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# Sex differences in energy expenditure in non-human primates

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Female mammals bear the energetic costs of gestation and lactation. Therefore, it is often assumed that the overall energetic costs are greater for females than they are for males. However, the energetic costs to males of intrasex competition may also be considerable, particularly if males maintain a much larger body size than females. Using data from 19 non-human primates, this paper examines the relationship between male and female energetic costs both in the short term (daily energy expenditure) and the long term (the energetic cost of producing a single offspring). It is shown that the major determinant of sex differences in energetic costs is body size dimorphism. In the long term, the energetic costs are often greater for females, but, when male body size exceeds female body size by 60% or more, male energetic costs are greater than those for females. That is, in highly sexually dimorphic species the energetic costs of gestation and lactation for the females are matched by the energetic costs to the males of maintaining a large body size.

**Keywords:** energy expenditure; sexual dimorphism; activity budgets; reproductive costs

## 1. INTRODUCTION

Adult primates, like all other mammals, require energy for daily body maintenance, survival and reproduction. Several primate studies have attempted to measure and compare the energetic costs within a species (Coelho 1974, 1986; Coelho *et al.* 1979; Altmann & Samuels 1992; Dasilva 1992; Leonard & Robertson 1994, 1997) but few have compared the energetic costs across primates (but see Coelho 1974; Coelho *et al.* 1979; Leonard & Robertson 1997) and no comparative studies have examined sex differences in energetic needs. Since female mammals must meet the energetic costs of gestation and lactation, the energy requirements of reproduction are often assumed to be greatest for females. For instance, Coelho (1986) stated that 'It is a physiological fact that the actual costs of reproduction (pregnancy and lactation) are borne only by the female primate; there is nothing physiologically comparable in the male' (p.153). Theories regarding a whole range of important issues, such as grouping patterns, feeding strategies and mating and parenting strategies, have stressed the importance of resource acquisition for females (e.g. Trivers 1972; Emlen & Oring 1977; Greenwood 1980; Wrangham 1980; Dunbar 1988). Since male reproductive success is viewed as being primarily dependent upon their ability to acquire females rather than resources, the energetic costs of male mating effort and the constraints this may impose on male behaviour are often overlooked.

Adult female energetic demands arise primarily from gestation, lactation and offspring care. Lactation is particularly energetically costly and females lose weight

during lactation in most wild populations (Altmann 1980; Bercovitch 1987; McFarland 1997). Hiraiwa-Hasegawa (1997) observed that, in many primate species, adult females feed for longer than males and prefer higher-calorie foods and suggested that this is due to the energetic demands of pregnancy and lactation. However, while the energetic costs incurred by males are likely to arise from rather different activities compared with females, they may be none the less substantial. Males incur energetic costs due to the demands of sperm production (Kenagy & Trombulak 1986), courtship, mate guarding and male–male competition. Male aggression, chasing and mate guarding are energetically costly activities and have been shown to result in weight loss in golden lion tamarins (Dietz *et al.* 1993). Mate guarding has been found to reduce male feeding efficiency in savannah baboons (Alberts *et al.* 1996) and Packer (1977) described how consorting male olive baboons often appear exhausted due to lack of food and sleep. In many species, male–male competition is manifest in the much larger size of the males compared with females (Leutenegger & Kelly 1977; Gaulin & Sailer 1984), which means that for males the costs of body maintenance will be relatively high. Thus, in sexually dimorphic species such as the gorilla, male energetic costs will be high, maybe even as high as female energetic costs. On the other hand, in species in which male and female body size are similar, such as the gibbon, the energetic costs of body maintenance will be similar for each sex. Therefore, the overall energetic costs are likely to be greater for females who must meet the energetic costs of pregnancy and lactation in addition to the costs of body maintenance. This reasoning suggests that the relationship between male and female energetic costs will vary with the degree of sexual dimorphism in body size.

