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Published By: The American Society of Ichthyologists and Herpetologists

URL: http://www.bioone.org/doi/full/10.1643/CE-11-177

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American Alligator Digestion Rate of Blue Crabs and Its Implications for Stomach Contents Analysis

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Stomach contents analysis (SCA) provides a snap-shot observation of a consumer’s diet. Interpretation of SCA data can be complicated by many factors, including variation in gastric residence times and digestion rates among prey taxa. Although some SCA methods are reported to efficiently remove all stomach contents, the effectiveness of these techniques has rarely been tested for large irregular shaped prey with hard exoskeletons. We used a controlled feeding trial to estimate gastric residency time and decomposition rate of a large crustacean prey item, the Blue Crab (Callinectes sapidus), which is consumed by American Alligators (Alligator mississippiensis), an abundant apex predator in coastal habitats of the southeastern United States. The decomposition rate of C. sapidus in the stomachs of A. mississippiensis followed a predictable pattern, and some crab pieces remained in stomachs for at least 14 days. We also found that certain portions of C. sapidus were prone to becoming caught within the stomach or esophagus, meaning not all crab parts are consistently recovered using gastric lavage techniques. However, because the state of decomposition of crabs was predictable, it is possible to estimate time since consumption for crabs recovered from wild alligators. This information, coupled with a detailed understanding of crab distributions and alligator movement tactics, could help elucidate patterns of cross-ecosystem foraging by the American Alligator in coastal habitats.

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Submitted: 7 December 2011. Accepted: 29 April 2012. Associate Editor: J. F. Schaefer.

© 2012 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CE-11-177
MATERIALS AND METHODS

American Alligators.—Eighteen (12 male and six female) *A. mississippiensis* (temporarily loaned to us from the St. Augustine Alligator Farm Zoological Park in St. Augustine, Florida) were housed in three outdoor concrete holding tanks (1.5 m high × 4 m wide × 1.5 m long) at the United States Geological Survey Southeast Ecological Science Center in Gainesville, Florida. Two days prior to transport study animals were fed Mazuri crocodilian diet pellets (Purina Mills, LLC) during their weekly feeding, and upon arrival, individuals were held for two days (without food) before the start of the feeding trial. Six *A. mississippiensis* were housed in each tank with flowing freshwater maintained at 20 cm depth throughout the study period. One wooden pallet atop four concrete blocks served as a basking area and dry dock within each tank, and 50% of each enclosure was covered with 15% shade cloth. *A. mississippiensis* ranged from 161–185 cm total length (mean ± SD = 176 ± 7 cm) and from 16–25.5 kg (mean ± SD = 22.5 ± 2.3 kg). In southeastern estuary dwelling populations, *A. mississippiensis* within this size range consume adult *C. sapidus*.

Blue Crabs.—Eighteen *C. sapidus* were purchased from a local seafood market and kept alive until force-fed to the alligators. Carapace width (measured spine-tip to spine-tip) of all *C. sapidus* was greater than 10 cm. Mass of *C. sapidus* ranged from 109–181 g (mean ± SD = 145.1 ± 19.9 g). Prior to being fed to *A. mississippiensis*, *C. sapidus* were immobilized by being placed on ice for 10 to 15 minutes, sectioned into quarters and chelipeds removed from the body. All body parts (i.e., four body sections and two chelipeds) were included in mass of *C. sapidus* force-fed to the alligators. Crabs were sectioned to 1) reduce the chance of possible injury to alligators during force-feeding and 2) to simulate the natural action of crushing by alligators during feeding events in the wild.

Study design.—Two days after transport from St. Augustine, FL, all 18 *A. mississippiensis* were force-fed one *C. sapidus* using a 1.25 cm diameter PVC pipe with domed end to carefully push sections of crab along the esophagus into the stomach cavity. Each *A. mississippiensis* was identified using internal passive integrative transponder (PIT) tags, and the wet mass of *C. sapidus* fed to each individual was recorded prior to force-feeding. Following feeding, three *A. mississippiensis* were quasi-randomly selected (one randomly from each of the three enclosures) and subjected to stomach flushing at 24, 48, 96, 144, 192, and 336 hours post-ingestion. All effluent produced from stomach flushings were collected in a large plastic container and stomach contents were recovered by pouring collected effluent through a 1 mm mesh sieve. We then removed any items from the stomach contents not identified as remains of *C. sapidus* (e.g., vegetation, rocks, sand, insect chitin) before measuring wet mass to the nearest 0.1 gram on an electric balance (PGI2002, Adam Equipment, Co. Ltd., Danbury, CT). We measured air temperature in two locations in each tank (“shaded” and “unshaded”) using HOBO pendant temperature loggers (Onset, Cape Cod, MA) to identify any potential differences among enclosures in abiotic conditions during the study period. We did not measure water temperature in all three tanks because the temperature loggers were not able to be recovered or were destroyed by the alligators in two of the tanks.

