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METABOLISM AND FOOD SELECTION OF EASTERN HOUSE FINCHES

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The establishment and dispersal of introduced species of birds is best documented by the many studies of the House Sparrow (*Passer domesticus*) (Johnston 1964, 1973; Hudson and Kimzey 1966; Selander and Johnston 1967; Johnston and Selander 1971, 1973; Johnston et al. 1972; Blem 1973, 1974, 1975), and the Eurasian Starling (*Sturnus vulgaris*) (Kessel 1953, 1957; Blem 1981). However, with very few exceptions (Lack 1949, Calhoun 1947), most of this research did not occur until many years after the populations were first established. The recent introduction of the House Finch (*Carpodacus mexicanus*) into the eastern half of the United States (Elliott and Arbib 1953, Aldrich and Weske 1978) and dispersal into Virginia (Blem and Mehner 1981) provided us the opportunity to examine avian adaptation to a new environmental regime as it occurred and not after the fact. The present study: (1) documents the metabolic response of Virginia House Finches to ambient temperature, photoperiod, and food composition; and (2) quantifies the poor tolerance of Virginia House Finches of low temperatures. The dependence of these birds on artificial food sources for survival may be a possible ecological basis for significant morphological differences, particularly increased bill size, which have arisen between the eastern race and the parental stock (Aldrich and Weske 1978, Aldrich 1982).

METHODS

All birds used in this study were trapped at feeders near Richmond, Virginia, in December 1980, or January 1982. They were kept in flight cages for several days at room temperature (25°C ± 2) and at a photoperiod of 12L:12D. All birds initially were given water and chick starter mash ad lib. In preparation for each metabolic test, birds were placed individually in small cages of hardware cloth (Martin 1967) and acclimated to the test temperature for at least 3 days. Each bird was weighed at the beginning of each test and given a known amount of test food, varying from 10–50 g depending on ambient temperature. Water was provided ad lib. All experiments were run in constant temperature cabinets where temperature was controlled to ±1°C; relative humidity did not exceed 50%. After 2 days, each bird was reweighed and the excreta and remaining food were collected, oven-dried, and weighed. The heat of combustion of food and feces was determined by bomb calorimetry. Gross energy intake (kJ of food consumed) and excretory energy (kJ of feces and urine) were calculated from appropriate weights and heats of combustion (see Kendeigh 1967, Kendeigh et al. 1977). Metabolized energy (gross energy intake minus excretory energy) and efficiency of utilization (metabolized energy/gross energy intake ×100) were computed for all measurements. Tests generally were run at 2, 7, 14, 20, 26, and 32°C and photoperiods of 12L:

TABLE 1

COMPOSITION OF FOODS USED IN METABOLIC STUDIES AND PREFERENCE TESTS OF HOUSE FINCHES

Food	kJ/g	Lipid (%)	Protein (%)	Ash (%)	Carbohydrate (%)
Chick mash	17.2	6.6	19.0	10.5	63.9
Chick mash + oil	20.5	25.3	15.0	8.4	51.3
Chick mash + soy	18.0	3.6	31.0	8.4	57.0
Milo	18.0	3.1	10.0	1.9	85.0
Millet	18.4	3.6	11.3	5.7	79.4
Sunflower	28.5	40.7	42.1	2.3	14.9

12D and 10L:14D with each of three different foods. The single exception was elimination of 2°C tests with protein-supplemented food; poor survival of birds tested at 7°C indicated that 2°C tests were impossible. Every test, including each combination of photoperiod, temperature, and food type, involved three replicates performed with each of four birds, except those tests in which birds died, whereupon the test was completed with the remaining birds. Fifteen different House Finches were used. The food types used were chick starter mash, fat-supplemented mash consisting of chick mash plus 20% (by weight) vegetable oil (shortening), and protein-supplemented mash composed of chick mash containing 50% ground soy meal. The percentage of protein in each food type was obtained by Kjeldahl analysis, lipids by Soxhlet extraction in 5:1 petroleum ether:chloroform, ash by combustion in a muffle furnace at 550°C, and carbohydrate by subtraction (Table 1). For comparative purposes, House Sparrows were tested in the same fashion as House Finches at temperatures of 7 and 14°C, and a photoperiod of 12L:12D, using all three foods. Nine different sparrows were used and two replicates were made for each bird at each combination of conditions.

