REPRINT FROM
Calif. Fish and Game, 64(4) : 255-267 1978.

FOOD SELECTION BY FIVE SYMPATRIC CALIFORNIA BLACKBIRD SPECIES [1]

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The percent volume of food items in stomachs and esophagi was tabulated for 875 adult and subadult blackbirds of five species (tricolored blackbird, *Agelaius tricolor;* red-winged blackbird, *A. phoeniceus;* yellow-headed blackbird, *Xanthocephalus xanthocephalus;* brown-headed cowbird, *Molothrus ater;* and Brewer's blackbird, *Euphagus cyanocephalus*) collected in the Sacramento Valley, California, 1967–72. Seeds of cultivated grains, chiefly rice (*Oryza sativa*), made up 24% to 54% of the annual diet of all species. Rice was eaten more than any other food by red-winged (43.7%), yellow-headed (38.0%), and tricolored blackbirds (37.8%). Water grass (*Echinochloa* spp) was the primary food of brown-headed cowbirds (45.9%), and wild oats (*Avena* spp) the primary food of Brewer's blackbirds (17.6%). Insects were eaten most in the spring and summer and made up 3 to 24% of the annual diet.

Statistical comparisons of percent volume for 11 major food classes (treating stomachs and esophagi separately) revealed many significant ($p \leq .05$) differences in food selection among species. Similar comparisons for six food classes also showed some significant differences among tricolor and red-wing sex and age classes. The differences among species and between sexes are likely related to differences in bill size and structure, which affect the size of seeds that can be handled efficiently and the ease of catching insects. The differences between adults and subadults are likely related to difference in feeding experience. The use of rice by red-wings and Brewer's has increased greatly since 1900 and 1931, mainly because of changes in crop acreages and continued conversion of marshes and fields to agricultural uses.

INTRODUCTION

Many agricultural damage problems by blackbirds involve several different species that often feed together in mixed flocks. Biologists generally recognize that not all blackbird species, or even all sex and age classes within a species, contribute equally to damage, but no detailed analysis has been made of the relative importance of these various groups for specific damage situations.

From 1964 through 1974, personnel of the U.S. Fish and Wildlife Service studied blackbird damage to rice in the Sacramento Valley of California. The problem is complex because five species (eight subspecies) of blackbirds are present, as resident and migrant populations, during the fall damage season: the tricolored blackbird, red-winged blackbird (*A. p. californicus, A. p. caurinus,* and *A. p. nevadensis*), yellow-headed blackbird, brown-headed cowbird (*M. a. artemisiae* and *M. a. obscurus*), and Brewer's blackbird.

Very little has been published on the foods of tricolored blackbirds, brown-headed cowbirds, and yellow-headed blackbirds in California, and food habits studies of red-winged and Brewer's blackbirds in California by Beal (1900), Bryant (1912), Soriano (1931), and others were done before the era of intensive rice culture. Studies were started in the fall of 1967 to determine the food of each blackbird species during the fall damage season and were later expanded to

[1] Accepted for publication June 1978.
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include all seasons. This paper summarizes the seasonal and annual foods of adults and flying young of all five species and examines differences in food selection among species and between tricolor and redwing sex and age classes. Data we gathered on the food of nestling tricolors have been reported elsewhere (Crase and DeHaven 1977).

STUDY AREA

Blackbirds were collected in Colusa, Glenn, and Butte counties, the major rice-growing areas of the Sacramento Valley. This area is intensively farmed. Rice is the primary crop, but grain sorghum (*Sorghum vulgare*), safflower (*Carthamus tinctorius*), barley (*Hordeum vulgare*), wheat (*Triticum aestivum*), and fruit and nut crops are also grown. Four wildlife refuges provide areas of natural marsh for nesting and roosting and also contain fields of rice and water grass grown to reduce waterfowl damage on nearby non-refuge lands. Several private gun clubs maintain areas of natural marsh. The Sacramento River, numerous irrigation canels, drainage ditches, and sinks provide additional semi-natural marsh habitat for blackbirds.

METHODS

About 80% of the 875 birds used for this study were shot at random from evening flightlines into major communal roosts or in adjacent staging areas. The remaining 20% were shot in loafing and breeding areas during spring when the birds do not congregate into large roosts. Birds were taken on 74 different days from September 1967 through June 1972 (averaging 11.8 birds/day) and during all months of the year. Each sample was frozen as soon as possible, usually within 2 hours of collection. For examination, each bird was thawed and dissected, and the contents of each esophagus and stomach (gizzard and proventriculus) were washed, assigned a number, air dried on blotter paper, and examined under low magnification. Food items were identified and segregated into piles, and the precentage of the total volume of each item was visually estimated.