RESULTS

We used the hose–Heimlich technique (Fitzgerald, 1989) to remove stomach contents from alligators. Individual alligators, with their mouths taped shut, were removed from tanks by hand and placed on a 2.5 m spine board (Med Tech Resources, Inc., Marietta, GA), using 5 cm wide smooth nylon Spider strips with Velcro stripping to secure alligators on to the spine board. The spine board and alligator were tilted at a 20° decline using stacked concrete blocks, head-end facing down, to assist in the flushing process. Once secured and in position, a 10 cm diameter schedule 40 PVC section wrapped in duct tape was inserted into the open mouth. We then reapplied mouth tape, securing the pipe section in place. Then, while holding the tongue down, a small (1.25 cm diameter) lubricated garden hose was inserted through the esophagus into the stomach cavity of the alligator. A constant low velocity flow of freshwater was used to fill the stomach cavity until visibly distended, after which a gentle massaging motion was used to flush effluent out of the stomach cavity and into the large plastic container. The process was repeated until stomach effluent ran clear of all food particles, three repetitions in most cases.

Once stomach contents were removed, remains of *C. sapidus* were separated, and wet mass was measured. We then calculated the proportion of mass still present in each stomach (recovered wet mass/initial wet mass). To assess the rate of digestion we evaluated two competing decay models (hyperbolic and exponential) using Akaike Information Criterion (Burnham and Anderson, 2004), corrected for small sample sizes (AICc), to determine which model resulted in lowest residual deviance when fit to the data. The hyperbolic function (1 model parameter) tested was slightly less complex than the exponential function (2 model parameters). We used the best fit model to describe the relationship between time since ingestion (24, 48, 96, 144, 192, and 336 hours) and proportion of undigested mass of *C. sapidus* recovered (three samples/interval). Additionally, at each stomach-pumping event we carefully noted which body parts were recovered and the state (e.g., thickness, texture, color, presence of soft tissue) of any remains. All data analysis was performed in R 2.13 (R Development Core Team, Vienna, Austria, http://www.r-project.org).

We used the hyperbolic function of the form \( y = 1/(1+k^{x}) \), where \( y \) = proportional mass remaining, \( x \) = hours since ingestion, and \( k \) = instantaneous rate of decay. Non-linear least squares regression revealed that the best fit for parameter (k) to be equal to 0.0848 \( (P < 0.001; \text{Fig. 1}) \). We recovered a mean ± SD of 34 ± 15.5%, 17.2 ± 0.05%, 10.4 ± 0.02%, 8.8 ± 0.05%, 6.9 ± 0.01%, and 4.6 ± 0.04% ingested mass after 24, 48, 96, 144, 192, and 336 hours post-ingestion, respectively. Using the model fit, we predicted 32.9%, 19.7%, 10.9%, 7.5%, 5.7%, and 3.4% mass recovered. Thus, we found over 90% of mass of *C. sapidus* to be digested or unable to be recovered after four days. The drastic decrease in recovered mass after 24 and 48 hours post-ingestion was most likely due to the inability to flush out the chelipeds (i.e., front pincers or claws) and other large sections of carapace. Missing chelipeds were presumably caught within the stomach or esophagus by spines or other sharp edges (Fig. 2), since these
body parts were far too large to pass through the duodenum into the lower intestine. We recovered only two out of six ingested chelae at the 24-hour post-ingestion flushing event; both of the recovered chelae were intact with no signs of thinning or softening of the shell. During the second flushing event (48 hours post-ingestion) we recovered no chelipeds or pieces thereof, only reddened sections of carapace, legs, and abdomen. During the third flushing event we recovered softened pieces of chelipeds, legs, carapace, and abdomen. The remainder of flushing events yielded only small, softened sections of chelae, legs, carapace, and abdomen. Coloration of recovered crab remains changed from no loss of color at the 24-hour event to bright red with blue hues still visible during the 48-hour event and eventually to yellow and washed out red/pink for the remaining flushing events (Fig. 2).

