

# CALORIC INTAKE OF NESTLING DOUBLE-CRESTED CORMORANTS

ERICA H. DUNN

ENERGY requirements of altricial nestlings should have effects on optimal reproductive strategy and foraging efficiency of adults, and on developmental physiology of nestlings (Royama 1966, Dunn 1973). Most food consumption studies measure weight of food intake without considering nutritional value. Because avian foods vary widely in digestibility, nutrition, and caloric content, such measures of food consumption of different species are not always comparable. In addition, many studies examine only total quantities of food eaten during growth (e.g. Kale 1965, Brenner 1968) or deal with birds raised in captivity (e.g. Kahl 1962, Junor 1965). The latter may not indicate natural levels of food consumption, as it is difficult to duplicate normal foods and feeding rates. For example Junor's (1965, 1972) studies indicate that the amount of food captive young Reed Cormorants, *Phalacrocorax africanus*, consume differs markedly according to the number of times per day they are fed.

I am aware of only a few studies to date that have estimated daily consumption of altricial nestlings under natural conditions (Royama 1966, Koelink 1972, van Balen 1973, Westerterp 1973), and only the latter provided data on the caloric value of the foods eaten.

This paper gives the results of a field study on food consumption of free-living nestling Double-crested Cormorants, *Phalacrocorax auritus*. (Unless noted otherwise, all references to cormorants mean this species.) Feeding frequency and size of food items were used to indicate quantities eaten, and analysis of food samples and digestive efficiency allowed conversion to caloric intake. The report is mainly descriptive, and the correlation of results to other aspects of the breeding strategy of cormorants will be reserved for a later paper.

## METHODS

A colony of about 250 pairs of cormorants on Duck Island, Isles of Shoals, New Hampshire (43° N, 70° 35' W) was studied during the 1972 breeding season. Periodic watches of known-age nestlings (up to 50 days after hatching) were conducted from a blind during all hours of daylight, for a total of 278 nest hours, or 445 nestling hours. On the average, 2 chicks were watched on each day of the nestling period for about 4.5 h. Data recorded for each young included time of feeding, number of feeding attempts during a given feeding session, and food related behavior. Because food is transferred by regurgitation to the young, whose head is inserted into the parent's throat, food items cannot be identified, but when a lump of food could be seen in the nestling's throat during swallowing, an estimate was

made of its length, width, and depth. Not all meals make a lump, as in the liquid meals given to the youngest birds, and a correction was later applied to overcome this difficulty.

When we arrived at the colony, the parent cormorants often regurgitated food at the nest site. These samples of food (which would presumably have soon been fed to the nestlings) were collected and frozen within 2 h. They were measured and weighed, and dimensions of the meals seen eaten by nestlings were compared to those of the samples to derive approximate weights (Royama 1966).

Food samples were homogenized, using a modification of the method described for large birds by Brisbin (1968). Each frozen meal was ground in a meat grinder, and a weighed portion of water was added before blending in a heavy duty blender. After thorough mixing, about 100 cc were removed for further analysis. This sample was weighed, freeze-dried, reweighed, and its water content calculated, allowing for the proportion of water added for mixing. Fat was extracted from a portion of the dried sample with petroleum ether in a Soxhlet apparatus. Caloric determinations of the remaining dry fat portion were conducted with a Phillipson oxygen micro-bomb calorimeter, with four replications from each meal. A value of 9.0 kcal/g was used for ether extractable fat in calculation of live weight caloric value (Odum et al. 1965).

Excretory losses were measured for 17 known-age young over 24-h periods. Each chick was brought to the laboratory and kept in a plastic lined cardboard box with a false floor of  $\frac{1}{2}$  inch hardware cloth. Young were fed every 3 or 4 h with weighed portions of eviscerated fish (pollack, *Pollachius virens*), and returned to the colony at the end of the experiment. Pollack were the only fish available to me during the experiment, and were eviscerated for longer storage. They occur in the natural diet and are of the same average composition, so digestive efficiency was probably similar to that for other natural foods. The plastic linings of the boxes were removed, dried, weighed, washed clean, redried, and reweighed to give the dry weight of a day's excreta, and samples of dried excreta were burned in the calorimeter. Caloric intake for the experimental period was calculated from the known weight of food consumption and appropriate caloric equivalent (Table 1), and digestive (assimilation) efficiency over a 24-h period was calculated as (kcal intake-kcal excreta)/kcal intake.

