

INFLUENCES OF TIME POSTMORTEM, FEEDING ACTIVITY, AND DIET ON DIGESTIVE ORGAN MORPHOLOGY OF TWO EMBERIZIDS

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ABSTRACT.—We conducted experiments to determine the effect of time postmortem, feeding activity, and diet on changes in digestive organ morphology in Dark-eyed Juncos (*Junco hyemalis*) and Harris' Sparrows (*Zonotrichia querula*). We measured digestive organs immediately, or at 30, 60, or 90 min postmortem, but detected no time-related differences in Dark-eyed Juncos. The small intestines of free-feeding Dark-eyed Juncos were longer than those of food-deprived birds. We found no significant diet-related differences in lengths of small intestines of Harris' Sparrows. Liver mass reflected energy intake of free-feeding versus food-deprived Harris' Sparrows. Received 4 August 1989, accepted 7 April 1990.

THE AVIAN literature abounds with descriptions of changes in digestive organ morphology. Researchers attributed changes in avian gizzard size to the texture and fiber content of the diet (Ziswiler and Farner 1972, Savory and Gentle 1976a, Kehoe and Ankney 1985), and reported a relationship between gizzard mass and body mass in northern Galliformes (Thomas 1984, Moss 1983). Leopold (1953) and Kehoe and Ankney (1985) suggested that a high-fiber diet causes increased lengths of small intestines, a conclusion reached by several researchers working on tetraonids (Moss 1974, Pendergast and Boag 1973, Pulliainen and Tunkkari 1983). A causal relationship between cecal size and dietary fiber was proposed (Leopold 1953) and supported with experimental evidence (Moss 1972, 1989; Savory and Gentle 1976b; Moss and Trenholm 1987; but see Remington 1989). Ziswiler and Farner (1972) contended that large-intestine length reflects the diet of avian species, and Savory and Gentle (1976a, b) could produce increases in large-intestine length by adding fiber to the diet of Japanese Quail (*Coturnix coturnix*).

Most pertinent reports on avian species have involved gallinaceous birds and waterfowl. Little attention has been focused on changes in gut morphology of passerines, or the influence of time postmortem or feeding activity on measurements of gut morphology. In this study, we examined the effects of time postmortem, feeding activity, and diet on digestive organ morphology of two emberizids, Harris' Sparrow

(*Zonotrichia querula*) and the Dark-eyed Junco (*Junco hyemalis*).

METHODS

Birds were captured during winter near Manhattan, Kansas. After capture, all birds were confined individually in 38 × 22 × 27-cm wire cages and placed in an environmental chamber under constant 10°C temperature, 10L:14D photoperiod, and 76–78% relative humidity. Water and a maintenance pelleted mash diet were provided *ad libitum* for at least 30 days before any experimentation. Before and during experiments, we measured mass to the nearest 0.01 g within 15 min of the onset of the light period. After birds were killed by cervical dislocation, we measured wing length (distance from proximal tip of carpo-metacarpus to tip of leading primary feather), and determined age (by skull ossification; Wiseman 1962) and sex (by examination of gonads).

We removed the gastrointestinal tracts and associated organs from the carcasses, and discarded the esophagus, proventriculus, and pancreas. The small intestine was isolated by separation at the gizzard and ileo-cecal junctions. The ceca were disjoined from the small intestine, and the large intestine was considered to be that portion from the ileo-cecal junction to and including the cloaca. Lengths of ceca (both combined), small intestine, and large intestine were measured to the nearest 1.0 mm using Leopold's straight ruler technique (Freehling and Moore 1987). One person measured the lengths of all intestines and ceca. Wet masses (patted dry) of small intestine, large intestine, ceca (both combined), gizzard (without contents), and liver were recorded to the nearest 0.1 mg. After measuring and determining wet mass, we dried intestines and associated organs at 65°C for 24 h, and

determined their mass again to the nearest 0.1 mg. Data were analyzed using analysis of variance (ANOVA) procedures, including ANOVA for repeated 4×4 Latin Squares (Cochran and Cox 1962). Fisher's protected least significant difference (LSD) (Ott 1984) was used for pairwise comparisons. The significance level for all tests was $P = 0.05$; means in the text are presented $\pm$ SE.

