

FOOD NICHE OVERLAP OF TWO IOWA MARSH ICTERIDS¹

DAVID K. VOIGTS²

Department of Zoology and Entomology
Iowa State University
Ames, Iowa 50010

Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) seem to establish mutually exclusive territories in fresh-water marshes. Red-winged Blackbirds tend to nest in dense vegetation and Yellow-headed Blackbirds nest in clumped vegetation over water (Orians and Willson 1964), but little is known concerning the evolution of this apparent segregation. One resource that could be over-exploited, leading to competition, is food; and mutually exclusive territories may reduce overlap in food use. Orians and Horn (1969) have quantified overlap in diet between Red-winged, Yellow-headed, and Brewer's Blackbirds (*Euphagus cyanocephalus*) nesting in central Washington. The present study measures overlap in diet between Red-winged and Yellow-headed Blackbirds throughout the nesting season in northwestern Iowa. Changes in prey availability and differences in foraging techniques also were studied because both can affect blackbird food habits and influence the degree of overlap.

DESCRIPTION OF THE STUDY AREA

This study was conducted in an area of concentrated nesting at Rush Lake, a semipermanent marsh in northwestern Iowa 15 miles S of Ruthven. The vegetation of this general area has been summarized by Hayden (1943).

In 1969, Rush Lake was nearing the "open stage" described by Weller and Spatcher (1965). Muskrats (*Ondatra zibethica*) had extensively opened the homogeneous stand of cattail (*Typha* sp.) in the deep-marsh zone, but a broad peripheral band of cattail remained and formed the major nesting area of the icterids. (Names for the zones follow Stewart and Kantrud 1971.) Typical floating vegetation was duckweed (*Lemna minor*), giant duckweed (*Spirodela polyrrhiza*), and slender riccia (*Riccia fluitans*) in very dense mats. Submerged plants were bladderwort (*Utricularia vulgaris*), coontail (*Ceratophyllum demersum*), and sago pondweed (*Potamogeton pectinatus*). Emergent plants of the very narrow, sparsely vegetated wet-meadow zone were sedges (*Carex* spp.), blue flag (*Iris virginica*), spikerush (*Eleocharis* spp.), and willows (*Salix* spp.).

Major upland vegetation adjacent to the marsh study area consisted of an open stand of primarily burr oak (*Quercus macrocarpa*), ash (*Fraxinus* spp.), and gooseberries (*Ribes* spp.) in thickets on the steep

marsh bank. About 200 yards from the study area on the marsh was an uncut hayfield of alfalfa (*Medicago sativa*), white sweet clover (*Mililotus alba*), and Timothy (*Phleum pratense*).

METHODS

Field work began 22 May 1969, when egg laying was nearing the peak, and continued through 4 July, when only two active Red-winged Blackbird nests remained on the study area. This area of concentrated blackbird nesting was searched systematically for nests at least every 10 days. Nest locations were marked by spraying paint on the tips of cattail leaves and with plastic marking tape. Nests were numbered on the supporting dead vegetation with a felt-tipped pen.

Food samples from nestling Yellow-headed and Red-winged Blackbirds were obtained with the pipe-cleaner neck-band method (Orians 1966, after Klujiver 1933). Neck bands were left in place approximately 1 hr.

Insect foods were identified to family by using the keys in Usinger (1963) for aquatic insects and in Borror and DeLong (1964) for terrestrial insects.

Aggregate volumes for each prey taxon were determined to the nearest 0.01 ml by displacement in 80% ethyl alcohol. Per cent of total volume has been used as an index of caloric value of prey (Snelling 1968) because most invertebrate tissues seem similar in calories per ash-free gram (Slobodkin 1961). It must be assumed that both Red-winged and Yellow-headed Blackbirds expend about the same energy in foraging and that assimilation efficiencies for any food item are similar for both species (Snelling 1968).

