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FOOD OF NESTLING TRICOLORED BLACKBIRDS

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Information on the food of nestling Tricolored Blackbirds (*Agelaius tricolor*), a colonial breeding species largely endemic to California, has been recorded for only a few scattered colonies and not in much detail. Tyler (1907) reported that adult Tricolored Blackbirds at a colony near Fresno, Fresno Co., gathered a "short, heavy worm" to feed their young. A few years later at a colony near Rancho Dos Rios, Stanislaus Co., Mailliard (1914) reported that milk-stage barley was "much prized as a food for the young," but he found that the stomachs of adults contained "mostly insects of several sorts (not determined), grasshoppers being largely in evidence." More recently, Payne (1969) stated that several hundred food items of nestlings from colonies near East Park Reservoir, Colusa Co., were almost entirely animal matter, one-half of which (by weight) consisted of grasshoppers; he listed other food items but did not quantify those observations.

During the breeding seasons of 1971, 1972, and 1975, we examined the stomach contents of Tricolored Blackbird nestlings from several locations within the Central Valley of California. This paper summarizes the foods of the nestlings we sampled, examines the relative importance of certain foods at different colonies, looks at the day-to-day variation of some foods at the same colony, and presents observations on the foraging behavior of adults.

METHODS

We collected 272 Tricolored Blackbird nestlings from 10 breeding colonies (nine locations) within the Central Valley: (1) Clay—1.6 km N Clay, Sacramento Co.; (2) Orland—4.8 km SW Orland, Glenn Co.; (3) Afton—3.2 km S Afton, Glenn Co.; (4) Angle Road—3.2 km ENE Herald, Sacramento Co.; (5) Butte Sink—8.0 km N Meridian, Sutter Co.; (6) Pig Farm—14.4 km SW Modesto, Stanislaus Co.; (7) Knights Landing—3.2 km N Knights Landing, Yolo Co.; (8) Folsom—2.4 km S Folsom, Sacramento Co.; and (9) Herald—0.8 km ENE Herald (table 1).

In 1971 and 1972, nestlings were taken throughout each colony at 5 ± 1 days of age, around midday (between 11:00 and 13:00), and were frozen until examination. In 1975, nestlings were collected from each colony at 3, 6, and 9 days of age, around midday, immediately injected with a 10% formalin solution, and frozen until examination. The contents of each stomach (gizzard and proventriculus) plus the negligible amount of food found in the esophagus were washed, assigned a number, air-dried on blotter paper, and examined under low magnification. Each food item was identified, segregated, and its percentage of the total volume was estimated visually. The aggregate percentage volumes (Martin et al. 1946) of selected major food items were compared among locations, and among days at the same location by single-classification analyses of variance (ANOVA) on arcsin-transformed data. Means were compared using the least significant difference (Steel and Torrie 1960); $P < 0.05$ was considered significant. Neff (1937), Orians (1961), Payne (1969), and DeHaven et al. (1975) present more complete data on breeding colony characteristics and Central Valley habitats.

In 1975 we injected 10% formalin into nestlings to prevent possible post-mortem digestion of soft food items (Dillery 1965). However, we could not detect any visual differences in the degree of preservation of food items from injected and noninjected nestlings, and the percentage volume of soft and hard food items did not differ significantly between the two types of nestlings (ANOVA; $P > 0.10$; $F = 2.54$

TABLE 1. Characteristics of 10 Tricolored Blackbird breeding colonies in the Central Valley, California.

Breeding colony	Date sampled	No. stomachs examined	No. breeding adults	Breeding substrate	Primary foraging substrate
Clay	27 May 1971	15	25,000	Cattail-Bulrush	Dry and irrigated pasture
Orland	15 June 1971	17	3000	Cattail	Dry grassland; creek
Afton 71	18 June 1971	35	5000	Cattail	Rice and wheat fields
Angle Road	9 May 1972	15	2500	Cattail	Dry and irrigated pasture
Butte Sink	10 May 1972	20	1000	Cattail	Dry grassland
Pig Farm	5 June 1972	30	25,000	Cattail	Dry and irrigated pasture
Knights Landing	8 June 1972	20	1500	Cattail	Ricefields
Folsom 75-3	16 May 1975	10	3000	Blackberry	Dry grassland; creek
75-6	19 May 1975	10	3000	Blackberry	Dry grassland; creek
75-9	22 May 1975	10	3000	Blackberry	Dry grassland; creek
Herald 75-3	5 June 1975	15	9000	Blackberry	Dry and irrigated pasture
75-6	8 June 1975	15	9000	Blackberry	Dry and irrigated pasture
75-9	11 June 1975	15	9000	Blackberry	Dry and irrigated pasture
Afton 75-3	6 June 1975	15	7500	Cattail	Rice and wheat fields
75-6	9 June 1975	15	7500	Cattail	Rice and wheat fields
75-9	12 June 1975	15	7500	Cattail	Rice and wheat fields

with 1,270 d.f.). Our data from injected and non-injected nestlings are therefore considered comparable.

