foraging a close relationship is needed between neighbouring birds. Play may therefore be important in maintaining this contact and in strengthening bonds between neighbouring birds so that conflict over food (the most critical resource and one which would be expected to strain any relationship) can be amicably resolved.

The amount of time spent inactive by Bearded Vultures increased in August and September despite the fact that the amount of time being spent on foraging by off-duty birds was increasing. This can be explained by the fact that on-duty birds were more visible, standing at the entrances of nesting potholes shading nestlings (rather than sitting tight on eggs) and progressively moving out of the nest and perching nearby on the cliff. As the nestling grew older so the on-duty bird left the nesting area for longer and longer periods to forage, and this is reflected in the decrease in inactivity in October and November. By mid-December young birds were making their first flights, and they perched inactive for long periods between one short flight and the next. This situation lasted for a few months until the young birds were foraging over a fairly large range (see Chapter 7).

8.4.2 Energetics

The energy requirements of Bearded Vultures given in this study were calculated from time-activity budgets. Craighead & Craighead (1956) have shown that species with body weight ranging from 100-200 g consume about 22% of their own weight in food per day, while species of 200-800 g consume about 13% of their own weight. Kendeigh *et al.* (1977) give equations based on mass and temperature for calculating the daily energy budget of birds:

$$DEB = 1{,}079\ W^{0{,}67} \quad \text{for } 30^{\circ}C$$

$$DEB = 8{,}059\ W^{0{,}50} \quad \text{for } 0^{\circ}C$$

There is no temperature station in the subalpine or alpine belts of the Drakensberg mountains. Extrapolation to 3000 m above sea level from the Cathedral Peak Forestry weather station at 1860 m (where an average decrease of 0,5° C is experienced with each increase of 100 m in altitude) gives a mean daily temperature of about 7,5°C. Using a mean body weight (W) of 5490 g, a DEB of 2298 kJ is obtained for non-breeding Bearded Vultures. This is within 5% of the value obtained in Table 8.7 using coefficients based on the time-activity budget, and while it lends support to these results, it must be borne in mind that the equations of Kendeigh *et al.* are based on very few measured DEB values.

Seasonal changes in the estimated daily energy expenditure are more pertinent when compared to the daily food requirements and the food availability for a breeding pair of Bearded Vultures.

During this study it was not possible to determine directly the daily food requirements of the Bearded Vulture. Hiraldo *et al.* (1979) give figures for the slightly heavier European Bearded Vultures of between 400-500 g per day, and state that "during the peak demand period, a pair raising a chick must obtain almost 1500 g per day".

The energy requirements of adult Whitebacked Vultures (with an average weight of 5,4 kg, which is only slightly smaller than the southern African Bearded Vulture) was between 1674-2093 kJ/day (Houston 1976). This represents between about 320-400 g of meat. Bearded Vultures probably expend a little more energy per day than do Whitebacked Vultures as they are slightly larger, spend more time in flight and live in a colder environment.

The daily energy expenditure of a pair of Bearded Vultures as calculated from the daily activity-time budget per month is shown in Figure 8.11. An estimate of the daily food requirement for each month of the year per breeding pair is calculated from these figures in the following way.

The Bearded Vulture's diet was estimated to consist of bone (with its associated marrow), muscle and skin in a ratio of 14:5:1, based on this study (see chapter 6) as well as that of Hiraldo et al. (1979), who found that 80% of all food brought to nests in Spain was bone and that 90% of stomach contents examined were bone. Examination of 50 Ethiopian birds showed that all had bones in their stomachs (Cramp & Simmons 1980). It should be remembered, however, that soft material is likely to be digested more quickly and would not be equally represented. As bones obtained by Bearded Vultures usually have some muscle and skin attached, the above ratio would seem to be realistic.