The index of Morisita (1959), as simplified by Horn (1966), has been used to quantify overlap in food between two species. In this study, the index also was used to measure diurnal and seasonal changes in the diet of each species. The following formula was used to calculate the index of overlap (C_{λ}):

$$C_{\lambda} = \frac{2 \sum_{i=1}^s x_i y_i}{\sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2}$$

This formula is appropriate when the data are expressed as the proportions x_i and y_i of respective samples from the diets of species x and y that are composed of prey taxon i (Horn 1966). A maximum value of 1 is possible when there is complete overlap. Totally different samples give an index value of zero.

Odonate emergence was studied with 16 box traps, 18 inches by 36 inches, made of wood frames and plastic screen (Voigts 1973). Traps were placed at the shore line and at random within three vegetative zones along four transects crossing areas used by both blackbird species. Traps were emptied on alternate days shortly after noon.

Foraging females were observed from a portable blind placed near a nest and from an automobile

¹ Journal Paper No. J-7351 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 1504.

² Present address: Ecological Services Group, Texas Instruments, Inc., R.F.D. 4, Ulster Landing Road, Saugerties, New York 12477.

TABLE 1. Diurnal patterns in the major foods of nestling blackbirds (3% or more of total volume for each species from each time period).

Major foods	Per cent of total volume									
	Time periods								Total number	
	06:00-08:59 ^a		09:00-12:59		13:00-16:59		17:00-21:00			
	RW		YH		Blackbird sp.				RW	YH
					RW		YH			
Nests sampled										
	12	11	14	22	18	20	6	13	50	66
Ephemeroptera										
Ephemeridae A ^b (Burrowing mayflies)							4.3		1	0
Odonata										
Lestidae A (Spread-winged damselflies)	8.5		15.4		7.2		3.3		18	0
Coenagrionidae A (Narrow-winged damselflies)	8.7	5.0	11.8	16.8	12.9	24.2	8.1	18.3	73	135
Orthoptera										
Gryllidae T (crickets)					6.6				1	0
Hemiptera										
Miridae T (Leaf bugs)	5.0								0	51
Homoptera										
Membracidae T (Treehoppers)	3.4		4.4				10.4		75	1
Aphididae T (Aphids)		3.5		6.4				3.6	173	991
Coleoptera										
Carabidae T (Ground beetles)	7.3	4.1				3.5			8	7
Scarabaeidae T (Scarab beetles)	9.0		16.7		6.2				4	0
Lepidoptera										
Noctuidae T (Noctuid moths)	21.1		7.2		20.5	3.9	25.1	8.6	22	7
Pyralidae U (Pyralid moths)				4.6	4.9	6.7		13.9	8	37
Unidentified T			14.9						19	2
Diptera										
Tipulidae A (Crane flies)	3.9				6.4		12.3	3.8	27	30
Chironomidae W (Midges)	18.0	26.8		15.2		10.1		11.2	194	702
Stratiomyidae A (Soldier flies)		8.5		21.6	7.2	14.9	9.5	12.4	24	123
Syrphidae T (Flower flies)				4.9				5.6	4	22
Ephydriidae A (Shore flies)	5.9			7.0		9.5			1	312
Anthomyiidae T (Anthomyiid flies)	7.4			4.1		5.5			14	136
Arachnida										
Araneida W (Spiders)	7.0	4.7	11.3	5.2	6.8		3.8	5.0	99	74
Unidentified U							4.3		6	13
Corn seeds T		8.2							1	4
Totals	3.35	3.40	3.90	7.76	5.12	8.25	2.11	3.38	890	2978

^a Central Daylight Saving Time.

^b A, primarily from the marsh; T, primarily from the uplands; W, widespread; U, unknown.

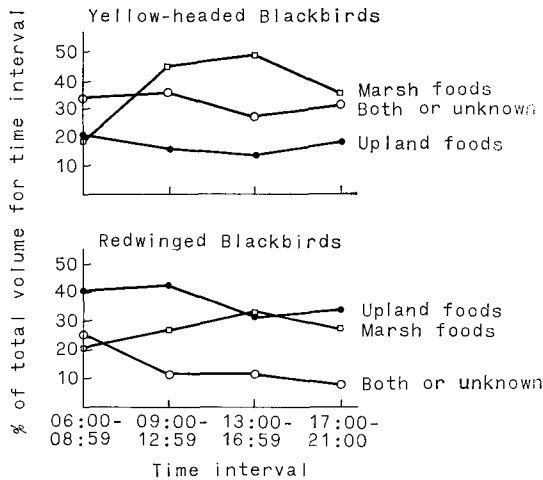


FIGURE 1. Diurnal patterns in major foods of nestlings.

parked on an adjacent road. An opening in the trees concentrated the birds flying to the hayfield foraging area.

