

A change in tongue volume with body size could be accomplished in several ways. If larger birds had longer tongues, volume could be increased by lengthening. A change in volume could also result from a change in the dimensions of the grooves in tongues of the same length. This appears to be the case for *N. verticalis* as compared with *N. venusta* (fig. 3), where tongues are the same length but the smaller *venusta* has a smaller tongue volume. For the larger *N. reichenowi*, the greater volume is achieved by a slightly longer tongue with much larger grooves (fig. 3).

Bill length and morphology appear to be well correlated with corolla length and morphology in nectar-feeding birds (Snow and Snow 1972, Wolf et al. unpubl. data). This co-evolutionary relationship presumably provides for ease in reaching and extracting nectar at the base of differently shaped flowers. Bill morphology among hummingbirds and sunbirds is so diverse that birds of similar sizes may have different bill lengths. If tongue morphology reflects such differences, birds of similar sizes could have different tongue volumes. It would be of interest to determine the extent to which this may relate to rates and efficiencies of nectar intake for such species visiting flowers with which they have co-evolved.

#### SUMMARY

The structure and function of sunbird tongues were compared with those of hummingbirds. In experiments with *Nectarinia kilimensis*, the rate of nectar intake from a feeder decreased with increasing "corolla" length, primarily as a result of less nectar obtained per lick. The grooves on the tongues of sunbirds vary in volume with body size such that the tongues of larger sunbirds could hold more nectar. However, the tongues of sunbirds appear to hold less nectar than those of smaller species of hummingbirds. Thus, hummingbirds, which expend more energy while hovering to consume nectar, may obtain more nectar/lick, but sunbirds' less costly method of perching while feeding should make their nectar extraction

more efficient despite proportionally smaller volumes of the tongue grooves.

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## CECAL FERMENTATION IN MALLARDS IN RELATION TO DIET

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The digestive system of birds enlarges in response to poor foods (high fiber content, relatively indigestible) and shrinks in response to high quality, easily digested foods (Leopold 1953, Lewin 1963, Gardarsson 1971, Miller 1975, Moss 1972, Pendergast and Boag 1973). Little work has been done on the associated changes in cecal fermentation in relation to diet quality.

The ceca of birds are probably the principal organs where microbial fermentation of cellulose and other constituents of the diet takes place (Suomalainen and Arhimo 1945, Beattie and Shrimpton 1958, Thornburn and Wilcox 1965, Annison et al. 1968, McBee and West 1969, Inman 1973). Ruminants produce volatile fatty acids (VFA's) from a similar fermentation process and the proportion of the different VFA's varies with different diets (McDonald et al. 1969: 117, and many others). More data are required

to understand fermentation processes in birds. It is possible that cecal VFA production increases in birds when the diet contains large amounts of fiber, and this may be a significant energy source (McBee 1970).

The purpose of this paper is to document the effect of three different diets on cecal VFA concentrations and cecal discharge rates in Mallards (*Anas platyrhynchos*).

#### MATERIALS AND METHODS

Forty-eight Mallards (progeny from a captive flock maintained at the United States Fish and Wildlife Service's Denver Wildlife Research Center, Denver, Colorado), five to six months old, were obtained from a captive flock that had been kept outdoors in a dirt floor enclosure since hatching. Turkey starter (Ralston-Purina turkey startena), whole maize, and limited natural foods in the enclosure were the only foods available to the ducks before the study began in October 1972.

The ducks were housed indoors at 20-22°C under a 12 hr photoperiod and assigned randomly to one of three communal pens with eight males and eight fe-

TABLE 1. Selected nutritional parameters of turkey starter, alfalfa pellets (rabbit chow), and whole maize as determined by proximate analysis, bomb calorimetry, and feeding trials.

	Turkey starter	Maize	Alfalfa (rabbit chow) <sup>d</sup>
Gross energy (Kcal/g)	4.53	4.44	4.21
Metabolizable energy (Kcal/g)	3.20 <sup>b</sup>	3.30-3.90 <sup>e</sup>	1.40 <sup>b</sup>
Crude protein (%) <sup>a</sup>	29.0	9.8	16.6
Petroleum ether extract (%)	7.9	4.4	1.4
Crude fiber (%)	4.0	2.2	25.6
Ash (%)	10.0	1.8	9.3
Nitrogen free extract (%)	49.0	81.8	47.1
Moisture (%)	8.6	9.2	9.3

<sup>a</sup> All percentages are based on dry weight, except moisture.

