BEHAVIORAL INTERACTIONS OF RED-WINGED BLACKBIRDS AND COMMON GRACKLES ON A COMMON BREEDING GROUND

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Ecologists have long been engaged in the study of relationships between species, but ethologists have all too often ignored interspecies relationships, with the result that the behavioral aspects of community ecology or competition are poorly known. The few recent detailed studies of interspecific behavior (Simmons, 1951; Rand, 1954; Lanyon, 1957; Selander and Giller, 1959, 1961; Moynihan, 1962, 1963; Orians and Collier, 1963; Orians and Willson, 1964) have exposed new approaches to investigations of ecological relationships (see Wynne-Edwards, 1962).

This study was undertaken to examine the nature and effects of behavioral interactions between two icterids, the Red-winged Blackbird (*Agelaius phoeniceus*) and the Common Grackle (*Quiscalus quiscula*), in a situation where the two species were breeding together in a small cattail marsh and were as a consequence potentially in competition.

Red-wings nest in a wide range of habitats, but usually are closely associated with marshes and, indeed, are often the "dominant species" of the Nearctic marsh avifauna (Allen, 1914). Grackles, while being quite adaptable in their nesting habits and utilizing a wide range of nesting substrates (see Bent, 1958), apparently only sporadically nest in marshes. Indeed, Beecher (1942), in analyzing nesting substrates of several species in relation to available edge growth, concluded that cattails were "pessimum" substrate for grackles and "supra-optimum" for Red-wings. Thus in a situation in which both species utilize marsh flora for nesting substrate, any interpretation of the relationships between the species must recognize that the habitat is typical for Red-wings and unusual for grackles.

The Study Area

The study was conducted during the spring and summer of 1962 and 1963 in a 2.4 acre (1 hectare) cattail (*Typha latifolia*) marsh on the east of Lake Wingra, in the University of Wisconsin Arboretum, Madison. This marsh is bordered by red osier dogwood (*Cornus stolonifera*) and black willow (*Salix nigra*), particularly on the side adjoining the lake, and is bordered on three sides by fairly dense stands of mixed hardwoods. Figure 1 illustrates the general features of the study area. It is the same marsh used by Nero (1956) and by Beer and Tibbitts (1950) in their studies of Red-wings. Grackles have nested in small numbers in this marsh since at least 1946 (J. Beer, pers. comm.). These first nests were

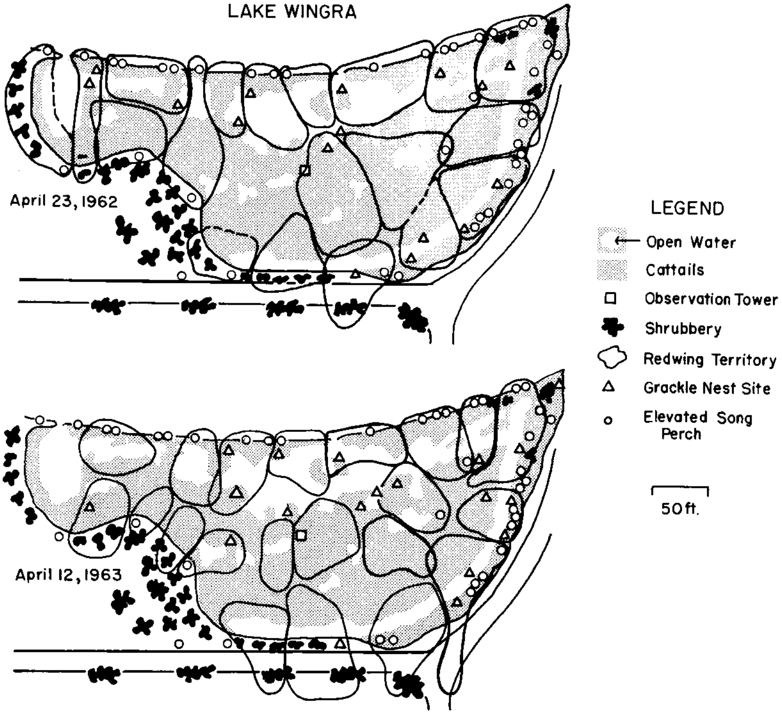

Figure 1. Grackle nest sites and Red-wing territory configurations in the East Wingra Marsh at the beginning of grackle nesting, 1962, 1963.

in dead dogwoods in the west end of the marsh, but by 1948 grackles were nesting in cattails in several places in the marsh.

Through most of the two breeding seasons studied there were about 20 to 25 male grackles and 18 to 22 female grackles directly associated with the marsh; other small groups of both sexes often frequented the marsh edges, especially early in the season, but these birds wandered in and out of the area and did not nest about the marsh. In 1962 there were 45 to 55 female Red-wings nesting in the marsh, while in 1963 about 50 to 60 females were present. In both years 21 male Red-wings held territories in the marsh.

METHODS

Observations were made with 7 × 35 binoculars from the edge of the marsh, from the roof of a car parked on the road bordering the marsh, and, mostly, from a 20-foot wooden tower located roughly in the center of the marsh. During the 1963 season a small battery-operated tape recorder was used to record observations, a technique particularly useful for recording the details of rapid behavioral sequences.

Extensive searches through the entire marsh were made rather often to locate nests. When nests were found their position was plotted on a map of the marsh, a numbered cloth or plastic tag was affixed to nearby vegetation, and subsequent visits were made two or three times per week.

INTRASPECIFIC BEHAVIOR

DISPLAYS

Both species have several well-defined displays which are regularly used in intraspecific situations, and since these displays are also seen in encounters between the species it may be helpful to describe several briefly. Similarities between the displays of the two species suggest homologous relationships and permit a parallel categorization. A detailed analysis of Red-wing displays is presented by Nero (1956), and Ficken (1963) has analyzed grackle displays.

