

RELATIONSHIPS OF AVIAN CECAL LENGTHS TO FOOD HABITS, TAXONOMIC POSITION, AND INTESTINAL LENGTHS¹

TERESA F. DEGOLIER

Department of Biological Sciences, Bethel College, St. Paul, MN 55112, e-mail: t-degolier@bethel.edu

SHEILA A. MAHONEY

Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL 33431

GARY E. DUKE

Department of Veterinary PathoBiology, University of Minnesota, St. Paul, MN 55108

Abstract. Body mass, intestinal lengths, and the occurrence and relative size of ceca from 154 species of birds representing 21 orders and a diversity of food habits were compared. Well-developed ceca occur in the Anseriformes, Galliformes, Gruiformes, Cuculiformes, Strigiformes, Caprimulgiformes, and Trogoniformes. The presence of well-developed ceca is less consistent in other orders and appears to be related to diet; herbivorous species whose diets contain large amounts of cellulose have well-developed ceca, whereas species having diets rich in soluble sugars and proteins tend to have poorly-developed or no ceca. We postulate that the relatively well-developed ceca in some non-herbivorous birds are associated with conservation of critical resources such as water and nitrogen.

Key words: *ceca, cellulose, chitin, food habits, intestinal lengths, taxonomy.*

INTRODUCTION

Ceca are outpouches of the alimentary canal originating at the junction of the small and large intestine. The occurrence and anatomy of these ceca in birds reveal considerable interspecific variation (Maumus 1902, Pinchon 1942, Naik 1962), which likely reflects functional differences among avian species. Papers presented during the First International Avian Cecal Symposium (Braun and Duke 1989) and a recent comprehensive review of avian cecal anatomy and function (Clench and Mathias 1995) indicate that avian ceca may function in: (1) bacterial fermentation, (2) nitrogen recycling, (3) osmoregulation, (4) nutrient absorption, (5) bacterial synthesis of vitamins, and (6) an immunological response.

The purpose of the present study was to measure cecal and intestinal lengths from a diverse population of birds representative of different taxa and various diets. The data were then used to explore relationships among cecal lengths and food habits and the species' taxonomic position in a wide range of bird orders. Additionally, the data may contribute to future studies attempting to better understand the relationship of cecal size and the digestibility of foodstuffs, colonic mo-

tility, and water availability (Braun and Duke 1989, Clench and Mathias 1995).

METHODS

STUDY SPECIMENS

A total of 602 avian specimens, mostly North American, representing 21 orders and 154 species were dissected, measured, and categorized. Salvaged and donated carcasses were frozen soon after death. No birds were sacrificed for this project. Data from other investigators for 17 galliform species (Leopold 1953), a Hoatzin *Opisthocomos hoatzin* (Grajal et al. 1989), and 8 shorebirds (Mahoney, unpubl. data) also were used.

MEASUREMENTS

Carcasses were weighed to the nearest 0.1 g prior to freezing. Upon thawing, intestinal lengths were recorded using methods previously described by Leopold (1953). Lengths were recorded to the nearest 0.1 cm and consisted of the following: (1) total intestine length (IN)—from the gastric pylorus to the caudal lip of the vent, (2) small intestine length (SI)—from the gastric pylorus to the ileocecalcolic (ICC) junction, (3) rectal-cloacal length (R)—from the ICC junction to the caudal lip of the vent, and (4) cecal length (CL)—from the ICC junction to the distal end of the longest cecum. Even though

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most avian species possess two ceca of approximate equal length (McLelland 1989), the origin of the ceca at the ICC junction is not always symmetrical, thus the rectal-cloacal length measurements were made from the most caudal cecum.

Similar cecal lengths can be found among various orders of birds of different body sizes. To better reflect the relative size of the ceca, CL also was presented as a percent of the total intestinal length ($CL/IN \times 100$).

CATEGORIES OF FOOD HABITS

Very few avian species are restricted to a single food; most feeding habits are influenced by food availability, seasonal changes, experience, and age. Determination of avian food habits herein was based upon stomach contents whenever they could be ascertained. To be consistent in assigning birds to food habit categories, the method of Wilson (1974) was used, viz., when a particular food type predominated in stomach samples from 51% or more of the individuals in a sample of that species, the species was assigned to that food category. In the absence of stomach contents, information from the literature was used (e.g., Martin et al. 1951, Erlich et al. 1988). The primary types of food in the given food categories are listed at the end of Table 1.

STATISTICAL ANALYSES

Mean body mass, cecal length, and the corresponding intestinal lengths for each of the 154 species were statistically compared using SAS (SAS Institute 1990). Previous analysis of species with large sample sizes such as Eastern Screech-Owl *Otus asio* ($n = 51$), Chuck-will's-widow *Caprimulgus carolinensis* ($n = 24$), and Yellow-billed Cuckoo *Coccyzus americanus* ($n = 23$) indicated that there were no significant differences in CL between the sexes in adults (Poppema 1990), thus data for sex were pooled within each species.

RESULTS

Mean \pm SE of body mass, IN, SI, R, CL, CL/IN, and the corresponding food habits of the 154 species are listed in Table 1. Cecal lengths of the species ranged from 73.0 cm in *Centrocercus urophasianus*, the Sage Grouse, to less than 1.0 cm in several of the species sampled. Ceca were present in 83% of the species examined,

and all were paired except for the single cecum observed in the Ciconiiformes, family Ardeidae.