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In this paper, sex differences in energy expenditure are examined using data from 19 non-human haplorhine primates. Sex differences in energy expenditure are assessed with respect to (i) total daily energy expenditure (DEE), and (ii) the energetic costs of producing and rearing offspring. These data are used to assess whether female energetic costs exceed male energetic costs and to what extent sexual dimorphism in body size determines sex differences in energy expenditure.

## 2. MATERIAL AND METHODS

In order to assess both short-term (DEE) and long-term (the energetic cost of reproduction) energy demands, the following data are required: male and female activity budgets, male and female body mass, day range, gestation length, weaning age and interbirth interval. The data, data sources and details of the data collection procedure can be found in an electronic appendix on the Royal Society Web site.

A complete data set was available for 19 haplorhine primates, representing a good cross-section of genera: seven Cebidae, eight Cercopithecidae, one Hylobatidae and three Hominidae. The data were restricted to haplorhine primates in order to create a data set for which the energetic costs of pregnancy, lactation and infant growth are likely to be broadly comparable. Strepsirhine data were not used, primarily because of differences in their reproductive physiology and behaviour in comparison with haplorhines. For instance, the milk composition of strepsirhines is generally more concentrated than that of haplorhine primates (Tilden & Oftedal 1997) and infant post-natal growth rates are high relative to the mother's body mass (Ross 1989). Behavioural variation within the strepsirhine group may also have an influence on female energetic costs; in particular species which do not carry their young may have lower costs than those which do carry them.

### (a) Daily energy expenditure

DEE is the sum of the energetic costs of all activities performed over the course of a single day. These costs are determined by two factors: the basal metabolic rate (BMR) and activity patterns. Kurland & Pearson (1986) showed that the Kleiber (1932, 1961) equation is appropriate for estimating the BMR ( $\text{kcal h}^{-1}$ ) from body mass  $W$  (kg) for haplorhine primates:

$$\text{BMR} = 70W^{0.75}. \quad (1)$$

The activity costs can be estimated from time-budget data using Coelho's (1974, 1986) energetic model:

$$\text{DEE} = \sum_{i=1}^n A_i, \quad (2)$$

where DEE is the daily energy expenditure ( $\text{kcal } 24 \text{ h}^{-1}$ ),  $A_i$  is the energetic cost (kcal) of an individual activity ' $i$ ' and

$$A_i = (D_i \times \text{BMR} \times T_i)100, \quad (3)$$

where  $T_i$  is the percentage of the day spent performing activity  $i$  and  $D_i$  is the energy constant for each activity, where  $D_{\text{sleep}} = 1.00$ ,  $D_{\text{rest}} = 1.25$ ,  $D_{\text{feed}} = 1.38$  and  $D_{\text{social}} = 2.35$  (Leonard & Robertson 1997).

The energy constants quoted above for sleeping, resting, feeding and socializing are estimates of the energetic costs of these activities and are based upon human studies. Very little is

known at present about the energetic costs of these activities in non-human primates, although it is unlikely that they will be the same as in humans. For instance, colobines have a folivorous diet and have specialized guts which may consume more energy during feeding and resting (since they will also be digesting during rest periods). Using human values means that the absolute energetic costs estimated by these equations may be slightly inaccurate. This is not a serious problem because the purpose of these analyses is to compare male and female energetic costs. Thus, even if we have underestimated the energetic costs of feeding for folivorous primates (for example) this will apply equally to males and females and, thus, the relationship between male and female energetic costs will be the same.

Because the energetic costs of movement depend upon speed and distance travelled, there is no energy constant for locomotion. Taylor *et al.* (1970) used a combination of body mass, time spent moving and day range to calculate the energetic cost of locomotion  $A_{\text{loc}}$  (kcal). This equation was used here to calculate  $A_{\text{loc}}$ , which was then incorporated into equation (2)

$$A_{\text{loc}} = (0.041 \times W^{0.60})R_D + (0.029 \times W^{0.75})T_{\text{loc}}, \quad (4)$$

where  $W$  is body mass (g),  $R_D$  is the day range (km) and  $T_{\text{loc}}$  is the time spent moving (h).