## RESULTS

*Caloric values.*—Table 1 identifies and lists the 28 samples of food collected after adult regurgitation, along with their water and fat contents and caloric values. The samples were evidently representative of the normal diet, as the species of fish involved are mainly the same as those eaten by cormorants in other parts of Maine and in other years (Lewis 1929, Mendall 1936, Scattergood 1950, Kury 1969).

Other fishes eaten by birds have higher fat contents than those in Table 1, ranging from about 5–12.5% fat by weight (calculated from Kahl 1964, Hunt 1972). Many of the meals regurgitated by cormorants are partially digested, suggesting that the adults probably extract some energy from the food before passing it on to the young.

The average caloric value of the food samples (last line of Table 1)

TABLE 1  
FREQUENCY AND COMPOSITION OF FOOD ITEMS REGURGITATED BY  
ADULT CORMORANTS

Food item	Representation in samples		Composition <sup>1</sup>		
	% by frequency <sup>2</sup>	% by wt. <sup>3</sup>	% by wt.		kcal/g fresh wt. ± SD
			H <sub>2</sub> O	fat	
Cunner <i>Tautoglabrus adspersus</i>	47 (8)	59.7	72.2 (6)	1.2 (5)	1.25 ± 0.24 (6)
Winter flounder <i>Pseudopleuronectes americanus</i>	29 (5)	15.5	71.5 (1)	1.1 (1)	1.26 ± 0.07 (1)
Grubby (Sculpin) <i>Myoxocephalus aenaeus</i>	6 (1)	2.4	72.3 (3)	0.5 (1)	1.22 <sup>4</sup>
Rock eel (Gunnel) <i>Pholis gunnellus</i>	6 (1)	0.3	67.5 (1)	0.1 (1)	1.40 <sup>4</sup>
American eel <i>Anguilla rostrata</i>	12 (2)	6.6	73.9 (2)	4.3 (2)	1.41 ± 0.13 (2)
Pollack <i>Pollachius virens</i>	6 (1)	9.8	78.0 (1)		1.05 ± 0.03 (1)
Mummichog <i>Fundulus heteroclitus</i>	12 (2)	5.8			1.01 <sup>5</sup>
Unidentified (partly digested)	(11)		73.5 (11)	0.8 (11)	1.32 ± 0.12 (11)
Averages <sup>6</sup>			73.8	1.2	1.14 ± 0.06 <sup>7</sup>

<sup>1</sup> Sample size is given in parentheses.

<sup>2</sup> The number in parentheses gives the number of regurgitations in which that species was recorded. Some samples (total of 28) had more than one species.

<sup>3</sup> Out of total of 17 samples in which species could be determined.

<sup>4</sup> Calculated by converting body composition to calories, using caloric equivalents of fat (9.0 kcal/g) and lean dry weight (4.8 kcal/g; from calorimetry of other fish samples), rather than from direct calorimetry.

<sup>5</sup> From Brisbin (1965).

<sup>6</sup> Weighted according to proportional representation by weight of each species in total collection of food.

<sup>7</sup> Total of 4.8 kg of fish sampled with direct calorimetry.

was 1.14 kcal/g fresh weight. The species of fish eaten by cormorants in the Gulf of Maine may change during the course of the season, involving a shift to silversides (*Menidia*, Scattergood 1950), or an increase in the proportion of cunner (Mendall 1936). The average caloric value of food through the season probably does not change significantly, as the caloric values of the fishes involved are quite similar (Table 1, Brisbin 1965).