The animal foods available at known foraging sites in the hayfield were sampled with an aerial insect net. A sweep-net sample consisted of 15 sweeps 6 ft long.

An attempt was made to group foods into generalized habitat categories by using data from sweep-net samples, visual observations, and life-history information. However, no sophisticated analysis of foraging habitat overlap was possible because some foods could not be assigned to a habitat type with certainty. Orians and Horn (1969) also had difficulty classifying some foods but were able to assign these foods to a habitat type by their association with other items in the sample. This procedure was not used at Rush Lake because individual females were observed to forage both on the marsh and in the uplands during a sampling period. Also, males were observed to feed nestlings foods gathered on the territory while their mates were foraging in the uplands.

RESULTS

FOOD OF NESTLING BLACKBIRDS

Yellow-headed and Red-winged Blackbirds fed their young almost exclusively on invertebrate foods, and aquatic insects were a significant part of the diets (table 1). Plant fragments and seeds occasionally were found in the samples, but most may have been taken accidentally. Diets of nestlings older than 6 days did not differ greatly from diets of younger nestlings, so I did not separate data according to age.

Both small rock fragments and empty snail shells were fed to nestlings, presumably as grit. The chance that empty shells were taken accidentally is slight because live snails were uncommon at Rush Lake and made up only a small part of the diets.

DIURNAL PATTERNS IN FOOD SELECTION

Food-habits data from this study were divided into four diurnal time periods, as described by Willson (1966), because blackbirds have been observed to forage more for odonates during midday emergence peaks (Orians 1966; Willson 1966; Orians and Horn 1969).

Data from each time period have been arranged in table 1 to show percentage composition by volume for each taxon considered to be a major food (as defined by Snelling 1968). The only foods important to both Red-winged and Yellow-headed Blackbirds in all time periods were narrow-winged damselflies (Coenagrionidae).

Although no dramatic temporal shift in food habits is evident in table 1, data on the most common prey taxa suggest changes in blackbird foraging patterns. The general pattern is shown in figure 1. In both species there was increased use of marsh foods and slightly decreased use of upland foods during midday. Aquatic narrow-winged damselflies, spread-winged damselflies (Lestidae), shore flies (Ephydriidae), and larval soldier flies (Stratiomyidae) were selected more between 09:00 and 16:59. Examples of terrestrial invertebrates selected less during midday are tree hoppers (Membracidae), aphids (Aphididae), and noctuid moths (Noctuidae). Finally, visual observations of foraging females indicated slightly more foraging in the hayfield before 09:00 and after 17:00 than during midday.

The index of overlap (Horn 1966) was used to quantify diurnal patterns in food use (table 2). A maximum value of 1.0 would indicate no change in food habits between two time periods. It seemed appropriate to express overlap indexes for both volume and enumeration because values computed for enumeration differed greatly from the values computed for volume. A bird usually will gather a large number of individuals when it is foraging on small animals such as aphids, and these large numbers from a few taxa greatly affect the index of overlap by enumeration. Also, if the counts for food items taken during both time periods were high but their volumes were small, then the overlap measured by enumeration would be greater than the overlap measured by volume. Conversely, if the counts from food taxa used in two time periods were low but their volumes were large, then the overlap measured by volume would be greater than when measured by enumeration. Finally, small insects, such as aphids, often were crushed, which must have reduced their measured volume.

TABLE 2. Index of overlap values comparing different times of the day for each blackbird species.

