

OVERLAP IN FOODS AND FORAGING OF FOUR SPECIES OF BLACKBIRDS IN THE POTHOLES OF CENTRAL WASHINGTON

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Abstract. Overlap in foods and foraging of four species of breeding blackbirds in the Potholes of central Washington was estimated from samples of food delivered to the nestlings obtained by the pipe-cleaner technique. Prey distribution and availability were sampled with emergence traps for aquatic species and by sweeping with a standard insect net for upland species. Overlap was estimated by the probability that an item of food drawn randomly from the diet of one species would be of the same prey category taken from the same habitat as an item drawn at random from the diet of another species. Because of the diurnal cycle of emergence of aquatic insects, overlaps were calculated for three periods of the day (pre-emergence, emergence and postemergence) and averaged for the final overlap value. The overall food overlap for three of the species is high for all periods of the day and there is little evidence for differential specialization within habitats. Habitat overlaps, however, are varied, being highest during the emergence period for Redwings and Yellowheads but highest during the afternoon between Redwings and Brewers. The total overlap values are very similar to the theoretical maximum values derived from competition theory by MacArthur and Levins.

An important though controversial axiom of ecology is that two ecologically very similar species cannot exist in the same environment if there is a shortage of resources essential to both. A large body of mathematics and laboratory experiments supports the axiom, but its validity under the fluctuating conditions of nature is still debated. The evidence supporting the importance of competitive effects in nature is mostly indirect (Hutchinson 1957, Orians and Collier 1963), but a number of features of community structure suggest that competition may be operating.

Many field studies have demonstrated that closely related species differ significantly in their ecology, but these studies have not suggested how much overlap is required before competitive exclusion could be expected. It is unlikely that random collection of data on the amount of overlap between organisms will solve the problem, but recently MacArthur and Levins (1967) have presented a theoretical model of limiting similarity among ecologically similar species. The purposes of our paper are (i) to raise some of the problems encountered in attempts to quantify degrees of overlap among species, (ii) to indicate some partial solutions to these problems, (iii) to present data on overlap in food delivered to nestlings of several species of blackbirds, and (iv) to interpret these data in the light of current theory.

Selection of overlap parameters

Since any two organisms can overlap in an almost infinite number of characteristics, some basis for the selection of those features to be used in assessing competitively significant interactions between them must be developed. For the present purposes, we are primarily interested in variables in which shortages could possibly occur. That is, temperature tolerances are not particularly critical for our concern because the ability of one kind of organism to tolerate a given range of temperatures in no way precludes similar tolerances in many other species. The ability to tolerate different temperatures *should* influence

the interactions between two species, but the results will express themselves in different efficiencies of utilization of resources that can be exhausted. Similarly, the overlap in oxygen requirements between two species of mammals would not be of particular interest, but this might be critical in studies of interactions between fish species.

Of the resources that can be overexploited, one of the most important is food. The measurement of the overlap between the diets of two species is complex because two individuals in the same environment may find different foods by foraging in different ways. Alternatively, they may obtain the same foods but in slightly different environments. It is not immediately obvious how these similarities and differences should be analyzed and interpreted. Nevertheless, the importance of food resources to all living organisms requires that attempts be made to improve our measurement and interpretation of the foods of coexisting species.

Blackbirds (Icteridae) are well suited for this kind of analysis. They are usually the most common passerine birds in their habitats, the nests are easily found, food samples are easily obtained with neck collars of pipe cleaners (Orians 1966; Willson 1966), and in the simple vegetation in which they breed they are readily observed. In addition, some of the species exert a direct behavioral effect upon one another through aggression (Orians and Collier 1963) and interspecific territoriality (Orians and Willson 1964).

This paper reports on the food and foraging of four species of blackbirds in a 30-km² area of channeled scabland in Grant and Adams Counties, Washington. The species studied were the Brewer Blackbird (*Euphagus cyanocephalus*), Red-winged Blackbird (*Agelaius phoeniceus*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and Western Meadowlark (*Sturnella neglecta*). The data reported here are part of an extended study of the blackbirds of western North America. Details of the social organization and foraging ecology of these species are being presented elsewhere (Horn 1968,

1969; Orians 1966; Orians and Christman 1968; Willson and Orians 1963; Willson 1966).

The topography of the study area, part of which lies on the Columbia National Wildlife Refuge, consists of basins and buttes scoured in basalt by floods during the Pleistocene when the present channel of the Columbia River was blocked by ice (Bretz 1959). The Columbia basin lies in the rain shadow of the Cascade Mountains and receives only about 200 mm of precipitation annually, most of it falling in the winter. During the main breeding period of the blackbirds (May–June) precipitation is very light though strong southwest winds are common when storms rage over the mountains.

The dominant natural vegetation of the area is sagebrush (*Artemisia tridentata*), bunchgrass (*Agropyron spicatum*) and bluegrass (*Poa* sp.). Due to heavy grazing in the area, much of the bunchgrass has been replaced by stands of cheatgrass (*Bromus tectorum*). In the more alkaline pans sagebrush is replaced by greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus viscidiflorus*) is common on sandy sites.