Song-spread.—Song-spread in both species is a fairly mild threat display and serves intraspecifically as a territorial or self-advertisement display. It is not uncommonly given by solitary birds, but it is usually delivered with greater intensity and frequency in the presence of other individuals of the same sex. In male Red-wings song-spread is usually associated with the *oak-a-lee* song; the wings and tail are spread and the contour feathers raised during the song (Figure 2, A). Song-spread in female Red-wings is similar to that of the male except in the accompanying vocalization; the female gives a series of shrill, high, rapidly descending trills, something on the order of *skraw-skraw-a-skree-skree-skree,* with each display.

In male grackles the song-spread display is quite similar to the above, but the vocalization is less elaborate and the raising of the head and body at the climax of the song contrast with the crouching position of the Red-wing (Figure 2, B). A similar display is given by female grackles, although the visual and vocal components are typically less pronounced.

Bill-tilt.—This display, or displays similar to it, is found in many of the Icteridae and in a number of other passerines (Nero, 1963; Andrew, 1961; Marler, 1961), and it apparently functions in maintaining a "critical distance." The display, which is given by both sexes, occurs only in the presence of other birds, usually members of the same sex. It is associated with territorial defense in the Red-wing (Figure 2, C), and with courtship and (infrequently) territorial defense in the grackle (Figure 2, D).

Dive.—In both species diving is a highly aggressive action, usually taking the form of a direct swooping flight toward another individual. Diving is much more common in Red-wings than in grackles, perhaps because of the smaller territory size of the latter, but in both species it

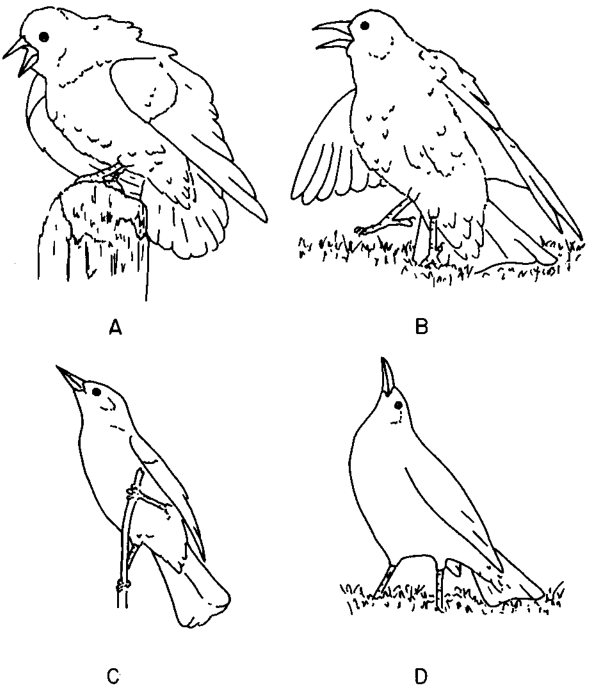

Figure 2. Song-spread and bill-tilt displays in Red-wing and grackle males. A, Red-wing song-spread; B, grackle song-spread; C, Red-wing bill-tilt; D, grackle bill-tilt. A and C after Nero (1956), B and D after Ficken (1963).

is relatively uncommon in normal intraspecific activities. This motor pattern may have given rise to such courtship displays as "sexual chases" in the Red-wing (Nero, 1956), and "leader flights," "chases," and "together flights" in the grackle (Ficken, 1963), all of which are characterized by pursuit of a female by several males.

Tail-flicking.—This display is given by both Red-wings and grackles of both sexes in response to a strange situation or a disturbance. In both species it consists of repeated upward flicks of the closed tail and is often accompanied by sharp call notes.

BREEDING BIOLOGY

Although I studied the breeding biology of each species fairly intensively, only those aspects which bear on interspecific behavior are discussed here.

Grackles are not typically marsh nesters, are strictly monogamous, and defend only a small territory directly about the nest site. Red-wings, on the other hand, are characteristic marsh nesters, are polygynous, and defend clearly circumscribed areas of from .06 to 2.0 acres against other males, females other than their mates, and, at times, fledgling Red-wings.

Adult male Red-wings usually arrive on the East Wingra Marsh about the second week in March, the first arrivals usually being birds which have previously bred on the marsh (Nero, 1956). Females arrive a week or two later. Adult male grackles generally arrive in the area two or three days after the male Red-wings, and are followed 5 to 10 days later by the adult females.

Territories are established by male Red-wings almost immediately upon their return, but the boundaries may undergo considerable fluctuations and may not become firmly established until nesting begins five or six weeks later. Red-wing territories vary in position, size, and shape, with respect to the availability of elevated singing perches, the extent of vegetational edge growth (cattail-open water interface), and population density. That territorial boundaries of Red-wings do fluctuate early in the season is important, because this affects the ease with which grackles may penetrate the marsh and establish their own small territories.

Red-wing courtship typically takes place in the territories after they have been initially established. Grackle courtship, on the other hand, takes place about the edges of the nesting area, and territories are formed only after the nest site has been selected by flights of the paired birds into the nesting area (the marsh). Thus grackle territories are nest-centered, with territorial aggressiveness decreasing with increasing distance from the nest, while Red-wing territories are large, with no definite center of activity, and defense is intense to the very edge of the clearly delineated area.

Grackles began nesting activities in the marsh 5 to 15 days before Red-wings (see Figures 3 and 4). Grackles took about a week more to construct their nests than Red-wings, and incubated the eggs a day or so longer (12–13 days). Grackles laid an average of 4.4 eggs per clutch in the marsh, about one or more egg per clutch than Red-wings. Grackle nestlings stayed in the nest two to five days longer than Red-wing nestlings, but left the marsh within a day or two after fledging, while Red-wing fledglings remained in the home territory for as long as two weeks after leaving the nest.

