

MIGRATORY DISPOSITION AND CHOICE OF DIET
BY THE YELLOW-RUMPED WARBLER
(*DENDROICA CORONATA*)

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ABSTRACT.—Because migration is a period of exceptional energy demand and surely exerts strong selective pressure for efficient foraging, we expected Yellow-rumped Warblers (*Dendroica coronata*) to be especially efficient foragers when in migratory disposition and to select a diet that more nearly achieves energy maximization relative to control individuals not in migratory disposition. We induced migratory disposition in experimental birds by artificially prolonging daylength, then provided both controls and experimentals with a choice among large, medium, and small larvae (*Tenebrio molitor*) that varied in calories per unit handling time. Diet choice was studied during the premigratory fattening period, as experimentals gained weight and deposited subcutaneous fat, and later as experimentals attained maximum weight and began to show nocturnal restlessness. Warblers in migratory disposition consumed more food items per feeding bout; handled items more rapidly, thereby increasing the net energetic value of the food they consumed; and fed selectively on more profitable items than control individuals. As a result of these adjustments in their food intake, Yellow-rumped Warblers in migratory disposition foraged more efficiently and came closer to achieving energy maximization during the premigratory fattening period and the subsequent migratory period. Received 19 November 1984, accepted 8 May 1985.

THE seasonal migrations that characterize much of our avifauna are unquestionably high-risk and energetically expensive events (Tucker 1971, Berthold 1975, Blem 1980). Migratory birds often must contend with fluctuations in resource availability (Schneider and Harrington 1981, Terrill and Ohmart 1984), heightened risk from predators, the likelihood of severe competition because energy-depleted migrants must compete among themselves and with residents at stopover sites (Kodric-Brown and Brown 1978, Schneider and Harrington 1981, Sutherland et al. 1982), the vicissitudes of weather (Richardson 1978), and possible orientational errors (Ralph 1978, McLaren 1981, DeSante 1983). How well migrants respond to the contingencies of migration undoubtedly has an impact on their survival and future reproductive success (see Greenberg 1980, Morse 1980, Duffy et al. 1981, Wood 1982, Metcalfe and Furness 1984). Consequently, behavior that reduces the risks associated with migration or enables a migrant to more efficiently meet energetic demands is likely to evolve in populations of migratory birds.

Because migration is clearly a period of exceptional energy demand and surely exerts strong selective pressure for efficient foraging,

migratory birds should be especially efficient foragers during migration. Efficiency is viewed in terms of increased calories consumed per unit handling time relative to a nonselective forager. While it may be reasonable to assume that fitness is correlated with feeding efficiency (hence the expectation that animals will be efficient in their foraging activities), individuals should be particularly efficient during periods when their feeding activities strongly affect fitness (see Schluter 1981, Sih 1982, Myers 1983). Migration is such a period.

We hypothesized that Yellow-rumped Warblers (*Dendroica coronata*) would select a diet when in migratory disposition that more nearly achieves energy maximization relative to control individuals not in migratory disposition. Migratory disposition refers to the specific physiological state responsible for a metabolic condition in which there is sufficient energy available for migration (Berthold 1975). The most striking feature of this state is the deposition of subcutaneous fat reserves. The principal mechanism in fat deposition is thought to be active hyperphagia, during which food intake increases dramatically and results in hyperlipogenesis (Berthold 1975, Blem 1980). Our results indicate that when migrants "en-

TABLE 1. Summary of data used to calculate the profitabilities associated with eating the different-size larvae for the two test periods.

Prey size	Cal/ larvae		Handling time ^a (s)		Profitability ^b (cal/s)	
			Premigratory	Migratory	Premigratory	Migratory
			Small (10-14 mm)	52.2	Control	11.14 ± 0.91
		Experimental	8.74 ± 0.53	10.76 ± 0.93	6.0	4.9
Medium (16-20 mm)	158.4	Control	22.58 ± 1.76	22.40 ± 1.31	7.0	7.1
		Experimental	19.92 ± 2.03	23.40 ± 1.71	7.9	6.8
Large (22-25 mm)	332.3	Control	98.88 ± 1.26	97.22 ± 1.58	3.4	3.4
		Experimental	98.26 ± 3.51	95.04 ± 9.57	3.4	3.5

^a Mean ± SD.