Food preference tests.—In preparation for each food preference test, birds were placed individually in the cages used for the metabolic tests, and given water and one of the three test foods ad lib. They were acclimated to test conditions for at least 3 days. At the beginning of each test, birds were presented with 10 g of each of the three types of mash in separate containers. The position of the food containers was systematically changed with each replicate to eliminate bias. Three replicates were completed with each bird. The amount of each food eaten was presumed to be the difference between weights of food at start and finish of each test. Test periods lasted 3 h. Control tests indicated that there was no weight change of foods under these conditions. This procedure was repeated on three different days to complete a given test. Four different tests were run, all on a photoperiod of 12L:12D, at temperatures of 7, 14, 20, and 26°C, using five different finches. The same procedure was repeated, using milo, white millet, and sunflower seed as the test foods. The composition of the seeds was determined as described for plain and supplemented chick mash above, and is listed in Table 1. Seed preference tests were run on a photoperiod of 12L:12D, at temperatures of 7, 14, and 20°C using four different finches with three replicates of each bird.

All analyses were performed by means of the Statistical Analysis System (SAS Institute 1982). A significance level of $P < 0.01$ was used in all tests. Covariance analyses of body weight and metabolism were computed with photoperiod, food, and sex included as clas-

TABLE 2
ANALYSIS OF COVARIANCE OF HOUSE FINCH BODY WEIGHT (G)

Source	df	Sum of squares	*F*
Model	10	68.5	3.02**
Error	108	244.9	
Total	118	313.5	
Sex	1	27.99	12.34**
Photoperiod	1	0.55	0.24
Food type	2	19.29	4.25**
Temperature	6	15.57	1.14

** $P \leq 0.01$.

sification variables (see Zar 1974), and weight, weight change, and ambient temperature included as covariants.

RESULTS

Body weight.—Covariance analysis indicates that sex and food type have significant effects on mean body weight during measurements of metabolism (Table 2). House Finches were able to maintain body weights at low ambient temperatures (i.e., below 20°C) only while being fed oil-supplemented mash (see Table 3), and mean body weight was significantly higher on this diet than on others ($t = 3.2$). Weight of the birds was lowest while being fed the unsupplemented mash and weight loss became more severe as ambient temperature decreased. At 2°C, 12L:12D, three of four birds being tested died. Weight losses of birds being fed soy-supplemented mash were minor until ambient temperatures of 7°C, when weight loss became severe and three of four birds being tested died, two on a photoperiod of 12L:12D and one at 10L:14D. An additional bird was removed from the 10L:14D photoperiod test due to extreme weight loss. The remaining birds were not tested at 2°C on the soy-supplemented mash; we assume they would not have survived. All deaths were preceded by large weight losses. The mean weight of six birds that died during the experiments was 16.1 g. The mean weight of 15 living birds (computed throughout all experiments, N = 282) was 20.0 ± 0.2 g (SE). Males (21.7 ± 0.2 g; N = 92) weighed more than females (20.6 ± 0.1; N = 190), and the difference is significant ($t = 4.9$). House Sparrows tested as "controls" maintained body weight under all conditions, but weighed significantly more ($t = 3.3$) when fed the oil-supplemented food.

Analysis of covariance indicates that differences in metabolized energy due to sex and photoperiod were not statistically significant; those data

TABLE 3
BODY WEIGHT, METABOLIZED ENERGY, AND EFFICIENCY OF USE IN HOUSE FINCHES

Temperature (°C)	N	Body weight[a] (g)	Metabolized energy[a] (kJ/day)	Efficiency[a] (%)
		Mash		
2	2	19.3 ± 2.5	65.5 ± 2.3	69.2 ± 0.6
7	8	20.0 ± 0.4	58.8 ± 3.1	71.3 ± 1.0
14	8	21.0 ± 0.4	44.2 ± 2.7	69.8 ± 1.1
20	8	20.8 ± 0.6	47.7 ± 1.9	73.2 ± 1.0
26	8	20.5 ± 0.5	37.4 ± 1.5	72.9 ± 0.8
32	4	20.7 ± 0.5	43.4 ± 3.1	72.6 ± 1.5
35	4	20.0 ± 0.3	38.1 ± 2.0	76.6 ± 0.4
		Soy-supplemented mash		
7	4	19.8 ± 0.6	41.8 ± 2.4	61.9 ± 2.3
14	4	20.3 ± 0.5	54.5 ± 2.2	62.3 ± 1.3
20	6	21.4 ± 0.5	50.8 ± 2.2	63.8 ± 1.8
26	8	21.6 ± 0.8	39.2 ± 3.2	61.1 ± 2.1
32	6	21.5 ± 0.8	47.1 ± 3.5	66.8 ± 1.5
		Oil-supplemented mash		
2	4	21.6 ± 0.7	91.0 ± 8.0	65.9 ± 1.8
7	4	21.5 ± 0.6	87.6 ± 2.6	74.8 ± 2.8
14	4	21.8 ± 0.3	74.3 ± 5.2	77.9 ± 1.3
20	6	21.7 ± 0.6	65.4 ± 5.5	74.3 ± 1.7
26	8	21.7 ± 0.6	52.5 ± 3.2	81.7 ± 0.8
32	6	21.7 ± 0.7	57.3 ± 4.4	79.3 ± 2.8