The nutrient value of feeds used in the experiments was determined by examining one sample of each by proximate analysis, moisture content by mass loss, ash by igniting dried samples at 600°C , crude fat by diethyl ether extraction (Cullison 1982), and crude protein by the Kjeldahl method (Perry 1984). Residue remaining after acidic and alkaline digestion was considered crude fiber (Nagy and Haufler 1980), and nitrogen-free extract less ash was the remaining fraction of the sample. Energy content was determined in an adiabatic oxygen bomb calorimeter.

EXPERIMENT I

Postmortem changes.—Thirty-two Dark-eyed Juncos were divided into two 16-bird groups. One group consisted of adult males, and the second contained juvenile males and females of unknown age. Wing length was used to separate adult males from females, and to separate juveniles from adults (Yunick 1981). Each group was assigned randomly to 4×4 Latin Squares. The blocking factors (rows and columns) in the Latin Squares were groups of birds and day of sacrifice, with day of sacrifice being common among squares. Water and a balanced mash were provided *ad libitum* during the experiment. Treatments consisted of killing specific birds and eviscerating them immediately or at 30, 60, or 90 min after death. Four birds from each group (8 birds) were killed at the onset of the light period each day, and measurements were made of digestive tracts and organs at predetermined postmortem times.

The data from the two Latin Squares were analyzed as repeated 4×4 Latin Squares with day of sacrifice common between squares and groups of birds nested within squares. Thus the model was

$$Y_{ijkl} = \mu + S_i + G_{(ij)} + D_k + T_l + e_{ijkl}$$

where Y_{ijkl} is the response observed in the i th square, for the j th group of birds, killed on the k th day, and eviscerated at the l th time, μ represents the overall mean of the response variable, S_i represents the effect of the i th square of birds (adult male or mixed immatures and females), $G_{(ij)}$ represents the j th randomly assigned group of birds within the i th square, D_k represents the effect of the k th day, T_l represents the effect of the l th time at evisceration, and e_{ijkl} represents the random error associated with the i, j, k , and l th observation and assumed to be distributed $N(0, \sigma^2)$.

EXPERIMENT II

Feeding activity.—Dark-eyed Juncos ($n = 64$) were divided randomly into four 16-bird groups, and each was assigned randomly to 4×4 Latin Squares. Birds were not segregated by sex or age. Water was provided *ad libitum* during all trials. Free-feeding and food-deprivation trials were conducted; each used two 16-bird groups. In food-deprivation trials, we removed food from the cage at the onset of the photoperiod on the day birds were to be killed; otherwise, the balanced mash was provided *ad libitum*. In the free-feeding trials, the balanced mash was provided *ad libitum* throughout. Four birds from each treatment group were killed each day either at onset or 3, 6, or 9 h after the beginning of the light period.

We measured the mass of each bird at the onset of the light period and when killed. Before we measured the intestines for length, we purged them of food. We recorded wet masses of small intestines before and after purging them. Measurements of intestines and associated organs were as described above.

The data from the four Latin Squares were analyzed by analysis of variance as pairs of repeated 4×4 Latin Squares. The model used in the analysis was

$$Y_{ijklm} = \mu + T_i + S_{(ij)} + D_k + G_{(ijl)} + H_m + e_{ijklm}$$

where Y_{ijklm} is the response observed for the i th feeding treatment, the j th square within the i th feeding treatment, the k th day, the l th group of birds within the j th square of the i th feeding treatment and the m th hour; μ represents the overall mean of the response variable; T_i represents the i th feeding treatment—deprived or full-fed; $S_{(ij)}$ represents the effect of the i th square within the j th feeding regime; D_k represents the k th day; $G_{(ijl)}$ represents the l th group of 4 birds that were sacrificed from the j th square on the i th treatment; H_m represents the m th hour at which evaluation occurred after onset of the photoperiod (0, 3, 6, or 9), and e_{ijklm} represents the random error associated with the i, j, k, l , and m th observation and assumed distributed $N(0, \sigma^2)$.