To examine food selection differences statistically, annual volume percentages for major food groups were compared among species and between sex and age classes for tricolors and red-wings. Comparisons were made by single-classification analyses of variance on arcsin-transformed data, and the means separated by Duncan's new multiple-range test; $p \leq 0.05$ was accepted as significant. For the among species comparison, each species was compared separately with every other species (10 species pairs) for each food item; the esophagi and stomachs were treated separately to remove digestion rates and percentage of empty esophagi as variables in the comparison. Eleven food classes were compared for stomach contents, and 10 for esophageal contents (esophageal grit could not be meaningfully compared); thus, 21 tests for food selection differences were made for each species pair. For the comparisons between sex and between age for tricolors and red-wings, the same tests were made for six food classes except that esophageal and stomach data were combined.

RESULTS

Plant Foods

Rice was an important food for all five blackbird species. In terms of volume, it ranked first in the annual diet of red-wings, yellow-heads, and tricolors, second in the diet of cowbirds, and third in the diet of Brewer's (Table 1). Generally, rice consumption was highest during the fall when maturing fields provided a super-abundant food source, but large amounts also were eaten during the winter when it was available as waste in harvested fields.

Water grass seed was the next most important blackbird food. It was eaten more than any other item by brown-headed cowbirds and was second in importance for red-wings, tricolors, yellow-heads, and Brewer's. Although the volume of water grass eaten was usually less than that of rice, the number of seeds taken was greater because rice seeds are four to five times larger than water grass seeds.

Seeds of cultivated grains (including rice) made up about one-half of the total annual food volume of red-wings, yellow-heads, and tricolors, one-third of the food of cowbirds, and less than one-fourth of the food of Brewer's blackbirds. Of these grains, sorghum was second in volume after rice and was eaten in similar percentages by all five species. Safflower, wheat, and cultivated oats were also eaten, but in relatively small amounts. The esophagi contained higher percentages of cultivated grains than did the stomachs. This may reflect some differential digestion (see Discussion), but, because most of our collections were from incoming flightlines to roosts, it may also be the result of the birds "filling up" on readily available food just before roosting.

Wild oats, a common weed along roads and ditches and in fallow fields, ranked first in the annual diet of Brewer's blackbirds. Oats were over 5% of the diet of tricolors but were found in only small amounts, or were absent, in red-wings, yellow-heads, and cowbirds.

Other wild seeds were eaten in small amounts by all species. Smartweed (*Polygonum* spp), pigweed (*Amaranthus* spp), filaree (*Erodium* spp), and Johnson grass (*Sorghum halepense)* were the most common, but Bermuda grass (*Cynodon dactylon)*, switch grass (*Panicum* spp), catchfly (*Silene* spp), bulrush (*Scirpus* spp), canary grass (*Phalaris* spp), and sprangletop (*Lepthochloa* spp) were also eaten.

Animal Foods

Insects made up most of the animal food of all species. Beetles (Coleoptera) were the main insect food of Brewer's, tricolors, and red-wings, whereas miscellaneous adult insects ranked highest for cowbirds and yellow-heads. Ground-dwelling beetles (Carabidae, Tenebrionidae, and Chrysomelidae) and water beetle larvae (Hydrophilidae) were the most important insect food of tricolors and red-wings, and ground-dwelling beetles and weevils (Curculionidae) were the insects eaten in the largest volumes by Brewer's. These beetle groups were also the primary food of tricolor nestlings from the same general area (Crase and DeHaven 1977). Brewer's blackbirds ate a much larger volume of grasshoppers and crickets (Orthoptera) than did the other four species. Generally, insects were eaten most abundantly during the spring and early summer, the blackbird breeding season. Hintz and Dyer (1970) have suggested that increased insect consumption by adult red-wings during the breeding season was related to both the increased availability of insects and the limited foraging time available to obtain their required energy (due to the demands of breeding activity).

TABLE 1. Percent Volume of Foods Found in the Esophagi and Stomachs of Five California Blackbird Species in Winter (Dec-Feb), Spring (Mar-May), Summer (Jun-Aug), and Fall (Sep-Nov). (Sample sizes are given in parenthesis.)

