. hammondi* and *E. difficilis* in other parts of its range, to our knowledge. However, the scanty data available suggest that *E. hammondi* forages at higher levels in the vegetation than *E. difficilis* wherever the two species occur (Johnson 1963, 1966a; Davis 1954; Bent 1942). In addition, Johnson (1966a) has shown that *E. hammondi* is very uniform in morphology and in choice of nesting habitat over its range. Specimens of *E. hammondi* collected by us are no exception (Johnson personally measured all of them) and the nesting habitat was typical except for those individuals that nested in aspen habitat. Selection has apparently not produced character displacement in the local population we studied, or in other areas of the

range with the exception of certain Pacific coastal ones (Johnson 1966a). On Vancouver Island, *E. hammondii* in the absence of *E. difficilis* had significantly longer bills than mainland populations. Isolation from the competitive effects of *E. difficilis* is apparently responsible for the shift in bill length.

All available evidence on the distribution of these species points to the conclusion that competition for food or other resources occurs between *E. hammondii* and *E. difficilis* when they occur sympatrically, differences in foraging niche and diet aside. Examination of nesting success and habitat use in the area of this study supports the above conclusion. We have shown above that *E. hammondii* had very poor nesting success in 1965 when *E. difficilis* was abundant. In the same year we found *E. hammondii* nesting in aspen habitat in low numbers, with equally poor nesting success. The following summer fewer *E. hammondii* were present, but nearly all occurred in aspen-conifer habitat and nesting success appeared to be better. *E. difficilis* was even less abundant than *E. hammondii* in 1966. Thus, *E. hammondii* may yield to *E. difficilis* in years when the latter species is abundant. In these years, nesting in aspen habitat occurs. When *E. difficilis* has low breeding densities, as in 1966, *E. hammondii* breeds in aspen-conifer habitat almost exclusively.

We cannot dismiss the possibility that the poor reproductive success of *E. hammondii* in aspen-conifer habitat in 1965 was due to intraspecific competition. This could also explain the presence of breeding pairs in aspen habitat in the same year. However, data on nesting success of *E. hammondii* in the absence of *E. difficilis* in aspen-conifer habitat are not available. Thus, it is not possible at this time to separate the influence of intra- and interspecific competition on the behavior of local populations of *E. hammondii*.

COMPETITIVE RELATIONSHIPS

The presence of *E. hammondii* in relatively large areas when *E. difficilis* is uncommon, rare, or absent, as described by Johnson (1966a), means that *E. difficilis* is not always the superior competitor. The apparent reversal of competitive advantage suggests that these two species actually have different, albeit subtle, habitat preferences. It is only on the edges of preferred habitats that sympatry and resulting competition will occur. The superior competitor will be the species for which the majority of the habitat is suitable. The other species will suffer under direct competition or be displaced to another habitat.

Hespenheide (1971b) found that three species of eastern flycatchers, the Eastern Wood Pewee (*C. virens*), the Least Flycatcher (*E. minimus*), and the Acadian Flycatcher (*E. virescens*) which all breed in deciduous forests, actually had different microhabitats. The latter two species occurred in very similar habitat, both preferring dense deciduous forest. However, *E. virescens* was found nesting in denser habitat than *E. minimus*. When vegetative characters were intermediate for the preference of the species, *E. virescens* apparently yielded to *E. minimus* and bred in different habitat.

Evidence for differences in habitat preference for the two *Empidonax* flycatchers studied here is circumstantial. Each species selects different nest sites. *E. hammondii* usually nests in conifer trees near the main trunk at heights from 15 to 40 ft (Davis 1954; Bent 1942). This was not exactly the case in the study area since nests in conifer trees were also found out on branches and only a few feet above the ground. Nests in aspen trees were above 30 ft and on the main stem.

E. difficilis nests low and in depressions in banks of streams or large rocks. Nests were also found on flaps of bark on aspen and conifer trees. Davis et al. (1963) list similar nest sites for this species. *E. difficilis* appeared to select open, unvegetated nesting sites compared to relatively vegetated sites chosen by *E. hammondii*. Further study is needed to determine if choice of nest site is indicative of differences in habitat preference.

BEHAVIORAL INTERACTIONS

It seems likely that behavioral interaction between *E. difficilis* and *E. hammondii* is the means by which displacement is accomplished. However, only two interspecific encounters were noted in both years of study and these occurred very early in territory establishment. Most interactions from then on were intraspecific and much more intense. Morse (1971) found that behavioral interactions between the Wood Thrush (*Hylochia mustelina*) and the Veery (*Catharus fuscescens*) and Hermit Thrush (*C. guttatus*) in Maine occurred early in territory establishment. Conflicts over territorial boundaries between these species were limited to this early period. The Wood Thrush dominated the other two species and apparently displaced them from habitat intermediate to each one's preferred habitat. Almost all interactions later on were intraspecific. Thus, it may be that very little interaction between species is sufficient to produce displacement in the subordinate species.

The expansion of *E. hammondi* into aspen habitat perhaps to escape competition from *E. difficilis* at first seems an appropriate response to pressure from *E. difficilis* in aspen-conifer habitat. No other species of *Empidonax* flycatcher breeds locally in aspen habitat and the only other abundant flycatcher, *C. sordidulus*, is larger by about 40%. Furthermore, we have shown above that *C. sordidulus* takes significantly larger insects than *E. hammondi*. In general, *C. sordidulus* takes longer foraging flights for insects and feeds in more open habitat than *E. hammondi*. These differences would seem to allow compatible coexistence of these species. However, even though the degree of ecologic difference in these species exceeds that for *E. difficilis* and *E. hammondi*, coexistence may still result in competition. Hesperheide (1971b) has shown that coexistence in eastern North American flycatchers is apparently only possible if the smaller species is half the size of the larger. He showed that the only regularly coexisting species in deciduous forests was one of the three small species, *C. virens*, *E. minimus*, or *E. virescens*, and the larger Great Crested Flycatcher (*Myiarchus crinitus*). Other cases of apparent coexistence of *C. virens* with smaller species were found to be in situations where the preferred habitats of the species interdigitated, forming a mosaic of habitats.