EXPERIMENT III

Diet influences.—Harris' Sparrows ($n = 35$) that had been fed a balanced mash for 30 days in the environmental chamber were divided randomly into four groups. Ten were fed sunflower (*Helianthus annuus*) seeds, 10 were fed white proso millet (*Panicum miliaceum*) seeds, 10 were fed the balanced mash, and 5 provided baseline information. The 5-bird group was killed on the first day of the trial, and pertinent measurements were made to characterize the experimental birds. Food (either sunflower seeds, millet seeds, or mash) and water were provided *ad libitum*. Water-soluble vitamin and mineral supplements were added

to the water of each bird each day to minimize dietary deficiencies due to single-seed diets.

Five birds in each of the 10-bird groups were maintained on their respective diets for 7 or 14 days, then killed. This yielded seven 5-bird groups: 1 baseline group, 3 groups fed different feeds for 7 days, and 3 groups fed different feeds for 14 days. Carcass mass was determined and wings measured, the birds were eviscerated, and their digestive tract and organs were measured as described previously. Food consumed was determined by subtracting spilled and uneaten food from the amount provided each bird.

One-way analysis of variance was used to compare the 7-treatment group means for the variables of interest. In the cases where the *F*-tests were significant, LSDs were used to separate treatment means. To compare feed main effects, the baseline group was dropped from the analysis and the remaining 6 groups were compared in a 3×2 factorial ANOVA with the 3 types of feeds constituting one factor, and time on feed the other. The error mean square from the 7-treatment ANOVA was used as the *F*-test denominator in the 3×2 factorial analysis.

RESULTS

The three foods used in the experiments varied in nutritional characteristics. Sunflower seeds had the highest energy content and the least fiber (Table 1). Millet seeds had twice the fiber content and approximately 60% of the energy content of sunflower seeds (Table 1).

DARK-EYED JUNCOS

Postmortem changes.—Cranial ossification was complete in some females; therefore, we could not age females accurately. Wing lengths of adult males (80.6 ± 0.4 mm) were significantly longer than those of juvenile males (75.3 ± 0.8 mm) and unknown aged females (75.1 ± 0.5 mm). The body mass of adult males (19.1 ± 0.3 g) was significantly greater than in juvenile males (17.8 ± 0.4 g) and unknown aged females (17.8 ± 0.5 g). Except for dry cecal masses, we detected no differences in length or mass of intestines or associated organs among adult males, juvenile males, or females of unknown age. Dry cecal mass of adult males (2.2 ± 0.1 mg) and females of unknown age (2.0 ± 0.2 mg) was significantly heavier than that of juvenile males (1.6 ± 0.2 mg). Because of the lack of differences among measurements of birds of different mass and among age/sex groups (except dry cecal mass),

TABLE 1. Selected nutritional characteristics of the three feeds.

Characteristic	Mash	Millet seeds	Sunflower seeds
Energy content ($\text{kJ} \cdot \text{g}^{-1}$) ^a	19.3	19.7	31.4
Crude protein (%)	24.9	11.4	25.7
Ether extract (%)	1.6	4.2	56.1
Crude fiber (%)	4.5	6.5	3.1
Ash (%)	6.8	3.8	3.3
Nitrogen-free extract (%)	62.2	74.1	11.8
Moisture (%)	12.5	12.9	6.3

^a All measurements in dry mass, except for moisture measurements.

data were pooled to determine effects of time postmortem on length and mass of intestines and associated organs.

Not one of the intestine lengths or associated organ masses was significantly different when measured immediately or at 30, 60, or 90 min after death (Table 2). The dry mass to wet mass ratios were fairly consistent over the 90-min time period for small intestines (0.25:0.22), gizzards (0.30:0.29), and livers (0.30:0.29), but decreased slightly with time for large intestines (0.17:0.12).