Mean cecal lengths within each food category are shown in Table 2. All food categories had species with ceca. Species that were assigned as herbivorous, omnivorous, and granivorous had the longest ceca, whereas nectarivorous and piscivorous species had the smallest ceca.

Mean cecal lengths within each order are shown in Table 3. Birds belonging to 19 of the 21 orders surveyed had ceca. The longest ceca, in descending order, were found in Galliformes, Anseriformes, Gruiformes, and Strigiformes. Ceca were only absent in the Psittaciformes and Piciformes. Some of the resulting standard errors are large at an ordinal level and likely indicate that factors other than taxonomic position influence cecal presence and size.

DISCUSSION

Our results support those of other studies that cecal development is related to diet, and that the longest ceca occurred in herbivorous species (Maumus 1902, Pinchon 1942, Naik and Dominic 1962), and that the relative length of the ceca may not be a reliable taxonomic character beyond the species level (McLelland 1989, Clench and Mathias 1995).

Our results indicate that well-developed ceca also occur in omnivorous and some granivorous species. However, this is due to the inclusion in both categories of Galliform species from Leopold's data (1953), in which he designates quails, partridges, and pheasants as "seed"-eating species (granivorous) that also consume greens, fruits, and insects (omnivorous.) Nevertheless, a common component of both diets is the insoluble carbohydrate, cellulose. Several studies have demonstrated that as the amount of cellulose in the diet increases, whether in natural or commercial diets, so do the lengths of the ceca (Lewin 1963, Moss 1972). If cecal length is an indicator of ingested cellulose, then species consuming the cell walls of higher plants would be expected to have well-developed ceca, and those species consuming nectar, fruits, and animal proteins would be expected to have less cecal development because these foods are easily digested by endogenous lipases, proteases, and carbohydrases (Duke 1986). Within the nectarivorous diet, which is rich in soluble sugars, and the insectivorous and piscivorous diets, contain-

TABLE 1. Mean (\pm SE) body mass, total intestine length (IN), small intestine length (SI), rectal-cloacal length (R), cecal length (CL), CL/IN \times 100, and diet of 154 species of birds. (n) = sample size, and where no parentheses appear, (n) = 1; — indicates data not available. All data are from this study unless otherwise noted.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL/IN (%)	Food category ^a
Gaviiformes							
Gaviidae							
<i>Gavia immer</i> (10)	1,797.6 \pm 163.6	157 \pm 7.8	149.8 \pm 7.5	6.9 \pm 0.4	5.3 \pm 0.3	3.4	Fish
Podicipediformes							
Podicipedidae							
<i>Podiceps nigricollis</i> (8) ^b	347.4 \pm 20.3	125.4 \pm 6.7	—	—	6.0 \pm 0.3	4.8	Carni AI
<i>Tachybaptus dominicus</i> (2)	202.2	79.5	76.2	3.3	0.4	0.5	Carni AI
<i>Podilymbus podiceps</i> (7)	291.9 \pm 31.7	83.9 \pm 5.8	80.4 \pm 5.7	3.5 \pm 0.6	0.3 \pm 0.0	0.4	Carni AI
Procellariiformes							
Diomedeidae							
<i>Diomedea immutabilis</i>	2,460.0	180.0	173.0	7.0	1.5	0.8	Fish
Hydrobatidae							
<i>Oceanites oceanicus</i>	144.8	42.8	41.6	1.3	0.4	0.9	Fish
Procellariidae							
<i>Calonectris diomedea</i> (3)	404.9 \pm 92.3	53.1 \pm 7.2	50 \pm 6.8	3.2 \pm 0.5	1 \pm 0.2	1.9	Fish
<i>Pterodroma hasitata</i>	—	69	65.5	3.5	0.5	0.7	Fish
<i>Puffinus lherminieri</i>	107.0	40.2	37.1	3.1	0.3	0.8	Fish
<i>P. gravis</i>	380	72.4	73.5	3.9	0.6	0.8	Fish
Pelecaniformes							
Pelecanidae							
<i>Pelecanus occidentalis</i> (9)	1,947.7 \pm 125.2	239.6 \pm 7	232.6 \pm 7.6	7.5 \pm 1.0	4.7 \pm 0.9	2.0	Fish
Sulidae							
<i>Sula bassanus</i> (7)	1,731.3 \pm 78.8	122.8 \pm 4.5	114.2 \pm 4.5	8.6 \pm 0.3	1.1 \pm 0.1	0.9	Fish
Phalacrocoracidae							
<i>Phalacrocorax auritus</i> (4)	803.3 \pm 69.3	127.7 \pm 9.7	118.9 \pm 8.8	8.8 \pm 1.7	1.1 \pm 0.2	0.9	Fish
Anhingidae							
<i>Anhinga anhinga</i> (19)	605.6 \pm 50.2	115.8 \pm 5.3	101.6 \pm 5.9	11.1 \pm 0.5	0.1 \pm 0.1	0.1	Fish