Scattered over the basins are large numbers of lakes and ponds most of which were completely dry prior to the advent of irrigation in the basin at the turn of the century. More extensive irrigation began in the region in 1951; many new lakes have been formed since then and water levels have risen in others due to a general rise in the underground water table. In many localities the sides of the lakes are too steep to permit the growth of emergent vegetation, but where the slope is more gradual there are patches of cattail (*Typha latifolia*). Stands of sedges (*Carex* sp.) and *Scirpus* border most areas of standing water and streams, and an open growth of willows (*Salix amygdaloides*), locally damaged by beaver activity, follows the streams.

The nests of the meadowlarks are scattered through most of the upland sagebrush areas, being located either under small sagebrush bushes or in small depressions in the ground. Breeding colonies of Brewer Blackbirds are found in patches of tall sagebrush where the right combination of lookout posts and stream and/or lakeside foraging areas are present (Horn 1969). The nests of the Yellow-headed Blackbird are placed exclusively in cattails in the Potholes. Red-winged Blackbird nests are found primarily in cattails, but also in sagebrush and, occasionally, in small willows. Virtually all nests of all species are readily accessible.

METHODS

Observations of the foraging localities and foraging techniques of the adult blackbirds were made from vantage points on the basaltic cliffs. Food samples were collected from the nestlings of all four species by the pipe-cleaner technique. During May and June 1965–66, the period considered in our analysis, we gathered 103 samples from Brewer Blackbirds, 86 samples from Red-winged Blackbirds, 57 samples from Yellow-headed Blackbirds and 16 samples from Western Meadowlarks. By a sample we mean the food obtained from the nestlings in one nest during a single sampling period, usually about 1 hr in duration. Food samples were taken to the laboratory for identification; the caloric contents of most of the common prey species were obtained by burning in a Parr Semi-micro Oxygen Bomb calorimeter.

The limitations of the food samples need be borne in mind. First, it is impossible for us to obtain samples from young less than 3 days old. Our samples, however, cover the main period of food delivery to the young prior to fledging. Second, the neck-collaring technique is not

equally efficient on all species. A higher percentage of the food delivered to nestling Redwings and Yellowheads is recovered in the samples than is the case for Brewers. Either the neck musculature of nestling Brewers is such that they are better able to work the collar loose enough to permit food to be swallowed or they do not beg as vigorously when collared. We are unable, therefore, to use the food samples to estimate the amount of food delivered per hour for any of the species. For this reason, the following analysis is based upon the assumption that the food obtained in the samples is representative of all the food delivered.

Similarly, though we have reason to suspect that the rate of food delivery is not constant during the day but is higher during the periods of maximum emergence of aquatic insects, there is no consistent indication of such a relationship in the food samples of any of the species. Therefore, we have had to assume that the rate of delivery of food to the nestlings is constant throughout the daylight hours. This assumption is necessary to estimate the caloric importance of the different types of food, but it is not critical to our discussion of overlap.

In comparing the food delivered to nestlings of different species we have erected categories based upon both the kind of food and the kind of habitat in which it was obtained. Because the vegetation in this area is structurally simple, it is possible to divide the foraging substrates into four discrete categories: (i) emergent aquatic vegetation (almost exclusively cattails), (ii) sedges bordering the ponds and streams, (iii) sagebrush, and (iv) upland dry grass. The structural simplicity of the vegetation greatly restricts the number of foraging techniques possible in the same habitat, though, as will be pointed out later, the different species of blackbirds may forage differently in one of the habitats.

The erection of suitable categories for the kinds of food taken by the birds is a more difficult problem. It would be possible, in most cases, with considerable effort, to carry the identifications of the insects and other food items to the generic or specific level, but there are convincing reasons for not doing so. First, the number of different food types in the samples of all the species of blackbirds is so large that fine taxonomic categorization would be extremely cumbersome. Moreover, the large number of species taken strongly suggests that the blackbirds, like most species of birds that have been studied intensively, probably take nearly all the insects within a certain size range that they encounter as they forage (MacArthur 1961). Assuming that blackbirds forage in such a manner that they maximize energy intake per unit of time and energy expended in foraging (MacArthur 1961, Emlen 1966), it is unlikely that their rate of energy intake could be increased, or even maintained, by selectively discriminating against certain prey types unless they are highly unsuitable for other reasons; i.e., they are toxic or extremely difficult to capture even when encountered.