Both species are usually single-brooded in the Madison area. Nest construction and incubation are performed entirely by the female in both species, but male grackles participate in feeding the nestlings, while male Red-wings take such a role only occasionally. In both species the fledglings are fed by both sexes, the male usually predominating.

Ecologically, the two species appeared to utilize the marsh in much the same manner. Nests of both species were usually on the edges of

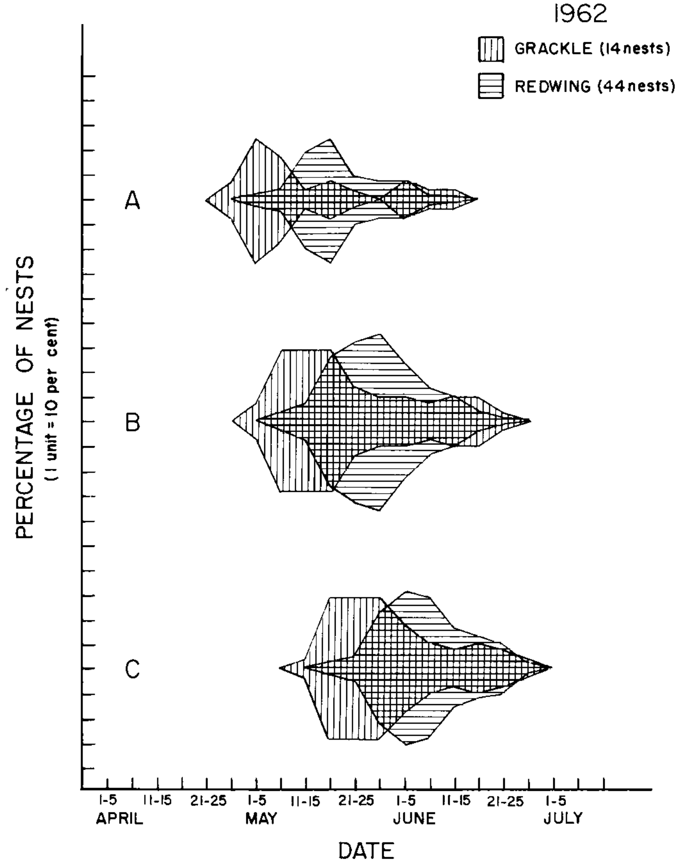

Figure 3. Chronology of Red-wing and grackle nesting in the East Wingra Marsh, 1962. A, nests being laid in; B, nests being incubated; C, nests with young.

cattail clumps bordering areas of open water and very few differences in the character of the substrate selected were detected. Both species constructed a cup-shaped nest with a bulky framework of interwoven cattails, a cup of mud or wet cattails, and a cup lining of slender grasses, rootlets, or hair. Grackle nests, however, were usually bulkier and heavier than Red-wing nests, and were normally built in somewhat denser cattail clumps than Red-wing nests. The average distance from water to nest rim for 34 grackle nests in the marsh was 20.0 inches (range, 9–27 inches), while 138 Red-wing nests averaged 23.7 inches up (range, 14–33 inches). Red-wing nests were usually exposed and well-lighted, while grackle nests often were somewhat hidden and usually shaded, perhaps as a result of their slightly lower position in dense clumps of cattails.

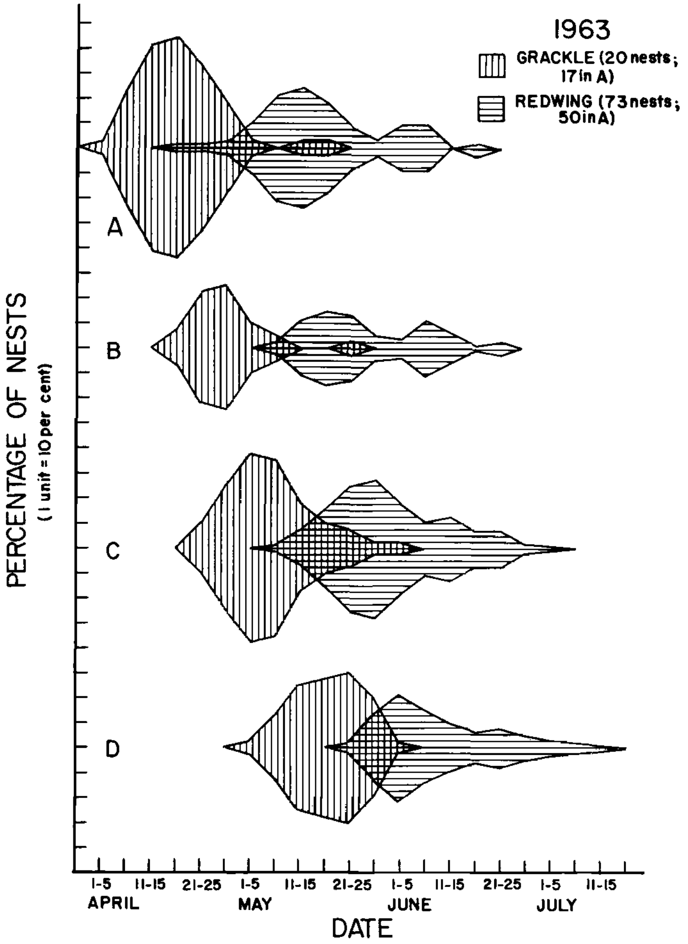

Figure 4. Chronology of Red-wing and grackle nesting in the East Wingra Marsh, 1963. A, nests being built; B, nests being laid in; C, nests being incubated; D, nests with young.

Both grackles and Red-wings appear to obtain the bulk of their food (Lepidopteran larvae) in the hardwood forests bordering the marsh, but both fed to a limited extent on emerging damselflies and dragonflies in the marsh.

