FOOD OF NESTLING YELLOW-HEADED BLACKBIRDS, CARIBOO PARKLANDS, BRITISH COLUMBIA

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Several techniques have been used for collecting food samples from wild birds, and the errors inherent in these different methods have been discussed by Hartley (1948). In the case of small passerines, which cannot be induced to disgorge the contents of their stomachs, food brought to the young has been collected either by the use of artificial nestlings (Promptow and Lukina, 1938; Betts, 1954, 1956) or by placing around their necks light metal collars too narrow to permit the nestlings to swallow the food brought by the parents (Kluijver, 1933; Lockie, 1955; Owen, 1956). Thus far, all successful uses of artificial nestlings have been with hole-nesting species. In this study I have collected food from nestling Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Redwinged Blackbirds (*Agelaius phoeniceus*) by wrapping segments of pipe cleaners around their necks (Willson and Orians, 1963; Willson, 1966). Attempts to induce the adults to feed artificial nestlings have failed, and Evans (1964) also was unable to obtain samples in this manner from sparrows.

The pipe-cleaner method has several important advantages. With minimal experience neck bands can be installed rapidly and adjusted to the size of the nestling. Moreover, the same nestlings can be sampled repeatedly during their stay in the nest. However, there are some important disadvantages that must be kept in mind when evaluating the data. First, I have thus far been unable to obtain good samples from nestlings younger than three days old. All attempts have resulted either in slippage of the food past the band or in strangulation of the young. Therefore, data are restricted to the period after the first few days of nestling life. Since the food brought during the first few days might be expected to differ from the food brought to older young, this is an important limitation.

Second, there is abundant evidence that at times, even with older nestlings, some food slips past the neck bands, although with careful installation this can be minimized. There is, at present, no way of measuring the extent of this loss. But smaller food items are probably more likely to pass than larger ones, so that samples may be biased in favor of larger food items. Also, if the rate of delivery has been rapid or the bands have been left on longer than usual, the young frequently cough up the food. Normally this can be picked up from the bottom of the nest or the surface of the water underneath; but it is possible that some of the food is lost or that it may even be eaten by the adult birds. Finally, although I have no direct evidence, it is possible that after food has accumulated in the throats of the nestlings for a time they may not beg as vigorously, with the result that the feeding rates of the adults decrease. Conversely, the lack of food in the stomach may induce more vigorous begging. It is also possible that the adults may eat some of the food they have brought if nestling response is reduced. At present it is impossible to determine the magnitude of these effects.

Thus, although I cannot determine the absolute rate of delivery from these food samples, it is possible to obtain information concerning *relative* rates of delivery provided that the errors mentioned above are equally important at all times of the day. Since this assumption appears reasonable, the data will be used to draw conclusions about relative rates of delivery of food to the nestlings and relative composition of the food at different times of day. This is the first of a series of papers analyzing the food of marsh-nesting blackbirds in various parts of the Pacific Northwest. Here I shall discuss the effects of weather, time of day, and lake productivity upon the foraging of blackbirds. Data from other areas and an analysis of foraging patterns of individual birds will be given elsewhere.

The data analyzed here were obtained at several lakes in the Cariboo Parklands of central British Columbia. With the exception of a small, isolated colony of Yellow-headed Blackbirds at Tachick Lake 160 miles to the northwest, this region forms the northwestern limits of the breeding range of this species. The Yellowhead is apparently a relatively recent immigrant to the area. Observations 40 to 60 years ago, summarized by Munro (1945), indicate that it was a rare straggler then, and it is uncertain that it bred. During the drought years 1931–1934, when many of the shallow lakes and sloughs either dried out or held water only briefly in early summer, Yellowheads became common in the Cariboo. For a marsh-nesting species this might seem to be a strange correlation, but Yellowheads do better during warm, sunny weather (see below). The drought years also resulted in the opening up of larger areas of grassland, an important supplementary feeding ground for these birds. Since then the Yellowhead has been a common breeding bird, arriving in late April and early May and departing in August (Munro, 1945).

The Cariboo is a gently rolling parkland, about 3000 feet in elevation, of lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*) interspersed with grassland and spruce bogs and dotted with many small lakes. These lakes include wide ranges in salinity, and many of them fluctuate in water level markedly from year to year. However, since blackbirds require emergent vegetation for their nests, they are restricted to lakes with relatively constant water level. Food samples were collected during a four-day period in June 1963 and a five-day period in June 1964. Observations on the breeding populations of blackbirds were also made on lakes at which no food samples were taken. All data on lake chemistry cited herein were generously provided by G. G. E. Scudder, who has been studying aquatic insects in many of these lakes.

Rush Lake, the most intensively studied lake, is roughly one-fifth mile in length, rimmed with bulrush (*Scirpus*), and surrounded by gently sloping, heavily grazed grassland except at the southeast corner where a pine-aspen wood comes down to the shore. The Yellowhead is the most common breeding passerine bird, but Long-billed Marsh Wrens (*Telmatodytes palustris*) were scattered through the denser stands of bulrush and one male Redwing held a territory in one corner of the lake adjacent to the pine-aspen wood. Nonpasserine species breeding on the lake include Eared Grebe (*Podiceps nigricollis*), Mallard (*Anas platyrhynchos*), Blue-winged Teal (*A. discors*), Redhead (*Aythya americana*), Scaup (*A. affinis*), Ruddy Duck (*Oxyura jamaicensis*), and American Coot (*Fulica americana*). The lake has a pH ranging between 8.5 and 9.0 and a conductivity ranging from 3000-4000 micromhos/cm.

