

OVERLAP IN FEEDING HABITS OF REDWINGED BLACKBIRDS AND COMMON GRACKLES NESTING IN A CATTAIL MARSH¹

JOHN C. SNELLING

WIENS (1965), in a study of the behavioral interactions of Redwinged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*) on a small cattail (*Typha latifolia*) marsh in Madison, Wisconsin, points out that the cattail habitat is "typical" for Red-wings and "unusual" for grackles, and that a potentially competitive situation exists in a marsh where the two species nest together. The emphasis of his study was on behavioral interactions and the effect of these interactions on reproduction. The purpose of the present investigation is to consider other parameters, namely food and feeding behavior, which may be very important in the relationships of Red-wings and grackles breeding on this cattail marsh. Indeed, as expressed by Orians and Collier (1963: 457), "Ecological compatibility, the prime requirement for sympatry, . . . is strongly influenced by such behavioral attributes as feeding behavior which vary remarkably in morphologically similar species." In addition, selected breeding biology data are presented from the years following Wiens' study to elucidate further the relationships of Red-wings and grackles on this marsh.

For extensive discussion of the breeding biology and displays of Red-wings see Beer and Tibbitts (1950) and Nero (1956). Peterson and Young (1950) and Ficken (1963) give corresponding discussions of grackles, and Wiens (1965) compares the two species.

THE STUDY AREA

The study area (Figure 1) is a 2.4 acre marsh on the southeast shore of Lake Wingra in the University of Wisconsin Arboretum, Madison. Cattail is the dominant vegetation, within which a resident population of muskrats (*Ondatra zibethicus*) maintains areas of open water. The immediate edge of the marsh, including the earthen dike separating it from Lake Wingra on the north, supports shrubs of black willow (*Salix nigra*) and red-osier dogwood (*Cornus stolonifera*), and scattered (mostly dead or dying) individuals of cottonwood (*Populus deltoides*) and river birch (*Betula nigra*). For other descriptions of this marsh see Beer and Tibbitts (1950), Nero (1956), and Wiens (1965).

The marsh is surrounded on the east, south, and west by a dense deciduous forest of the Southern Lowland type (Curtis, 1959), the most important tree species being cottonwood, black willow, and river birch, with a

¹ Journal Paper No. 78, University of Wisconsin Arboretum.

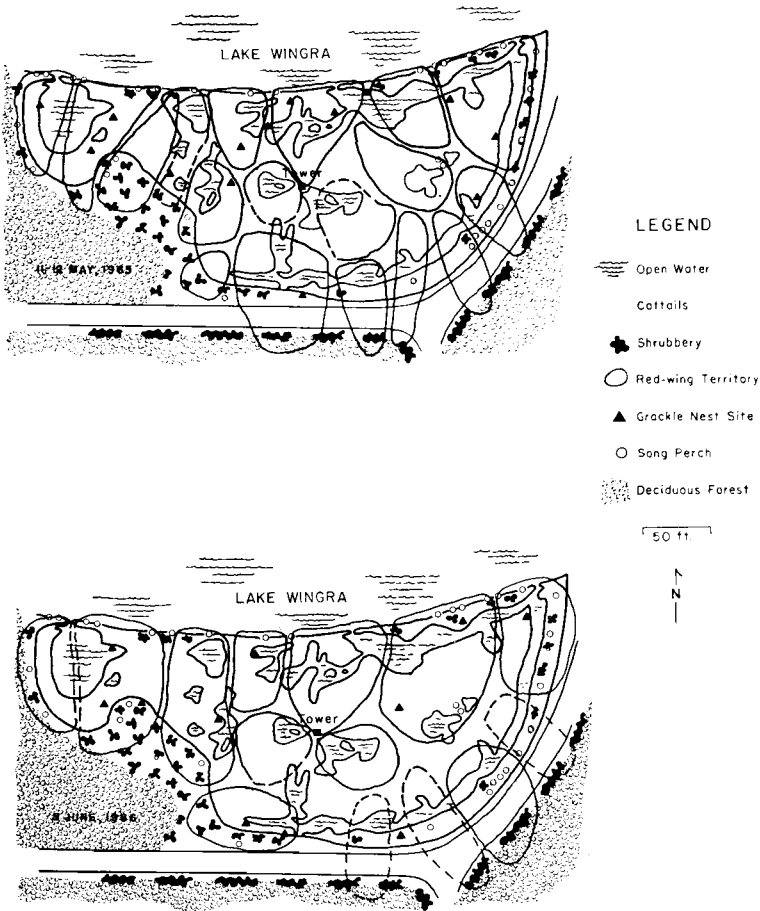


Figure 1. Red-wing territory configuration and grackle nest sites at East Wingra Marsh, 1965 and 1966.

dense understory of honeysuckle (*Lonicera tartarica* × *morrowii*). On the south and east the woods extend only about 300 feet, beyond which is a hydric fen composed of bluejoint (*Calamagrostis canadensis*), reed canary grass (*Phalaris arundinacea*), reedgrass (*Phragmites communis*), sedges (*Carex* spp.), *Aster simplex*, nettle (*Parietaria* sp.), and goldenrod (*Solidago gigantea*). As will be shown later this fen was an important foraging area for female Red-wings.

What little is known of the history of grackles nesting in the cattails of Wingra Marsh is summarized by Wiens (1965). Nesting pairs have been recorded since 1946, but reliable estimates of the total breeding population are available only for 1957 when 12 nests were found, and from 1962 to

1966. The trend has generally been toward increased utilization of this marsh habitat with the possible exception of the last three years (see below).

Grackles have also been observed nesting in small numbers at two other marshes in the Madison area.

METHODS

The field work of this investigation was accomplished during the 1965 and 1966 breeding seasons. As in previous studies of blackbirds at East Wingra Marsh, breeding biology was studied fairly intensively. Observations were begun in mid-March with the arrival of Red-wing males, and continued until the end of July when most blackbirds had left the marsh. Activities on the marsh were observed with the aid of 6 × 30 binoculars and a 20× spotting scope from a 20-foot wooden tower located roughly at mid-marsh, and from the roof of an automobile parked along the edge of the marsh. In both years the configurations of male Red-wing territories (most of the territory holders were color-banded in 1965) were plotted at monthly intervals on a map of the marsh. This was accomplished by connecting points where males displayed, especially where they bill-tilted (Wiens, 1965) to neighboring males.

Nests were found by traversing the marsh systematically, twice weekly in 1965, once a week in 1966, and were marked with a small paper tag affixed to nearby vegetation at least 3 feet away. A form was kept for each nest giving the location, dates of visits, the condition (construction, eggs, young, etc.) at each visit, and a record of food samples obtained from the nestlings.

The food brought to the nestlings was sampled daily at most nests in 1965. A 1-inch length of pipe cleaner was looped around the neck of the nestling tight enough to prevent swallowing of food delivered (cf. Orians, 1966; Willson, 1966). After about one hour the accumulated food bolus was removed and placed in a vial of 70 per cent ethyl alcohol. When white pipe cleaners were used 11 Red-wing and 1 grackle young were removed from their nests by the parents. Substitution of flesh-colored pipe cleaners solved this problem. It is suggested that the white objects in the nest released nest sanitation behavior of the female, in this case with adverse results. I tried to sample all daylight hours (ca. 0500 to 2100 hours) with equal frequency, but most samples were collected between 0900 and 1900 hours.