Surprisingly, the energetic costs of locomotion are not particularly sensitive to differences in locomotor systems. Taylor (1980) showed that the energetic costs of running are very similar for a wide variety of animals, including lizards, insectivores, monotremes, marsupials and specialized cursorial mammals such as gazelles and cheetahs (see also Heglund 1980; Coelho 1986). Thus, equation (4) should provide reasonable and comparable estimates of the energetic costs of locomotion for most of the taxa used in these analyses. However, brachiation is more energetically expensive than quadrupedal locomotion for larger bodied animals such as gibbons (Parsons & Taylor 1977) and, thus, the energetic costs may be underestimated for large, arboreal primates. The costs of infant carrying are not included in equation (4), since this would require very specific data on infant weight and carrying times which are not available for most species.

The energetic cost of each individual activity (feeding, resting, moving, sleeping and socializing) was calculated using equations (3) and (4). Summing the energetic costs of each activity (equation (2)) provided an estimate of the total DEE. The data (including that discussed in §2(b)) were analysed using SPSS for Windows. Pearson's correlation was used to assess the strength of the relationship between male and female energetic costs and all tests were two-tailed.

### (b) The energetic cost of reproduction

The energetic cost of reproduction is defined as the sum of the energetic costs of every activity that contributes to the production of a single, surviving offspring (Key 1998). It includes the energy expended on intrasexual competition for mates and parental care in addition to the DEE. It is difficult to assess the energetic costs of intrasexual competition directly. Here it is assumed that, in species in which male–male competition is high, males will be larger (Trivers 1972). Therefore, body size will reflect the energetic costs of intrasexual competition. Other costs associated with male–male competition, such as risk of injury, are not easily translated into energetic terms and cannot be incorporated into this type of analysis. The costs of parental care will differ for each sex and will usually be considerably greater for females. In most

instances the costs of parental care are negligible for males, with the possible exception of the smaller monogamous cebids for which the energetic costs of male care (i.e. infant carrying and protection) may be underestimated. Gestation length and lactation length were used to estimate the energetic costs of parental care for females.

The female interbirth interval was used to measure the length of a reproductive event, since this reflects the mean amount of time a female invests in each offspring (all species used in this analysis typically produce only one infant per litter). The mean energy expended during the time it takes a female to produce an offspring was calculated for males. This method has the advantage of comparing male and female energetic costs over an equivalent time-period. Of course, an individual male could sire one, several or no offspring during this time. However, assuming a 1:1 sex ratio, the mean time that males take to produce an offspring will be the same as the mean time that females take to produce an offspring.

The energy expenditure per reproductive event was calculated for males and females by modifying the equations for DEE. Across mammals, gestation is estimated to increase DEE by between 20 and 30% (Gittleman & Thompson 1988). Here an average value of 25% was used, as suggested by Portman (1970). The energetic costs of lactation are far more variable, ranging between 30 and 149% of DEE (Gittleman & Thompson 1988) for mammals. Portman (1970) suggested that lactation costs are *ca.* 50% for primates, an observation supported by Muruthi *et al.*'s (1991) finding that the energy intake of pregnant or lactating female baboons was, on average, 57% higher than that of cycling females. In most cases the milk of haplorhine primates is dilute compared with other mammals and, thus, the energetic costs of lactation are relatively low (Oftedal 1984). However, this is not uniformly the case: in callitrichids the energetic costs can be *ca.* 100% greater during lactation than at other times (e.g. *Saguinus oedipus* (Kirkwood & Underwood 1984) and *Callithrix jacchus* (Nievergelt & Martin 1999)). In this respect, the callitrichids appear to be more similar to strepsirhines, which generally have energy-rich milk (Tilden & Oftedal 1997). Since the sample used here includes neither callitrichids or strepsirhines, an energetic cost of lactation of 50% was used.

