

## Energy Allocation in Mammalian Reproduction<sup>1</sup>

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**SYNOPSIS.** On behavioral, hormonal, and physiological grounds, mammalian reproduction can be compartmentalized into the following continuous sequence of events: mating (courtship, estrous), gestation, parturition, lactation, post-lactational parental care, and maternal recovery. We point out that comparing the relative allocation of energy for these events across mammals is difficult because of life history variability (*e.g.*, litter size, birth weight), allometry, phylogeny, and individual variation. We review the empirical and theoretical literature on each of these events with respect to: different methodologies in measuring energy use; broad patterns of energy consumption across diverse mammalian taxa; and, identification of particular reproductive characteristics (*e.g.*, birthing, parental care) which may be costly but have yet to receive energetic measurements. Although most studies have considered gestation and lactation the critical reproductive events for energy expenditure, variation in these events is substantial and almost certainly is a function of relative allocation of time to gestation *vs.* lactation as well as the presumed energetic costs of mating, birthing and parental care. In addition, repeated observations show that behavioral compensation is an extremely important strategy for minimizing energy requirements during reproduction. From this review, we argue that more complete analyses will come from (1) incorporating energetic measurements in studies of mammalian behavior and (2) including mechanisms of behavioral compensation into physiological studies.

### INTRODUCTION

Energy use during mammalian reproduction has received considerable attention in recent years (see Harvey, 1986; Loudon and Racey, 1987), particularly in association with studies of sexual selection, sex allocation, and parental investment. Studies usually fall into one of two broadly defined categories: those concerned primarily with evolutionary (=fitness) consequences (*e.g.*, Clutton-Brock *et al.*, 1982; Ortiz *et al.*, 1984) or those interested in the energetic (=physiological) costs associated with varying reproductive patterns (*e.g.*, Smith and McManus, 1975; Glazier, 1985*b*; Mattingly and McClure, 1985). Evolutionary biologists and behavioral ecologists have been primarily concerned with parental investment, defined as costs to an individual's future reproductive success result-

ing from a current reproductive event (Trivers, 1972). Parental investment has typically been assessed via either behavioral parameters, such as suckling frequency or duration (*e.g.*, Ortiz *et al.*, 1984; Costa and Gentry, 1986), or net production (*e.g.*, litter mass at birth or weaning). In contrast, physiologists have studied energetic costs of reproduction by monitoring caloric intake, net production, metabolic rate, and/or daily energy expenditure (DEE) during specific reproductive events (usually gestation or lactation), in an attempt to understand the energetic consequences of variation in parameters such as body size, litter size, and fecundity (*e.g.*, Glazier, 1985*a, b*; Mattingly and McClure, 1985). One aim of this paper is to emphasize the importance of both behavioral and physiological techniques for the study of energy use during reproduction. We hope to show that (1) precise measurements of energetic constraints and consequences of reproductive behaviors must be incorporated into studies of mammalian behavior and (2) behavioral flexi-

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bility (*e.g.*, in duration and/or frequency) may dramatically alter the relative energetic costs of specific reproductive events (see also Goldstein, 1988). Although we primarily address problems related to mammalian reproduction, we believe a general merging of energetics and behavioral perspectives, encompassing multiple measures of costs, will foster more complete analyses of the costs of reproduction in most organisms (see also Bronson, 1979; Calow, 1981, 1984; Altmann, 1983, 1986; Knapton, 1984; Bennett, 1986; Costa and Gentry, 1986; Halliday, 1987).

#### PROBLEMS AND PERSPECTIVES IN THE COSTS OF MAMMALIAN REPRODUCTION

On behavioral (Eisenberg, 1981), hormonal (Rosenblatt and Siegel, 1983) and physiological (Millar, 1977) grounds, mammalian reproduction can be compartmentalized into the following continuous sequence of reproductive events: mating (courtship, estrous period), gestation, parturition, lactation (suckling period), post-lactational parental care, and post-lactational/post-parental care maternal recovery. Most energetic studies have focused on either caloric consumption or maternal metabolic rate, in conjunction with changes in maternal (during gestation) and offspring mass, during only one reproductive event (usually gestation or lactation). Although an evolutionary perspective requires that relative values of these measures be used in comparisons of energetic costs of mammalian reproduction, both within and between species, recent detailed studies show that, for several reasons, comparative statements are difficult to make.