*Digestive efficiency.*—Table 2 gives the caloric value of dried excrement and digestive efficiency of young when eating pollack. Digestive efficiency increases with age, as it does for young Starlings, *Sturnus*

TABLE 2  
CALORIC VALUE OF EXCRETA AND DIGESTIVE EFFICIENCY IN NESTLING  
DOUBLE-CRESTED CORMORANTS<sup>1</sup>

Age (days)	kcal/g dry excreta $\pm$ SD	% digestive efficiency (over 24 h)
3-4	3.31 $\pm$ 0.00	
7-8	2.20 $\pm$ 0.23	
9-10	2.29 $\pm$ 0.06	
11-12 (2)		79.9
12-13 (2)	2.34 $\pm$ 0.09	
14-15		81.0
14-15	2.066	
15-16		81.0
20-21 (5)		88.1
38-39 and 45-46 (2)	3.15 $\pm$ 0.46	
Averages	2.53 $\pm$ 0.11	84.9

<sup>1</sup>Each 24-h experimental period covered 2 days of age. The number in parentheses indicates the number of young when more than one was tested. Two samples were tested for each bird, except for age 14-15 days.

*vulgaris* (Westerterp 1973) and Herring Gull chicks, *Larus argentatus* (MS). Average digestive efficiency and caloric value of dried excrement are similar to those for other fish-eating birds (Uramoto 1961, Kahl 1964, MS), but digestive efficiency is higher and caloric density of excrement lower than the corresponding figures for seed- and insect-eating species (Dunn 1973).

*Feeding frequency.*—Feeding of very small cormorant nestlings is stimulated by peeping and uncoordinated head waving of the young. The parent responds by arching the neck, taking the head of the chick into its mouth, and regurgitating food. Older nestlings have a hoarser call, and beg by standing and waving the bill back and forth, sometimes hitting the adult's gular pouch. Occasionally the older birds flap their wings while begging. When feeding occurs, the nestling thrusts its head well into the parent's throat. This is typical of other pelecaniform birds, and is similar to the feeding behavior Snow (1963) described for the Shag, *Phalacrocorax aristotelis*.

Feedings occur in bouts, with several insertions of the nestling's head into the mouth of the adult. Bouts usually last less than 10 min, and are separated by at least a half hour. There may be as many as five or six head insertions in a bout during the early stages of the nestling period, but older chicks generally show only one or two. The larger young may be more easily fed, perhaps because the whole fish given to them is simpler to regurgitate than the semiliquid food provided to newly hatched young.

Feeding of young each day did not begin before 0600 and ended around

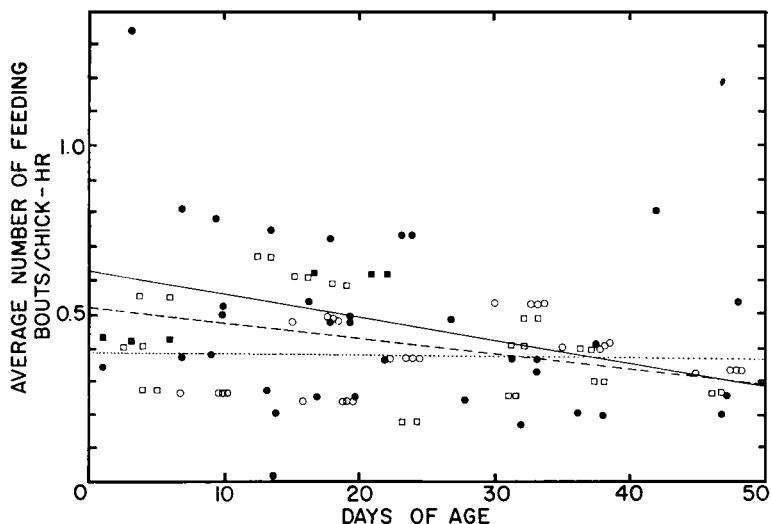


Fig. 1. Hourly feeding frequency of individual nestlings. Symbols represent different brood sizes: one, solid circles and solid line; two, open squares and dashed line; three and four, solid squares (3) and open circles (4) with dotted line. None of the slopes of the regression lines for different brood sizes was significantly different from 0 ( $P < 0.05$ ), nor was the slope for all data combined.