Food samples from each nestling were examined separately in the laboratory under a dissecting microscope. Individual prey items were segregated according to family where possible and in some cases to genus or species. The word *taxon* hereafter signifies the most specific category to which a prey item has been assigned. Their numbers and mean lengths were recorded, and the combined volume of all individuals of each prey taxon was determined to the nearest .01 ml by displacement in ethyl alcohol.

Field investigation during 1966 was concentrated on watching Red-wing and grackle nests with young from the tower or car top for 1-hour periods, and dictating notes on important activities into a tape recorder. Thus the nest was under constant observation during the hour. The delivery of food, foraging location of the parent birds, and other aspects of feeding behavior were recorded. Red-wing nests were watched during all daylight hours; fewer observations were made of grackle nests.

RESULTS

Size of breeding populations.—The Red-wing population reached a maximum of 22 males with territories on 27 April 1965, but only 18

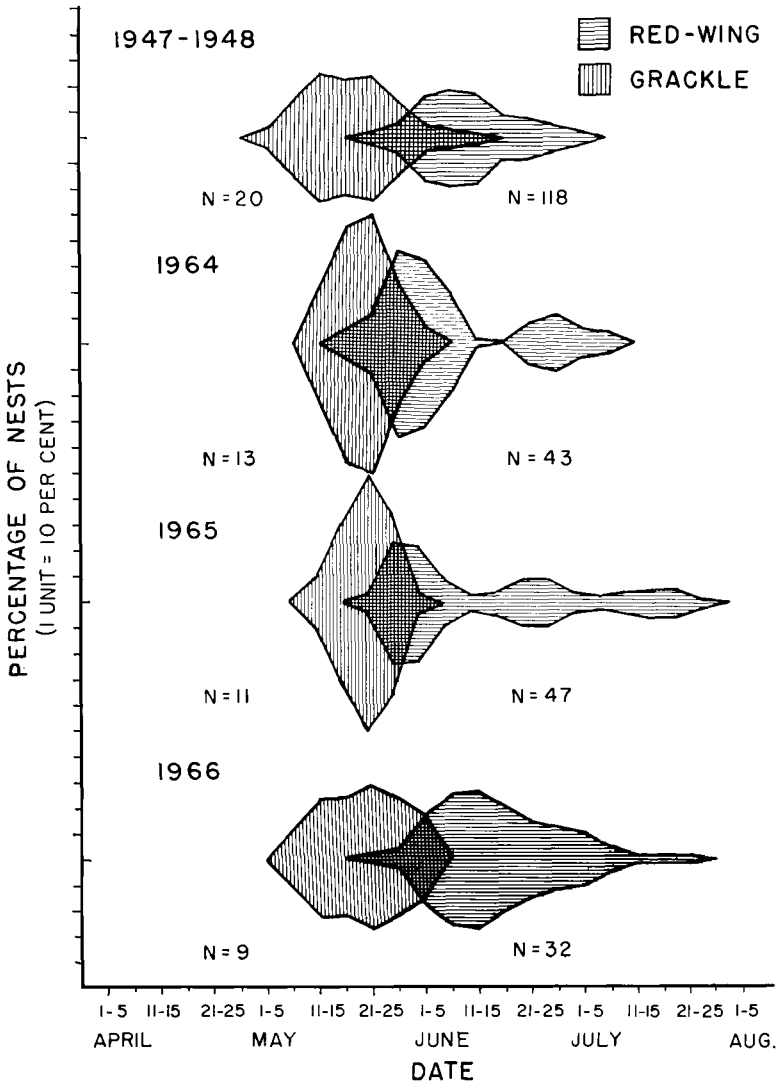


Figure 2. Chronology of Red-wing and grackle nests with young at East Wingra Marsh. Data of 1947-1948 from 1947 Red-wing nesting on the Marsh (Beer and Tibbitts, 1950), and from the average of 1947 and 1948 grackle nestings in a nearby white cedar (*Thuja occidentalis*) plantation (Peterson and Young, 1950). Data of 1964 from J. A. Wiens (MS). Data of 1965 and 1966 from this study. N is the number of nests.

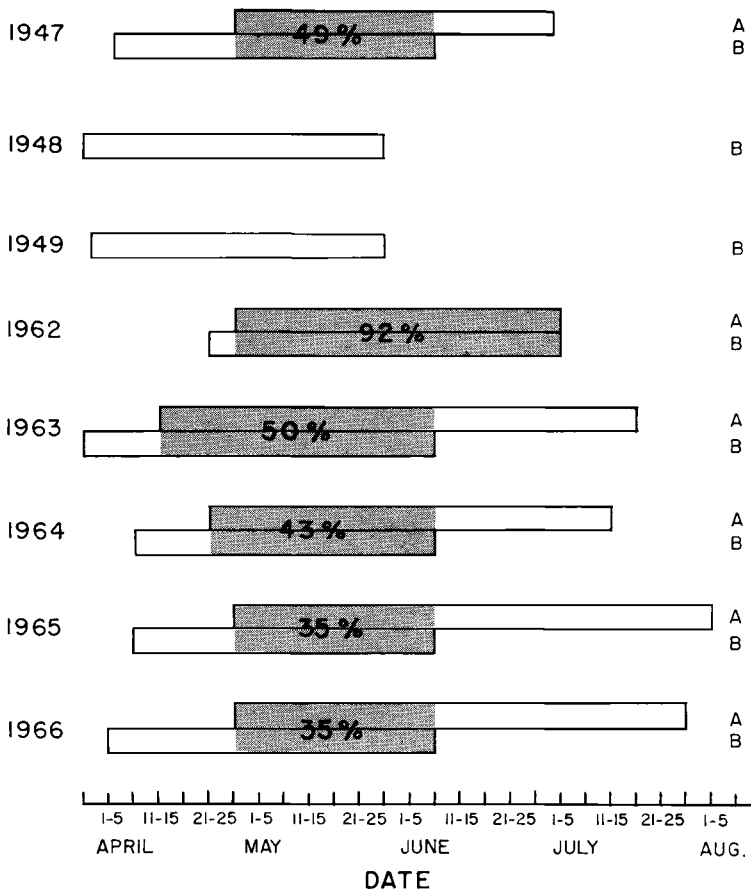


Figure 3. Extent of overlap in the breeding periods (nest building through young flying) of Red-wings and grackles in the Madison area. A, Red-wing; B, grackle. Period of overlap shaded and per cent given. Red-wing data from East Wingra Marsh (1947 data from Beer and Tibbitts, 1950). Grackle nestings of 1947 and 1948 in a white cedar plantation; 1949 nesting in honeysuckle (Peterson and Young, 1950). 1962 and 1966 nestings at East Wingra Marsh (1962 and 1963 data from Wiens, 1965; 1964 data from J. A. Wiens, MS).

territorial males were present from 11 May through the remainder of the breeding season (Figure 1). On 7 May 1966 18 territorial males were present, but on 8 June only 14 were found (Figure 1), and the number decreased to 12 on 28 June. Nero (1956) found 17 to 25 territorial males during the years of his study (1948 to 1953), and Wiens (1965) reports 21 territorial male Red-wings for both 1962 and 1963. Thus the male Red-wing population was relatively low during the present investigation.