RESULTS AND DISCUSSION

General food habits. Animal matter averaged over 86% of the total volume of all nestling food (table 2), and beetles (Coleoptera) were the major animal order represented. Ground-dwelling beetles of three families were the most prominent (31.1%), followed by water beetle larvae (18.4%), and grasshoppers and crickets (Orthoptera, 10.2%). Weevils averaged 8.3% of the total volume but were found in more stomachs (38.2%) than water beetle larvae (37.5%) and orthopterans (26.5%). All classes of beetles comprised more than 60% of the total food volume.

Of the other food categories, mollusks and miscellaneous plant material averaged 4.7% and 5.0% of the total volume, respectively, and all others made up about 3% or less (table 2). Small mollusks have been previously recorded as food items of Redwinged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Orians 1966, Orians and Horn 1969, Mott et al. 1972). However, much of the mollusk material that we found was meatless fragments of fresh-water clam shell and was likely used at grit. The miscellaneous plant category consisted largely of dried grasses and may have been either nest material eaten by the nestlings or grasses incidentally picked up by adults gathering other food.

Our results differ from those of Mailliard (1914), Neff and Wilson (1940), and Payne (1969), who indicated that grasshoppers might be the primary insect food of both adults and nestlings. Orians (1961) further suggested that the locust plagues that presumably occurred in the valley grasslands before the invasion of European man could have provided the abundant and easily available food supply required by the Tricolored Blackbird's colonial breeding system. We do not know whether the food of nestlings has actually changed since the earlier studies, or whether the differences in foods consumed are explainable by our observation that different colonies often rely on different foods; yearly variations in the availability of some insect groups or other normal variations could also account for differences. De-

TABLE 2. Foods of 272 Tricolored Blackbird nestlings from 10 breeding colonies in the Central Valley, California during 1971, 1972, and 1975.

Food item	Percent of total volume	Percent frequency of occurrence
Animal		
Coleoptera		
Ground-dwelling beetles[a]	31.1	86.8
Water beetles[b]		
Larvae	18.4	37.5
Adults	0.9	8.5
Weevils[c]	8.3	38.2
Other coleoptera larvae	2.1	9.6
Orthoptera	10.2	26.5
Diptera	0.3	2.9
Hemiptera	2.8	13.6
Lepidoptera larvae	0.8	2.2
Miscellaneous larval insects	3.6	13.2
Miscellaneous adult insects	0.5	1.5
Arachnida	2.4	10.7
Mollusca	4.7	39.3
Other animal matter	T	0.4
TOTAL COLEOPTERA	60.8	98.5
TOTAL INSECT	79.0	100.0
TOTAL ANIMAL MATTER	86.1	100.0
Plant		
Oats (*Avena* spp.)	2.1	13.2
Wheat (*Triticum* spp.)	3.1	9.9
Rice (*Oryza sativa*)	0.4	5.1
Wild seeds	0.6	13.6
Miscellaneous plant	5.0	42.6
TOTAL CULTIVATED GRAIN	5.6	25.7
TOTAL WILD SEEDS	0.6	13.6
TOTAL PLANT MATTER	11.2	63.6
Grit		
TOTAL GRIT	2.7	27.6

[a] Carabidae, Tenebrionidae, and Chrysomelidae.
[b] Hydrophilidae.
[c] Curculionidae.

TABLE 3. Results of statistical comparisons of six foods (percent of total volume) of 5-day old (±1 day) Tricolored Blackbird nestlings from 10 breeding colonies in the Central Valley, California.[a]

GROUND-DWELLING BEETLES

	(%)	KL	A-75	Or	H-75	AR	A-71	F-75	PF	BS
KL	6.5									
A-75	7.8	○								
Or	13.8	○	○							
H-75	14.5	○	○	○						
AR	37.7	×	×	×	×					
A-71	42.1	×	×	×	×	○				
F-75	52.3	×	×	×	×	○	○			
PF	54.0	×	×	×	×	×	×	○		
BS	55.0	×	×	×	×	×	×	○	○	
Cl	56.1	×	×	×	×	×	×	○	○	○