	Tricolored blackbird					*Red-winged blackbird*					*Brown-headed cowbird*				
Food Item	*Win. (37)*	*Spr. (35)*	*Sum. (90)*	*Fall (105)*	*Annu. (267)*	*Win. (100)*	*Spr. (99)*	*Sum. (16)*	*Fall (168)*	*Annu. (384)*	*Win. (29)*	*Spr. (38)*	*Sum. (43)*	*Fall (20)*	*Annu. (130)*
Rice	37.4	47.9	16.8	49.1	37.8	48.4	25.7	36.1	64.5	43.7	49.3	28.4	3.4	21.6	25.7
Sorghum	8.4	0.9	11.9	9.0	7.6	18.3	1.2	12.0	3.3	8.7	8.6	0.7	18.7	2.1	7.5
Safflower	0.0	0.0	1.6	2.3	1.0	0.0	4.0	0.0	1.8	1.4	0.0	0.0	0.0	0.6	0.2
Wheat	7.2	0.0	0.4	0.0	1.9	0.0	1.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Other grain	0.0	0.0	0.0	2.4	0.6	0.0	0.0	0.0	T	T	0.0	0.0	0.0	0.0	0.0
Oats	10.6	0.0	9.1	1.7	5.4	0.9	6.4	0.0	T	1.8	0.2	0.2	0.0	0.8	0.3
Water grass	22.1	13.4	12.2	21.7	17.4	16.9	26.5	37.3	18.7	24.8	33.2	23.5	62.0	65.0	45.9
Smartweed	1.0	0.4	0.8	2.4	1.2	1.5	1.1	0.6	3.2	1.6	1.6	0.7	5.6	1.0	2.2
Pigweed	0.0	T	0.0	0.5	0.2	0.0	T	0.0	0.0	T	0.0	0.0	0.0	0.0	0.0
Johnson grass	0.0	0.0	2.3	0.6	0.7	0.1	0.1	0.0	0.2	0.1	0.4	0.0	0.4	0.0	0.2
Other wild seeds	1.7	2.6	1.1	1.4	1.7	0.6	6.2	0.6	1.9	2.3	2.2	26.7	1.5	1.8	8.0
Misc. plant	0.0	T	T	T	T	0.0	0.0	0.0	T	T	0.0	0.1	0.0	0.0	T
Total cultivated grain	53.0	48.8	30.3	62.7	48.7	66.7	32.1	48.1	69.6	54.1	57.8	29.2	22.1	24.3	33.4
Total wild seed	35.4	16.5	25.6	28.4	26.5	20.1	40.4	38.5	24.1	30.1	37.7	51.1	69.5	68.6	56.7
Total plant	88.4	65.3	55.9	91.1	75.2	86.8	72.5	86.6	93.7	84.9	95.5	80.3	91.6	92.9	90.1
Coleoptera															
Ground beetles	2.4	9.7	6.1	1.8	5.0	1.7	6.1	1.1	0.4	2.3	0.4	1.8	0.6	0.4	0.8
Weevils	0.5	2.5	0.3	0.2	0.9	0.2	2.4	0.0	0.1	0.7	0.0	0.3	0.0	0.0	T
Water beetles															
Adults	0.2	0.4	0.2	0.0	0.2	0.0	0.4	0.0	0.0	0.1	0.0	0.4	0.0	0.1	0.1
Larvae	0.0	6.5	18.6	0.1	6.3	0.0	1.3	5.8	0.0	1.8	0.0	0.2	0.0	0.0	T
Orthoptera	0.0	1.9	5.6	0.5	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	T
Diptera	0.3	0.3	0.2	0.2	0.2	0.6	1.1	0.0	0.3	0.5	T	0.4	0.0	0.0	0.1
Hemiptera	0.0	0.2	0.6	0.2	0.2	0.1	T	0.6	0.2	0.2	0.0	0.0	0.0	0.4	0.1
Misc. insects															
Adults	0.2	0.8	3.0	3.3	1.8	0.4	0.8	1.4	3.0	1.4	T	0.8	1.8	3.0	1.4
Larvae	0.2	1.6	3.4	0.5	1.4	0.2	4.7	1.6	0.1	1.6	0.0	0.9	0.0	0.1	0.2
Arachnida	0.0	2.1	1.0	0.3	0.8	0.5	0.1	0.7	0.3	0.4	0.1	0.0	0.0	0.1	T

TABLE 1—*Continued*

Mollusca	0.0	0.2	0.2	0.2	0.2	0.0	T	0.0	0.1	T	0.0	0.2	0.0	0.3	0.1
Misc. animal	0.4	1.7	T	T	0.6	0.6	0.2	0.0	T	0.2	0.0	0.0	0.0	0.0	0.0
Total beetles	3.0	19.1	25.3	2.1	12.4	1.9	10.2	6.9	0.5	4.9	0.4	2.7	0.6	0.6	1.1
Total insects	3.8	23.9	38.1	6.9	18.2	3.2	16.9	10.5	4.0	8.6	0.5	4.9	2.6	4.1	3.0
Total animal	4.2	27.9	39.3	7.5	19.7	4.4	17.3	11.1	4.4	9.3	0.6	5.2	2.6	4.5	3.2
Grit	7.4	6.6	4.5	1.4	5.0	8.8	10.2	2.4	2.1	5.9	4.1	14.5	5.7	1.8	6.5