At Rush Lake in 1963, mid-day samples were taken on 14 June, early-morning and late-afternoon samples on 15 June, mid-day samples on 16 June, and early-morning samples on 17 June. Sampling times were not identical on different days, the early-morning period ranging from 0650 to 0950, the mid-day period from 1045 to 1645, and the late-afternoon period from 1930 to 2140. The same seven nests were sampled each sampling period, but two additional nests were sampled on 17 June. During this period the weather was uniformly warm and dry with light variable winds and temperatures ranging from night-time lows in the mid-fifties to highs between 75 and 85°F. Warm dry weather also prevailed for several weeks prior to the sampling period. Thus, in these samples effects of changing weather conditions and variability due to differences in foraging patterns of individual females were minimized. Nests were not regularly watched during the sampling period, and it is not known how much of the food was delivered by the males. But, as is usually the case (Willson, 1963), the contribution of the males was probably considerably less than that of the females.

In 1964, early-morning (0725-0950) samples were taken on 23 and 25 June, mid-day samples (0930-1250) on 22 and 26 June, and late-afternoon samples (1625-1855) on 23 and 25 June at Rush Lake. Insofar as possible the same nests were sampled each time, but young fledged from several nests during the sampling period and young in other nests reached sampling age. In contrast to the previous year, the weather in 1964, both during and prior to the sampling period, was cold and wet. Showers fell on 22, 24, and 26 June, and the temperature never reached 70°F during the five-day period. Night-time temperatures were low, falling to 36°F on 23 June, 41°F on 24 June, 40°F on 25 June, and 35°F on 26 June.

Early-morning (0650-0845) and late-afternoon (1650-1940) samples were also taken on 26 June, and on 22 and 26 June, respectively, at Westwick Lake, a long, narrow lake lying about three miles north of Rush Lake. It is also rimmed with bulrush and surrounded mostly by grassland, but spruce woods border the lake along about half of its south side and at the SE corner. A very lightly grazed pasture was immediately adjacent to the sampling area. The pH of the lake ranges from 8.1 to 8.8, and the conductivity from 1250 to 1900, averaging 1640 micromhos/cm. The Yellowhead is also the most common breeding passerine on Westwick Lake, but marsh wrens are present and Redwing territories occur wherever the lake is bounded by woods.

At Rush Lake, 37 samples, covering 52¾ hours of food delivery, were obtained in 1963. In 1964, 91 samples, covering 101 hours of food delivery, were obtained. The 32 samples taken at Westwick Lake in 1964 cover 31¾ hours of food delivery. In addition, less abundant data obtained from a Redwing nest on Rush Lake and from Yellowhead nests at a marsh at 150 Mile House, 15 miles to the east, are presented for comparison. Throughout this discussion the term "sample" refers to all the food brought to all the nestlings in one nest during a sampling period of from 1 to 1½ hours.

The overall results of the food samples taken at Rush Lake are shown in tables 1 and 2, which illustrate the importance of odonates for the Yellowhead population in both years. In 1963, 56.4 per cent of all prey items were odonates (mostly a coenagrionid damselfly, *Enallagma*), and in 1964, 38.2 per cent of all prey items were odonates. In 1963, 33 (89.2 per cent) of the samples contained *Enallagma*, and six samples (16.2 per cent) consisted entirely of it; in 1964, 80 samples (88.6 per cent) contained *Enallagma*, and 21 samples (22.3 per cent) consisted entirely of it. Other important insects included the cerambycid beetle *Toxotus obtusus*, Trichoptera, and Diptera (1964). Little is known of the life history and daily cycle of *Toxotus obtusus*. Its host plants are unknown, but its presence in open grasslands suggests that, like other species in the genus, its larvae are soil inhabitors, feeding on the roots of small plants. Adults are known to be active from May to July (J. A. Chemsak, personal communication), but the period of emergence at Rush Lake is completely unknown.

TABLE 1
FOOD BROUGHT TO NESTLING YELLOWHEADS, RUSH LAKE, BRITISH COLUMBIA, 14–17 JUNE 1963

Class	Order	Family	Number of specimens: Larvae	Pupae	Tenerals	Adults	Order total
Insecta	Odonata	(Anisoptera)	2			1	532
	"	(Zygoptera)	138		280	111	
	Homoptera	Cicadellidae				2	2
	Heteroptera	Miridae				1	5
	"	Lygaeidae				2	
	"	Gerridae			1		
	"	?	1				
	Coleoptera	Dytiscidae	52			2	171
	"	Cerambycidae				99	
	"	Curculionidae				7	
	"	Carabidae				5	
	"	Elateridae				1	
	"	Hydrophilidae				2	
	"	Scarabaeidae				3	
	Trichoptera					74	74
	Lepidoptera		2			5	7
	Diptera	Ephydridae		1		2	75
	"	Syrphidae				2	
	"	?		1			
	"	Chironomidae			20	7	
	"	Ceratopogonidae			7	7	
	"	Stratiomyidae				2	
	"	Dolichopodidae			1	14	
	"	Cyclorrhapha			1		
	"	Simuliidae				3	
	"	Muscidae				4	
	"	Otitidae				1	
	"	Tachinidae			1	1	
	Hymenoptera	Formicidae				4	9
	"	Ichneumonidae				3	
	"	Braconidae				2	
Arachnoidea	Araneida					43	43
	Hydracarina					1	1
Gastropoda	Pulmonata					23	23
							942