The four species of blackbirds are similar enough in size that all of them regularly utilize the same range of prey sizes. Therefore we have not attempted to erect categories of prey based on size. If prey are taken in roughly the frequency that they are encountered in a given environment, the most useful grouping of prey would be according to whether they will be encountered by a bird foraging in a specific way. Accordingly, we have attempted to establish our categories of prey by this criterion. Thus, all of the insects found on the stems of upland grasses, or all insects obtained from the sedges at the edge of a pond are grouped together. By this criterion, members of a single species may be placed in dif-

ferent categories depending upon their age and the time of day they were taken. For example, damselfly larvae are inevitably taken from the edges of the ponds, either on emergent vegetation or the sedge borders. The teneral, however, leave the marshes as soon as they are able to fly and may be picked up on the sagebrush bushes in the afternoon. Adults are usually taken in sagebrush bushes where they roost for the night. Conversely, some unrelated taxa are lumped because their microhabitats and behaviors are similar.

Many of the food items are restricted to a specific habitat, but others cannot be assigned to a location with precision. In these cases we have examined the other items in the sample and assigned the doubtful ones by association. For example, a spider found in a food sample together with a large number of damselfly larvae and dytiscid larvae is assigned to the emergent vegetation, while a spider in a sample together with several grasshoppers is assigned to the dry grass.

In addition we have used our knowledge of the foraging behavior of the blackbirds to aid us in our assignment of foods to habitat. For example, the legs of the Brewer Blackbird are not properly proportioned for efficient foraging on stalks of cattails; moreover, individuals foraging close to cattails are usually chased away by Redwings or Yellowheads. During the peak periods of damselfly emergence the Brewers forage almost exclusively at the sedge edges of the ponds and streams. Accordingly we have assigned damselfly larvae and teneral to the sedge habitat when they are found in Brewer samples but to the emergent vegetation when they are found in Redwing and Yellowhead samples. The assignments of food items to habitat and the criteria by which they were made are summarized in Appendix A. The actual numbers of food items of the different categories assigned to the four habitats during three major periods of the day are summarized in Appendix B.

A qualitative estimate of the food available to the birds was made in the following ways. While walking through the marshes to check nests and collect food samples, we made general notes on the number of teneral insects flushed. Ten emergence traps (Cook and Horn 1968) on a small lake near a colony of Brewer Blackbirds provided a more accurate picture of the diurnal pattern of emergence of damselflies which form the bulk of the food samples of several of the blackbirds for an important part of the day. Some sweep sampling with a standard insect net was done in the upland habitats, but as yet we have insufficient data to estimate relative abundances of the insects there.

RESULTS

Of the four species of blackbirds, the meadowlark is the most singular, foraging almost entirely on terrestrial insects many of which are obtained by digging (Table 1). A foraging meadowlark will walk slowly over the ground examining holes. Upon finding one it places any food already in its bill on the ground, digs into the hard desert soil with its long, powerful bill, extracts the food items, picks up the other food, and continues its search.

The other species of blackbirds do forage on the uplands, but they obtain a smaller percentage of their prey from that area, get very little of it by digging, and regularly search for and capture aquatic insects that have moved away from the water. For these reasons the overlap between the food and foraging techniques of the meadowlark and the other three species is very low. In the following analyses we shall be concerned strictly with the other three species.

TABLE 1. Food of nestling Western Meadowlarks, Columbia National Wildlife Refuge, 1964

Taxon		Larvae or nymphs	Adults	Total
Ephemeroptera.....			2	2
Hemiptera.....	Pentatomidae		16	16
	Reduviidae		1	1
	Scutellaridae		1	1
	other	1	2	3
Diptera.....	Asilidae		1	1
	Culicidae		2	2
	other	11	4	15
Lepidoptera.....	Hesperiidae	2		2
	Noctuidae	2		2
Coleoptera.....	Dytiscidae	1		1
	other	16	26	42
Orthoptera.....	Acrididae	18	32	50
	Gryllidae		4	4
	Tettigoniidae	11	21	32
Hymenoptera.....		1	21	22
Spiders.....			36	36
Scorpionida			2	2
Gastropoda.....			4	4
				238

The Brewer Blackbird also has long legs and forages primarily by walking either on relatively bare ground or over the short sedges bordering the lakes and streams. It is, on the other hand, extremely awkward in foraging from vertical stalks of cattails, and we have never observed it to extract prey by digging into the soil. Like the other species, however, it does flip over dried cattle dung.

The Redwing and Yellowhead are very similar in general proportions, differing only in size, the Yellowhead being larger. Both are adept at foraging from the vertical surfaces of emergent aquatic vegetation by grasping either one or two stalks. Because of their shorter legs, however, they walk more slowly on the ground and progress with greater difficulty through the low sedges favored by the Brewers. Unlike the other species, Redwings regularly forage in trees, but this is a minor feature of their behavior in the Potholes owing to the scarcity of trees.

Temporal pattern of foods and foraging

In large part, nestling blackbirds are fed emerging aquatic insects, but this resource is not uniformly available during the day. Rather there is a striking daily cycle of emergence of many of the species, particularly the most important items. The average catches of emerging damselflies from 10 shore traps set on 1 lake in the Potholes during late May 1966 are shown at the bottom of Figure 1. The peak in emergence during the mid- and late-morning hours is clearly indicated. During bad weather the time of emergence may be delayed and heavy rain may inhibit it entirely, but in the Potholes at this time of the year heavy overcast and rain are extremely rare; hence the pattern illustrated is typical of most days while the blackbirds are feeding their young.