The energetic cost per reproductive event for females was calculated using the following:

$$E_F = DEE((T_{\text{gest}} \times 1.25) + (T_{\text{lact}} \times 1.5) + (T_{\text{ibi}} - T_{\text{gest}} - T_{\text{lact}})), \quad (5)$$

where  $E_F$  is the female energy expenditure per reproductive event (kcal),  $T_{\text{gest}}$  is the length of gestation (days),  $T_{\text{lact}}$  is the length of lactation (days) and  $T_{\text{ibi}}$  is the interbirth interval (days).

The gestation and lactation times were multiplied by 1.25 and 1.50, respectively, to account for the increased energy costs associated with these activities. The term  $(T_{\text{ibi}} - T_{\text{gest}} - T_{\text{lact}})$  reflects the amount of time spent between births in which females are neither pregnant or lactating. In some species the gestation and lactation phases overlap; however, this equation remains appropriate if it is assumed that during this time the costs of gestation and lactation are cumulative.

The male energy expenditure per female reproductive event was calculated using the following equation:

$$E_M = DEE \times T_{\text{ibi}}, \quad (6)$$

where  $E_M$  is the male energy expenditure per female reproductive event (kcal).

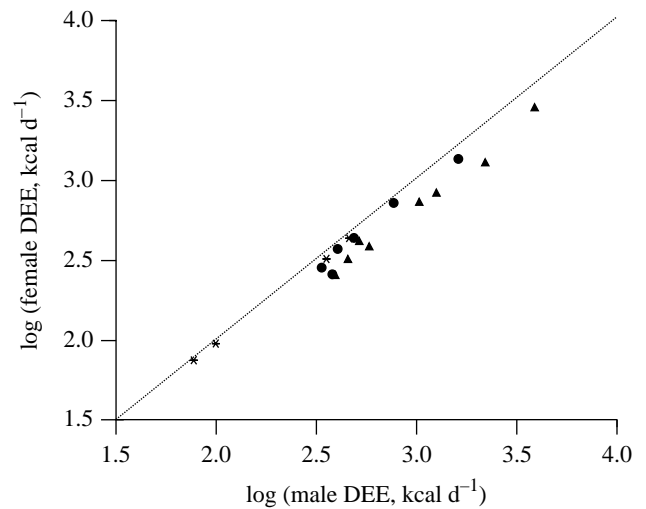


Figure 1. Comparison of male and female DEE. Markers denote the level of sexual dimorphism in body mass (male body mass/female body mass). Low dimorphism (asterisk) is categorized by scores of less than 1.15, medium dimorphism (filled circles) by scores between 1.15 and 1.5, and high dimorphism (filled triangles) by scores greater than 1.5. Points below the isometric line (shown) indicate higher male DEE than female DEE, while points above the line indicate higher female DEE.

### 3. RESULTS

#### (a) Daily energy expenditure

DEE refers here only to those energetic costs that arise from daily body maintenance and does not include the costs of pregnancy and lactation (see §2(a)). As shown in figure 1, there is a close correlation between male and female DEE ( $r=0.988$ ,  $p<0.0001$  and  $n=19$ ) and male expenditure is, in every case, greater than female expenditure. The variation in the relationship between male and female DEE appears to be explained by the sex differences in body mass. In species in which males and females are of similar body size, the daily energetic costs for each sex are very similar. In contrast, male DEE greatly exceeds that of females in species in which there is high body size dimorphism. This relationship is not surprising given the large role of body mass in determining the BMR and, therefore, the daily energetic costs. In fact, the relationship between DEE and body mass is so close (linear regression  $r=0.995$ ,  $p=0.000$  and  $n=38$ ), that body mass  $W$  (kg) could be used to estimate DEE (kcal) using the following equation:

$$\log \text{DEE} = 0.75 \log W + 1.97. \quad (7)$$

#### (b) The energetic cost of reproduction

While male DEE is generally higher than female DEE, this does not take into consideration the energetic costs of pregnancy and lactation for the female. The energetic cost of reproduction includes all of these costs and, thus, provides a more meaningful comparison of male and female energy demands. As shown in figure 2, there is a very close correlation between the energetic cost of reproduction for males and females ( $r=0.986$ ,  $p=0.000$