^b Premigratory = test period during which experimental birds gained weight and deposited subcutaneous fat. Migratory = test period after experimental birds attained maximum body weight and began to show nocturnal restlessness.

ter" migratory disposition they adjust their feeding behavior in several ways to maximize energy gain, foraging more efficiently than congeners not in migratory disposition. Diet choice was studied as the experimental birds gained weight and deposited subcutaneous fat (the premigratory fattening period) and later when experimental birds attained maximum body weight and began to show nocturnal restlessness (the so-called migratory period).

MATERIALS AND METHODS

Yellow-rumped Warblers are North American migrants whose breeding range extends from Alaska and northern Canada through coniferous forest into the northern United States. They winter abundantly through the southern half of the United States east of the Great Plains and south to Panama and are common in south-central Mississippi, where this study was conducted. Birds were mist-netted during late fall 1983 near Hattiesburg, Mississippi. Prior to experimentation, birds were housed 4 to a cage (1 m³) under winter (LD 10:14) photoperiod while being fed a diet of commercial monkey biscuits (Zupreem), mealworms, and supplemental vitamins and minerals. The first week of January, we divided birds into control and experimental groups and housed them singly in activity cages (40 cm³). Cages were equipped with movable perches attached to micro-switches so that activity could be monitored using an Esterline Angus event recorder.

Migratory disposition, including body weight increase, subcutaneous fat deposition, and nocturnal restlessness, was induced in the experimental birds ($n = 5$) in January with artificially prolonged daylengths. Daylength was increased by 1-h daily increments until a 16-h day was reached (LD 16:8). Controls ($n = 5$) remained on a short-day (winter)

photoperiod, maintained rather constant weight throughout the experiment, and did not display nocturnal restlessness. The ability to induce a migratory state in experimental birds enabled us to conduct simultaneously feeding tests with controls and experimentals.

Food items consisted of small, medium, and large *Tenebrio molitor* larvae. The caloric value of the three food sizes was determined by bomb calorimetry (see Table 1). Samples of the three sizes were dried to constant weight (8.8 mg/small larva, 26.4 mg/medium larva, and 65.8 mg/large larva) in an evacuated desiccator at room temperature to reduce the possibility of losing easily volatilized lipids. Each sample was then exploded in a Parr adiabatic calorimeter and cal/g determined. The net energy value (profitability, E_i/h_i) associated with each food size was determined by dividing the average handling time (h_i) into the caloric value (E_i). Handling times for the small, medium, and large larvae (i.e. time from picking up a larva until it was swallowed) were sampled for control and experimental birds during both the premigratory fattening period and the migratory period (see Tables 1, 2). Handling time reflected, for the most part, time necessary to manipulate the item before swallowing. Once oriented properly, larvae were consumed rapidly. While the photoperiod was being shifted for experimental birds and before the start of the experiment, we familiarized all birds with a range (8-26 mm) of food sizes that encompassed sizes used in the study.

Tests were conducted during the premigratory fattening and the migratory periods of experimental birds. During the experiment, the birds were deprived of their normal diet in the morning and tested approximately 2 h later. Birds were transferred within their "home" cage to the test cage (60 cm³) and allowed to acclimate for 5 min before the food dish (30 cm diameter) containing 25 each of the small, medium, and large larvae was uncovered by remote

control. Individuals were allowed to forage for only 18 min so that the relative distribution of food classes would not be grossly distorted and satiation effects would be minimized. The rate of consumption did not measurably decline over the test period. Experimentals and controls were tested in random order on each of 10 test days from 30 January to 9 February (pre migratory period) and again over 10 test days from 21 February to 1 March 1984 (migratory period).

RESULTS

During the pre migratory fattening period, before the onset of nocturnal restlessness, experimental birds gained, on average, 4.5 g, which represented a 36% increase over average pretest weight (see Table 2). Their mean rate of food intake under test conditions was 8.18 ± 0.84 (SD) larvae/trial. Because these warblers could obtain 6.0 cal/s handling time from small, 8.0 cal/s handling time from medium, and only 3.4 cal/s handling time from large larvae at this time, we expected them to feed preferentially on the most profitable, medium larvae. When given an opportunity to choose, four of the experimentals clearly preferred the medium over the small larvae and all birds tended to ignore the largest larvae (Table 2, Fig. 1). Warbler E45 selected small larvae as often as it selected medium larvae.

