

BODY COMPOSITION, FAT RESERVES, AND FASTING CAPABILITY OF CAPE GANNET CHICKS

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ABSTRACT.—Age-related changes in lipid, water, and non-lipid content and energy density of four major body parts (integument, viscera, leg and pectoral muscles, and carcass) of Cape Gannet chicks, juveniles, and adults were studied. The proportion of water was typically high for neonates and decreased during development to near adult levels at fledging. The percentage of lean dry matter remained almost constant for muscles and carcass but decreased in viscera and integument due to fat deposited during growth. Energy density was linearly related to age ($\text{kJ/g} = 4.46 + 0.076 \text{ Age (days)}$, $r^2 = 0.845$, $P < 0.001$). Fasting capability (FC) of chicks (survival time when using only their lipid reserves, calculated from lipid mass and field metabolic rate) increased exponentially up to 70 days of age ($\text{FC} = 0.6e^{0.05 \text{ Age}}$, $r^2 = 0.815$, $P < 0.001$). Newly fledged birds have a fasting capability between 8–16 days and adults only 1–2 days. Time between consecutive feeds, from field observations at the nest, for chicks 21–40, 41–60 and 61–80 days old were 11.9 ± 0.7 h, $N = 74$; 16 ± 1.1 h, $N = 50$; and 20 ± 0.6 h, $N = 35$, respectively. The results are contrary to the hypothesis that fat deposits are an insurance against an unpredictable fast, although they may serve for this purpose. Fat deposits may be the physiological consequence of the temporal pattern of feeding by adults, or they may serve as energy sinks to increase energy requirements relative to the nutrient and protein requirements of chicks. Received 16 May 1991, accepted 23 Mar. 1992.

Seabirds share a number of characteristics that set them apart from most other birds such as low clutch size, deferred maturity and slow chick growth. It is thought that these characteristics are related to the unpredictable, patchy, and fluctuating nature of the food resources that seabirds exploit. Lack (1968) proposed that due to a limitation in the ability of adults to supply food, the pattern of development of the chicks is characterized by slow growth and the accumulation of large fat deposits. These fat deposits are interpreted as an insurance against the poor feeding conditions occasionally experienced by adults when foraging at sea (Lack 1968). Two predictions that can be drawn from Lack's hypothesis are tested in this paper: (1) a close match between fasting capability (i.e., fat deposits) and maximum time between consecutive feeds should be expected, and (2) assuming that the lean dry mass is well regulated by controls on somatic growth, the fat deposits should exhibit some variability as a consequence of chicks consuming their fat deposits during fast periods, so it is reasonable to expect a higher variance in fat deposits than in lean dry mass. On the other hand, Ricklefs (1979) suggests that pro-

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longed and unpredictable fasting is not the main force acting upon selection for large fat deposits in seabird chicks but that it may be a by-product of the energy-rich and nutrient-poor diet of most seabirds. Large fat deposits thus may be accumulated by seabird chicks as energy sinks to allow the chick to increase its energy requirements relative to the requirements of protein and other nutrients (Ricklefs 1979). Also, chicks are apparently fed more regularly than has been presumed (e.g., Ricklefs et al. 1985, Stempniewicz and Jezierski 1987, Taylor and Konarzewski 1989). In this case there is no reason to expect a close relationship between lipid deposits and fasting time, and variances of lipid and lean dry matter should be similar.

Gannets and boobies (Sulidae) are large altricial seabirds (Nelson 1978). Chicks are cared for intensively by both parents at the nest for 11 weeks (Peruvian Booby *Sula variegata*) to more than 20 weeks (Abbott's Booby [*Sula abbotti*]), with most species attending the young for ca 13 weeks. Post-fledging care is a characteristic of boobies but not of gannets (Nelson 1978). Growth of sulid chicks has been described for all species, but such studies have traditionally emphasized ontogenetic changes in body mass, and wing and culmen length. Changes in body composition and energy requirements have been studied only in Northern Gannets ([*Sula bassanus*]; Montevecchi et al. 1984), although energetic requirements for growth of Cape Gannets (*Morus capensis*) have been studied by Cooper (1978). In this paper, I describe age-related changes in lipid, water and non-lipid content and energy density of four major body parts (integument, internal organs, leg and pectoral muscles, and carcass) of Cape Gannet chicks, juveniles, and adults. Field data for foraging rate are also analyzed to test predictions from Lack's (1968) hypothesis (see above).

