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DIGESTIBILITY OF THREE FISH SPECIES BY DOUBLE-CRESTED CORMORANTS[1]

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Abstract. I determined daily energy requirements of captive Double-crested Cormorants (*Phalacrocorax auritus*) and their metabolizable energy coefficients (MECs) for three fish species: channel catfish (*Ictalurus punctatus*), gizzard shad (*Dorosoma cepedianum*), and bluegill (*Lepomis macrochirus*). Ad libitum intake ranged from 264 to 503 g·bird^{-1}·day^{-1} among tests, resulting in metabolizable energy values of 616 to 1,334 kJ·kg^{-1}·day^{-1}. Ninety percent of the marker carmine red was recovered in 48 hr, suggesting that collection periods should be ca. three days to determine digestion efficiencies. Estimated MECs ranged from 77.9% to 89.2% among fish diets, with bluegill < channel catfish = gizzard shad. No seasonal differences were found for MECs of catfish. Nitrogen corrections reduced MECs to approximately 75% for bluegill, 78% for gizzard shad, and 79% for channel catfish.

Key words: Digestion; Dorosoma cepedianum; *fish-eating birds;* Ictalurus punctatus; Lepomis macrochirus; *metabolizable energy coefficient; nitrogen correction;* Phalacrocorax auritus.

INTRODUCTION

In the last decade, North American populations of Double crested-Cormorants (*Phalacrocorax auritus*) increased in size (Ludwig 1984, Vermeer and Rankin 1984) such that cormorants are of concern to inland commercial fisheries (Bayer 1989). One method to assess the extent of damage by vertebrates to agricultural crops involves bioenergetic modeling to estimate energy requirements of wild populations (Otis 1989). Currently, no field data are available that quantify daily energy requirements of wild cormorants. However, values derived from measures of basal metabolism of captive birds (545 kJ·bird^{-1}·day^{-1}, Henneman 1982) and predictive equations of field metabolism for seabirds (1,380 kJ·bird^{-1}·day^{-1}, Nagy 1987 [eq. 16], but see Nagy 1989) offer a range of estimates for consideration for 1.5 kg birds.

Also needed in a bioenergetic model of cormorant impact at fisheries are estimates of digestion efficiencies for energy (termed metabolizable energy coefficients, MECs) of the commonly consumed fish species to translate daily energy budgets into the amount of food consumed (Kendeigh et al. 1977). Piscivorous birds tend to have relatively high MECs, ranging from 54% (Cooper 1978) to nearly 90% (Dunn 1975), but converging on 75% (Furness 1978). Metabolizable energy coefficients may vary with bird species (Jackson 1990) and age (Heath and Randall 1985), fish species consumed (Jackson 1986), body mass of the bird (Schmidt-Nielson 1984), or its metabolic demands (Ellis 1984). For example, 11- to 21-day old Double-crested Cormorant chicks fed pollack (*Pollachius virens*) had age-related increases in MECs from 79.9% to 88.1% (Dunn 1975). Yearling cormorants fed herring (*Clupea harengus*) had MECs of 72.9% (Cummings 1987). The differences could be due to age, diet, body mass or even gravimetric methodology (Montevecchi and Piatt 1987). Additionally, seasonal variation in MEC has been hypothesized for wintering or migratory birds with the rationale that energy or nutrients may be differentially absorbed due to seasonal variation in metabolic demands (Zimmerman 1968).

My objectives for this study were to estimate with captive Double-crested Cormorants daily energy requirements, the MECs of three commonly consumed fish species (channel catfish [*Ictalurus punctatus*], gizzard shad [*Dorosoma cepedianum*], and bluegill [*Lepomis macrochirus*], Bivings et al. 1989), and to determine whether seasonal differences exist in MECs of the channel catfish diet. I will suggest how these data may be used in a preliminary bioenergetics model of cormorant consumption of fish.