In contrast, odonates form only a small fraction of the food brought to nestling Yellowheads at Westwick Lake (table 3). Only nine samples (28.1 per cent) contained odonates, none were exclusively odonates, and odonates comprised only 1.1 per cent of individual prey items delivered. Dipterans, on the other hand, were present in 100 per cent of the samples, 53.1 per cent of the samples consisted entirely of Diptera, and 96.1 per cent of all individual prey items were Diptera. Unfortu-

TABLE 2
FOOD BROUGHT TO NESTLING YELLOWHEADS, RUSH LAKE, BRITISH COLUMBIA, 22–26 JUNE 1964

Class	Order	Family	Number of specimens				Order total
			Larvae	Pupae	Tenerals	Adults	
Insecta	Ephemeroptera	—				9	9
	Odonata	(Anisoptera)	6				1051
	"	(Zygoptera)	364		512	169	
	Orthoptera	Locustidae	2				2
	Homoptera	Cercopidae	2				6
	"	Cicadellidae	1			2	
	"	Delphacidae				1	
	Heteroptera	Gerridae	4			7	23
	"	Corixidae				1	
	"	Saldidae				1	
	"	Lygaeidae	1				
	"	?	2			7	
	Coleoptera	Cerambycidae				261	408
	"	Dytiscidae	78				
	"	Curculionidae				15	
	"	Staphylinidae				1	
	"	Cleridae				4	
	"	Elateridae				1	
	"	?				48	
	Trichoptera	—				339	339
	Lepidoptera	Pyralidae	5				6
	"	?				1	
	Diptera	Asilidae				2	827
	"	Syrphidae				1	
	"	? (mostly Chironomidae)	24	5	20	775	
	Hymenoptera	Ichneumonidae				1	12
	"	?				11	
Arachnoidea	Araneida					7	7
Crustacea	Amphipoda					17	17
Gastropoda	Pulmonata					27	27
							2734

nately no mid-day samples, when odonates would be expected to be the most important, are available from Westwick Lake, but it is unlikely that additional samples would greatly alter the picture. Unlike Rush Lake, Westwick Lake produces few odonates, and few emerging tenerals or cast skins were noted during the sampling period, while tenerals were present in large numbers at Rush Lake during the middle and latter parts of the day.

TABLE 3

FOOD BROUGHT TO NESTLING YELLOWHEADS, WESTWICK LAKE, BRITISH COLUMBIA, 22–26 JUNE 1964

Class	Order	Family	Number of specimens				Order total
			Larvae	Pupae	Tenerals	Adults	
Insecta	Odonata	(Anisoptera)	1				17
	"	(Zygoptera)	5		3	8	
	Heteroptera	Gerridae				1	3
	"	Corixidae				1	
	"	?				1	
	Coleoptera	Cerambycidae				10	27
	"	Dytiscidae	9				
	"	Curculionidae				1	
	"	?				7	
	Lepidoptera	Noctuidae	1				3
	"	?				2	
	Diptera	Drosophilidae				1	1504
	"	Asilidae				3	
	"	? (mostly Chironomidae)	7	12	14	1467	
Arachnoidea	Araneida					2	2
Gastropoda	Pulmonata					9	9
							1565

The concentration of sampling at three different times of the day permits analysis of diurnal variations in the food delivered to the young. As seen in figures 1 and 2, the total rate of delivery at Rush Lake in both years increased during the day, reaching a peak in the late afternoon. The same trend, although less striking, was apparent at Westwick Lake (fig. 3). Also there were striking diurnal changes in the species composition of the food samples at Rush Lake. *Toxotus*, most strongly represented in the morning samples, was almost completely absent from the mid-day samples, and only a few were taken in the evening samples. Trichoptera and Diptera were found almost entirely in the evening samples. Damselflies were found in all periods, but the percentage of the food comprised by them was conspicuously larger in the middle of the day when 92 per cent (1963) and 94 per cent (1964) of all food items were damselflies. All mid-day samples contained damselflies, and 25 samples (54.3 per cent) consisted entirely of them. Early-morning and late-afternoon samples had, on the average, fewer damselflies, and some samples were completely without them.

Correlated with the great preponderance of damselflies in the mid-day samples, the total number of prey taxa (mostly insect families) represented in the food samples was smallest in the mid-day samples, larger in the early-morning samples, and greatest in the late-afternoon samples. A precise comparison of the food samples can be obtained by the use of the standard diversity index from information theory, where Diversity $(H) = -\Sigma p_i \log p_i$ (Shannon and Weaver, 1949). The use of this