METHODS

Body composition.—Analysis of body composition of Cape Gannets was based on 21 chicks, two fledglings caught two days after fledging, and three adults caught at the end of the breeding season. Birds were collected, under permit, at Malgas Island (33°03'S, 17°55'E), South Africa, between 1987–1989 and kept frozen until analysis. Thawed birds were dissected into four major components: integument (skin plus down, feathers removed), viscera (all internal organs, stomach contents removed), leg muscles plus pectoral muscles, and carcass. Each of the four body components was ground and homogenized and then air-dried at 50°C to constant mass. Wet and dry masses were obtained. Dried material was powdered (or ground and homogenized when fat content was too high), and two aliquots for fat analysis were taken. Lipid content was determined by hexane extraction (2 g of dried material in 25 ml of hexane) for 45 min at 70°C and then centrifuged. From the liquid phase, 2 ml were dried for 30 min at 100°C, and the residues weighted. This method extracts mainly triglycerides and other nonpolar lipids. Phospholipids and cholesterol are not removed by hexane extraction (Fishing Industry Research Inst., UCT, pers. comm.).

The following definitions are used in this paper: water = wet mass – dry mass; lipid =

dry mass \times extracted mass/aliquot mass; lean wet mass = wet mass - lipid; lean dry mass = dry mass - lipid; lipid index = lipid/lean dry mass; and water index = water/lean dry mass. Energy equivalents of tissue were calculated using the conversion factors: 38 kJ g⁻¹ lipid and 20 kJ g⁻¹ lean dry matter (Ricklefs 1974).

Fasting capability.—Fasting capability of birds relying solely on their lipid stores was calculated based on a field metabolic rate (FMR) of 1264 kJ/day for chicks, and FMR = 3380 kJ/day for adults (Adams et al. 1991). For fledglings the FMR of adults was used, though it may underestimate their fasting capability. It was also assumed that the lipid mass equivalent to lipid index of 0.1 was not available for energy generation (Taylor and Konarzewski 1989). This figure was derived from body composition analysis of adult birds of different species starved to death. Such analysis showed the presence of a petroleum ether-extractable material equal to 0.5–2% of the wet body mass that gives lipid indices lower than 0.1 (Evans 1969, Chaplin 1974, Wishart 1979, Jenni and Jenni-Eiermann 1987).

Time between consecutive feedings.—For chicks older than 20 days, adult arrival at the nest after a foraging trip was used as an estimate of time between two consecutive feeds, since feeding of chicks older than 20 days is almost exclusively associated with the arrival of a bird at the nest. Data for two all-day watches of a group of nests (chicks aged 30–60 days) support this assumption: of 39 arrivals witnessed, 36 (92.3%) were followed by chick feeding within 30 min, three did not involve chick feeding and two cases of chick feeding were not associated with adult arrival. Parents usually feed the chick between 1–5 times within 30 min of arrival, but for the purpose of the present analysis, this was considered as a single feeding bout.

Data on adult arrival at the nest were obtained by regularly checking a group of nests every 30 min during daylight hours (and in two opportunities, every 1 h during the night). The time of arrival of a bird was recorded to within 30 min. Birds were dye-marked to recognize members of a pair. These observations were carried out for two to four days consecutively at different stages of chick development. Overnight observations revealed that no shifts at the nest or mate arrival occurred at night.

Unless otherwise stated, variations about means are given as the standard error followed by the sample size.

RESULTS

Body composition.—Changes in water, lipid, and lean dry matter for muscles, viscera, integument, and remaining carcass are shown in Fig. 1. During the nestling period, pectoral and leg muscles were characterized by a large proportion of water ($80.2 \pm 0.5\%$, $N = 21$) and lean dry matter ($17.9 \pm 0.8\%$), and small amounts of lipid ($1.9 \pm 0.1\%$). The carcass had a similar pattern, the average composition being $73.5 \pm 1.0\%$, $23.2 \pm 0.7\%$ and $3.3 \pm 0.4\%$ of water, lean dry matter and lipid, respectively. These proportions were different for the integument ($63.1 \pm 2.7\%$, $18.9 \pm 1.0\%$ and $17.9 \pm 2.5\%$ of water, lean dry matter, and lipid, respectively) and viscera ($73.5 \pm 1.7\%$, $17.0 \pm 0.6\%$ and $9.5 \pm 1.7\%$ of water, lean dry matter and lipid, respectively). The proportion of lipid content in pectoral and leg muscles, carcass, internal organs, and integument ($4.7 \pm 1.8\%$ $N = 2$, $5.7 \pm 1.3\%$, $32.4 \pm 13\%$ and $53.5 \pm 3.9\%$, respectively) of fledglings were markedly higher than those in adults ($3.6 \pm 1.8\%$ $N = 3$, $2.6 \pm 0.2\%$, $4.3 \pm 0.4\%$ and $18.7 \pm 1.6\%$, respectively). The proportion