There is no comparable cycle of insect abundances in the upland areas, but in those areas not too distant from the water the availability of food is influenced by the movement away from the water of teneral insects, particularly odonates and dipterans, during the afternoon hours. This accounts for the fact that the blackbirds may forage in the uplands during the afternoon and yet obtain many aquatic insects.

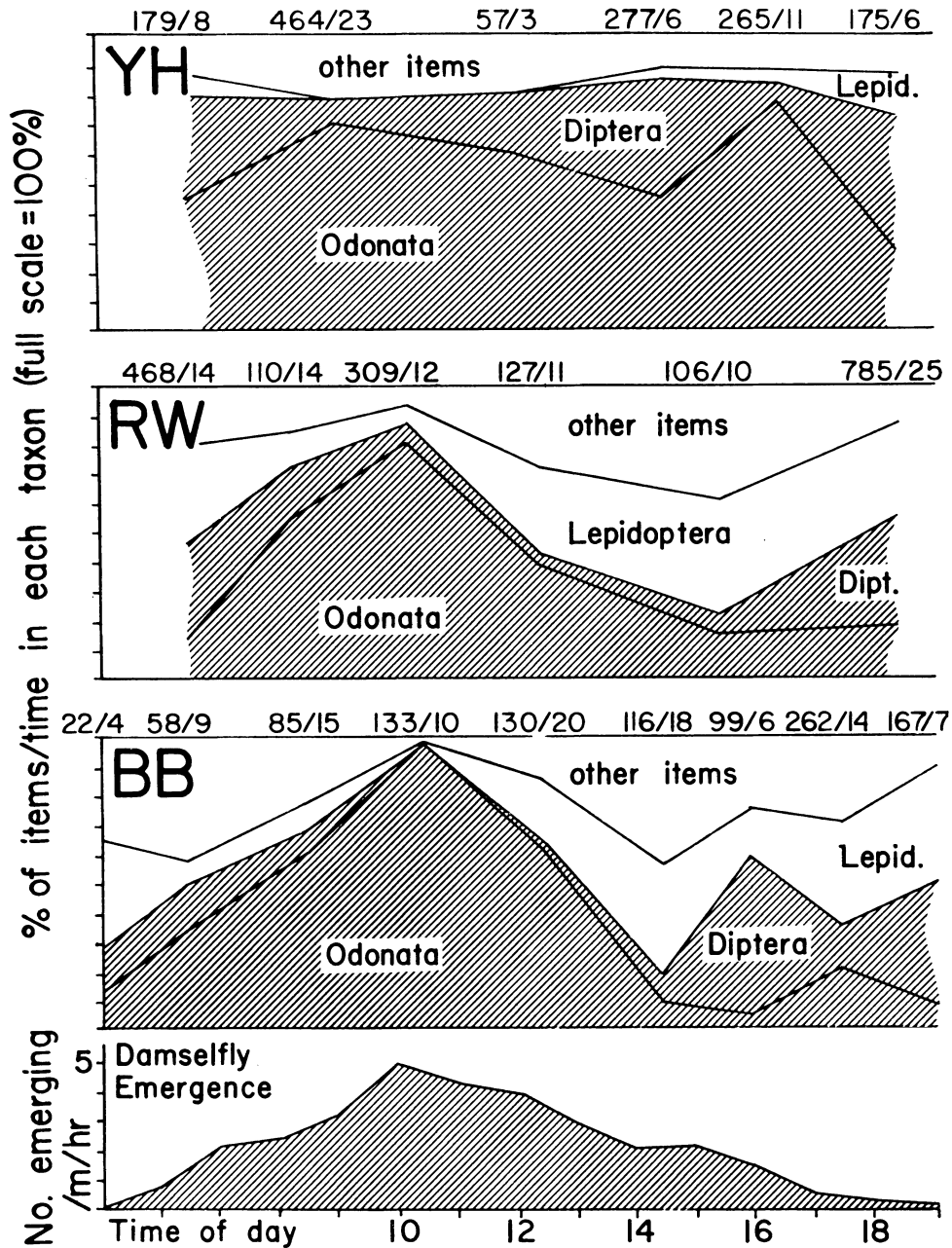


FIGURE 1. Diurnal changes in food of nestling blackbirds and emergence of damselflies at the Potholes. Damselfly emergence is plotted as the number of nymphs emerging per meter of pond edge per hour. The numbers above the diets for each species of blackbird indicate the number of prey items (larger number) and the number of samples (smaller number) which each point represents. Aquatic insects of the two most common insect orders are hatched to provide a rough picture of the importance of aquatic feeding for the blackbirds at different times of the day.