Little information is available on the energy content

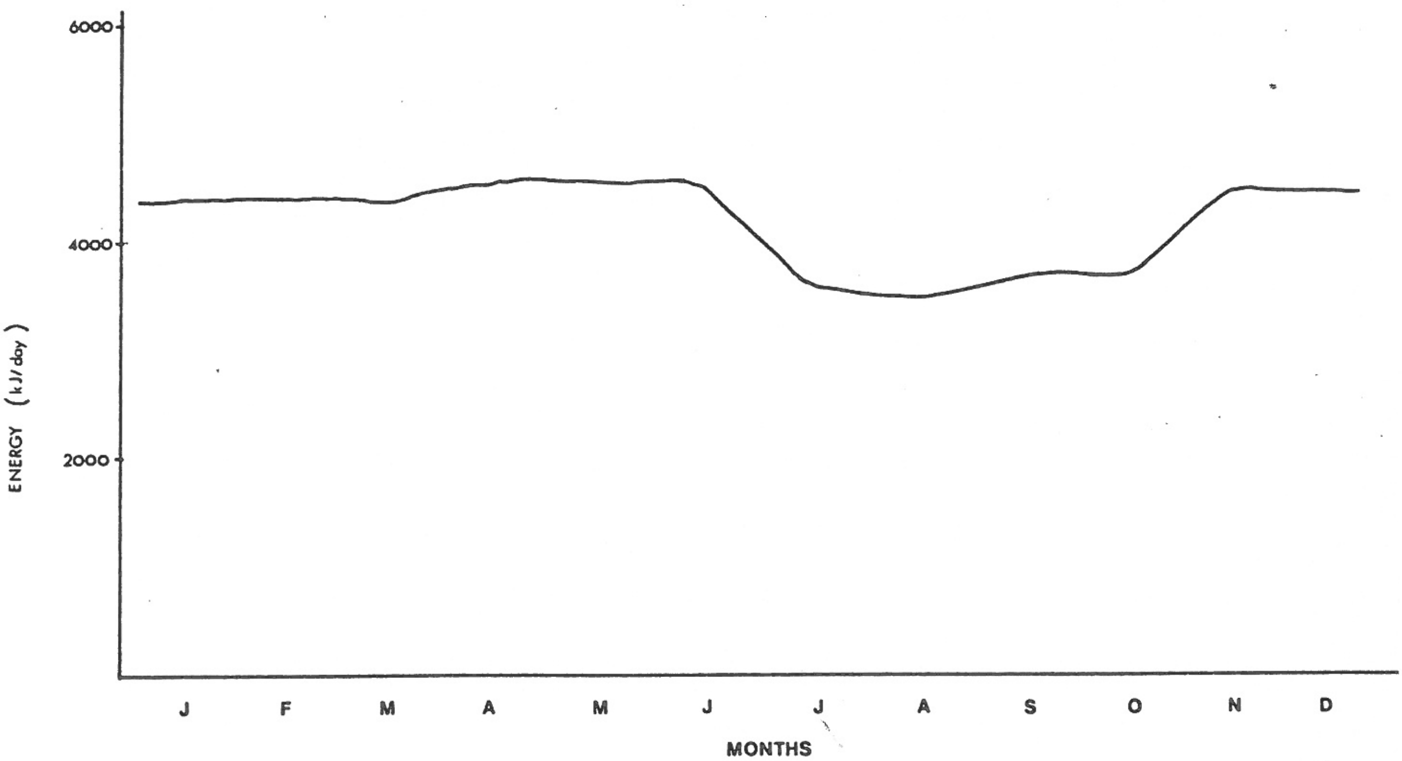

FIGURE 8.11. Average daily energy expended by a pair of breeding Bearded Vultures per month, calculated from the daily activity-time budget as explained in the text.

of prey components. Variations occur from species to species as well as between different age classes within a species. Values for the energy content of meat are 5,2; 6,1 and 7,0 kJ/g wet weight (Houston 1976; Komen 1984; C.W. Sapsford pers. comm. respectively), while for skin and fur of laboratory mice the figure is about 12,0 kJ/g (C.W. Sapsford pers. comm.). The cleaned but not de-oiled skeleton of a laboratory mouse contained about 16,5 kJ/g dry mass (= about 8,4 kJ/g wet weight), and ash free (i.e. an indication of the energy contained in the marrow) gave about 28,5 kJ/g. As bones get larger so the amount of energy per gram decreases e.g. Vervet Monkey *Cercopithecus pygerythrus* longbones contain about 8,0 kJ/g and ribs about 5,9 kJ/g while the longbones and ribs of the Red Duiker *Cephalophus natalensis* contain about 2,5 and 2,9 kJ/g respectively (C.W. Sapsford pers. comm.).