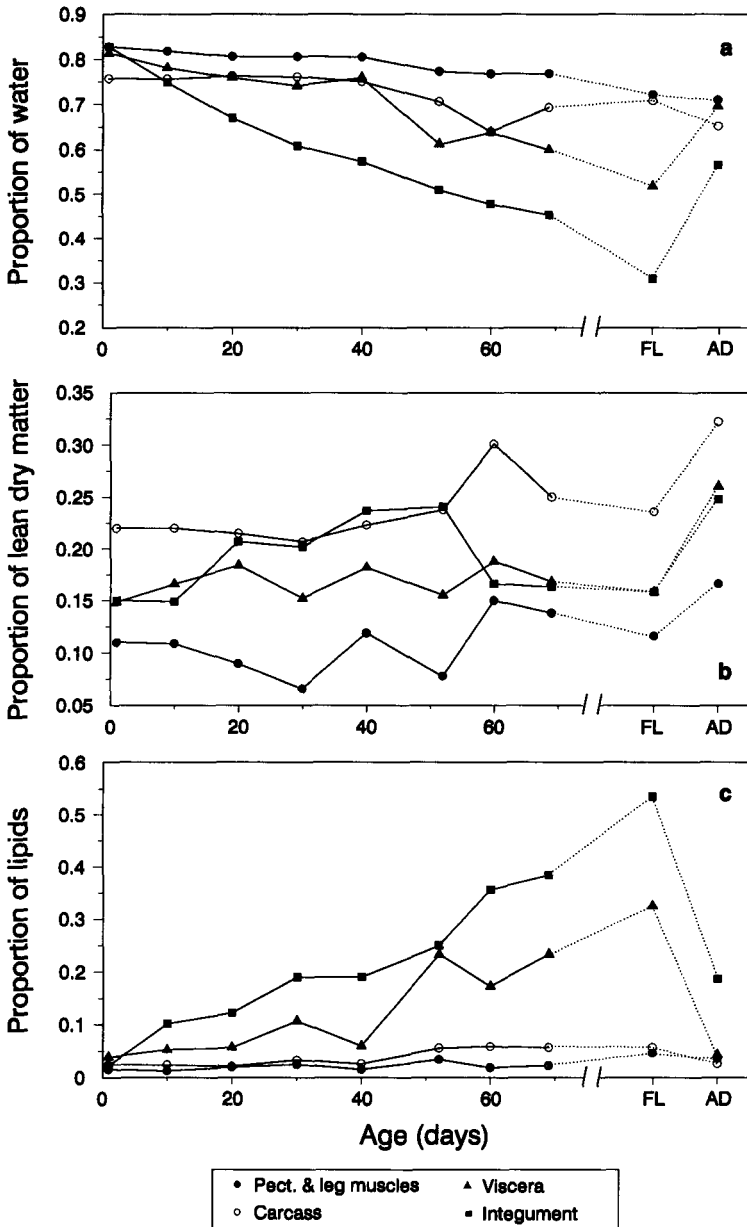


FIG. 1. Changes in lipid (L), lean dry mass (LF) and water (W) content of four major body parts of Cape Gannet chicks as function of age. Contents of fledglings (FL) and adults (AD) are also indicated. Sample sizes are as follows (age:N): 1:3; 10:3; 20:3; 30:3; 40:4; 52:1; 60:3; 69:1; FL:2; and AD:3.