TABLE 1. Continued.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL/IN (%)	Food category ^a
Ciconiiformes							
Ardeidae							
<i>Ixobrychus exilis</i> (2)	61.5	68.5	54.6	4.3	0.0	0.0	Fish
<i>Botaurus lentiginosus</i>	248.0	113.9	108.5	5.4	0.7	0.6	Fish
<i>Egretta thula</i> (2)	289.3	97.3	91.7	5.6	0.7	0.7	Carni AI
<i>E. rufescens</i>	786.0	198.0	188.9	9.6	1.8	0.9	Fish
<i>E. caerulea</i>	253.6	98.0	90.8	7.2	0.6	0.6	Fish
<i>Butorides striatus</i>	178.8	91.0	82.0	9.0	0.0	0.0	Fish
<i>Ardea herodias</i> (2)	1,914.0	193.1	182.3	10.8	1.0	0.5	Fish
<i>Nycticorax nycticorax</i> (2)	486.9	127.9	118.8	9.2	1.0	0.8	Fish
<i>Nyctanassa violacea</i>	511.0	137.1	126.1	11.0	0.4	0.3	Carni AI
<i>Bulbulcus ibis</i> (8)	220.7 ± 13.0	55.2 ± 2.6	48.8 ± 2.5	5.3 ± 0.1	0.2 ± 0.1	0.4	Fish
Ciconiidae							
<i>Mycteria americana</i>	1,800.0	295.5	285.0	10.5	0.6	0.2	Fish
Threskiornithidae							
<i>Eudocimus albus</i> (12)	611.9 ± 34.5	103.0 ± 3.4	96.9 ± 3.3	5.9 ± 0.2	0.5 ± 0.0	0.5	Carni AI
<i>Ajaia ajaja</i>	1,543.0	161.6	154.8	6.8	0.8	0.5	Fish
Phoenicopteriformes							
Phoenicopteridae							
<i>Phoenicoperus ruber</i> (3)	1,878.3 ± 119.0	266.5 ± 21.0	259.0 ± 20.8	7.5 ± 0.3	9.0 ± 1.2	3.4	Carni AI
<i>Phoeniconaias minor</i> (4) ^b	1,158.0 ± 137.8	317.8 ± 24.8	228.8 ± 65.8	5.8 ± 6.6	3.2 ± 0.3	1.0	Diatoms
Anseriformes							
Anatidae							
<i>Anas discors</i>	250.3	106.1	99.5	6.7	6.6	6.2	Grain
<i>A. fulvigula</i> (4)	543.9 ± 237.8	142.0 ± 9.1	132.2 ± 8.7	9.8 ± 0.5	12.6 ± 0.7	8.9	Carni AI
<i>A. americana</i>	530.0	144.4	137.0	7.4	22.5	15.6	Herb
<i>A. platyrhynchos</i> (2)	929.5	169.5	154.9	12.0	16.1	9.5	Grain
<i>Aythya collaris</i> (9)	612.1	126.9 ± 3.0	117.0 ± 3.0	10.0 ± 0.3	13.3 ± 0.3	10.5	Herb
<i>Aix sponsa</i>	537.3	109.5	101.5	8.0	8.9	8.1	Carni AI
<i>Cairina moschata</i> (8)	585.0 ± 162.1	137.9 ± 12.9	127.8 ± 11.8	9.8 ± 1.5	12.8 ± 1.2	9.3	Omni
<i>Mergus serrator</i> (4)	461.4 ± 50.9	144.6 ± 12.8	137.4 ± 12.9	8.3 ± 1.4	2.8 ± 0.6	1.9	Fish
Falconiformes							
Cathartidae							
<i>Cathartes aura</i> (3)	2,097.0 ± 22.2	130.5 ± 3.9	—	—	0	0.0	Carni TV