Feeding activity.—Initial masses of food-deprived (18.4 ± 0.3 g) and free-feeding (18.5 ± 0.4 g) birds did not differ, but 3 h after the onset of the light period, the mass of free-feeding birds increased to 20.2 ± 0.6 g, which was significantly greater than the 17.9 ± 0.2 g of food-deprived birds. By hour 9, the mass of free-feeding birds was 20.4 ± 0.4 g, significantly more than the 16.5 ± 0.3 g of food-deprived birds.

There was no significant difference in the lengths of small intestines of free-feeding and food-deprived birds at the start of the light period, but from the third hour on, the lengths of the small intestine of free-feeding birds were significantly longer than those of food-deprived birds (Table 3, Fig. 1). Wet masses of small intestines of food-deprived birds and those of small intestines without contents of free-feeding birds did not change or differ with time. After 3 h into the light period, however, each was significantly lighter than wet masses of small intestines with contents. We observed no significant differences in dry masses of the small intestines from free-feeding or food-deprived birds throughout the 9-h experiment.

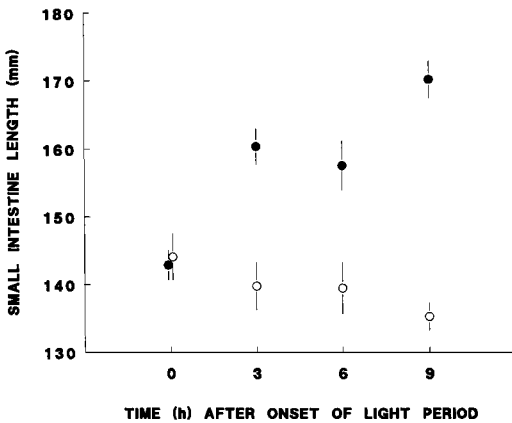


Fig. 1. Mean ($n = 8$) lengths of small intestines from free-feeding (closed circles) and food-deprived (open circles) Dark-eyed Juncos killed at various times after onset of the light period. Vertical lines extend ± 1 SE.

No significant changes occurred in the lengths or wet masses of large intestines of free-feeding and food-deprived birds. The dry masses of large intestines of free-feeding and food-deprived birds did not differ at the start of the experiment, but the dry masses of large intestines from

free-feeding birds were significantly greater than those of food-deprived birds 9 h after the onset of the light period (Table 3).

Lengths and wet masses of ceca from free-feeding and food-deprived birds did not differ during the 9-h experiment. Dry mass, however, of ceca of free-feeding birds was greater than that of food-deprived birds throughout the experiment (Table 3). No significant differences were detected in the wet or dry masses of gizzards (Table 3).

Although liver wet masses of food-deprived and free-feeding birds were not significantly different at the start of the experiment, they declined during the experiment for food-deprived birds and increased for free-feeding birds (Fig. 1). Liver wet mass was significantly heavier in free-feeding birds from the third hour onward (Table 3). An identical pattern of change was observed in dry masses of livers (Table 3).

HARRIS' SPARROWS

Diet influences.—At the start of this 14-day experiment, wing lengths of birds assigned to each diet did not differ. Initial masses of the three diet groups did not differ significantly. Birds

TABLE 2. Mean ($\pm$ SE) wing lengths (mm), body masses (g), and digestive organ lengths (mm) and masses (mg) from Dark-eyed Juncos ($n = 8$) taken at selected times postmortem.