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MATERIALS AND METHODS

FEEDING TRIALS

Adult Double-crested Cormorants were borrowed from a wildlife rehabilitation center for three test periods (June and August 1990, and February 1991). Cormorants had body masses of 1.48 to 2.10 kg. Four birds were tested each month with one to three species of fish. Cormorants were kept in a group holding cage (4 × 4 × 2 m) under a covered outdoor aviary. Prior to conducting digestion trials, cormorants were fed thread herring (*Opisthonema oglinum*) ad libitum for a three-week cage acclimation period. Thread herring was the diet offered at the wildlife rehabilitation center and was familiar to the cormorants. Channel catfish was purchased from commercial producers. Gizzard shad, bluegill, and thread herring were caught from wild stock. The available gizzard shad were too large to be swallowed by cormorants, so they were cut into 15 × 2 × 2 cm pieces to approximate the size of juvenile gizzard shad, which comprise a large proportion of gut contents in wild Double-crested Cormorants (Bivings et al. 1989). All fish were frozen, then thawed for each feeding. Although frozen fish may digest differently than fresh fish because of prior tissue damage due to freezing and thawing (Jackson et al. 1987), they were used to reduce costs of the study and to prevent parasite infection of captive cormorants (B. Suto, Suncoast Seabird Sanctuary, St. Petersburg, FL, pers. comm.). No additional vitamins or salt were provided to the cormorants during the cage acclimation or test periods.

Individual digestion cages (1.5 m^3), with wire flooring (2.5 cm mesh), were constructed as satellites to the main holding cage. A single plastic "T" perch was attached to the floor of each digestion cage to encourage cormorants to stand in one spot during the collection periods. I trained cormorants to enter digestion cages voluntarily by serving their meals in the cage. Plastic sheets were placed under the wire floor of each cage to collect droppings. Environmental conditions were similar in June and August tests, with air temperatures ranging between 20° and 35°C each day. In February, air temperatures were highly variable with lows between −5° and +15°C, and daily highs between +10° and +27°C. The thermoneutral zone of captive cormorants ranges from 20° to 40°C in the day and 18° to 40°C at night (Henneman 1982). Thus, energy demands were not similar among months of testing.

Fish were given to cormorants on a free-feeding basis. Daily records were kept of number and mass of fish offered to and rejected by the cormorants. In June, cormorants refused to eat channel catfish and so were force-fed meals equivalent to 10% body mass (150 to 200 $g \cdot bird^{-1} \cdot day^{-1}$). In August trials, cormorants voluntarily ate each fish species and were offered approximately 500 g $fish \cdot bird^{-1} \cdot day^{-1}$. In February, cormorants were offered approximately 700 g $fish \cdot bird^{-1} \cdot day^{-1}$, higher than August to meet increased energy demands.

Passage of channel catfish through the gut of cormorants was determined with six birds (two in June, four in August) by measuring transit time and calculating mean residence time of a single dye-marked fish that was fed with a full meal. Carmine dye was used as a liquid-phase marker (Kotb and Luckey 1972, Duffy et al. 1985). Transit time is the time between consumption of marked food and first appearance of the marker in the feces; mean residence time is the average time that a sample of feces, collected at a specific point, remained in the gut (Warner 1981). A gelatin capsule containing 0.5 ml of 10% carmine red solution was inserted in a thawed fish. At 10:00 EST, one marked fish was fed to each cormorant as it perched in its digestion cage. Casts and feces were collected for 48 hr. Marker concentration was determined at 520 nm with a spectrophotometer. Total solids were collected for 28 hr from two birds fed the carmine dye in June to compare movement of solid and liquid phases of digesta. Mean residence times (MRT) of the liquid marker and total solids were calculated with the equation:

$$MRT = \sum x_t \cdot t_t / \sum x_t$$

where t_t = time t, and x_t = the amount of marker or solid excreted at time t (Warner 1981).

An attempt to determine the transit time of bluegill was also made by marking the solid phase of digesta with pieces of plastic flagging (Robbins 1983). Plastic is presumed to be insoluble throughout the gut and is often used as a particulate marker (Warner 1981). Four small pieces of colored flagging tape (5 mm^2) were inserted into the body cavity of a fish. Each of four cormorants was hand fed one marked bluegill per day for a four-day period. Different colors of flagging were used each day. Feces and casts were

collected and checked for colored flagging for five days after the first flagging was fed to the birds. Note that the two food markers, dyeing and flagging, are not comparable techniques: dye marks the liquid phase and flagging marks the solid phase of digesta.

