

ENERGETIC REQUIREMENTS FOR GROWTH AND MAINTENANCE OF THE CAPE GANNET (AVES; SULIDAE)

J COOPER

Percy FitzPatrick Institute of African Ornithology, University of Cape Town

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ABSTRACT

Energetic requirements for growth and maintenance of the Cape gannet (*Sula capensis*) were studied by hand-rearing captive chicks and keeping juveniles in captivity at constant mass. Daily gain in mass was linear until 60 days of age; after 82 days the chicks lost mass prior to attaining fledging age (97 days). Daily relative growth decreased with age. Food intake increased to 70 days and thereafter decreased. Guano production increased to 50 days. Relative food intake decreased with age. Energy content of guano and assimilation efficiency showed no clear changes with age. Mass recession prior to fledging may be related to the lack of post-parental care. Hand-reared gannets grew at an optimum rate when compared with field growth rates from the literature. Juvenile birds were maintained on a diet forming 12,4% of body mass at an assimilation efficiency of 74,2%. Aviary-existence maintenance was 2,4 times standard metabolic rate. The cost of free living in an adult gannet is roughly estimated to be $4,5 \times \text{SMR}$, corresponding to a food intake of 20% of body mass.

INTRODUCTION

The Cape gannet (*Sula capensis*) feeds on pelagic shoaling fish (Rand 1959) which are of commercial importance. The South African population is considered to have decreased in numbers in recent years and to be in competition with the fishing industry for the same species of fish (Jarvis 1970). The gannet cannot normally rear more than one chick to optimum fledging mass in one annual breeding season and it is probable that food supply is a limiting factor that has influenced breeding productivity (Jarvis 1974).

The energetic requirements for growth have not been previously studied for the Cape gannet, or for any other sulid, and are known for few piscivorous birds (Cooper 1977). The mass of food needed to hand-rear a captive Cape gannet chick is given by Jarvis (1971) but metabolized energy cannot be calculated from his data since guano production was not measured. The daily food intake of adult Cape gannets has been estimated from the mass of stomach contents of birds shot at sea and birds induced to regurgitate on land (Rand 1959; Jarvis 1970).

This paper deals with the energetic requirements for growth and maintenance of the Cape gannet, based on data obtained through hand-rearing captive chicks and from captive juveniles maintained at constant mass.

METHODS

Two newly hatched Cape gannet chicks were collected at Bird Island, Lambert's Bay (32°05'S/18°07'E), on 25 January 1974. Their age was estimated to be five and six days respectively. The chicks were reared by hand until 97 days old (the mean fledging period: Jarvis 1974).

The chicks were fed exclusively on a diet of anchovy (*Engraulis capensis*) supplemented with a multi-vitamin and mineral supplement (Vi-daylin M) at five-day intervals. The mean individual mass of the fish was 12.0 g ($n = 56$). Anchovies form an important part of the diet of the Cape gannet (Rand 1959; pers. obs.) and are caught commercially.

The chicks were hand-fed to near satiation from eight to two times a day, the number of meals decreasing with age. They were not fed at night. The chicks were given whole fish at room temperature, except when very young, when they were fed pieces of slightly warmed fish. The fish was not pre-digested. The chicks could partially regulate their food intake by refusing to beg or to swallow fish.

Young chicks were kept indoors and were at first artificially brooded, using a 100 W light bulb as a heat source. Older chicks (+ 65 days) were kept out-of-doors but were protected from wind and direct insolation. Chicks were weighed daily in the early morning before being fed. Measurements of culmen, wing, tarsus and tail were taken at five-day intervals.

Samples (five fish) of the food fed to chicks were analysed for water and energy contents at five-day intervals. On the same day excreta (guano) were collected by keeping the chicks individually for 24 h in small cages fitted with wire mesh floors over aluminium foil trays of known mass. The dry mass of guano produced was obtained by drying the foil trays and their contents to a constant mass in a forced-draught oven set at 50°C. Portions of each chick's guano and the oven-dried food sample were analysed for energy content using an adiabatic bomb calorimeter.