Time periods compared	Red-winged blackbird		Yellow-headed blackbird	
	Enumeration	Volume	Enumeration	Volume
06:00-08:59 and 09:00-12:59	0.25	0.55	0.56	0.53
09:00-12:59 and 13:00-16:59	0.33	0.62	0.50	0.89
13:00-16:59 and 17:00-21:00	0.11	0.62	0.63	0.60
06:00-08:59 and 17:00-21:00	0.08	0.58	0.82	0.60

While the data in table 1 and figure 1 indicate no dramatic shift in foraging patterns, a low index of overlap values (table 2) shows the effect of subtle changes in prey utilization when nearly all time periods are compared. Much similarity is suggested by the high overlap index for volume of 0.89 when the two midday periods for Yellow-headed Blackbirds are compared.

SEASONAL CHANGES IN FORAGING

Low index values show that changes in diet occurred between different segments of the nesting season (table 3). These changes may be explained by data for the major food taxa (table 4) which show a tendency for Yellow-headed Blackbirds to forage more in the uplands and for Red-winged Blackbirds to forage more within their marsh territories as the nesting season progressed.

Before 20 June, the most important foods of nestling Yellow-headed Blackbirds were aquatic narrow-winged damselflies, larval soldier flies, and widespread adult midges (Chironomidae). After 20 June, the ubiquitous midges and the readily available soldier flies continued to be very important foods, but aphids, anthomyiid flies (Anthomyiidae), and flower flies (Syrphidae) from the nearby hayfield also became important.

Before 20 June, noctuid moths, gathered in the brush and trees, were the most important prey of Red-winged Blackbirds. After 20 June, most foods from terrestrial sources declined in importance while damselflies and larval soldier flies increased.

Data from insect emergence traps in place from 7 June to 4 July help to explain these seasonal changes in feeding habits (table 5). The location for emergence of narrow-winged

damselflies changed from plant stems in the central marsh to the shoreline as the nesting season progressed. Spread-winged damselflies were not trapped until late in the nesting season when they emerged only along the shoreline. Evidently, blackbirds foraged more within their marsh territories in response to the increased availability of odonates.

Data from two sweep-net samples taken at known foraging sites in the hayfield indicated much similarity in the upland insects available during the middle and late parts of the nesting season (Voigts 1970), but these insects were not used to any great extent by Yellow-headed Blackbirds until late in the nesting season when availability of the emerging odonates declined in the central marsh.

Because Red-winged Blackbirds rarely fed in the hayfield and no samples were taken in the trees where they foraged, nothing is known concerning the availability of their principal upland foods. Red-winged Blackbirds did begin to forage more on the marsh and along the brushy border, however, when the emergence of odonates along the shore increased.

OVERLAP IN FOOD UTILIZED BY THE TWO BLACKBIRD SPECIES

The total overlap index according to volume is between 0.46 and 0.49 (tables 6 and 7). Because Red-winged and Yellow-headed Blackbirds probably are similar enough to use the same foods (Orians and Horn 1969), other factors must be reducing the amount of overlap. The period showing the least overlap in food is 09:00-12:59 (table 6). This indicates the relatively small importance of daily emergence peaks to these blackbirds because this is the period when the most teneral (newly

TABLE 3. Index of overlap values comparing different segments of the nesting season for blackbirds at Rush Lake.

Dates compared	Red-winged blackbird		Yellow-headed blackbird	
	Enumeration	Volume	Enumeration	Volume
22 May-6 June and 7 June-20 June	0.12	0.38	0.13	0.44
7 June-20 June and 21 June-4 July	0.31	0.55	0.70	0.35

TABLE 4. Seasonal patterns in the major foods of nestling blackbirds at Rush Lake expressed in per cent of total volume fed to young (3% or greater).