Bearded Vultures generally swallow smaller bones whole, while larger ones are dropped onto rocky sites to crack them open. While it is advantageous to swallow small bones whole thereby saving time on the removal of marrow and adhering soft material, there is an upper limit to the size of bones that a Bearded Vulture can swallow. The energy value of small bones, which contain a relatively low inorganic component, is remarkably high, higher in fact than red meat and compares favourably to liver which contains about 8,8 kJ/g (C.W. Sapsford pers. comm.). While larger bones may also be eaten after being broken into smaller pieces, the number of longbone fragments found at ossuaries attests to the fact that once the marrow has been consumed (adhering muscle and skin are usually removed before dropping), the bone fragments are often discarded. Being oily, these bone fragments contain some energy, but the high inorganic content makes them less attractive as an energy source, eaten only when hungry or by young birds. Bearded Vultures scoop out marrow and do not always eat the rest of the bone. They are thus using a very high-energy source of food. An average figure of 6,7 kJ/g wet weight was therefore chosen to represent the energy content of the bone and marrow component of the Bearded Vulture's diet. The average figures adopted for the energy contents of meat and skin were 5,8 and 11,7 kJ/g respectively. From 100 g of food, therefore, a Bearded Vulture would obtain on average about 670 kJ.

The assimilation efficiency of diurnal raptors and owls is generally given in the range of 70-80% (Gessaman 1973; Mosher & Matray 1974; Sapsford & Mendelsohn 1984), although for captive nestling Cape Vultures, Komen (1984) gives a somewhat higher figure of 86,5%. Because of the high inorganic content of the Bearded Vulture's diet, an assimilation figure at the bottom of the accepted range, i.e. 70% was adopted. Thus, for every 100 g of food eaten the actual amount of energy obtained is in the order of 473 kJ. Using these figures, the basic daily food requirement to provide for the average energy expenditure per month for a breeding Bearded Vulture was determined; during the non-breeding season this was calculated to be 464 g of food and during the breeding season was about 405 g (ranging between about 365 g in the incubation stage to 475 g during the stage when the nestling was left unattended on the nest). These figures are only slightly lower than those given by Hiraldo et al. (1979) for the larger European Bearded Vulture, and similar to the daily food requirement of the similar sized Whitebacked Vulture (Houston 1976).

To determine the overall food requirements of a pair of breeding Bearded Vultures two further aspects have to be taken into account, namely the energy required to produce a clutch of eggs and the amount of food required to feed the nestling until it is independent.

The cost of egg-laying is small, each egg weighing about 3% of the weight of the adult bird. A two-egg clutch represents about 2135 kJ (649 kJ/100g, extrapolated from figures available for domestic chickens as given by Paul & Southgate (1978) and Watt & Merrill (1975)), and at an assimilation efficiency of 70%, requires about 450 g of food.

The food intake of nestling Bearded Vultures from hatching until independence has been extrapolated from figures obtained for the food intake of nestling Whitebacked Vultures (Houston 1976). This extrapolation can be justified on the grounds that the species are of comparable weights, and the lengths of the nestling periods are very similar, i.e. 120-130 days (Maclean 1985). The figures for daily food intake have been increased by about 10%, however, to account for the large bone component in the Bearded Vulture's diet with its high inorganic content and lower assimilation efficiency compared to the diet of griffon vultures which consists almost entirely of muscle and viscera, as well as the lower ambient temperatures encountered by Bearded Vultures as compared to Whitebacked Vultures. For the first two months after leaving the nest the young vulture obtains all its food from its parents. During the first month it spends most of the day perched inactive, thereafter becoming more and more active. For the purpose of determining the food requirements of a pair of adults and the additional food they need to feed their offspring it was assumed that after the second month out of the nest (i.e. March) they provide decreasing amounts of food to the young bird, which begins to find its own food in increasing amounts, and at the time of independence (i.e. June) parents are providing only 10% of its requirements.

When all these figures of the food requirements are added together, an indication of the daily food requirements of a breeding pair of Bearded Vultures is obtained for each month of the year (Figure 8.12). It is apparent that two periods of particularly high food demand occur, (i) from September to November when the nestling is growing rapidly and the pair need to obtain about 1335 g of food per day during the peak demand period, and (ii) from February to April when the dependent young bird has become active and before it is capable of providing a significant contribution towards its own food requirements. During this period the pair need to obtain about 1270 g of food per day.