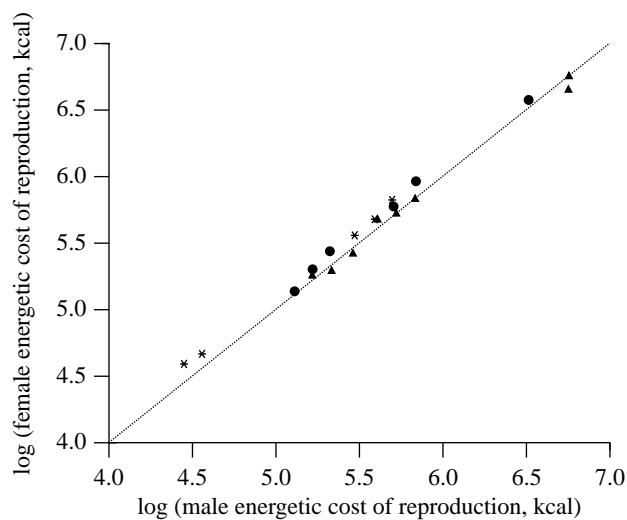


Figure 2. Comparison of male and female energetic cost of reproduction. Markers denote the level of sexual dimorphism as specified in figure 1. Points below the isometric line indicate higher male energetic costs and points above the line indicate higher female energetic costs.

and  $n=19$ ). However, now that reproductive costs have been included, female energy demands are often higher than male energy demands. As with DEE, sexual dimorphism in body size appears to explain most of the variation in male and female energetic costs: in species in which body size dimorphism is low or medium female energetic costs per reproductive event exceed those of males, whereas in highly dimorphic species, male and female costs are very similar.

Figure 3 illustrates the strong correlation between sexual dimorphism in energy expenditure ( $E_M/E_F$ ) and sexual dimorphism in body mass ( $r=0.946$ ,  $p=0.000$  and  $n=19$ ). As body size dimorphism increases, male energetic costs also increase relative to females. Since body mass is correlated with DEE (see above), gestation length (Martin & MacLarnon 1988), lactation length (Lee *et al.* 1991) and the interbirth interval (Ross 1988; Key 1998), this relationship is expected. Even when males are up to 60% larger than females, the female energetic costs of reproduction exceed those of males (i.e.  $E_M/E_F < 1.0$ ) due to the high costs of gestation and lactation. However, when male body size is more than 60% greater than female body size, the energetic costs of reproduction for males are similar to or exceed those for females. In very sexually dimorphic species, such as *Cercopithecus mitis* (blue monkey) and *Erythrocebus patas* (patas monkey), in which males are 90% larger than females, the male energetic costs exceed the female energetic costs by 10%. In the most extreme case, orang-utans (*Pongo hygmaeus*), the male energetic costs of reproduction are *ca.* 30% higher than the female energetic costs. This estimate applies only to the larger male orang-utans; smaller males will clearly incur lower costs. In fact, the very high estimates found here for large male orang-utans may explain the occurrence of small males in orang-utan populations (Rodman & Mitani 1987).