The numbers of female Red-wings and both male and female grackles actively using the marsh were approximated by recording the numbers of nests. Nests and numbers of female Red-wings should be equivalent, possible re-nesting excepted, because Red-wings are rarely double-brooded in this area (Nero, 1956). Grackles are usually monogamous and single-brooded (Peterson and Young, 1950; Wiens, 1965). In 1965 there were 69 active (with one or more eggs) Red-wing nests, and in 1966 there were 55 such nests. In both years at least 10 nests were started, but never completed. In 1964 Wiens (MS) found 62 active Red-wing nests. The numbers of active grackle nests were 14 and 13 in 1965 and 1966. This compares with 16 in 1964 (Wiens, MS) and 17 and 19 in 1962 and 1963 (Wiens, 1965).

Male Red-wing territories during grackle nesting and the locations of grackle nests for 1965 and 1966 are mapped in Figure 1. Wiens (1965) reports that grackle nests were usually located at the periphery of male Red-wing territories, a generalization not convincingly supported by the few data presented here.

Nesting chronology.—The temporal relationships of Red-wing and grackle nesting at Wingra Marsh for 1964 to 1966 are shown in Figures 2 and 3. The peaks of grackle nesting activity generally preceded those of Red-wings by 10 to 20 days (Figure 2). Also, the period of Red-wing breeding was considerably more extended than that of the grackle (Figure 3), partly because of a few Red-wing second nestings.

Figure 3 also shows the extent of overlap in breeding, and the grackle breeding periods in two arboreal colonies (nests in honeysuckle and white cedar) one half mile north of the marsh. Timing of the nesting of both species remained fairly constant for all years and places with the exception of 1962 when grackles continued nesting later at Wingra Marsh and Red-wings ended nesting early, partly because of destructive winds at the peak of Red-wing nesting (Wiens, 1965). The extent of overlap appears to have decreased during the last 5 years.

Figure 4 shows similar data for the periods in which both species had young in the nest, the period of greatest significance in terms of potential competition for food resources. Note again the trend toward decreasing overlap in the breeding cycles of the two species, i.e. toward breeding asynchrony.

Data in Figure 2 from Red-wings at Wingra Marsh in 1947, and from grackles nesting in the nearby white cedar plantation in 1947 and 1948, may be used as a baseline by which to place in proper perspective the trend toward asynchrony at Wingra Marsh in the last 5 years. For these former years the peaks in Red-wing and grackle nestings were 20 to 25 days apart. The overlap in total breeding periods and nestling

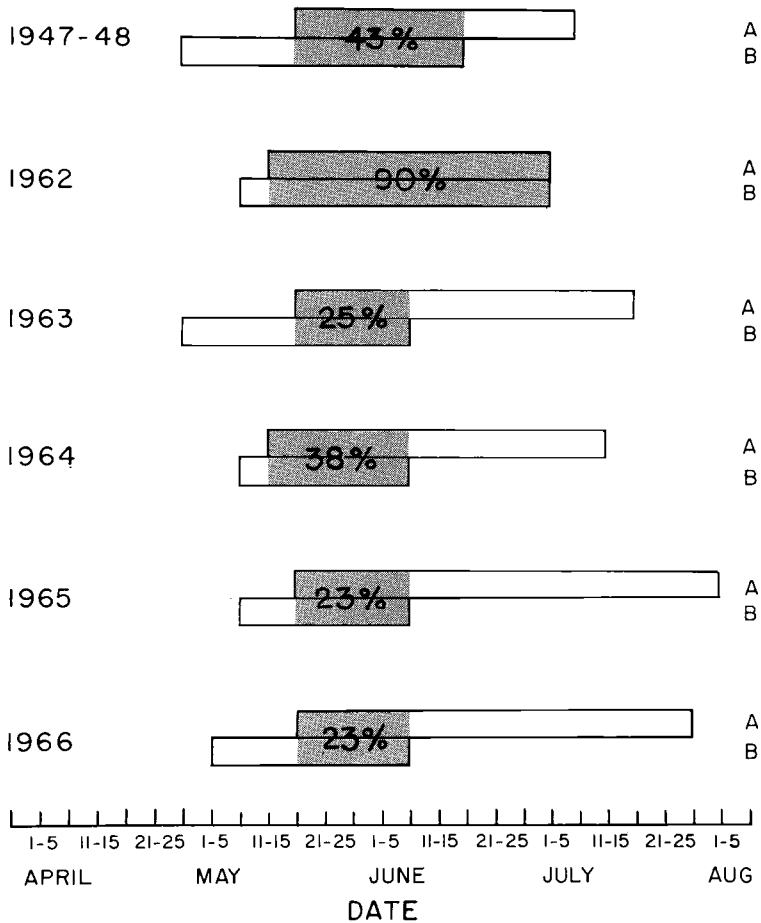


Figure 4. Extent of overlap in nestling periods of Red-wings and grackles at East Wingra Marsh. A, Red-wing; B, grackle. Period of overlap shaded and per cent given. Grackle data of 1947-1948 are the average of 1947 and 1948 nestings in a nearby white cedar plantation (Peterson and Young, 1950). Red-wing data of 1947 from Beer and Tibbitts (1950). Data for 1962 and 1963 from Wiens (1965); 1964 data from J. A. Wiens (MS).

periods (Figures 3 and 4) fails to confirm the trend suggested by the 1962 to 1966 data. The data for grackles may not be comparable to marsh nesting grackles, as nesting substrate may affect the timing of breeding.

Breeding asynchrony may be an effective mechanism in precluding interspecific competition for food or any other resource. Whether or not Red-wing and grackle breeding at Wingra Marsh is becoming asynchro-

nous, the data of 1963 to 1966 show an average overlap of only 40 per cent in the entire breeding cycle of both species. Wiens (1965) reports that segregated Red-wing and grackle colonies in the Madison area in 1962 and 1963 were well synchronized with the integrated colonies. A more thorough study of this problem is needed.

The food of nestling Red-wings and grackles.—Although the food habits of adult Red-wings and grackles are well known (Beal, 1900; Neff and Meanley, 1957; Meanley, 1961; Bird and Smith, 1964), the literature on food of nestlings is sparse (Gabrielson, 1915; Hamilton, 1951; Neff and Meanley, 1957; Willson and Orians, 1963; Orians, 1966).

A total of 113 Red-wing and 39 grackle food samples, representing 501 and 221 nestling hours of sampling respectively, were obtained at Wingra Marsh in 1965; a *food sample* is defined as the food collected from the gullets of all nestlings in a single nest during a sampling period of 1 to 2 hours.

Table 1 presents a list of all prey items found in the food samples, as well as the per cent occurrence (presence or absence), per cent frequency (by numbers), and per cent by volume of each prey taxon in the diet.

Data from the Red-wing food samples were divided to separate food collected during the period when both species were feeding young in the marsh (hereafter referred to as the *overlap period*) from that collected later. Young grackles leave the marsh a day or two after leaving the nest (Wiens, 1965). The above separation is deemed useful because of seasonal shifts of prey abundance (especially insects) in the habitat. Only food taken during the overlap period is strictly comparable.

Both Red-wings and grackles fed their nestlings principally on invertebrate animals. Vegetable matter occurred in only 7.9 per cent of the Red-wing samples and comprised 2.2 per cent of total volume, while 66.6 per cent of the grackle samples contained vegetable matter (18.6 per cent volume), principally white bread (Table 2). The mean lengths of animal food items from 123 Red-wing and 82 grackle prey taxa were found to be 10.09 ($\pm .65$ SE) and 9.79 ($\pm .79$ SE) mm. respectively, and were not significantly different ($t = .29, p > .5$).