At the same time, control birds consumed fewer larvae per foraging bout (5.84 ± 1.03 larvae/trial) and took significantly longer to handle small (one-tailed $t = 5.12$, 8 df, $P < 0.0005$) and medium larvae (one-tailed $t = 2.21$, 8 df, $0.025 < P < 0.05$) than warblers in migratory disposition (Tables 1, 2). The difference in feeding rate between controls and experimentals at this time also was statistically significant (one-tailed $t = -3.95$, 8 df, $0.001 < P < 0.0025$). One-tailed Student's t -tests were applied because we expected experimentals to handle larvae more rapidly than controls, which would, in part, influence relative consumption rates. Moreover, with one exception (C47), controls failed to exhibit a noticeable preference for a particular size despite E_i/h_i differences among the larvae comparable to values calculated for experimental birds (see Table 2). A contingency Chi-square analysis confirmed the significant difference ($\chi^2 = 41.03$, 2 df, $P < 0.001$) in choice frequencies between control and experimental groups: warblers in migratory disposition clearly preferred to eat more profitable items than war-

blers not in migratory disposition. Examination of the observed and expected frequencies suggested that the significant disagreement between control and experimental data might have been largely a result of the disproportionate number of more profitable, medium larvae taken by experimental birds. However, when the medium data were ignored momentarily and the Chi-square analysis subdivided, a statistically significant difference remained between control and experimental warblers ($\chi^2 = 19.67$, 1 df, $P < 0.001$). Presumably, the difference was a function of the choices among all size classes. Regardless, control birds consumed fewer calories per unit handling time than did experimental birds.

Between 20 and 25 days following the photoperiod change, the migrants began to display nocturnal migratory activity that marked the onset of the migratory period. Experimental birds decreased their rate of food intake (6.88 ± 0.52 larvae/trial), yet continued to be highly selective in their diet choice (see Table 2; Fig. 1). According to a paired-sample t -test, the decline in feeding rate from the pre migratory fattening period to the migratory period was statistically significant (one-tailed $t = 7.14$, 4 df, $0.0025 < P < 0.001$). The proportion of more profitable, medium larvae consumed rose from 56% to 62% during these feeding trials, while the consumption of small larvae decreased somewhat; large larvae were again virtually ignored. The change in preferences among the experimental birds that occurred after the pre migratory period was statistically significant according to Chi-square contingency analysis ($\chi^2 = 24.87$, 2 df, $P < 0.001$). Although the E_i/h_i ranking among the different food sizes remained unchanged from one test period to the next for experimentals, profitabilities decreased somewhat because of increased handling times—most noticeable for the small and medium larvae (Table 2). Paired-sample t -tests suggested that the experimental birds were able to handle medium (one-tailed $t = -7.09$, 4 df, $0.0025 < P < 0.001$) and small larvae (one-tailed $t = -3.25$, 4 df, $0.025 < P < 0.01$) at a significantly faster rate during the pre migratory fattening period. The same cannot be said for large larvae; experimental birds continued to avoid this size despite a decrease in handling time from the pre migratory to the migratory period.

Control birds continued to feed less selectively and to consume significantly fewer lar-

TABLE 2. Diet choice and handling times for Yellow-rumped Warblers in migratory disposition (experimental) and controls during the pre-migratory fattening period (as experimental gained weight and deposited fat) and later when experimental attained maximum body weight and began to display *Zugunruhe* (migratory period).