TABLE 1. Continued.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL/IN (%)	Food category ^a
Accipitridae							
<i>Accipiter striatus</i>	81.6	36.0	—	—	0	0.0	Carni TV
<i>A. cooperii</i>	411.6	46.5	40.0	6.5	0.1	0.2	Carni TV
<i>Buteo platypterus</i>	227.2	60.0	52.0	8.0	0.1	0.2	Carni TV
<i>B. lineatus</i> (3)	459.7 ± 75.7	96.9 ± 5.1	—	—	0.0	0.0	Carni TV
<i>B. jamaicensis</i>	912.0	87.0	—	—	0.0	0.0	Carni TV
<i>Pandion haliaetus</i> (3)	1,104.5 ± 113.5	204.0 ± 62.5	193.2 ± 66.0	10.8 ± 4.2	0.5 ± 0.2	0.3	Fish
Falconidae							
<i>Falco sparverius</i> (5)	87.7 ± 3.5	35.6 ± 3.2	—	—	0.0 ± 0.0	0.1	Insect
<i>F. mexicanus</i>	338.0	65.5	—	—	0.0	0.0	Carni TV
Galliformes							
Phasianidae							
<i>Colinus virginianus</i> (7)	161.1 ± 18.9	74.7 ± 8.5	66.7 ± 8.5	8.0 ± 1.1	11.3 ± 1.3	15.1	Omni
<i>Phasianus colchicus</i> (4)	1,397.8 ± 300.3	118.5 ± 5.5	109.6 ± 5.3	8.9 ± 0.5	21.1 ± 2.7	17.8	Omni
<i>Bonasia umbellus</i> (7)	397.9 ± 44.4	104.3 ± 5.3	93.2 ± 5.1	11.1 ± 0.5	41.8 ± 3.0	40.1	Omni
<i>Meleagris gallopavo</i> (5)	6,775.0 ± 1,580.9	232.8 ± 18.6	220.0 ± 18.0	12.8 ± 0.8	46.5 ± 4.5	20.0	Omni
<i>Lagopus lagopus</i>	525.0	103.5	91.0	12.5	47.0	45.4	Herb
<i>L. mutus</i> ^e	502.0	115.0	104.0	11.0	47.0	40.9	Herb
<i>Canachites canadensis</i> ^e	576	116	105	11	40	34.5	Herb
<i>Pediocetes phasianellus</i> ^e	850.0	135.5	121.0	14.5	49.0	36.2	Herb
<i>P. phasianellus</i> × <i>Tympanuchus cupido</i> ^e	898	133	119	14	47	35.3	Herb
<i>T. cupido</i> ^e	1,120	131	117	14	45	34.4	Grain
<i>Dendragapus fuliginosus</i> ^e	1,250	138	120	18	50	36.2	Grain
<i>Centrocercus urophasianus</i> ^e	1,427	148.3	135	13.3	73	49.2	Grain
<i>Tetra urogallus</i> ^e	2,500	177	159	18	52	29.4	Grain
<i>Callipepla squamata</i> ^e	175.0	68.5	59.0	9.5	10.5	15.3	Grain
<i>Lophortyx gambelii</i> ^e	188.0	89.5	81.0	8.5	11.3	12.6	Grain
<i>L. californica californica</i> ^e	173.0	86.0	77.1	8.9	13.9	16.2	Grain
<i>L. californica brunescens</i> ^e	192.0	93.7	85.7	9.0	16.5	17.6	Grain
<i>Oreortyx picta</i> ^e	250.0	88.0	76.5	11.5	17.5	19.9	Grain
<i>Cyrtonyx montezumae</i> ^e	186.0	53.5	46.0	7.5	11.5	21.5	Omni
<i>Perdix perdix</i> ^e	395.0	67.3	59.0	8.3	19.0	28.2	Grain
<i>Alectoris graeca</i> ^e	576.0	86.0	77.5	8.5	19.0	22.1	Grain
<i>Chrysolophus pictus</i>	366.7	72.7	65.0	7.7	9.6	13.2	Grain
<i>Gallus gallus</i> (21)	2,045.0	191.5 ± 7.8	185.8 ± 6.4	10.4 ± 0.4	18.3 ± 0.7	9.6	Grain

TABLE 1. Continued.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL:IN (%)	Food category ^a
Gruiformes							
Rallidae							
<i>Gallinula chloropus</i> (12)	225.3 ± 29.9	126.7 ± 55.4	64.1 ± 6.3	7.2 ± 0.6	11 ± 1.1	8.7	Herb
<i>Porphyrio martinica</i> (12)	163.9 ± 18.6	47.7 ± 4	42.9 ± 3.9	4.8 ± 0.3	3.5 ± 0.3	7.3	Omni
<i>Rallus longirostris</i> (4)	129.7 ± 14	40.9 ± 1.6	36.5 ± 1.9	4.4 ± 0.3	5.0 ± 0.2	12.2	Carni AI
<i>Porzana carolina</i> (6)	51.2 ± 7.3	38.2 ± 5.6	35.1 ± 5.5	3.1 ± 0.3	3.4 ± 0.3	8.9	Herb
<i>Laterallus jamaicensis</i>	18.5	19.7	17.7	2.0	1.2	6.1	Insect
<i>Fulica americana</i> (5)	383.8 ± 26.7	92.8 ± 8.4	85.1 ± 8.3	7.7 ± 0.7	15.3 ± 1	16.5	Omni
Aramidae							
<i>Aramus guarauna</i> (2)	591.6	71.0	67.0	4.0	5.9	8.3	Carni AI
Charadriiformes							
Haematopodidae							
<i>Haematopus palliatus</i>	461.0	93.2	87.1	6.1	4.9	5.3	Carni AI
Charadriidae							
<i>Charadrius vociferus</i> (8)	25.6 ± 9	24.6 ± 2.7	21.5 ± 2.4	3.1 ± 0.4	2.8 ± 0.4	11.4	Insect
<i>Pluvialis squatarola</i>	158.6	81.3	77.5	3.8	2.3	2.8	Insect
Scolopacidae							
<i>Calidris alba</i> (2)	51.5 ± 2.5	28.1 ± 1.7	24.9 ± 1.6	3.2 ± 0.1	3.0 ± 0.5	10.7	Insect
<i>C. pusilla</i> (2)	22.5	26.3	22.9	3.4	2.5	9.5	Insect
<i>C. melanotos</i>	27.6	25.5	23	2.5	1.9	7.5	Insect
<i>C. canutus</i>	102.6	40.6	36.5	4.1	4.1	10.1	Insect
<i>Arenaria interpres</i>	79.4	42.5	40.0	2.5	4.1	9.7	Insect
<i>Gallinago gallinago</i> (9)	69.3 ± 5.8	31.9 ± 2.2	27.9 ± 1.9	4.0 ± 0.6	2.7 ± 0.3	8.5	Insect
<i>Phalaropus tricolor</i> (6) ^b	61.2 ± 3.1	34.0 ± 1.6	—	—	3.9 ± 0.2	11.5	Carni AI
Recurvirostridae							
<i>Recurvirostra americana</i> (6) ^b	320.5 ± 10.7	74.3 ± 4.2	—	—	6.7 ± 0.3	9.0	Omni
Laridae							
<i>Rhynclops niger</i> (4)	288.2 ± 52.7	44.7 ± 2.2	41.5 ± 2.2	3.1 ± 0.2	0.9 ± 0.1	2.0	Fish
<i>Larus californicus</i> (5)	470.0 ± 9.1	106.4 ± 3.9	—	—	0.5 ± 0.3	0.5	Insect
<i>L. atricilla</i> (11)	267.5 ± 17	54.6 ± 3.6	50.7 ± 3.6	3.9 ± 0.2	0.5 ± 0.1	0.9	Carni AI
<i>L. argentatus</i> (5)	787.9 ± 85.8	96.5 ± 6.4	90 ± 6.5	6.5 ± 0.5	1.1 ± 0.2	1.1	Omni
<i>L. delawarensis</i> (10)	359.7 ± 12.2	74.1 ± 1.9	69.0 ± 1.9	5.0 ± 0.4	0.9 ± 0.0	1.2	Omni
<i>L. hyperboreus</i>	1,132.0	123.5	116.5	7.0	1.0	0.8	Omni
<i>Sterna fuscata</i>	—	46.9	44.4	2.5	0.2	0.4	Fish