A series of two- to four-day digestion trials were conducted to obtain estimates of metabolizable energy (ME) and MEC for energy for each test diet. A digestion trial consisted of offering a single meal, followed by collection of (1) food that was spilled and rejected, (2) food that was consumed, but regurgitated (casts or pellets), and (3) feces and urine 24 hr later. The procedure was repeated daily. For three days between digestion trials, birds were fed the next fish species to be tested to allow clearance of the prior test diet. Replicates of the digestion trials were performed 5 to 14 June 1990 (channel catfish and bluegill, only), 29 July to 15 August 1990 (all three fish species), and 17 to 20 February 1991 (channel catfish only).

SAMPLE ANALYSES

Uneaten food, regurgitated pellets, and droppings (termed excreta to indicate the combined feces and urine) were collected from food trays and plastic sheets. A thin film of excreta remained on the plastic sheets after scraping, but comprised <1% of the total dry matter of the collections. Each sample was weighed while wet, then dried at 60°C until it reached constant mass. From these data, a partial dry mass measurement was calculated. Samples were then stored in separate, inert plastic bags at −20°C.

Samples of the test diets, uneaten food, pellets, and excreta were ground to 1 mm particles with a Wiley mill. Dry matter content (% DM as received) was determined by drying the partially dry samples at 105°C for 8 hr (Association of Official Agricultural Chemists 1991). Although some volatile lipids may be lost at 105°C, the temperature was used to ensure that all moisture evaporated from the partially dry samples. Total dry matter was calculated with the equation,

$$\text{Total DM} = (\%\ \text{partial DM}) \times (\%\text{DM as received}). \quad \text{(eq. 1)}$$

Organic matter content (% OM) was measured by burning dry samples at 500°C for 3 hr (Association of Official Agricultural Chemists 1991). Energy content ($kJ \cdot g^{-1}$ dry matter, ash-free) was measured by igniting samples under 25 atmospheres oxygen in a plain jacket calorimeter (Parr Instrument Co. 1960). Nitrogen content was determined by Kjeldahl analysis (Association of Official Agricultural Chemists 1991). Two replicates per sample were performed and a 2% relative error was accepted.

Metabolizable energy was calculated with the equation,

$$\text{ME} = \text{Energy Consumed} - (\text{Energy in Feces} + \text{Urine}). \quad \text{(eq. 2)}$$

Because the body masses of cormorants ranged between 1.48 and 2.1 kg, the measure of ME was standardized as $kJ \cdot kg^{-1} \cdot day^{-1}$.

Metabolizable energy coefficients (MECs) were calculated for each bird on each diet over the three to four days of testing, using the equation,

$$\text{MEC} = (\text{Energy Consumed} - (\text{Energy in Feces} + \text{Urine})) \div \text{Energy Consumed}. \quad \text{(eq. 3)}$$

MECs were corrected to nitrogen balance because urinary energy depends on total nitrogen metabolism. Nitrogen corrections are needed to allow comparisons of MECs among birds with varying nitrogen demands, such as growing chicks, egg laying adults, or molting birds (Sibbald 1982). The following equation was used,

$$\text{MEC}_N = (\text{Energy Consumed} - (\text{Energy in Feces} + \text{Urine}) - N) \div \text{Energy Consumed}, \quad \text{(eq. 4)}$$

where N is a correction factor calculated as

$$(N_{IN} - N_{OUT}) \times 36.5. \quad \text{(eq. 5)}$$

In equation 5, N_{IN} is the mass of nitrogen in food, N_{OUT} is the mass of nitrogen in feces and urine, and 36.5 kJ/g is the energy value for urinary nitrogen in poultry (Sibbald 1982) and is assumed to be valid for other birds.

A cormorant had to consume >10% of its body mass in wet fish per day to be considered as feeding normally. If during the course of a digestion trial, any bird failed to eat >10% of its body mass in fish, then all data for that bird on that diet were dropped from the analyses.