[a] Values are means ± 1 SE.

were pooled and reanalyzed using food as a class, and weight, weight change, and temperature as covariants. Metabolized energy is most affected by temperature, followed by food type, weight change, and weight, in that order, as judged by the portion of the total sum of squares attributable to these variables (Table 4). The multiple regression model that accounted for the greatest amount of variation indicated that metabolized energy (ME, in kJ) was inversely correlated with temperature, and directly correlated with both weight and weight change as follows:

$$\text{ME} = 51.8 + 1.7 \text{ weight (g)} + 14.6 \text{ weight change (g)} - 0.8 \text{ temperature (°C)} - 7.9 \text{ food}$$

where food is treated as a classification variable; oil-supplemented mash = 1, soy-supplemented mash = 2, unsupplemented mash = 3 ($R^2 = 0.56$). Least squares means (estimates of sample means corrected for effects of covariants) ± 1 SE indicate that the House Finch metabolizes significantly

TABLE 4

ANALYSIS OF COVARIANCE OF METABOLIZED ENERGY OF HOUSE FINCHES

Source	df	Sum of squares	*F*
Model	12	1677.4	22.9**
Error	106	647.5	
Total	118	2324.9	
Weight	1	26.3	4.0**
Temperature	6	690.4	18.8**
Weight change	1	99.1	16.2**
Food type	2	283.9	23.2**
Sex	1	12.3	2.0
Photoperiod	1	0.003	0.01

** $P < 0.01$.

more energy per day from the oil-supplemented diet (65.7 ± 1.7 kJ) than from soy-supplemented (48.5 ± 1.3 kJ) or unsupplemented diets (47.3 ± 0.8 kJ; see Table 3). Analysis of residuals indicated that there was no further source of temperature-related variation not accounted for, and that the data are linear with respect to temperature. House Sparrows likewise metabolized more of the oil-supplemented mash than the other foods (Table 5).

Arcsine transformations of efficiency ratios were computed and tested using analysis of covariance. As before, the three food types, sex, and photoperiod were treated as covariants. Differences in efficiency due to sex, photoperiod, and weight change were not significant (Table 6), and these data were pooled. Reanalysis using food as a class, and temperature and weight as covariants indicated that energetic efficiency was, by far, most influenced by food type, then by temperature, and lastly by weight, as judged by the portions of the total sums of squares attributable to each of these variables. The "best" multiple regression model ($R^2 = 0.50$) shows energetic efficiency to be inversely correlated with weight and positively correlated with temperature as follows:

$$\text{TEFF} = 1.27 - 0.01 \text{ weight (g)} + 0.003 \text{ temperature (°C)} - 0.08 \text{ food}$$

where TEFF is arcsine-transformed efficiency, and food is treated as a classification variable as above.

Least squares means indicated that the birds used the oil-supplemented mash most efficiently, unsupplemented mash second, and soy-supplemented mash least efficiently. A large amount of variation in energetic efficiency remains unaccounted for by the "best" regression model. How-

TABLE 5

METABOLIZED ENERGY AND EFFICIENCY OF USE OF HOUSE SPARROWS AS MEASURED IN THIS STUDY AND AS PREDICTED FROM EQUATIONS IN BLEM (1973, 1976A)

Temperature (°C)	N	Metabolized energy (kJ)[a]		Efficiency (%)[a]	
		This study	Predicted	This study	Predicted
		Mash			
7	5	96.2 ± 4.0	98.7	72.4 ± 5.4	76.2
14	5	72.4 ± 4.1	86.2	71.5 ± 4.2	75.1
		Soy-supplemented mash			
7	4	94.1 ± 6.2	96.7	64.5 ± 1.9	66.1
14	4	85.8 ± 8.1	90.0	64.0 ± 4.3	64.8
		Oil-supplemented mash			
7	5	146.0 ± 7.3	—	77.9 ± 5.4	83.0
14	6	138.1 ± 9.4	—	79.9 ± 2.8	82.1

[a] Values are means ± 1 SE.

ever, analysis of residuals indicated that there was no further source of temperature-related variation not accounted for, and that the data are linear with respect to temperature.