First, even though mammalian reproductive events appear discrete, intrinsic variability in parameters such as birth weight, litter size, weaning age, weaning weight, and inter-birth interval, both within and across species, often confound comparisons of energy expended during reproduction. For example, larger litters demand greater energy expenditures during lactation (Millar, 1978; Mattingly and McClure, 1982; Glazier, 1985*b*) and, in some small mammals, produce slow mater-

nal recovery from reproduction (Elwood and Broom, 1978).

Second, most mammalian reproductive events and various energetic constituents are correlated with body size (see Eisenberg, 1981; Calder, 1984; Millar, 1984; Schmidt-Nielson, 1984; Gittleman, 1986). Resting metabolism (Kleiber, 1961), existence metabolism (Kendeigh, 1969), birth and weaning masses (Millar, 1977), birth weight (Leitch *et al.*, 1959), and gestation length (Kihlström, 1972; Eisenberg, 1981), among others, demonstrate an exponential relationship to body size where the exponent of these relationships is  $< 1.0$ . In contrast, functions describing capacity terms, for example digestive capacity (Kleiber, 1961) and storage capacity (Calder, 1984), bear a nearly linear relationship to body mass. These allometric relationships affect the relative ability of mammals differing in size to respond to periods of energy deprivation or abundance. All else being equal, a larger mammal can store proportionally more energy and, likewise, draw upon proportionally more reserves than a small mammal (Lindstedt and Boyce, 1985); as extreme examples, some large mammals such as lactating gray seals (Davies, 1949), rutting red deer (Mitchell *et al.*, 1976), and many lactating seals (Bartholomew, 1952; Bowen *et al.*, 1985) exclusively depend on an ability to fast through reproductive events. Many large mammals store energy for carryover from one reproductive event to another, usually from pregnancy to lactation, which may confound the relative cost of each. This carryover is a particularly difficult problem when pregnancy and lactation events are studied separately.

Third, comparative studies have repeatedly shown that phylogeny is an important component to life history evolution (see Stearns, 1983; Harvey and Clutton-Brock, 1985; Gittleman, 1986, 1988*a*). Life history factors are often coupled with energetic constraints (see McNab, 1980; Lindstedt and Calder, 1981; Calder, 1984), and it follows that phylogeny may play an important role in setting energetic costs, even at lower taxonomic (familial, generic) levels. For example, Kenagy and Bartholomew's (1985) study of reproductive pat-

terns in five coexisting desert rodents shows that, although the diurnal antelope ground squirrel (*Ammospermophilus leucurus*) is sympatric with four nocturnal heteromyids, its timing of reproduction and reproductive effort are more similar to marmotine squirrels (ground squirrels, marmots, prairie dogs, chipmunks) than to the heteromyids. As the authors conclude, "The comparison of *A. leucurus* with *D. merriami* [kangaroo rat] illustrates the importance of considering whole suites of functional, reproductive, and life history traits when one examines adaptation to a particular environment. It also shows that the fixity of a series of characters in the genotype can be a barrier ("phylogenetic constraint") to the evolution of a major change in life history."

Fourth, experimental studies make it apparent that within single populations individuals vary considerably in the quality and quantity of maternal care, energy utilization, and ability to produce milk, all of which will tilt the balance of energy costs (Bronson and Rissman, 1986; Thompson and Nicoll, 1986). In domestic rats, for example, we know that such variation relates to heredity, neonatal development, prior maternal experiences (age), and psychological state (e.g., Denenberg *et al.*, 1962; Morton *et al.*, 1963). Although individual differences provide case studies for examining adaptive allocation of energy in fitness terms, *i.e.*, life-time reproductive success (see Charnov, 1982; Clutton-Brock, 1985; Stewart, 1986), small sample sizes and high variability should demand caution, even when extrapolating between closely related species.

