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## Functional Review and Macrostructure of the Caecum in Ardeidae

Lola R. Mildren

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# Capstone of Lola R. Mildren

Submitted in Partial Fulfillment of the Requirements for the Degree of

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Nova Southeastern University

Halmos College of Arts and Sciences

Functional review and macrostructure of the caecum in Ardeidae

By

Lola R. Mildren

A Capstone

Submitted to the Faculty of

Nova Southeastern University

Halmos College of Arts and Sciences

In partial fulfillment of the requirements for the degree  
of Masters of Science with a specialty in:

Marine Science

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## **Abstract**

Situated on the lower digestive tract, caeca typically project cranially from the juncture of the small and large intestine. Recent studies have proposed that the role of caeca in the avian system is to act as fermentation chambers to synthesize vitamins, modulate gut microflora, and absorb nutrients; however, functionality differs with diet. Caeca are a typical characteristic of the avian gastrointestinal tract, with varying sizes and shapes, or even rudimentary or absent in some species. Caeca are notably singular and relatively small in Ardeids. Morphometric consistency in the number and presence of caeca on the lower intestinal tract of Ardeids was determined on a sample of 70 birds obtained from South Florida wildlife rehabilitation centers. This study also reports the findings of caeca length relative to morphometric and intestinal measurements. Caecum length relative to tarsus length was found to be significantly different between Cattle Egrets and Green Herons along with Green Herons and Great White Herons. Caecum length relative to small intestine length was significantly different between Great Egrets and Cattle Egrets. In order to further the understanding of Ardeid caeca, next steps include further research into the function of caeca in piscivorous birds and an in-depth look at the bacteria found in the avian caecum. In particular, future studies can be aimed at understanding why Green Herons differ so greatly from other Ardeids.

**Keywords:** Ciconiiformes, Pelicaniformes, Ardeidae, caeca, avian gastrointestinal tract

## Introduction

### *Wading Birds*

Wading birds are a large and diverse group. Generally accepted as being an ancient lineage, fossil records show the earliest herons and ibises dating from 60 to 54 million years ago during the late Paleocene and early Eocene epochs (Lowe, 1954). Although individual morphologies differ within the grouping, many of these modern species are found within the Order Ciconiiformes. Order members have conservative anatomical characters indicative of kinship in descent, including the positioning of the palatine bones, the presence of diastatony, the presence of small caeca, the possession of 16-20 cervical vertebrae, and the presence of only one pair of sternotracheal muscles in the syrinx (Lowe, 1954; Bock, 1956). Most of these birds are of substantial size with long necks, legs, and toes with special adaptations for wading in shallow waters. Widely distributed and often abundant, Ciconiiformes are conspicuous and graceful birds in their open habitats or in the air. Ciconiiforms subsist mainly on animal prey like fishes, small mammals, birds, and reptiles, which are typically swallowed whole then regurgitated later as pellets full of indigestible substances. Ciconiiforms are relatively silent birds that use croaks, grunts, shrieks, or clattering to communicate within their colonies. Gregarious in nature, Ciconiiformes will sometimes form large single or mixed-species aggregations for nesting and foraging. Flock feeding can be advantageous for wading birds for several reasons, such as: increased foraging success, reduced energy expenditure, enhanced predator detection, and protection from predators (Green and Leberg, 2005). Ciconiiformes comprises the three main families of Ardeidae (herons, egrets, and bitterns), Ciconiidae (storks), and Threskiornithidae (ibises and spoonbills).

Threskiornithidae consists of approximately 30 species and are generally the shortest of the long-legged group. They populate most warm regions except South Pacific islands, wading in shallow lagoons, lakes, bays, and marshes (Lowe, 1954; Bock, 1956). Medium in overall size, they have a distinctive long, slender, down-curved or spatulate bill with slit-like nostrils located laterally and basally to allow breathing while feeding and grooved surfaces that aid in feather cleaning (Hancock *et al.*, 2010). The Threskiornithidae adaptation of schizorhinal split cranial morphology allows for free movement of the upper mandible for tactile foraging (Del Hoyo *et al.*, 1992). The middle toe claw is cupped for use in feather maintenance and the hind toe is

reduced and elevated for more walking rather than perching. Reproduction and nesting sites are variable in this group, with nests in trees, low bushes, among reeds, or even on the ground with clutch sizes of three or four ovoid eggs. Ibis chicks are downy at hatching and go through two down plumages while remaining in their nests until fully grown (Lowe, 1954).

Ciconiidae consists of 20 species of large, stoutly built wading or walking birds. Most storks occur in the Old World, with only one species, the Wood Stork (*Mycteria americana*) being represented in North America. Storks have long necks with large, heavy, straight or curved bills. The middle and outer toes have partial webbing and the hind toe is smaller and raised compared to other families in Ciconiiformes. Boldly black and white in plumage, some stork species totally lack head feathers. Diet is varied and may be sought on dry land, in marshes, or in shallow water. Wood Storks in particular target fish prey by plowing the water with partly submerged open mandibles while wading shallow waters (Lowe, 1954). Nest choice is variable with some species choosing tall trees, cliffs, or buildings for their clutches of three to six eggs. Lacking a syrinx, storks utilize bill clattering as a mode of communication, particularly at or near the nest (Del Hoyo *et al.*, 1992).

Ardeidae consists of approximately 60 species and is the most diverse of the Ciconiiformes (Frederick, 2001). In comparison to other Ciconiiformes, Ardeids have a slimmer body with a long neck, a wide variation in display feathers on the head, neck, and back, and a pectinate middle toe claw for preening and feather maintenance, which ultimately aids flight aerodynamics. Ardeids resemble the other families included in the order Ciconiiformes in being long-legged, long-necked, and mostly aquatic, but differ in the characteristics of their feathers, beaks, and necks (Mock *et al.*, 1977). Specialized feathers are found in all herons and can be separated into three major types: lanceolate, filamentous, and aigrette (Bock, 1956). Most herons have occipital plumes consisting of a tuft of long feathers extending posteriorly. Found in both sexes throughout the breeding period, plumes function in courtship and pair bond displays. Ardeid bills are long and pointed for the spearing method they use to catch prey (Bock, 1956). Rather than being pierced by the spear-like bill, prey is grasped between the mandibles (Bock, 1956). Ardeid necks have adaptations between the sixth and seventh cervical vertebrae to accommodate the rapid forward thrusting of the bill. Vertebrae in front of this position have horizontal zygapophyses, and those beyond the sixth position shift backward to a vertical arrangement (Bock, 1956; Mock *et al.*, 1977). This unique morphological specialization on the

sixth cervical vertebra also allows for a kink in heron necks to maintain an “S” shape in flight (Mock *et al.*, 1977; Schreiber and Burger, 2001). Herons present two claw types: one is a short, strongly curved claw and the second is long and only slightly curved (Bock, 1956). Species with longer claws tend to also have longer toes and this characteristic is correlated with the habitat in which the heron lives, nests, and roosts in. Generally aquatic, these birds are strongly associated with shallowly flooded wetlands, where they contribute to important ecosystem functions such as accelerating nutrient cycles at feeding grounds, regulating fish populations, and providing organic subsidies such as feces or dropped food for biological transport pathways (Miranda *et al.*, 1997, Michelutti *et al.*, 2010).

### *Study Species*

Coastal habitats tend to support many different species of herons, which theoretically, any two species resembling each other too closely in habitat requirements could lead to the species with more efficient methods to drive the second species to extinction (Gause, 1943; Willard, 1977). Coexistence of heron species in a given habitat forces them to develop behavioral differences to share resources and avoid direct competition (Willard, 1977). Some of these ecological and behavioral adaptations include varied hunting depth based on leg length, varied feeding behaviors and techniques, feeding aggregations (Willard, 1977).

The Great Blue Heron (*Ardea herodias*) is the largest heron in North America and almost double the body mass of any other species of heron (Butler, 1997). They are geographically distributed across North America, rarely venturing far from bodies of water and living year-round on beaches, streams, rivers, and marshes (Butler, 1997). Great Blue Herons nest in old-growth areas and estuaries, wade on beaches and streams, and hunt in marshes and mangrove forests, thus, heron eggs act as sentinels to provide a means of monitoring contaminants in the rivers and oceans (Butler, 1997). Great Blue Herons feed anywhere they can get prey, including the terrestrial plane, and although fish are the preferred prey, their typical diet can consist of smaller prey within striking distance such as amphibians, reptiles, rodents, birds, shrimp, crabs, and aquatic insects, which they forage for by wading slowly or standing motionless in an upright position, waiting for approach (Short and Cooper, 1985; Kushlan, 1976). They utilize a variety of feeding behaviors including probing, pecking, walking at slow or fast speeds, flying short distances and alighting, hovering over water to pick up prey, jumping from perches, and floating

on the water's surface (Short and Cooper, 1985). Great Blue Herons typically hunt in solitary or in large social groups within intertidal mud and sandflats, intertidal reedbeds, wetlands, and tidal flats. Flock feeding is highly correlated with colonial nesting, which allows for stronger active defense and higher nest success rates (Short and Cooper, 1985). Limited to southernmost Florida and the Florida Keys, Great White Herons (*Ardea occidentalis* or *A. herodias occidentalis*) have an all-white plumage and a dark beak that can range from grey to pink with greyish or yellow legs. Great White Herons are currently treated as one of four distinctive and separate subspecies reproductively isolated from Great Blue Herons due to spatial and temporal differences in breeding (McGuire *et al.*, 2019). In Florida Bay and the Florida Keys extending beyond Florida Bay's western boundary, mixed pairs do occur, although blue-blue and white-white pairs are more common (McGuire *et al.*, 2019).

The Great Egret (*Ardea alba*) is a large, white migratory heron that is present on Florida coasts year-round, but can also be found throughout coastal areas within the Americas. Cosmopolitan Great Egrets inhabit freshwater, estuarine, and marine wetlands, where they are extremely adaptable as generalist foragers (Kushlan, 1976). Starting around mid-February to early March, Great Egrets nest in mixed-species colonies ranging from a few pairs to thousands of individual birds, including other species of herons, spoonbills, cormorants, and pelicans (Chapman and Howard, 1984). With fish constituting nearly 83% of their diet, Great Egrets employ a mainly passive hunting technique while standing still or wading in shallow water and hunting mainly minnow-sized fishes (Chapman and Howard, 1984). Prey also includes crustaceans, small birds, snails, frogs, snakes, and aquatic insects (Mock, 1980; Kaufman, 2001; Chapman and Howard, 1984). Because their legs are longer than other herons, they can forage in slightly deeper water than other conspecifics (Chapman and Howard, 1984). Much like the case of the Great Blue Heron, individual fish are caught through a rapid thrust of their bill singly, in mixed-species flocks, or in single-species groups (Mock, 1980; Chapman and Howard, 1984). Feeding grounds are determined by success, oftentimes being used repeatedly or, if success is low, Greats Egrets may move to other areas (Chapman and Howard, 1984). Most observations of group feeding have been recorded during specific environmental conditions, such as lowered water levels leading to prey concentration (Chapman and Howard, 1984).

The Cattle Egret (*Bubulcus ibis*) is a small, stocky, short-legged heron with long, slightly curved claws (Bock, 1956). Cattle Egrets are an abundant, strongly migratory species that are

widely distributed and common in Florida year-round (Patankar *et al.*, 2007). Unlike the other Ardeids that are mainly aquatic, gregarious Cattle Egrets usually forage in small flocks in dry fields, marshes, farms, and highway edges, and are highly associated with grazing livestock, where their insect prey are flushed out from grasses and caught (Meyerriecks, 1959; Fogarty and Hetrick, 1973). Cattle Egrets also form large flocks to pick at freshly ploughed fields to seize disturbed insects (Patankar *et al.*, 2007). Their diet mainly consists of insects such as grasshoppers, crickets, and flies, but they also feed on snakes, nestling birds, and small fishes (Kaufman, 2001). With a predominantly insectivorous diet, Cattle Egrets can be considered as a biological pest control, which makes them advantageous in an agro-ecosystem (Patankar *et al.*, 2007). Cattle Egrets nest and breed in both mixed colonies with cormorants and other Ardeid species or entirely in monospecific colonies (Metallaoui *et al.*, 2019; Patankar *et al.*, 2007). Unlike the mixed species colonies, monospecific nest sites may not be located near a water body (Patankar *et al.*, 2007).

The Green Heron (*Butorides virescens*) is a stocky, short-legged heron with shorter and more strongly curved claws than the Cattle Egret. They have a dark crest, streaked fore neck and breast, rich rufous side neck plumage, and a greenish varicolored back and wings (Bock, 1956). Largely a bird of tropical and warm temperate areas, Green Herons are migratory in northeastern North America and found year-round in warmer climates (Fraser and Ramsay, 1996). They are a common and widespread species in both fresh and salt water habitats, particularly near the edges of wetlands in shallow waters or concealed in vegetation. Small and hunch-backed, Green Herons forage mostly in solitary by stalking or standing still, waiting for prey to approach; however, they have been observed plunging into deeper pools, and capturing aerial prey from a perched position (Kaufman, 2001; Fraser and Ramsay, 1996). Utilizing feathers or small twigs on the water's surface as bait, Green Herons are generalist predators predominately feeding on small fish, snails, tadpoles, crayfish, and small frogs (Kaufman, 2001; Wheelock, 1906; Fraser and Ramsay, 1996). Intermediately social, Green Herons generally breed as either solitary pairs or in small colonies with old nests persisting for many years to be reused or as platforms for male courtship displays (Fraser and Ramsay, 1996).

The Tricolored Heron (*Egretta tricolor*) is a medium-sized, dark heron distinguished by its mix of blue-grey and lavender coloring with a white rump and belly (Hancock and Kushlan, 1984). They are typical along the northeastern Atlantic coast and permanent residents of the Gulf

coast. The Tricolored Heron is a coastal bird of shallow marshes and shores, swamps, mudflats, and bays (Hancock and Kushlan, 1984). They typically forage for prey in shallow waters as primarily solitary hunters. Wading thigh deep, their typical feeding behaviors include walking slowly, standing and waiting, and walking quickly (Hancock and Kushlan, 1984). Using a long, thin dagger-like bill, the Tricolored Heron mainly feeds on small fishes, but amphibians, crustaceans, gastropods, and insects are also consumed (Hancock and Kushlan, 1984).