The energetic requirement for maintenance of the Cape gannet was calculated by feeding two captive juvenile birds at a level to maintain constant mass for a period of 15 days. The birds were weighed daily and meal sizes were varied to maintain constant mass. The juveniles were the same birds reared as chicks and were 120 and 121 days old at the commencement of the experiment. The birds had completed feather growth. Feeding, weighing and guano collection regimes were as described above for chicks, with the exception that guano production was measured at three-day intervals.

RESULTS

Change in mean daily body mass of the hand-reared chicks is shown as a moving average of three (Figure 1). Increase in mass was approximately linear until 60 days of age; between 60 and 82 days increase was less rapid. Between 82 and 97 days the chicks lost mass. The mean mass at 97 days (fledging) was 93% of the maximum mass at 82 days. The mean daily gain in mass and the mean daily percentage growth, or instantaneous relative growth (Kahl 1962),

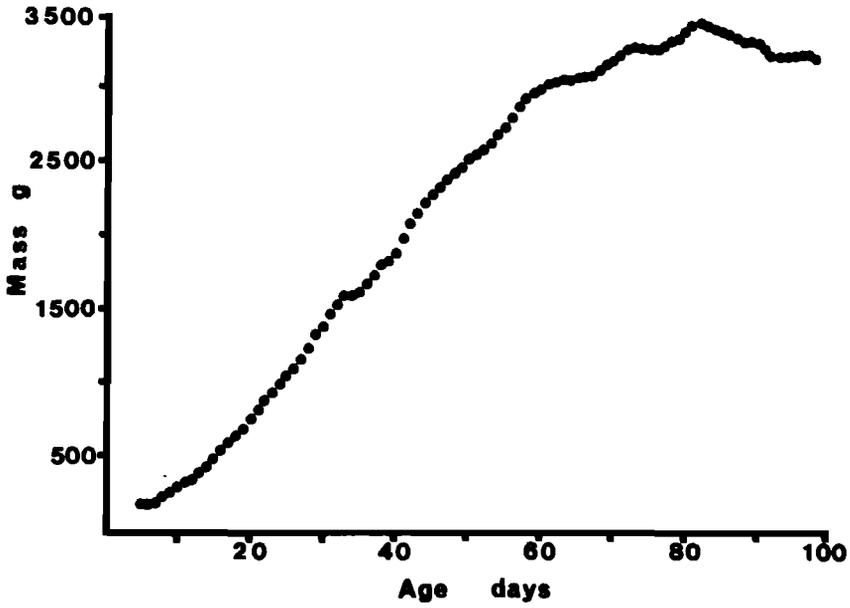


FIGURE 1.

Increase in body mass of two hand-reared Cape gannet chicks.

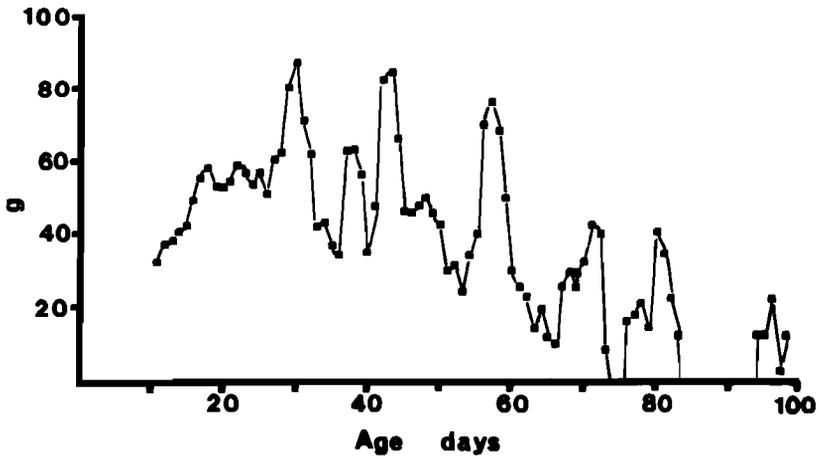


FIGURE 2.