Major foods	22 May-6 June		7 June-20 June		21 June-4 July	
	RW	YH	Blackbird species		RW	YH
			RW	YH		
			Nests sampled			
	8	14	14	38	28	14
Odonata						
Lestidae A ^a (Spread-winged damselflies)					17.1	
Coenagrionidae A (Narrow-winged damselflies)		25.0	6.4	20.1	13.4	
Orthoptera						
Gryllidae T (Crickets)			7.3			
Hemiptera						
Miridae T (Leaf bugs)						5.4
Homoptera						
Membracidae T (Treehoppers)	5.1		5.1			
Aphididae T (Aphids)				3.1		8.1
Coleoptera						
Carabidae T (Ground beetles)	11.1	5.6	5.6	3.6		
Scarabaeidae T (Scarab beetles)			6.8		12.6	
Curculionidae T (Weevil)	9.4	3.8				
Lepidoptera						
Noctuidae T (Noctuid moths)	35.0	5.1	29.5		10.8	
Pyralidae U (Pyralid moths)	12.8	5.9		8.9	3.2	
Unidentified T			5.8			
Diptera						
Tipulidae A (Crane flies)		4.8			3.6	
Chironomidae W (Midges)		8.6	12.8	18.1		9.9
Stratiomyidae A (Soldier flies)		17.5		13.6	6.8	22.9
Syrphidae T (Flower flies)		3.0				8.1
Ephydriidae A (Shore flies)				9.6		3.9
Anthomyiidae T (Anthomyiid flies)						15.0
Arachnida						
Araneida W (Spiders)	6.8	3.8	3.8	3.9	9.8	4.3
Mollusca						
Pulmonata A (Snails)	6.0					
Unidentified	5.1					
Corn seeds						3.0
Total Volume	1.17	3.72	4.68	14.01	7.77	4.67

^a A, primarily from the marsh; T, primarily from the uplands; W, widespread; U, unknown.

TABLE 5. Seasonal and spatial patterns in the emergence of odonates trapped at Rush Lake.

Zone trapped	7 June-20 June				21 June-4 July			
	A	Li	Le	C	A	Li	Le	C
Shoreline				3	1	6 ^a	16 ^a	
Dense cattail				22	2		4 ^a	
Opened cattail	1			11			4 ^a	
Cattail-water edge				6		1	5	

^a Difference in emergence rate between time periods is significant ($P=0.10$).
 Key: A, Aeshnidae; Li, Libellulidae; Le, Lestidae; C, Coenagrionidae; four traps were used in each zone.

emerged insects) should be available, and both blackbird species should be concentrating their foraging on these susceptible teneral (Orians and Horn 1969). It is evident that Red-winged and Yellow-headed Blackbirds selected many of the same foods, but during different parts of the nesting season, because each segment of the nesting season has a low index of overlap value while the total overlap is higher (table 7). Both species adjusted their foraging patterns and utilized more aquatic insects when the emergence of odonates increased within their marsh territories (tables 4 and 5). Also, the birds were observed to use different techniques while foraging on the marsh. Red-winged Blackbirds foraged by moving swiftly through the vegetation about 1-3 ft above the substrate. Yellow-headed Blackbirds usually foraged near the waterline by slowly moving around cattail clumps and by searching on floating dead vegetation. Finally, upland foraging areas differed. Only Red-winged Blackbirds utilized the invertebrates in the trees and shrubs, and most of the birds using the hayfield were Yellow-headed Blackbirds. This must have affected the foods of nestlings.

DISCUSSION

FOOD AS A POSSIBLE SOURCE OF COMPETITION

Orians and Willson (1964) have suggested that possible foraging areas of Red-winged and Yellow-headed Blackbirds also are reduced by the mutually exclusive territories of the other species. It is probable that Red-winged Blackbirds would expand their foraging area greatly if Yellow-headed Blackbirds were eliminated (Willson and Orians 1963; Robertson 1972). Yellow-headed Blackbirds would be affected less if the situation were reversed because they seem less efficient at foraging in dense vegetation and do not usually use trees and dense brush for foraging (Willson and Orians 1963). Because these theories suggest restriction of

TABLE 6. Index of overlap values comparing foods of Red-winged and Yellow-headed Blackbirds at Rush Lake during different times of the day.

Time periods	Overlap values	
	Enumeration	Volume
06:00-08:59	0.88	0.56
09:00-12:59	0.04	0.25
13:00-16:59	0.40	0.48
17:00-21:00	0.04	0.48
Total overlap	0.38	0.49

the fundamental niche of each species, they satisfy the criteria for existence of competitive displacement (Miller 1967; Colwell and Futuyma 1971). However, these theories do not quantify the degree of interspecific competition.