The diurnal changes in food delivered to nestlings of the three species of blackbirds are shown in Figure 1. The major insect groupings are indicated on the diagrams; "other items" are small mollusks, spiders, and insects that show no diurnal variations in the samples. Of the three species, the Yellowhead forages primarily upon aquatic insects during the entire day, bringing more than 80% aquatics at all times. By contrast, both the

Redwing and the Brewer capture many terrestrial organisms during the early morning and mid-to-late-afternoon hours. Many of these prey items are captured in sagebrush bushes and dry, upland grass.

Because the temporal pattern of odonate emergence is such a major factor influencing the availability of foods and foraging behavior of the birds, we have divided the day into three periods: early morning, prior to the emer-

gence of large numbers of aquatics (0400-0700); mid-morning, during the main emergence (0700-1300); and afternoon, after the major emergence (1300-1900). The quantities of data available for analysis do not permit finer subdivisions of the day; moreover, it is unlikely that finer subdividing would reveal anything not clearly indicated by a tripartite division.

Food-habitat overlap

The total food obtained from the nestling food samples is given, in terms of per cent composition both by numbers and calories, in Table 2. Both forms of presentation are of intrinsic interest. The numbers of different prey items may be a better indication of the amount of time the birds have foraged in different environments while the caloric proportions stress the energetic importance of the larger insects. Thus, though orthopterans and cicadas are numerically insignificant in the food delivered to the nestlings, they do contribute a major portion of the total energy delivered to nestling Redwings and Brewers. On the other hand, though larger numbers of dipterans and lepidopteran larvae (mostly very small pterophorid larvae) are captured, they contribute relatively less to the total energy budget of the young because of the small average sizes of the individuals. Odonates are fairly large insects and consequently they are important both in terms of numbers and calories delivered.

TABLE 2. Food of nestling blackbirds in the potholes (per cent of daily total)^a

Taxon	Items			Calories		
	Yellow-head	Red-wing	Brewer	Yellow-head	Red-wing	Brewer
Odonata.....	56	37	34	64	35	34
Orthoptera.....	1	2	7	3	7	24
Cicadidae.....	1	3	1	4	23	11
Lepidoptera.....	4	30	24	3	14	13
Diptera.....	24	13	21	6	5	5
Other insects.....	7	5	7	4	3	3
Araneae.....	4	7	5	10	9	9
Other items.....	3	3	1	6	4	1
Totals: items.....	1417	1905	1072			
samples.....	57	86	103			

^aSamples have been corrected to comparable sampling per hour.

Based upon the food and habitat categories discussed earlier, we have calculated the overlap in foods delivered to the nestlings using the overlap of Morisita as modified by Horn (1966). The calculations are outlined fully in Appendix C. Separate calculations have been made for each of the three major periods of the day; the results are shown in Table 3. All three species of blackbirds are exploiting a similar food supply, and this is expressed in the fact that the overall food overlap for all species for all periods of the day is high. The overall food overlap is particularly high during the midmorning hours when all species are feeding almost entirely upon emerging damselflies. It is also very high for Redwings and Brewers during the afternoon when both are obtaining primarily lepidopteran larvae and orthopterans from the sage brush and dry grass.

Habitat overlaps, however, are more varied. As indicated above, habitat overlap is very high between Redwings and Yellowheads in the midmorning and between Redwings and Brewers in the afternoon when both are obtaining the same items in the same environments. The

TABLE 3. Overlap in food foraging habitat of blackbirds in the Potholes. See Appendix C for formulas

Type of overlap	Species compared	Time of day			Time-weighted average
		0400-0700	0700-1300	1300-1900	
Habitat	YH-RW	.88	.97	.56	.79
	RW-BB	.93	.18	.99	.65
	BB-YH	.80	.21	.60	.48
Food (overall)	YH-RW	.73	.97	.64	.79
	RW-BB	.68	.75	.96	.82
	BB-YH	.71	.84	.66	.74
Food (within-habitat)	YH-RW	.79	.93	.83	.86
	RW-BB	.72	.36	.96	.67
	BB-YH	.57	.10	.76	.46
Total	YH-RW	.72	.91	.48	.70
	RW-BB	.67	.06	.95	.54
	BB-YH	.47	.02	.46	.29

Yellowhead overlaps less with the other two species during the afternoon as it forages primarily on the marshes while the others are mostly exploiting the uplands. The overlap in this case may be even less than we have indicated since some of the adult odonates assigned to the sagebrush may have been captured by Yellowheads in the cattails.

The lowest habitat overlaps occur between Brewers and the other two species during the midmorning hours when Brewers forage almost entirely at the sedgy edges of ponds and streams while the other species forage primarily in the emergent vegetation. However, both Redwings and Yellowheads forage along the sedgy edges even when Brewers are also exploiting the area, so that the actual habitat overlap is greater than given in the tables, but we are unable to say by what factor the estimate should be altered.

A total overlap for the three species may be obtained by considering each combination of food and habitat as a separate resource. This analysis reveals that the Redwing is intermediate between the other two species in its exploitation of the environment, overlapping by at least 50% with both of the other two species. Brewers and Yellowheads have a much lower total overlap and at no time of day does the amount of overlap get as high as 50%.