The Snowy Egret (*Egretta thula*) is a medium-sized white heron that occurs continuously along the Atlantic coasts and the California Pacific coast. Snowy Egrets have black bills and legs along with bright yellow facial lores and feet throughout the non-breeding season; while in breeding condition, toes become orange-red and lores grow reddish-pink with the conspicuous lengthening of the head, neck, and back plumes (Hancock and Kushlan, 1984). Snowy Egret habitat varies considerably from dry grasslands for feeding to coastal areas, as long as the habitat borders or is flooded by water. Breeding is not restricted to coastal areas and occurs wherever suitable wetlands are extensive (Hancock and Kushlan, 1984). Typical in fresh and coastal areas, they occur in inland river basins, valleys, marshlands, swamp, and mangroves (Hancock and Kushlan, 1984). Snowy Egrets are highly colonial yet aggressively territorial, often nesting in mixed species colonies and displaying defense behaviors vigorously with crest raising, forward displays, and face off fighting (Hancock and Kushlan, 1984). Diet is diverse and sought out in open aquatic habitats with a more active pursuit than other heron species. Typical prey consists mainly of shrimp, but small fishes, fiddler crabs, mollusks, insects, crayfish, and frogs are also taken (Hancock and Kushlan, 1984).

The Little Blue Heron (*Egretta caerulea*) is a small-medium sized heron that has slate-blue plumage with a reddish-brown head and neck and grey-green legs. They differ from other dark-colored herons in that their first year is spent in entirely white plumage (Hancock and Kushlan, 1984). They are common along the eastern Atlantic and Gulf coasts along with the Mississippi basin, where they nest and feed in marshes, swamps, ponds, shores, and meadows. Their diverse diets include fishes, amphibians, insects, and substrate-crawling invertebrates (Hancock and Kushlan, 1984).

The Reddish Egret (*Egretta rufescens*) is a medium-sized, dimorphic heron that comes in both a dark and white form (Hancock and Kushlan, 1984). They are common throughout in coastal South Florida, the coastal Gulf, the Bahamas, the Caribbean, and Central America.

Reddish Egrets nest and feed in open marine flats and shorelines with very few records inland (Hancock and Kushlan, 1984). They are one of the most active-feeding herons with varied methods of hunting including running, hopping, open wing feeding, foot raking, and underwing feeding (Hancock and Kushlan, 1984). They prey mainly on smaller fishes like minnows, mullet, killfish, and pinfish (Hancock and Kushlan, 1984).

As an outgroup from Ardeids, the White Ibis (*Eudocimus albus*) is a large wading bird with long legs and a football-shaped body. They are almost entirely white with dark green-tipped wings and reddish legs and bills. They are wide-ranging birds with distribution throughout the coastal eastern Atlantic and Gulf. They are highly sociable and often roost and feed in flocks with large nesting colonies. They forage by walking slowly in shallow water or on land through touch while probing with their long, decurved bills (Kushlan and Kushlan, 1975). In coastal Florida, crayfish, crabs, insects, and small fishes make up the majority of prey (Kushlan and Kushlan, 1975).

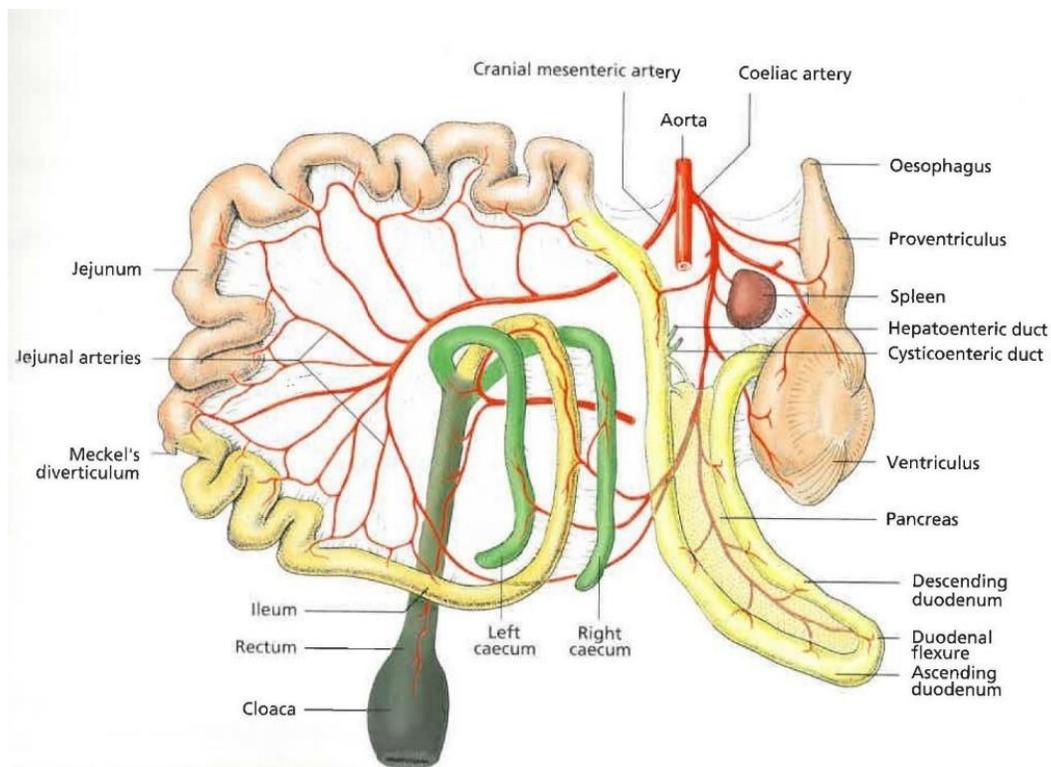
### *The avian alimentary canal*

In order to benefit from the physical and chemical characteristics of a wide variety of food types, the avian gastrointestinal (GI) tract has had to evolve much more than other animal orders (Hamdi *et al.*, 2013). Like mammals, the avian gastrointestinal tract is a double-ended open tube that begins at the beak and ends at the vent (Zaher *et al.*, 2012). Evolution of the avian GI tract has had to fit within limitations to facilitate flight, and thus, birds evolved a lightweight beak and muscular ventriculus to replace the dense bone, musculature, and dental features of reptiles and mammals (Hamdi *et al.*, 2013). Comparatively shorter and thus lighter than that of mammals, the compact avian GI tract fits flight requirements by being coiled near the bird's center of gravity with rapid digestive processes to support the high metabolic rate of birds (Hamdi *et al.*, 2013). Compact and lightweight, the avian proventriculus and ventriculus are unique among vertebrates providing a suitable environment for the breakdown of the size and molecular complexity of a bird's diet (Langlois, 2003).

Digestive systems convert food into elements that can easily be absorbed across the intestinal wall into the blood stream providing all of the nutrients, vitamins, and minerals vital to supporting life (Crompton and Nesheim, 2016). Digestion is aided by enzyme secretion throughout the alimentary tract thereby releasing simple sugars from carbohydrates, amino acids,

and free fatty acids (Crompton and Nesheim, 2016). To become accessible to these enzymes, food must be liquefied and softened, seeds must be opened, and lipids need to be broken down (Crompton and Nesheim, 2016). In the case of digestive enzymes being unable to break down certain food material, specialized areas in the lower digestive tract and caeca contain microorganisms to assist with digestion to produce small molecules for absorption (Crompton and Nesheim, 2016). The gastrointestinal tracts of birds differ among species to account for different diet specifications.

Upon consumption, food is transported from the beak through various components of the digestive system. The gastrointestinal tract is composed of the mouth, esophagus, crop, proventriculus, ventriculus, intestine, caeca, rectum, and finally, cloaca, though some of these structures may be rudimentary or absent during the evolution of some species (Zaher *et al.*, 2012). The thin-walled, flexible esophagus extends down the neck from the laryngeal mound into the thoracic cavity and terminates in the proventriculus, with the cervical component lying dorsal to the trachea (König *et al.*, 2016; Zaher *et al.*, 2012). At the thoracic inlet, immediately before its entry to the body cavity, the esophagus widens to form the crop, a spindle-shaped dilatation, which typically lies ventrally. The crop generally acts as temporary storage of ingesta, as well as a tool for softening and predigesting hard to digest food particles. The crop wall has a similar structure to the esophagus, and it contains mucus-producing crop glands similar to the ones found in the esophagus (König *et al.*, 2016). Muscles in the crop contract forcefully to propel the foodstuff into the stomach, which has different forms depending on the diet of the bird.



**Figure 1.** Gastrointestinal tract of a chicken *Gallus gallus domesticus* showing the end of the esophagus leading into the proventriculus and ventriculus. With the chemical breakdown of food in the ventriculus, ingesta is pushed out into the duodenum, through the jeuno-ileum, and follows the intestine until exit. (Source: König et al., 2016)

The avian “stomach” is comprised of the proventriculus, the intermediate zone, the ventriculus, and the pylorus (Langlois, 2003). The proventriculus, which is functionally equivalent to the mammalian stomach in producing digestive enzymes, is the fusiform, glandular compartment extending from the esophagus without a clear anatomical boundary, lying against the liver and to the right of the spleen (Langlois, 2003). Among avian species, this organ varies in size and shape with relatively smaller organs in granivorous birds and large sizes in carnivores and piscivorous birds. Carnivorous birds have a highly expandable, single, sac-like proventriculus with very little muscle to allow for the rapid ingestion of large quantities of animal protein. Grain- and plant-eating birds have two distinctly divided stomachs, the glandular proventriculus and the muscular ventriculus, while fruit-eating species have a rudimentary diverticulum (König *et al.*, 2016). Non-carnivorous birds lack longitudinal folds that are characteristic of the mucosal surface of the esophagus along the surface of the proventriculus but

is rather lined with mucous-secreting cells (Langlois, 2003). The proventriculus and ventriculus meet at a juncture called the intermediate zone, where food undergoes rhythmic contractions to force ingesta through the narrow gastric isthmus and into the ventriculus (Turk, 1982; König *et al.*, 2016). The ventriculus, or gizzard, is a muscular compartment that is most prominent in seed-eating bird species (Crompton and Nesheim, 2016) and does not have an equivalent in the mammalian gastrointestinal tract (Langlois, 2003). Replacing the function of teeth, ventricular contractions grind and liquefy foods exposing them to digestive enzymes (Crompton and Nesheim, 2016). Seed and plant-eating birds ingest grit to aid maceration by providing an abrasive surface, which is continuously renewed as it wears down (Langlois, 2003; Neshiem, 2006). Development of the ventriculus varies among species with two basic types: well-developed and distinct from the proventriculus in granivores, insectivores, and herbivores, or poorly developed and uniform in thickness in carnivores and piscivores (Langlois, 2003). The ventriculus of non-carnivorous species consist of four semiautonomous smooth muscle regions alternately contract muscles to grind food (Houston and Duke, 1987.) Ventriculi of carnivorous birds lack the four muscular regions and has no clear distinction from the proventriculus (Langlois, 2003). Frugivores and nectarivores vary in terms of ventriculus development and tend to lean to well- or poorly developed depending on species (Langlois, 2003). Connecting the ventriculus to the duodenum is the pylorus, which regulates the rate of passage of food by slowing down the movement of large particles into the duodenum from the stomach (Langlois, 2003).

The avian small intestine is a long, coiled mass divided into three parts: duodenum, jejunum, and ileum. The U-shaped duodenum starts at the pyloric region of the stomach, which opens into the duodenum through a guarded pyloric orifice to slow the movement of large particles into the duodenum (Zaher *et al.*, 2012; Langlois, 2003). The elongated duodenal loop encases the pancreas, which is attached to each arm of the loop. The jejunum and ileum, termed the jejuno-ileum, are very long and coiled into loops on the right posterior quadrant of the body cavity, beginning at the caudal end of the duodenum where bile and the pancreatic ducts are located (König *et al.*, 2016; Zaher *et al.*, 2012). The external diameter of the jejunum and ileum is roughly uniform, and thus the transition between the two sections can be difficult to recognize by the rudimentary Meckel's diverticulum (Zaher *et al.*, 2012). The Meckel's diverticulum is where the yolk sac was attached during the embryonic development and appears as a small

projection on the jejunum's outer surface. The large intestine consists of the caeca and a short rectum and begins at the ileo-caecal-colic junction, where the small and large intestine meet (Zaher *et al.*, 2012). The large intestine aids in control of the rate of flow of the digesta fluid along the intestine and also in the filling and emptying of the caeca (Turk, 1982). The final intestinal segment is the rectum, which passes to the cloaca, passing digestive and urogenital systems (König *et al.*, 2016).

#### *Anatomy and physiology of the avian caeca*

Found on the final segment of the intestine, caeca are intestinal outpockets along the lower digestive tract that project from the ileo-caecal-colic junction with separate lateral or ventrolateral openings into the colon. Typically paired, the right caecum and the left caecum usually lie at the same level of the gut; however, in some species, the openings are positioned at marginally different levels (McLelland, 1989). Caeca are a common characteristic of the avian digestive tract, and although they can be absent in some species, caeca are found in a diverse array of sizes and forms (Svihus *et al.*, 2013). From their bases, caeca are loosely connected to the terminal part of the ileum by mesentery and a fold of the ileocaecal ligament, generally directed cranially (McLelland, 1989; Clench and Mathias, 1995).

Because of the presence of large populations of bacteria within them, caeca are hypothesized to act as fermentation chambers that function to synthesize vitamins, modulate gut microflora, absorb nutrients, and act as an immunological response (DeGolier *et al.*, 1999; Svihus *et al.*, 2013). With a pH of 6.0-6.6, caeca are essentially sacs of anaerobic bacteria, protozoa, fungi, and other micro- and macro-organisms (Hill, 1971; Clench and Mathias, 1995). Caeca contain both beneficial and disease-causing forms of organisms, although some have been demonstrated as pathogenic (Clench and Mathias, 1995). Most notably, the pathogenic caecal microorganism *Eimeria tenella* alters caecal motility and causes irreparable physical damage to tissue (Clench and Mathias, 1995). Among the most common macroscopic parasites are nematodes, ringworms, and pinworms, which are swallowed as larvae and move from the upper gut to the colon, and finally into the caeca (Clench and Mathias, 1995).

As with other aspects of avian morphology, caeca were not described until the late 19<sup>th</sup> and early 20<sup>th</sup> centuries, with descriptions mostly coming as an incidental byproduct to other studies (Clench and Mathias, 1995). Caecal physiology knowledge is based on studies of

gallinaceous birds and waterfowl because they are large enough to easily study, readily available, economically important, and behaviorally amenable (Clench and Mathias, 1995). Although not well understood, and historically regarded as vestigial, useless ancestral remnants, caeca may contribute to osmoregulatory function and the recycling of nitrogen from urine (e.g., Björnhag, 1989). Browne (1922) stated that caeca could only be filled with fluid digesta and small particles, which could not directly pass from the small intestine into the caeca, but rather pass through the narrow ileum into the colon, where the pressure finally decreases and takes a retrograde path into the caeca from the colon (Browne, 1922; Björnhag, 1989). This retrograde flow of urine into the caeca can possibly provide a more efficient recovery of electrolytes, water, and nutrients, and provide a nitrogen source for the caecal microbes during periods when the bird's diet may be lacking (Akester *et al.*, 1967; Hill, 1971). Thus, the intestinal avian caecum acts as a blind-ended sac with a meshwork of long, interlocking villi at its entrance that functions as a sieve, permitting fluid and small particles to enter the caecal cavity as colonic contents are selectively passed through the caecal sphincter (Clench and Mathias, 1995). These contents are prevented from migrating up the large intestine into the ileum by the contracted ileal sphincter. Because of the blind-ended nature of the caecum, contents can be held for greater lengths of time than in the main intestine, through which digesta moves quickly (Clench and Mathias, 1995). Fluid held in the caeca has time to be absorbed and the molecules and solid particles in the solution can be acted on by bacteria, fungi, and other micro-organisms (Clench and Mathias, 1995). The caeca therefore may serve as a site for the absorption of water and nitrogenous components (Clench and Mathias, 1995). In caecal studies of domestic turkeys *Meleagris gallopavo f. domestica*, the main emptying of the caeca occurs twice daily, after the bird awakens in the morning and early afternoon, suggesting a long residence time for caecal contents (Svihus *et al.*, 2013; Moss, 1989).