Interspecific Behavior

Behavioral interactions between Red-wings and grackles occurred throughout the breeding season, but were more frequent during the early part of courtship than after the initiation of nesting (Figure 5). Most

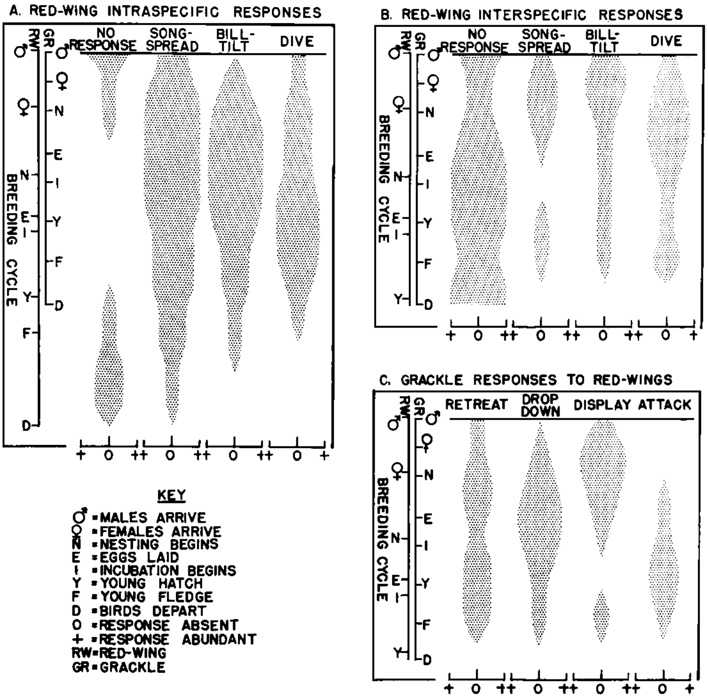

Figure 5. Approximate frequencies of basic interspecific responses with respect to Red-wing and grackle breeding cycles in 1963. A, Red-wing responses to territory intrusions by other Red-wings; B, Red-wing responses to territory intrusions by grackles; C, grackle responses to Red-wing displays. Frequencies for a response indicate the relative frequency through the breeding season of that response only, and do not relate to its frequency in the total response repertoire of the species.

interactions between the two species were initiated by the Red-wings and were apparently the result of grackle trespasses into Red-wing territories. Such intrusions occurred most often in connection with grackle courtship and with their efforts to reach their nests or feed fledgling grackles.

Grackle courtship in the marsh involved two characteristic behavior patterns, the "mutual perch" displays and "pair formation flights." The "mutual perch" displays were usually performed in small mixed groups in the tall willows and dogwoods about the marsh edges. Male grackles showed a distinct tendency to give these displays from prominent perches in these trees (= song perches), but individual males or pairs showed no attachment to particular song perches, and there was no evidence of any grackle territoriality connected with these perches. Many of these trees were also used as song or display perches by the resident (i.e., territory-holding) Red-wing males, and thus were included in Red-wing territories and strongly defended intraspecifically by the Red-wings. Grackles displaying in these trees, however, almost never elicited any response from resident Red-wings (Table 1), even when the two birds were only a few feet apart.

Grackle "pair formation flights" followed the typical pattern, one or more females leading a group of males out over the marsh. Often these flights ended with the grackles alighting in the cattails (and thus in Red-wing territories). Early flights into the marsh were apparently made at random with respect to Red-wing territories, but as courtship progressed, and as Red-wing territories became increasingly well defined, grackle flights became directed into areas along the edges of Red-wing territories. Detailed records were kept for 42 grackle "pair formation flights" into the marsh which occurred between the arrival of females and the initiation of nesting activities: of these flights 13 (31 per cent) ended in areas outside Red-wing territories (although such areas comprised less than 15 per cent of the usable marsh area); 15 (36 per cent) ended fewer than 5 feet into a territory; 9 (21 per cent) ended 5 to 10 feet inside a territory; and only 5 (12 per cent) ended more than 10 feet into a territory. Deep penetrations by grackles into Red-wing territories always elicited a response (usually a dive), while penetrations of only a few feet were met with a wider range of responses, and not uncommonly the resident Red-wing male made no observable response (Table 1). By a week or 10 days after the beginning of grackle courtship the flights showed a distinct orientation to Red-wing territorial edges or areas of poorly defined territories, and no penetrations of more than 10 feet were observed. Grackle flights connected with nest site selection were similarly oriented, and apparently the subsequent placement of most grackle nests depended on the location of Red-wing territory boundaries as well as vegetational characteristics (Figure 1). Some Red-wing territories continued to fluctuate after the establishment of grackle nest sites, however, so a few grackle nests eventually became located well within Red-wing territories.

With the initiation of nest construction the activities of grackles became more closely associated with their nest sites, and flights out into the cattails were usually made by a single female or pair. The response of Red-wing males to these grackles was rather variable. On numerous occasions grackles approaching their nests elicited no observable response from the resident Red-wings, and the frequency of such seeming "indifference" increased with the beginning of Red-wing nesting activity and the concurrent increase in Red-wing intraspecific territorial activity (Figure 5). In some cases the behavior of the resident Red-wings actually suggested "avoidance" of the grackles; the Red-wing male dropped down

TABLE 1
RED-WING DISPLAY RESPONSES TO GRACKLES DURING GRACKLE COURTSHIP AND NESTING, 1962, 1963

Target or situation	*Instances of display response of Red-wing male*				
	Dive	*Bill-tilt*	*Song-spread*	*Tail-flick**	*No response**
Grackle male	34	17	16	unusual	usual
Grackle female	55	25	16	unusual	usual
Grackle group	1	5	6	usual	nearly always
Position of grackles:					
on elevated song perch	2	6	8	unusual	nearly always
flying overhead	1	0	1	rare	nearly always
above Red-wing	1	22	14	not recorded	not recorded
below Red-wing	88	23	20	not recorded	not recorded
high in cattails	77	30	20	not recorded	not recorded
low in cattails	10	15	12	not recorded	not recorded
not in territory	1	2	0	unusual	nearly always
less than 5 ft. into terr.	32	16	15	usual	usual
5–10 ft. into territory	48	27	16	usual	unusual
more than 10 ft. into terr.	6	1	1	unusual	never
grackle approaching its nest	68	27	19	usual	usual

* Not quantified.

into the cattails or flew to another part of the territory when grackles made shallow intrusions. On other occasions, however, Red-wing males responded aggressively to grackles approaching their own nests. By far the most prevalent expression of aggression at this time was a dive (Table 1), although dives were often mixed with bill-tilts, song-spreads, and tail-flicks in complex display sequences.