DISCUSSION

There are two cases in which two of the species show high overlap in both food and habitat at the same time of the day. One of these cases (the midmorning overlap of Redwings and Yellowheads) occurs when emerging damselflies are most abundant and can be interpreted as a convergence upon a temporarily superabundant food supply. The other case (afternoon overlap between Redwings and Brewers) does not, however, represent similar convergence, though the number of insects in the sagebrush and dry grass is probably highest then because of the movements of teneral aquatic insects away from the ponds and streams. We do have evidence which suggests that the two species may be foraging in different ways at that time, but this difference is not expressed in either the habitat categories we have established or the food groupings we have found most useful. The Brewer Blackbird forages in sagebrush in one of two ways. Either it walks on the ground underneath the bushes and searches for and captures insects on the branches above, or it forages on the tops of the denser bushes. The Redwing,

on the other hand, being a smaller bird with shorter legs, regularly forages by moving among the branches of the bushes. Apparently the same kind of insects are encountered by all techniques, and, since we have not subdivided a sagebrush bush as a foraging substrate, these differences, though possibly of competitive significance, do not influence our calculations. More quantitative data on the distribution of insects in sagebrush and the foraging of the birds will have to be gathered before this problem can be analyzed more precisely.

In most cases, the estimates of overall food overlap and within-habitat food overlap are extremely similar. This can be interpreted (Appendix C) to mean that when foraging in the same environment, birds of all three species obtain roughly the same food in the same proportions. Therefore, for our purposes, a division of the overlap into its food and habitat components is sufficient to obtain useful estimates of the degree of overlap among the species. Suppose, however, that the foraging efficiencies of the birds varied in opposite directions in the different substrates so that, say, Redwings obtained primarily orthopterans in the dry grass and odonates in the sedges while Brewers captured primarily odonates in the dry grass and orthopterans in the sedges. In this event, a calculation of food and habitat overlaps would show very high overlap, whereas the actual overlap would be extremely low. While it is unlikely that two ecologically similar species would really behave in the manner just suggested, it cannot be concluded a priori that more subtle differences of this kind are not operating in a particular case. Therefore, a test which can reveal the importance of different foraging behaviors in different habitats is an important part of any analysis of overlap. We believe that the test we have used may be a valuable way of doing so.

Our data show that the three species of blackbirds are responding to the temporal and spatial heterogeneity of the environment in very different ways. The Yellowhead forages almost exclusively among marsh vegetation and the insects available in it. During the spring of 1965 there was an irruption of cicadas (*Okanagana luteobasalis*) in the Potholes, and both the Redwings and the Brewers (but not Yellowheads) responded by searching for and capturing these extremely large insects. During the afternoon hours that year, cicadas formed at least 25% of the energy delivered to nestling Redwings and about 10% of the energy delivered to nestling Brewers. The importance of the cicadas to the Redwings may have been higher because of the greater ability of female Redwings to capture cicadas among the denser branches of the sagebrush bushes.

Since a clumped nesting pattern is probably the result of a temporally and spatially variable food supply (Horn 1968), the opportunism of the Brewer Blackbird is to be expected. The Redwing is a species primarily oriented toward marshes in most of its range, but it does regularly breed and forage in uplands and, in all environments where it has been studied, obtains a significant amount of its food away from the marshes. As a result it is able to breed in more humid regions where the marshes are in general less productive and within a given region it can be found on lakes of low productivity (Orians 1966). As a species it appears to have been under considerable selection to respond to changes in food availability in upland environments.

The Yellow-headed Blackbird, however, is a species that forages almost exclusively on aquatic insects over most of its range. Its geographical range is limited to arid and semiarid regions and within a given region it is restricted to highly productive lakes (Orians 1966). In

some areas Yellowheads obtain more of their food from the uplands, but on the whole the species seems less able to supplement the food available on the marshes with alternative sources.

The highest total overlap occurs between the Redwing and the Yellowhead. These species are also most similar morphologically and overlap most in their nesting sites. These results accord with the fact that they are interspecifically territorial and support the interpretation of Orians and Willson (1964) that the degree of overlap between these two species is sufficient to have given selective advantage to interspecific exclusion behavior. Foraging Brewer Blackbirds are chased away when they attempt to capture food within the territories of Redwings or Yellowheads, but we have no evidence that the size and locations of colonies of Brewers is influenced by interactions with birds of the other species. Colony locations are explicable on the basis of the combination of large sagebrush bushes, lookout perches and suitable foraging areas (Horn 1969). The reasons for the failure of more elaborate interspecific exclusion behaviors to develop may include the following: First, the defense of a section of emergent vegetation involves defense of both the nesting substrate and major foraging substrate for Redwings and Yellowheads. Therefore, a reduction in the density of breeding birds of the two species combined can be achieved at a relatively low energy cost per individual. The major foraging substrate of the Brewers, however, provides no nesting sites for any of the species, and, moreover, its generally linear distribution makes it more difficult to defend. In addition, for a male Redwing to prevent a colony of Brewer Blackbirds from establishing itself in the general area would require that he spend long hours away from his territory and mates. It is difficult to imagine conditions under which such behavior could result in an increase in fitness. Orians and Willson (1964) suggested that the major factor influencing the probability that two ecologically similar species would be interspecifically territorial was the structural simplicity of the vegetation which renders general visibility good and makes defense relatively inexpensive. Our results on the interaction of these three species of blackbirds suggests that the spatial distribution of patches in the environment may also play an important role in determining the costs of exclusion and, hence, the degree of overlap required before such behavior is favored by natural selection.