During the study, air temperature averaged for all three tanks ranged from 17.0°C to 45.2°C in the shaded portions and 17.7°C to 46.7°C in the unshaded portions. For the one tank in which the water temperature logger survived, the water temperature ranged from 21.6°C to 32.2°C. Air temperatures in the shaded portions of each tank were significantly lower than in the unshaded portions of each tank (Mann-Whitney rank sum test: all P < 0.007) but we detected no differences in air temperature between the shaded portions of each tank or the unshaded portions of each tank (Kruskal-Wallis one-way ANOVA on ranks: all P > 0.3). Therefore, it is unlikely that differences in temperature between the three tanks affected digestion rates of alligators sampled from each tank. Temperature variability was chiefly due to day–night fluctuations, as daily mean air temperatures for all tanks ranged only 2.7°C during the study period.

FIG. 1. Proportion of Callinectes sapidus recovered during stomach pumping at 24, 48, 96, 144, 192, and 336 hours post-ingestion. The dotted line is the fitted regression trend-line and regression equation is reported on graph.

DISCUSSION

American Alligators are abundant, large-bodied, opportunistic predators and scavengers that are ubiquitous throughout aquatic habitats of the southeastern United States (Mazzotti and Brandt, 1994). As such, they are reputed to exert top-down control on prey populations (Bondavalli and Ulanowicz, 1999). However, an important step toward understanding the ecological roles of alligators and other crocodilians is to accurately identify the relative importance of particular prey items which can be used to designate use of particular habitats (e.g., blue crab—estuarine habitats, crayfish—freshwater habitats). In this study we quantified

Fig. 1. Proportion of Callinectes sapidus recovered during stomach pumping at 24, 48, 96, 144, 192, and 336 hours post-ingestion. The dotted line is the fitted regression trend-line and regression equation is reported on graph.

Fig. 2. Photographs of representative remains of Callinectes sapidus recovered during stomach flushing events at (A) 24 hours post-ingestion, (B) 48 to 96 hours post-ingestion, and (C) 144 to 336 hours post-ingestion.
the digestion rate of a common prey species eaten by alligators occupying coastal habitats, and found that the digestion process for this species followed a predictable pattern.

The greatest amount of digestion of *C. sapidus* (82.8%) occurred between 0 and 48 hours post-ingestion, as previously hypothesized. This period was associated with the total disappearance of all muscle and other soft tissues, but some of the loss of mass of *C. sapidus* was likely attributable to an inability to recover certain hard parts from the stomachs as well. Between 48 and 336 hours after ingestion, only 12.6% of the initial mass was digested, and this period was associated with the slow disappearance of the chitinous exoskeleton. Though digestion during this latter period was slow, we observed stark qualitative differences in the color of carapace parts recovered as they transitioned from natural bright red and blue hues still present at 48 hours post-ingestion to ruddy yellow/red hues present thereafter. A small portion of the initial crab mass (mean = 4.6%), consisting entirely of small pieces of softened carapace, persisted in the stomach until at least 336 hours post-ingestion. Our study was unable to determine exactly how long it would take for one *C. sapidus* to become entirely digested and therefore undetectable.

The pattern of digestion we observed is similar to patterns of digestion of other prey species of *A. mississippiensis*. Barr (1997) studied the digestive rates of snakes, insects, birds, mammals, turtles, salamanders, frogs, snails, fish, and crayfish fed to *A. mississippiensis* and found that time to complete digestion or almost complete digestion (<0.05% of mass remaining) ranged from 30 hours for very soft-bodied prey (frog) to 312 hours for prey with hard parts (turtle). We demonstrated that remains of *C. sapidus* may persist in the stomach for at least 336 hours. In comparison to the digestion rate of the only crustacean (crayfish, *Procambarus* sp.) tested by Barr (1997), our results demonstrate remains of *C. sapidus* may persist at least 156 hours longer in the stomach cavity. Additionally, Barr (1997) reported chelipeds were the only crustacean body portions recovered after 108 hours post-ingestion; however, we recovered portions of legs, carapace, abdomen, and chelipeds of *C. sapidus* 96 hours post-ingestion. The implication of these findings for SCA of *A. mississippiensis* is that *C. sapidus* could become over-represented during analyses of prey volume or mass because portions have the potential to accumulate in the stomach and persist for long periods of time.