TABLE 1. Continued.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL/IN (%)	Food category ^a
<i>S. maxima</i> (8)	260.5 ± 15.7	65.8 ± 1.9	62.1 ± 1.8	3.7 ± 0.3	0.9 ± 0.1	1.4	Fish
<i>S. caspian</i> (2)	423.2	83.7	78.8	4.9	0.8	1.0	Fish
<i>S. antillarum</i>	24.8	23.0	20.5	2.5	0.2	0.9	Fish
<i>S. hirundo</i>	76.3	36.4	33.2	3.2	0.6	1.7	Fish
Alcidae							
<i>Fratercula cirrhata</i>	913.5	84.5	79.0	5.5	0.6	0.7	Fish
Columbiformes							
Columbidae							
<i>Zenaidura macroura</i> (7)	100.7 ± 14.1	49.5 ± 3.6	—	—	0	0.0	Grain
<i>Z. asiatica</i>	140.1	56.0	—	—	0	0.0	Grain
<i>Streptopelia risoria</i>	119.4	52.0	47.0	5.0	0.2	0.4	Grain
<i>Columba livia</i> (9)	286.0 ± 39.4	84.3 ± 5.4	80.3 ± 5.2	3.9 ± 0.3	0.5 ± 0.05	0.6	Grain
<i>Columbina passerina</i> (4)	32.3 ± 3.2	31.3 ± 3	—	—	0	0.0	Grain
Psittaciformes							
Psittacidae							
<i>Myiopsitta monachus</i> (3)	376.6 ± 283.9	52.6 ± 4.9	—	—	0	0.0	Grain
<i>Melopsittacus undulatus</i> (3)	36.6 ± 6.2	22.0 ± 4.8	—	—	0	0.0	Grain
<i>Nymphis hollandicus</i> (3)	76.0 ± 6.2	41.4 ± 0.4	—	—	0	0.0	Grain
<i>Cacatua galerita</i>	589.0	130.5	—	—	0	0.0	Grain
<i>C. sulfurea</i>	180.7	52.0	—	—	0	0.0	Grain
<i>Psittacus erithacus</i> (2)	429.8	114.0	—	—	0	0.0	Grain
Cuculiformes							
Cuculidae							
<i>Coccyzus americanus</i> (23)	46.0 ± 3.2	30.9 ± 1.2	26.2 ± 0.9	4.2 ± 0.3	3.7 ± 0.1	12.0	Insect
<i>Geococcyx californianus</i> (4)	171.1 ± 28.3	45.8 ± 2.7	38.9 ± 2.3	6.9 ± 0.5	6.5 ± 0.3	14.2	Insect
<i>Crotophaga ani</i> (2)	70.0	29.7	26.8	3.1	2.9	9.8	Insect
Opisthocomidae							
<i>Opisthocomos hotzini</i> ^d	750	82.2	64.4	17.8	4.0	4.9	Herb
Strigiformes							
Tytonidae							
<i>Tyto alba</i> (5)	419.6 ± 26.4	57.0 ± 11.0	51.4 ± 10.5	5.6 ± 1.1	6.9 ± 1.3	12.1	Carni TV