WATER-BEETLE LARVAE

	(%)	Cl	Or	F-75	BS	PF	H-75	AR	A-71	A-75
Cl	0.0									
Or	0.0	○								
F-75	0.0	○	○							
BS	1.0	○	○	○						
PF	3.3	○	○	○	○					
H-75	7.0	○	○	○	○	○				
AR	14.0	×	×	×	×	×	○			
A-71	30.3	×	×	×	×	×	×	×		
A-75	34.5	×	×	×	×	×	×	×	×	
KL	69.0	×	×	×	×	×	×	×	×	×

WEEVILS

	(%)	BS	A-75	F-75	KL	A-71	Cl	H-75	Or	AR
BS	0.2									
A-75	0.2	○								
F-75	0.5	○	○							
KL	2.0	○	○	○						
A-71	5.3	×	×	×	○					
Cl	6.0	×	×	×	×	○				
H-75	9.8	×	×	○	○	○	○			
Or	21.5	×	×	×	×	×	○	×		
AR	22.3	×	×	×	×	○	○	○	○	
PF	26.8	×	×	×	○	○	○	○	×	○

ORTHOPTERA

	(%)	AR	Cl	PF	F-75	KL	A-75	A-71	BS	Or
AR	0.0									
Cl	0.3	○								
PF	0.7	○	○							
F-75	1.5	○	○	○						
KL	3.5	○	○	○	○					
A-75	4.7	○	○	○	○	○				
A-71	9.1	○	○	×	○	○	○			
BS	16.5	×	×	×	×	×	×	○		
Or	26.5	×	×	×	×	×	×	×	×	
H-75	31.8	×	×	×	×	×	×	×	×	○

HEMIPTERA

	(%)	Cl	Or	A-71	AR	PF	KL	F-75	H-75	BS
Cl	0.0									
Or	0.0	○								
A-71	0.0	○	○							
AR	0.0	○	○	○						
PF	0.0	○	○	○	○					
KL	0.0	○	○	○	○	○				
F-75	0.5	○	○	○	○	○	○			
H-75	2.0	○	○	○	○	○	○	○		
BS	2.8	○	○	○	○	○	○	○	○	
A-75	14.5	×	×	×	×	×	×	×	×	×

ARACHNIDA

	(%)	Cl	Or	A-71	AR	BS	KL	PF	H-75	A-75
Cl	0.0									
Or	0.0	○								
A-71	0.0	○	○							
AR	0.0	○	○	○						
BS	0.0	○	○	○	○					
KL	0.0	○	○	○	○	○				
PF	0.2	○	○	○	○	○	○			
H-75	0.3	○	○	○	○	○	○	○		
A-75	1.5	○	○	○	○	○	○	○	○	
F-75	19.5	×	×	×	×	×	×	×	×	×

[a] Means were compared using arcsin-transformed data. For each comparison between two colonies, "×" indicates that the means were significantly different ($P < 0.05$); "○" indicates non-significant differences. Zero values could not be compared by analysis of variance but are assumed to have the same differences as the lowest numerical value for that food item. Cl = Clay, Or = Orland, A-71 = Afton 71, AR = Angle Road, BS = Butte Sink, PF = Pig Farm, KL = Knights Landing, F-75 = Folsom 75-6, H-75 = Herald 75-6, A-75 = Afton 75-6.

Haven et al. (1975) have suggested a decline in Tricolored Blackbird numbers in recent years that might be the result of declining or changing food supplies.

Differences among colonies. The colonies differed significantly in the percentages eaten of the six most common animal foods (table 3). For example, weevils were eaten in large amounts (>20%) at the Orland, Angle Road, and Pig Farm colonies, but were less important (<10%) at the other seven. Similar differences among colonies were recorded for ground-dwelling beetles, water beetle larvae, orthopterans, hemipterans, and arachnids (mostly spiders). Only 6-day-old nestlings from the 1975 colonies were used in these comparisons to keep age of young constant. Plant foods were not examined statistically because of their small contribution to the total food at each of the colonies we sampled.

Four sources of variation need to be considered in terms of the differential utilization of food items at different colonies: (1) seasonal variations in the availability of food items over the time span in which the samples were taken; (2) yearly variations in the abundance of some food items; (3) location-related differences in the foraging substrate and thus the available food supply; and (4) day-to-day variations at the same colony related to foraging behavior.