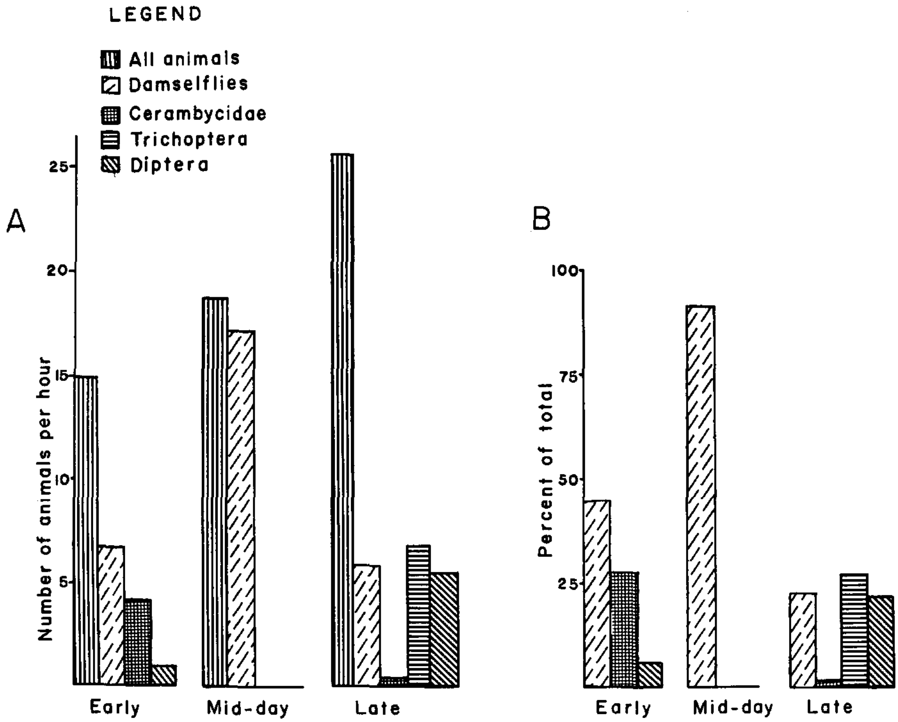

Figure 1. Diurnal variation in food brought to nestling Yellow-headed Blackbirds, Rush Lake, British Columbia, 1963. A, number of prey animals delivered per hour; B, percentage composition of food samples.

index in ecology was first suggested by Margalef (1958), and it has been used by Crowell (1961, 1962) and MacArthur and MacArthur (1961) as a measure of diversity of foraging locations in birds and by Paine (1962) as a measure of diversity of the food of predatory gastropods.

The diversity of the food delivered to nestling Yellowheads at Rush Lake was lowest in the mid-day samples, intermediate in the early-morning samples and highest in the evening samples (table 4). However, there are only half as many samples from the evening as there are from either of the other two periods in 1963, and since this index is sensitive to changes in sample size, the evening diversity is probably an underestimate. Horn (personal communication) has suggested that another index from information theory, redundancy, defined as $1 - H/H_{max}$ where H_{max} is taken as the logarithm of N (in this case number of prey taxa), is a useful estimate of the degree of specialization of a diet, which may, under certain circumstances, give different results than the diversity index. The redundancy indexes from Rush Lake (table 4) confirm the extreme specialization of foraging during the middle of the day and the much more generalized foraging during the late afternoon. Considering the striking differences in weather, the results are very similar for the two years.

Naiads, tenerals, and adult damselflies were well represented in the food samples, but their relative importance varied markedly at different times of the day (fig. 4).

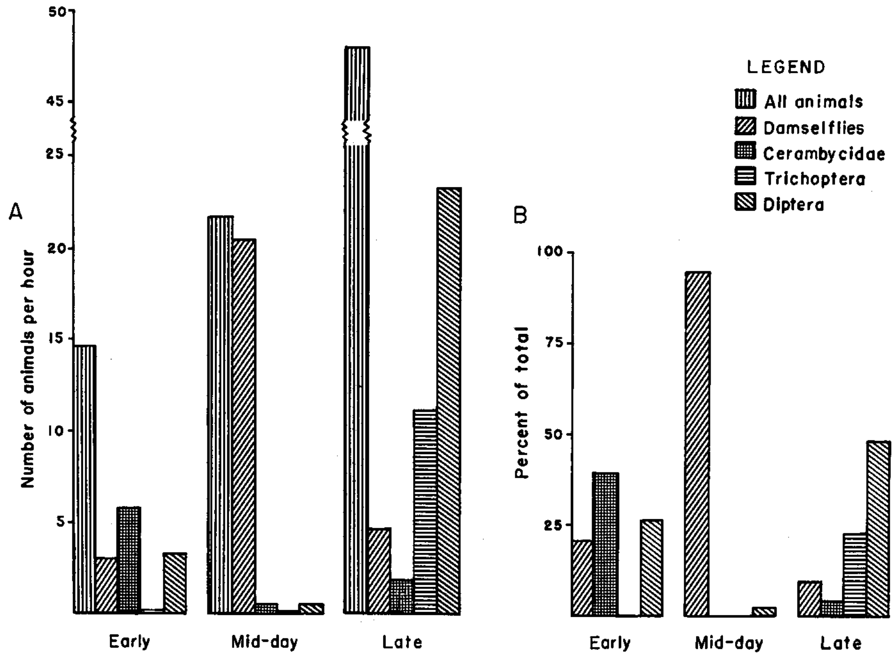

Figure 2. Diurnal variation in food brought to nestling Yellow-headed Blackbirds, Rush Lake, British Columbia, 1964. A, number of prey animals delivered per hour; B, percentage composition of food samples.

Naiads were taken most commonly during the early and mid-day periods, while tenerals were by far the most common in the mid-day samples. The number of adults taken was considerably less than the number of tenerals, but the relative number of adults increased during the day, becoming most important in the evening samples.