A standard diversity index (Paine, 1963) from information theory

$$H = - \sum P_i \ln P_i$$

where H equals diversity and

P_i equals the fraction of the total numbers of all prey taxa comprised by the numbers of the i th prey taxon (animal material only)

was used to measure feeding diversity. Values obtained were 3.17 for Red-wings and 2.62 for grackles for food collected while both species

TABLE 1
FOOD OF RED-WING AND GRACKLE NESTLINGS AT EAST WINGRA MARSH, 1965

Per cent occurrence is the per cent of the total samples in which a prey taxon was present. Per cent frequency is the number of individuals of a prey taxon divided by the total number of individuals of all taxa. Key: A, food collected while both species were feeding young (20 May to 10 June); B, food collected from 11 June to 30 July; R_w, Redwinged Blackbird; Gr, Common Grackle, n, nymph (naiad); t, teneral; a, adult; l, larva; p, pupa.

Prey taxa	% Occurrence			% Frequency			% Volume			
	A	B	R _w	A	B	R _w	A	B	R _w	
	R _w	Gr	R _w	R _w	Gr	R _w	R _w	Gr	R _w	
ANIMAL MATTER										
NEMATODA	.67	2.56		.29	.19	.03		.01		
ANNELIDA										
Oligochaeta										
Opisthophora										
Lumbricidae		28.20		1.17	4.35	.03		9.13		
Lumbricus	.67									
Hirudinea										
MOLLUSCA	8.00	53.85	9.41	— ^s	— ^s	— ^s		.81		
Gastropoda (Pulmonata) ¹										
ARTHROPODA										
Arachnida										
Araneae	.67		.39	.29		.22		.03		.02
Ditynidae			.39			.11				.02
Gnaphosidae	.67	2.56	.39	.87	.19	.85		.01		.04
Clubionidae	1.33	5.13	.78	.58	.38	.64		.08		.14
Thomisidae			.39			.11				.07
Salticidae			.39			.11				.02
Agelenidae	.67		.39	.29		.42				
Pisauridae										
Lycosidae										
Pirata spp.	1.33	5.13	1.18	.87	.38	.33		.12		.09
Undetermined			1.96			.67		.37		.79
Therididae			1.18			.44				.07

TABLE 1 (CONTINUED)

Prey taxa	% Occurrence			% Frequency			% Volume		
	A	B	Rw	A	B	Rw	A	B	Rw
	Rw	Gr	Rw	Rw	Gr	Rw	Rw	Gr	Rw
Araneidae	.67		3.92	.29		1.55	.53		1.11
Tetragnathidae									
<i>Tetragnatha</i> spp.	.67		2.35	.29		.78	.03		.14
Linyphiidae			1.57			.78			.09
Undetermined	1.33	7.69	1.96		.57	.56	.03	.03	.07
Oplitoness									
Ischyropsalidae									
<i>Phalangium</i> spp.	.67	2.56	3.14	1.46	.19	3.22	.21	.06	1.64
Acarina			.39			.11			.02
Crustacea									
Isopoda									
Oniscoidea									
<i>Tracheoniscus</i>									
<i>rathkei</i>	1.33	10.26	.39	.87	2.46	.22	.53	.46	.32
Decapoda									
Astacidae									
<i>Cambarus</i> spp.		2.56			.19			.20	
Diplopoda		7.69			.95			.19	
Insecta									
Odonata									
Aeschnidae	.67			.58t	.76n	.44n	3.17	5.26	1.39
Libellulidae	2.00	10.26	1.18	.58n	.38t		5.76		
				.58t	.19n				
				.29t	.19t		2.64	1.19	
Cordulegasteridae	.67	5.13							
Coenagrionidae	9.33	20.51	9.41	3.79n	.57n	2.11n	4.95	1.44	8.69
				3.79t	1.13t	6.55t			
				9.33a	2.46a	6.22a			
				.29t	.11n		1.08		.02
Unidentified	1.33		.39	.58a					

TABLE 1 (CONTINUED)

Prey taxa	% Occurrence			% Frequency			% Volume				
	R _w	A	Gr	B	R _w	Gr	A	R _w	Gr	B	R _w
Orthoptera											
Locustidae				9.41				3.44n			43.21
								.89a			
Coleoptera											
Carabidae				1.96				1.55a			2.04
Hydrophilidae				1.96	1.171			.561	.53		1.46
Scydmaenidae	2.00		2.56			.19a				.01	
Scaphididae			2.56			.19a				.01	
Elateridae			2.56			.19a				.02	
Helodidae	1.33			.78	.581			.221	.05		.04
Endomychidae				1.96				2.66a		.16	.32
Alleculidae			2.56			.191					
Scarabaeidae											
Phyllophaga			38.46	.39		4.92a		.11a	.48	27.19	1.43
Undetermined	.67				.29a						
Chrysomelidae											
Donacia											
<i>emarginata</i>				.39				.22a			.39
Curculionidae			12.82			2.08a				.29	
Undetermined			12.82	1.18		1.51a		.11a		.21	.39
Corrodentia			2.56			.19a				.10	
Neuroptera											
Sialidae											
<i>Chauliodes</i>											
<i>pectinicornis</i>	.67				.29a					1.69	
Lepidoptera											
Nymphalidae											
<i>Vanessa</i>											
<i>atalanta</i>				.78				.33p			3.64
Undetermined				2.35				1.111			4.89

TABLE 1 (CONTINUED)

Prey taxa	% Occurrence			% Frequency			% Volume		
	A	B	Rw	A	B	Rw	A	B	Rw
	Rw	Gr	Rw	Rw	Gr	Rw	Rw	Gr	Rw
Lycenidae	12.00	5.13	4.31	.29a	.38l	.11a	31.99	.47	10.18
Noctuidae		38.46		11.66l	8.51l	1.66l		13.78	
Notodontidae			.39	.58p		.44p			1.07
Geometridae						.11p			
<i>Nematocampa</i>									
<i>limbata</i>	1.33			.58l			.37		
<i>Aksoiphila</i>									
<i>homotaria</i>	5.33	10.26	.39	12.25l	2.46l	.11l	11.32	1.18	.29
Undetermined	14.66	38.45	1.96	18.95l	7.00l	1.22l	20.42	3.57	2.04
Pyralidae	2.00	2.56		.29l	.19l		2.17	.20	
				1.17p					
Ethmiidae			.39			.22l			.43
<i>Ethmia</i> spp.	.67	15.39		.29l	1.32l		.21	.52	
Unidentified	.67			.29l			.26		
Tortricidae	.67	2.56		.29l	.19l		.05	.02	
Yponomeutidae		5.13	.39	.58l	.38l	.11l	1.90	.17	.07
Undetermined	2.66			.58p					
Diptera									
Tipulidae			.39			.22l			.43
<i>Megistocera</i> spp.		2.56	1.96		.19l	.11l		.01	1.02
Undetermined						1.11p			
Trupaneidae									
<i>Eurosta</i>	.67			.29l			.37		.41
<i>solidaginis</i>	5.33	48.72	1.96	7.87a	15.69a	.33p	.66	1.55	
Chironomidae						3.55a			

TABLE 1 (CONTINUED)