In a theoretical analysis of optimal foraging patterns in patchy environments, MacArthur and Pianka (1966) suggested that an organism might be expected to respond to competition by decreasing the number of patches in the environment in which it foraged but not to decrease the number of prey types it captures. Our data (Table 3) provide limited support for this prediction. The blackbirds in the Potholes do indeed differ to a greater extent in their foraging habitats than in their overall choice of food types. We hope to subject this theory to a more critical test by making use of the differing intensities of competition that accompany the temporal changes in the abundance of damselflies. However, this test must wait until we are able to measure the intensity of competition with data that are independent of our measures of food and habitat overlap.

MacArthur and Levins (1967) have derived a theoretical criterion for the limiting similarity of coexisting species. This criterion applies to species that can be linearly ordered with respect to their resources, as the Yellowhead, Redwing, and Brewer blackbirds can be. Furthermore, the species must be similar enough, as we must assume the blackbirds are, that the environment

would support about the same number of individuals of each species in the absence of the others. MacArthur and Levins' criterion predicts that the blackbirds are as similar as coexisting species can be if the sum of the YH-RW overlap and the RW-BB overlap equals 1 plus the BB-YH overlap. The total overlaps of Table 3 fit this criterion almost exactly ($YH-RW + RW-BB = 1.24$; $1 + BB-YH = 1.29$). In view of the numerous assumptions we have made in calculating these overlaps, we find their agreement with the theory remarkable. The theory may indeed describe nature accurately; alternatively the theory may be flexible enough to accommodate any data when the ordering of the species is determined from the relative magnitudes of their overlaps. Although the theory is not subject to a critical test, an accumulation of many weak tests like ours might strongly support the theory.

As a final point, we wish to emphasize that the analysis of the data on food and habitat aspects of overlap among these species of blackbirds has depended heavily upon our broad general knowledge of the birds, their foraging behavior and the distributions of insects in the environment. Without this basic biological information, the use of overlap indexes can be of limited usefulness in interpreting the relationships between species. Erection of categories and the assignment of data to them can be no better than the knowledge of the investigator of the system.

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APPENDIX A. Habitat groupings of insects found in blackbird food samples.^a

Habitat category	Insects assigned to habitat category when in:	
	Redwing and Yellowhead samples	Brewer samples
Emergent aquatic vegetation	Odonate larvae and teneralis, gastropods, dipteran larvae, dytiscid larvae	Nothing
Sedge edges	Most Anisoptera teneralis, ichneumonids, some Trichoptera, mycetophilid and sciarid Diptera, most spiders	Odonate larvae and teneralis, mycetophilid and sciarid Diptera, ichneumonids, Trichoptera most spiders, some hemipterans by association
Sagebrush	Odonate adults, most adult Diptera, Lepidoptera larvae, katydids, orb-weaving spiders, cicadas, ephemeropterans, most Coleoptera, raphidiids, some Hemiptera and Hymenoptera by association (Reduviidae, Tenthredinidae, Diprionidae).	Same as Redwing and Yellowhead samples.
Dry grass	Grasshoppers, some beetles burrowing spiders	Grasshoppers, crickets, some beetles, burrowing spiders, cicada nymphs

^aMany items have been assigned to different habitats than indicated in this table when they were associated in a food sample with key items restricted to one of the habitats.

APPENDIX B. Numbers of prey individuals of the different taxa assigned to the four habitats, (a) during the early morning preemergence period (0400-0659) ...

Taxon	Emergent vegetation			Grass-sedge edge			Sagebrush			Dry upland grass		
	YH*	RW	BB	YH	RW	BB	YH	RW	BB	YH	RW	BB
Anisoptera (L) ^a	6	5				3						
Anisoptera (T)	1	4		4								
Anisoptera (A)												
Zygoptera (L)	28	9										
Zygoptera (T)	38	10				16						
Zygoptera (A)							10	40	5			
Diptera		4		2	1		70	139	12			
Lepidoptera							16	152	13			
Orthoptera								4	8	1	2	3
Cicadidae								5	2			
Other insects and spiders												
Other items	3			7	3		12	44	18			

... (b) during the midmorning emergence (0700-1259),

Anisoptera (L)	9	6				7						
Anisoptera (T)						7	19	3				
Anisoptera (A)									2	1	1	
Zygoptera (L)	122	70				151						
Zygoptera (T)	210	259				95						
Zygoptera (A)	7					3	3	10				
Diptera	2	14		2		5	56	26	2			
Lepidoptera								69	37			
Orthoptera									2			5
Cicadidae								15	3			
Other insects and spiders	6	4		63	20	12	7	30	14			
Other items	28	8				5			1			

... (c) during the afternoon postemergence period 1300-2000).