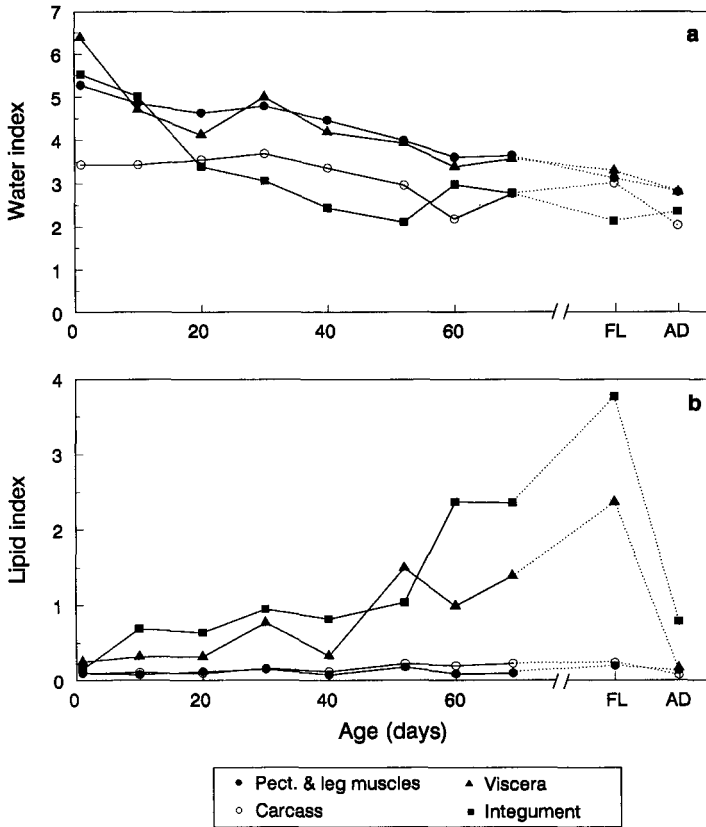


FIG. 2. Relative changes of (a) water index (water g/lean dry matter g) and (b) lipid index (lipid g/lean dry matter g) of four major body parts of Cape Gannet chicks as function of age. Figures for fledgling (FL) and adults (AD) are indicated. Sample sizes as in Fig. 1.

of lean dry matter of pectoral and leg muscles and carcass remained almost constant throughout the nestling period (Fig. 1b).

Water index (which is independent of the fatness level) decreased and approached adult levels in all four major body parts (Fig. 2a). The water index of the neonate (whole chick) is 4.0, which is similar to those of precocial species (range 3 to 4) (Ricklefs et al. 1980). Among the major body parts analyzed, only the viscera are within the range of altricial species (6 to 8), whereas the integument and leg plus pectoral muscles are between the range of precocial and altricial birds. The steady decrease in the water index is directly proportional to an increase in its functional maturity (Ricklefs 1979).

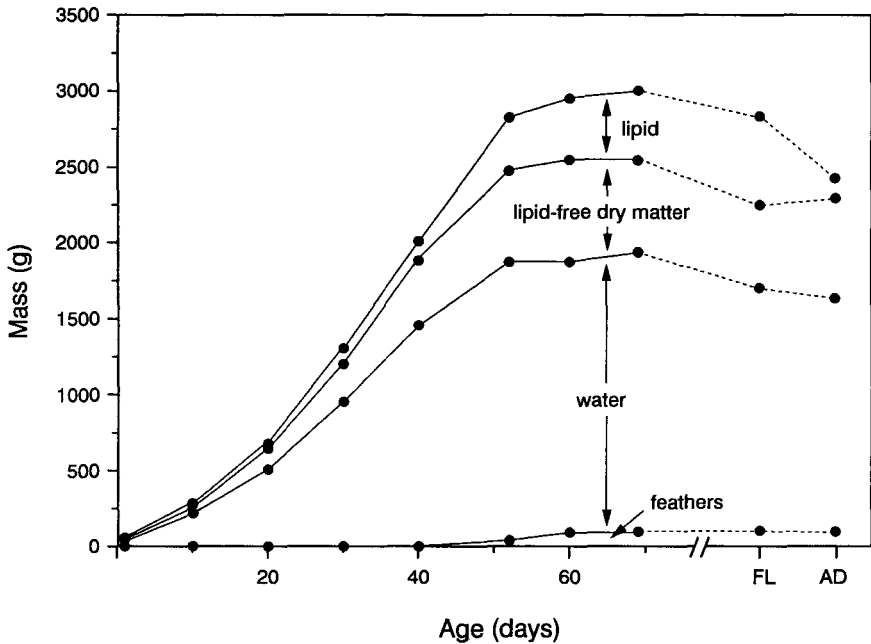


FIG. 3. Overall changes in feathers, water, lean dry matter, and lipid content of Cape Gannet chicks as function of age. Contents for fledgling (FL) and adults (AD) are indicated. Sample sizes as in Fig. 1.