Prey taxa	% Occurrence			% Frequency			% Volume		
	A	B	Rw	A	B	Rw	A	B	Rw
	Rw	Gr	Rw	Rw	Gr	Rw	Rw	Gr	Rw
Stratiomyidae									
<i>Stratiomyia</i> spp.	1.33	5.13	9.80	1.171	.381	3.551	3.65	.48	6.89
Undetermined	4.00			3.991		1.22a	.64		
			.39	.58a		.11a			.17
Tabanidae		2.56	.78		.19a	.22a		.01	.11
Pipunculidae			.39			.11a			.29
Syrphidae			.39			.11a			.02
Drosophilidae	.67	2.56	.78	.29a	.19a	.11a	.26	.04	.04
Tachinidae	.67	2.56		.291	.191	.33a	.03	.01	.04
Undetermined					.19a				
Hymenoptera									
Argidae	2.66	2.56	.39	2.921	.191	.111	.69	.10	.04
Formicidae									
<i>Campoplex</i>									
<i>herculeanus</i>		7.69			.76a			1.02	
Undetermined		2.56	.39		.57a	.111		.21	.11
Undetermined		2.56			.19a			.01	
Homoptera									
Cercopidae	.61	43.59	1.57	.29a	21.55n	.67a	.03	3.55	.14
Fulgoridae					8.33a				
Cicadellidae	2.66	2.56	2.75	2.33n	.19a	.56n	.71	.01	.73
				.58a		1.66a			
Aphididae	.67		3.53			43.84a	.03		.52
Undetermined			1.18	.29n		.11n			.05
						.22a			
Hemiptera									
Anthocoridae	.67			.29n			.11		
				.291					

TABLE 1 (CONTINUED)

Prey taxa	% Occurrence			% Frequency			% Volume			
	A	B	Rw	A	B	Rw	A	B	Rw	
	Gr	Rw	Gr	Gr	Rw	Gr	Gr	Rw	Gr	
Naucoridae		.78			.22h					.27
Undetermined	5.13		.38l					.02		
CHORDATA										
Osteichthyes	28.20		— ³		.44			7.01		.05
Undetermined		.78								
VEGETABLE MATTER										
Seeds	2.66	.39	2.46	1.75	.11	.11	.11	.38	.12	.02
Green leaves	2.56		.19							
Domestic		.88	— ³	— ³	— ³	— ³	— ³	12.82	.77	.42
Bread	43.59		.19							
Corn chip	2.56		— ³					1.30		
Noodles	2.56		— ³					1.18		
Popped corn	5.13		— ³					1.18		
Peanut fragments	7.69	1.18	2.84	100.43	.78	99.95	100.03	1.98	99.47	2.07
Total ²			100.28							100.44

¹ Mostly shell fragments.

² Per cent totals differ from 100 by rounding error.

³ Not quantified.

TABLE 2
THE IMPORTANCE OF VEGETABLE MATERIAL IN THE DIET OF RED-WING AND
GRACKLE NESTLINGS AT EAST WINGRA MARSH, 1965

	% Occurrence	% Volume
Red-wing	7.9	2.2
Grackle	66.6	18.6
bread	43.6 ¹	12.8 ¹

¹ From Table 1.

were feeding young. When these values are compared with the value ($H = .06$ to $.39$ depending on the time of day) Orians (1966) reports for Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) in British Columbia, it is clear that Red-wings and grackles at Madison are diverse and relatively unspecialized feeders.

For quantification of the extent of overlap in the diet of Red-wings and grackles a coefficient of similarity

$$C = \frac{2w}{a + b}$$

where w is the sum of all food types in the diet which both species share in common,

a is the sum of all food types in the diet of Red-wings, and

b is the sum of all food types in the diet of grackles,

used by Bray and Curtis (1957) for comparing upland forest communities in Wisconsin, and later used by Beals (1960) to measure the similarity of forest bird communities, was applied. As used here, when C equals zero there is no overlap, and when C equals one there is 100 per cent overlap. The value obtained ($C = .52$) indicates about 52 per cent overlap in the total diets of Red-wings and grackles when both species were feeding young on the marsh.

Because of the diversity of food taken by Red-wings and grackles, the most important prey taxa should be compared if anything meaningful is to be said about dietary overlap and competition for food. The importance of a food item is directly related to the net energy it yields when metabolized, or approximately the caloric value of the food item, less the number of calories expended in its procurement. Of course many factors complicate this simplified working definition of importance, such as the distance a bird travels to a food source, the distribution of food items at the source, and the amount of metabolic energy actually obtained from a food item of known caloric value. Also such components of food as water, minerals, and total nitrogen are disregarded in this definition.

For the present study neither the caloric values of food items nor the energy expended in their procurement are well enough known. The assump-

TABLE 3

FOOD OF RED-WING AND GRACKLE NESTLINGS AT EAST WINGRA MARSH, 1965
 The "important" (3 per cent or greater per cent volume) prey taxa of Red-wings and grackles while both species were feeding young at East Wingra Marsh, 1965. Values given are the per cent of the total volume in the diet. Data from Table 1.

Prey taxon	Red-wing	Grackle	Red-wing
	20 May to 10 June		11 June to 30 July
ANIMAL MATTER			
ANNELIDA			
Oligochaeta			
Opisthophora			
Lumbricidae			
<i>Lumbricus</i> spp.		9.13	
ARTHROPODA			
Insecta			
Odonata			
Aeschnidae	3.17		
Libellulidae	5.76	5.26	
Coenagrionidae	4.95		8.69
Orthoptera			
Locustidae			43.21
Coleoptera			
Scarabaeidae			
<i>Phyllophaga</i> spp.		27.19	
Lepidoptera			
Nymphalidae			
<i>Vanessa</i>			
<i>atalanta</i>			3.64
Undetermined			4.89
Noctuidae	31.99	13.78	10.18
Geometridae			
<i>Alsophila</i>			
<i>pometaria</i>	11.32		
Undetermined	20.42	3.57	
Diptera			
Stratiomyidae			
<i>Stratiomyia</i> spp.	3.65		
Undetermined			6.89
Homoptera			
Fulgoridae		3.55	
CHORDATA			
Osteichthyes		7.01	
VEGETABLE MATTER			
Bread		12.82	
TOTAL	81.26	82.31	77.50

tions are made that both Red-wings and grackles expend about the same amount of energy in foraging, and that the assimilation efficiencies for any particular food item are the same for both young Red-wings and grackles. As all available evidence indicates that insect tissues are very similar in terms of calories per ash-free gram (Slobodkin, 1961) the per cent by volume of the diet each taxon comprises is used as an index of its importance.

TABLE 4
COMPARISON OF FORAGING AND PROVISIONING ACTIVITIES OF
RED-WINGS AND GRACKLES AT EAST WINGRA MARSH

Activity	Red-wing		Grackle	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
Adults attending each nest	0	1	1 or 2	1
Rate of food delivery trips/hour	6.23 ($\pm .98$ SE)		2.01 ($\pm .57$ SE)	4.06 (± 1.16 SE)
trips/nestling/hour	2.87 ($\pm .52$ SE)			1.77 ($\pm .39$ SE)
Foraging on marsh (% of observation time)	n.d.	16	0	4
Absent from marsh (% of observation time)	n.d.	45	70	57

n.d. = not determined.

Table 3 shows the most important prey taxa of Red-wings and grackles according to the above criterion. In the Red-wing diet during the overlap period in nesting, the order Lepidoptera was most important, families Geometridae and Noctuidae comprising 63.73 per cent of the total volume. Larvae of a single species of the former, *Alsophila pometaria*, made up 11.32 per cent of the total volume.