Five late-afternoon samples (1620-1830) were taken 16 June 1963 at a marsh near 150 Mile House. This marsh was surrounded by pine-aspen woods and an extensive ungrazed, wet sedge meadow. General observations during the sampling period indicated that the foraging females gathered much of the food for the nestlings from the wetter portions of the sedge meadow. This is reflected in the large number of sawfly larvae (Hymenoptera:Symphyta) represented in these food samples (table 5).

On 15 June 1963 early-morning and late-afternoon food samples were obtained from the one Redwing nest on Rush Lake, which contained three nine-day-old young. This information is scanty, but it does suggest that the foraging patterns of that particular female Redwing were very similar to those of the female Yellow-heads on the same day; that is, *Toxotus obtusus* was dominant in the early-morning sample while the late-afternoon sample contained a wide variety of insects (table 6). This corresponds to data obtained elsewhere where the two species breed on the same marshes, indicating that there is great overlap in the food taken (Willson and Orians, 1963; Orians, unpublished).

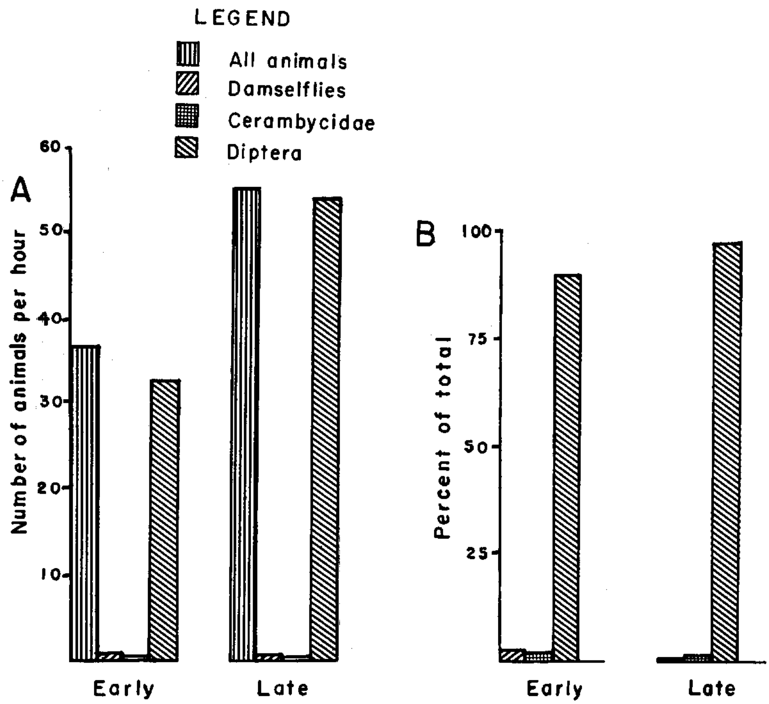

Figure 3. Diurnal variation in food brought to nestling Yellow-headed Blackbirds, Westwick Lake, British Columbia, 1964. A, number of prey animals delivered per hour; B, percentage composition of food samples.

DISCUSSION

Effects of weather on the survival of nestlings. General observations indicate that feeding conditions were excellent for Yellowheads during the sampling period in 1963. Despite rather heavy sampling all young survived, and six of the seven nests were fledging four young and the seventh three. Moreover, none of the nests contained runts, a common feature of nests if foraging conditions are poorer. In 1964, however, most nests contained runts, and there was considerable starvation of nestlings, particularly in larger broods. Moreover, mortality was significantly heavier ($P < .05$) at Westwick Lake than at Rush Lake (table 7). High nestling mortality, particularly during cold, rainy weather, is characteristic of other areas of the Pacific Northwest (Willson, 1966).

Mortality during cold, rainy weather could be due to exposure and chilling, to poorer feeding conditions, or to a combination of the two. Generally, Yellowheads do not brood their young in cold, wet weather, and the young often become chilled (Willson, 1966). However, since nestlings at Rush Lake and Westwick Lake were exposed to the same inclement weather in 1964, the data suggest that there is an interaction between exposure and adequacy of nutrition of the young. Well-fed young will grow more rapidly, will have a more favorable surface-to-volume ratio, and can more readily afford to divert energy to temperature control.

TABLE 4
DIVERSITY AND REDUNDANCY IN THE FOOD BROUGHT TO NESTLING YELLOWHEADS AT RUSH LAKE

Time of day	Diversity ($-\Sigma p_i \log_{10} p_i$)		Redundancy ($1 - H/H_{max}$)	
	1963	1964	1963	1964
Early morning	0.684	0.694	0.461	0.466
Mid-day	0.188	0.131	0.809	0.863
Late afternoon	0.912	0.715	0.345	0.291

Effects of lake productivity on the distribution of breeding blackbirds and the survival of nestlings. Productivity of the Cariboo lakes was not directly measured in this study, but indirect measures were obtained in two ways. First, the conductivity of the water of most of the lakes was determined during and prior to this study by G. G. E. Scudder. Conductivity is directly correlated with the concentration of dissolved solids in the water (Juday and Birge, 1933; W. T. Edmondson, personal communication), and Rawson (1961) demonstrated a strong correlation between total dissolved solids and productivity of plankton in a series of lakes in Saskatchewan. Therefore, it is reasonable to assume that the productivity of the Cariboo lakes increases with increasing conductivity of the water, but with reference to the black-