	Yellow-headed blackbird					Brewer's blackbird				
Food item	*Win. (0)*	*Spr. (12)*	*Sum. (2)*	*Fall (10)*	*Annu. (24)*	*Win. (23)*	*Spr. (19)*	*Sum. (4)*	*Fall (24)*	*Annu. (70)*
Rice	—	80.6	0.0	35.5	38.0	20.0	11.9	0.0	26.2	14.5
Sorghum	—	0.0	3.0	31.3	11.4	26.0	0.5	0.0	2.8	7.3
Safflower	—	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.9	0.4
Wheat	—	0.0	0.0	0.0	0.0	0.0	3.3	0.0	3.1	1.6
Other grain	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oats	—	0.0	0.0	0.0	0.0	2.7	25.3	36.0	6.5	17.6
Water grass	—	7.8	76.3	16.4	33.5	15.1	15.9	8.8	27.5	16.8
Smartweed	—	0.1	0.0	4.2	1.4	0.2	0.0	0.0	0.9	0.3
Pigweed	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	T	T
Johnson grass	—	0.0	0.0	5.2	1.7	1.3	0.0	0.0	0.5	0.4
Other wild seeds	—	0.2	0.0	T	T	2.6	10.0	3.5	2.5	4.6
Misc. plant	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total cultivated grain	—	80.6	3.0	64.7	49.4	46.0	16.7	0.0	32.9	23.9
Total wild seed	—	8.0	76.3	25.8	36.7	21.9	51.3	48.3	38.0	39.9
Total plant	—	88.6	79.3	90.5	86.1	67.9	68.0	48.3	70.9	63.8
Coleoptera										
Ground beetles	—	0.3	0.3	0.0	0.2	6.0	14.7	13.8	8.0	10.6
Weevils	—	0.0	0.0	0.2	T	0.0	2.8	5.0	1.1	2.2
Water beetles										
Adults	—	0.4	0.0	0.0	0.1	0.0	0.2	0.0	0.0	T
Larvae	—	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.3
Orthoptera	—	0.0	0.0	0.0	0.0	0.0	0.0	23.8	2.6	6.6

TABLE 1.—*Continued*

Food item	Yellow-headed blackbird *Win. (0)*	*Spr. (12)*	*Sum. (2)*	*Fall (10)*	*Annu. (24)*	Brewer's blackbird *Win. (23)*	*Spr. (19)*	*Sum. (4)*	*Fall (24)*	*Annu. (70)*
Diptera	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.5
Hemiptera	—	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.6
Misc. insects										
Adults	—	0.0	20.0	6.9	9.0	T	0.3	0.0	10.6	2.8
Larvae	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arachnida	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mollusca	—	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.2	0.2
Misc. animal	—	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.3
Total beetles	—	0.6	0.3	0.2	0.4	6.0	18.9	18.8	9.0	13.2
Total insects	—	0.6	20.3	7.2	9.4	6.1	21.5	42.6	24.5	23.7
Total animal	—	0.6	20.3	7.2	9.4	7.8	21.5	42.6	24.6	24.1
Grit	—	10.2	0.0	2.0	4.1	23.9	10.7	9.2	3.7	11.9

Grit

Mineral grit was about 5% of the total food volume for all species except Brewer's, for which it was about 12%. The figure for Brewer's is probably an overestimate of actual intake because 89% of the esophagi for this species were empty (see Discussion). Grit intake for all species was generally highest during the spring and lowest during the fall. This contrasts with the findings of Bird and Smith (1964) and Mott et al. (1972), who found that the least amount of mineral grit was picked up when insects were a large portion of the diet.

Species Differences

In the examination of food selection differences among blackbird species, the number of significant differences between species pairs ranged from 1 (5%) to 19 (90%) (Figure 1). Only one food class, grain sorghum, did not show at least one significant difference among species (Table 2).

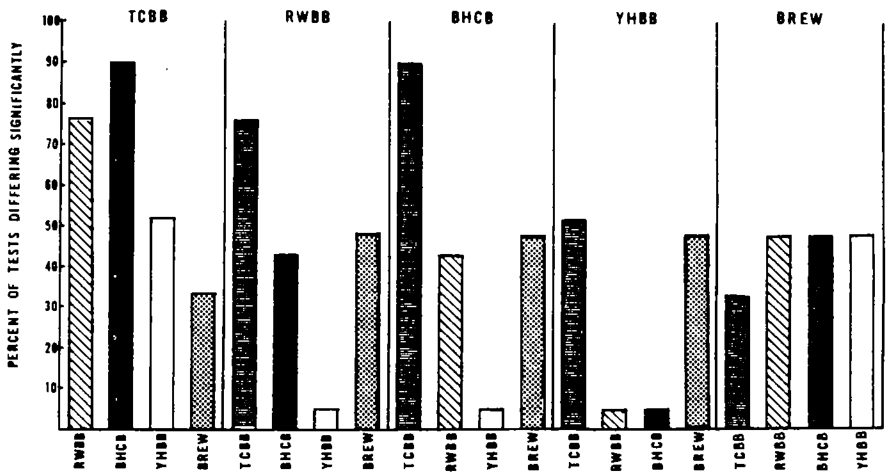

FIGURE 1. Differential consumption of 11 food classes, testing esophageal and stomach contents separately (21 tests), by five blackbird species in the Sacramento Valley, California; TCBB = tricolored blackbird, RWBB = red-winged blackbird, BHCB = brown-headed cowbird, YHBB = yellow-headed blackbird, BREW = Brewer's blackbird.