The scarabaeid beetle genus *Phyllophaga* was the most important taxon in the grackle diet, comprising 27.19 per cent by volume. Noctuidae (13.78 per cent), bread (12.82 per cent), and the genus *Lumbricus* (9.13 per cent) when combined with the above yield a total of 62.92 per cent of the total volume in the diet.

The Red-wing diet after grackles finished feeding young on the marsh was apparently quite different from that of the overlap period. Three families from three orders (Orthoptera, Locustidae; Lepidoptera, Noctuidae; Odonata, Coenagrionidae, in that order of importance) comprised 62.08 per cent of the total volume.

The observed difference could be due to one or both of two phenomena. There may have been marked changes in prey availability after grackles stopped nesting, or the Red-wings may choose different prey (character displacement of Brown and Wilson, 1956) in response to competition with grackles. The former is known to be a definite possibility. The latter, although a tempting hypothesis, is not supported by the facts. Table 3 shows that the diet of grackles and Red-wings was more similar during the overlap period than afterward. If Red-wings altered their food preference during the period of overlap, then their subsequent diet should be most similar to that of the grackles.

Parental foraging and provisioning of nestlings.—Table 4 compares the data collected during 13 hours spent observing six separate grackle nests

with young with those obtained in 27 hours of watching nine Red-wing nests with young.

Male Red-wings feed flying young (Nero, 1956; Wiens, 1965), but rarely, if ever, do they assist in feeding nestlings; and no instance was observed in this study. Male grackles, on the other hand, fed nestlings one half as often as did females. Female Red-wings spent 16 per cent of their time foraging on the marsh. An additional 45 per cent of their time was spent off the marsh, but the amount of foraging there was undetermined. Both Nero (1956) and Wiens (1965) state that most of the Red-wings' food at East Wingra Marsh was obtained off the territory. In Utah, on the other hand, Lindford (1935) reported that most food was obtained on the territories. In Washington up to 90 per cent of the foraging was done on areas off the marsh according to Willson and Orians (1963). These differences are regional and should not necessarily be considered contradictory. Male grackles were not seen foraging on the marsh, and females did so during only 4 per cent of the observation time. The large number of odonates in their diet strongly suggests, however, that grackles must forage a good deal in a marshy or riparian habitat. Female grackles spent 57 per cent and males spent 70 per cent of their time off the marsh. The provisioning rate of female Red-wings was $2.87 (\pm .52 \text{ SE})$ feeding trips to the nest per nestling per hour, while both grackle sexes (together) made $1.77 (\pm .39 \text{ SE})$ trips per nestling per hour. Gross (in Bent, 1958) reports the provisioning rate of "Bronzed" Grackles as six trips per hour, which is comparable with the data collected here (Table 4). Orians (1961) states that female Red-wings in California visited the nest with food four times each hour on the average. Comparable data from this study run slightly higher (Table 4).

The female Red-wing does all the provisioning. Two birds, on the other hand, regularly care for nestling grackles, and at least one extra male assisted in feeding at two nests on East Wingra Marsh in 1966. The incidents of three attendants per nest may represent irregularities such as the cooperation of male grackles from disturbed nestings, but insofar as this occurs it is significant in terms of reproductive efficiency.

Foraging off the marsh was observed only incidentally. Grackles were often seen flying across Lake Wingra toward Vilas Park one half mile to the north, and also along the east edge of the lake. Presumably much of the bread, corn chips, noodles, and peanuts found in the nestlings' gullets were obtained at the "Vilas Park feeding ground" (picnic tables) Nero (1956) mentions. Dead (?) fish and some aquatic insects were undoubtedly obtained along the lake edge. One female grackle was watched accumulating green objects, presumed to be Lepidoptera larvae, in the upper branches of a large willow on the south edge of the marsh.

Red-wings were often seen searching the branchlets and leaves of honeysuckle and other shrubs to the south, east, and west of the marsh where the larval geometrid *Alsophila pometaria*, as well as other geometrids and noctuids, were abundant on the foliage in early June. On several occasions Red-wings were also seen foraging along a strip of grass on either side of the road bordering the marsh. Typically the bird walked along the ground in a deliberate manner, probing under debris; when an insect flushed the forager jumped into the air and hawked it. Presumably homopterans, locustids, and adult coenagrionids were taken in this manner. A fen one half mile southeast of the marsh (see THE STUDY AREA) was apparently the destination of many female Red-wings from the marsh. Probably the bulk of the locustids were obtained at this site, for one female Red-wing that brought in little else but grasshoppers almost always left and returned over the intervening wooded tract. On several occasions females were noted searching the leaves and yellow flowers of a bed of water lilies (*Nuphar variegatum*) 20 feet north of the marsh. The birds hopped from leaf to leaf just before each submerged, peering into the blossoms. Flies of the family Syrphidae, present in 0.39 per cent of the Red-wing food samples, were often seen in the flowers of these lilies.

Further inferences about foraging areas and habits of both species may be gained from the prey types themselves. It is interesting that only grackles took earthworms (*Lumbricus* spp.) which occurred in 28.20 per cent of the samples. These were undoubtedly taken on the ground, probably in the surrounding lowland forest. As Red-wings should have no more difficulty than grackles in capturing earthworms (Becher, 1951), the most logical explanation conforms with the casual observation that Red-wings frequented the forest floor less often than grackles. June beetles (*Phyllophaga* spp.), another prey taxon taken almost exclusively by grackles (in 38.46 per cent of the grackle samples and in none of the concurrent Red-wing samples), were locally abundant in the forest especially in mid-May. Adult June beetles according to Swain (1952) feed by night on the foliage of such deciduous trees as oak, elm, willow, and poplar, and hide in the soil of pastures or other grasslands during the day. Either the Red-wing is not as adept at digging these beetles out of hiding, does not forage where they occur, or finds them too large. Grackles removed the head and elytra before feeding these beetles to their young.

Nesting success.—Table 5 presents the Red-wing and grackle nesting success data for 1964, 1965, and 1966. The per cent of Red-wing eggs which produced flying young in 1964 (40.7) is comparable to that reported by Wiens (1965) in his 1962–1963 study, and similar to most published records, but nesting success in 1965 and 1966 was low (17.8 and 33.2 per cent). Grackle nests at East Wingra Marsh also had poor success in all

TABLE 5
COMPARISON OF RED-WING AND GRACKLE NESTING SUCCESS AT
EAST WINGRA MARSH, 1964 TO 1966

Year	Nests ¹			Eggs ²		
	No. ²	Hatched eggs	Young flying	Laid	Hatched	Young flying
Red-winged Blackbirds						
1964 ³	62	44 (70.9)	28 (45.2)	209	145 (69.4)	85 (40.7)
1965	69	45 (65.2)	19 (27.5)	241	140 (58.1)	43 (17.8)
1966	55	32 (58.2)	25 (45.5)	187	94 (50.3)	62 (33.2)
Common Grackles						
1964 ³	18	13 (72.2)	6 (33.3)	75	50 (66.6)	19 (25.3)
1965	15	12 (80.0)	6 (40.0)	61	43 (70.5)	18 (29.5)
1966	14	12 (85.7)	3 (21.4)	51	31 (60.8)	6 (11.8)

¹ Percentages given in parentheses.

² Nests with one or more eggs.

³ J. A. Wiens, MS.

3 years, and produced only about half as many flying young per egg laid as they did in 1962 and 1963.