Parameter	Time postmortem (min)				Experimental SE
	0	30	60	90	
Wing length	77.3 $\pm$ 1.2*	77.6 $\pm$ 1.1	78.7 $\pm$ 1.1	77.9 $\pm$ 1.2	1.1
Body mass	18.7 $\pm$ 0.4	18.1 $\pm$ 0.6	18.0 $\pm$ 0.6	19.0 $\pm$ 0.6	0.5
Small intestine					
Length	142.1 $\pm$ 2.1	140.2 $\pm$ 3.1	138.5 $\pm$ 3.6	143.3 $\pm$ 3.0	3.0
Wet mass	650.0 $\pm$ 34.3	653.8 $\pm$ 51.2	585.0 $\pm$ 27.4	637.5 $\pm$ 50.1	40.8
Dry mass	159.7 $\pm$ 8.3	147.5 $\pm$ 13.9	129.1 $\pm$ 5.9	141.3 $\pm$ 8.9	9.3
Large intestine					
Length	13.6 $\pm$ 1.4	12.0 $\pm$ 1.0	13.2 $\pm$ 1.5	15.1 $\pm$ 1.0	1.2
Wet mass	40.0 $\pm$ 3.8	40.0 $\pm$ 6.0	36.2 $\pm$ 5.0	43.8 $\pm$ 5.0	4.9
Dry mass	6.8 $\pm$ 0.6	5.4 $\pm$ 0.4	4.7 $\pm$ 0.8	5.4 $\pm$ 0.5	0.5
Ceca (combined)					
Length	5.1 $\pm$ 0.4	5.8 $\pm$ 0.3	5.3 $\pm$ 0.7	6.5 $\pm$ 0.5	0.5
Dry mass	2.2 $\pm$ 0.2	2.1 $\pm$ 0.2	1.9 $\pm$ 0.2	2.1 $\pm$ 0.2	0.2
Gizzard					
Wet mass	582.5 $\pm$ 22.4	613.8 $\pm$ 23.1	582.5 $\pm$ 28.0	606.3 $\pm$ 17.4	22.7
Dry mass	174.6 $\pm$ 7.6	175.8 $\pm$ 10.3	165.9 $\pm$ 8.9	176.5 $\pm$ 6.9	8.4
Liver					
Wet mass	637.5 $\pm$ 29.7	757.5 $\pm$ 50.1	750.0 $\pm$ 29.1	746.3 $\pm$ 36.2	36.3
Dry mass	190.3 $\pm$ 8.1	218.5 $\pm$ 16.0	212.6 $\pm$ 6.0	216.9 $\pm$ 12.9	10.8

* Means within a row are not significantly different ($P = 0.05$).

TABLE 3. Mean ($\pm$ SE) lengths (mm) and masses (mg) of digestive organs from free-feeding and food-deprived Dark-eyed Juncos ($n = 8$) killed at various times after onset of the light period.