Bird	Weights ^a (g)		Pre-migratory fattening period						Migratory period					
	Pre-test	Mig	Diet choice ^b			Handling time (s)			Diet choice ^b			Handling time (s)		
			SM	MD	LG	SM	MD	LG	SM	MD	LG	SM	MD	LG
Experimental														
E41	11.0	15.8	23	53	5	19.2 ± 3.8	90.0 ± 23.2	9	46	10	11.3 ± 2.1	23.7 ± 3.1	79.0 ± 27.4	
E42	12.5	16.2	31	42	11	21.2 ± 3.4	99.0 ± 14.6	18	45	7	10.5 ± 1.4	24.2 ± 3.3	98.1 ± 17.2	
E43	13.0	19.0	26	41	4	22.8 ± 4.0	104.0 ± 25.7	13	42	9	12.1 ± 2.0	23.6 ± 3.8	101.0 ± 23.8	
E44	13.1	16.9	20	45	14	18.4 ± 3.0	92.3 ± 15.9	25	35	8	9.9 ± 2.8	20.5 ± 2.9	94.1 ± 20.0	
E45	12.2	16.0	41	47	6	8.1 ± 2.0	106.0 ± 19.7	21	53	3	10.0 ± 1.8	25.0 ± 3.9	103.0 ± 24.0	
Control														
C46	13.0	13.2	17	13	17	24.6 ± 4.0	97.1 ± 23.0	16	18	15	9.7 ± 2.0	23.8 ± 3.7	97.5 ± 19.8	
C47	13.5	14.0	19	28	11	22.2 ± 3.0	100.0 ± 22.3	30	20	14	11.4 ± 1.8	23.5 ± 2.9	98.1 ± 25.0	
C48	13.2	12.5	12	19	21	24.0 ± 3.9	95.6 ± 19.0	20	15	16	12.0 ± 2.1	22.4 ± 3.5	98.7 ± 22.0	
C49	12.5	12.7	31	28	15	20.2 ± 3.7	102.0 ± 25.3	26	27	10	11.8 ± 1.5	21.7 ± 3.0	97.2 ± 23.1	
C50	13.0	12.8	20	25	16	21.9 ± 3.2	99.7 ± 20.9	19	20	17	10.3 ± 1.7	20.6 ± 3.5	94.6 ± 21.8	

^a Pretest = weight prior to induction of migratory disposition in experimental; Mig = weight once experimental began to display *Zugunruhe*.

^b Number of larvae consumed over 10 feeding trials.

^c Mean ± SD.

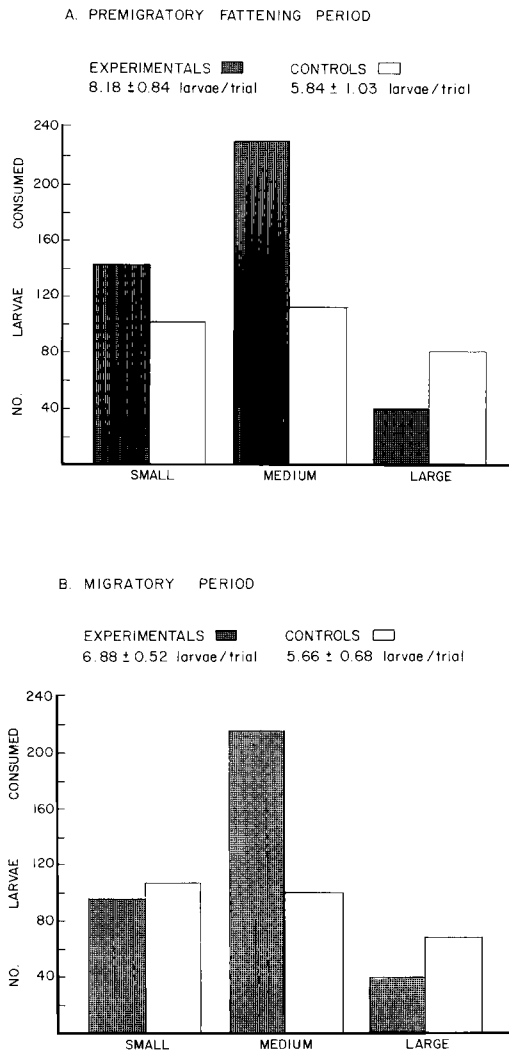


Fig. 1. Feeding preference of experimental ($n = 5$) and control ($n = 5$) birds for large, medium, and small *Tenebrio molitor* larvae during the premigratory fattening period (A) and the migratory period (B). Preferences are based on 10 feeding trials per bird for each test period. Mean feeding rates \pm SD also are given.