Energetic efficiencies of House Sparrows were similar to those found by Blem (1976a) using similar diets, and metabolized energies were similar to those found by Kendeigh and Blem (1973) for the winter-adapted House Sparrow (Table 5). Like the finches, the sparrows metabolized by far the larger proportion of calories from the oil-supplemented diet. Also like the finches, calories metabolized from the unsupplemented and soy-supplemented mashes were nearly equal, although the soy-supplemented mash was slightly higher. Although the differences are not statistically significant, House Sparrows seemingly metabolized all three diets at 7 and 14°C more efficiently than the finches.

Food preference.—The percentage of oil-supplemented food chosen at each test temperature was greater than either of the other test foods. Statistical comparisons of preferences are not possible in a conventional fashion; percentages of food selected are interdependent since preference of one food precludes others being selected during individual tests. Even so, the great difference between the amount of oil-supplemented mash and the other types chosen over the series of tests, leads us to seriously question the null hypothesis of no difference in food preference. Oil-supplemented mash constituted 88–92% of the total weight of food eaten, while neither of the other mashes ever amounted to more than 6% of the total.

TABLE 6
ANALYSIS OF COVARIANCE OF EFFICIENCY OF USE OF HOUSE FINCHES[a]

Source	df	Sum of squares	*F*
Model	12	0.457	17.5**
Error	106	0.220	
Total	118	0.676	
Weight	1	0.015	6.9**
Temperature	6	0.110	8.4**
Weight change	1	0.001	0.5
Food type	2	0.382	87.8**
Sex	1	0.003	1.3
Photoperiod	1	0.002	0.8

** $P < 0.01$.

[a] The ratio, metabolized energy/gross energy intake, was transformed by the arcsine procedure (Zar 1974).

In seed preference tests, finches chose sunflower seeds almost exclusively at all temperatures. At 7°C, sunflower seeds comprised 82.4% by weight of the seeds chosen; at 14°C they comprised 99.3%, at 20°C, 100.0%. Millet comprised the remaining percentage of seeds. No milo was eaten at any temperature.

DISCUSSION

Birds invading new areas must make a variety of adjustments to unfamiliar environments. One of the most serious of these is exploitation of new food sources. In much of the United States, and particularly in centers of human population density, the food placed in bird feeders represents a major nutritional resource which may permit the existence of birds not otherwise capable of finding energy sources. We believe the House Finch is such a species.

The House Finch first appeared in Virginia in 1962 and became a breeding species in the Richmond area by 1978 (Blem and Mehner 1981). Today it is a very common permanent resident in urban areas of central Virginia; nearly every city block in Richmond has a male House Finch singing on territory in the spring. We suggest this rapid spread has been aided by artificial food sources provided by humans and perhaps also by the altered microclimate available around human habitations. In the Richmond area, hundreds of House Finches gather at local feeders and are present throughout the winter. A variety of foods may be found in such feeders, but the commonest ingredients are sunflower seeds, white and red millet, and milo. We are aware of little data regarding the food habits of eastern House Finches, but our impression from field studies is that the species shows a definite preference for artificial food sources (also see Aldrich and Weske 1978). Under natural conditions we have observed House Finches feeding on the seeds of the sweet gum (*Liquidambar styraciflua*) and on unidentified weed seeds, but such observations are not common.

Without artificial food sources we believe that mid-winter survival of House Finches in the newly colonized part of the range would be difficult. Observations by Elliot and Arbib (1953), Katholi (1967), and Aldrich and Weske (1978) support the notion that present eastern House Finch populations generally are sedentary and subject to mid-winter mortality. In Richmond, during two periods of extreme cold in the winter of 1981–82, there were several reports of House Finch mortality at more than one locality, including one observation of 20–30 dead or dying finches at a single location (perhaps 10% of a wintering flock visiting a local feeder; M. O'Bryan, pers. comm.). Additionally we have observed that the number of finches visiting feeders in the Richmond area decreases over winter (unpubl.).

Evaluating the nutritional quality of wild bird food has only recently been attempted and we are aware of only a few studies that provide useful information on nutritional quality of natural foods for small passerines. Willson and Harmeson (1973) suggested that seeds may be selected according to east of handling, but in their study, Cardinals (*Cardinalis cardinalis*) chose foods with higher caloric content at lower ambient temperatures. No correlation was found between energetic efficiency and seed preference. Blem (1976a) found significant relationships between food composition and energetic efficiency in the House Sparrow. Specifically, there is a strong positive correlation between energetic efficiency and fat content of food and a negative correlation between protein content and efficiency. Williams and Hansell (1981) found that Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*) metabolizes dried mealworms more efficiently than chick starter mash. Browning (1981) showed that the Field Sparrow (*Spizella pusilla*) and the Cardinal could choose high quality seeds over those of lesser nutritional quality. However, the seeds they used were very different morphologically, and choices may have been due to differences in the birds' ability to handle the different seeds. Several authors have noted a preference of birds for seeds high in fat (Kear 1962, Conley and Blem 1978).