STATISTICAL ANALYSES

Although the primary goal was to determine daily energy needs and MECs of Double-crested Cormorants on each of three fish diets, hypotheses were tested to identify fish-related differences in these variables. Normality and homo-

TABLE 1. Characterization of fish used in digestion trials, including size, dry matter (DM, % fresh weight), organic matter (OM, % dry matter), nitrogen (N, % dry matter), and energy content (kJ/g dry, ash-free [dmaf], and kJ/g fresh weight). Dashes (—) indicate analyses not performed.

Fish species	Month	Length (cm)		Mass (g)		Determinations			Energy content	
		$\bar{x}$	SD	$\bar{x}$	SD	% DM	% OM	% N	$kJ \cdot g^{-1}$ dmaf	$kJ \cdot g^{-1}$ fresh
Channel Catfish	June	8.3	(0.5)	5.8	(0.3)	21.65	81.02	—	25.013	4.38
(*Ictalurus punctatus*)	August	20.1	(1.5)	65.2	(7.3)	26.39	88.12	13.88	28.518	6.63
	February	17.5	(2.6)	34.5	(2.8)	25.49	83.76	13.52	28.123	6.00
Gizzard Shad (*Dorosoma cepedianum*)	August	30.4	(4.3)	145.5	(9.8)	29.41	80.62	14.16	27.844	6.60
Bluegill (*Lepomis macrochirus*)	June	15.7	(3.1)	73.1	(5.2)	24.19	71.97	—	23.349	4.06
	August	13.1	(4.1)	58.8	(25.0)	24.51	70.66	11.50	23.223	4.02

scedasticity were evaluated with normal probability plots and Bartlett's tests, respectively (Sokal and Rohlf 1981). Correlation or regression analyses were used to identify relationships between dependent variables. Repeated-measures analyses of variance were used to test the hypothesis of no difference in treatment means for each dependent variable.

RESULTS

Dry matter, organic matter and energy contents of the fish diets are shown in Table 1. The 17.5 to 20 cm channel catfish had the highest energy contents on a dry, ash-free basis, but were similar to gizzard shad on a fresh weight basis. On average, body mass of the cormorants varied <5% within all digestion trials, except the February trials when the birds gained 11.5% in five days of channel catfish feeding. Thus the February birds were not in energy balance.

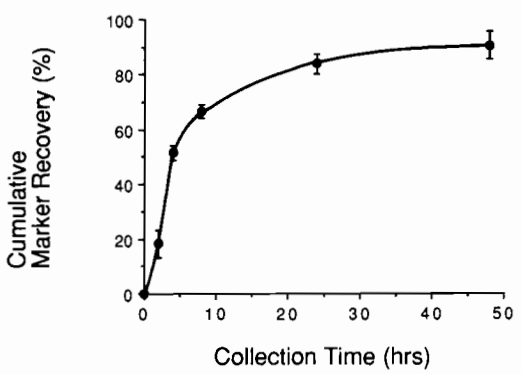

FIGURE 1. Mean (±SD) cumulative recovery over 48 hr of a liquid-phase marker, carmine red dye, in the feces of six Double-crested Cormorants (*Phalacrocorax auritus*) fed channel catfish (*Ictalurus punctatus*).

Mean transit time (or the time between consumption of marked food and first appearance of the marker in the feces) of carmine dye in the gastrointestinal tracts of six Double-crested Cormorants was <2 hr (Fig. 1). Cumulative recovery of the liquid phase marker was 51.55% (±2.5) at 4 hr, 83.83% (±3.7) at 24 hr, and 90.55% (±4.9) at 48 hr (Fig. 1). This suggested that a collection period for estimating MECs should be >48 hr and perhaps 72 hr to obtain 95% of digesta from a single meal.

Mean residence time of the solid and liquid phases of channel catfish increased with collection time; solids remained in the digestive tract longer than the liquid phase (Fig. 2). In both cormorants, a pulse of the liquid-phase marker appeared 24 hr after administration, suggesting gastric emptying of the prior day's meal into the intestines after the current day's meal.