Measurement	Time (h) after onset of light period				Experimental SE
	0	3	6	9	
Small Intestine					
Length					
Food-deprived	144.1 ± 3.4A*	139.8 ± 3.5A	139.5 ± 3.8A	135.3 ± 2.0B	3.0
Free-feeding	142.9 ± 2.2A	160.4 ± 2.6C	157.6 ± 3.6C	170.3 ± 2.7D	
Wet mass					
Food-deprived	608.7 ± 27.9A	624.4 ± 32.3A	542.7 ± 31.1A	501.9 ± 32.7A	64.8
Free-feeding					
(minus contents	512.8 ± 49.6A	553.5 ± 31.9A	494.9 ± 65.6A	562.4 ± 97.1A	
Free-feeding					
(with contents)	512.8 ± 49.6A	1,035.3 ± 43.9B	938.1 ± 65.2B	1,101.7 ± 51.9B	
Dry mass					
Food-deprived	158.1 ± 9.4	160.1 ± 6.3	127.1 ± 6.6	129.5 ± 7.1	13.0
Free-feeding	128.7 ± 12.4	162.5 ± 21.0	151.0 ± 18.3	176.6 ± 23.1	
Large Intestine					
Length					
Food-deprived	8.5 ± 0.7	9.0 ± 1.0	8.5 ± 0.6	8.8 ± 0.6	0.8
Free-feeding	9.3 ± 0.8	10.8 ± 0.8	9.3 ± 1.0	11.1 ± 0.7	
Wet mass					
Food-deprived	27.2 ± 2.2	25.4 ± 2.3	21.5 ± 3.2	21.0 ± 2.8	2.2
Free-feeding	20.8 ± 1.6	25.5 ± 1.1	18.7 ± 1.4	23.2 ± 2.9	
Dry mass					
Food-deprived	6.1 ± 0.6AB	6.2 ± 0.6AB	5.5 ± 0.7BC	4.3 ± 0.7C	0.6
Free-feeding	4.8 ± 0.2BC	7.3 ± 0.4A	6.3 ± 0.5AB	7.2 ± 0.7A	
Ceca (combined)					
Length					
Food-deprived	5.5 ± 0.5	5.3 ± 0.5	6.0 ± 0.5	5.6 ± 0.6	0.5
Free-feeding	6.0 ± 0.4	6.8 ± 0.5	6.6 ± 0.8	6.1 ± 0.4	
Wet mass					
Food-deprived	5.3 ± 0.9	5.8 ± 0.8	4.6 ± 0.6	5.0 ± 0.8	0.8
Free-feeding	6.4 ± 0.8	6.5 ± 0.6	6.6 ± 0.8	5.3 ± 0.8	
Dry mass					
Food-deprived	1.3 ± 0.1A	1.6 ± 0.1ABC	1.5 ± 0.3AB	1.3 ± 0.1A	0.1
Free-feeding	1.8 ± 0.2BC	1.8 ± 0.1BC	1.9 ± 0.1C	1.6 ± 0.1C	
Gizzard					
Wet mass					
Food-deprived	640.1 ± 29.8	588.5 ± 20.0	572.4 ± 19.9	580.0 ± 35.3	23.9
Free-feeding	599.1 ± 13.8	591.7 ± 26.3	612.8 ± 22.9	601.4 ± 24.4	
Dry mass					
Food-deprived	181.2 ± 7.9	169.2 ± 6.0	166.8 ± 7.7	171.2 ± 10.7	7.2
Free-feeding	171.9 ± 4.5	163.0 ± 7.1	172.5 ± 6.6	174.1 ± 7.0	
Liver					
Wet mass					
Food-deprived	655.1 ± 28.8AB	708.3 ± 43.8A	569.2 ± 18.2BC	533.1 ± 29.3C	38.6
Free-feeding	684.0 ± 28.8AB	890.7 ± 53.9D	920.2 ± 63.5D	1,054.4 ± 42.9E	
Dry mass					
Food-deprived	204.5 ± 9.8AB	217.3 ± 15.0A	177.0 ± 6.0B	166.4 ± 6.2B	13.1
Free-feeding	211.7 ± 7.6A	285.8 ± 19.4C	327.9 ± 25.1D	382.2 ± 15.5E	

^a Means unlettered or with the same letter, compared both horizontally between hours and vertically between feeding regimes for the same digestive organ, are not significantly different ($P = 0.05$).

TABLE 4. Mean ($\pm$ SE) lengths (mm) and masses (mg) of small intestines, large intestines, and combined ceca from Harris' Sparrows ($n = 5$) fed 1 of 3 feeds for 7 or 14 days.

Day/food	Length	Mass	
		Wet	Dry
Small Intestine			
Day 0			
Mash	170.0 ± 2.3 ^a	966.9 ± 60.6	126.6 ± 7.4
Day 7			
Mash	177.8 ± 5.4	1,097.2 ± 47.9	114.3 ± 5.5
Millet	173.0 ± 6.7	1,025.1 ± 71.4	107.4 ± 10.3
Sunflower	168.6 ± 4.5	1,100.2 ± 48.4	101.2 ± 9.2
Day 14			
Mash	172.4 ± 4.9	1,082.0 ± 61.4	114.2 ± 10.6
Millet	164.6 ± 1.9	915.1 ± 53.7	98.6 ± 4.9
Sunflower	181.0 ± 9.2	1,154.1 ± 58.4	107.5 ± 10.6
Experimental SE	5.0	57.5	8.5
Large Intestine			
Day 0			
Mash	14.0 ± 1.2	44.4 ± 3.2	6.6 ± 0.5
Day 7			
Mash ^b	15.5 ± 1.3	53.1 ± 6.7	6.7 ± 0.5
Millet	15.8 ± 2.1	48.1 ± 5.1	6.0 ± 0.8
Sunflower	14.0 ± 1.3	44.3 ± 5.1	6.1 ± 0.5
Day 14			
Mash	14.2 ± 1.6	43.3 ± 5.9	4.9 ± 0.6
Millet ^b	15.3 ± 1.0	46.9 ± 8.5	6.0 ± 0.4
Sunflower	14.4 ± 1.3	57.7 ± 2.4	7.0 ± 0.8
Experimental SE	1.4	5.3	0.6
Ceca (combined)			
Day 0			
Mash	6.8 ± 0.7	5.1 ± 1.1	1.5 ± 0.3
Mash ^b	6.5 ± 0.3	5.2 ± 0.9	1.4 ± 0.2
Day 7			
Millet	6.6 ± 0.2	5.1 ± 1.3	1.6 ± 0.3
Sunflower	6.6 ± 0.3	5.2 ± 0.9	1.4 ± 0.2
Day 14			
Mash	7.2 ± 0.2	4.7 ± 0.9	1.3 ± 0.1
Millet	7.0 ± 0.3	4.2 ± 0.2	1.3 ± 0.1
Sunflower	6.6 ± 0.4	4.5 ± 0.5	1.3 ± 0.1
Experimental SE	0.3	0.8	0.2