Considering some of the unavoidably small sample sizes for some of the comparisons, it appears that the Brewer's and tricolor are most alike in their food habits, and their food habits in turn differ most from that of the cowbird. The tricolor and red-wing showed a large difference in food selection considering their close phylogenetic relationship. The few statistical differences between yellow-heads and the other four species are probably partly due to the small sample size for this species. Likewise, the large number of empty Brewer's esophagi may have affected the number of significant differences between this and the other species. At any rate, each species apparently has its own pattern of utilizing the available food supply.

TABLE 2. Differences in Consumption of Major Food Items (percent of total annual volume in the esophagi and stomachs) Among Five California Blackbird Species.*

Food Item	*Tricolored blackbird*	*Red-winged blackbird*	*Brown-headed blackbird*	*Yellow-headed blackbird*	*Brewer's blackbird*
		Esophagus			
N =	(173)	(294)	(96)	(21)	(8)
Rice	43.0^{a}	55.2^{b}	30.5^{c}	47.7^{b}	22.8^{c}
Grain sorghum	9.6^{a}	8.8^{a}	9.2^{a}	14.4^{a}	16.5^{a}
Oats	5.0^{a}	2.1^{b}	0.3^{b}	0.0	5.8^{ab}
Water grass	12.4^{a}	19.8^{b}	43.2^{c}	34.7^{ab}	5.4^{ab}
Cultivated grains	57.1^{a}	66.5^{b}	40.0^{c}	62.1^{d}	39.3^{abc}
Wild seeds	19.9^{a}	24.8^{a}	55.7^{b}	36.7^{a}	13.1^{a}
Plant matter	77.0^{a}	91.3^{b}	95.7^{b}	98.8^{b}	52.4^{a}
Ground-dwelling beetles	3.0^{a}	1.1^{b}	0.4^{b}	0.0	2.5^{ab}
All beetles	13.6^{a}	1.8^{b}	0.5^{b}	0.3^{b}	6.9^{ab}
All insects	19.6^{a}	7.5^{b}	2.9^{b}	0.5^{b}	22.4^{a}
		Stomach			
N =	(267)	(384)	(130)	(21)	(70)
Rice	34.0^{x}	35.7^{y}	22.0^{z}	29.3^{xy}	13.6^{z}
Grain sorghum	6.3^{x}	8.3^{x}	6.4^{x}	8.8^{x}	6.1^{x}
Oats	5.6^{x}	1.6^{y}	0.3^{y}	0.0	17.8^{z}
Water grass	20.8^{x}	28.4^{x}	47.7^{y}	35.0^{x}	17.9^{x}
Cultivated grains	43.0^{x}	45.3^{y}	28.5^{z}	38.1^{xy}	22.5^{z}
Wild seeds	31.3^{x}	35.3^{xy}	57.7^{z}	39.3^{x}	41.6^{y}
Plant matter	74.3^{x}	80.6^{y}	86.2^{y}	77.4^{x}y	64.1^{x}
Ground-dwelling beetles	6.2^{x}	3.0^{y}	1.1^{y}	0.4^{y}	11.2^{z}
All beetles	11.9^{x}	6.7^{y}	1.5^{y}	0.5^{y}	13.5^{x}
All insects	17.6^{x}	9.4^{y}	3.0^{z}	14.5^{yz}	23.3^{x}
Grit	8.1^{x}	9.9^{x}	10.6^{x}	8.0^{xy}	13.0^{y}

* Means compared using arcsin-transformed data. Within each food item and organ, means followed by different superscript letters are significantly different ($p \leq 0.05$). Zero values cannot be compared by analysis of variance.

Sex Differences

For both tricolors and red-wings, six food classes were compared for differential selection by sex (Table 3). Both tricolor and red-wing males ate significantly more rice, cultivated grain, and plant matter than did females of the same species. The females of both species ate significantly more wild seed than did males. In addition, tricolor females ate significantly more insect matter than did tricolor males.

Age Differences

For tricolors and red-wings, differences in consumption of the same six food groups between age classes (adult vs. subadult) were less pronounced than differences among species and between sexes (Table 3). For both species, the two age classes ate almost identical percentages of rice and cultivated grain, but subadult tricolors ate significantly more wild seed and significantly less insect matter than did adults. For red-wings, there were no significant differences between adults and subadults in consumption of wild seed, plant matter, beetles, or insect matter.

TABLE 3. Sex and Age Differences in the Consumption of Selected Food Items (percent of total annual volume, esophagi and stomachs combined) by Tricolored and Red-winged Blackbirds.