In addition to the above difficulties, few studies have directly measured energy costs in mammalian reproduction and the methods vary greatly from study to study (Randolph *et al.*, 1977; Millar, 1978; McClure and Randolph, 1980; Glazier, 1985a, b; Costa and Gentry, 1986; Kunz and Nagy, 1987). Thus, our discussion of the relative energetic costs of reproductive events will focus on: (1) different methodologies in measuring energy use, (2) broad patterns of energy consumption, across diverse taxa, for specific reproductive events, and (3) identification of partic-

ular reproductive characteristics (e.g., male ejaculate; parturition; paternal care) which may be costly but have yet to receive energetic study.

#### ENERGETICS OF MAMMALIAN REPRODUCTIVE EVENTS

##### *Mating*

Mating behavior includes interactions between a male and female in a situation that leads to copulation. These interactions include investigatory behavior (mate searching), mounting, lordosis, intromission, ejaculation and any observable postcopulatory interactions. Although each of these behaviors has been extensively analyzed from hormonal, neural, evolutionary, and genetic approaches (Beach, 1965; Diakow, 1974), energetic studies are still lacking. This is ironic considering that some of the earliest studies in ethology used energetic terms. For example, a classic paradigm in studies of mating tested for the number of ejaculates before an individual reached "exhaustion" (e.g., Beach and Jordan, 1956; Tiefer, 1969), with the presumption that a male's energetic capacity was practically "unlimited."

Apparently only one study has directly measured energy consumption during the mammalian mating period. Kenagy (1987), working with golden-mantled ground squirrels (*Spermophilus saturatus*), found that energy expenditure (kJ/day; measured using doubly labeled water) in males is  $2.5 \times \text{BMR}$  and in females  $2.0 \times \text{BMR}$ , the difference mainly due to greater body mass in males. The total energy expenditure during mating is only slightly greater than periods outside of reproduction.

Many behavioral studies have suggested that the energetic costs of mating are significant. Males of larger species tend to show significant increases in activity levels (frequency and duration), decline in feeding, and loss of as much as 20% body weight during mating (McCullough, 1969). In male red deer the proportion of daytime spent grazing fell from 44% outside of the breeding season to less than 5% during the rut (Clutton-Brock *et al.*, 1982); similar patterns are observed in other ungulates

(Struhsaker, 1967; McCullough, 1969). In general, females do not appear to incur large energetic demands while mating. Nevertheless, some energetic costs are suggested because stress induced situations, such where food resources decline, correlate with decreases in length of breeding season, breeding success, and estrous cycling (see Sadleir, 1969). It should be pointed out that a primary problem in assessing energy usage during mating events is the brief time-frame in which they occur. Thus, it is especially difficult to separate the costs of mating per se from other daily activities.

With respect to mate access and reproductive success (RS), some indirect measures indicate the importance of metabolic rate. In European rabbits there is a positive correlation between resting metabolic rate (RMR) and social status among groups of males organized in a stable hierarchy; the costs of body maintenance appear to be higher for high-ranking males with increased values of RS (Bell, 1983, 1986). However, subordinate tree-shrews (*Tupaia glis*) and deer mice (*Peromyscus maniculatus*) have lower rates of metabolism than dominants (Farr and Andrews, 1978a, b; Fuchs and Kleinknecht, 1986). Certainly, there are several other interrelated variables which influence higher RS in dominant males (e.g., access to better breeding areas; earlier start to breeding: see Rutberg, 1986); nevertheless, these high metabolic rates in dominants and subordinates of different species may reflect alternative energetic constraints rather than contradictory data. Thus, in *Tupaia* and *Peromyscus* subordinates may have high RMRs due to stress from continual testing of the hierarchy whereas in rabbits subordinates may be more passive.

It is often assumed that most of the energetic costs of mating in males is associated with searching for prospective mates and male-male conflicts. Although sperm are vastly smaller and the cost of testicular growth is negligible, numerous studies now indicate that ejaculate cost in terms of some behavioral and physiological measures is significant (Dewsbury, 1982). Sperm production is generally limited in terms of:

reduced numbers of sperm in successive ejaculates (Dewsbury and Sawrey, 1984), often for periods of up to a week, and limitations of other hormonal substances critical to successful mating; in humans, when weight loss is in the range of 25% normal body weight, sperm production ceases (Frisch, 1984). Furthermore, repetitive copulation for pregnancy initiation, female choice and control, and risks of searching for a mate all entail *presumed* energetic costs and limit male reproductive capacity (see Dewsbury, 1982). Specific energetic measurements, yet to be completed, may provide critical constraints on copulatory abilities and, interestingly, may suggest causal explanations for alternative breeding strategies in males (see Gibson and Guinness, 1980).