2000 EDT (as also found by Lewis 1929 and Mendall 1936). The average hourly feeding frequency of nestlings is shown in Fig. 1. Siblings watched from a blind could rarely be distinguished from each other, so each point represents the average feeding rate per young at nests containing broods of the indicated size and age. None of the slopes of the regression equations for feeding rates to different brood sizes was significantly different from 0 ( $P < 0.05$ ), although sometimes single young appeared to be fed more often than nestlings in larger broods ever were. The larger, older nestlings in multiple broods may have been fed more often than their smaller siblings, so that older nestlings were fed as frequently as single offspring. This is supported by my observation that the youngest chick was frequently underweight for its age and often died. The same is true for Shag chicks (Snow 1960).

Feeding frequency for an individual chick varies widely from day to day. Feeding times are evenly distributed with respect to time of day when tested by Chi-square, but there is a significant tendency ( $P < 0.001$ ) for feeding times to be concentrated in the first few hours after high tide. Other authors have noted concentrations of feeds near noon (Mendall 1936) or late in the day (Snow 1963).

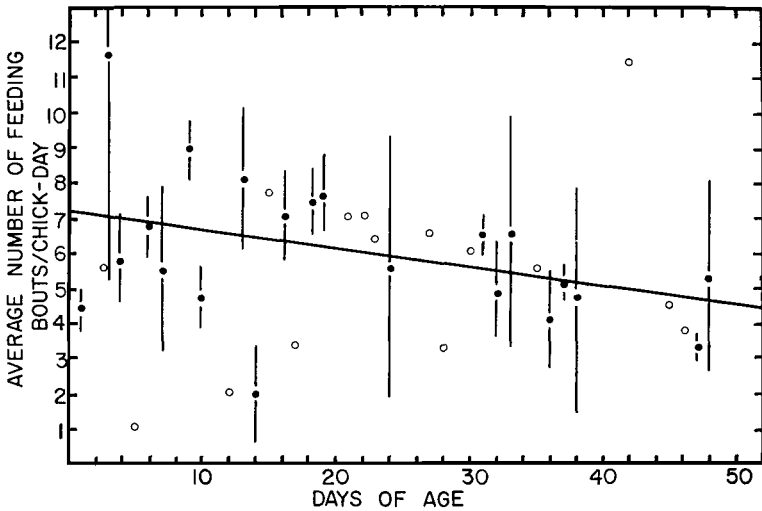


Fig. 2. Average daily feeding frequency for nestling Double-crested Cormorants. All brood sizes combined, and based on an observed 14-hour feeding day. Open symbols represent averages for days with fewer than 10 h of observation, and are not included in the regression. The slope of the regression equation ( $Y = -0.05X + 7.19$ ) is not significantly different from 0 ( $P < 0.05$ ). SE of the estimate is 1.97, and SE of means used in the regression are shown by the vertical bars.

Fig. 2 shows the average feeding frequency per chick per day (all brood sizes combined). The slope of the regression is not significantly different from zero ( $P > 0.05$ ), but was used in further calculations as the best estimate of feeding rate. The data are remarkably similar to those for Shag chicks (Snow 1963).

*Food consumption.*—Fig. 3 shows the sizes and weights of food samples collected from adult regurgitations. Length, width, and depth were measured, and volume calculated as if each sample were a rectangular solid. Estimated dimensions of meals seen swallowed by young in the field were then compared to the regression line in Fig. 3 to derive approximate weights.

Fig. 4 shows the estimated weights for the meals seen swallowed by individual nestlings. On the average, young received similarly sized meals regardless of brood size, but meal size variation is large. Average meal weights for each age (all brood sizes combined) clearly show an increase in meal weight with age, and the increase is sigmoid (Fig. 4). Various sigmoid curves were fitted to the averages (Ricklefs 1967) to give an estimate of average value for meal weights throughout the nestling period, and the logistic shown in Fig. 4 gave the best fit. Average meal weights