As outlined in Table 1, a literature review by Clench and Mathias (1995) found that caeca are a common feature of the avian gastrointestinal tract. Observed differences in the occurrence and physical characteristics of avian caeca suggests considerable interspecific variation (Svihus *et al.*, 2013; DeGolier *et al.*, 1999).

**Table 1.** Table of the available knowledge on caeca of each avian taxonomic order.

<b>Taxonomic Order</b>	<b>Caeca Size</b>	<b>Comments</b>	<b>Source</b>
Tinamiformes	Large	Large and ornate	Clench and Mathias, 1995
Sruthioniformes	Large	Large and very long caeca	Clench and Mathias, 1995
Rheiformes	Large	Very long with less internal spiral folding	Clench and Mathias, 1995
Casuariiformes	Moderate	Relatively short with sacculations	Clench and Mathias, 1995
Apterygiformes	Large	Large and wide caeca	Clench and Mathias, 1995
Anseriformes	Large and Moderate	Reduced in some species	Clench and Mathias, 1995; Degolier <i>et al.</i> , 1999
Galliformes	Large	Well developed	Clench and Mathias, 1995; Degolier <i>et al.</i> , 1999
Gaviiformes	Moderate	Moderately sized, paired caeca	Clench and Mathias, 1995
Sphenisciformes	Small/vestigial		Clench and Mathias, 1995
Procellariiformes	Small/vestigial	Single in some species; Variable	Clench and Mathias, 1995
Podicipediformes	Moderate and Small/vestigial		Clench and Mathias, 1995
Phoenicopteriformes	Small/vestigial	Very little information known	Degolier <i>et al.</i> , 1999
Phaethontiformes		Very little information known	
Ciconiiformes	Small/vestigial	Single in some species	Clench and Mathias, 1995
Pelecaniformes	Small/vestigial	Single in some species	Clench and Mathias, 1995
Accipitriformes	Small/vestigial		Ritzman, 2014
Otidiformes		Very little information known	

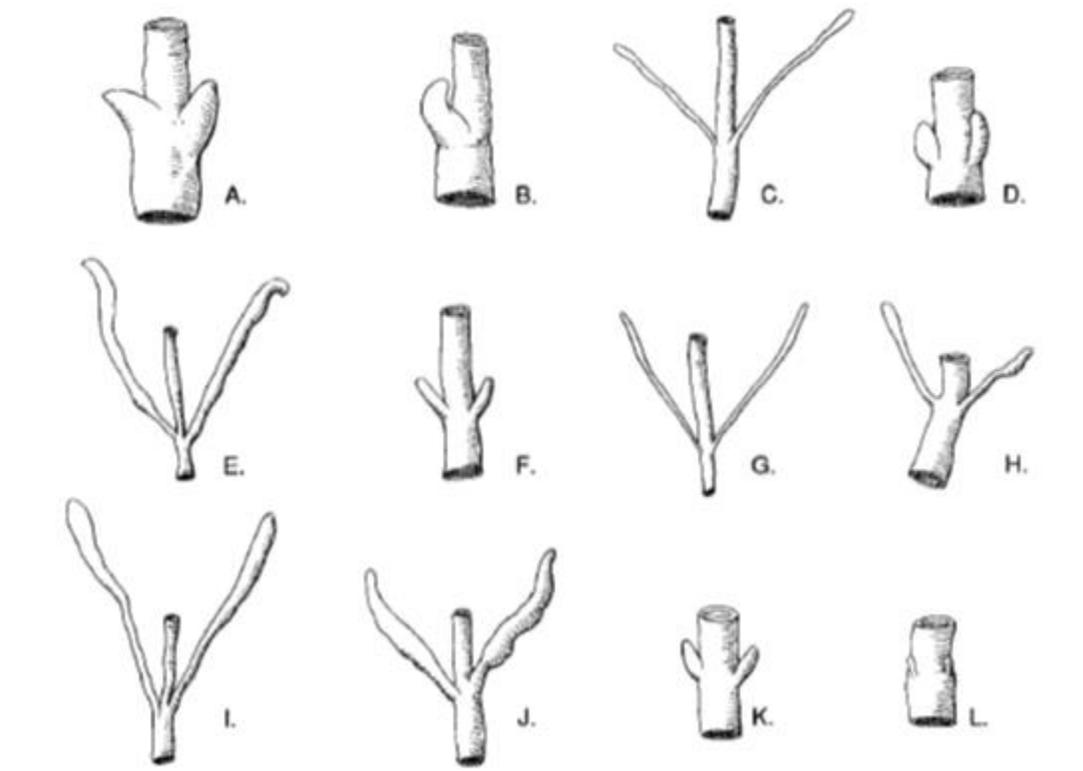
Gruiformes	Large		Clench and Mathias, 1995; Degolier <i>et al.</i> , 1999
Charadriiformes	Large, Moderate, and Small/vestigial	Variable	Clench and Mathias, 1995
Columbiformes	Absent		Clench and Mathias, 1995
Opisthocoformes	Large	Well-developed caeca	Degolier <i>et al.</i> , 1999
Cuculiformes	Large, Moderate, and Absent	Variable	Degolier <i>et al.</i> , 1999
Strigiformes	Large		Clench and Mathias, 1995
Caprimulgiformes	Large		Clench and Mathias, 1995
Apodiformes	Absent		Degolier <i>et al.</i> , 1999
Coliiformes	Absent		Clench and Mathias, 1995
Trogoniformes	Moderate		Clench and Mathias, 1995
Coraciiformes	Moderate, Small/vestigial, and Absent	Variable	Clench and Mathias, 1995; Degolier <i>et al.</i> , 1999
Piciformes	Absent		Clench and Mathias, 1995
Falconiformes	Small/vestigial		Clench and Mathias, 1995; Ritzman, 2014
Psittaciformes	Absent		Clench and Mathias, 1995
Passeriformes	Small/vestigial		Clench and Mathias, 1995

Observed in most avian species, caeca come in various sizes and forms, but can also be absent altogether (Svihus *et al.*, 2013; Clench and Mathias, 1995). Most bird species have a single pair of caeca, often fingerlike in shape. Caeca can be symmetrical or asymmetrical, with the right caecum usually longer, and a few groups (notably Ardeidae) possess one single, unpaired caecum (McLelland, 1989; Magnan, 1911). Naik and Dominic (1962), in a limited scope, suggested the degree of development of caeca has a connection to their diet. Omnivorous and herbivorous groups, such as Galliformes and Anseriformes, find caeca to be highly developed and resemble the intestine in length (Naik and Dominic, 1962). Granivorous groups like Columbiformes and Psittaciformes tend to have vestigial, non-functional, or even absent caeca. In piscivorous groups like Ciconiiformes and Procellariiformes, caeca are vestigial or entirely absent. Carnivores display two distinct forms of caecal development: Strigiformes have well-developed, glandular caeca that are devoid of lymphoid tissue, and Accipitriformes caeca are small, lacking glands, and infiltrated by lymph cells. Insectivore groups like Cuculiformes and Coraciiformes show extreme variation in the degree of caecal development; however, the vast majority of intestinal caeca are vestigial and non-glandular, or even totally absent (Naik and Dominic, 1962; McLelland, 1989). Caeca tend to be more conspicuous in plant-eating birds where they act as sites for microbial fermentation of non-digestible plant-cell walls (Houston and Duke, 1987). In some bird species, adaptive caeca will change in size to accommodate the nature of their diet (Svihus *et al.*, 2013; Crompton and Nesheim, 2016). The length and width of caeca increase dramatically as birds adapt to a fiber-rich, less digestible diet during winter than when in the spring when young plants are available (Crompton and Nesheim, 2016). Redig (1989) determined that the caeca of gallinaceous birds require around two to four months to accommodate a new diet; however, some birds are subject to decreased weight and increased mortality rates during this adaptation period.

#### *Diversity of caeca in Ardeids*

Order Ciconiiformes has small caeca with many lymphocytes, coined the “lymphoid” type (Clench and Mathias, 1995). Ardeid caeca are variable, appearing reduced, small, or rudimentary. The heron family usually has a single, small caecum, 0.4-1.0 cm in length; however, some individuals may reveal a second rudimentary caecum in the wall of the intestine (Clench and Mathias, 1995; DeGolier *et al.*, 1999). In contrast to the typical lateral opening,

Ardeidae's single, visible caecum opens into the intestine dorsally (McLelland, 1989; Naik, 1962).



**Figure 2.** Illustrations of various avian caeca reproduced from Clench and Mathias (1995). There is a wide range of morphological diversity based on diet. (A) Little Cormorant (*Microcarbo niger*), piscivorous; (B) Cattle Egret (*Bubulcus ibis*), insectivorous; (C) Cotton Teal (*Nettapus coromandelianus*), omnivorous; (D) Crested Serpent Eagle (*Spilornis cheela*), carnivorous; (E) Common Quail (*Coturnix coturnix*), herbivorous; (F) Collared Dove (*Streptopelia decaocto*), granivorous; (G) Redwattled Lapwing (*Vanellus indicus*), insectivorous; (H) Common Koel (*Eudynamys scolopaceus*), insectivorous; (I) Spotted Owlet (*Athene brama*), insectivorous; (J) Indian Roller (*Coracias benghalensis*), omnivorous; (K) Oriental Skylark (*Alauda gulgula*), granivorous and insectivorous; (L) Gray Wagtail (*Motacilla cinerea*), insectivorous.

Biological and ecological studies on herons and egrets have burgeoned in recent years because these species can be utilized as indicators of anthropogenic disturbances in wetland and

coastal ecosystems (e.g., Abdullah *et al.* 2017; Massa *et al.*, 2014). With such little knowledge on the caeca of Ardeidae, the primary objective of this study was to determine whether there was morphometric consistency in the number and presence of caeca on the lower intestinal tract of Ardeids. Further, because the birds within the Ardeid group differ in total sizes, the secondary objective was to determine if the relative length of the caecum differs between Ardeid species in terms of scaling on the small intestine.

## **Materials and Methods**

### Collection:

All bird specimens were collected from four wildlife rehabilitation centers in South Florida: South Florida Wildlife Center (SFWC) in Fort Lauderdale, Pelican Harbor Seabird Station (PHSS) in Miami, and Florida Keys Wild Bird Rehabilitation Center (FKWBC) in Tavernier. The specimens died from either undergoing treatment at the wildlife centers, euthanasia upon admittance (EOA) due to physical condition or traumatic impairment or were pronounced dead upon arrival (DOA). Bird specimens were collected from these wildlife centers under FFWCC permits LSSC-12-00075 and LSSC-18-00062, USFWS permit MB8290-A-0, and a USFWS LOA to D.W. Kerstetter.

Bird specimens used in this study included Great Blue Herons (GBHE), Great White Herons (GWHE), Great Egrets (GREG), Cattle Egrets (CAEG), Snowy Egrets (SNEG), Green Herons (GRHE), Tricolored Herons (TCHE), and White Ibises (WHIB) (the four letters in parentheses pertain to the official American Ornithologists' Union "alpha codes" for each species, per AOS, 2017). As specimens were collected from agencies and not captured, sample size was dependent upon specimens donated.

### Laboratory Processing:

#### *Bird Processing:*

Upon collection of specimens from the wildlife rehabilitation centers, these birds were assigned a unique identification number along with the ornithological standard four-letter species code, tagged with this information, and placed in standard laboratory freezers (*ca.* -10°C) for

storage. To prepare the specimens for dissection, they were transferred to the ca. 20°C laboratory refrigerator for thawing. All birds were dissected immediately upon thawing. Before the dissection took place, morphometric measurements such as weight, tarsus length, wing chord, esophagus length, middle toe and claw lengths, tail length, and beak dimensions were recorded on datasheets for each specimen. Senar and Pascual (1997) determined that tarsus length was a good predictor of overall body size, so for the purpose of this study, tarsus length was used to determine overall body size among bird specimens. Additionally, information including wildlife center (geographic location), date of collection, date of processing, age-class (juvenile or adult), and observable or previously noted injuries were recorded.

#### *Caecum Analysis:*

After initial measurements and processing photographs were taken, the dissection proceeded by making an incision below the sternal keel and cutting along the ribs to open up the internal cavity. The coracoids were cut to open the bird from esophagus to large intestine and have full range of motion within the bird's abdominal cavity. After taking note of the bird's sex, the gastrointestinal tract was examined, including the large intestine, small intestine, ventriculus, and proventriculus.

Measurements of the length of the large intestine, length to the ileum, length to the jejunum, and length to the duodenum, along with the length of the proventriculus and dimensions of the ventriculus, were recorded. The caecum at the junction of the small and large intestine was removed (including 1 inch of intestinal tissue on either side), photographed and measured, then stored in formalin to fix and store the sample.

#### Statistical Analysis:

Recorded measurements were collated and uploaded into the program RStudio (version, year), where descriptive statistics were conducted to calculate the range, mean, and standard deviation for tarsus length, duodenum length, jejunum length, ileum length, small intestine length, large intestine length, and caecal length. Further, ratios of the caecum length to tarsus length and small intestine length were calculated to determine consistency among Ardeid species. A correlation test was run to determine if the wing chord length and tarsus length were correlated. A t-test was run to determine how age class and body size affects caeca length in

White Ibis samples. Then a one-factor ANOVA test was run to determine how the caeca measurements relative to the tarsus lengths and small intestine measurements varied by bird group.

## Results

### Specimen Collection

A total of 70 individual bird specimens belonging to two taxonomic families were collected and sampled. As summarized in Table 2, Great Blue Herons had the highest number of collected individuals (n=16), followed by Great Egrets (n=12), Green Herons (n=11), Cattle Egrets (n=11), Great White Herons (n=8), White Ibis (n=7), Snowy Egrets (n=3), and Tricolored Herons (n=2) (Table 1). The distribution of bird specimens varied among the three wildlife centers with the Florida Keys Wild Bird Center contributing the most specimens (n=51), followed by the South Florida Wildlife Center (n=18), and Pelican Harbor Seabird Station (n=1).

**Table 2:** Total number of each wading bird species dissected for this study, including the size (via tarsus length) and the number of specimens obtained from each wildlife center. \*White Ibis is a comparative outgroup.