A theoretical model devised by MacArthur and Levins (1967) to quantify niche similarity was used by Orians and Horn (1969) to measure overlap in foods of three blackbird species. Given several assumptions, the model predicts that two adjacent species of a linear arrangement can coexist in a variable environment if their α levels of competition are not much in excess of 0.50, provided the shape of the utilization curves are symmetrical. An increased overlap should prevent coexistence. In the present study, the index of overlap values for total foods, which are equal to α levels (Orians and Horn 1969), was between 0.46 and 0.49 when based on volume. However, the shape of the utilization curves is not known because the food overlap between Red-winged Blackbirds and Common Grackles (*Quiscalus quiscula*), the next icterid species in this linear arrangement, was not studied. Therefore, the values obtained in this study can be considered only as first approximations of the amount of niche overlap. Because food niche overlap values were rather close to the theoretical maximum, it is probable that foraging isolation would not have been possible without the presence of mutually exclusive territories that restricted the foraging areas of the other species.

TABLE 7. Index of overlap values comparing foods of Red-winged and Yellow-headed Blackbirds at Rush Lake during different segments of the nesting season.

Dates	Overlap values	
	Enumeration	Volume
22 May-6 June	0.16	0.23
7 June-20 June	0.24	0.28
21 June-4 July	0.63	0.28
Total overlap	0.38	0.46

GEOGRAPHICAL DIFFERENCES IN
FOOD HABITS

Recent workers have presented evidence for dramatic diurnal changes in foraging by blackbirds that coincided with emergence patterns of odonates (Orians 1966; Willson 1966; Orians and Horn 1969). During my study, no pronounced diurnal foraging patterns were observed, and several foods were consistently important. Snelling (1968) and Robertson (1971), working with Red-winged Blackbirds nesting over water in Wisconsin and New York, also have indicated much foraging for terrestrial invertebrates.

There are several possible reasons for these differences. First, there are basic climatological differences between the geographical areas studied. The areas studied by Orians (1966), Willson (1966), and Orians and Horn (1969) have relatively dry and unproductive uplands. This may force a greater dependence on the marsh for food. The comparatively lush and diverse uplands in the eastern United States provide very large and diverse prey populations for foraging blackbirds. During this study, blackbirds exploited upland food supplies for extended periods when the abundance of marsh odonates was low.

Second, the greater use of odonates as food might indicate marshes with a higher basic productivity. Orians (1966) suggested that the emergence rate of odonates could be used as an index to compare productivities of different marshes. Unfortunately, this comparison is not possible because Orians and Horn (1969) had data from the shore of a pond with almost no emergent vegetation (Cook and Horn 1968), whereas I trapped only in marshes with emergent vegetation. Emergent vegetation would increase places of possible emergence, and a lack of emergent vegetation would concentrate emerging insects along the shoreline. Also, the traps used by Orians and Horn were in place for only 4.5 days (Horn 1968); so there are no comparable data for the rest of the nesting season.

Another suggested way of comparing productivity of marshes is comparing measures of specific conductance, which is directly related to total dissolved solids (Orians 1966). In that study, Orians found that Yellow-headed Blackbirds did not nest in marshes with a specific conductance of less than 1100 micromhos/cm. Six samples of water measured for conductivity from the Rush Lake, Iowa, study area ranged from 390 to 760 micromhos/cm at 25°C. Because basic productivity is correlated with abundance of different nutrients that make up a small part of the total

dissolved solids, specific conductance is not a precise measure of productivity when used alone to compare widely separated areas with large climatic and geological differences (Larkin and Northcote 1958; Rawson 1961).

SUMMARY

Food habits of nestling Red-winged and Yellow-headed Blackbirds were studied throughout the nesting season at Rush Lake, Iowa. Most food items were invertebrates, and aquatic insects were especially important. Only small changes in diurnal feeding habits were observed, and these changes did not appear to respond to diurnal patterns of odonate emergence reported elsewhere (Orians 1966; Orians and Horn 1969).

Diets responded to the changing rate of odonate emergence as the nesting season progressed. Terrestrial foods seemed to serve as supplementary energy sources and were used to a greater extent when odonate emergence rates were low.