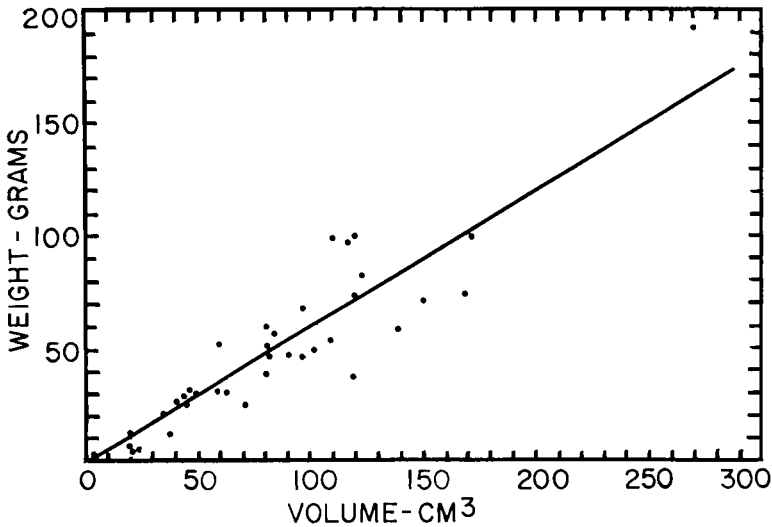


Fig. 3. Weights and estimated volumes of food items regurgitated by adults. Volumes were calculated from length, depth, and width, as if rectangular solids.  $Y = 0.63X - 3.69$ , SE of estimate is 15.44.

from this curve were then multiplied by the corresponding feeding rates per chick per day (Fig. 2) to obtain total weight of food consumption per chick per day. This was converted to kcal by multiplying by 1.14 kcal/g (Table 1), giving the first estimate of caloric intake through the nestling period shown in Fig. 5. Because feeding rate declines slightly while meal weight apparently levels off before the end of the nestling period, the estimated total caloric intake per chick declines somewhat after 4 weeks. Comparable decreases in food at the end of the nestling period have been reported in certain other birds (Royama 1966, Tickell 1968, Koelink 1972).

Examination of data on the energy lost in excretion and on that required by nestling cormorants for growth and metabolism (Dunn 1973) suggest that the estimate for energy intake in Fig. 5 is too low in the early part of the nestling period. This is not surprising, as the smallest chicks are fed a semiliquid food and the meal cannot be detected as a lump in the nestling's throat. A conservative upward correction was therefore calculated, representing average known energetic requirements during the period when measured food intake was certain to be too low. That I had to apply a correction indicates that the field methods were inadequate for assessing quantities of semiliquid food, but they should work for most other species of birds. I am unable to compare my cor-

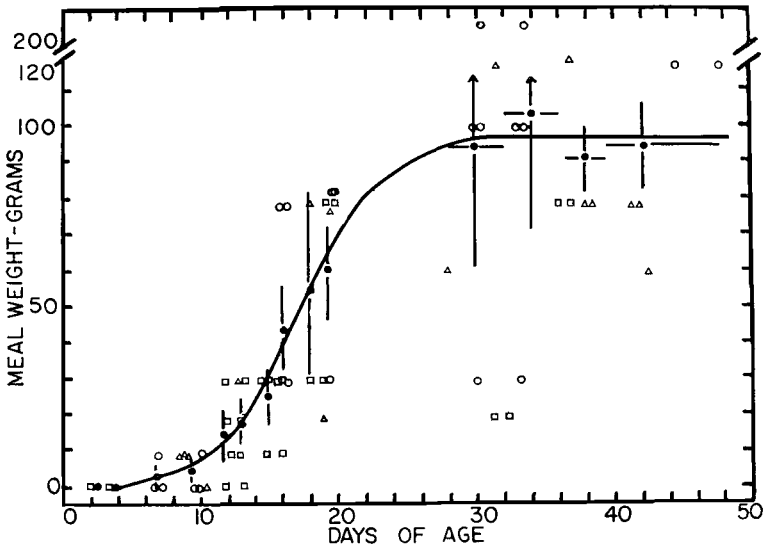


Fig. 4. Estimated weights of meals observed swallowed by nestlings. Open symbols represent meal weights derived from estimated dimensions (from Fig. 3) of individual meals observed swallowed by young in different brood sizes: one, triangle; two, square; four, circle. The solid symbols show averages (all brood sizes combined) for the day(s) indicated. Vertical bars show the SE of the means, assuming field estimates of volume are totally accurate (i.e. as this error is unknown, it is not calculated into the SE). The line shows a logistic curve fit to the averages by Ricklefs' (1967) graphical method.

rection to results from other species, as my figures for caloric intake are the only ones available for the first quarter of the nestling period.