Human interference was probably an important factor at the marsh during the present investigation. At least four types of interference were observed. First, especially in 1965 when nests with young were visited almost daily, some predator (probably raccoon, *Procyon lotor*) systematically destroyed nests and removed eggs and young, presumably found by following human scent or broken cattails. Second, food sampling once a week had a slight retarding effect on the growth of nestlings. Third, as noted earlier, parents removed some nestlings with white food collars. And fourth, the extremely low number of flying grackle young produced in 1966 (11.8 per cent) may be partially explained by desertion caused by capturing adults at the nest and marking them with paint for more accurate identification while foraging; this definitely caused the failure of one nest with eggs and two others with young.

DISCUSSION AND CONCLUSIONS

Interspecific competition.—The East Wingra Marsh icterid populations are interesting ecologically because of the recency of the apparent grackle invasion. Also the lack of similar concentrations of marsh-nesting grackles in the Madison area, and the fact that Wingra grackles make themselves as inconspicuous as possible while inside the boundaries of a Red-wing territory (see below), suggest that these grackles are utilizing unusual and somewhat adverse habitat.

Although the word *competition* is widely used in the ecological literature, much misunderstanding of its meaning has existed (see Birch, 1957 and

Milne, 1961), and Andrewartha (1961) would even abandon its use altogether. As Milne (1961) points out, part of the problem is that very few authors have bothered to define what they mean by competition, and even if a good definition is found, its interpretation may vary.

The most widely accepted definition recently stated by Milne (1961) says that competition occurs when two species try to gain a supply of the same limited resource. Another definition suggested by Elton and Miller (1954) stresses above all the effect of two interacting or interfering species on the reproductive success or survival of one or both. Although the second definition might logically be considered to be a consequence of the situation delineated by the first and to follow directly from it, this need not be the case. If, other things being equal, the result of two interacting species is the lowering of reproductive success (or survival) of one or both, then competition between them is clearly shown. But if under similar circumstances such effects are not evident, this is not proof of the absence of competition. As Darwin pointed out in his *Origin of species* (1859), ultimately competition may take three courses. New forms, either by immigration or evolution, may 1) eliminate the forms with which they compete, 2) be eliminated by them, or 3) become ecologically isolated, in which case competition ceases. It is clear then that competition ultimately results in evolutionary change, extinction or emigration through disadvantage in reproduction, or survival to one or both of the competing species.

Thus I favor a flexible concept of competition that relies on either or both of the above definitions. Often it is difficult to show reduced survival of one species; likewise it is often difficult to show that a shared resource is in limited supply. Actually the two definitions compliment each other.

Another problem is that interspecific competition is such a strong ultimate factor that it is quickly selected against, so we rarely observe it directly (R. B. Root, pers. comm.). Generally competition is demonstrated only indirectly by its effects through compensatory adjustments in the various forms of niche divergence. The relatively short time during which Red-wings and grackles have nested together in East Wingra Marsh precludes the possibility of any measureable niche divergence, and the differences that have been noted merely show that these two icterids are no more closely related than their inclusion in separate genera implies.

What evidence exists of direct competition at East Wingra Marsh? As no change in reproductive performance attributable to competitive interference is discernible, we must look to joint utilization of resources in short supply.

Competition for food.—No data are available on prey abundance at Wingra Marsh or the nearby foraging areas, and only a small amount of information about the foraging habits of Red-wings and grackles has been

TABLE 6

FOOD OF RED-WING AND GRACKLE NESTLINGS AT EAST WINGRA MARSH, 1965
 Red-wing and grackle utilization of important¹ overlapping prey orders while both species were feeding young at East Wingra Marsh, 1965. Values given are per cent frequency. Data from Table 1.

Prey taxon	Red-wing			Grackle		
	Naiad	Teneral	Adult	Naiad	Teneral	Adult
Odonata						
Libellulidae	.58	.58		.76	.38	
	Larva	Pupa	Adult	Larva	Pupa	Adult
Lepidoptera						
Noctuidae	11.66	.58	.29	8.51		
Geometridae						
<i>Nematocampa</i>						
<i>limbata</i>	.58					
<i>Alsophila</i>						
<i>pometaria</i>	12.25			2.46		
Undetermined	18.95			7.00		

¹ See Table 3.

obtained. Potential competition is suggested by overlap in the taxa the two species eat and by the important taxa they take during the overlap period (Tables 3 and 6). Lepidoptera (families Geometridae and Noctuidae) formed an important prey order for both species, as did Odonata (families Libellulidae and Coenagrionidae).

Table 6 presents more detailed information on the utilization of the two important prey orders (Lepidoptera and Odonata) taken by both Red-wings and grackles. Both species took mostly larvae of Lepidoptera and the naiads and tenerals of Odonata. The only apparent difference in the utilization of these shared prey is that they appear to have been more important in the diet of Red-wings than grackles. Thus the two species are potential competitors for noctuids, geometrids, libellulids, and coenagrionids insofar as the supply is limited, but a number of authors (Beal, 1900; Tinbergen, 1949; Skutch, 1949; Andrewartha and Birch, 1954; Lack, 1954) have pointed out that food is usually superabundant and not a limiting factor to bird populations during the breeding season.

Also the diversity of food the Red-wings and grackles take at Wingra Marsh argues against the sole dependence of these species on a small number of prey taxa. And finally as both species have been shown to utilize different foraging areas to some extent, significant competition for food seems unlikely. A more complete evaluation of competition for food on this marsh must await further investigation of prey abundance in the habitat.

Competition for space.—Wiens (1965) points out that most behavioral

interactions between Red-wings and grackles at East Wingra Marsh were initiated by Red-wings diving at grackles intruding into Red-wing territories. Grackles were rarely aggressive to Red-wings, and usually responded to Red-wing dives or threats with evasive action, making themselves inconspicuous.

Although the presence of grackles had no apparent effect on Red-wing courtship, nesting patterns, or nest placement, and had only slight effects on Red-wing territory configuration, some aggressive neglect (Hutchinson and MacArthur, 1959; Ripley, 1961) was noted that apparently affected the success of a few Red-wing nests. Wiens (1965) concludes that cattail-nesting grackles may be considered to have small nest-centered territories and that the territories of both species are to some extent mutually exclusive. Simmons (1951) points out that interspecific territorialism, like distinctive habitat preferences or divergence of food habits, may be a way of reducing competition.

Casual observations during the present investigation were generally in agreement with the interpretations of Wiens (1965). But after reviewing the evidence suggesting the absence of competition for food at East Wingra Marsh, reevaluation of the Wiens (1965) data and other observations made in the present study point to a resource that is in short supply and that both species utilize, namely space. Both Red-wings and grackles need places to build their nests and each requires a territory around the nest, but the Red-wing certainly needs more space than does the grackle. I suggest, therefore, that both species are actively competing for space, the Red-wing to maintain territorial integrity established by its prior arrival, and the grackle to establish its small nest-centered territory. Conclusive proof might be obtained by removing all Red-wings and noting the effect on grackle nesting density. Over the past two decades grackles apparently have had a slight competitive advantage. Future observations would help to ascertain whether this trend will continue.

SUMMARY

The food habits and foraging behavior of Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*) breeding concurrently on a small cattail marsh in Madison, Wisconsin, were studied during the 1965 and 1966 breeding seasons, particularly to investigate potential food competition between the two species.

The size of the breeding populations of both species was slightly lower than in previous studies at this marsh. Nesting asynchrony suggested by the breeding chronology of 1963 was substantiated in the present investigation, but data from 1947 (grackles nesting in a white cedar plantation) failed to substantiate a long-term trend of increasing asynchrony.