When young grackles fledged they rapidly moved away from the nest site, staying in the marsh only a day or two. Red-wing males were never seen to respond to grackle fledglings even though they were often well within Red-wing territories and only a few feet from Red-wing males. Adult grackles arriving to feed such young, however, were almost always vigorously displayed to or chased from the territory by the Red-wing.

Female Red-wings are somewhat unusual among passerines in that they establish nest-centered "sub-territories" within their mate's territory, from which they repel all other Red-wing females (Nero, 1956). Female Red-wings were observed to give bill-tilts to female grackles near the Red-wings' nest site on several occasions, but away from the nest site female Red-wings rarely responded to grackles unless their mates did, in which case they moved about nearby giving disturbance calls and tail-flicking.

Grackles were rarely aggressive to Red-wings although several times they dived at Red-wings (of either sex) two or three feet from the grackle nest. Generally the grackles tolerated Red-wings (and other grackles as well) when they were more than four feet from the nest.

TABLE 2

GRACKLE RESPONSES TO RED-WING INTERSPECIFIC DISPLAYS GIVEN DURING THE GRACKLE COURTSHIP AND NESTING PERIOD, 1962, 1963

Grackle response	*Red-wing male display*			
	Dive	*Bill-tilt*	*Song-spread*	*Tail-flick**
Dives at Red-wing	9	1	0	never
Bill-tilt	2	19	2	never
Song-spread	0	1	5	rare
Drops into cattails	48	6	2	rare
Flies away	26	6	5	rare
Tail-flick*	never	unusual	unusual	unusual
None	6	11	14	usual

* Not quantified.

Grackles generally responded to Red-wing aggression with evasive actions or, occasionally, displays. They usually made no observable response to Red-wing song-spreads, but bill-tilts often elicited a grackle bill-tilt in return. Red-wing dives usually resulted in the grackles' dropping down low into the cattails or flying away (Table 2).

EFFECTS OF INTERACTIONS OF REPRODUCTION

Behavioral interactions between species might be expected to affect various aspects of their reproduction, since they require energy normally available for intraspecific activities. The initiation of breeding activities could be retarded, nest placement or territory configuration altered, pairing or nesting patterns changed, feeding and brooding rates reduced, or nesting success affected. Several instances have been recorded where interspecific interactions apparently have reduced the reproductive efficiency or lowered the population density of a species (Ripley, 1959, 1961; Orians and Collier, 1963; Wynne-Edwards, 1962).

EFFECTS OF THE PRESENCE OF GRACKLES ON RED-WING REPRODUCTION

Many authors (including Bent, 1958; Davis, 1944; Poor, 1946) have noted predatory habits in the grackle. Indeed, Roberts (1932: 321) has suggested that grackle predation in some areas may be so great as to "prevent most other species making their home in the vicinity of a colony," and Meanley and Webb (1963) proposed that grackles were probably responsible for most of the predation on Red-wing eggs in Chesapeake tidal marshes. On the Wingra marsh there was no evidence that grackles were predators on Red-wing eggs or young; their responses to Red-wings were usually non-aggressive (Figure 5, Table 2).

The presence of grackles in the marsh had no observable effects on the nature of Red-wing pair formation or nesting procedure. Displays used in courtship or territorial behavior were also indistinguishable from those observed in "grackle-free" Red-wing colonies or reported in the literature. There were slight modifications of Red-wing territory boundaries to accommodate the small grackle territories, but I doubt that grackle activity had any major effects on Red-wing territory configuration, or on the exact placement of Red-wing nests.

Figures 3 and 4 show that Red-wing breeding cycles in 1962 and 1963 were very similar with respect to timing. In the same two years the breeding cycles of the grackles were markedly dissimilar, even though female grackles arrived (and courtship began) about the same time each year. The constancy of Red-wing breeding in relation to the varying period of contact with grackles in the two years indicates that interactions had little effect on the timing of Red-wing breeding, a conclusion further supported by comparison of the 1963 breeding chronology in the Wingra marsh with that in a "grackle-free" marsh a few miles away. In both marshes the various aspects of Red-wing nesting activity began and reached peaks at about the same time.

A more complex type of reproductive interference could result from the release of excessive aggressive behavior of Red-wings in the presence of grackles, leading to a neglect of the nest or young by the Red-wings. Such behavior has been termed "aggressive neglect" by Hutchinson and MacArthur (1959) and Ripley (1961). In the marsh female Red-wings were often attracted to Red-wing—grackle interactions, and in 1962 several females nesting in areas of grackle activity repeatedly left their nests to join in the interspecific responses of their mates. In three of these nests the eggs became addled or the nestlings died. This suggests the operation of aggressive neglect on at least a small scale. Breeding success in the entire marsh, however, was not markedly lower than that found for Red-wings breeding in the absence of grackle activity in this region (Table 3). Such comparisons must be made cautiously though, because Red-wing nesting success may vary considerably with regard to locality, season, vegetative substrate, and nest height (Case and Hewitt, 1963; Meanley and Webb, 1963). The low nesting success of Red-wings in the marsh in 1963 is at least partially the result of two violent windstorms in early June.