The statistical accuracy of the curve in Fig. 5 is difficult to calculate, as the curve is derived from multiplication of average caloric value by lines and curves fitted to feeding rate, meal weight according to volume, and meal weight according to age of young, each with its own confidence limits (Ewens pers. comm.). Approximate statistical accuracy can be calculated by multiplying the means observed for each age (rather than the lines fitted to these means over the entire nestling period) and calculating SE for the resulting daily mean caloric intakes. Such calculations indicate an average SE of 34% of the mean, or approximate 95% confidence intervals of  $\pm 65\%$ . This is poor from a statistician's point of view, but the curve in Fig. 5 may not be as worthless as the statistic implies. The poor statistical accuracy results from the high variability in certain measurements, particularly meal weight and feeding rate, which in turn results from my having studied chicks in all conditions of brood size, health, weather, tide level, etc. Statistical variability can be reduced



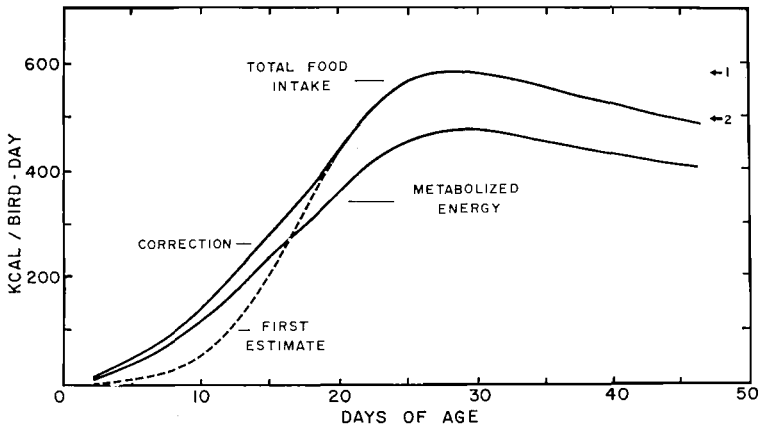


Fig. 5. Estimated average energy intake of free-living cormorant nestlings. Correction based on known energetic requirements for growth and metabolism, to be presented elsewhere. Metabolized energy of corrected caloric intake calculated from 85% digestive efficiency. Arrow 1: estimated caloric intake of free-living adults. Arrow 2: estimated metabolizable energy of free-living adults.

by increasing the number of observations, but this was impractical under the prevailing field conditions. Another way to reduce variability would have been to observe only healthy nestlings in a particular brood size (as was done in growth studies by van Balen (1973) or in the energy budget study of Westerterp (1973)), but I wanted to obtain an average figure for caloric intake over the entire colony. The wide confidence intervals of Fig. 5 indicate that caloric intake of any single nestling would be exceedingly unlikely to follow the curve indicated. Still I am confident that the relatively large number of observations in this study are sufficient to have given a reasonably accurate figure for average intake for all nestlings combined. In addition, the curve checks out well with the rest of the nestling energy budget (Dunn 1973), and certain estimates by other authors also corroborate those presented here.

Estimates of proportional food intake for free-living adults and juveniles of several species of cormorants range from about 20–30% (Wetmore 1927; Lewis 1929; Madsen and Spärch 1950; du Plessis 1957; Junor 1965, 1972). If food intake of free-living adults is taken to be equivalent to an average of 25% of body weight, and caloric value of food is the same as in Table 1, then the adults require around 580 kcal/day (arrow 1 in Fig. 5). Assuming the same digestive efficiency as in nestlings, metabolizable energy would be about 495 kcal/day (arrow 2 in Fig. 5). Free-living energy requirements have been estimated to be from about 20% to about 50% higher than those for captive birds (Ura-

moto 1961, Kale 1965, Willson and Harmeson 1973), so captive requirements of adults should be closer to those estimated for nestlings at the end of growth. These chicks are probably about as active as captive adults would be. Thus, the estimate of energy intake for nestlings in Fig. 5 seems reasonable for the latter stages of the nestling period.