Species	n	Tarsus Length ( $\bar{x} \pm SD$ ; cm)	South Florida Wildlife Center	Pelican Harbor Seabird Station	Florida Keys Wild Bird Center
Great Blue Heron	16	16.97 $\pm$ 2.99	6	0	10
Great White Heron	8	18.113 $\pm$ 1.97	0	1	7
Green Heron	11	4.38 $\pm$ 0.442	5	0	6
Great Egret	12	13.93 $\pm$ 1.206	2	0	10
Cattle Egret	11	7.082 $\pm$ 0.433	3	0	8
Snowy Egret	3	9.33 $\pm$ 1.617	1	0	3
Tricolored Heron	2	9.0 $\pm$ 0.707	1	0	1
*White Ibis	7	7.714 $\pm$ .628	1	0	6

### Correlation

A correlation test was run to determine if tarsus length and wing chord length were correlated, but for each bird specimen group, the two variables consistently proved to not be significantly correlated. Correlation p-values for tarsus length and wing chord length were taken for Cattle Egrets, Great Blue Herons, Great White Herons, Green Herons, Snowy Egrets, and White Ibises, respectively: (p=0.7681, p=0.3058, p=0.7681, p=0.1115, p=0.332, p=0.3333, p=0.815).

### T-test

Unlike Ardeids, White Ibis plumage distinctly differs between age classes. Through use of a t-test, White Ibis samples were used to determine that age class does not significantly affect caeca size (p-value = 0.28) or body size (p-value = 0.37).

### Morphometric Data

Of the 63 Ardeid specimens, the presence of a singular caecum was consistent within this group, with the exception of one Green Heron, which was observed to be lacking any caecal tissue. Further research into this observation noted however that the caecum could be so reduced so that it is hidden within the intestinal lining (Clench and Mathias, 1995; DeGolier *et al.*, 1999). This particular Green Heron was a malnourished adult female that came into the wildlife center with a fractured vertebrae, which according to Redig's (1989) research, could suggest leading to a reduced caecum. Of the seven outgroup specimens, each White Ibis showed two uniform, prominent caeca on either side of the intestine.

Measured in millimeters, on average, Great White Herons had the largest tarsus length ( $181.1 \pm 19.7$ ) followed closely by Great Blue Herons ( $169.7 \pm 29.99$ ), then Great Egrets ( $139.3 \pm 12.06$ ), Snowy Egrets ( $93.3 \pm 16.17$ ), Tricolored Herons ( $90 \pm 7.07$ ), White Ibises ( $77.14 \pm 6.28$ ), Cattle Egrets ( $70.82 \pm 4.33$ ), then finally Green Herons ( $44.36 \pm 4.54$ ) (Table 3).

Measured in grams, Great White Herons had the heaviest weight ( $1863 \pm 459.6$ ), followed closely by Great Blue Herons ( $1700 \pm 425.8$ ), then Great Egrets ( $869.1 \pm 287.9$ ) and White Ibises ( $577.1 \pm 71.48$ ). Lower in weight were the Tricolored Herons ( $392 \pm 4.35$ ), Snowy Egrets ( $331.9 \pm 41.07$ ), Cattle Egrets ( $249.1 \pm 47.7$ ), and Green Herons ( $133 \pm 40.64$ ) (Table 3).

**Table 3.** The mean, range, and standard deviation of the tarsus length (in millimeters) and weight (in grams) for each bird species for this study.

<b>BIRD (N=)</b>	<b>TARSUS LENGTH (MM)</b>			<b>WEIGHT (GRAMS)</b>		
	<b>Mean</b>	<b>Range</b>	<b>Std. Dev</b>	<b>Mean</b>	<b>Range</b>	<b>Std. Dev</b>
<b>GBHE (N=16)</b>	169.7	125	29.99	1700	1500	425.8
<b>GWHE (N=8)</b>	181.1	68	19.69	1863	1200	459.6
<b>GREG (N=12)</b>	139.3	35	12.06	869.1	1100	287.9
<b>CAEG (N=11)</b>	70.82	13	4.33	249.1	148	47.67
<b>GRHE (N=11)</b>	44.36	13	4.55	133	119	40.64
<b>SNEG (N=3)</b>	93.33	28	16.17	331.9	80.8	41.07
<b>TCHE (N=2)</b>	90	10	7.071	392	61.3	4.35
<b>*WHIB (N=7)</b>	77.14	17	6.28	577.1	200	71.48

## Intestinal Measurements

Measurements were taken in centimeters (cm) from the large intestine, to the ileum, to the jejunum, and finally to the opened duodenal loop. The small intestine comprises the ileum, jejunum, and duodenum, which was individually added up for each bird and used as a separate measurement. Additionally, the caecum was measured through the clipping of an inch on each side of the intestinal tissue and lined up against a ruler after all measurements were recorded. Intestinal measurements were taken for 16 Great Blue Herons, 8 Great White Herons, 12 Great Egrets, 11 Cattle Egrets, 11 Green Herons, 3 Snowy Egrets, 2 Tricolored Herons, and 7 White Ibises. Data are presented as mean length (cm) and standard deviation.

### *Large Intestine*

Great Blue Herons ( $9.07 \pm 2.31$ ) and Great White Herons ( $9.06 \pm 0.67$ ) were very similar in large intestine lengths (Table 4). The White Ibis ( $6.46 \pm 1.32$ ), Tricolored Heron ( $6.25 \pm 1.06$ ), and Snowy Egret ( $6.23 \pm 0.81$ ) were similar in mid-range large intestine lengths, followed by the smaller large intestine measurements of Green Herons ( $5.65 \pm 1.01$ ), Great Egrets ( $5.45 \pm 0.91$ ), and Cattle Egrets ( $4.62 \pm 1.02$ ) (Table 4).

### *Ileum*

Great Blue Herons had the largest ileum sizes ( $81.28 \pm 13.26$ ), followed by Great Egrets ( $76.25 \pm 13.89$ ), Great White Herons ( $71.63 \pm 13.75$ ), and Tricolored Herons ( $54.5 \pm 16.26$ ) (Table 4). Smaller ileum measurements of the White Ibises ( $36 \pm 4.20$ ), Green Herons ( $33.5 \pm 6.31$ ), Snowy Egrets ( $31.12 \pm 9.41$ ), and Cattle Egrets ( $22.58 \pm 5.80$ ) were measured accordingly (Table 4).

### *Jejunum*

Great Blue Herons ( $71.16 \pm 16.88$ ), Great Egrets ( $68.67 \pm 16.10$ ), Great White Herons ( $65.25 \pm 14.11$ ), and Tricolored Herons ( $64 \pm 33.94$ ) had the largest jejunum measurements followed by Snowy Egrets ( $34.67 \pm 11.59$ ), White Ibises ( $33.97 \pm 5.82$ ), Green Herons ( $30.36 \pm 8.33$ ), and Cattle Egrets ( $17.08 \pm 3.34$ ) (Table 4).

### *Duodenum*

The small duodenal loop was largest in Great Egrets ( $27.83 \pm 8.5$ ), Great White Herons ( $27.44 \pm 9.77$ ), and Great Blue Herons ( $26.75 \pm 6.42$ ), followed by Tricolored Herons ( $19.5 \pm 0.71$ ), White Ibises ( $17.93 \pm 2.17$ ), Snowy Egrets ( $16 \pm 5$ ), Green Herons ( $14.27 \pm 2.75$ ), and Cattle Egrets ( $10.88 \pm 6.29$ ) (Table 4).

### *Small Intestine*

Overall, the small intestine was largest in Great Blue Herons ( $179.2 \pm 24.2$ ), Great Egrets ( $172.8 \pm 27.6$ ), Great White Herons ( $164.3 \pm 30.7$ ), and Tricolored Herons ( $138 \pm 50.91$ ), followed by White Ibises ( $87.9 \pm 8.57$ ), Snowy Egrets ( $81.83 \pm 21.58$ ), Green Herons ( $78.14 \pm 11.89$ ), and Cattle Egrets ( $50.55 \pm 8.56$ ) (Table 4).

### *Caecum*

Finally, the caecum was largest in Great Blue Herons ( $0.98 \pm 0.39$ ), Great White Herons ( $0.86 \pm 0.26$ ), Tricolored Herons ( $0.85 \pm 0.06$ ), and Great Egrets ( $0.82 \pm 0.35$ ) (Table 4). Caeca were smaller in Snowy Egrets ( $0.57 \pm 0.06$ ), Green Herons ( $0.47 \pm 0.12$ ), White Ibises ( $0.43 \pm 0.16$ ), and Cattle Egrets ( $0.36 \pm 0.11$ ) (Table 4).

### *Ratio of Caecum Length to Tarsus Length*

The caecum length compared to the tarsus length was largest in Tricolored Herons ( $0.116 \pm 0.032$ ), Green Herons ( $0.096 \pm 0.037$ ), Snowy Egrets ( $0.063 \pm 0.016$ ), and Great Blue Herons ( $0.061 \pm 0.029$ ) (Table 5). The scaling of the caecum to the tarsus was smaller in Great Egrets ( $0.058 \pm 0.025$ ), White Ibises ( $0.055 \pm 0.017$ ), Cattle Egrets ( $0.52 \pm 0.017$ ), and Great White Herons ( $0.048 \pm 0.017$ ) (Table 5). A Kruskal-Wallis one-way analysis of variance test deemed a significant difference between group means ( $p=0.01968$ ) with the non-parametric multiple comparisons hoc test revealing significant differences between Cattle Egrets and Green Herons and Green Herons and Great White Herons (Figures 3 and 4).

### *Ratio of Caecum Length to Small Intestine Length*

The caecum length compared to small intestine length was largest in Cattle Egrets ( $0.007 \pm 0.003$ ), Tricolored Herons ( $0.006 \pm 0.0003$ ), Green Herons ( $0.006 \pm 0.001$ ), and Great Blue

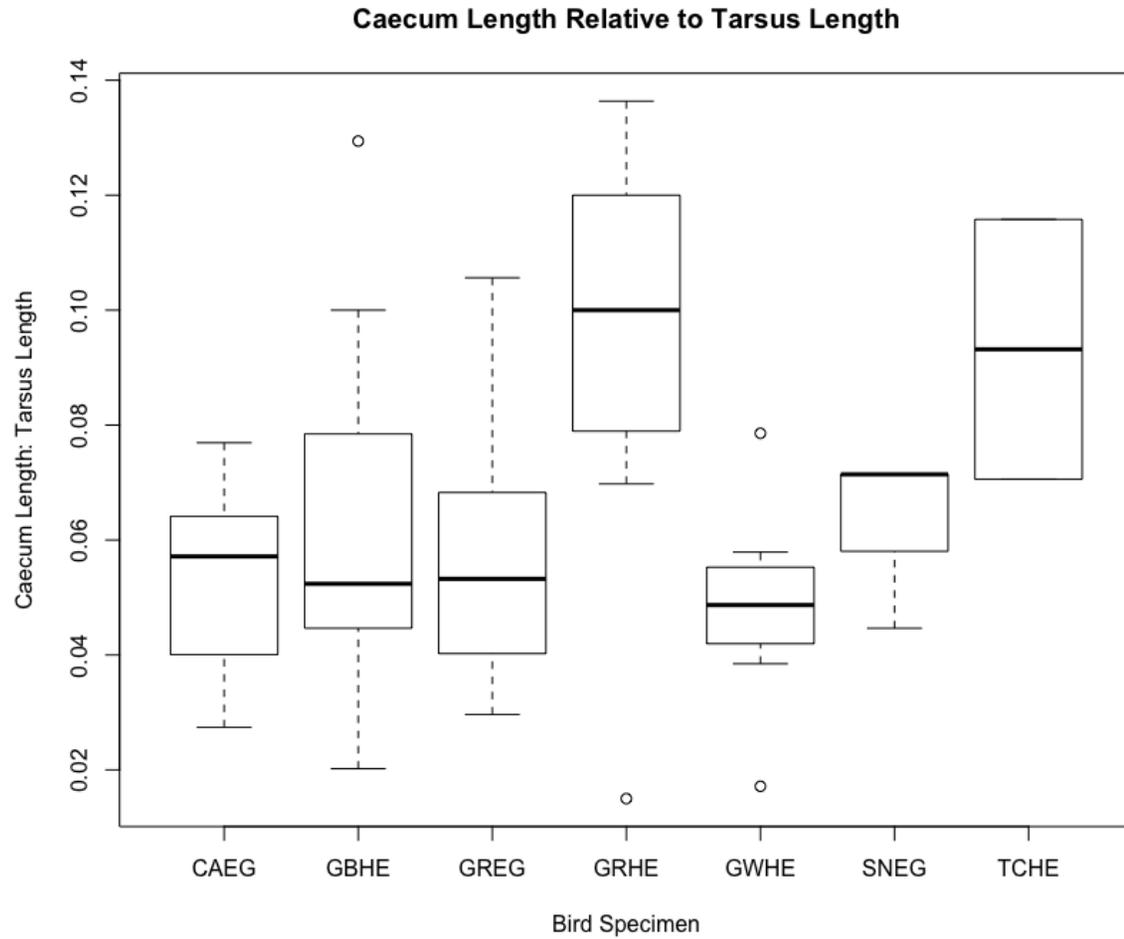
Hérons ( $0.005 \pm 0.002$ ) (Table 5). Great White Herons ( $0.005 \pm 0.002$ ), White Ibises ( $0.005 \pm 0.002$ ), Great Egrets ( $0.005 \pm 0.002$ ), and Snowy Egrets ( $0.004 \pm 0.001$ ) had the lowest ratios of caeca length to small intestine length (Table 5). A one-factor ANOVA test revealed a significant difference among the bird specimen groups ( $p=0.03214$ ), and further, a Tukey's Honest Significant Difference test showed Great Egrets and Cattle Egrets to display significant differences ( $p=0.03214$ ) (Figures 5 and 6).

**Table 4.** The mean, range, and standard deviation of the duodenum, jejunum, ileum, small intestine, large intestine, and caeca measurements in centimeters for each bird specimen group. Species codes below follow the ornithological standard four-letter naming respectively: Great Blue Heron, Great White Heron, Great Egret, Cattle Egret, Green Heron, Snowy Egret, Tricolored Heron, and White Ibis.