Food item	*Sex*				*Age*			
	Tricolored blackbird		*Red-winged blackbird*		*Tricolored blackbird*		*Red-winged blackbird*	
	Male	*Female*	*Male*	*Female*	*Adult*	*Subadult*	*Adult*	*Subadult*
N =	(143)	(124)	(230)	(154)	(224)	(43)	(329)	(55)
Rice	47.6^{a}	28.0^{b}	49.5^{x}	37.8^{y}	38.1^{a}	37.5^{a}	43.8^{x}	43.6^{x}
Cultivated grain	58.4^{a}	38.0^{b}	62.0^{x}	46.2^{y}	48.4^{a}	49.0^{a}	54.3^{x}	53.9^{x}
Wild seeds	22.3^{a}	30.7^{b}	26.2^{x}	35.4^{y}	18.8^{a}	34.2^{b}	29.2^{x}	32.4^{x}
Plant matter	79.4^{a}	71.0^{b}	87.7^{x}	82.1^{y}	65.2^{a}	85.2^{b}	83.4^{x}	86.2^{x}
Beetles	10.8^{a}	13.0^{a}	4.1^{x}	5.7^{x}	20.0^{a}	4.8^{b}	5.4^{x}	4.4^{x}
All insects	15.6^{a}	20.8^{b}	7.6^{x}	9.6^{x}	27.7^{a}	8.7^{b}	8.7^{x}	8.5^{x}

• Means compared using arcsin-transformed data. Within each food item and sex or age class, means followed by different superscript letters are significantly different ($p \leq 0.05$).

DISCUSSION

Potential Sources of Bias

Bartonek and Hickey (1969), Dirschel (1969), and Swanson and Bartonek (1970) have shown differences in the food composition of esophagi and gizzards in several species of waterfowl, mostly because of differential retention rates of hard and soft food items. Moreover, Beer and Tidyman (1942) showed that gallinaceous birds use small, hard seeds as grit and Mott et al. (1972) suggested that hard parts of insects (e.g., beetle mandibles) may also function as grit in the gizzards of blackbirds.

In view of these findings, we conducted laboratory tests with tricolors and found that relatively soft cultivated grains (rice and sorghum) are fully digested within 2 to 4 hr, whereas harder wild seeds, such as water grass, are only about 50% digested at 8 hr. Small, very hard seeds of species such as smartweed remain completely undigested after 12 hr. Swanson and Bartonek (1970) recommended that only esophageal contents be used in avian food habits studies. Such a method would be impractical for blackbirds because they feed in many different habitats and locations and may consume different foods at different times of the day (Willson 1966). Esophageal contents in our study would largely reflect only those foods eaten just before the birds entered the roost. Stomach contents, on the other hand, would reflect the foods eaten earlier in the day but would contain unrepresentative percentages of those most resistant to digestion.

In calculating the aggregate percent volume of foods eaten for Table 1, we tried to lessen the above sources of bias associated with single-organ analyses by averaging the esophageal and stomach contents together for each bird whose esophagus contained food (all stomachs contained food). The resulting data contain a slight to moderate bias toward stomach contents for each species depending upon the proportion of birds with empty esophagi, but the bias is less than with a single-organ analysis. For tricolors, red-wings, cowbirds, and yellowheads, 65, 77, 74, and 88% of the birds, respectively, had food in the esophagus. Only 11% of the Brewer's blackbirds had food in the esophagus, however, so the data for this species are the most heavily weighted toward stomach contents.

Differential Food Selection

Lack (1954, 1966), Kear (1962), and Schoener (1965) have found that closely related species of birds occupying the same area generally rely on different foods. However, the presence of a super-abundant food supply can mask the feeding differentiation evolved in natural systems (Lack 1954). Brown (1969) has aptly pointed out that the food of wild birds is a compromise between what they prefer and what is available.

In the Sacramento Valley, rice is a super-abundant food for much of the year. In addition to thousands of acres of ripening rice available during late summer and fall, large amounts of waste rice are available in fields during the winter and perhaps into spring. Wild-growing blackbird foods, particularly water grass, are kept at a minimum by the combination of rice monoculture and intensive agricultural weed control programs. It is not surprising, therefore, to find rice as a prominent food in the diet of blackbirds in the area. What is surprising is the large amount of water grass eaten. It appears that cowbirds, and to a lesser extent the other four species, must preferentially select or search for water grass for it to be such a large portion of the annual diet. Despite the abundance of cultivated grains, the many significant differences in food consumption show that the five blackbird species have maintained a large degree of differential food selection. Thus, it appears that mechanisms evolved in natural systems to subdivide the food subniche are still operative, to some degree, in the agricultural environments created by modern man.

The actual mechanisms of feeding differences among bird species have been shown to be related primarily to differences in bill size (which is related to body size) and bill structure, which affect the size of seeds that can be handled efficiently and the ease of catching insects (Kear 1962; Hespenheide 1966; Newton 1967, 1973; Brown 1969; Willson 1971, 1972; Willson and Harmeson 1973). Differences in bill structure and size exist among all five blackbird species we studied and, therefore, offer the best explanation of their feeding differences. The finch-like bill of cowbirds is the most adapted for seed eating, and the longer, thinner bills of red-wings, tricolors, and Brewer's blackbirds are more generalized for some insect gathering (Beecher 1951). Hence, cowbirds ate higher percentages of seeds and fewer insects than did these other three species. Even among congeneric species, bill structure apparently influences the diet. The tricolor has a longer and thinner bill than that of the closely related red-wing (Davis 1954, Orians 1961) and ate more insects than did the latter species. In addition to structure differences, the bills of yellow-heads and red-wings are larger than those of tricolors and Brewer's, whose bills are larger than the cowbirds'. Thus, the cowbird may select more water grass than would the other four species simply because the small water grass seeds are easier for it to handle than the larger seeds of the cultivated grains.