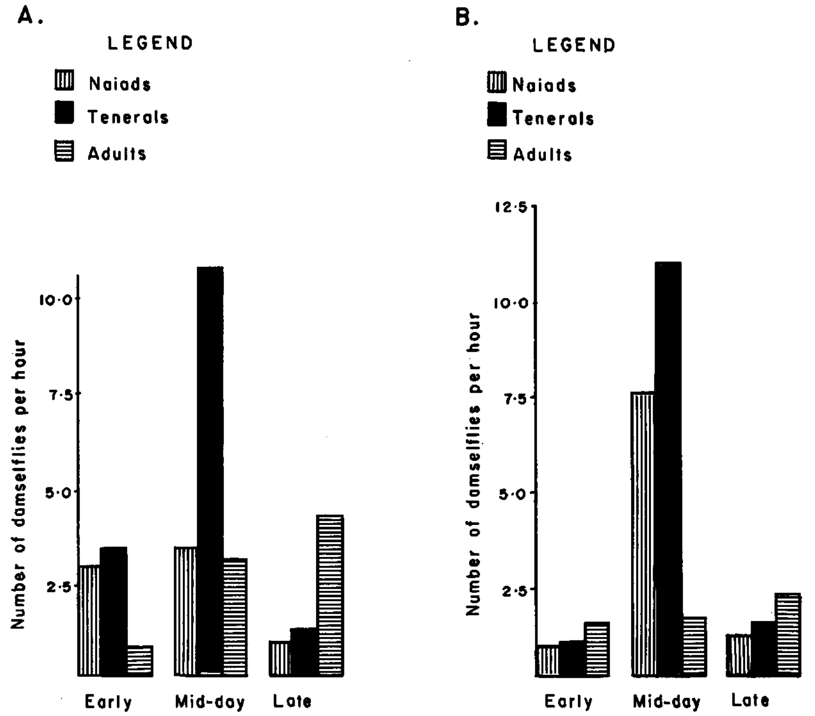

Figure 4. Diurnal variation in age composition of damselflies brought to nestling Yellow-headed Blackbirds, Rush Lake, British Columbia. A, 1963; B, 1964.

TABLE 5
FOOD BROUGHT TO NESTLING YELLOWHEADS, 150 MILE HOUSE, BRITISH COLUMBIA, 16 JUNE 1963

Class	Order	Family	Number of specimens				Order total
			Larvae	Pupae	Tenerals	Adults	
Insecta	Odonata	(Anisoptera)					22
	"	(Zygoptera)	2		2	18	
	Orthoptera		1				1
	Heteroptera	Cicadellidae				2	4
	"	Saldidae				1	
	"	Miridae				1	
	Coleoptera	Chrysomelidae				1	5
	"	Carabidae				3	
	"	Helodidae				1	
	Trichoptera					1	1
	Diptera	Rhagionidae				8	15
	"	Stratiomyidae				5	
	"	Chironomidae				1	
	"	Tipulidae				1	
	Hymenoptera	(Symphyta)	15				15
Arachnida	Araneida					10	10
	Phalangida					3	3
Gastropoda	Pulmonata					3	3
							79

birds only that productivity which is finally channelled into certain aquatic insects, particularly odonates, is of real importance. However, since odonate larvae attack and eat a wide range of animal foods (Pritchard, 1964), production of odonates probably also increases with increasing conductivity.

This view is strengthened by our general observations on the abundance of emergent aquatic insects at the various lakes. At Rush Lake, for example, damselflies were present in great abundance every afternoon, while at Westwick Lake very few damselflies were seen during any of our visits. Therefore, although I have no exact measurements of the productivity of emergent insects on these lakes or the actual number emerging per unit area during the study periods, the following discussion is predicated upon the assumption that lakes of higher conductivity produce more food for blackbirds than do lakes of lower conductivity.

The lakes of the Cariboo Parklands range in conductivity from less than 100 to more than 40,000 micromhos/cm. However, breeding Yellowheads and Redwings are restricted to the range between 600 and 3500 micromhos/cm (table 8). A rough indication of the breeding density of the blackbirds on the various lakes is given by the number of plusses on table 8. But the total breeding population is not necessarily larger on a lake with more plusses since differences in the total area of emergent vegetation may more than compensate for differences in population density. At conductivities above 4000 micromhos/cm emergent vegetation (*Scirpus* and *Typha*) cannot grow, and the birds are deprived of nest sites and sites from

TABLE 6

FOOD BROUGHT TO NESTLING REDWINGS, RUSH LAKE, BRITISH COLUMBIA, 15 JUNE 1963

Class	Order	Family	Number of individuals				Order total
			Larvae	Tenerals	Pupae	Adults	
A. *Morning sample* (0730–0920)							
Insecta	Coleoptera	Cerambycidae (*Toxotus*)				21	21
"	Lepidoptera		2				2
B. *Evening sample* (2030–2150)							
Insecta	Odonata	Coenagrionidae		5		9	14
"	Heteroptera	Gerridae	1				1
"	Coleoptera	Dytiscidae	1				1
"	Trichoptera	Limnophilidae	1			4	5
"	Diptera	Chironomidae			14		16
	"	Ephydridae	1		1		
							60

which the emerging insects can be gleaned. The lower limits are probably set by low productivity.