Finally, perhaps the most extreme example of the evolutionary and energetic costs of mating are in the marsupials, where post-mating mortality occurs in males of several species of *Antechinus*. Such mortality is partly caused by gastrointestinal ulceration and suppression of the immune system brought on by stress. But there also appears to be an energetic reason. Using doubly labeled water, Nagy *et al.* (1978) showed that there is no substantial increase in daily energy expenditure during the mating season. However, since the resting metabolic rate may increase in males by 17% at the time of mating (Cheal *et al.*, 1976), there may be a reduction in energy spent on other activities. There is indirect evidence that energy used in mating may substitute for a reduction in feeding (Lee and Cockburn, 1985).

#### Gestation

Total energy investment during pregnancy involves many components including net production of fetal, uterine, placental, and mammary tissue, production costs ("the work of growth" [Brody, 1945]), and increased maintenance costs associated with these new tissues (*i.e.*, the metabolism of added mass). Direct measurement of each of these components is difficult and generally has been restricted to laboratory or domesticated species (e.g., McC. Gra-

ham, 1964; Myrcha *et al.*, 1969; Studier *et al.*, 1973; Havera, 1979; Oftedal, 1985). Neonatal mass (birth weight) is often employed as an indirect measure of uterine and placental tissue masses and consequently may estimate the energetic cost of pregnancy (Millar, 1977, 1981; Oftedal, 1985; Kunz, 1987; Kurta and Kunz, 1987). Caloric consumption studies reveal considerable variation in net production of fetal and placental tissues. Production efficiency ranges from about 10–15%, with domestic mammals clustering at the high end and wild mammals tending towards the low end of the range (Myrcha *et al.*, 1969; Studier *et al.*, 1973; Oftedal, 1985); placental and uterine proliferations account for about 20% of the net caloric investment during gestation (Oftedal, 1985). However, although the relative size of neonate(s) may serve as a useful first approximation of energy consumption during gestation, significant changes in maintenance requirements, due to increased mass and/or increased specific metabolic rates, cannot be detected solely through examination of net production; these may involve significant energetic expenditures during gestation (Partridge *et al.*, 1986; Thompson and Nicoll, 1986; Nicoll and Thompson, 1987).

Studies of the energetic costs of gestation have focused on caloric intake, sometimes augmented with respirometry (*e.g.*, Randolph *et al.*, 1977). Measurement of caloric intake by itself can produce misleading estimates of reproductive costs. Digestive efficiencies do change slightly during gestation and lactation, although the low magnitude of these changes usually leads to dismissal of their importance (*e.g.*, Oftedal, 1985; but see Mattingly and McClure, 1982). Of greater significance, however, is the potential for compensation, via reallocation of energy from some nonreproductive level of activity or thermoregulatory (maintenance) expenditure.

It is difficult to compare caloric intake data between species (or individuals) without knowledge of (1) ambient temperatures during measurement, (2) limits of thermoneutrality (or natural nest temperatures), and (3) variation in activity levels before and after reproduction. In some

white rats, for example, there was little or no difference in food consumption between pregnant and non-reproductive females (Slonaker, 1925; Wang, 1925); however, activity (=wheel running) was 57–96% lower in the pregnant individuals. Thus, at least some species may shift allocation of energy from activity to gestation by reducing the frequency and/or duration of certain behaviors (Racey, 1981, 1982); without integration of behavioral and energetic data, this tactic can result in an underestimation of the total energy allocated to gestation. A combination of caloric consumption, respirometry, and time budgets of behavior, before and during gestation (reproduction) is a requisite for assessment of the allocation of energy to maintenance, "the work of growth" (Brody, 1945), and net production during gestation. Respirometry may be particularly important because some species, especially those with low basal metabolic rates (Nicoll and Thompson, 1987; but see Nagy and Montgomery, 1980), show increased resting metabolic rates during gestation, presumably as a result of costs associated with growth of the fetus. However, this increased metabolism is not due to a differentially high rate of metabolism in fetal tissue (Kleiber, 1961).