<sup>b</sup> Values from Pintails (*Anas acuta*) (Miller 1974).

<sup>c</sup> Values from domestic fowl (*Gallus domesticus*) converted to metric from McDonald et al. (1969) pp. 160, 376.

<sup>d</sup> Contains small percentages of added minerals and grain.

males in each pen. All ducks were fed a mixture of turkey starter and maize for a one week adjustment period before starting the experiments. The birds were then individually weighed and marked with numbered plastic leg bands. The experimental period commenced at this time and continued for 21 days. During this period, the ducks in group number one were fed solely on turkey starter (a balanced control diet), group two on whole maize (high energy and low fiber content, relatively easily digested), and group three on alfalfa pellets (high fiber and low energy content, relatively indigestible) (Ralston-Purina rabbit checkers) (table 1). The foods were provided freely in communal feeding trays and water was provided in large tubs for bathing and drinking. Food and water were changed daily. Food consumption was calculated by weighing the food remaining at the end of each day and subtracting this value from the weight of food originally supplied. No grit was provided.

On day 21, all ducks except one male and one female randomly selected from each group (which were needed for the second part of this study) were sacrificed by cervical dislocation. All ducks were immediately weighed, the abdomens of each incised, and the ceca extracted. The contents of both ceca were squeezed into a pre-weighed centrifuge test tube and immediately frozen.

Cecal samples were thawed, weighed, and mixed with 20% meta-phosphoric acid equal to half the sample weight. Samples were then centrifuged at 15,000 rpm for 15 min and the clear supernatant was injected in 2  $\mu$ l amounts directly into a gas chromatograph column (1/8 in by 6 ft stainless steel with 15% FFAP on acid washed 70/80 chromosorb W DMCS) (Palmquist 1965). The chromatograph used was an Aerograph HY-FI model 600-D equipped with a hydrogen flame detector. Results were recorded on a Honeywell-Brown Elektronik strip chart recorder. The concentrations of acetic (acetate), propionic

(propionate), butyric (butyrate), valeric (valerate), and isovaleric (isovalerate) volatile fatty acids were determined by comparison with a standard and recorded in mmol/l.

The six Mallards left alive from the original groups were put in individual metabolism cages under the same environmental conditions described above and given the same foods that they had been receiving for the previous 21 days. The number of cecal droppings per bird per day was determined over a six-day period. Cecal droppings are recognized by color (dark brown from starter-fed ducks, dark green from alfalfa-fed ducks, light orange-brown from maize-fed ducks) and by their shapeless, liquid-like masses (Moss and Parkinson 1972).

A parametric two-way analysis of variance (Remington and Schork 1970) was conducted on the data to assess the influence of food and sex individually and in combination (interaction) upon VFA concentrations. A rigorous statistical analysis of the cecal dropping data was not conducted because of the small number of birds used in the experiment. A nonparametric Kruskal-Wallis one-way analysis of variance was used in this case (Siegel 1956).

## RESULTS AND INTERPRETATION

**Body Weights and Food Consumption.** Each group of ducks lost weight on average during the 21-day period, but these losses were generally small (2 to 50 g) and significant ( $P < 0.05$ ) only in the maize-fed group. Food consumption by the maize and turkey starter-fed ducks was similar at 53 and 57 g (dry weight) per bird per day, respectively, while the ducks fed alfalfa ate about 97 g per bird per day (Miller 1975).

**Volatile Fatty Acid Production.** Acetate was found in the greatest concentration in the cecal samples on all diets, followed in decreasing order by propionate and then butyrate. Valerate concentrations followed those of butyrate and exceeded those of isovalerate on the turkey starter and maize diets, but isovalerate exceeded valerate on the alfalfa diet (table 2).

The results of the two-way analysis of variance demonstrate that VFA concentrations were significantly influenced by food type. The alfalfa diet produced higher concentrations of propionate, butyrate, and total VFA ( $P < 0.01$ ) than either maize or turkey starter (table 2). Valerate and isovalerate concentrations did not follow this pattern, but they were relatively unimportant since, combined, they made up less than 5% of the total VFA on all diets.