#### DISCUSSION

Caloric value of food and digestive efficiency of the consumer are significant, although much neglected, aspects of food consumption studies. The measurement of metabolizable energy is important, as this figure represents the actual energy available to nestlings for growth, thermoregulation, and activity. Different foods vary in caloric content, and may change throughout the nestling period (Royama 1970), even though remaining constant in this study. In addition, digestive efficiency ranges from 30–85% for different foods (Dunn 1973) and may increase during nestling growth (Westerterp 1973). This study also reaffirms the importance of measuring size of food items, as feeding frequency alone cannot give an accurate representation of total food consumption (Royama 1966, Koelink 1972, Westerterp 1973).

Very little is known of avian nutrition (Fisher 1972), but food composition is also clearly of importance to nestling development. Fishes have a high protein content, which is important for nestling growth (Johnson 1971, Lemmetyinen 1972), and cormorants show very rapid growth for birds of their size (Ricklefs 1968). Adults regurgitate bones, but nestlings digest them, which may also contribute to rapid growth by providing necessary minerals (van Dobben 1952).

Cormorant young, because they grow fast, use large amounts of energy in growth, but the pattern of growth is such that food intake at no time exceeds that estimated for free-living, nonbreeding adults (Fig. 5). Average fledging success for various species of cormorants is about one to two chicks per pair per year (Serventy and White 1943, Snow 1960, Kury 1969, Vermeer 1969), so each parent must, on average, at least double its usual feeding effort during the breeding season (both parents feed the young). Because the parent works to increase its foraging effort, it probably increases its own food consumption over that in the nonbreeding season, so perhaps foraging effort is more than doubled. Variation in the doubling of foraging would occur, of course, depending on fledging success and on whether nonbreeding, free-living costs differ from those estimated here.

Koelink (1972) suggested that Pigeon Guillemots, *Cephus columba*, also double their foraging efforts when feeding their broods of one or two young. Siegfried (1972) suggested the same increase for Cattle

Egrets, *Bubulcus ibis*. Corresponding estimates for the Great Tit, *Parus major*, assuming an average brood size of 10 young, taking food requirements for healthy young from van Balen (1973), and taking caloric values of foods and adult requirements from Gibb (1957), suggest that each Great Tit parent must increase its foraging efforts by 50–80% (assuming free-living energy costs to be 20–50% higher than those in captivity).

Although the estimates for increase in foraging effort of breeding over nonbreeding birds appear remarkably similar, they should by no means be interpreted as having general significance. The costs of foraging, or of increasing foraging, may differ widely and represent very different proportions of each species' time and energy budget. In addition, the energetic and nutritional return per degree of effort can vary widely (Dunn 1973, Willson and Harmeson 1973).

Available food supply is extremely difficult to measure, but knowledge of the amount of food eaten by a bird population allows a minimum estimate of food in the environment (e.g. Uramoto 1961, Kahl 1964). If each pair of Double-crested Cormorants on the Isles of Shoals colony of 250 pairs raised two young and timing of the breeding season were synchronized, then the total amount of fish taken by that colony (for both parents and young) at the peak of nestling food demand would be at least 510 kg per day.

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#### SUMMARY

Food intake was measured for Double-crested Cormorant nestlings at a colony in New Hampshire. Fishes constitute the entire diet, which had an average caloric content of 1.14 kcal/g fresh weight. The adults evidently digest some fat before regurgitating the food to the young. Digestive efficiency of the nestlings averages 85%.

Young are fed about six times a day, and meal size increases during the first half of the nestling period. Total food intake peaks when the young are about 4 weeks old and declines thereafter.

It is estimated that cormorants with average nesting success must about double their nonbreeding foraging efforts to raise nestlings. At

the peak of nestling food demand, the colony studied probably removes about 510 kg of fish from the surrounding ocean each day.

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*Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104. Present address: Long Point Bird Observatory, Box 160, Port Rowan, Ontario, Canada. Accepted 22 July 1974.*