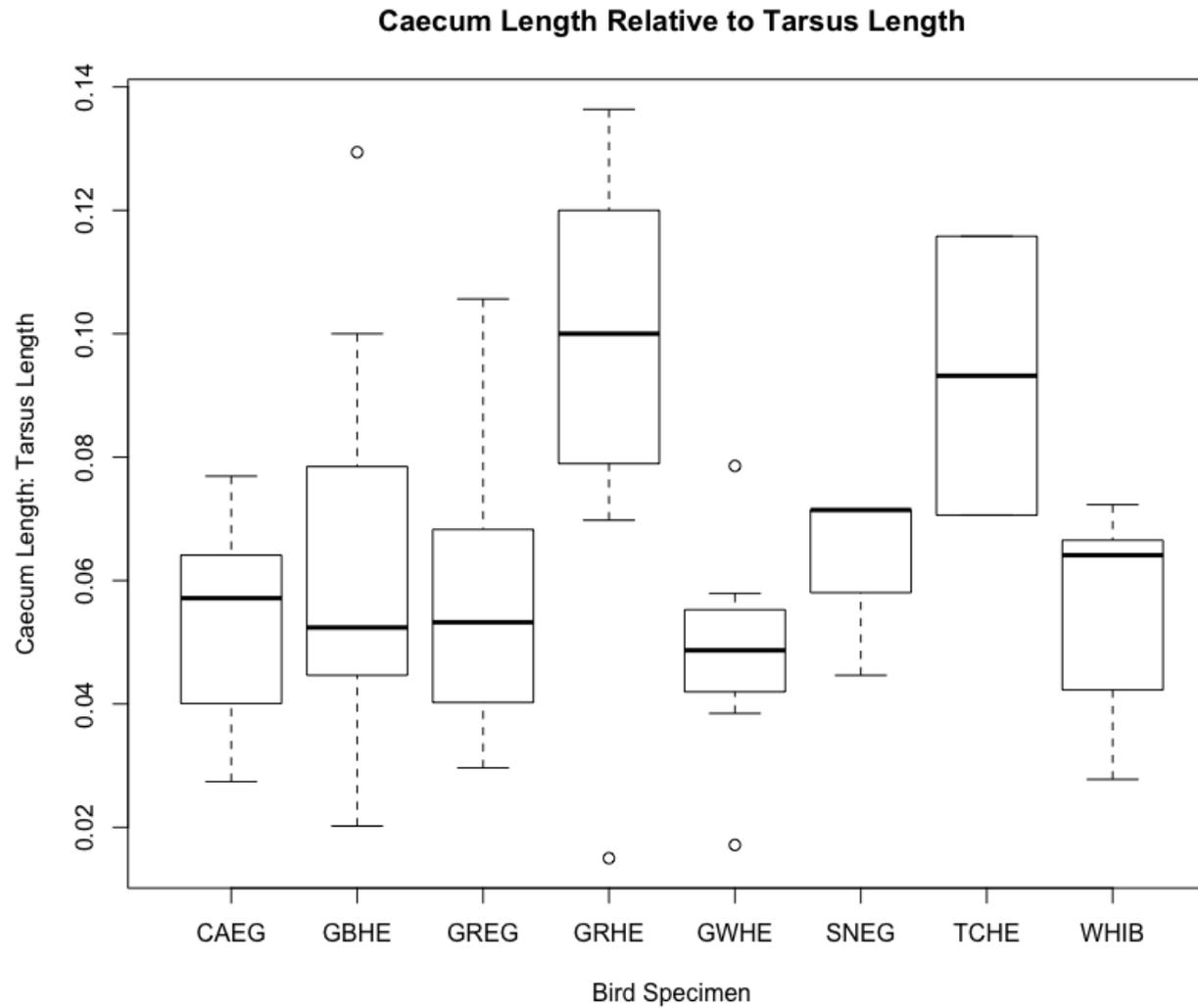
BIRD (N=)	DUODENUM (CM)			JEJUNUM (CM)			ILEUM (CM)			SMALL INTESTINE (CM)			LARGE INTESTINE (CM)			CAECA (CM)		
	Mean	Range	Std. Dev	Mean	Range	Std. Dev	Mean	Range	Std. Dev	Mean	Range	Std. Dev	Mean	Range	Std. Dev	Mean	Range	Std. Dev
<b>GBHE</b> (N=16)	26.75	28	6.424	71.16	62	16.88	81.28	50	13.26	179.2	99	24.2	9.07	9.5	2.31	0.98	1.2	0.39
<b>GWHE</b> (N=8)	27.44	27	9.774	65.25	44	14.11	71.63	44	13.75	164.3	93.5	30.7	9.06	2	0.67	0.86	0.8	0.26
<b>GREG</b> (N=12)	27.83	28.5	8.505	68.67	50	16.1	76.25	42.5	13.89	172.8	85	27.6	5.45	3.3	0.91	0.82	1.1	0.35
<b>CAEG</b> (N=11)	10.88	22	6.29	17.08	12	3.34	22.58	20	5.8	50.55	28	8.56	4.62	3	1.02	0.36	0.3	0.11
<b>GRHE</b> (N=11)	14.27	9	2.75	30.36	31	8.3	33.5	23	6.31	78.14	35	11.89	5.65	3.7	1.01	0.47	0.3	0.12
<b>SNEG</b> (N=3)	16	10	5	34.67	21	11.59	31.17	17	9.41	81.83	41.5	21.58	6.23	1.6	0.81	0.57	0.1	0.06
<b>TCHE</b> (N=2)	19.5	1	0.71	64	48	33.9	54.5	23	16.26	138	72	50.91	6.25	1.5	1.06	0.85	0.5	0.06
<b>WHIB</b> (N=7)	17.93	5.5	2.168	33.97	18.2	5.82	36	12	4.2	87.9	23.2	8.57	6.46	4	1.32	0.43	0.4	0.16

**Table 5.** Mean, range, and standard deviation of the pairwise comparisons of the caeca length to the tarsus length and the caeca length to the small intestine length of each bird specimen group.

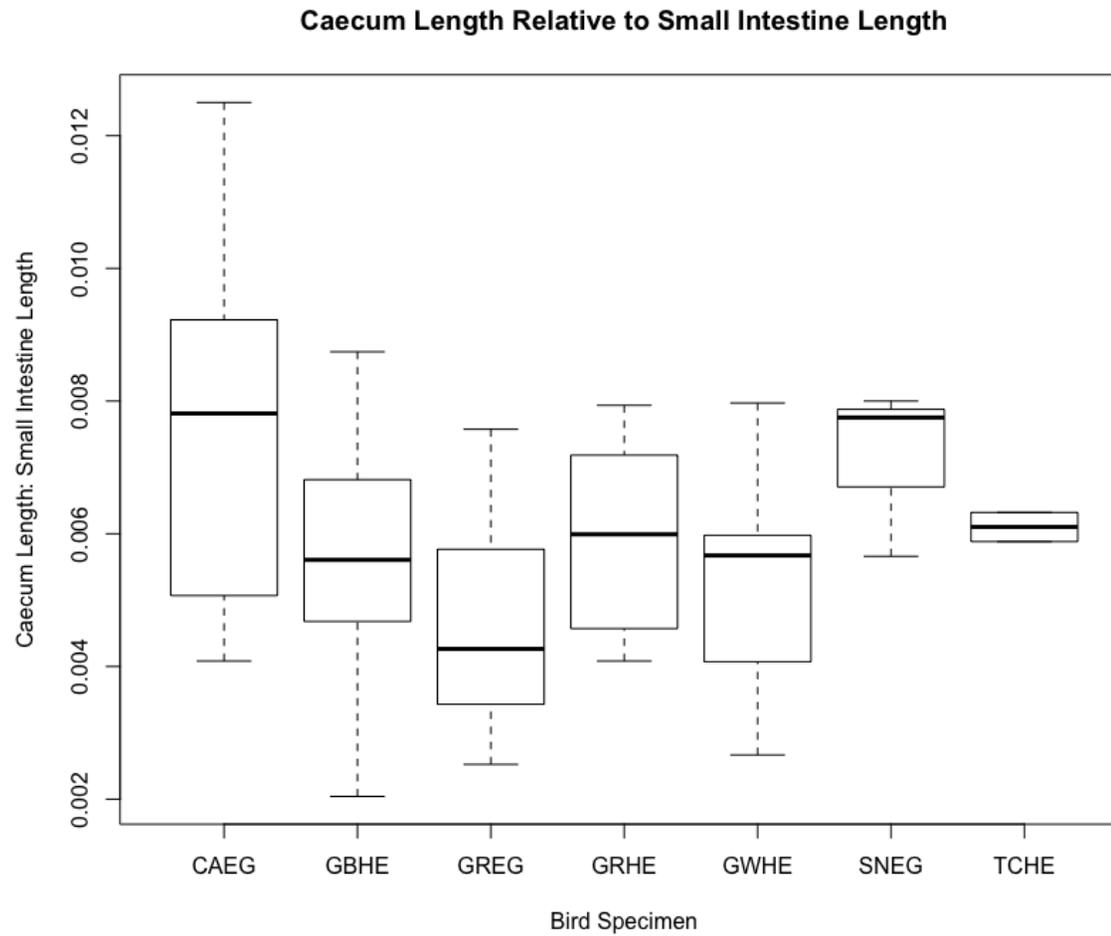
<b>BIRD (N=)</b>	<b>CAECA LENGTH: TARSUS LENGTH (CM)</b>			<b>CAECA LENGTH: SMALL INTESTINE (CM)</b>		
	<b>Mean</b>	<b>Range</b>	<b>Std. Dev</b>	<b>Mean</b>	<b>Range</b>	<b>Std. Dev</b>
<b>GBHE (N=16)</b>	0.061	0.109	0.029	0.005	0.007	0.002
<b>GWHE (N=8)</b>	0.048	0.061	0.017	0.005	0.005	0.002
<b>GREG (N=12)</b>	0.058	0.076	0.025	0.005	0.005	0.002
<b>CAEG (N=11)</b>	0.052	0.05	0.017	0.007	0.008	0.003
<b>GRHE (N=11)</b>	0.096	0.121	0.037	0.006	0.004	0.001
<b>SNEG (N=3)</b>	0.063	0.027	0.016	0.004	0.002	0.001
<b>TCHE (N=2)</b>	0.116	0.045	0.032	0.006	0.0004	0.0003
<b>*WHIB (N=7)</b>	0.055	0.045	0.017	0.005	0.006	0.002



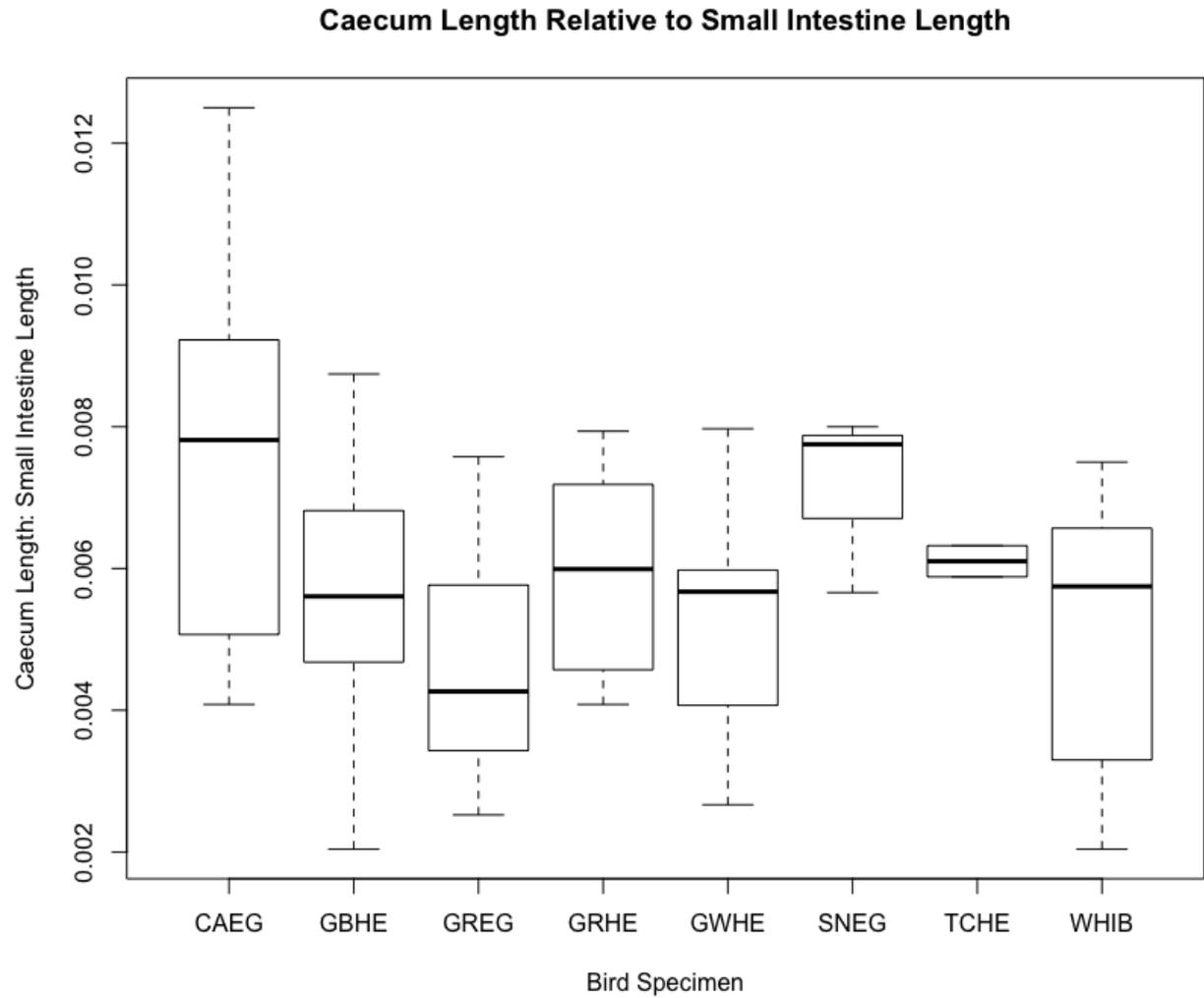
**Figure 3.** Caecum length scaled to tarsus length for each bird specimen group with outliers displayed by small circles. Error bars on Tricolored Herons are notably small due to reduced sample size. Green Herons are significantly different from Cattle Egrets and Great White Herons ( $p=0.001968$ ).