The plastic flagging tape that was inserted in the body cavities of bluegill did not pass through the cormorants as intended. Instead, the tape was regurgitated with pellets of bones or pieces of fish. Flagging tape was recovered one or two days after being fed to each cormorant. Of 15 casts collected during 20 bird-days (4 birds × 5 collection days), nine contained flagging. Six casts were collected with one-day old flags and three casts with two-day old flags. Other pieces of flagging were found on plastic sheets near bits of regurgitated fish, and were ejected on the day of feeding.

Unlimited access to food resulted in intakes that varied in fish species and with month of testing. Cormorants ate fish in several "meals"

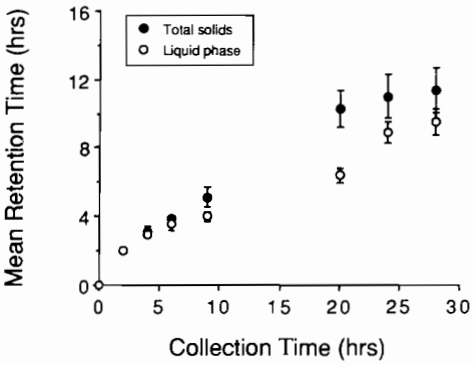

FIGURE 2. Mean retention times of total solids and liquid-phase marker in the feces of two Double-crested Cormorants (*Phalacrocorax auritus*) fed channel catfish (*Ictalurus punctatus*).

during the day. A typical pattern was for each bird to eat about half the available fish at first, then one or two fish every 4–6 hr thereafter. Voluntary intake of wet channel catfish increased from 347 (±15) g·bird^{-1}·day^{-1} in August to 503 (±29) g·bird^{-1}·day^{-1} in February (Table 2). Voluntary intake of bluegill was approximately 300 g·bird^{-1}·day^{-1} in June and August (Table 2). In August, the only trial when all three fish were tested with the same four birds, intake differed significantly ($F_{2,8}$ = 8.5; P = 0.01). Mean intake of gizzard shad was 264 (±16) g·bird^{-1}·day^{-1}, 12% to 24% lower than that of bluegill and channel catfish, respectively. Averaged across all birds, diets and days in captivity, voluntary intake was 283 (±25) g·bird^{-1}·day^{-1} (n = 52 days).

Daily masses of excreta varied among birds and diets (Table 2). Mass of excreta was correlated with wet intake among diets in each month of testing (June: r = 0.53, df = 15, P = 0.04; August: r = 0.56, df = 14, P < 0.001; February: r = 0.53, df = 15, P = 0.04). In the August trials, energy in the excreta did not differ among fish diets ($F_{2,8}$ = 2.34; P = 0.16).

Metabolizable energy varied in the warm weather (June and August) feeding trials from 616 (±22) kJ·kg^{-1}·day^{-1} for cormorants eating bluegill to 1,282 (±52) kJ·kg^{-1}·day^{-1} for cormorants eating channel catfish (Table 2). In February, daily ME was 1,334 kJ·kg^{-1}·day^{-1} (±45). In August, there were significant differences in MEs among diets ($F_{2,8}$ = 40.5; P < 0.001), with catfish = gizzard shad > bluegill.

Excluding the force-fed birds in the June channel catfish trials (for which only two days' data

TABLE 2. Weighted mean (±SE) mass of birds used in digestion trials, intake of wet fish, dry matter excretion, energy of the excreta, metabolizable energy, and metabolizable energy coefficients (MECs) of Double-crested Cormorants (*Phalacrocorax auritus*) fed one of three fish species, channel catfish (*Ictalurus punctatus*), gizzard shad (*Dorosoma cepedianum*), or bluegill (*Lepomis macrochirus*), during three trials. Dashes (—) indicate analyses not performed.