^a Means within a column for a specific organ are not significantly different ($P = 0.05$).

^b $n = 4$.

consumed 9.97 ± 0.81 g of mash per day, significantly more than millet (7.00 ± 0.38 g). Both values were significantly greater than the 4.92 ± 0.20 g of sunflower seeds consumed per day. On the seventh day of the experiment, none of the bird groups had gained or lost a significant amount of mass. At the end of the 14-day experiment, birds fed millet had lost an average of 2.2 ± 0.9 g, and those fed balanced mash had

lost an average of 0.9 ± 0.2 g. Birds fed sunflower seeds, however, had gained an average of 0.3 ± 0.8 g.

Neither length nor mass of small or large intestines or combined ceca was changed significantly by diets (Table 4). Gizzard mass of birds on different diets varied during the 14-day experiment (Table 5). No significant changes were detected in gizzard masses of birds on the

TABLE 5. Mean ($\pm$ SE) masses of gizzards and livers from Harris' Sparrows ($n = 5$) provided 1 of 3 feeds for 7 or 14 days.

Day/food	Gizzard mass		Liver mass	
	Wet	Dry	Wet	Dry
Day 0				
Mash	969.9 $\pm$ 29.0B ^a	283.6 $\pm$ 7.7B	1,209.4 $\pm$ 43.2AB	369.5 $\pm$ 14.3AB
Day 7				
Mash	949.5 $\pm$ 28.4AB	274.1 $\pm$ 5.6AB	1,301.1 $\pm$ 125.9AB	399.1 $\pm$ 26.6B
Millet	890.2 $\pm$ 30.4A	262.1 $\pm$ 13.4A	1,177.6 $\pm$ 126.0ABC	362.1 $\pm$ 36.7ABC
Sunflower	1,054.1 $\pm$ 12.4BC	316.3 $\pm$ 7.0BC	875.3 $\pm$ 43.3D	271.9 $\pm$ 13.9D
Day 14				
Mash	1,016.4 $\pm$ 57.8BC	292.4 $\pm$ 17.5BC	1,340.7 $\pm$ 97.6A	414.3 $\pm$ 25.8B
Millet	927.1 $\pm$ 56.3AB	267.0 $\pm$ 17.3AB	949.4 $\pm$ 87.3CD	299.4 $\pm$ 22.2CD
Sunflower	1,134.7 $\pm$ 62.9C	326.8 $\pm$ 17.0C	1,073.3 $\pm$ 50.9BCD	324.8 $\pm$ 16.5BCD
Experimental SE	39.6	10.8	82.0	22.3

^a Means with the same letter within a column are not significantly different ($P = 0.05$).

mash diet. Gizzard masses of birds on millet decreased significantly by the seventh day, but by the fourteenth day they were similar to the original mass. Gizzards from birds fed sunflower seeds increased significantly in mass during the 14-day experiment (Table 5). Except for a significant seventh day decrease in liver masses of birds provided sunflower seeds, no diet-related trends were noted in wet or dry liver masses of Harris' Sparrows.