The validity of these results is dependent upon the accuracy of the assumptions underlying the model. As has already been discussed, the energetic costs of

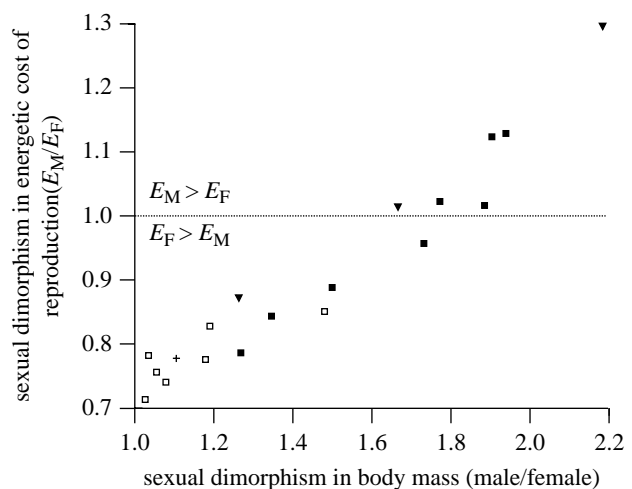


Figure 3. The relationship between sexual dimorphism in the energetic cost of reproduction ( $E_M/E_F$ ) and sexual dimorphism in body mass (male mass/female mass). Open squares, Cebidae; filled squares, Cercopithecidae; plus sign, Hylobatidae; and inverted filled triangles, Hominidae.

pregnancy, lactation, locomotion and activities such as feeding and resting are likely to vary between species. Considerably more research needs to be carried out into the energetic costs of these activities in non-human primates. For reasons already discussed (see § 2(b)) lactation costs may be particularly variable. Here it has been assumed that lactation elevates the daily energy demands by 50%, a value that would appear reasonable for most haplorhine primates which produce fairly dilute milk. However, in humans lactation only increases the daily energy requirements by 25% (FAO-WHO-UNO 1985). In contrast, callitrichids and most strepsirhines produce energy-dense milk and, therefore, the energetic costs of lactation may be considerably higher than 50%. Nievergelt & Martin (1999) estimated that, in common marmosets, lactation elevates the female daily energy requirements by 100%.

Figure 4 shows how varying the energetic costs of lactation between the estimated minimum and maximum values of 25 and 100% of DEE would affect the results. Using a minimum value, the results are similar to those already discussed: when males are between 30 and 50% larger than females, the male and female energetic costs are almost identical, while higher levels of sexual dimorphism result in high male energetic costs compared to females. When the maximum value for the cost of lactation is used, the female energetic costs nearly always exceed those of males, even in species in which body size dimorphism is high. Taken at face value, this suggests that, in strepsirhines and callitrichids, the costs of producing energy-rich milk will result in much greater female energetic costs compared to males. However, Tilden & Oftedal (1997) noted that the strepsirhines with the richest, energy-dense milk tend to be 'parkers' that leave their infants unattended for long periods. In these cases high lactation costs may be balanced by less frequent nursing and low infant transport costs. Similarly, male care giving in callitrichids may compensate for the high lactation costs for females

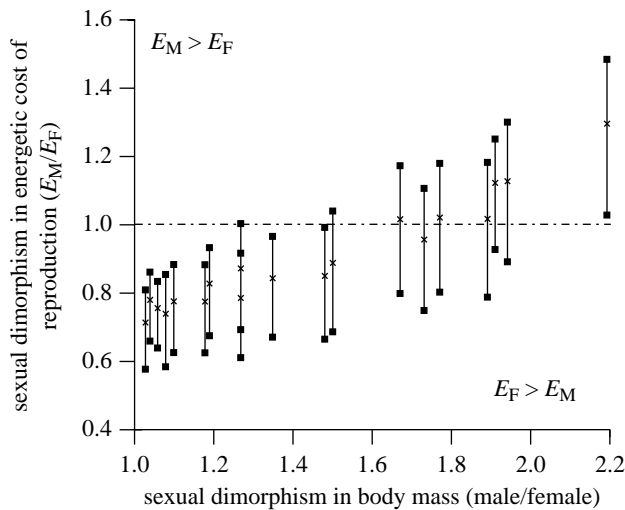


Figure 4. The effect of varying the energetic cost of lactation on the relationships shown in figure 3. Whiskers denote the range of values of energy dimorphism using the minimum and maximum estimates for the energetic cost of lactation as described in the text. Original estimates are indicated by crosses.

although the evidence for this is at present ambivalent (Tardif 1997; Sanchez *et al.* 1999).