Mean daily gain in mass of hand-reared Cape gannet chicks.

are shown in Figures 2 and 3 as moving averages of three. Mean daily gain in mass showed numerous fluctuations but was highest in the period of linear growth. Mean daily relative growth decreased rapidly with age up to 30 days and thereafter decreased more gradually, showing a number of fluctuations.

Growth of wing, culmen and tarsus is shown in Figure 4. The wing increased linearly throughout the growth period. At 'fledging' (97 days) chick B had a wing length (maximum chord) of 443 mm. This had increased to 457 mm when measured at 142 days of age. Culmen increased less rapidly after approximately 50 days of age. Chick B increased its culmen from 81 to 84 mm between 97 and 142 days of age. Tarsus length increased most rapidly up to 30 days of age. Tarsus of chick B increased from 67 to 69 mm after fledging.

Mean daily food intake in grams wet mass is shown as a moving average of three in Figure 5 and in Table 1. Food intake increased to 70 days and thereafter decreased. Several short-term fluctuations occurred. Mean relative food intake (Kahl 1962) is plotted as a moving

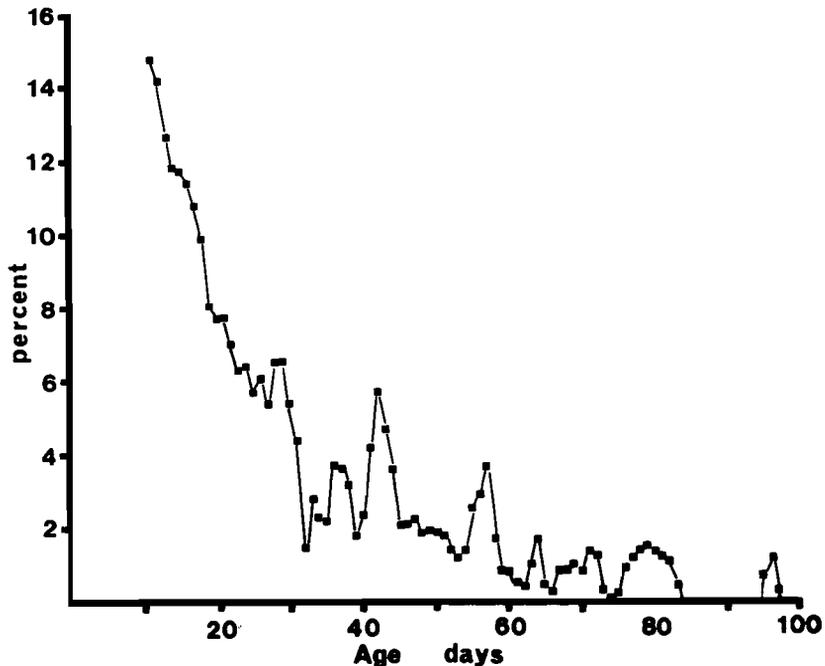


FIGURE 3.

Mean daily relative growth of hand-reared Cape gannet chicks.

$$\left(= \frac{\text{mean daily gain in mass}}{\text{mean daily mass}} \times 100 \right)$$

average of three in Figure 6 and showed a steady decrease over the whole growth period from approximately 50 to 10%.

The mean mass of dry guano produced at five-day intervals is shown in Figure 7 and Table 1. The drop in guano production at about 60 days of age is related to a drop in food intake (Table 1). Guano production increased from approximately 15 to 65 g per day. Mean food and energy intake, guano and energy excreted, metabolized energy and assimilation efficiency (Kushlan 1977a), or percentage metabolizable energy, at different ages are shown in Table 1. The energy content of guano showed no clear trends with age of chick.

Total food and energy intake, guano production, metabolized energy and mean assimilation efficiency for the whole growth period are shown in Table 2. The two hand-reared chicks were fed approximately 37,5 kg of fish each during the 88-day period of rearing and each produced approximately 4,5 kg of dry guano. Overall, mean assimilation efficiency was 76,1%.