EFFECTS OF THE PRESENCE OF RED-WINGS ON GRACKLE REPRODUCTION

The courtship and pair formation behavior of grackles were apparently unchanged by Red-wing activity in the marsh, perhaps because most of the displays were given in the trees bordering the marsh where Red-wing interference was slight. Grackles showed a definite tendency, however, to orient their courtship and nest site selection flights to areas not in-

TABLE 3

COMPARISON OF RED-WING AND GRACKLE NESTING SUCCESS ON THE EAST WINGRA MARSH WITH NESTING SUCCESSES OF EACH SPECIES IN UNMIXED COLONIES

	Year	*Nests*[1]			*Eggs*[1]		
		No.	*Hatched eggs*	*Fledged young*	*Laid*	*Hatched*	*Young fledged*
				Red-winged Blackbirds			
Grackles present:	1962	62	51 (82.3)	38 (61.2)	221	168 (76.0)	109 (49.3)
	1963	76	52 (68.4)	36 (47.4)	255	162 (63.5)	92 (36.0)
Grackles absent:	1941[2]	—	—	—	563	418 (74.3)	335–7 (59.7)
	1941[2]	—	—	—	577	405 (70.2)	340–4 (59.3)
	1947[3]	91	78 (85.7)	57 (63.6)	325	258 (79.4)	170 (52.3)
	1959[4]	238	—	83 (35.0)	730	393 (53.8)	204 (28.0)
	1960[4]	280	—	67 (24.0)	902	402 (44.6)	162 (18.0)
				Common Grackles			
Red-wings present:	1962	15	13 (86.6)	8 (53.3)	65	56 (86.1)	33 (50.6)
	1963	18	14 (77.8)	12 (66.7)	81	61 (75.3)	44 (54.3)
Red-wings absent:	1947[5]	26	—	12 (45.0)	117	84 (71.8)	51 (44.0)
	1948[5]	15	—	8 (53.3)	73	53 (72.6)	31 (42.5)
	1949[5]	21	—	14 (66.7)	98	72 (73.4)	53 (54.1)

[1] Percentages given in parentheses.
[2] Smith, 1943; Cook County, Illinois.
[3] Beer and Tibbitts, 1950; Madison.
[4] Young, 1963; Stoddard, Wisconsin.
[5] Petersen and Young, 1950; Madison.

cluded in Red-wing territories, and the placement of grackle nests showed a corresponding correlation with the edges of Red-wing territories (Figure 1). This pattern of nesting distribution was probably a result of Red-wing aggression in the more central portions of their territories.

The manner of nest approach by marsh-nesting grackles was considerably modified from that seen in "normal" colonies. In normal situations grackles approach the nest by flying directly to the nest area and quietly move to the nest site at nest level. In the Wingra marsh grackles would alight in the cattails 10 to 25 feet from the nest and move slowly through the cattails toward the nest, approaching well below nest level with repeated tail-flicks. Such a slow, "inconspicuous" pattern of nest approach might function to reduce interspecific interference.

Red-wing aggressiveness apparently had little effect on the timing of grackle nesting. Grackle nesting activity on the marsh began considerably earlier in 1963 than in 1962 (Figures 3 and 4), although the birds arrived on the marsh and started courtship at about the same time each year. The reasons for the inconsistent timing of grackle breeding activity and the contrasting consistency of Red-wing breeding activity are not clear, but it is probable that the two species responded to environmental conditions in different ways. In 1963 grackle nesting chronology at the

Wingra marsh corresponded closely with that of a colony of about 70 pairs nesting close by in a plantation of 20-foot red cedars (*Juniperus virginiana*) where Red-wings were absent.

Grackle nesting success in the marsh agrees fairly well with the success of tree-nesting grackle colonies in other years at Madison (Table 3). In 1963 the grackles completed nesting before the two violent windstorms which affected Red-wing breeding success.

DISCUSSION

Interspecific competition is usually if not always resolved, in the long run, by means other than interspecific aggression (see, for example, Crombie, 1947; Svärdson, 1949; Wynne-Edwards, 1962; Hamilton, 1962; Moynihan, 1963). Where ecological overlap is slight, interspecific aggression may involve an "undesirable" expenditure of time and energy (Dixon, 1961; Orians and Collier, 1963) and perhaps give rise to aggressive neglect (Udvardy, 1951; Ripley, 1961). Yet if ecological competition is great, interspecific aggression may lead to the establishment of mutually exclusive territories between the species. Through such interspecific territorialism aggressive contacts between the species may be reduced to the frequency of intraspecific contacts. Even a slight reduction in the amount of interspecific competition through territorial segregation could be selectively advantageous in enabling the species to retain both their ecological attributes and their sympatric distribution.

Numerous examples of interspecific territorialism have been noted in birds (Simmons, 1951; Johnson, 1963; Orians and Willson, 1964). Often these involve species breeding in structurally simple vegetation (such as marshes or grasslands) where there are few opportunities for diversification of foraging techniques and, hence, presumably few ways to avoid competition (Orians and Willson, 1964). Whether or not true interspecific territorialism existed between Red-wings and marsh-nesting grackles was rather difficult to determine, because of the very small and vaguely defined territories of the grackles. Interspecific territorial aggression was often noted in both species, however, and presumably even partial territorial exclusion between the species might contribute to their successful cohabitation of the marsh habitat.

Selander and Giller (1963) have proposed that in certain cases interspecific territorial aggression may be the fortuitous result of the release of territorial behavior by morphological or behavioral similarities between the species. With such "mistaken identity" the aggressor is presumably responding to sign stimuli which have only a partial resemblance to the "optimal stimulus" presented by a member of the same species (Tinbergen, 1939). Such aggression is especially likely when the threshold of the fighting response is low or aggressive "motivation" is high, as is the case during the breeding season. The interspecific responses of the Red-wings and grackles observed in this study, however, indicated a more complex cause than mistaken identity, for Red-wing aggression was directed at grackles with a fairly high frequency and consistency (Figure 5, Table 1). In addition, Red-wings often responded to grackles by diving (Table 1), and activity which was generally replaced by ritualized displays in intraspecific clashes. Hinde (1952) has noted that diving is rare in intraspecific contacts in several European tits (*Parus*), but occurs fairly often in interspecific encounters.