Fish	Month	No. birds: days	Body mass (kg)		Intake (wet g·d^{-1})		Excretion (dmaf g·d^{-1})		Fecal energy dmaf (kJ·g^{-1})		Metabolizable energy (kJ·kg^{-1}·day^{-1})		MEC (%)		Nitrogen corrected MEC (%)	
			$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)
Catfish	June	4:2	1.59	(0.13)	160	(5)*	7.87	(0.39)	14.81	(0.42)	377	(38)	83.38	(0.01)	—	
	August	4:4	1.60	(0.05)	347	(15)	18.06	(1.44)	14.22	(0.32)	1,283	(52)	89.03	(0.72)	79.67	(0.68)
	February	3:3	1.92	(0.04)	503	(29)	32.27	(2.13)	14.08	(0.08)	1,334	(45)	85.04	(0.90)	78.64	(0.81)
Shad	August	3:4	1.57	(0.04)	264	(16)	14.87	(0.55)	15.29	(0.24)	1,011	(133)	89.24	(1.07)	77.60	(0.87)
Bluegill	June	2:3	1.53	(0.03)	307	(24)	17.93	(3.31)	13.80	(1.34)	673	(117)	80.25	(0.03)	—	
	August	4:4	1.57	(0.03)	301	(13)	17.76	(1.00)	14.83	(0.27)	617	(36)	77.89	(1.59)	74.68	(1.51)

* Force-fed birds.

are available), MECs ranged from 77.9% to 89.2% among diets and trials (Table 2). In August, MECs differed significantly among diets ($F_{2,8}$ = 29.33; $P < 0.001$) with channel catfish = gizzard shad > bluegill (Table 2). Mean MECs of channel catfish did not differ between the August and February trials when cormorants voluntarily ate catfish (t = 2.33, df = 5, P = 0.07). Nitrogen corrections reduced the MECs to approximately 75% for bluegill, 78% for gizzard shad, and 79% for channel catfish (Table 2). Nitrogen corrected MECs (y) were directly related to % OM (x) of the fish. The relationship is described by the equation

$$y = 54.25 + 0.29x$$
$$(r^2 = 0.99,\ P < 0.01,\ n = 4).$$

DISCUSSION

Voluntary intake of fish by Double-crested Cormorants varied almost two-fold between the February channel catfish and the August gizzard shad digestion trials. The difference could be related to increased energy expenditures due to higher costs of thermoregulation in cooler weather. However, increased intake of catfish in February was offset by increased defecation, resulting in relatively close estimates of ME among August and February catfish trials and August gizzard shad trials. Thus, captive cormorants may have increased intake during February for reasons other than energy requirements.

The average intake of 283 g fish·bird^{-1}·day^{-1}, calculated with 52 days' data when birds were held either in groups (maintenance) or in individual digestion cages (tests), falls within the range of 225 to 450 g fresh fish·bird^{-1}·day^{-1} estimated by captive care facilities (B. Suto, Suncoast Seabird Sanctuary, pers. comm.). Assuming 80% MEC_N and 6 kJ·g fresh catfish, the observed average intake is nearly identical to predictions derived from Nagy's (1987) field metabolic rate equations for 1.5 kg seabirds (287.5 g fish·bird^{-1}·day^{-1}). The value slightly exceeds the 230 to 247 g·bird^{-1}·day^{-1} predicted for 1.8 kg cormorants (Schramm et al. 1987).

Intake can be influenced by many competing factors. Diet-related factors affecting intake are size and shape of the fish, foraging effort required to catch the fish, handling time (e.g., spines on channel catfish), palatability, and nutrient content of the fish. Bird-related factors that influence intake include familiarity, preferences, metabolic requirements, and social facilitation of feeding. Channel catfish and gizzard shad had similar energy and organic matter contents (on a fresh weight basis) and were more energy-dense than bluegill. In vitro tests demonstrated that these two fish species degraded faster than bluegill in artificial digestion liquor (Brugger 1992). Thus, from a benefit/cost standpoint, channel catfish and gizzard shad probably offer the most energy return for the least digestive effort, when compared with bluegill. Based on intake and anecdotal observations of the relative state of excitement of birds offered catfish, cormorants appeared to prefer eating channel catfish once they learned about it. I predict that if trials were conducted with naive cormorants, they would prefer catfish over gizzard shad or bluegill.