Lipid index (Fig. 2b) increased steadily during chick growth for the integument and viscera, reaching a maximum value in fledglings, whereas it remained more and less constant for pectoral and leg muscles and carcass.

Overall increases in water, lipid, and lean dry matter are shown in Fig. 3, and the energy equivalents of these components are illustrated in Fig. 4a. The energy density (Fig. 4b) was linearly related to chick age ($\text{kJ/g} = 4.46 + 0.076 (\text{SE} = 0.008) \text{Age (days)}$, $r^2 = 0.845$, $N = 21$, $P < 0.001$). The relationship for the North Atlantic Gannet ($\text{kJ/g} = 3.35 + 0.16\text{Age}$) (Montevecchi et al. 1984) was significantly different (ANCOVA: $F_{\text{slopes}[1,31]} = 56.9$, $P < 0.001$; and $F_{\text{adjusted means}[1,31]} = 38.7$, $P < 0.001$; homogeneity of variances test, $F_{\text{max}[2,19]} = 0.79$, $P > 0.05$). The energy density of adults (7.5 ± 0.2 , $N = 3$) was similar to that of a 40-day-old chick, which is ca 58% of the figure reported by Montevecchi et al. (1984) for the North Atlantic Gannet. The lipid fraction accounted for ca 45–65% of the energy stored in the tissues of 50–70-day-old chicks and ca 65% of that of fledglings, but only 27% of adults.

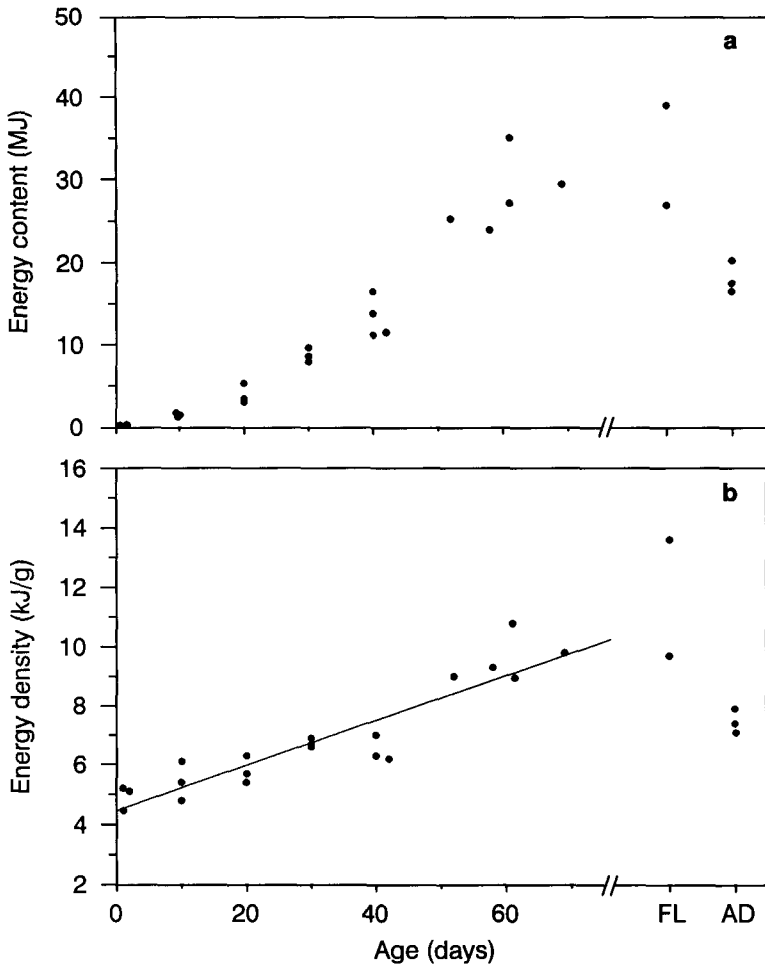


FIG. 4. Changes in (a) energy content and (b) energy density (kJ/g) of Cape Gannet chicks as function of age. Contents for fledglings (FL) and adults (AD) are indicated.