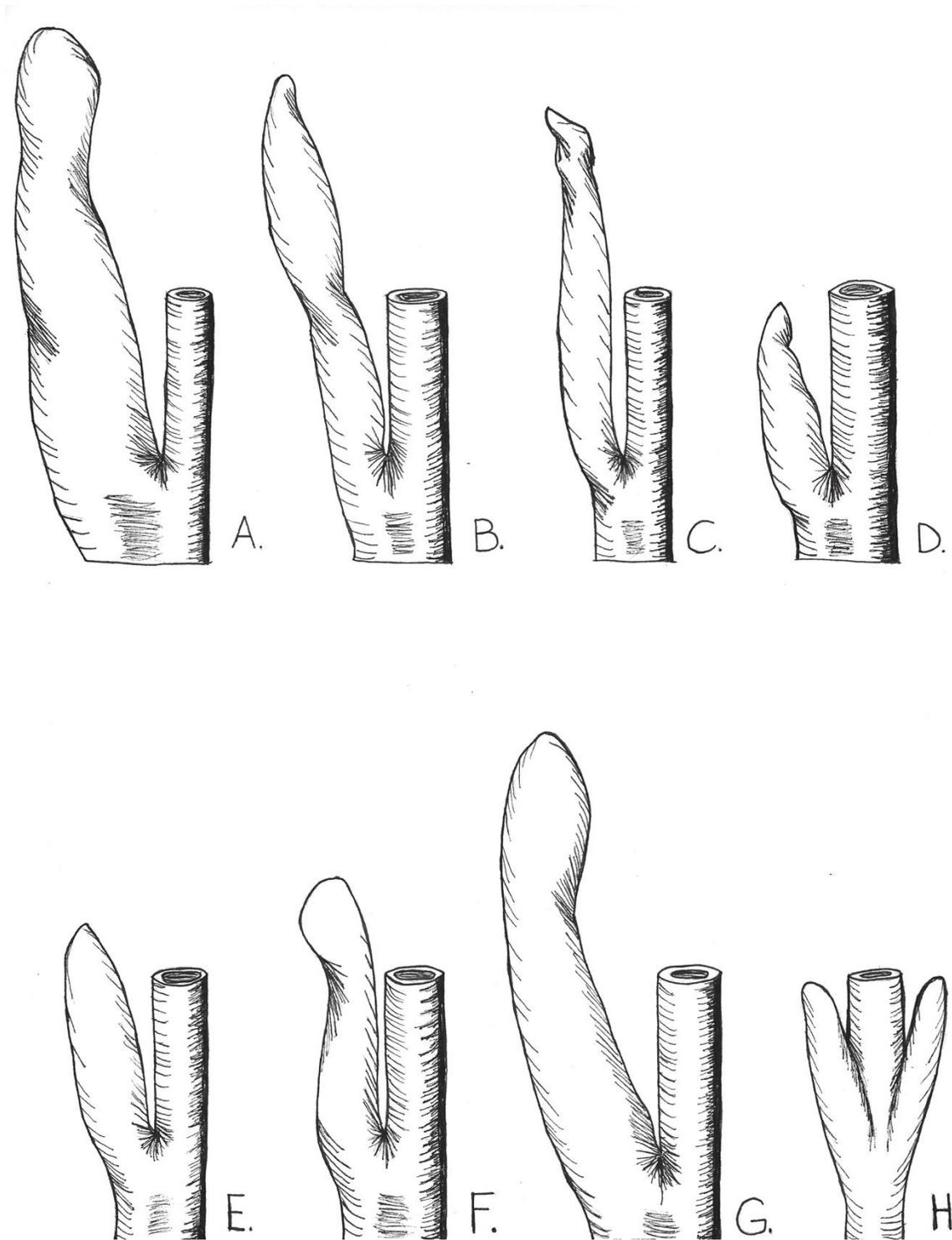
**Figure 4.** Caecum length scaled to tarsus length for each bird specimen group with outliers displayed by small circles. White Ibis outgroup is included with no significant differences.



**Figure 5.** Caecum length scaled to small intestine length for each bird specimen group. Error bars on Tricolored Herons are notably small due to reduced sample size. Great Egrets are significantly different from Cattle Egrets (0.03214).



**Figure 6.** Caecum length scaled to small intestine length for each bird specimen group. White Ibis outgroup is included with no significant differences.



**Figure 7.** Illustrations of the caecae of the Ardeids observed in this study: (A) Great Blue Heron (*Ardea herodias*); (B) Great White Heron (*Ardea herodias occidentalis*); (C) Great Egret (*Ardea alba*); (D) Cattle Egret (*Bubulcus ibis*); (E) Green Heron (*Butorides virescens*); (F) Snowy Egret (*Egretta thula*); (G) Tricolored Heron (*Egretta tricolor*); (H) White Ibis (*Eudocimus albus*).

## Discussion

### *Morphometric Measurements*

Among the Ardeid samples, morphometric consistency was met in terms of a singular caecum on the junction of the ileo-caecal-colic junction in all samples except for one Green Heron. This exception is likely explained by Redig's (1989) research on caeca decreasing in size with a reduced or new diet and with my observation of the malnourished condition of the Green Heron specimen. With the White Ibis outgroup species, morphometric consistency was met again with all seven specimens meeting the paired caeca specification that is noted in family Threskiornithidae.

With Great White Herons being treated as a subspecies of Great Blue Herons, there is little surprise that their tarsus lengths and weights were so similar and recorded as the largest among all the species groups. Great Egrets were consistently recorded as the third largest of the sampled bird specimens for all morphometric measurements. Likely due to their insect-heavy diet, White Ibises were higher in weight compared to the Tricolored Herons, Snowy Egrets, Cattle Egrets, and Green Herons, but averaged a lower tarsus length. While Snowy Egrets and Tricolored Herons reversed in rank of measurements, Cattle Egrets and Green Herons always ranked smallest, respectively.

### *Intestinal Measurements*

Intestinal measurements varied among the sample groups with Great Blue Herons, Great White Herons, and Great Egrets typically dominating the largest position followed closely by Tricolored Herons. The large intestine was recorded longest in the largest birds: Great Blue Herons and Great White Herons, and surprisingly smallest in Great Egrets and Cattle Egrets, respectively. The length from the large intestine to the ileum was largest again in the largest birds: Great Blue Heron, Great Egret, and Great White Heron, and smallest in the Green Herons, Snowy Egrets, and Cattle Egrets. The length of the jejunum followed suit with ileum sizes with largest lengths in the largest birds: Great Blue Heron, Great Egret, and Great White Heron, and smallest lengths in White Ibises, Green Herons, and Cattle Egrets. The duodenal loop length again favored the Great Egrets, Great White Herons, and Great Blue Herons, and was recorded shortest in Snowy Egrets, Green Herons, and Cattle Egrets. The total length of the small intestine

showed longest in the largest birds: Great Egrets, Great White Herons, and Great Blue Herons, and shortest in the morphometrically small birds: Snowy Egrets, Green Herons, and Cattle Egrets. Caeca were found to be largest in predominantly piscivorous Great Blue Herons and Great White Herons and smallest in predominantly insectivorous White Ibises and Cattle Egrets.

The relative length of the caecum to the tarsus length was largest in Tricolored Herons which was unsurprising due to the large size of the caeca compared to the small morphometric size, though with only two samples, this could be negligible. After Tricolored Herons, Green Herons and Snowy Egrets had the highest ratios of caeca length to tarsus, indicating that their caecae are large for their morphometric size. At the other end of the spectrum, relative caecum length to tarsus length was smallest in Cattle Egrets and Great White Herons. Green Herons were significantly different from Cattle Egrets and Great White Herons ( $p=0.01968$ ), and could pose a starting point for future research questions. Relative length of the caecum to small intestine was largest in Cattle Egrets, which in general had the smallest caecae and shortest small intestines. Further, the Cattle Egrets were significantly different from Great Egrets ( $p=0.03214$ ). Snowy Egrets had the smallest caecum length scaled to the small intestine length.

The degree of development in caeca are thought to have a connection with diet, with highly developed caeca in omnivorous and herbivorous groups; vestigial, non-functional caeca in granivorous groups; mostly vestigial and non-glandular, but with extreme variation in degree of development in insectivorous groups; and vestigial or absent caeca in piscivorous groups (Naik and Dominic, 1962; McLelland, 1989). In the scope of this study, the singular caecum of piscivorous Great Blue Herons, Great White Herons, Great Egrets, Green Herons, Snowy Egrets, Cattle Egrets and Tricolored Herons is unsurprising as Clench and Mathias (1995) observed the trait within this family. White Ibises and Cattle Egrets were the two predominantly insectivorous groups, with corresponding smallest caeca lengths, likely due to their insect-heavy diet. Cattle Egrets tend to have a more varied diet that includes fish, and piscivorous Family Ardeidae is known for their singular caecum, which could explain the unpaired caeca in Cattle Egrets (Clench and Mathias, 1995). Naik and Dominic (1962) found that among insectivorous groups, extreme variation was the norm among caeca lengths and number, which could explain why the White Ibis would have two rudimentary caeca as opposed to the singular vestigial caeca found in the Ardeids.

## Conclusion

With much of our caecal knowledge being compiled from relatively sparse records or as a byproduct of other studies, there are significant gaps in our knowledge of the functionality and usage of the avian, particularly Ardeid, caeca (Clench and Mathias, 1995). Though a widespread family, Ardeidae is often overlooked as a study species because they are difficult to sample and not generally recognized as economically beneficial. Although wading birds may not be the first choice for human economic gain, interactions between wading birds and adjacent organisms can provide humans direct and indirect benefits while having a positive effect on biodiversity through various ecosystem services such as regulating fish populations, providing information on food web interactions, and nutrient cycling (Green and Elmberg, 2014). Wetlands provide valuable ecosystem services such as water purification, fixation of run-off nutrients, flood prevention, aquifer recharge, and fishery maintenance, yet aquatic birds in these habitats are often overlooked in their roles overseeing these processes (Green and Elmberg, 2014). Terrestrial and aquatic systems are strongly interdependent, thus interdisciplinary research between aquatic ecologists and ornithologists should be pursued to ensure that proper understanding and management includes aquatic birds as having top down and bottom up influence in aquatic food webs (Green and Elmberg, 2014). Occurring in all continents except Antarctica and being among the most visible of wetland species, wading birds have been proven to be a low-cost, practical shortcut in assessing many biological questions regarding trophic ecology, and thus, determining how food abundance and availability influence their niche relations (Kushlan *et al.* 1985; Ruiz-Guerra and Echeverry-Galvis, 2019).

A fixture in coastal habitats, wading birds come close to human settlements and anthropic pressure which can lead to conflict with humans or human activities in estuary habitats (Crozier and Gawlick, 2003). As ecosystems are increasingly impacted and changing, we need to assess the human influence on biodiversity and ecological functions (Kushlan, 1993; Cheek, 2006). With inevitable global change possibilities, wading birds could be beneficial in understanding how such changes like sea level rising and variable precipitation could potentially negatively affect wading bird reproductive performance or access to feeding areas with possible timing shifts and unreliable availability of prey (Kushlan 1986; Frederick and Collopy, 1989; Butler *et al.*, 1998). In the 1970s, wading bird were used as indicators of environmental conditions, foraging ecology, and contaminants (Kushlan, 1992; Kahl, 1971). A focal point for future studies

could be on the differences between Ardeids and how their usage of habitats affects their biology, as well as comparing caeca sizes between island-based and mainland-based wading birds.

## Literature Cited

- Abdullah, Muhammad, Rashid A. Khan, Muhammad Rafay, Tanveer Hussain, Tahira Ruby, Fariha Rehman, Sangam Khalil, and Sohail Akhtar. "Habitat Ecology and Breeding Performance of Cattle Egret (*Bubulcus ibis*) in Faisalabad, Pakistan." *Pakistan Journal of Zoology* 49, no. 5 (2017). <https://doi.org/10.17582/journal.pjz/2017.49.5.1863.1870>.
- Akester, A. R., R. S. Anderson, K. J. Hill, and G. W. Osbaldiston. "A Radiographic Study of Urine Flow in the Domestic Fowl." *British Poultry Science* 8, no. 3 (1967): 209-15. doi:10.1080/00071666708415670.
- Björnhag, Göran. "Transport of Water and Food Particles through the Avian Ceca and Colon." *Journal of Experimental Zoology* 252, no. S3 (1989): 32-37. doi:10.1002/jez.1402520506.
- Bock, Walter Joseph. "A generic review of the family Ardeidae (Aves). American Museum novitates; no. 1779." (1956).
- Browne, T.G. "Some Observations on the Digestive System of the Fowl." *Journal of Comparative Pathology and Therapeutics* 35 (1922): 12-32. [https://doi.org/10.1016/s0368-1742\(22\)80002-3](https://doi.org/10.1016/s0368-1742(22)80002-3).
- Butler, Robert William. *The Great Blue Heron: A Natural History and Ecology of a Seashore Sentinel*. Vancouver, BC: UBC Press, 1997.
- Butler, R. W., R. I. G. Morrison, and F. Delgado. "The distribution and abundance of coastal seabirds, wading birds, and birds of prey on the coast of Panama." *Atlas of Nearctic Shorebirds and Other Waterbirds on the Coast of Panama* (RIG Morrison, RW Butler, ES Delgado and RK Ross, Eds.) Canadian Wildlife Service, Ottawa (1998): 69-89.
- Chapman, Brian R., and Rebecca Howard. *Habitat Suitability Index Models. Great Egret. Vol. 28*. Fish and Wildlife Service, 1984.
- Cheek, Michael David. "Wading bird foraging ecology in a disturbed mangrove estuary in northwest Ecuador: commercial shrimp ponds vs. natural mangrove mudflats." (2006).
- Clench, Mary H., and John R. Mathias. "The avian cecum: a review." *The Wilson Bulletin* (1995): 93-121.
- Clench, Mary H. "The Avian Cecum: Update and Motility Review." *Journal of Experimental Zoology* 283, no. 4-5 (1999): 441-47. doi:10.1002/(sici)1097-010x(19990301/01)283:4/53.0.co;2-8.
- Crompton, D. W. T., and M. C. Nesheim. "Survey of the Avian Alimentary Tract." (2016).
- Crozier, G.E. and Gawlik, D.E., 2003. Wading bird nesting effort as an index to wetland ecosystem integrity. *Waterbirds*, 26(3), pp.303-324.

- Degolier, Teresa F., Sheila A. Mahoney, and Gary E. Duke. "Relationships of Avian Cecal Lengths to Food Habits, Taxonomic Position, and Intestinal Lengths." *The Condor* 101, no. 3 (1999): 622-34. doi:10.2307/1370192.
- Del Hoyo, Josep, Josep Del Hoyo, Andrew Elliott, and Jordi Sargatal. *Handbook of the birds of the world*. Vol. 1, no. 8. Barcelona: Lynx edicions, 1992.
- Michael J. Fogarty, Willa Mae Hetrick, Summer Foods of Cattle Egrets in North Central Florida, *The Auk*, Volume 90, Issue 2, 1 April 1973, Pages 268–280, <https://doi.org/10.1093/auk/90.2.268>
- Fraser, David Frank, and Leah R. Ramsay. *Status of the Green Heron in British Columbia*. Ministry of Environment, Lands, and Parks, Wildlife Branch, 1996.
- Frederick, Peter. "Wading Birds in the Marine Environment." *Marine Biology of Marine Birds*, 2001, 617-55. doi:10.1201/9781420036305.ch19.
- Frederick, Peter C., and Michael W. Collopy. "The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades." *The Condor* 91, no. 4 (1989): 860-867.
- Gause, G. F. "The struggle for existence. Hafner, New York." Reference from (1934).
- Gibbs, James P., and Linda K. Kinkel. "Determinants of the Size and Location of Great Blue Heron Colonies." *Colonial Waterbirds* 20, no. 1 (1997): 1-7. doi:10.2307/1521757.
- Green AJ, Elmberg J. 2014. Ecosystem services provided by waterbirds. *Biol Rev.* 89:105–122. doi:10.1111/brv.12045.
- Green, M. Clay, and Paul L. Leberg. "Flock formation and the role of plumage colouration in Ardeidae." *Canadian Journal of Zoology* 83, no. 5 (2005): 683-693.
- Hamdi, H., El-Ghareeb, A.W., Zaher, M. and AbuAmod, F., 2013. Anatomical, histological and histochemical adaptations of the avian alimentary canal to their food habits: II-Elanus caeruleus. *Int. J. Sci. & Engineering Research*, 4(10), pp.1355-1364.
- Hancock, James, James A. Kushlan, and M. Philip Kahl. *Storks, ibises and spoonbills of the world*. A&C Black, 2010.
- Hancock, James, and James Kushlan. *The Herons: Handbook*. Croom Helm, 1984.
- Hill, K. J. 1971. The physiology of digestion, p. 25-49. In D. J. Bell and B. M. Freeman [eds.] *Physiology and biochemistry of the domestic fowl*. Vol. I. Academic Press, New York.
- Houston, David C., and Gary E. Duke. "Physiology A. Gastrointestinal." In *Raptor: Research and Management Techniques*, 267-77. 1st ed. Washington, D.C.: Institute for Wildlife Research, National Wildlife Federation, 1987.