Analysis of variance failed to detect a higher concentration of acetate in the alfalfa-fed group at the 0.01 level of significance (significance at the 0.10 level was attained). The mean concentration of acetate (males and females combined) in the alfalfa-fed group (84.5 mmol/l) was approximately 10 mmol/l greater than the combined means of the maize- (76.0 mmol/l) and turkey starter- (74.5 mmol/l) fed groups, a sizeable difference. The failure to verify this difference statistically resulted from the low mean acetate concentration in the alfalfa-fed females (77.0 mmol/l) as opposed to the males (92.1 mmol/l), together with the large variance in the female data of this group (table 2). This depressed mean and wider variance resulted from an unusually low acetate concentration (49.1 mmol/l) recorded for one of the individual females. This value was the lowest single acetate concentration recorded for any duck in the three groups. Two of the females accounted for acetate concentrations over 90 mmol/l,

TABLE 2. Volatile fatty acids in the ceca of Mallards fed turkey starter, maize, and alfalfa pellets; average concentration (mmols/l) and percentage of total VFA's.

Food	Sex(N)	Individual volatile fatty acids					Total VFA <sup>b</sup>
		Acetate	Propionate	Butyrate	Valerate	Isovalerate	
Turkey starter							
Concentration	M(7)	75.9 ± 5.8 <sup>a</sup>	26.2 ± 2.8	13.7 ± 1.6	2.7 ± 0.3	2.3 ± 0.3	120.8 ± 9.1
% of total		62.8 ± 1.4	21.7 ± 0.7	11.3 ± 0.5	2.2 ± 0.3	1.9 ± 0.1	
Concentration	F(7)	73.2 ± 5.3	24.8 ± 3.4	13.7 ± 1.5	2.2 ± 0.1	1.9 ± 0.3	115.8 ± 5.3
% of total		63.2 ± 2.1	21.4 ± 1.0	11.8 ± 0.5	1.9 ± 0.2	1.6 ± 0.2	
Maize							
Concentration	M(7)	78.7 ± 3.3	22.1 ± 1.1	11.3 ± 0.7	2.4 ± 0.2	1.5 ± 0.2	115.9 ± 5.2
% of total		67.8 ± 1.1	19.1 ± 0.4	9.7 ± 0.2	2.1 ± 0.1	1.3 ± 0.1	
Concentration	F(7)	73.3 ± 4.0	20.0 ± 1.8	11.2 ± 1.1	2.2 ± 0.2	1.4 ± 0.2	108.1 ± 5.2
% of total		67.8 ± 0.6	18.5 ± 0.5	10.2 ± 0.4	2.0 ± 0.1	1.3 ± 0.1	
Alfalfa							
Concentration	M(7)	92.1 ± 3.7	31.8 ± 1.4	20.8 ± 0.8	1.9 ± 0.2	2.1 ± 0.2	148.7 ± 5.6
% of total		61.9 ± 0.8	21.4 ± 0.5	14.0 ± 0.4	1.3 ± 0.1	1.4 ± 0.1	
Concentration	F(7)	77.0 ± 7.3	30.6 ± 3.5	19.1 ± 2.6	1.5 ± 0.1	1.9 ± 0.2	130.1 ± 14.8
% of total		59.2 ± 1.3	23.5 ± 0.9	14.7 ± 0.6	1.2 ± 0.1	1.5 ± 0.1	
F ratios <sup>c</sup> (concentration)							
Food		2.442	8.764 <sup>e</sup>	24.885 <sup>e</sup>	9.719 <sup>e</sup>	5.929 <sup>e</sup>	6.586 <sup>e</sup>
Sex		3.734	0.575	0.385	6.605 <sup>d</sup>	2.083	2.649
Interaction		0.887	0.016	0.285	0.358	0.256	0.419

<sup>a</sup> Mean ± standard error.<sup>b</sup> Total VFA includes the five VFA's listed in table only.<sup>c</sup> Degrees of freedom: Food factor—2, sex factor—1, interaction—2, residual—36.<sup>d</sup> Significant ( $P < 0.05$ ).<sup>e</sup> Significant ( $P < 0.01$ ).

well within the male data. The lack of statistical significance appears to be a function of small sample size and unexplained variability of response by the one group of females. A larger sample size would have probably averaged out much of this variability making statistical verification of differences likely. Therefore, a higher concentration of acetate should probably be expected on a diet of alfalfa for females as well as males.