TABLE 1. Continued.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL/IN (%)	Food category ^a
Strigidae							
<i>Otus asio</i> (51)	83.2 ± 2.9	27.9 ± 0.7	24.0 ± 0.6	3.9 ± 0.1	4.4 ± 0.1	15.87	Insect
<i>O. kennicottii</i> (4)	79.7 ± 7.5	26.2 ± 2.4	24.5 ± 2.4	3.7 ± 0.2	4.1 ± 0.2	15.7	Carni TV
<i>Bubo virginianus</i> (5)	1,057.2 ± 15.6	88.4 ± 10.2	78.8 ± 7.9	5.6 ± 0.6	9.9 ± 0.8	11.2	Carni TV
<i>Athene cucularia</i> (7)	117.9 ± 150.5	34.3 ± 1.7	31.2 ± 1.8	3.2 ± 0.3	4.6 ± 0.3	13.4	Insect
<i>Strix varia</i> (3)	651.0 ± 54.0	76.2 ± 10.6	69.8 ± 11.4	6.4 ± 0.8	8.9 ± 0.6	11.7	Carni TV
Caprimulgiformes							
Caprimulgidae							
<i>Caprimulgus carolinensis</i> (24)	89.1 ± 4.1	27.6 ± 1	22.9 ± 0.9	4.7 ± 0.2	4.3 ± 0.2	15.6	Insect
<i>C. vociferus</i> (2)	34.3	17.9	13.0	4.9	2.4	13.4	Insect
<i>Chordeiles minor</i> (10)	56.7 ± 4.4	21.4 ± 1.1	17.5 ± 1	3.9 ± 0.3	3.3 ± 0.2	15.4	Insect
<i>C. acutipennis</i>	46.4	21.1	18.1	3.0	2.6	12.3	Insect
Apodiformes							
Trochilidae							
<i>Archilochus colubris</i>	28.6	5.6	4.2	1.4	0.1	1.8	Nectar
<i>Calypte anna</i>	3.0	6.0	4.0	2.0	0.3	5.0	Nectar
Trogoniformes							
Trogonidae							
<i>Trogon strigilatus</i>	—	23.3	18.3	5.0	3.6	15.5	Insect
<i>T. violaceus</i>	—	45.0	20.1	4.0	2.8	6.2	Insect
<i>T. collaris</i>	—	72.7	20.0	4.0	3.2	4.4	Insect
Coraciiformes							
Alcedinidae							
<i>Ceryle alcyon</i> (8)	221.8 ± 112.4	97.2 ± 4.3	—	—	0	0.0	Fish
Coraciidae							
<i>Coracias caudata</i>	—	24.7	22.1	2.6	3.7	15.0	Insect
Piciformes							
Picidae							
<i>Melanerpes carolinus</i> (12)	52.6 ± 2.5	26.4 ± 0.6	—	—	0.0	0.0	Insect
<i>Colaptes auratus</i> (4)	78.9 ± 7.1	29.5 ± 0.9	—	—	0.0	0.0	Insect
<i>Dryocopus pileatus</i> (2)	178.3	51.0	—	—	0.0	0.0	Insect
<i>Sphyrapicus varius</i> (9)	38.9 ± 2.1	28.7 ± 2.4	—	—	0.0	0.0	Insect
<i>Selenidra nattereri</i>	149.3	2.06	—	—	0.0	0.0	Insect

TABLE 1. Continued.

Taxon (n)	Body mass (g)	IN (cm)	SI (cm)	R (cm)	CL (cm)	CL/IN (%)	Food category ^a
Passeriformes							
Hirundinidae							
<i>Hirundo rustica</i>	31.4	14.6	13.2	1.4	0.3	2.1	Insect
<i>Tachycineta bicolor</i> (2)	15.4	15.8	14.1	1.7	0.4	2.5	Insect
<i>Progne subis</i> (2)	30.3	17.8	—	—	0.0	0.0	Insect
Corvidae							
<i>Corvus corax</i>	874.0	112.3	103.5	8.8	2.0	1.8	Omni
<i>Cyanocitta cristata</i> (2)	61.0	36.8	33.3	3.3	1.1	3.0	Omni
Turdidae							
<i>Hylocichla mustelina</i>	51.7	24.6	22.0	2.6	0.5	2.0	Insect
<i>Catharus ustulatus</i>	42.1	20.2	17.1	3.1	0.2	1.0	Insect
<i>Turdus migratorius</i>	76.6	28.0	25.5	2.5	0.3	1.1	Insect
Laniidae							
<i>Lanius ludovicianus</i> (3)	28.7 ± 0.3	28.7 ± 2.9	26 ± 2.7	2.7 ± 0.2	0.3 ± 0.1	1.1	Insect
Vireonidae							
<i>Vireo flavifrons</i>	20.0	15.0	14.0	1.0	1.0	6.7	Insect
Parulidae							
<i>Parula americana</i>	4.3	9.9	—	—	0.0	0.0	Insect
Emberizidae							
<i>Geothlypis trichas</i>	6.3	11.0	—	—	0.0	0.0	Insect
<i>Junco hyemalis</i>	28.6	24.7	22.7	2.0	0.3	1.2	Grain
Icteridae							
<i>Quiscalus quiscula</i> (4)	81.1 ± 35.5	32.2 ± 3.5	32.3 ± 2.7	3.0 ± 0.1	0.4 ± 0.2	1.2	Omni
<i>Q. major</i>	178.2	49.2	46.2	3.0	0.7	1.4	Omni
Thraupidae							
<i>Piranga olivacea</i>	34.8	20.0	—	—	0.0	0.0	Insect
Fringillidae							
<i>Coccothraustes vespertinus</i>	80.0	51.0	48.0	3.0	0.2	0.4	Grain

^a Primary types of foods in assigned food categories: Herb (herbivore)—greens, including the leafy parts of aquatic and terrestrial plants, needles. Grain (granivore)—seeds, including grains, sunflower seeds, conifer seeds, nuts. Insect (insectivore)—terrestrial invertebrates, including insects, spiders, snails, slugs, worms, millipedes, sowbugs. Carni-TV (carnivore; terrestrial vertebrates)—small terrestrial vertebrates including lizards, snakes, salamanders, frogs, small birds, rodents, carrion. Carni-TV (carnivore; terrestrial vertebrates)—small terrestrial vertebrates including lizards, snakes, nectar. Fish (piscivore)—fish, including fry and eggs. Diatom (diatomivore)—diatoms and matter high in silicate concentration.