Thus, we postulate that the flycatchers studied here will exhibit fine differences in habitat preference that are responsible for the lack of coexistence over most of their common ranges. Occasional contact in areas where particular physical conditions produce a mosaic of habitats or where habitats abut along broader zones results in competitive interactions which probably reinforce differences in habitat preference rather than produce character displacement. This is a parallel situation to that described by Hesperheide (1971b) for eastern forest flycatchers.

Other western species of *Empidonax* are also largely allopatric as a result of differences in habitat preference. The Gray (*E. wrightii*) and Dusky (*E. oberholseri*) Flycatchers prefer piñon-juniper or sagebrush and broken coniferous forest habitats or aspen and mahogany woodland habitats, respectively (Johnson 1966b). These species are found in microsympatry only where their preferred habitats join to form a vegetational mosaic. In these areas, interspecific territorial behavior restricts each species to its preferred habitat patch (Johnson 1966b). It is not clear whether the behavioral interactions between these species are indicative of potential com-

petition for food. Johnson (1966b) felt that lack of demonstrable character displacement in bill lengths (ratios mostly 1.13–1.16) confirmed a lack of long-term competition in these species. Ashmole (1968) has objected by claiming that interspecific territoriality in these two species precludes competition for food and therefore no selective advantage for character displacement exists. However, interspecific territories may not preclude competition for food in birds which feed on highly mobile prey, as flycatchers do, that may regularly pass through several microhabitats. We have shown above that differences in foraging microhabitat are probably not sufficient to prevent competition between *E. hammondi* and *E. difficilis* in our study area. It remains to be demonstrated that competition for food between *E. wrightii* and *E. oberholseri* is eliminated by habitat differences when in sympatry.

It is noteworthy that differences in foraging ecology alone have not resulted in widespread sympatry of small flycatchers as is the case in other groups of insectivorous birds, such as warblers in the genus *Dendroica* (MacArthur 1958). Foraging on the wing for relatively large insects compared to the smaller size of insects taken by foliage-gleaning birds is probably an indication that food is relatively less abundant for flycatchers. Schoener and Janzen (1968) and Hesperheide (1971a) have shown that larger sized insects are relatively much less abundant than smaller ones. In addition, the flycatching habit may necessitate taking only large insects in order to make the energy intake per prey worth the effort. Coexistence between two flycatcher species may be possible only if they have very little overlap in the size of foods taken with the larger species taking much larger prey, or if they are interspecifically territorial as is the case for *E. wrightii* and *E. oberholseri* in eastern California and southern Nevada (Johnson 1966b). Thus, the combination of foraging on aerial prey that are large but not very abundant appears to have had a major influence on the pattern of distribution of flycatchers wherever they are found.

SUMMARY

Coexisting populations of the congeneric flycatchers *E. difficilis* and *E. hammondi* were studied during the breeding season in 1965 and 1966 in southern Colorado mountains. The study area is on the eastern edge of the range for both species at this latitude. The two *Empidonax* flycatchers are found together only

rarely, even though they have extensively overlapping ranges. We examined the circumstances under which local coexistence was possible in our study area. A third and slightly larger flycatcher, *C. sordidulus*, was also studied because of possible interactions with *E. hammondii*.

The study area contained a mosaic of habitats formed primarily by the physical ruggedness of the study area. We found *E. difficilis* and *E. hammondii* occupying overlapping territories in aspen-conifer habitat. *E. difficilis* was more than twice as abundant as *E. hammondii* in 1965, but both species had similar abundances in 1966 when the overall population sizes of both species decreased. *E. hammondii* also nested in aspen habitat in the presence of *C. sordidulus*, but occurred in lower numbers in 1966 than in 1965.

Coexistence was accompanied by differences in the foraging niche. *E. hammondii* fed significantly higher than *E. difficilis* in aspen-conifer habitat but with more than 50% overlap. The size of food items in the diets of each species was not significantly different. *E. hammondii* fed in the same vertical zone as *C. sordidulus* in aspen habitat, but the latter species took significantly larger prey. Both the situations found for *E. difficilis* and *E. hammondii* in aspen-conifer and for *E. hammondii* and *C. sordidulus* in aspen habitat suggest that coexistence for these species is possible by subdivision of the foraging niche in the first case, and by subdivision of food resources in the second.

However, the nesting success of *E. hammondii* in 1965 was low in the presence of a high population of *E. difficilis*. Also, about 63% of the breeding population of *E. hammondii* nested in aspen habitat in 1965, where nesting success was even poorer. In 1966, *E. hammondii* had better nesting success in aspen-conifer habitat in the presence of a greatly reduced population of *E. difficilis*. It was also observed that only 33% of the population of *E. hammondii* bred in aspen habitat in 1966. Thus, it appeared that *E. difficilis* displaced *E. hammondii* to some degree from aspen-conifer habitat. Thus, *E. difficilis* appears to be the superior competitor in our study area. Local coexistence is most likely a temporary and unstable situation in which *E. hammondii* is at a disadvantage.

It is postulated that each species of flycatcher actually has slightly different habitat preferences and that in localities where habitat is intermediate in composition coexistence may be observed but with one or the other species being at a competitive disadvantage. How-

ever, in the preferred habitat, one species is presumably able to exclude the other.

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