Bill structure and size may also influence the feeding habits of tricolor and red-wing sexes. Selander (1966) found that sex-related feeding differences in woodpeckers (*Centurus* spp) were due to sexual dimorphism of the feeding apparatus. In the tricolor and red-wing, females are smaller than males and have smaller bills (Davis 1954, Orians 1961). This may explain why females ate significantly more of the small wild seeds, and males more of the larger cultivated grains.

Differential habitat utilization may also account for some of the feeding differences among species and between sexes. Brewer's blackbirds, in particular, are often found loafing and feeding along roadsides and other waste areas, whereas the other four species are most often found in mixed-species flocks near fields, marshes, or riparian situations. In addition, flock segregation by sex, which has been reported at various seasons for yellow-heads (Willson 1966, Crase and DeHaven 1972), red-wings (Meanley 1961, Orians 1961), tricolors (DeHaven et al. 1975), and Brewer's (Bent 1958), may increase intersexual feeding differences if the male and female flocks, with their different bill sizes, forage in different habitats.

Differences in size of bird and structure of bill do not adequately explain the differential consumption of wild seeds and insects by subadult and adult tricolors because the bill and other structures are generally full grown in passerines by the fall and winter months (Marshall 1948, Power 1970). Brown (1969) suggested that young birds may inherit the ability to recognize food by certain cues, such as seed color, size, and shape. However, such instinctual responses could be modified by experience with other available foods (Newton 1973). Therefore, young tricolors might recognize certain wild seeds as food but would have to learn to eat the larger, cultivated grains. Proficiency in catching insects might also be learned in that the more experienced an individual becomes, the more adept he would be at successfully securing a food item that attempts escape.

Relationship To Agriculture

Our study shows changes in the diet of California's red-winged blackbirds since earlier studies by Beal (1900) and Soriano (1931). They reported more wheat and oats than we found; Beal did not mention rice and Soriano found only small amounts. Beal also found a higher proportion of animal matter than we did, but Soriano's figures were similar to ours.

Three factors likely account for most of these differences. First, the acreages of the various grain crops have changed considerably. There was no cultivated rice in California during Beal's studies in the late 1800's, and fewer than 40,500 ha (100,000 acres) in the 1930's. Rice is now one of the dominant grains in the Sacramento Valley (Johnston and Dean 1969). Second, there have been continuing drainage and destruction of natural marsh areas, thereby reducing the availability of native marsh foods. And last, the birds examined by Beal and Soriano were from a larger geographic area and more varied habitats than were the birds we examined.

The diet of Brewer's blackbirds in California as reported by Soriano (1931) was not as strikingly different from our data as that of the red-wing. We found less wheat and filaree but more rice and water grass than did Soriano. Again, differences in study areas and changes in agriculture probably account for most of these differences.

Neff and Meanley (1957) and Meanley (1971) studied the foods of red-wings and cowbirds in a situation similar to ours—the rice fields of Arkansas and Louisiana. Rice was 45% of the red-wing's annual diet in Arkansas and 67% in Louisiana. These proportions are similar to those we found for California red-wings. However, rice was 46% of the brown-headed cowbird's annual diet in Arkansas versus only 26% of our study.

The feeding differences between blackbirds of different species, sexes, and ages mean that some groups are more responsible for agricultural damage than others. Although we were primarily concerned with rice damage, the feeding differences that we found likely exist in many, if not all, damage situations. Mott et al. (1972), for example, found that red-wing males were responsible for more corn damage in South Dakota than were females. However, selective control of only the "damaging" groups would be practically impossible. Chemical repellents such as methiocarb (Mesurol ®) (DeHaven et al. 1971, Guarino 1972, Crase and DeHaven 1976) offer the most promising method of safely protecting crops. Since they simply render the crop unpalatable, they do not harm those birds not causing damage and those that may actually be helping the farmer by consuming large numbers of insects throughout much of the year.

ACKNOWLEDGMENTS

We thank W. Harry Lange and Lynn J. Shaw, University of California, Davis, for help in the identification of insects and in the computer analysis of the data, respectively. Bruce M. Browning, California Department of Fish and Game, identified many of the seeds. We also thank co-workers Richard R. West, Paul P. Woronecki, Joseph L. Guarino, Willis C. Royall, Jr., Jerome F. Besser, and Ann H. Jones for help during various phases of the project.

REFERENCES

Bartonek, J. C., and J. J. Hickey. 1969. Food habits of canvasbacks, redheads, and lesser scaup in Manitoba. Condor 71(3): 280–290.