^b S. A. Mahoney (unpubl. data).

^c A. S. Leopold (1953).

^d Grajal et al. (1989).

TABLE 2. Mean (\pm SE) cecal length (CL) of 154 bird species grouped by food habit categories (see the end of Table 1 for types of food in assigned food categories and for the sample size of individual species).

Diet	No. species	CL (cm)
Herbivore	10	28.4 \pm 6.4
Granivore	28	11.0 \pm 2.9
Insectivore	40	1.9 \pm 0.3
Carnivore (small vertebrates)	11	2.7 \pm 1.2
Carnivore (aquatic invertebrates)	14	4.2 \pm 1.1
Omnivore	17	13.5 \pm 4.2
Nectarivore	2	0.2 \pm 0.1
Piscivore	31	1.0 \pm 0.2
Diatominivore	1	3.2

ing animal protein and lipids, many species have poorly developed or non-existent ceca (Table 2).

Some protein consumers, however, have very well-developed ceca. For example, members of Cuculiformes, Caprimulgiformes, and Trogoniformes are primarily insectivorous, and Gruiformes and Strigiformes consume animal proteins from a variety of small vertebrate species (Table 1). A possible factor linking cecal presence and length to these diets may be chitin, the insoluble component of arthropod exoskeletons. Chitin is analogous to cellulose, in that both are structural carbohydrates considered to be insoluble in many digestive systems because of a beta-1,4 glycosidic linkage between individual monomer units (Muzzarelli 1977). Given that the well-developed ceca found in herbivorous birds that regularly consume cellulose also contain cellulolytic microbes (Soumalainen and Arhimo 1945, McBee and West 1969, Gasaway 1976), it would be useful to investigate whether the well-developed ceca found in non-herbivorous birds that consume chitin also contain chitinolytic microbes that function similarly.

There are several avian orders, however, whose members do not have well-developed ceca, i.e., Procellariiformes and Passeriformes (Table 1) and Sphenisciformes (Poppema 1990), but do contain endogenous chitinases secreted by either the gastric mucosa (Jackson et al. 1992, Place 1996) or pancreatic tissue (Staley 1986) that allow for chitin digestibility. Perhaps endogenous chitinases have eliminated the need for ceca to serve as a host site for bacterial digestion of chitin.

The presence of large ceca in non-herbivorous species may reflect other functions. Ceca from

TABLE 3. Mean (\pm SE) cecal length (CL) of 154 bird species grouped within each of the 21 orders sampled (see Table 1 for the sample size of individual species).

Order	No. species	CL (cm)
Gaviiformes	1	5.3
Podicipediformes	3	2.2 \pm 1.7
Procellariiformes	6	0.7 \pm 0.2
Pelecaniformes	4	1.8 \pm 1.0
Ciconiiformes	13	0.6 \pm 0.1
Phoenicopteriformes	2	6.1 \pm 2.9
Anseriformes	8	11.9 \pm 2.3
Falconiformes	9	0.08 \pm 0.05
Galliformes	24	32.0 \pm 3.9
Gruiformes	7	6.4 \pm 2.0
Charadriiformes	23	2.1 \pm 0.4
Columbiformes	5	0.1 \pm 0.1
Psittaciformes	6	0.0 \pm 0.0
Cuculiformes	4	4.3 \pm 1.1
Strigiformes	6	6.5 \pm 1.0
Caprimulgiformes	4	3.2 \pm 0.4
Apodiformes	2	0.2 \pm 0.1
Trogoniformes	3	3.2 \pm 0.2
Coraciiformes	2	1.9 \pm 1.9
Piciformes	5	0.0 \pm 0.0
Passeriformes	17	0.5 \pm 0.1

herbivorous Anseriformes, Galliformes, and Gruiformes have been histologically classified as "intestinal" in that they are similar anatomically to the small intestine (Naik 1962). In contrast, the large ceca in the non-herbivorous species (Strigiformes, Cuculiformes, Caprimulgiformes, Trogoniformes) are classified as "glandular," in that they contain an abundance of goblet cells and are capable of profuse secretory activity (Naik 1962). At a macroscopic level, these ceca appear thinner, more sac-like, and contain more fluid than the intestinal type (Poppema 1990). Chaplin (1989) demonstrated that the removal of these glandular types of ceca implicated a vital role of these ceca in water balance of thermally stressed Great Horned Owls *Bubo virginianus*. Little research has focused on non-herbivorous birds with well-developed ceca as compared to herbivorous birds with well-developed ceca. Thus, the challenge remains to further explore the relationship between cecal size and water balance in species containing glandular ceca. For example, is there evidence of glandular ceca changing size in response to water and/or heat stress as do the lengths of intestinal type ceca in response to diet quality (Lewin 1963, Moss 1972)? How does the alimentary canal adapt following cecectomy of glandular ceca? Do the tissues compensate for the loss of

cecal surface area by increasing length or number of villi? Do the tissues respond physiologically by enhancing existing transport mechanisms for water and electrolytes?