Food from nestlings of both species was sampled using a pipe cleaner collar to prevent swallowing. Animal matter (chiefly insects) predominated in the diets of both Red-wings and grackles. Vegetable material occurred in only 7.9 per cent of the samples of the former, and while 66.6 per cent of the grackle samples contained vegetable matter (mostly bread), it comprised only about 18.6 per cent of the total intake by volume. Both species were found to be unspecialized feeders, as the information theory diversity index for Red-wings and grackles was 3.17 and 2.62 respectively. A coefficient of similarity commonly used in plant ordinations gave an estimate of 52 per cent overlap in the two diets. More detailed examination of the important prey taxa of both species, as determined by the per cent of the total intake by volume, showed moderate overlap in the Lepidoptera (families Geometridae and Noctuidae), and in the Odonata (families Coenagrionidae and Libellulidae). The above Lepidoptera (mostly larvae) accounted for 63.73 and 17.35 per cent of the total intake by volume of Red-wings and grackles respectively, while Odonata were less important.

Observations at nests with young showed that grackles foraged on the marsh only 4 per cent of the time. Female Red-wings (males did not feed nestlings) spent 16 per cent of the time foraging on the marsh. The provisioning rate of grackles was 1.77 trips per nestling per hour, while young Red-wings were fed at the rate of 2.87 trips per nestling per hour. The principal Red-wing foraging areas were the shrubbery in an adjacent Southern Lowland Deciduous Forest, the marsh itself, and grass around the marsh and 300 yards to the southeast. Grackles were known to scavenge at Vilas Park one half mile north and were believed to forage on the floor of the deciduous forest as well as around the lake edge.

Nesting success (per cent flying young per egg laid) of both species was lower for the years of this study than for other years and locations. Human interference (nest visits and food sampling) was probably a factor.

Competition, at least for food, probably did not exist between Red-wings and grackles at Wingra Marsh because of the diversity of food both species take and because of differences in foraging locations. It is suggested that both Red-wings and grackles were competing actively for space.

ACKNOWLEDGMENTS

I am grateful to John T. Emlen, Jr. for his guidance throughout the study, and especially for critically reading the manuscript. Special thanks are also due to John A. Wiens who gave valuable council not only during the formative period of this study, but also through its completion, and who allowed the inclusion in this paper of some of his unpublished data. Gordon H. Orians also gave advice, while Marlin P. Johnson and Susan E. Reichert gave generously of their time and by identifying certain invertebrates. Any possible errors in the identification of food items are solely my responsibility.

Use of the East Wingra Marsh study area was made possible by the University of Wisconsin Arboretum Committee. This study was made in partial fulfillment of the requirements for the degree of Master of Arts at the University of Wisconsin, and was supported in part by two summer grants from the Wisconsin Alumni Research Fund.

LITERATURE CITED

- ANDREWARTHA, H. G. 1961. An introduction to the study of animal populations. Chicago, Univ. Chicago Press.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Chicago, Univ. Chicago Press.
- BEAL, F. E. L. 1900. Food of the Bobolink, blackbirds, and grackles. U. S. Dept. Agr. Bull., **13**.
- BEALS, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull., **72**: 156-181.
- BEECHER, W. J. 1951. Adaptations for food-getting in the American blackbirds. Auk, **68**: 411-440.
- BEER, J. R., AND D. TIBBITTS. 1950. Nesting behavior of the Red-wing Blackbird. Flicker, **22**: 61-77.
- BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Natl. Mus., Bull. **211**.
- BIRCH, L. C. 1957. The meanings of competition. Amer. Nat., **91**: 5-18.
- BIRD, R. D., AND L. B. SMITH. 1964. The food habits of the Red-winged Blackbird, *Agelaius phoeniceus*, in Manitoba. Canadian Field-Nat., **78**: 179-186.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr., **27**: 325-349.
- BROWN, W. L., JR., AND E. O. WILSON. 1956. Character displacement. Syst. Zool., **5**: 49-64.
- CURTIS, J. T. 1959. The vegetation of Wisconsin. Madison, Univ. Wisconsin Press.
- DARWIN, C. 1859. The origin of species. New York, New American Library.
- ELTON, C., AND R. S. MILLER. 1954. An ecological survey of animal communities: with a practical system of classifying habitats by structural characteristics. J. Ecol., **42**: 460-496.
- FICKEN, R. W. 1963. Courtship and agonistic behavior of the Common Grackle, *Quiscalus quiscula*. Auk, **80**: 52-72.
- GABRIELSON, I. N. 1915. Notes on the Red-winged Blackbird. Wilson Bull., **27**: 293-302.
- HAMILTON, W. J. 1951. The food of nestling Bronzed Grackles, *Quiscalus quiscula versicolor*, in central New York. Auk, **68**: 213-217.
- HUTCHINSON, G. E., AND R. MACARTHUR. 1959. Appendix: on the theoretical significance of aggressive neglect in interspecific competition. Amer. Nat., **93**: 133-134.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.
- LINDFORD, J. H. 1935. The life history of the Thick-billed Red-winged Blackbird, *Agelaius phoeniceus fortis*, Ridgeway, in Utah. Unpublished M.S. thesis, Salt Lake City, Univ. of Utah.
- MEANLEY, B. 1961. Late-summer food of Red-winged Blackbirds in a fresh tidal-river marsh. Wilson Bull., **73**: 36-40.
- MILNE, A. 1961. Definition of competition among animals. In Mechanisms in biological competition. Symp. Soc. Exp. Biol., **15**: 40-61.

- NEFF, J. A., AND B. MEANLEY. 1957. Blackbirds and the Arkansas rice crop. Arkansas Agr. Exp. Sta. Bull. **584**.
- NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. Wilson Bull., **68**: 5-37, 129-150.
- ORIAN, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr., **31**: 285-312.
- ORIAN, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor, **68**: 321-337.
- ORIAN, G. H., AND G. COLLIER. 1963. Competition and blackbird social systems. Evolution, **17**: 449-459.
- PAYNE, R. T. 1963. Trophic relationships of 8 sympatric predatory gastropods. Ecology, **44**: 63-73.
- PETERSON, A., AND H. YOUNG. 1950. A nesting study of the Bronzed Grackle. Auk, **67**: 466-476.
- RIPLEY, S. D. 1961. Aggressive neglect as a factor in interspecific competition in birds. Auk, **78**: 366-371.
- SIMMONS, K. E. L. 1951. Interspecific territorialism. Ibis, **93**: 407-413.
- SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis, **91**: 430-455.
- SLOBODKIN, L. B. 1961. Preliminary ideas for a predictive theory of zoology. Amer. Nat., **45**: 147-153.
- SWAIN, R. B. 1952. The insect guide. New York, Doubleday and Co.
- TINBERGEN, L. 1949. Bosvogels en insecten. Ned. Bosbouw Tijdschr. **4**: 91-105 (not seen).
- WIENS, J. A. 1965. Behavioral interactions of Red-winged Blackbirds and Common Grackles on a common breeding ground. Auk, **82**: 356-374.
- 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. Abstracts, Proc. 16th Intern. Congr. Zool., **3**: 342-346.

*Department of Zoology, University of Wisconsin, Madison, Wisconsin.
Present address: Section of Systematics and Ecology, Division of Biological Sciences, Cornell University, Ithaca, New York 14850.*