Although previous studies suggested the hose–Heimlich technique is near 100% effective in recovering crocodilian stomach contents (Fitzgerald, 1989; Rice et al., 2005), it may be less effective for irregularly shaped prey that have jagged edges or spikes, such as *C. sapidus* or *Limulus polyphemus* (Horseshoe Crab), another common prey species in coastal habitats (J. Nifong, unpubl.). At the 24-hour pumping events, we only recovered two of six ingested claws, and the two recovered were lacking only a small portion of their associated muscle tissue. The natural coloration of the chelipeds was still present and the chitin did not appear to be affected over such a short period of time. Thus it is unlikely that the four unrecovered claws had been completely digested. It is more likely that they were stuck somewhere in the stomach or esophagus. Additionally, no remains or scat were observed in the enclosures. The implication of this finding is that if an *A. mississippiensis* or other crocodilian species recently ingested (i.e., within 48 hours) a *C. sapidus* or a similar large-bodied crustacean, the use of the hose–Heimlich technique to gather stomach contents could result in under-representation of crustacean prey in the diet for analyses by volume or mass.

*Callinectes sapidus* mainly inhabit coastal or estuarine habitats characterized by brackish or fully-marine waters and are only occasionally found in completely freshwater riverine habitats (Cameron, 1978; Hines, 2007), whereas *A. mississippiensis* inhabiting coastal areas are capable of regularly moving long distances between marine, estuarine, and freshwater habitats, including isolated freshwater wetlands on barrier islands and within dune swales (Tamarack, 1988; Rosenblatt and Heithaus, 2011; J. Nifong, unpubl.). Therefore, we infer that because the decomposition of *C. sapidus* followed a predictable chronological pattern, pieces of *C. sapidus* recovered from stomachs of wild *A. mississippiensis* could be used as indicators of recent habitat use. For example, if an *A. mississippiensis* was captured in a freshwater tributary of an estuary or isolated wetland and its stomach contained fully intact claws of *C. sapidus* with muscle tissue still attached, then based on the results from our study it would be likely that the alligator ingested the crab within the previous 48 hours in the brackish or marine portions of the estuary and then traveled to the freshwater tributary where it was captured. Conversely, if that same alligator’s stomach only contained a few soft, ruddy-hued pieces of carapace of *C. sapidus* then one could possibly conclude that the crab had been ingested between 4–14 days prior. Of course, the proper interpretation of the presence and state of decay of pieces of *C. sapidus* in the stomach of an alligator as an indicator of habitat use would be dependent on a detailed understanding of habitat use of *C. sapidus* in the same location, as *C. sapidus* are known to occasionally travel into fresh and brackish regions of coastal rivers, especially during the breeding season (Cameron, 1978). Additionally, we conducted this study using a single prey item within a narrow (two-week) timeframe at ambient temperatures well below the potential maximal temperatures experienced by individuals in the wild (i.e., July and August). Given this context, it is likely that decomposition rates will increase slightly with increasing temperature and possibly decrease in the presence of other prey items, especially if alternate prey items contain large amounts of non-digestible structures (e.g., mammalian hair, fish scales, etc.). Adjustment of digestive rates due to increased ambient temperatures, however, may not be clear-cut when taking into account the thermoregulatory ability of crocodilians.

We demonstrated that *C. sapidus* can persist in the stomach of an *A. mississippiensis* for at least 14 days and that decomposition of *C. sapidus* follows a predictable pattern that is characterized first by the disappearance of muscle tissue and later by the softening and gradual disappearance of the chitinous exoskeleton. We also demonstrated that certain crab body parts are difficult to recover from stomach contents using the hose–Heimlich technique, most likely because of their irregular shape and large size. These findings indicate that SCA of populations of coastal *A. mississippiensis* could be biased toward under-representation of *C. sapidus* if recently ingested (<48 hours) and over-representation if the crab was not recently ingested (>48 hours). We recommend that in future studies of crocodilian stomach contents, all recovered prey items that have hard parts be partitioned into “old” and “new”
categories based on known taxon-specific digestive rates. Then, separate analyses can be used for each group of prey items to more fully identify possible differences and similarities in feeding habits between individuals. This will result in more fine-scale knowledge of crocodilian functions in food web and ecosystem dynamics and may provide greater insight into crocodilian-mediated habitat connectivity.

ACKNOWLEDGMENTS

We thank the United States Geological Survey Southeast Ecological Science Center for allowing the use of holding tanks and the St. Augustine Alligator Farm Zoological Park for loaning study animals. Research was conducted under an award from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration, Award No. NA10NOS4200022. This research study was also supported in-part by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research Program under Grant No. DEB-9910514. We give special thanks to R. Douglass, K. Torregrosa, and R. McCarville for their technical assistance. Finally, our research was conducted in accordance with recommendations from Institutional Animal Care Use Committee protocol #USGS/SESC 2011-03, and any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED