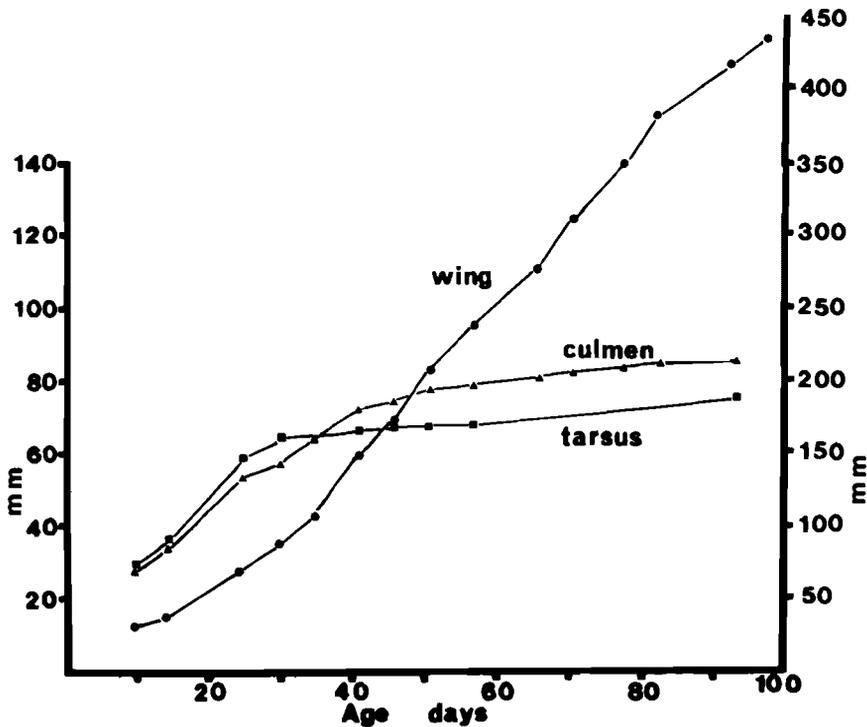


FIGURE 4.

Mean growth of culmen, tarsus and wing in hand-reared Cape gannet chicks.
Scale for culmen and tarsus on left, for wing on right.

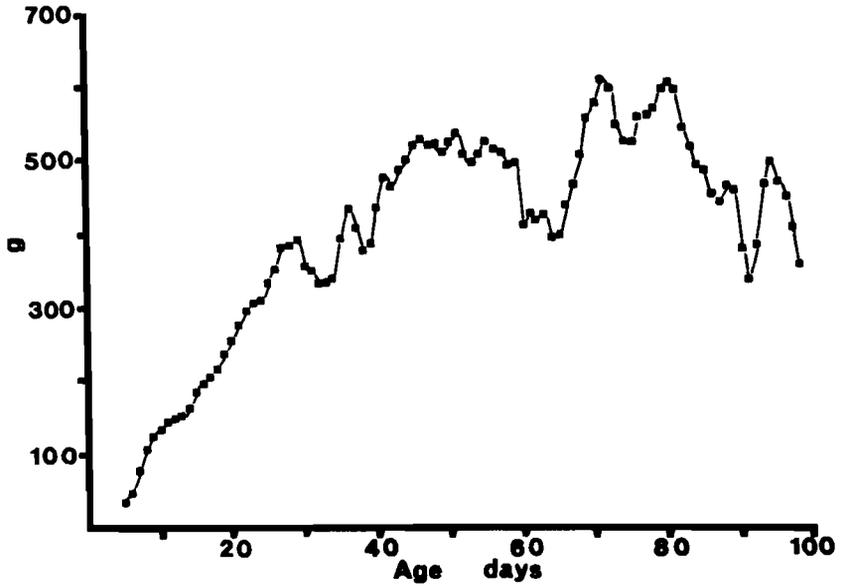


FIGURE 5.
Mean daily food intake of hand-reared Cape gannet chicks.