The variances of lipid and lean dry matter of chicks 20–70 days old were compared, after adjusting for their magnitude, by dividing each value by its respective sample mean. This ensures that both data sets have the same mean so that the variances can be compared using a simple ratio. The variance ratio lipid/lean dry matter was $0.764/0.259 = 2.945$, $F_{0.025[14,14]} = 2.983$ (two-tailed test), indicating that the variances were not significantly different.

Fasting capability.—Fasting capability (FC) of chicks increased expo-

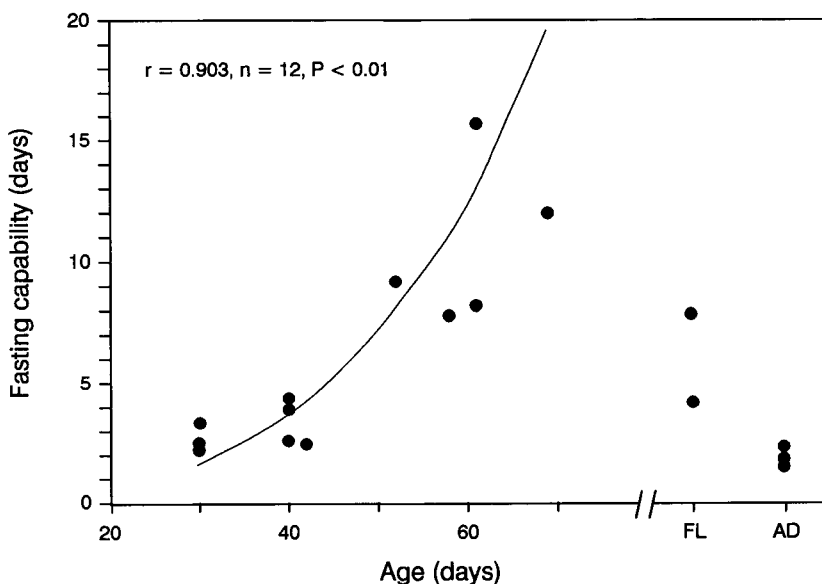


FIG. 5. Estimated fasting capability of chicks, fledglings, and adults assuming that they rely solely on their lipid stores. See text for details of calculations.

nentially up to 70 days of age according to the model: $FC = 0.6e^{0.05Age}$ ($SE_b = 0.01$; $r^2 = 0.815$; $N = 12$; $P < 0.01$) (Fig. 5). The fat deposits of chicks aged 30–40 days would supply their energetic needs for 2–4.5 days, for chicks 50–70 days old the fat deposits would last for 8–16 days. The two fledglings analyzed had reserves to last them for 4–8 days, whereas lipid reserves of adults would provide them with energy for, at most, one or two days (Fig. 5).

Time between consecutive feedings.—Frequency distribution of time between consecutive feedings for three age classes are shown in Fig. 6. The longest period recorded was 31 h for a 70-day-old chick. The peculiar frequency distribution for chicks 61–80 days old is due to the two adults arriving at the nest within a few hours of each other after long foraging trips (typically > 18 h), thus producing the peak observed at ≤ 6 h. The mean time between feeds for chicks 21–40, 41–60 and 61–80 days old were 11.9 ± 0.7 h, $N = 74$; 16.0 ± 1.1 h, $N = 50$; and 17.5 ± 1.2 h, $N = 44$ (20.0 ± 0.6 h, $N = 35$ excluding short intervals), respectively. When compared with the fasting capability of chicks (Fig. 5), it is clear that chicks had substantially more fat reserves than were needed to survive the observed intervals between consecutive feedings.