- Kahl, M. P. "Social behavior and taxonomic relationships of the storks." *Living Bird* 10 (1971): 151-170.
- Kaufman, Kenn. *Lives of North American Birds*. Boston: Houghton Mifflin, 2001.
- König, H. E., H. G. Liebich, R. Korbel, and C. Klupiec. "Digestive System (apparatus Digestorius)." In *Avian Anatomy: Textbook and Colour Atlas*, 93-116. 2nd ed. (2016)
- Kushlan, James A. "Colonial waterbirds as bioindicators of environmental change." *Colonial waterbirds* (1993): 223-251.
- Kushlan, James A. "Population Biology and Conservation of Colonial Wading Birds." *Colonial Waterbirds* 15, no. 1 (1992): 1-7. doi:10.2307/1521348.
- Kushlan, James A., and Marilyn S. Kushlan. "Food of the White Ibis in southern Florida." *Florida field naturalist* 3, no. 3 (1975): 31-38.
- Kushlan, James A., Gonzalo Morales, and Paula C. Frohring. "Foraging niche relations of wading birds in tropical wet savannas." *Ornithological Monographs* (1985): 663-682.
- Kushlan, James A. Feeding Behavior of North American Herons, *The Auk*, Volume 93, Issue 1, 1 January 1976, Pages 86–94, <https://doi.org/10.1093/auk/93.1.86>
- Kushlan, James A. Feeding ecology of wading birds. National Audubon Society, 1978.
- Kushlan, James A. "Responses of wading birds to seasonally fluctuating water levels: strategies and their limits." *Colonial Waterbirds* (1986): 155-162.
- Langlois, Isabelle. "The Anatomy, Physiology, and Diseases of the Avian Proventriculus and Ventriculus." *Veterinary Clinics of North America: Exotic Animal Practice* 6, no. 1 (2003): 85–111. [https://doi.org/10.1016/s1094-9194\(02\)00027-0](https://doi.org/10.1016/s1094-9194(02)00027-0).
- Lowe, Frank A. *The Heron*. London: Collins, 1954.
- Magnan, Antoine. *Le tube digestif et le régime alimentaire des oiseaux*. Vol. 3. Librairie scientifique A. Hermann et fils, 1911.
- Massa, Carolina, Moira Doyle, and Roberta Callicó Fortunato. "On How Cattle Egret (*Bubulcus ibis*) Spread to the Americas: Meteorological Tools to Assess Probable Colonization Trajectories." *International Journal of Biometeorology* 58, no. 9 (2014): 1879–91. <https://doi.org/10.1007/s00484-014-0790-z>.
- Mayr, Ernst. "Is the Great White Heron a Good Species?" *The Auk* 73, no. 1 (1956): 71-77. doi:10.2307/4081639.

- McGuire, Heather L, Sabrina S Taylor, and Frederick H Sheldon. "Evaluating the Taxonomic Status of the Great White Heron (*Ardea herodias occidentalis*) Using Morphological, Behavioral and Genetic Evidence." *The Auk* 136, no. 1 (2019). <https://doi.org/10.1093/auk/uky010>.
- McLelland, John. "Anatomy of the Avian Cecum." *Journal of Experimental Zoology* 252, no. S3 (1989): 2-9. doi:10.1002/jez.1402520503.
- Metallaoui, Sophia, Hamdi Dziri, Abderazzak Bousseheba, Salim Heddami, and Haroun Chenchouni. "Breeding ecology of the Cattle Egret (*Bubulcus ibis*) in Guerbes-Sanhadja wetlands of Algeria." *Regional Studies in Marine Science* 33 (2020): 100979.
- Meyerriecks, Andrew J. "Foot-Stirring Feeding Behavior in Herons." *The Wilson Bulletin* 71, no. 2 (1959): 153-58.
- Michelutti, N., J. M. Blais, M. L. Mallory, J. Brash, J. Thienpont, L. E. Kimpe, M. S. V. Douglas, and J. P. Smol. "Trophic Position Influences the Efficacy of Seabirds as Metal Biovectors." *Proceedings of the National Academy of Sciences* 107, no. 23 (2010): 10543-0548. doi:10.1073/pnas.1001333107.
- Miranda, Leopoldo, and Jaime A. Collazo. "Food Habits of 4 Species of Wading Birds (Ardeidae) in a Tropical Mangrove Swamp." *Colonial Waterbirds* 20, no. 3 (1997): 413. doi:10.2307/1521591.
- Mock, Douglas, Christopher J. Risley, and Robert B. Payne. "Systematics and Evolutionary Relationships among the Herons (Ardeidae)." *Bird-Banding* 48, no. 1 (1977): 81. doi:10.2307/4512300.
- Mock, Douglas W. "Communication Strategies of Great Blue Herons and Great Egrets." *Behaviour* 72, no. 3-4 (1980): 156-69. doi:10.1163/156853980x00096.
- Moss, R. "Gut Size and the Digestion of Fibrous Diets by Tetraonid Birds." *Journal of Experimental Zoology* 252, no. S3 (1989): 61-65. doi:10.1002/jez.1402520510.
- Mosso, E. D., A. T. R. de Montaner, A. H. Beltzer, and E. B. De Carlo. "Anatomical and histological aspects of the digestive tract of the black-crowned night-heron *Nycticorax nycticorax hoactli* Gmelin, 1789 (Aves: Ardeidae)." *Revista Ceres (Brazil)* (1994).
- Naik, D. R., and C. J. Dominic. "A study of the intestinal caeca of some Indian birds." M. Ss. thesis (1962).
- Naik, D. R., and C. J. Dominic. "The Intestinal Caeca of Some Indian Birds in Relation to Food Habits." *Die Naturwissenschaften* 49, no. 12 (1962): 287. doi:10.1007/bf00622441.
- Patankar, Pratyush, Isha Desai, Kavita Shinde, and B. Suresh. "Ecology and Breeding Biology of the Cattle Egret *Bubulcus Ibis* in an Industrial Area at Vadodara, Gujarat." *Zoos Print Journal* 22, no. 11 (2007): 2885–88. <https://doi.org/10.11609/jott.zpj.1566.2885-8>.

- Redig, Patrick T. "The Avian Ceca: Obligate Combustion Chambers or Facultative Afterburners?—The Conditioning Influence of Diet." *Journal of Experimental Zoology* 252, no. S3 (1989): 66-69. doi:10.1002/jez.1402520511.
- Ritzman, Tracey K. "Raptor Gastroenterology." In *Gastroenterology, Veterinary Clinics of North America: Exotic Animal Practice*. London: Elsevier Health Sciences, 2014.
- Ruiz-Guerra, Carlos, and María Ángela Echeverry-Galvis. "Prey consumed by wading birds in mangrove swamps of the Caribbean coast of Colombia." *Journal of Natural History* 53, no. 29-30 (2019): 1823-1836.
- Schreiber, E. A. and J. Burger (Eds.). 2001. *Biology of Marine Birds*. CRC Press, Boca Raton, Florida.
- Senar, J. C., and J. Pascual. "Keel and tarsus length may provide a good predictor of avian body size." *ARDEA-WAGENINGEN*- 85 (1997): 269-274.
- Short, Henry L., and Robert J. Cooper. *Habitat suitability index models: great blue heron*. No. 82/10.99. US Fish and Wildlife Service, 1985.
- Snipes, Robert L. "Morphology of the Mammalian Cecum and Colon." In *Intestinal Absorptive Surface in Mammals of Different Sizes*, pp. 39-50. Springer, Berlin, Heidelberg, 1997.
- Svihus, B., M. Choct, and H.I. Classen. "Function and Nutritional Roles of the Avian Caeca: A Review." *Worlds Poultry Science Journal* 69, no. 2 (2013): 249-64. doi:10.1017/s0043933913000287.
- Turk, D. E. "The Anatomy of the Avian Digestive Tract as Related to Feed Utilization." *Poultry Science* 61, no. 7 (January 1982): 1225–44. <https://doi.org/10.3382/ps.0611225>.
- Waite, David William, and Mike Taylor. "Exploring the avian gut microbiota: current trends and future directions." *Frontiers in microbiology* 6 (2015): 673.
- Wheelock, Irene G. "Nesting Habits of the Green Heron." *The Auk* 23, no. 4 (1906): 432–36. <https://doi.org/10.2307/4070432>.
- Willard, David E. "The feeding ecology and behavior of five species of herons in southeastern New Jersey." *The Condor* 79, no. 4 (1977): 462-470.
- Zaher, Mostafa, Abdel-Wahab El-Ghareeb, Hamida Hamdi, and Fathia AbuAmod. "Anatomical, histological and histochemical adaptations of the avian alimentary canal to their food habits: I- *Coturnix coturnix*." *Life Sci. J* 9, no. 3 (2012): 253-275.

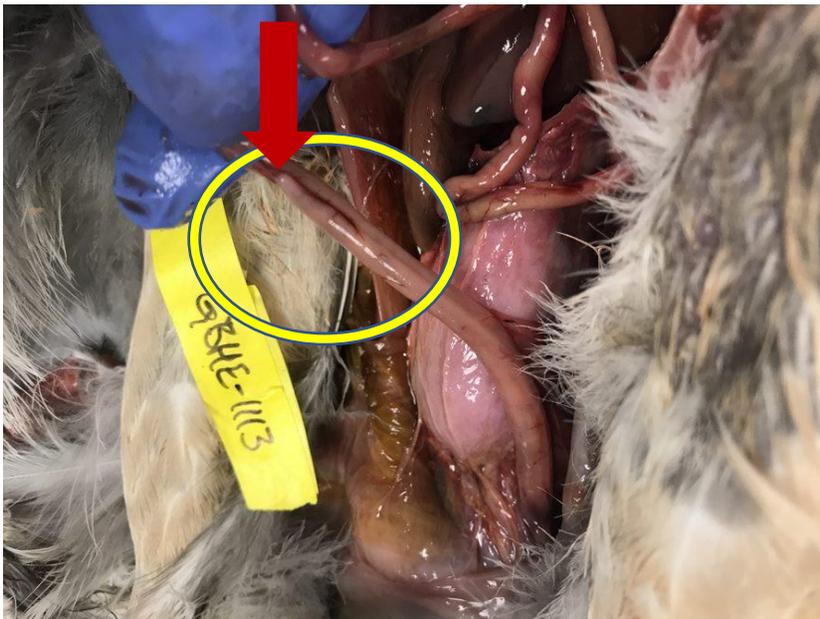
## Appendix

### Caeca Figures

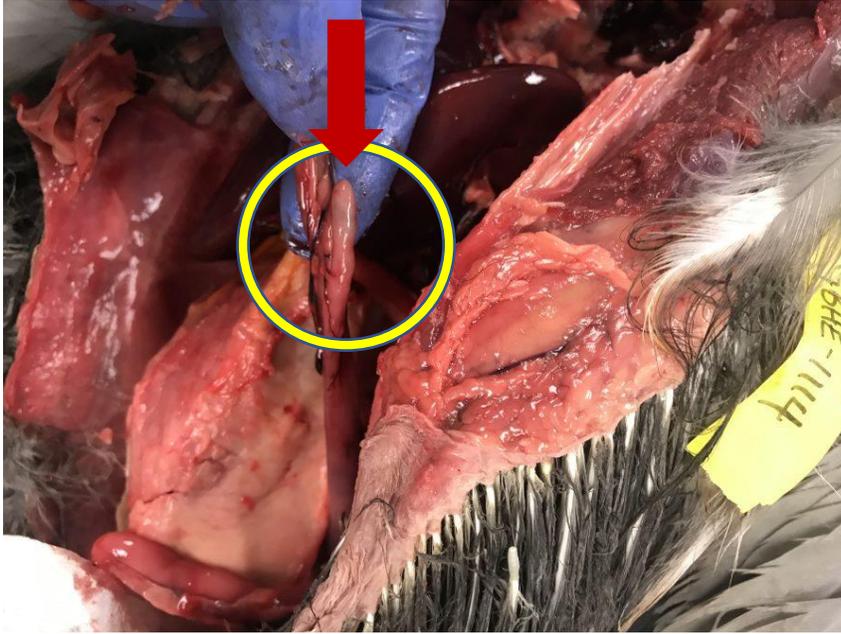
#### *Great Blue Herons*



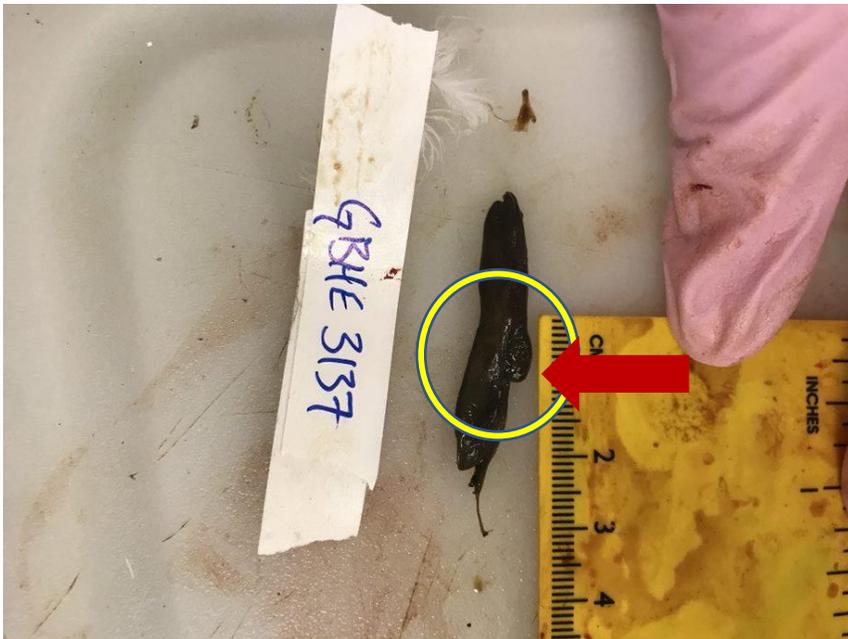
**Appendix Figure 1.** In situ photograph of caecum found on Great Blue Heron 1109 from May 28, 2019.