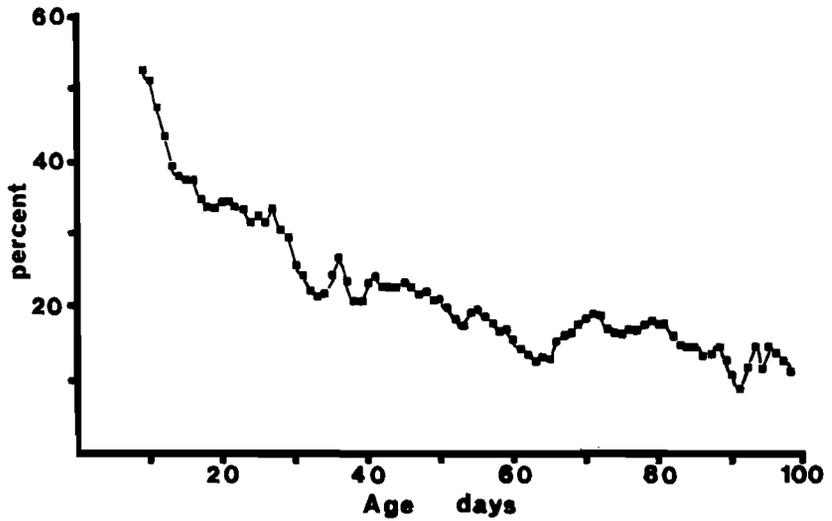


FIGURE 6.
Mean relative food intake of hand-reared Cape gannet chicks.

$$\left(= \frac{\text{mean daily food intake}}{\text{mean daily mass}} \times 100 \right)$$

TABLE 1.

Mean food and energy intake, guano and energy excreted, metabolized energy and assimilation efficiency in hand-reared Cape gannet chicks.

Age (days)	Food intake (g wet mass)	Food dry mass/wet mass ratio	Energy content of food (kJ/g dry mass)	Energy intake (kJ)	Guano excreted (g dry mass)	Energy content of guano (kJ/g dry mass)	Energy excreted (kJ)	Metabolized energy (kJ)	Assimilation efficiency (%)
9-10	123	0,26	20,3	649	16,2	12,4	200	449	69,2
14-15	199	0,27			20,3				
19-20	258	0,26	21,0	1 409	30,1	12,1	364	1 045	74,2
24-25	312	0,30			36,9				
29-30	375	0,36	22,8	3 078	46,9	14,9	699	2 379	77,3
34-35	393	0,30			46,6				
40-41	493	0,28	23,0	3 175	53,8	11,7	629	2 546	80,2
45-46	550	0,30			65,6				
50-51	512	0,27	22,0	3 041	68,5	15,2	1 041	2 000	65,8
56-57	402	0,27			43,2				
60-61	473	0,27	24,0	3 065	48,6	11,8	573	2 492	81,3
65-66	385	0,27			48,8				
70-71	587	0,27	22,4	3 550	64,4	12,3	792	2 758	77,7
77-78	502	0,31			55,5				
82-83	478	0,28	23,0	3 078	64,2	12,6	809	2 269	73,7
87-88	454	0,29			67,2				
92-93	502	0,28	22,1	3 106	60,3	12,9	778	2 328	75,0
98*	450	0,29	22,9	2 988	68,7	12,1	831	2,157	72,3

* Based on one bird only.

TABLE 2.

Total and daily average food and energy intake, guano and energy excreted, metabolized energy and mean assimilation efficiency in hand-reared Cape gannet chicks over 88 days of growth.

	Food intake (g wet mass)	Energy intake (kJ)	Guano excreted (g dry mass)	Energy excreted (kJ)	Metabolized energy (kJ)	Assimilation efficiency (%)
Total	37 498	243 587	4 544	58 163	185 424	—
Daily average	426	2 768	52	661	2 107	76,1

TABLE 3.

Mass, food and energy intake, guano and energy excreted, metabolized energy and assimilation efficiency of two captive juvenile Cape gannets fed at maintenance level for fifteen days.

	Mass		Food intake wet mass (g/day)		Estimated energy intake (kJ/day)		Guano excreted dry mass (g/day)		Energy excreted (kJ/day)		Metabolized energy (kJ/day)		Assimilation efficiency (%)	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Mean	2 806	2 704	339	340	2 229	2 243	46,8	44,8	584	572	1 645	1 671	73,8	74,5
Standard deviation	16	17	7	7	50	46	1,8	2,0	23	95	—	—	—	—
Range	2 780 to 2 830	2 680 to 2 730	324 to 350	327 to 352	2 138 to 2 310	2 158 to 2 323	45,0 to 49,1	42,9 to 47,4	554 to 619	510 to 733	—	—	—	—
No. observations	15	15	14	14	14	14	5	5	5	5	—	—	—	—

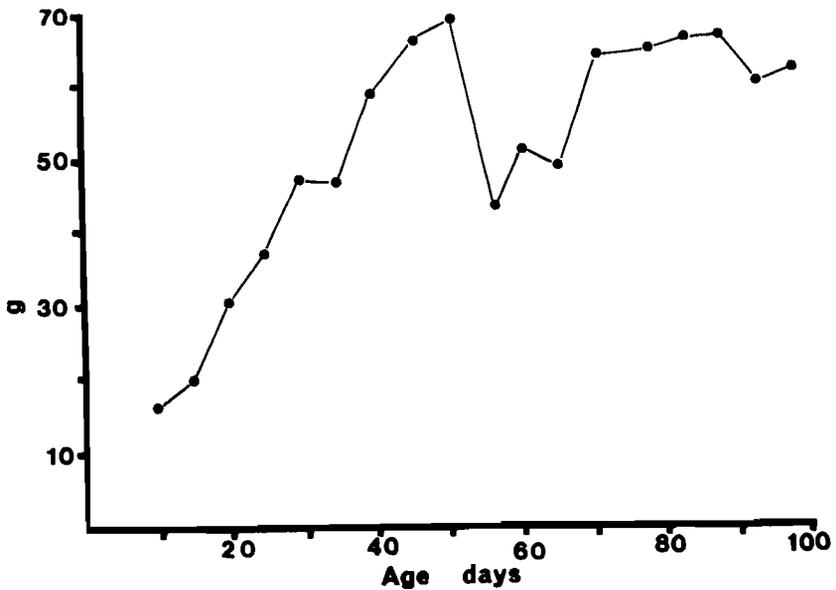


FIGURE 7.

Mean guano production (g dry mass) of hand-reared Cape gannet chicks, measured over five-day periods.

Data on maintenance requirements in captivity are given in Table 3. The juveniles consumed a mean of 340 g of fish per day (12.4% of body mass) and produced approximately 46 g of dry guano per day. Gross energy intake was 2236 kJ/day, of which 1658 kJ/day was metabolized. Mean assimilation efficiency was therefore 74.2%.

DISCUSSION

Cape gannet chicks in the wild grow in a similar manner to hand-reared chicks, with a decrease in mass occurring after approximately 80 days. The mean fledging mass of 451 chicks was 2920 ± 335 g (Jarvis 1974). The two hand-reared chicks weighed 3270 g and 3210 g when 97 days old (mean fledging age). It is evident that the hand-reared gannet chicks grew at an optimum rate when compared with naturally reared birds. Jarvis (1971) hand-reared a Cape gannet chick until 97 days old. This bird also lost mass after 80 days although it was fed to satiation. Decrease in mass was related to a decrease in food intake, a pattern similar to that for the two chicks reported here (Figure 5, Table 1). Decrease in food intake is related to an unwillingness in the chick to eat, rather than to a decrease in the parental feeding rate, a pattern occurring in several hand-reared piscivorous species (Harris 1976; Schreiber 1976; Cooper 1977; Greichus *et al.* 1977). Decrease in body mass prior to fledging is recorded for the northern gannet (*S. bassana*) by Nelson (1964). Decrease in mass prior to fledging is common in oceanic species of birds, which tend to be aerial foragers and have well-developed flight capabilities at the time of fledging (Ricklefs 1968). It may be a disadvantage for a fledgling to be too heavy while it is learning to fend for itself (Harris 1976). It is noteworthy that there is no post-fledging parental care in Cape gannets (Jarvis 1974). Cormorants, which have extensive post-fledging parental care (Snow 1960; pers. obs.), apparently show little or no mass recession prior to fledging, although loss in mass may occur after fledging (Snow 1960; Dunn 1975a; Berry 1976; pers. obs.). The presence of post-fledging care obviates the need for the fledgling to be at the optimum mass to fend for itself.