We did not quantify seasonal and yearly variations in the available food supply, but they did not appear to seriously affect the overall food brought to the colonies during the period sampled. For example, ground-dwelling beetles were an important food during each of the 3 years sampled, and throughout the entire breeding season each year (table 3). Other, less common, food items also failed to show any large seasonal or yearly pattern of utilization. However, such variations could occur—local grasshopper abundance can vary greatly, depending on spring precipitation (Andrewartha and Birch 1954). At all 10 colonies, the primary foods were ground-dwelling beetles, weevils, water beetle larvae, grasshoppers, or some combination. Such use of diverse foods would allow the Tricolored Blackbird to exploit alternate food sources during those years when some foods are limited by weather or other conditions.

Location-related differences in the foraging substrate are probably responsible for many of the differences in foods among colonies. The Afton and

TABLE 4. Statistical comparison of six foods (percent of total volume) of Tricolored Blackbird nestlings collected at 3, 6 and 9 days of age from three breeding colonies in the Central Valley, California.[a]

Breeding colony		No. of stomachs examined	Ground-dwelling beetles	Water beetle larvae	Weevils	Orthoptera	Hemiptera	Arachnida
Folsom	75-3	10	35.0^{a}	0.0^{a}	0.5^{a}	0.0^{a}	8.0^{a}	24.0^{a}
	75-6	10	52.3^{b}	0.0^{a}	0.5^{a}	1.5^{a}	0.5^{b}	19.5^{a}
	75-9	10	26.8^{a}	0.0^{a}	4.7^{b}	14.5^{b}	1.0^{b}	16.5^{a}
Herald	75-3	15	24.1^{x}	19.3^{x}	3.3^{x}	24.3^{x}	0.3^{x}	0.3^{x}
	75-6	15	14.5^{x}	7.0^{x}	9.8^{x}	31.8^{x}	2.0^{y}	0.3^{x}
	75-9	15	18.4^{x}	3.3^{y}	10.5^{x}	14.7^{x}	0.0^{x}	0.7^{x}
Afton	75-3	15	10.0^{r}	43.8^{r}	0.3^{r}	12.1^{r}	17.3^{r}	1.0^{r}
	75-6	15	7.8^{r}	34.5^{r}	0.2^{r}	4.7^{r}	14.5^{r}	1.5^{r}
	75-9	15	14.6^{r}	41.8^{r}	0.1^{r}	6.3^{r}	5.9^{r}	0.0^{r}

[a] Means were compared using arcsin-transformed data. For each food item from one colony, means followed by different superscript letters were significantly different ($P < 0.05$). Zero values could not be compared by analysis of variance but are assumed to have at least the same differences as the lowest numerical value for that colony and food item.

Knights Landing colonies were located in the rice district of the upper Sacramento Valley, and water beetle larvae were an important food at both colonies. The Orland, Butte Sink, and Herald colonies were bordered by foothill grassland and the greatest volumes of grasshoppers were fed to nestlings at these colonies. However, the Clay, Angle Road, and Folsom colonies were also surrounded by foothill grassland but grasshoppers were not an important food. Irrigated pastures and other wet areas close to these colonies appeared to provide a more abundant food source (ground-dwelling beetles) than that furnished by the surrounding grassland as we observed the adults foraging in these areas instead of the arid grassland.

Differences within colonies. Some within-colony differences in the percentages of the six most common animal foods were also significant (table 4), but they were neither as large nor as frequent as among-colony differences. These differences do not appear to represent changes in prey selection related to nestling age or to seasonal trends in availability. Rather, we think that they represent day-to-day fluctuations in the percentage composition of some foods in the diet, which in turn reflect the substrates on which the adults foraged.

In general, adults of both sexes forage in flocks concentrated at sites of abundant food within 6 km of the breeding colony. Small colonies (1000–2000 birds) generally have only one or two such flocks active at one time while large colonies (15,000 or more) may have a dozen or more. Such flock feeding behavior would allow the colony to locate and quickly exploit new sites of locally abundant food as old ones become depleted. Our observations of foraging adults during repeated visits to colonies in 1975 revealed that only occasionally (two instances in nine visits) were the flocks feeding at the same locations as during previous visits. This would account for the day-to-day variation in some foods within colonies and, to a lesser degree, some of the among-colony differences.