In addition to maintaining water balance during environmental stress, the ceca and rectum recycle nitrogen, especially in species that do not consume large amounts of dietary nitrogen in the form of protein (Braun and Campbell 1989, Karasawa 1989). Although it appears as a functional redundancy in the lower gut (Braun and Duke 1989), a positive correlation of cecal and rectal-cloacal lengths might indicate that the ceca are functioning as an extension of the lower gut in stressful conditions (Poppema 1990). Our analysis, however, was limited because the sample size was frequently insufficient to yield significant statistical power. The addition of other data (McLelland 1989, Clench and Mathias 1995) to the data herein, could be used in an allometric analysis regressing log transformations of mean cecal length values (dependent variable) upon body mass and other intestinal lengths (independent variables), and might enhance our understanding as to what extent cecal length is determined by taxonomic and/or dietary factors.

Thus, the following predictions should be tested: if species are (1) from a water-stressed environment (e.g., Galliformes ingesting large amounts of dry food, with limited access to drinking water), or (2) from saltwater/hypersaline environments and risk osmotic dehydration (e.g., Podicipediformes, Charadriiformes, Procellariiformes), or (3) those whose natural diet is low in protein and nitrogen and high in fiber (e.g., Galliformes species and granivorous birds), then there should be a high correlation between cecal and rectal-cloacal lengths if the cecal surface area is functioning as an extension of the functional surface area of the lower intestine. Conversely, if species (1) ingest large quantities of protein (e.g., in insect and vertebrate muscle), or (2) have access to sufficient fresh water from their diet, then cecal length would not be expected to correlate well with rectal cloacal length.

It is important to note that similar cecal lengths can be found within the various orders of birds having different intestinal lengths. Again, to better understand the functional importance of the presence and length of the avian ceca, perhaps it should be asked, to what extent

do the ceca increase the functional surface area of the alimentary canal? For example, the cecal length of *Athene cunicularia*, the Burrowing Owl, is 4.6 ± 0.3 cm and the intestinal length is 34.3 ± 1.7 cm. This cecal length represents a 13.4% extension of the intestinal length and likely contributes more to potential nutrient digestion, absorption, nitrogen recycling, and water balance than do the ceca of the *Pelecanus occidentalis*, the Brown Pelican, whose similar cecal length is 4.7 ± 0.9 cm, but intestinal length is 239.6 ± 7.0 cm, which extends the surface area of the alimentary canal less than 2%.

Most taxonomic diversity in the occurrence and length of the ceca can be resolved by reviewing the diets of individual species. For example, all Anseriformes examined had well-developed ceca except *Mergus serrator*, the Red-breasted Merganser (2.8 ± 0.6 cm), a piscivorous species consuming little fiber (Table 1). All other species examined in this order eat a diversity of greens, grains, seeds, aquatic vegetation, and aquatic invertebrates. Likewise, in the Podicipedidae, the Eared Grebe *Podiceps nigricollis* has well-developed ceca (6.0 ± 0.3 cm) as compared to the ceca of the Least Grebe *Tachybaptus dominicus* (0.4 cm) and the Pied-billed Grebe *Podilymbus podiceps* (0.3 ± 0.03 cm). Whereas *P. nigricollis* consumes marine invertebrates (Mahoney and Jehl 1985), *T. dominicus* and *P. podiceps* primarily consume fish, whose digestion can be completed in the stomach and small intestine.

Much diversity in cecal development exists in the Charadriiformes (Tables 1, 3). Piscivorous species examined from the family Alcidae and Laridae have poorly-developed ceca (means of 0.6 cm and 0.7 ± 0.3 cm, respectively) but the cecal length of species examined from the Haematopodidae (4.9 cm), Charadriidae (2.5 cm), Scolopacidae (3.2 ± 0.8 cm), and Recurvirostridae (6.7 cm) are comparatively well-developed. These latter species consume large quantities of chitin as found in aquatic insects, crayfish, shrimp, snails, bivalves, and other marine invertebrates.

Consistent with earlier reviews (McLelland 1989, Clench and Mathias 1995), we found no ceca present in the Psittaciformes and Piciformes examined. Among the Coraciiformes, no ceca were observed in the piscivorous Belted Kingfisher, *Ceryle alcyon* (Alcidinidae), but rel-

atively well-developed glandular ceca (3.7 cm, or 14.9% increase in intestinal length) were present in the insectivorous Lilac-breasted Roller *Coracias caudata* (Coraciidae).

These same reviews report that ceca are apparently absent in the order Apodiformes. Specifically, no ceca have been observed in the genus *Apus* (Mitchell 1901) nor in *Aeronautes* (Marshall 1906). In contrast, we found small ceca, 0.1 cm and 0.3 cm, in two species examined, i.e., the Ruby-throated Hummingbird *Archilochus colubris* and Anna's Hummingbird *Calypte anna*, respectively. These ceca would appropriately be categorized as poorly developed or vestigial ceca based on their length (McLelland 1989). Such evidence further reinforces the caveat that the relative length of the ceca or the presence/absence of the ceca is not a reliable taxonomic character beyond the species level.

The goals of this study were to contribute to the developing knowledge base on avian cecal lengths and also to suggest operative relationships between avian cecal lengths and food habits, taxonomic position, and/or other intestinal lengths. The variation that exists in cecal presence, shape, histology, and size implies that avian ceca may have many useful functions. Attempts to explain and couple such structural and functional diversity will be most successful if the ecology and phylogeny of the subject avian species also are considered.

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