Beal, F.E.L. 1900. Food of the bobolink, blackbirds, and grackles. U.S. Dept. of Agr., Biol. Surv. Bull. No. 13. 77p.

Beecher, W. J. 1951. Adaptations for food-getting in the American blackbirds. Auk 68(4): 411–440.

Beer, J., and W. Tidyman. 1942. The substitution of hard seeds for grit. J. Wildl. Manage. 6(1): 70–82.

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Nat. Mus., Bull. 211. 549p.

Bird, R.D., and L. B. Smith. 1964. The food habits of the red-winged blackbird, *Agelaius phoeniceus,* in Manitoba. Can. Field-Natur. 78(3): 179–186.

Brown, R.G.B. 1969. Seed selection by pigeons. Behavior 34(3): 115–131.

Bryant, H. C. 1912. Birds in relation to a grasshopper outbreak in California. Univ. Calif. Publ. Zool. 11(1): 1–20.

Crase, F. T., and R. W. DeHaven. 1972. Current breeding status of the yellow-headed blackbird in California. Calif. Birds 3(2): 39–42.

———. 1976. Methiocarb: Its current status as a bird repellent. Proc. 7th Vert. Pest Cont. Conf., Monterey, California. March 9–11. pp. 46–50.

———. 1977. Food of nestling tricolored blackbirds. Condor 79(2): 265–269.

Davis, J. 1954. Seasonal changes in bill length of certain passerine birds. Condor 56(3): 142–149.

DeHaven, R. W., F. T. Crase, and P. P. Woronecki. 1975. Breeding status of the tricolored blackbird, 1969–72. Calif. Fish Game 61(4): 166–180.

DeHaven, R. W., J. L. Guarino, F. T. Crase, and E. W. Schafer, Jr. 1971. Methiocarb for repelling blackbirds from ripening rice. Int. Rice Comm. Newsletter 20(4): 25–30.

Dirschel, H. J. 1969. Foods of lesser scaup and blue-winged teal in the Saskatchewan River Delta. J. Wildl. Manage. 33(1): 77–87.

Guarino, J. L. 1972. Methiocarb, a chemical bird repellent: a review of its effectiveness on crops. Proc. 5th Vert. Pest Cont. Conf., Fresno, California. March 7-9. pp. 108–111.

Hespenheide, H. A. 1966. The selection of seed size by finches. Wilson Bull. 78(2): 191–197.

Hintz, J. V., and M. I. Dyer. 1970. Daily rhythm and seasonal change in the summer diet of adult red-winged blackbirds. J. Wildl. Manage. 34(4): 789–799.

Johnston, W. E., and G. W. Dean. 1969. California crop trends: yields, acreages, and production areas. Univ. Calif. Agr. Exper. Sta., Ext. Service Circ. 551. 126p.

Kear, J. 1962. Food selection in finches with special reference to interspecific differences. Proc. Zool. Soc. London 138: 163–204.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London. 343p.

———. 1966. Population studies of birds. Oxford Univ. Press, London. 341p.

Marshall, J. T., Jr. 1948. Ecologic races of song sparrows in the San Francisco Bay region. Part II. Geographic variation. Condor 50(6): 233–256.

Meanley, B. 1961. Late-summer food of red-winged blackbirds in a fresh tidal-river marsh. Wilson Bull. 73(1): 36–40.

———. 1971. Blackbirds and the southern rice crop. U.S. Fish and Wildl. Service, Resource Publ. 100. 64p.

Mott, D. F., R. R. West, J. W. DeGrazio, and J. L. Guarino. 1972. Foods of the red-winged blackbird in Brown County, South Dakota. J. Wildl. Manage. 36(3): 983–987.

Neff, J. A., and B. Meanley. 1957. Blackbirds and the Arkansas rice crop. Arkansas Agr. Exper. Sta., Bull. No. 584. 89p.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109(1): 33–98.

———. 1973. Finches. Taplinger Publ. Co., New York. 288 p.

Orians, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr. 31(3): 285–312.

Power, D. M. 1970. Geographic variation of red-winged blackbirds in central North America. Univ. Kansas Mus. Natur. Hist. 19(1): 1–83.

Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19(2): 189–213.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68(2): 113–151.

Soriano, P. S. 1931. Food habits and economic status of the Brewer and red-winged blackbirds. Calif. Fish Game 17(4): 361–395.

Swanson, G. A., and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of blue-winged teal. J. Wildl. Manage. 34(4): 739–746.

Willson, M. F. 1966. Breeding ecology of the yellow-headed blackbird. Ecol. Monogr. 36(1): 51–77.

———. 1971. Seed selection in some North American finches. Condor 73(4): 415–429.

———. 1972. Seed size preference in finches. Wilson Bull. 84(4): 449–455.

Willson, M. F., and J. C. Harmeson. 1973. Seed preferences and digestive efficiency of cardinals and song sparrows. Condor 75(2): 225–234.

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