Estimates of transit time and mean residence times demonstrate a long period of food retention in the gut of cormorants and are similar to those determined for Jackass Penguins (*Spheniscus demersus*) and Cape Gannets (*Morus capensis*) fed *Tilapia sparminii* (Duffy et al. 1985, Laugksch and Duffy 1986). Cormorants have a simple gut structure, with a large sac-like proventriculus, minor ventriculus, 1 to 2.5 m long intestines, and rudimentary cecae (K. E. Brugger, unpubl. data). Because of structural simplicity, boluses of marker and solids that appeared 24 hr after a meal probably represent proventricular emptying and subsequent movement of intestinal contents from the bird after consumption of a new meal (Duke 1986).

Cormorants egested bony pellets when they ate channel catfish and bluegill, but not when they ate thread herring or gizzard shad. Egestion of pellets is common in carnivorous and piscivorous birds and serves to eject non-nutritive or bulky material from the proventriculus and ventriculus (Duke et al. 1975). Egestion of pellets did not occur daily. Based on collection intervals of nondigested plastic flagging, the cormorants may have collected hard parts in the proventriculus for one or two days. This suggests that the use of pellets to quantify diet of wild cormorants might result in a bias toward bony fish species and a failure to identify soft-bodied fish or other organisms.

Double-crested Cormorants fed channel catfish, bluegill, and gizzard shad had high MECs in comparison with other piscivorous and carnivorous species (Karasov 1990). My estimates (uncorrected for nitrogen retention) are 16%

higher than those determined for 9- to 12-month old cormorants fed herring (Cummings 1987), yet corroborate values for nestling Double-crested Cormorants fed pollack (Dunn 1975). Nitrogen corrections reduced MECs by 3.2% to 11.6%, similar to the reduction in MEC found for White-chinned Petrels (*Procellaria aequinoctialis*, Jackson 1986). The discrepancy between apparent and nitrogen-corrected MECs could yield underestimates of fish consumption by Double-crested Cormorants at commercial fisheries, thus nitrogen corrections of MECs are especially important for modeling energy requirements in birds. These data support earlier generalizations that fish-eating birds have MECs that converge on 75% (Furness 1978).

PRELIMINARY BIOENERGETIC MODEL

A bioenergetic model to estimate cormorant effects on catfish ponds requires several sets of data, such as estimates of individual energy demands by age- and sex-classes, population composition, diet composition, availability of fish resources and aquacultural and economic information to convert fish consumption by cormorants to the desired output. The endpoint of a model may predict proportional fish losses, monetary losses, or offer decision making criteria for choosing management strategies to improve fish production and cormorant protection.

Assuming an average daily energy demand of 1,380 $kJ \cdot bird^{-1} \cdot day^{-1}$ (with no variation due to sex, age, or season), a hypothetical diet composed of 50% catfish, 25% shad, and 25% sunfish (note that diet typically reflects relative fish abundance, Craven and Lev 1985), and the fish energy contents and MEC_N obtained above, then an average Double-crested Cormorant should eat 320 $g\ fish \cdot day^{-1}$, 160 g of which would be catfish. Cormorants in the Mississippi delta tend to specialize on 10–20 cm fingerlings (Glahn and Dixson 1990), which may weigh 15–80 g. Current replacement cost is about \$0.20 per fingerling. Thus, in this scenario, a single cormorant would take 2–11 catfish per day at a cost of \$0.40 to $\$2.20 \cdot bird^{-1} \cdot day^{-1}$. Little information is available to quantify standing crop or fish losses due to cultural practices (aeration, water temperature, disease), thus the proportional losses of catfish to fish-eating birds relative to background losses currently cannot be determined.

Data needed to refine this preliminary model include a definition of the geographic area of concern and temporal limits to the model (such as the season when cormorant-fish interactions occur), weather parameters, cormorant parameters such as daily activity budgets, population composition and densities, and food habits, fish parameters such as species abundance, standing crop of 10–20 cm size classes, survivorship, and replacement rates, and economic information on alternative cultural techniques. Research is in progress at many sites to develop the necessary database for accurately modeling cormorant effects on local fisheries, thus more precise models should soon be available.

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