Social displays of animals are rarely released by a single sign stimulus, but rather are the result of simultaneous presentation of a number of species-specific social releasers, a "heterogenous summation" (Tinbergen, 1948). Simmons (1951) has advocated that mannerisms and general outline or shape are of prime importance in releasing interspecific responses, while plumage color and pattern are of secondary significance. Interspecific territorial aggression is by no means restricted to those species which are morphologically similar (Orians and Collier, 1963), but in general, species that hold mutually exclusive territories have similar postures and/or vocalizations which enable them to elicit mutual aggressive responses (Johnson, 1963).

Presumably a grackle intruding in a Red-wing territory does not provide as complete a set of releasers for the resident Red-wing as does another Red-wing. Still, grackles seem to produce a reasonably close facsimile of the aggregate of social releasers of Red-wing threat displays, for the responses of Red-wings to grackles were not observably different, qualitatively, from those induced by other Red-wings. In the closely-related Great-tailed and Boat-tailed grackles (*Cassidix mexicanus* and *C. major*) males regularly hold mutually exclusive territories, and all of the displays normally used in intraspecific interactions appear in interspecific encounters as well (Selander and Giller, 1961). On the other hand, Gordon Orians informs me (pers. comm.) that where Red-wings and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) breed together in Washington species-specific territorial displays are only occasionally used in interspecific encounters, most contacts involving simple supplanting attacks. Hinde (1952) has noted that the displays usually given in intraspecific situations by European tits do not occur in encounters between species.

Hinde thinks that the fighting drive is much more strongly activated than the fleeing drive in interspecific skirmishes of tits, and that in order to activate both drives to approximately equal levels the particular stimulus conformation presented by conspecific individuals is required. Thus displays such as "head up" (analogous to icterid bill-tilt), which seem to depend on such an equilibrium between the two drives, do not appear in encounters between species. The fleeing or withdrawal tendency is noted often in Red-wings engaging in interspecific encounters with grackles; its activation (perhaps due to the resemblance of the grackle stimulus configuration to that of the Red-wing), interacting with the predominating attack tendency, may create the "equilibrium" necessary for such displays as bill-tilting to appear.

In discussing the nature of the responses of Song Sparrows (*Melospiza melodia*) to other species on their territories, Nice (1943) noted an increasing tolerance of specific intruders after an initial period of aggressiveness, and suggested that this was the result of a habituation of the aggressive impulse after repeated exercise on a harmless visitor. The decrease in frequency or intensity of Red-wing responses to grackles with seasonal advancement (Figure 5) could be the result of seasonal variations in aggressiveness rather than an indication of habituation. It is perhaps worth noting, however, that two banded Red-wing males, residents on the marsh in former years and thus birds with "previous experience" with grackles, were among the least aggressive to intruding grackles. Orians and Collier (1963: 454) have noted that aggressive responses of male Red-wings to Tricolored Blackbirds (*Agelaius tricolor*) invading their territories were intense but ineffectual, and gradually subsided.

Habituation would seem to be selectively disadvantageous when interspecific ecological competition was intense and where environmental resources were limited, but could be advantageous in so far as it reduced distractions to nesting activity as visualized in the concept of aggressive neglect. As already noted, however, interspecific aggression may be advantageous where it operates as a dispersive or density-limiting mechanism.

ACKNOWLEDGMENTS

I wish to express appreciation to Dr. John T. Emlen (for guidance, suggestions, and timely encouragement throughout the study), to Dr. Gordon H. Orians (for suggestions on the manuscript), and to John Dallman (for helpful suggestions regarding the illustrations). The University of Wisconsin Arboretum Committee provided research facilities in the University of Wisconsin Arboretum. This study was made in partial fulfillment of the requirements for the degree of Master of Science at the University of Wisconsin, and was supported in part by a grant from the National Science Foundation. This is Journal Paper No. 62, University of Wisconsin Arboretum.

SUMMARY

During the spring and summer of 1962 and 1963 the nature and effects of behavioral interactions between Red-winged Blackbirds (*Agelaius*

phoeniceus) and Common Grackles (*Quiscalus quiscula*) were studied in a small cattail marsh at Madison, Wisconsin, where the two species nested in close association. The vegetation substrate constituted typical and apparently optimal nesting habitat for Red-wings, unusual and marginal habitat for grackles.

Most interactions between the two species were initiated by the Red-wings. Grackles were generally tolerated on the Red-wing singing perches about the edges of the marsh, but were attacked or displayed to when they penetrated the marsh, especially early in the season.

Direct attack or diving was the most common Red-wing response. Bill-tilting and song-spread (threat displays), and tail-flicking (a "disturbance" display) occurred less often. Not infrequently Red-wings made no definite counter-response to shallow penetrations of grackles into their territories, and occasionally their behavior indicated avoidance of the grackles. Female Red-wings rarely responded to grackles in the marsh unless their mates did, but on several occasions they attacked or bill-tilted to female grackles near the Red-wing nest sites.

Grackles were rarely aggressive toward Red-wings, but a few instances of interspecific display about grackle nests were observed. Grackles typically responded to Red-wing dives or threats with evasive actions or occasionally species-characteristic displays.

The presence of grackles in the marsh had no apparent effects on Red-wing courtship, nesting patterns, or nest placement, and only slight effects on Red-wing territory configuration. No predation by grackles was observed. The initiation of breeding activities by Red-wings was not observably retarded by the presence of the grackles, and breeding success was similar to that found in Red-wing colonies not exposed to grackles. Several nest failures, however, may have been due to Red-wing participation in persistent interspecific conflicts.