In the present study it appears that the composition of food affected survival of low ambient temperature. No mortality occurred in birds fed the oil-supplemented diet and the ability of finches to extract energy from this food was greatly enhanced in comparison to soy-supplemented or unsupplemented mash. Inspection of metabolic data further illustrates this. Simple regression equations were computed for birds being fed each of the three foods. It is obvious that the high protein content of soy-supplemented mash interferes with efficiency of utilization at 7°C and metabolic rates of all finches are elevated at 32–35°C. Eliminating metabolic rates at these temperatures, final equations are:

$$\begin{array}{ll} \text{mash} & M = 54.88 - 0.43\,T; \\ \text{soy + mash} & M = 61.43 - 0.78\,T; \\ \text{oil + mash} & M = 85.52 - 1.19\,T \end{array}$$

where M = metabolism in $\text{kJ}\cdot\text{bird}^{-1}\text{day}^{-1}$ and T = ambient temperature in °C. There is a visible progression of increasing slopes and intercepts that is directly correlated with fat content of the food, and, to a degree, inversely correlated with protein content. It is obvious that much more energy is metabolized from the oil-supplemented food even though its caloric content is not a great deal higher (Table 1).

Metabolized energy of birds fed soy- and oil-supplemented mashes increased at 32°C over measurements at 26°C. Since this did not occur in birds fed plain mash, we suggest that there may have been greater effects of specific dynamic action associated with the supplemented foods (see Blem 1976a). Metabolized energy of finches fed chick mash was similar in the range 26–35°C. These results suggest the thermal neutral zone commonly found in measurements of the standard metabolism of endotherms, but which is relatively unknown in measurements of metabolized energy (West 1962). Salt (1952) found the thermal neutral zone in California House Finches to be 24–27°C. Perhaps increased levels of metabolized energy at temperatures above 30°C reflect heat stress, especially in those birds being fed high protein food with its associated specific dynamic action.

Our data indicate that metabolized energy and efficiency of utilization of House Finches are both significant functions of food composition. Significantly, food type has a prominant effect on body weight of House Finches even when the effects of temperature, sex, and photoperiod are accounted for (Table 2). Metabolized energy and efficiency of utilization were highest on the oil-supplemented diet, presumably because of the ease of assimilation and relatively great efficiency of lipid metabolism in birds (see Blem 1976b). It appears likely that natural selection favors increased handling abilities for those seeds whose availabilities and compositions promote survival and we believe that this is true in the case of the eastern House Finch. Aldrich (1982) has shown that the eastern race of the House Finch has a larger average bill size than the parental stock. It is logical that those individuals best able to handle sunflower seeds, a large food particle relative to other foods available to the House Finch, would be those birds with larger bills (see Willson 1971).

Our evidence for the relationship between food preference, cold tolerance, and bill size in House Finches is, of course, not direct. We have shown: (1) food composition is extremely important in the efficiency with which House Finches extract energy from food; (2) foods high in lipid are more efficiently used; (3) cold tolerance is enhanced by foods high in lipid; (4) eastern House Finches prefer foods high in lipid, including sunflower seeds; and (5) survival of extreme cold weather in mid-winter is a particular problem of recently established eastern House Finch populations. Dawson et al. (1983) also indicate that eastern House Finch populations are in the midst of evolution of increased cold tolerance. We have not shown a correlation between bill size and efficiency of handling sunflower seeds, although it has been suggested many times that bill size and size of food items are correlated (see Willson 1971).

SUMMARY

The eastern race of the House Finch (*Carpodacus mexicanus*) tolerates low winter temperatures very poorly. Laboratory tests indicate that their metabolism and cold tolerance is, at least partially, a function of food composition. In the laboratory, oil-supplemented chick mash was preferred over soy-supplemented or unsupplemented mash and was more efficiently metabolized. House Finches select sunflower seeds over millet and milo and this preference may be related to the distinctly higher fat content of the former. Evolution of larger bill size in the eastern race of the House Finch may be due to preference for sunflower seeds at bird feeders in winter, increased cold tolerance as a result of this choice, and the increased range of permanent residency of this species.

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