Anisoptera (L)	2	1				2	1					
Anisoptera (T)						1						
Anisoptera (A)									1			
Zygoptera (L)	69	10				26						
Zygoptera (T)	206					47	37			1		
Zygoptera (A)	26					3		62	128	25		
Diptera	62	25						150	211	179		
Lepidoptera								38	322	214		
Orthoptera								3	7		4	15
Cicadidae								4	10	4		2
Other insects and spiders	3			34	10	3		38	82	89		
Other items	9	26				5						

*YH=Yellow-headed Blackbird, RW=Red-winged Blackbird, BB=Brewer Blackbird, L=larvae, T=teneral and A=adults.

APPENDIX C. Decomposition and interpretation of overlap indices.

In the following decomposition of overlap indices, we estimate probabilities using a model appropriate to sampling with replacement, since the samples that we have taken from young blackbirds are less than 1/100 of what the adults bring in. Ours may not be the most efficient estimates available, but we only use probabilities intuitively to interpret the resulting overlaps, which are treated as single measurements rather than as estimates of population parameters. Unfortunately, we don't know how the numbers on which we base our measurements

vary in nature. Therefore, until we have more data and keener biological judgment, statistical efficiency is trivial. An alternative view is expressed by Pielou (1966), and alternative estimators are discussed by Simpson (1949) and Morisita (1959).

Let x_{ij} be the proportion of a sample of species X 's diet that consists of food j taken from habitat i . y_{ij} is similarly defined for species Y . For notational convenience we define the proportion of species X 's food that is taken from habitat i as $X_i = \sum_j x_{ij}$, and the proportion of food j in species X 's diet as $X_j = \sum_i x_{ij}$. We use corresponding notation for species Y .

The probability that two items taken randomly from the diets of each species will be the same food from the same habitat is $P(F+H) \approx \sum_i \sum_j x_{ij} y_{ij}$. Similarly, $P(H) \approx \sum_i X_i Y_i$ is the probability that randomly drawn items from the diets of both species will come from the same habitat, and $P(F) \approx \sum_j X_j Y_j$ is the probability that they will be the same food, regardless of the habitat they come from. The "laws" of probability tell us that $P(F+H) = P(H) \cdot P(F^*H)$, where $P(F^*H)$ is the probability that the same food will be represented by two items drawn randomly from the diets of both species in the same habitat.

From the data x_{ij} and y_{ij} we can now estimate $P(F+H)$, $P(H)$, $P(F)$, and $P(F^*H)$. $P(F+H)$ measures the total overlap in food and habitat. $P(H)$ and $P(F)$ measure the overlaps in habitat and food respectively. If each of the types of food were equally distributed among the habitats, and if species X and Y foraged in the same way in each habitat, then $P(F^*H)$ would equal $P(F)$. Thus $P(F^*H)$ measures the average overlap in foraging techniques, weighted by the amount of time spent in each habitat and the relative abundances of food types in that habitat.

Each of the above probabilities can be calculated for a single species as well as for a pair of species. For example, $P_x(F) \approx \sum_j X_j^2$, the probability that two items randomly drawn from the diet of species X will be the same food, provides a measure of the food specialization of species X ; that is, the inverse of "niche breadth" (Levins 1968) relative to food.

The competitive overlap that is ecologically most interesting is the overlap between two individuals of different species relative to the overlap between individuals of the same species. When each of the overlap probabilities is divided by the average of the corresponding specialization probabilities for each of the species concerned, we have the overlap measure of Morisita (1959) as modified by Horn (1966) which is the average of the estimates of the α of competition equations used by MacArthur and Levins (1967).

In Table 3 we have calculated: Habitat overlap = $2P(H)/[P_x(H) + P_y(H)]$, overall food overlap = $2P(F)/[P_x(F) + P_y(F)]$, within-habitat food overlap = $2P(F^*H)/[P_x(F^*H) + P_y(F^*H)]$, and total overlap = $2P(F+H)/[P_x(F+H) + P_y(F+H)]$. Interpretation of the overall food, habitat, and total overlaps is straightforward. If the habitat overlap is great, then species X and Y are exposed to about the same average distribution of food, and within-habitat food overlap can differ substantially from overall food overlap only if the foraging techniques of X and Y differ within

each habitat. Thus, the ratio of within-habitat food overlap to overall food overlap measures the similarity of foraging techniques of species X and Y . Any difference in the habitats exploited will, of course, affect the calcu-

lated within-habitat food overlap. Thus, the interpretation of within-habitat food overlap is unclear if there is little habitat overlap, but in this case the overlap in foraging techniques is ecologically uninteresting.