Increase in assimilation efficiency with age has been observed in a number of species and appears to be related to a decrease in the energy content of the guano (Cooper 1977). However, although assimilation efficiency initially increased in the Cape gannet, energy content of guano did not decrease (Table 1) as it did for the jackass penguin, *Spheniscus demersus* (Cooper 1977). This accentuated the decrease in metabolized energy after 80 days of age and must have contributed to the mass recession prior to reaching fledging age. Although jackass penguins decreased their food intake they did not show a mass recession, neither did double-crested cormorants (*Phalacrocorax auritus*) studied by Dunn (1975a, b). Both these species showed decreases in the energy content of guano with age and increases in digestive efficiency throughout the growth period, in contrast to the Cape gannet. Mass recession may therefore be related to a relatively stable energy content of guano as well as to a voluntarily reduced food intake.

The hand-reared Cape gannets consumed a total of 37.5 kg of fish during the 88-day period of rearing, a mean of 426 g per day. A Cape gannet chick reared by Jarvis (1971) for

the same period consumed only 29,5 kg (322 g per day). The latter chick attained a mass of approximately 2 750 g at 97 days, substantially less than that of the chicks reported here and lower than the mean fledging mass in the wild (Jarvis 1974). Hand-reared jackass penguins consumed more food during the growth period than those reared naturally and attained a higher fledging mass (Cooper 1977). However, captive white ibis (*Eudocimus albus*) did not grow as fast as wild birds and were lighter at fledging (Kushlan 1977a).

Jarvis (1974), in artificial twinning experiments, has shown that the Cape gannet cannot normally rear more than one chick and normally lays one egg. Twins had lower fledging masses and suffered greater post-fledging mortality. Jarvis (1974) relates this to the available food supply. The data presented here help to confirm this view: growth rate and fledging mass are related to food intake. Adult gannets at the breeding colony with undigested stomach contents contained 350 g of fish (Jarvis 1970). It is apparent that two parents, supplying up to 700 g to two chicks, would not be able to rear them at the optimum rate shown by hand-rearing, but could rear one chick at that rate. This supports the argument of Lack (1954) that clutch size is related to the maximum number of chicks that can survive, since artificially twinned chicks had a lower survival rate than normal (Jarvis 1974).

Juvenile Cape gannets were maintained at a constant mass when fed a mean of 340 g of fish per day, or 12,4% of body mass, with a mean assimilation efficiency of 74,2%. Uramoto (1961) maintained a carrion crow (*Corvus corone*) in captivity on a diet of fish and obtained an assimilation efficiency of 81,2%. Kahl (1964) maintained wood storks (*Mycteria americana*) on fish with an intake of 16,2% of body mass at 79% assimilation efficiency. Captive white ibis had an assimilation efficiency of 79,7% (Kushlan 1977b). Common mergansers (*Mergus merganser*) have been maintained in captivity on a daily food intake of live fish varying from 18 to 38% of body mass (White 1957; Latta & Sharkey 1966). Turning to carnivores in general, Siegfried (1969) maintained cattle egrets (*Ardeola ibis*) on a diet forming 17,8% of body mass and an assimilation efficiency of 95%. In most aviary-existence measurements of metabolic rates (e.g. Uramoto 1961; Kahl 1964; Siegfried 1969; Kushlan 1977b) the captive birds were able to exercise and to take short flights. In the case of the Cape gannets reported here, the birds' activities were restricted by the size of their cages to standing and preening.