For pregnant rodents, increase in mean daily caloric intake over non-reproductive rates ranges from 18–25% (*e.g.*, Kaczmarzki, 1966; Migula, 1969; Myrcha *et al.*, 1969; Mattingly and McClure, 1982) and at least one of these species may store energy as fat for use during lactation (*i.e.*, *Sigmodon hispidus*: Randolph *et al.*, 1977; see also Mattingly and McClure, 1985). For most rodents, stored fat is not important for gestation. White-footed mice (*Peromyscus*) with food availability 80–90% of ad lib had no effect on body weight or fat content, but nevertheless fecundity significantly decreased (Merson and Kirkpatrick, 1981); similar effects of reduced fecundity associated with lowered food reserves are found in other small mammals (see Kenagy and Bartholomew, 1985). Fat storage may be of importance to bats, however, because of their unavoidably high activity levels and obvious flight costs. For

example, in some species (*e.g.*, big brown bat, *Eptesicus fuscus*) the fraction of body fat increases by as much as 68% in one week during mid-pregnancy (Stack, 1985) and if storage is unavailable foetal growth rates and pregnancy rates often decline (Racey, 1973; Kurta, 1986). Although the causal mechanisms of these results are not known, it appears from more extensive data on other species that smaller mammals may be more "hard-wired" to gestation length itself rather than storage. After controlling for body size, birth weight, litter size, and body temperature (Racey, 1981), increases in ingestion rates correlate most closely with gestation length (*e.g.*, Millar, 1977, 1978; McClure, 1987).

In contrast to rodents, larger mammals (ungulates) buffer the costs of gestation by laying down fat reserves prior to conception (see Frisch, 1984); if storage is not adequate, pregnancy rates decline (peary caribou: Thomas, 1982; barren ground caribou: Dauphine, 1976; wild and domestic reindeer: Klein and White, 1978). Well-fed pregnant ewes with heavy fat reserves had only about half the foraging intake of lean ewes (Reid, 1961). Ingestion rates during gestation are generally not as high as during lactation (see Fleming *et al.*, 1981), thus the inference being that milk production is more costly; indeed, because gestation costs are less (particularly per day), this may explain why, rather than have flexible lactation periods, in some taxa gestation is extended during harsh ecological conditions (*e.g.*, hystricomorphs: Short, 1985) or gestation varies in relation to dominance status (*e.g.*, anthropoid primates: Altmann, 1986).

Although the birthing period is brief relative to other reproductive events, behavioral, hormonal, and energetic changes indicate some costs. Peak rates of energy use by pregnant mammals typically occur within the few days preceding parturition. In domestic cattle, heat loss increases significantly (200–300 kcal/day) during labor and parturition due to some combination of increased fetal activity and the onset of fetal thermoregulation (Brockway *et al.*, 1963; Oftedal, 1985). Thus, energetic costs of parturition may be an important com-

ponent of the daily energy budget of a female mammal and, in the least, may influence the ability of a female to expend energy during early lactation.

#### Lactation

Milk production represents the single most influential and unique feature of mammalian reproduction (Maynard Smith, 1977; Pond, 1977; Daly, 1979). The complexity of energy transfer and energy use during lactation has motivated a wide array of physiological and behavioral studies. In addition to measuring caloric intake, labeled water, analysis of milk composition and production/consumption have been widely employed to estimate the energy requirements for lactation (Oftedal, 1985; Gittleman and Oftedal, 1987; Kunz and Nagy, 1987); respirometry has been used to a lesser extent (*e.g.*, Thompson and Nicoll, 1986). Measurements of the caloric content of milk have been combined with either behavioral indices of suckling rates (frequency and duration) or changes in mass of suckling young and mother (Ortiz *et al.*, 1984; Gittleman and Oftedal, 1987). However, analyses of milk production do not assess metabolic costs of milk production or maternal maintenance (*e.g.*, increased rates of maternal metabolism) and will tend to underestimate overall costs of lactation (also see discussion in Oftedal, 1985).