Although differences in habitat selection and foraging behavior have reduced competition, niche overlap has been further reduced by the evolution of mutually exclusive territories. It is probable that food niche overlap has been reduced to below the theoretical maximum for two coexisting species.

ACKNOWLEDGMENTS

I am very grateful to Milton W. Weller who provided guidance, criticism, and encouragement throughout the research and preparation of the manuscript. Page Music Burt helped with difficult insect identifications. Statistical analysis was done by David Jowett and Jim Mellon of the Statistical Laboratory and Agriculture Experiment Station, Iowa State University. Henry S. Horn, David L. Trauger, and Larry D. Wing critically read the manuscript and provided valuable suggestions for its improvement.

LITERATURE CITED

- BORROR, D. J., AND D. M. DELONG. 1964. An introduction to the study of insects. Rev. ed. Holt, Rinehart, and Winston, Inc., New York.
- COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567-576.
- COOK, P. P. JR., AND H. S. HORN. 1968. A sturdy trap for sampling emergent Odonata. *Ann. Entomol. Soc. Amer.* 61:1506-1507.
- HAYDEN, A. 1943. A botanical survey in the Iowa Lake Region of Clay and Palo Alto counties. *Iowa State Coll. J. Sci.* 17:277-416.
- HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *Amer. Nat.* 100:419-424.
- HORN, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). *Ecology* 49:682-694.

- KLUJIVER, H. N. 1933. Dijkstra tot de biologie en de ecologie van den spreeuw (*Sturnus vulgaris vulgaris* L.) gedurende zijn voortplantingstijd. Versl. Meded. Plantenziektenk. Wageningen, 69: 1-145. Original not available; cited in Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.
- LARKIN, P. A., AND T. C. NORTHCOLE. 1958. Factors in lake typology in British Columbia, Canada. Verh. Int. Ver. Limnol. 13:252-263.
- MACARTHUR, R., AND R. LEVINS. 1967. The limiting similarity, convergence, and divergence of co-existing species. Amer. Nat. 101:377-385.
- MILLER, R. S. 1967. Pattern and process in competition. Adv. Ecol. Res. 4:1-74.
- MORISITA, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci., Kyushu Univ., Ser. E Biol. 3: 65-80.
- ORIAN, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68:321-337.
- ORIAN, G. H., AND H. S. HORN. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50:930-938.
- ORIAN, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. Ecology 45:736-745.
- RAWSON, D. S. 1961. A critical analysis of the limnological variables used in assessing the productivity of northern Saskatchewan lakes. Verh. Int. Ver. Limnol. 14:160-166.
- ROBERTSON, R. J. 1971. Optimal niche space of the Red-winged Blackbird. Ph.D. thesis, Yale Univ., New Haven, Connecticut.
- ROBERTSON, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. Can. J. Zool. 50:247-263.
- SLOBODKIN, L. B. 1961. Preliminary ideas for a predictive theory of ecology. Amer. Nat. 95:147-153.
- SNELLING, J. C. 1968. Overlap in feeding habits of Red-winged Blackbirds and Common Grackles nesting in a cattail marsh. Auk 85:560-585.
- STEWART, R. E., AND H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U. S. Bur. Sport Fish. Wildl. Resour. Publ. 92.
- USINGER, R. L., [ed.]. 1963. Aquatic insects of California. Univ. California Press, Berkeley, California.
- VOIGTS, D. K. 1970. Comparative food habits of two Iowa marsh Icterids. M. S. thesis, Iowa State Univ., Ames, Iowa.
- VOIGTS, D. K. 1973. An odonate emergence trap for use in marshes. Proc. Iowa Acad. Sci. 80: 67-68.
- WELLER, M. W., AND C. S. SPATCHER. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa Agric. Home Econ. Exp. Stn. Spec. Rep. 43.
- WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36:51-77.
- WILLSON, M. F., AND G. H. ORIAN. 1963. Comparative ecology of Red-winged and Yellow-headed Blackbirds during the breeding season. Proc. Int. Congr. Zool. 16:342-346.

Accepted for publication 19 December 1972.