Because of the comparatively long flights needed for adults to gather food, Orians (1961) noted that the Tricolored Blackbird's colonial breeding system required more energy of individuals than the territorial breeding system of the closely related Red-winged Blackbird. He also noted that the Tricolored Blackbird makes up for some of this energy differential by using less energy for territorial defense. Hinde (1961) has called the flock feeding behavior of adults that we observed "local enhancement." Such flock behavior apparently allows individuals to find food quickly and without extensive searching (Emlen and DeLong 1975). Therefore, the flock feeding behavior of Tricolored Blackbirds may be another adaptation to lessen the energy requirements of food gathering on the individual.

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THE RELATION OF HUNTING SITE CHANGES TO HUNTING SUCCESS IN GREEN HERONS AND GREEN KINGFISHERS

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Considerable information is available on the feeding habits of herons and kingfishers (e.g., Skutch 1957, 1972, Meyerriecks 1960, 1966, 1971, Slud 1964, Jenni 1969, Recher and Recher 1972, Kushlan 1973, Tjomlig 1973). Several authors suggest that herons which hunt by standing and waiting and by wading or walking slowly will eventually move to a new location if no prey approach closely enough to be attacked; however, nothing is said about the tendency to move or stay after an attempt at prey capture. Kingfishers, which hunt from perches and attack more distant prey than do herons, sometimes move to a new location, both after an attempt and when no attempt has been made. To our knowledge, no one has investigated quantitatively the relationship between moving to a new location and hunting success at the previous location, for either herons or kingfishers. Our purpose was to study this relationship in Green Herons (*Butorides striatus*) and Green Kingfishers (*Chloroceryle americana*).

METHODS

We conducted our study at a shallow, 7-acre, artificial lake on the grounds of the Centro Agronomico Tropical de Investigacion y Enseñanza near Turrialba, Costa Rica (9°53′N, 83°38′W), at an altitude of 700 m. It is near the lower limit of the premontane wet forest life zone (Tosi 1969). The east shore and most of the north shore of the pond are overgrown by dense stands of papyrus (*Cyperus papyrus*). A small island containing several small clumps of bamboo (*Bambusa* sp.) is located in one corner. Water lilies (*Nymphaea* spp.) and floating mats of aquatic fern (*Salvinia auriculata*) interspersed with small patches of open water and mud islands cover about 80% of the surface. The rest is covered by emergent vegetation up to 1 m high. The vegetation was described in detail by Jenni and Collier (1972). Approximately 15 bamboo poles, projecting 0.5–2 m above the surface, are scattered throughout the lake.

Between 29 March and 26 June 1974 we watched two individually identifiable (one was banded; one had a misshaped foot), but unsexed, adult Green Herons for about 15 h each. Observation periods ranged from 3 to 102 min ($\bar{X}$ = 73 min, N = 25 sessions). Between 5 October and 12 December 1974 we watched adult Green Kingfishers for 12 h. During this period we saw only one male and one female at the same time, and we assumed that all our observations were of the same male (9 h) and female (3 h). Observation periods ranged from 5 to 78 min ($\bar{X}$ = 22 min, N = 32 sessions). Additionally, we casually observed both species throughout 1974; these observations showed that species differences discussed below existed throughout the year and were not a product of the different times of data collection.

We noted when the observed bird changed locations or attempted to catch prey and we recorded the time to the nearest 5 s. We also recorded whether attacks were successful. For each location change, we calculated either the period of time an individual spent at a location before and after an attack or the period of time it remained at a location without attacking. The time a heron spent eating was deducted from the total time spent at the location where it ate. Eating time was always less than 5 s for the kingfishers and was not recorded.

RESULTS

We combined the data for both individuals of each species because we found no significant individual differences for any of the parameters measured (Mann-Whitney U tests). The herons hunted mostly from the small mud islands and from rocks along the shore and infrequently from the bamboo poles, emergent vegetation and sides of a small skiff. They used the standing-and-waiting technique almost exclusively during our observations, but occasionally walked slowly along the shore. Herons always took prey less than 1 m away. The kingfishers hunted primarily from the bamboo poles, papyrus, and the bamboo trees on the island, and occasionally also from the emergent vegetation and rocks. Most of these perches were 1–2 m above the water but ranged from 0.3–5 m. We also saw kingfishers make several attempts after hovering 4–6 m above the water's surface. Both the heights of the perches and the hovering differ from Slud's (1964) report that these birds dive from low perches and not from hovers. Kingfishers took prey up to 6 m away. The minimum distance between locations was approximately 4–5 m for herons and 2–3 m for kingfishers; both species flew between locations.

The median lengths and ranges of times spent at locations are listed for the two species in Table 1. Three aborted attempts by kingfishers, in which the bird dove toward, but did not enter the water, are included as unsuccessful attempts. The ranges in