Sex apparently had no influence on VFA concentrations. Concentrations were consistently higher in males than females, but these differences were small and results of the two-way analysis of variance show that the differences were significant ( $P < 0.05$ ) only for valerate (table 2). Valerate made up such a small percent of total VFA (1–2%), however, that these results should not be over emphasized.

TABLE 3. Average number of cecal droppings (number/bird/day) from a pair of Mallards fed turkey starter, a pair fed maize, and a pair fed alfalfa pellets over a six-day period.

Sex	Turkey starter	Maize	Alfalfa pellets
M	1.50 ± 0.22 <sup>a</sup>	1.20 ± 0.17	4.50 ± 0.76 <sup>b</sup>
F	1.33 ± 0.42	1.33 ± 0.33	4.00 ± 1.09 <sup>b</sup>

<sup>a</sup> Mean ± standard error.<sup>b</sup> Significantly larger ( $P < 0.01$ ).

The small F-ratios for interaction (table 2) indicate that the differential response to the three foods was essentially constant for the two sexes and no interaction between sex and food occurred.

*Cecal Discharge Rates.* The number of cecal droppings discharged by the male and female Mallards fed alfalfa was significantly greater ( $P < 0.01$ ) than the number discharged by the other ducks (table 3).

## DISCUSSION

My data, although not conclusive, suggest that VFA production in response to the alfalfa diet was different from either maize or turkey starter. The absence of information on VFA absorption rates in waterfowl makes conclusions concerning production rates inadvisable, but the higher VFA concentrations in the alfalfa-fed group may be part of a generalized response by Mallards to increase digestive capacity and nutrient utilization, which allows survival on low energy, fibrous foods. Increases in food consumption rates and gut enlargement have been shown to be part of this response (Miller 1975). The cecal discharge data suggest that some aspect of the alfalfa diet, possibly low energy or other nutritive deficiency, caused a speedup in throughput times for material entering the ceca. Whether or not this faster turnover of cecal substrate was simply a reflection of the faster consumption rates observed, or a more complex response to qualitative and quantitative changes in microbial fermentation employed to increase the

TABLE 4. Comparison of total VFA and molar proportions of individual VFA's in the ceca of various galliform birds and Mallards.

Species	Diet	Avg. total VFA	Avg. acetic	Avg. propionic	Avg. butyric	Source
Mallards ( <i>Anas platyrhynchos</i> )	Starter	121 (7) <sup>a</sup> (mmol/l)	63 (7)	22 (7)	11 (7)	This study
	Maize	116 (7) (mmol/l)	68 (7)	19 (7)	10 (7)	This study
	Alfalfa	149 (7) (mmol/l)	62 (7)	21 (7)	14 (7)	This study
Domestic Fowl ( <i>Gallus domesticus</i> )	Lay feed pellets	107 (3) (mmol/Kg) <sup>b</sup>	56 (10)	29 (10)	10 (10)	Annison et al. 1968
Willow Ptarmigan ( <i>Lagopus lagopus</i> ) <sup>c</sup>	Willow buds and twigs	36 (8) (mmol/Kg)	—	—	—	McBee & West 1969
Red Grouse ( <i>L. l. scoticus</i> )	Heather	37 (3) (mmol/l)	60 (3)	13 (3)	17 (3)	Moss & Parkinson 1972

<sup>a</sup> Sample sizes in parentheses.

<sup>b</sup> Note: For comparative purposes, a kilogram (Kg) and a liter (l) of cecal substrate are considered equivalent; therefore, mmol/Kg and mmol/l are roughly equivalent.

<sup>c</sup> Subspecies not specified.

digestive contribution of the ceca in time of stress, remains to be discovered. Increased production of VFA's probably contributes to the energy budget of ducks (it has been demonstrated that cecal VFA's are absorbed and metabolized in fowl [*Gallus domesticus*], Annison et al. 1968). Nevertheless, it must be shown that accelerated VFA production yields products that are absorbed and metabolized at rates greater than normal to clearly demonstrate that the contribution to the energy budget provided by cecal VFA's increases with decline in food quality.