#### 4. DISCUSSION

Theoretical considerations suggest that, in mammals, female energetic costs should be higher than male energetic costs. This is because females are biologically obliged to meet the energetic costs of gestation and lactation. However, male energetic costs may also be high, particularly if they have to maintain a large body size. This paper has compared male and female energetic costs in a number of haplorhine primates in order to assess sex differences in energy demands. It has been shown that there is a very close correlation between body mass and energetic costs, suggesting that body mass is the principal determinant of energetic requirements. This implies that sex differences in DEE are determined primarily by body size dimorphism. Thus, DEE is similar for males and females in species which are monomorphic in body size, while male daily energetic costs exceed those of females in sexually dimorphic species. In the longer term, females must meet the additional energetic costs of lactation and gestation. This means that, in species which have low or medium body size dimorphism, the long-term female energetic costs are greater than male energetic costs. However, in highly sexually dimorphic species the overall energetic costs for each sex are very similar and, in some cases, the male energetic costs of reproduction are much greater than for females.

It appears that, in highly sexually dimorphic species, the energetic costs to females of lactation and gestation are matched or exceeded by the energetic costs to males of maintaining a larger body size. A study by Kenagy (1987) on energy expenditure in golden-mantled ground squirrels, which are highly body size dimorphic, lends support to this conclusion. He found that the energetic costs of lactation for females are huge; at peak lactation

female energy expenditure is 82% higher than at the time of mating. However, the DEE for males is much greater than for females and Kenagy (1987) concluded that, when all factors are considered, male and female energy requirements over a breeding season are virtually identical. Far more studies of this type are required to test the predictions made in this paper. Moreover, we need a much better understanding of how activity patterns, diet, body size, life history and milk composition covary in order to balance energy intake and expenditure. However, the models presented here underline the importance of examining mammalian energetics from the perspective of both sexes.

In retrospect, the conclusion that the relationship between male and female energetic costs varies with sexual dimorphism in body mass may seem nothing short of obvious. Yet, few authors have recognized the importance of energy intake to males, even in the most sexually dimorphic species. An exception is Bercovitch & Nürnberg's (1996) study of rhesus macaques, which showed that only males with sufficient body fat were able to sire offspring successfully. Bercovitch & Nürnberg (1996) suggested that, as with females, body fat provides males with a buffer against the energetic stress associated with reproduction. They concluded that male feeding behaviour is a primary rather than secondary determinant of male reproductive success. The models presented here suggest that this may be particularly true in sexually dimorphic species, in which the males' need to grow and support their large body size will mean that their resource needs will approach or even be greater than the resource requirements of females. Although this study is restricted to haplorhine primates, this prediction may carry implications for other taxa. Males of species where sexual dimorphism is typically high may have to make crucial 'decisions' about trade-offs between resource acquisition and mate acquisition. The high energetic cost of supporting a large body size may explain why males that are not living in bisexual groups often live in all-male groups rather than travelling alone. These 'bachelor' groups are found in many mammalian species, including primates (Pusey & Packer 1987), ungulates (e.g. Clutton-Brock *et al.* 1982) and cetaceans (Pryor & Shallenberger 1991; Wells 1991). It is usually assumed that these bachelor groups form primarily for predator defence and, in primates, to enable alliance formation prior to attempted immigration into a breeding group (Clutton-Brock *et al.* 1982; Pusey & Packer 1987). However, it is also possible that they play an important function in resource acquisition, as has been suggested for Hanuman langurs (Rajpurohit *et al.* 1995). Further research into the reasons why males group together may throw some light on this question.

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