From table 8 it can be seen that Yellowheads were not breeding on any of the Cariboo lakes with conductivities less than 1100 micromhos/cm while Redwings were found breeding on lakes with conductivities as low as 625 micromhos/cm. The smaller size of the Redwing means that less food is needed per hour for successful breeding and may be the principal reason why it is able to breed on lakes lower in productivity than is the Yellowhead (Willson and Orians, 1963). More productive lakes are probably also better for Redwings, but Cariboo lakes with conductivities above 1500 micromhos/cm are dominated by Yellowheads, sometimes to the complete exclusion of Redwings (the species are interspecifically territorial; Orians and Willson, 1964). On these lakes Redwing territories are found only where woodland borders the lake, and usually very few Redwings are present. Munro (1945) gives data for Rush Lake and Westwick Lake in 1942 showing populations of the two species similar to those in 1963 and 1964. Although lakes with conductivities in the range of 1100-1700 micromhos/cm support large populations of Yellowheads, breeding was not as successful as at Rush Lake.

There is strong evidence that nestling Yellowheads were less well fed at Westwick Lake (conductivity = 1640) than at Rush Lake (conductivity = 3430) in 1964, despite the higher rate of delivery of individual prey items at Westwick Lake. The main food items at Rush Lake are large insects (*Enallagma* and *Toxotus*), and each individual provides much more energy than the tiny Diptera (mostly *Chironomidae*) that are almost exclusively brought to the nestlings at Westwick Lake. Calorimetric determinations in the laboratory indicate that one female *Toxotus* is worth about six and one male *Toxotus* about four *Enallagma*. On the other hand, one *Enallagma* is worth about 40 midges so that, assuming equal assimilation efficiencies for the different kinds of insects, at least several times as much energy was being delivered to each nest per hour at Rush Lake. Moreover, the general condition of the nestlings at Westwick Lake appeared to be poor. Their fecal material, rather than being

TABLE 7

LOSSES OF YOUNG YELLOW-HEADED BLACKBIRDS, CARIBOO PARKLANDS, BRITISH COLUMBIA, 22 JUNE–26 JUNE 1964

Number of young lost	Original number of young			
	1	2	3	4
Westwick Lake (16 nests, 47 young)				
0	1	3	1	–
1	–	2	3	2
2	–	–	–	4
% surviving	100	80	75	58
Mean loss = 0.94/nest.				
Rush Lake (16 nests, 53 young)				
0	1	–	6	2
1	–	–	2	3
2	–	–	–	2
% surviving	100	–	92	75
Mean loss = 0.56/nest.				

semisolid and firmly encased in a sac, was liquid and not encased. Consequently it could not be removed from the nests by the adults and fouled the bottoms of the nests and the ventral portions of the nestlings. Also, more of the nestlings at Westwick Lake were cold to the touch than at Rush Lake, and there was heavier mortality (table 7).

Unfortunately there are no other lakes with conductivities of 2500-3500 micromhos/cm with which to compare Rush Lake. Westwick Lake was not studied in 1963, but adjacent Sorenson Lake (conductivity 1470 micromhos/cm) was checked on 14 June. One-hundred and fifteen fresh Yellowhead nests were found, and 95 of these were empty. Only one nest contained young, and they were poorly fed. On 16 June, when the oldest nestling was at least three days old, it was no larger than a normal one-day-old nestling, and virtually no food was brought to the young during a lengthy sample period. Nesting success of Yellowheads at Near Phalarope Lake (conductivity, 1600 micromhos/cm) in 1964 was also poor. Only one nest contained young on 24 June, and there were many empty nests. Thus, although many more data are needed, the available evidence suggests that breeding failure may be fairly common on lakes at the lower end of the conductivity range occupied by the Yellowhead and that yearly fluctuations in climate have a much smaller effect on lakes with higher conductivity.

Effects of time of day on the foraging of blackbirds. The marked differences in the composition of the food samples taken at different times of the day at Rush Lake could be explained in several ways: (1) The birds may forage in different places and thus encounter different prey; (2) The birds may forage in the same places but encounter different prey at different times of the day; or (3) The birds may forage in the same places and encounter the same prey but select different items at different times of the day. Since detailed observations of the foraging behavior of the adults were not made and no measurements were taken of prey availability, it is impossible to distinguish clearly among these possibilities or to determine their

TABLE 8

BLACKBIRD BREEDING POPULATIONS AND CONDUCTIVITY OF LAKE WATER, CARIBOO PARKLANDS, BRITISH COLUMBIA

Lake	Conductivity		Redwinged		Yellowhead
Opposite Crescent	82 micromhos/cm.		–		–
Springhouse 6	272 "		–		–
Near Rock	465 "		–		–
Racetrack	480 "		–		–
Hayfield	625 "		+		–
Springhouse 8	650 "		–		–
Box 17	846 "		–		–
Near Opposite Crescent	850 "		–		–
Springhouse 2	970 "		++		–
Box 22	1,100 "		+		+ (1 male only)
Near Box 22	1,300 "		+		–
Riske Creek	1,350 "		+		+
Sorenson	1,470 "	Redwing	+		++
Near Phalarope	1,600 "	territories	–		++
Westwick	1,640 "	only	+		++
Box 89	1,720 "	adjacent	–		++
Rock	1,790 "	to trees	–		++
Rush	3,430 "		+		+++
Boitano	4,940 "		–	no	–
Box 20-21	7,050 "		–	emergent	–
Phalarope	9,000 "		–	vege-	–
Box 4	13,100 "		–	tation	–

relative roles. However, it is possible, on general theoretical grounds and by a consideration of the ecology of the prey species, to suggest likely possibilities.