**Appendix Figure 2.** Image of Great Blue Heron 1113 unpaired caecum dissected on June 4, 2019.



**Appendix Figure 3.** Unpaired caecum of Great Blue Heron 1114 dissected on June 4, 2019.



**Appendix Figure 4.** Unpaired caecum of Great Blue Heron 3137 dissected on June 1, 2020.

*Great White Heron*

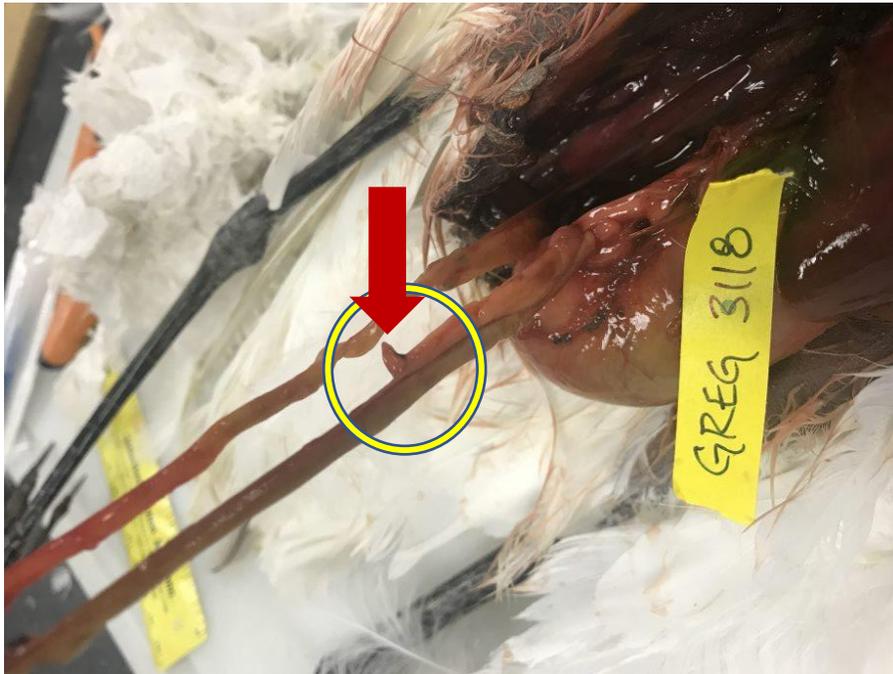


**Appendix Figure 5.** Unpaired caeca of Great White Heron dissected on June 14, 2019.



**Appendix Figure 6.** Internal view of intestines of male Great White Heron 3131, dissected on February 19, 2020.

*Great Egret*

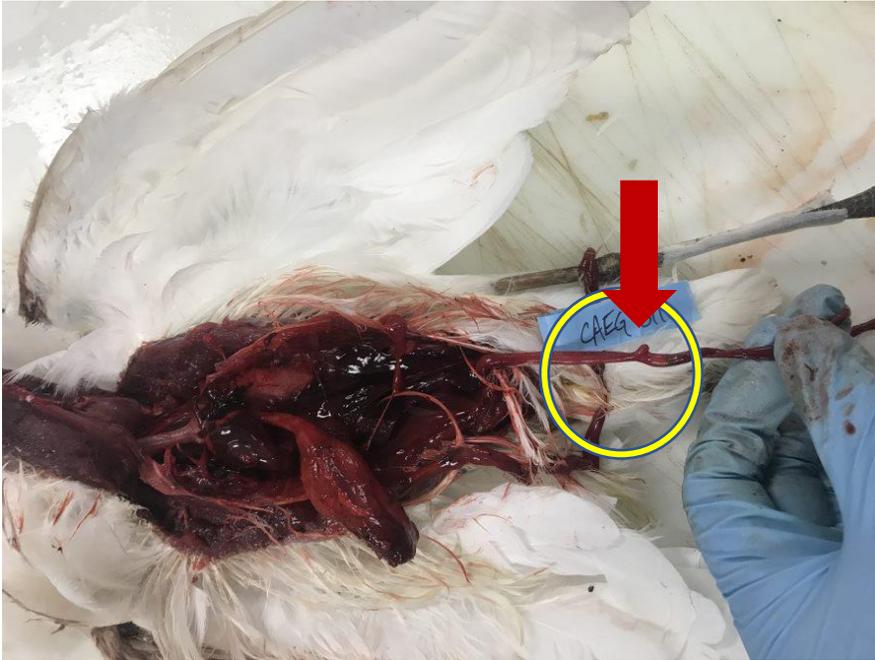


**Appendix Figure 7.** Unpaired caecum of Great Egret 3118 dissected on October 21, 2019.



**Appendix Figure 8.** Unpaired caecum of Great Egret 3118 dissected on October 21, 2019.

*Cattle Egret*

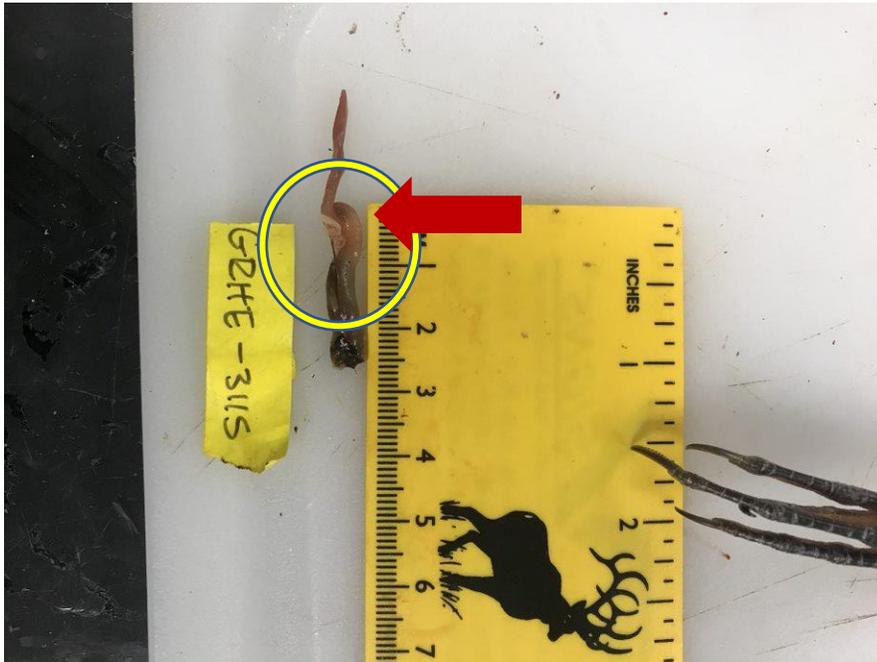


**Appendix Figure 9.** In situ caecum found on Cattle Egret 3111 dissected May 28, 2019.



**Appendix Figure 10.** Close up image of caecum and large intestine of Cattle Egret 3111.

*Green Heron*

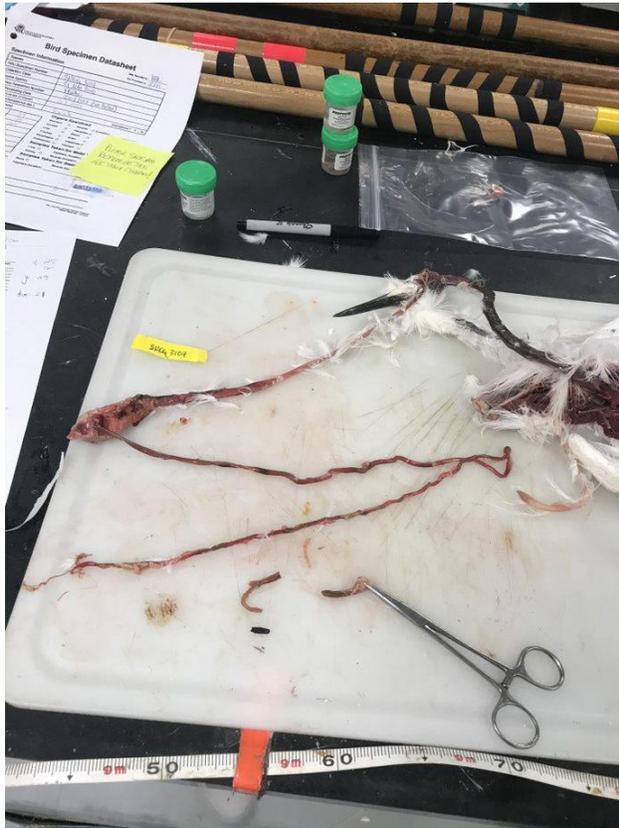


**Appendix Figure 11.** Unpaired caecum of Green Heron 3115 dissected on May 4, 2020.

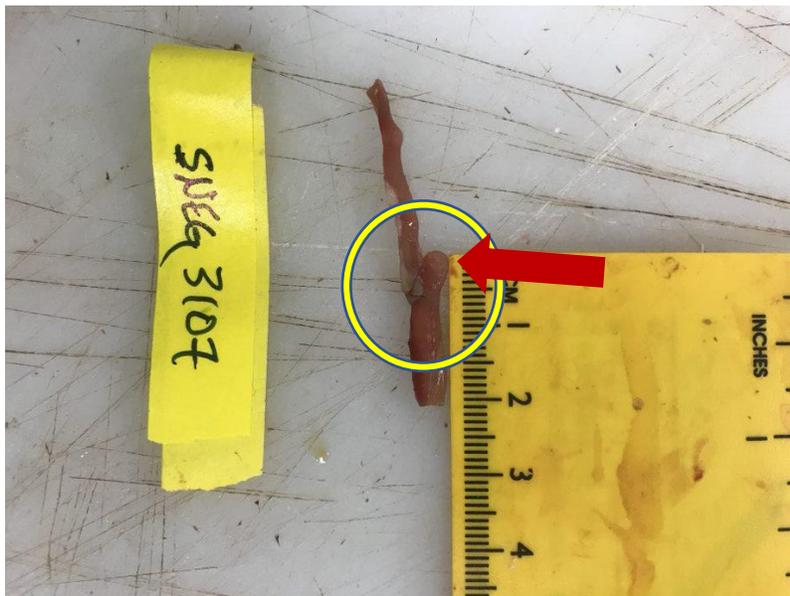


**Appendix Figure 12.** Unpaired caecum of Green Heron 3112 dissected on June 28, 2019.

*Snowy Egret*



**Appendix Figure 13.** Gastrointestinal tract of Snowy Egret 3107 dissected on June 8, 2020.



**Appendix Figure 14.** Unpaired caecum of Snowy Egret 3107 dissected on June 8, 2020.

*Tricolored Heron*

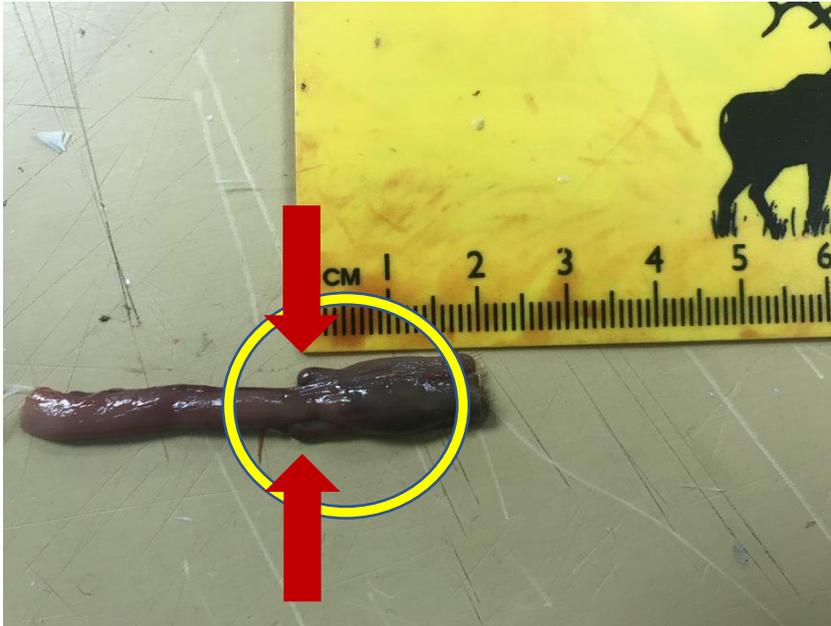


**Appendix Figure 15.** Unpaired caecum of Tricolored Heron 3001 dissected on July 20, 2020.

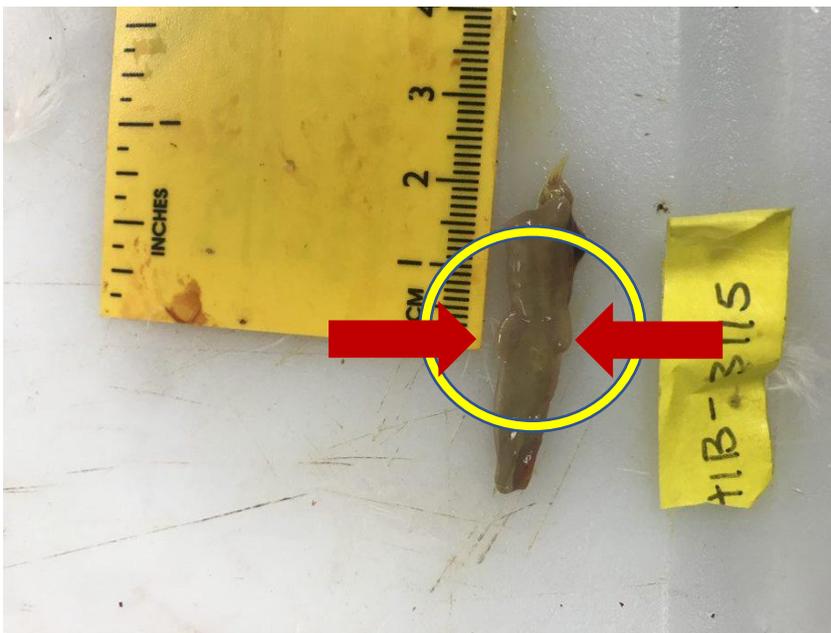


**Appendix Figure 16.** Unpaired caecum of Tricolored Heron 1000 dissected on July 20, 2020.

*White Ibis*



**Appendix Figure 17.** Paired caeca of White Ibis 3114 dissected on March 18, 2020.



**Appendix Figure 18.** Paired caeca of juvenile White Ibis 3115 dissected on May 4, 2020.