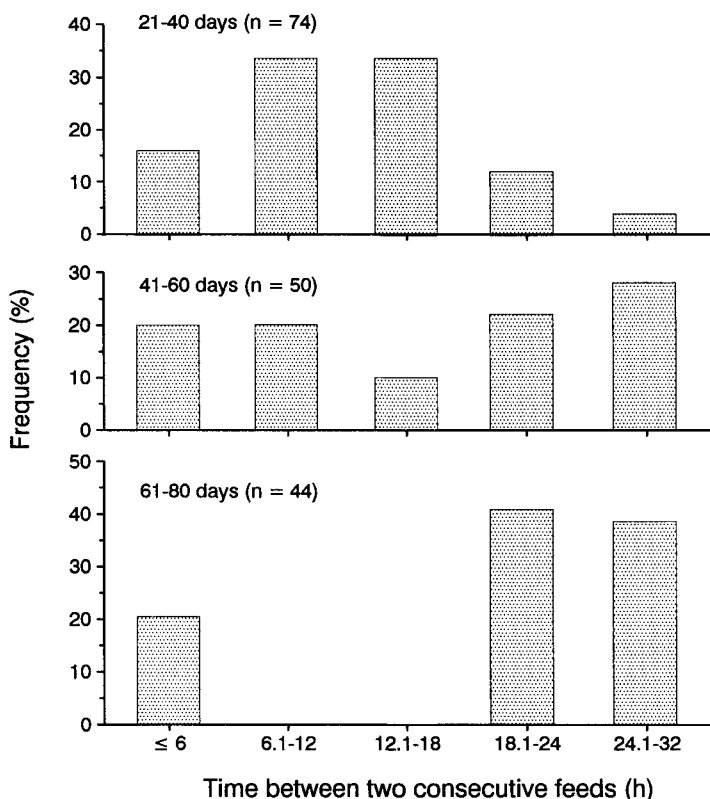


FIG. 6. Frequency distribution of time between two consecutive feedings for three age classes of Cape Gannet chicks.

DISCUSSION

Kirkham and Montevicchi (1982) distinguish three stages of energy partitioning in North Atlantic Gannet nestlings that are also clearly discernible in Cape Gannet chicks. During the first stage, spanning the initial five weeks, the energy delivered to chicks is used primarily for internal organ, skeletal, and muscular development. During this stage, chicks achieve thermal independence and have reached nearly adult dimensions. The second stage covers the period from about the 5th to the 10th week of the nestling period. At this stage, energy is used primarily for feather development and the deposition of substantial fat reserves. There is little development during the final stage which covers the last five weeks of the nestling period. Wings, feathers and pectoral muscles reach maturation, and chicks usually lose mass during this stage.

Adults typically lost mass during the breeding season (pers. obs.), and this must be reflected in their fat deposits. Adults were lean, and their small fat reserves would give them energy for two days at most. Adams et al. (1991), using the doubly labeled water technique, found that, at least during part of the breeding period, adults have a negative energy balance.

Lipid reserves of chicks, expressed as fasting capability, show that they greatly surpass what is required for potential needs, particularly so for chicks older than 50 days. Similar results have been reported previously for other seabirds, e.g., Sooty Tern (*Sterna fuscata*) (Ricklefs and White 1981), Leach's Storm-petrel (*Oceanodroma leucorhoa*) (Ricklefs et al. 1981), North Atlantic Gannet (Montevicchi et al. 1984), and Little Auk (*Alle alle*) (Taylor and Konarzewski 1989). These studies and my results support Ricklefs' (1979) hypothesis that large fat deposits may serve as energy sinks, increasing the chick's energy requirements relative to its requirements of protein and other nutrients, rather than as insurance against unpredictable fasting as proposed by Lack (1968). Occasionally, feeding frequencies could be greatly decreased (e.g., by bad weather spells) or the food provided by parents could be of low calorific value; in such cases fat deposits can make the difference between surviving or not. The adaptive significance lies in the frequency of such events.

Schaffner (1990) suggested that a feeding regime characterized by large but infrequent meals may be the main cause of large fat deposits. Intermittent feeding in poultry resulted in increased lipogenesis, lowered basal metabolic rates and slower growth (e.g., Cohn 1963, Nir et al. 1979).

Even if fat deposits are not crucial for nestlings, in terms of being an energy source, they may be important for juveniles. Recently fledged gannets must rely solely on their reserves until they learn the necessary skills to capture (by plunge-diving) enough food to balance their negative energy budget. In fact, the highest mortality reported for Cape Gannets occurs soon after fledging (Oatley et al. 1992) and it is related to the chick mass at fledging (Jarvis 1974). This factor may also have helped to shape patterns of growth of seabirds, favouring selection of large fat deposits. However, many seabirds lose part of their large fat reserves during a pre-fledgling fast (Lack 1968), indicating that lower body mass is required for efficient flight. Obviously, a fledging bird must compromise between flight efficiency and energy reserves.

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