The calculated standard metabolic rate (SMR) of a Cape gannet weighing 2,75 kg is 681 kJ/day (Lasiewski & Dawson 1967). The captive juvenile gannets metabolized energy at a mean rate of 1 658 kJ/day (Table 3) or $2,4 \times \text{SMR}$, Kahl (1964) obtained a similar figure of $2,7 \times \text{SMR}$ for wood storks and Siegfried (1969) $3 \times \text{SMR}$ for cattle egrets. Hulscher (1974) obtained a figure of $4,3 \times \text{SMR}$ for captive oystercatchers (*Haematopus ostralegus*). A comparable figure for white ibis was only $1,6 \times \text{SMR}$ (Kushlan 1977b). The low figure obtained for Cape gannets can be attributed to the very low level of exercise when compared with most of the other studies.

There are few estimations of the increased energy cost of free living over aviary-existence of piscivores; Hulscher (1974) estimated a 1,4 times increase for oystercatchers, while Kahl (1964) estimated a 1,5 times increase. These are comparable to $6 \times \text{SMR}$ and $4 \times \text{SMR}$ respectively. However, Kushlan (1977b) estimated the free existence energy cost of white ibis to be only $1,9 \times \text{SMR}$.

Cape gannets are aerial foragers that can fly long distances in search of food (Rand 1959) and therefore may be expected to have relatively high energy demands when compared with wood storks, cattle egrets, oystercatchers and white ibis which mainly forage while walking (Kahl 1964; Siegfried 1971; Hulscher 1974; Kushlan 1977b). The energy cost of flapping flight ranges from 9–14 \times SMR (Raveling & LeFebvre 1967; Tucker 1972; King 1974). Cape gannets forage only during the day (Rand 1959) and tend to leave the breeding colony an hour after sunrise and return approximately one to two hours before sunset, an interval of approximately 12 hours during the breeding season (pers. obs.). If on-land activity (incubation, feeding the chick, roosting) is taken to cost 3 \times SMR (King 1974) and flying 12 \times SMR, then the overall energy cost of free existence would be 8 \times SMR, or 3.3 times the measured aviary-existence metabolic rate. This equates to a theoretical food intake of 1 130 g. Rand (1959) estimated average daily food intake to be 350 g, and a similar figure was estimated by Jarvis (1970). Cape gannets fly in small groups and take advantage of the updraft from swells. They fly by alternately flapping and gliding and usually remain close to the water surface (pers. obs.). Thus they are apparently conserving energy by a number of methods: slipstreaming (Lissamen & Schollenberger 1970), gliding (Baudinette & Schmidt-Nielsen 1974) and ground effect (Withers & Timko 1977). Combined, these factors will reduce the cost of flying by an unknown, but probably large amount. Gliding flight in the herring gull (*Larus argentatus*) had an energy cost of approximately two times resting metabolism (Baudinette & Schmidt-Nielsen 1974) while flapping flight in the laughing gull (*L. atricilla*) was six to eight times resting metabolism (Tucker 1972). In the Cape gannet the energy cost of gliding would therefore be approximately 5 \times SMR. Cape gannets also roost at sea for an unknown period of time during the day. Taking these factors into account the daily energy cost of a free-living Cape gannet is certain to be less than 8 \times SMR. Purple martins (*Progne subis*) use gliding and soaring extensively at a mean energy cost of flight of 5.7 \times SMR (Utter & LeFebvre 1970).

If a figure of 4.5 \times SMR (twelve hours at 6 \times SMR, twelve hours at 3 \times SMR) is taken as the cost of free-living existence, then a food intake of 638 g per day or approximately 20% of body mass is required. This figure is similar to that estimated for the daily food intake of the partially piscivorous white ibis: 21% of body mass (Kushlan 1977b) as well as the wood stork (21%) (Kahl 1964). A captive common murre (*Uria aalge*) that was allowed to catch live fish in an aquarium maintained its mass (650 g) on an intake of 28% of body mass per day (Sanford & Harris 1967). Since a surplus of fish was supplied the situation approaches free-living conditions. The larger Cape gannet would require relatively less food.

Clearly, a study is needed of the time-activity budget of the Cape gannet, coupled with measurements of metabolic rates at different activity levels, before a more accurate estimate can be made of the energy cost of free living.

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