**Comparisons with Other Species.** The VFA concentrations found in the Mallards of this study are similar to those reported for fowl (Annison et al. 1968), but considerably higher than those of Red Grouse (*Lagopus lagopus scoticus*; Moss and Parkinson 1972) and Willow Ptarmigan (*Lagopus lagopus*; McBee and West 1969) (table 4). However, the

Mallards of this study had much smaller ceca than those of grouse (not fowl) when expressed in terms of body weight (table 5). Even if cecal fermentation is more active in Mallards than grouse, it is doubtful that it would compensate for smaller ceca.

**Volatile Fatty Acid Mixtures.** In ruminants, as the percentage of roughage increases in the diet, acetate increases at the expense of propionate, while the reverse occurs when starches are added to the diet (McDonald et al. 1969:117, Rook 1964, and others). The opposite result was noted for the Mallards, however, as the high starch diet (maize) yielded the greatest proportion of acetate and the lowest of propionate, while the alfalfa diet yielded the reverse (table 2).

Although the presence of VFA's in the ceca of Mallards proves that microbial fermentation occurs, probably in the ceca themselves (Annison et al.

TABLE 5. Comparison of ceca sizes among various galliform birds and Mallards.

Species	Avg. body weight (grams)	Avg. length (both ceca combined <sup>a</sup> ) (cm)	% of body weight (both ceca combined <sup>a</sup> )	Source	
Mallards <sup>c</sup> ( <i>Anas platyrhynchos</i> )	Starter-fed	1244 (Im ♂)	28	2.3	Miller 1975
	Maize-fed	1256 (Im ♂)	30	2.4	Miller 1975
	Alfalfa-fed	1243 (Im ♂)	40	3.2	Miller 1975
Domestic Fowl ( <i>Gallus domesticus</i> )	1800 (Ad ♀)	32	1.8	Sunde et al. 1950 (weight) Beattie & Shrimpton 1958 (ceca length)	
Willow Ptarmigan ( <i>Lagopus lagopus</i> ) <sup>b</sup>	625 (Ad ♂)	110	17.6	McBee & West 1969	
Red Grouse ( <i>L. l. scoticus</i> )	600 (Ad ♂)	144	24.0	Moss & Parkinson 1972 (weight) Moss 1972 (ceca length)	
Spruce Grouse ( <i>Canachites canadensis</i> )	533 (Ad ♂)	82	15.4	Pendergast & Boag 1973	
Ruffed Grouse ( <i>Bonasa umbellus</i> )	569 (? ♀)	80	14.1	Leopold 1953	

<sup>a</sup> Determined by doubling the length of single cecum values unless both were available.

<sup>b</sup> Subspecies not specified.

<sup>c</sup> Data from wild Mallards are not available.

1968), it does not indicate precisely what has been fermented because the end products of crude fiber, simple carbohydrate, and protein fermentation are not completely understood (Annison et al. 1968, Maynard and Loosli 1969:55). The ceca receive a substrate of still questionable composition (McBee 1970, Annison et al. 1968) which has escaped digestion in the upper digestive tract. Whether or not this substrate and its associated microbial population, vary fundamentally in composition with diet quality is unknown.

#### SUMMARY

Volatile fatty acid concentrations in the ceca and rates of production of cecal droppings were determined in three groups of Mallards, one of which was fed turkey starter, one maize, and the other alfalfa pellets. Acetate was highest in concentration followed by propionate, then butyrate, and then valerate and isovalerate in all groups. Total and individual VFA concentrations were generally greatest in the alfalfa-fed ducks. The concentrations of VFA's in Mallards were higher than those reported for Red Grouse and Willow Ptarmigan, but similar to chickens. Mallard ceca are shorter than those of wild gallinaceous birds, when expressed in relation to body weight. Cecal discharge rates were most rapid in the Mallards fed alfalfa. The high VFA concentrations and cecal discharge rates observed in the Mallards fed alfalfa appear to be part of a general response, including gut enlargement and increased food consumption rate, to allow maximum utilization of foods of poor quality.

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