The aggressive behavior of Red-wings to grackles had several observable effects on grackle reproductive behavior. Grackle courtship flights and nest sites became oriented with respect to Red-wing territory edges. The pattern of nest approach by grackles was considerably modified from that seen in "normal" grackle colonies. Grackle courtship and pair formation, breeding schedules, and breeding success were apparently unaffected by Red-wing activities.

Territories of both species were to some extent mutually exclusive. Species-characteristic displays were used in interspecific as well as intraspecific territorial defense, indicating that each species produced a reasonably close approximation of the releasers of the threat displays of the other species.

LITERATURE CITED

ALLEN, A. A. 1914. The Redwinged Blackbird: a study in the ecology of a cattail marsh. Proc. Linnaean Soc. New York, **24–25:** 43–128.

ANDREW, R. J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. Ibis, **103a:** 313–348, 549–579.

BEECHER, W. J. 1942. Nesting birds and the vegetation substrate. Chicago, Chicago Ornith. Soc., 69 pp.

BEER, J. R., AND D. TIBBITTS. 1950. Nesting behavior of the Redwinged 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:** 1–549.

CASE, N. A., AND O. H. HEWITT. 1963. Nesting and productivity of the Red-winged Blackbird in relation to habitat. Living Bird, **2:** 7–20.

CROMBIE, A. C. 1947. Interspecific competition. J. Anim. Ecol., **16:** 44–73.

DAVIS, M. 1944. Purple Grackle kills English Sparrow. Auk, **61:** 139–140.

DIXON, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. Pp. 179–216 *in* Vertebrate speciation (W. F. Blair, ed.). Austin, Univ. Texas Press.

FICKEN, R. W. 1963. Courtship and agonistic behavior of the Common Grackle, *Quiscalus quiscula*. Auk, **80:** 52–72.

HAMILTON, T. H. 1962. Species relationships and adaptations for sympatry in the avian genus *Vireo*. Condor, **64:** 40–68.

HINDE, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour Suppl. 2. Leiden, E. J. Brill.

HUTCHINSON, G. E., AND R. MACARTHUR. 1959. Appendix: on the theoretical significance of aggressive neglect in interspecific competition. Amer. Nat., **93:** 133–134.

JOHNSON, N. K. 1963. Biosystematics of sibling species of flycatchers in the Empidonax hammondii-oberholseri-wrightii complex. Univ. Calif. Publs. Zoöl., **66:** 79–238.

LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publs. Nuttall Ornith. Club, No. **1:** 1–67.

MARLER, P. 1961. The evolution of visual communication. Pp. 96–121 *in* Vertebrate speciation (W. F. Blair, ed.). Austin, Univ. Texas Press.

MEANLEY, B., AND J. S. WEBB. 1963. Nesting ecology and reproductive rate of the Red-winged Blackbird in tidal marshes of the upper Chesapeake Bay region. Chesapeake Sci., **4:** 90–100.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Colls., **143(7):** 1–140.

MOYNIHAN, M. 1963. Inter-specific relations between some Andean birds. Ibis, **105:** 327–339.

NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. Wilson Bull., **68:** 5–37, 129–150.

NERO, R. W. 1963. Comparative behavior of the Yellow-headed Blackbird, Red-winged Blackbird, and other icterids. Wilson Bull., **75:** 376–413.

NICE, M. M. 1943. Studies in the life history of the Song Sparrow. II. The behavior of the Song Sparrow and other passerines. Trans. Linn. Soc. New York, **6:** 1–328.

ORIANS, G. H., AND G. COLLIER. 1963. Competition and blackbird social systems. Evolution, **17:** 449–459.

ORIANS, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. Ecology, **45**: 736–745.

PETERSEN, A., AND H. YOUNG. 1950. A nesting study of the Bronzed Grackle. Auk, **67**: 466–476.

POOR, H. 1946. Predation by grackles. Proc. Linn. Soc. New York, **54–57**: 54–55.

RAND, A. L. 1954. Social feeding behavior of birds. Fieldiana: Zoology, **36(1)**: 1–71.

RIPLEY, S. D. 1959. Competition between sunbird and honeyeater species in the Moluccan Islands. Amer. Nat., **93**: 127–132.

RIPLEY, S. D. 1961. Aggressive neglect as a factor in interspecific competition in birds. Auk, **78**: 366–371.

ROBERTS, T. S. 1932. The birds of Minnesota. Vol. 2. Minneapolis, Univ. Minn. Press.

SELANDER, R. K., AND D. R. GILLER. 1959. Interspecific relations of woodpeckers in Texas. Wilson Bull., **71**: 107–124.

SELANDER, R. K., AND D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed grackles. Condor, **63**: 29–86.

SELANDER, R. K., AND D. R. GILLER. 1963. Species limits in the woodpecker genus *Centurus* (Aves). Bull. Amer. Mus. Nat. Hist., **124**: 213–274.

SIMMONS, K. E. L. 1951. Interspecific territorialism. Ibis, **93**: 407–413.

SMITH, H. M. 1943. Size of breeding populations in relation to egg laying and reproductive success in the Eastern Red-wing (*Agelaius p. phoeniceus*). Ecology, **24**: 183–207.

SVÄRDSON, G. 1949. Competition and habitat selection in birds. Oikos, **1**: 157–174.

TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. Trans. Linn. Soc. New York, **5**: 1–95.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull., **60**: 6–51.

UDVARDY, M. D. F. 1951. The significance of interspecific competition in bird life. Oikos, **3**: 98–123.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. New York, Hafner.

YOUNG, H. 1963. Age-specific mortality in the eggs and nestlings of blackbirds. Auk, **80**: 145–155.

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