DISCUSSION

We found a lack of age- and sex-related differences in digestive organ morphology in wintering Dark-eyed Juncos, which is consistent with reports of Gier and Grounds (1944) on House Sparrows (*Passer domesticus*), Kirkpatrick (1944) on Ring-necked Pheasants (*Phasianus colchicus*), and Leopold (1953) on California Quail (*Callipepla californica*). The practice of pooling avian digestive organ mass and length data appears justified if they are collected during non-breeding periods. We believe that measurements of digestive organ morphology can be recorded up to 90 min postmortem—or perhaps longer—without loss of accuracy. However, if histological information is required, measurements and fixation should be done immediately after death to avoid autolysis (Fenwick 1982).

Although we measured several organs of avian digestive tracts, we will concentrate on changes of the small intestine because it constitutes approximately 85% of the length of the emberizid digestive tract, and it serves as a pri-

mary site for digestion in most birds. We noted few significant changes in size of ceca or gizzards in either species. Liver masses increased in free-feeding birds during the 9-h period in Experiment II, and decreased in birds provided millet in Experiment III; both presumably reflect changes of stored liver glycogen.

The effects of food consumption on small intestine length could explain some of the contradictory results of changes in digestive organ morphology reported in the literature. We did not attempt to separate time effects from food consumption effects. We believe effect of time of day on small-intestine length was minimal, because small-intestine lengths of food-deprived birds did not change during the 9-h experiment. The lengths of small intestines of free-feeding birds after initial feeding (except between hours 6 and 9) were also unchanged. Birds in the free-feeding mode began feeding at the onset of the light period and continued to feed throughout the light period.

Changes in small-intestine length in birds during winter are commonly attributed to changes in diet, specifically an increase in fibrous content (Davis 1961; Moss 1972, 1974; Pulliainen and Tunkkari 1983). However, no change was reported in small-intestine lengths in Ring-necked Pheasants (Kirkpatrick 1944) or Sage Grouse (*Centrocercus urophasianus*; Hupp and Braun 1984) in spring, when low-fiber food replaces high-fiber food in the diet. Our results may shed light on this apparent inconsistency. During winter, many nonmigratory birds in temperate zones are forced to consume food

continuously to meet energy needs. Presumably the digestive tracts of these birds are distended throughout the day. In less stressful periods, most birds feed only in early mornings and late evenings, and their intestinal tracts are distended only during those periods. If bird collections are made without regard to feeding patterns, biases in measurements of gut length can result. For example, continuously feeding birds (free-feeding in Experiment II) collected in late morning or early afternoon would have elongated intestinal tracts. In the same birds on an early-morning-and-late-afternoon feeding regime, the intestinal tracts would not be distended at midday. Some of the autumn to winter changes in lengths of intestinal tracts reported in the literature could reflect such differences in feeding patterns.

Savory and Gentle (1976a) reported lengthening of small intestines of Japanese Quail when fiber was added to the diet. Although the fibrous content of the three feeds we used varied by a factor of 2, we detected no changes in intestinal length related to fiber content. Increased fiber in foods is commonly accompanied by a decrease in energy content, a situation that could cause changes in avian feeding patterns. If the increased fibrous diet in Japanese Quail (Savory and Gentle 1976a) caused birds to feed more frequently, the observed gut lengthening could have been enhanced by measurements taken when the small intestines were filled with food.

The amount of food consumed may cause changes in gut size (Fell 1969, Pulliainen 1976, and Pulliainen and Tunkkari 1983). In our experiments, birds consumed 12 g of mash, 7 g of millet, or 5 g of sunflower seeds per day. If only the quantity of food consumed caused gut size change, the birds on mash should have developed longer intestinal tracts than birds on millet or sunflower. We detected no such changes in Harris' Sparrows.

We support the widely held belief that changes in dietary fiber content alter the morphology of avian digestive systems. Whether or not our results can be extended to other passerine species is unknown. The presence of food in the small intestine reflected feeding activity patterns, and appeared to be an important factor in observed changes in small-intestine length. We recommend that studies of avian digestive morphology consider avian feeding activity

patterns, and that the digestive tract contents be removed before measurements are made.

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