vae on average (5.66 ± 0.68 larvae/trial; one-tailed $t = -3.19$, 8 df, $0.005 < P < 0.01$) than experimentals during the migratory period (see Table 2; Fig. 1). A contingency Chi-square analysis indicated that the differences in preferences between control and experimental birds were statistically significant ($\chi^2 = 63.06$, 2 df, $P < 0.001$). Subdivision of the contingency

analysis by excluding the choice data for the more profitable, medium larvae supported the null hypothesis that the remaining preferences were independent of treatment ($\chi^2 = 2.38$, 1 df, $0.10 < P < 0.25$). Manipulation of the results in this way confirmed the suspicion that the preference for medium larvae was primarily responsible for the discrepancy between the behavior of control and experimental birds at this time.

DISCUSSION

Migratory birds display the remarkable ability to accumulate lipid reserves very rapidly in response to the heavy energetic demands of migration (see King 1972). Berthold (1975) and Blem (1980) concluded that hyperphagia is principally responsible for this fat deposition. Other mechanisms, such as increased digestive efficiency, increased assimilation efficiency, changes in locomotor activity, temporary decreases in basal energy requirements, or shifts to higher-energy foods, apparently play non-essential roles. We found that Yellow-rumped Warblers in migratory disposition not only consumed more larvae per feeding trial, while handling larvae more rapidly, but also fed more selectively on profitable items relative to control birds not in migratory disposition. As a result of these adjustments in their food intake, warblers in migratory disposition foraged more efficiently and came closer to achieving energy maximization during both the premigratory fattening period and the migratory period after they attained maximum body weight and began to show nocturnal restlessness. Yellow-rumped Warblers choose food items on the basis of energetic costs and benefits, and, more significantly, they do so when feeding considerations are likely to have considerable impact on survival and future reproductive success (see Kushlan 1978, Griffiths 1981, Dugan 1982). Needless to say, caution must be exercised when extending the results of this laboratory study to the field (see Zach and Smith 1981, Schluter 1981). The spectrum of prey available to a foraging migrant in the field, for example, is surely quite different from that found in our experimental setting (see Graber and Graber 1983; Moore unpubl. data). Moreover, larvae were easy to locate during the feeding experiments in the laboratory; hence, search costs under-

standably were ignored, an assumption unlikely to hold in the field.

The frequency with which experimental birds consumed small larvae, particularly during the premigratory fattening period, and avoided large larvae during both test periods may reflect a "rule-of-thumb" relationship between volume rate of food intake and rate of net energy gain (see Hainsworth and Wolf 1979). If the food items naturally available to a Yellow-rumped Warbler in migratory disposition differ little in energy value, increasing the rate of food intake necessarily would increase energy gain. Graber and Graber (1983) recently reported that spring warblers foraged selectively while en route through Illinois, choosing either smaller size classes of larvae or smaller species of prey out of proportion to their availability. Handling ease, itself, could serve as a proximate cue to profitability. Kaufman and Collier (1981), for example, found a significant correlation between preference for seeds without hulls and hulling time; rats slowest at removing seed hulls showed the strongest preference for seeds without hulls. Our results suggest that migrants will be more likely to behave according to this rule of thumb when they are putting on fat in preparation for long-distance flight or replenishing depleted lipid reserves at stop-over sites. Once our experimental birds deposited subcutaneous fat and attained maximum body weight, they became less hyperphagic; handling times for both small and medium larvae increased, and the rate of consumption for both sizes decreased. King (1961) detected hyperphagia among captive White-crowned Sparrows (*Zonotrichia leucophrys*) only during the period of premigratory fat deposition (see also Morton 1967). Presumably, the new level of energy reserve can be maintained without increasing intake as long as total energy expenditure does not increase. Obviously, the energy expenditure from a night's migratory flight is considerably greater than that associated with a night of nocturnal restlessness in a laboratory cage. Yellow-rumped Warblers in migratory disposition did continue to discriminate larvae on the basis of profitability after premigratory fat deposition and consequently continued to gain more energy relative to control birds. In summary, our experimental results are intuitively pleasing in light of the energetic demands of migration. Efficient foraging behav-

ior assures that the lipid reserves so critical to a successful migration will be rapidly deposited prior to migration and rapidly restored when depleted en route.

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