First, in most cases I can be fairly certain whether a given prey item was captured in the bulrushes or on the adjacent grassland, the only two habitats exploited by foraging blackbirds. For example, all *Toxotus* were probably taken from the grassland and all *Enallagma*, Hemiptera, Dytiscidae, Trichoptera, and many of the Diptera were probably taken in the bulrushes. Using these assumptions I have estimated that in 1963 at Rush Lake about 68 per cent of the prey in the morning samples, 99 per cent of the prey in the mid-day samples, and 91 per cent of the prey in the late-afternoon samples were captured on the marsh. Corresponding values for 1964 are 54, 97, and 90 per cent. Thus, much of the difference between early-morning samples and those taken at other times of the day can be explained by assuming that the birds foraged more in the grassland, and this assumption is supported by casual observations of the foraging birds.

To explain the difference between mid-day and late-afternoon samples other factors must be invoked. If a bird forages so as to maximize the number of calories captured per unit effort expended, certain predictions can be made. If larger prey items are readily available, a more rapid rate of delivery of energy to nestlings can be achieved if the bird concentrates its attention on these larger prey and ignores smaller items unless they are unusually abundant. The largest insect commonly available on Rush Lake was *Enallagma*, and, in general, the species composition of the food samples can be correlated with their daily activity cycle.

Yellowheads are able to capture fully adult damselflies only with great difficulty and are, for the most part, dependent upon the day's emergence for their major food supply. Like most other temperate zone odonates, *Enallagma* emerges for the most part during the morning hours. Thus, early in the morning only those damselflies that emerged the previous day are available, and although these are now strong fliers, they may be more vulnerable to predation early in the morning when they are still cold. However, newly emerging naiads soon become available and are important in the food captured during the morning hours. In clear, warm weather metamorphosis proceeds rapidly, and by mid-day tenerals are available in large numbers and comprise the bulk of the insects brought to the young. By late afternoon they have hardened considerably and are probably tabulated as adults that now increase in importance as blackbird food. Thus, there is good reason to believe that damselflies are probably just as common in the late afternoon as during the middle of the day but that they are more difficult to catch in the late afternoon and therefore are less available then. Conversely, there is no reason to believe that the Hemiptera, dytiscid larvae, and Hymenoptera were more available during the late afternoon. These prey items are mostly much smaller than damselflies, and it is a reasonable assumption that these smaller prey items were bypassed during the middle of the day and were only taken when the larger damselflies were less available. Trichoptera and Diptera, however, were conspicuously more abundant in the marshes during the late afternoon, and their marked increase in the food samples may merely reflect their increased availability.

Although the number of items delivered to each nest per hour was greater in the evening samples, the amount of energy, as determined by caloric analysis of representative insects, was less than half that delivered during the middle of the day. Thus, feeding conditions may actually have been much poorer in the late afternoon than during the middle of the day. More precise comparisons will be possible when assimilation efficiencies of nestling blackbirds for a variety of insects have been determined.

Similar data are reported for the European Swift (*Apus apus*) by Lack and Owen (1955). This species also utilizes insect populations whose distribution and abundance vary considerably with weather and time of day. Swifts take smaller insects mainly in poor weather, even though there are more small insects in fair weather, presumably because during fair weather many larger insects are available and the swifts select these. Also, although the size of meals was the same in poor and good weather, the adults took longer to collect a meal in poor weather. Moreover, during bad weather the peak in feeding frequency came later in the day, suggesting that during fair weather, when the young are well fed, they beg less from their parents who are therefore less stimulated to bring more food (Lack and Owen, 1955). More extensive data on a larger number of species of birds may reveal that, in general, higher food species diversities are good indicators of poorer feeding conditions, and the converse.

SUMMARY

In June of 1963 and 1964 food samples were taken from nestling Yellow-headed Blackbirds in the Cariboo Parklands, British Columbia, by placing segments of pipe cleaners around their necks tightly enough to prevent swallowing of the food.

Weather was fair and warm in 1963 but cold and rainy in 1964. Damselflies (*Enallagma*) were the most important food items at Rush Lake, a lake of high productivity, but Diptera comprised 96 per cent of the food at Westwick Lake, a lake of lower productivity. Nestling survival was better during the warm, dry weather of 1963, and mortality was proportionally higher at Westwick Lake than at Rush Lake in 1964. In the Cariboo, Yellow-headed Blackbirds are restricted to lakes of higher productivity than Redwinged Blackbirds, and the available evidence indicates that survival of young is better on the more productive lakes. At Rush Lake the diversity of the food samples was greatest in the late-afternoon, intermediate in the early-morning, and lowest in the mid-day samples when damselflies constituted over 90 per cent of all prey items. Correlated with the morning emergence of metamorphosing damselflies, naiads and tenerals were proportionally more common in the mid-day samples, and adults were proportionally more common in the late-afternoon samples. The data are consistent with the hypothesis that the adult blackbirds foraged more in the grassland early in the morning than later in the day and turned to smaller insects primarily late in the afternoon when damselflies were harder to catch.

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