Lactation is generally considered the most expensive aspect of reproduction for a female mammal (*e.g.*, Hanwell and Peaker, 1977; Millar, 1977, 1978; Randolph *et al.*, 1977; Oftedal, 1985). Mean caloric intake during lactation ranges from 66–188% greater than for non-reproductives (*e.g.*, McC. Graham, 1964; Kaczmarski, 1966; Migula, 1969; Stebbins, 1977; Randolph *et al.* 1977; Millar, 1978; Mattingly and McClure, 1982; Sadleir, 1982; Glazier, 1985*a, b*). These levels may vary directly with litter size (*e.g.*, Smith and McManus, 1975; Millar, 1978; Sadleir, 1982) and may be over 200% in digestively inefficient species (*e.g.*, the folivorous "carnivore," the red panda, *Ailurus fulgens*: Gittleman, 1988*b*; see also Studier, 1979). Peak levels of energy use may approach 2.5–5 times those of non-reproductive females (see ref-



erences above). However, despite high energy expenditures during lactation, net production ranges from about 15–45% (see Smith and McManus, 1975; Mattingly and McClure, 1982; Glazier, 1985b; Oftedal, 1985) which is similar to, or even slightly higher than, gestation.

Behavioral changes parallel caloric intake results. Numerous studies, particularly of larger species, show that feeding bout lengths may increase by as much as 30%; frequency of feeding, and increased food selection are associated with the onset of lactation (see Clutton-Brock *et al.*, 1982; Dunbar, 1984; Duncan *et al.*, 1984; Berger, 1986). However, as previously mentioned, fat deposition prior to breeding or during gestation may supplement energy needs during lactation (see also Pond, 1984; Vernon and Flint, 1984; McClure, 1987) and may affect litter size, sex ratio, offspring size and brain size at weaning (*e.g.*, McC. Graham, 1964; Widdowson, 1981; McClure, 1987).

Lactation also imposes significant demands to water balance, particularly for mammals from xeric habitats (*e.g.*, Soholt, 1977). The water in milk may be partly recycled via the young (Friedman and Bruno, 1976): in rats, if micturation is prevented by urethral ligation, the transfer of water from mother to pups is greatly reduced, and the mother's water intake increases. As would be predicted, when a lactating female is deprived of water intake (*e.g.*, during hibernation), the degree of water recycling is higher (*e.g.*, black bears, *Ursus americanus*: Oftedal, in preparation).

As in gestation, there is evidence that some species divert energy from activity or maintenance to reproduction by reducing time allocations. In bats, even though the total energy expenditure during lactation may increase by 20–40% (see Anthony and Kunz, 1977; Kunz, 1987), females may shift energy expenditure from maintenance metabolism, via relaxation of homeothermy, to lactation, thus avoiding or minimizing increased food consumption. In brown long-eared bats (*Plecotus auritus*) the rate of increase in both absolute energy expenditure and expenditure relative to basal metabolism were similar during preg-

nancy and lactation (Racey and Speakman, 1987).

The daily rates of energy transfer are most spectacular in some marine mammals where females lactate intensively for relatively brief periods (four weeks or less), fast from food and water during lactation, produce energy-rich milk with high fat content, and wean their pups abruptly (see Fedak and Anderson, 1982; Bonner, 1984; Ortiz *et al.*, 1984; Costa *et al.*, 1986; Costa and Gentry, 1986). Prior to weaning, the sole source of nutrients for the developing pup is mother's milk. Thus, the total amount of milk and metabolic energy expended by a female during the entire lactation period can be calculated by extrapolating the daily milk (via pup water flux and milk composition) and metabolic expenditure rates. Costa *et al.* (1986) show that, in elephant seals (*Mirounga angustirostris*), the high energy cost of lactation is reflected by females losing approximately 42% of their body mass and expending 4,330 mJ even though lactation only lasts 26.5 days. Further metabolic savings are achieved by minimizing activity levels: females spend considerable amounts of time asleep and remain within a few meters of the parturition site for the entire lactation period. Such energy saving mechanisms, especially the lowered dependence on food energy intake to offset lactation costs, may be a critical strategy allowing for the elephant seal's remarkable return in population numbers (see Costa *et al.*, 1986). Unfortunately, there are no measurements of the energetic costs of gestation in marine mammals.

Three caveats need to be made with the general presumption that lactation is expensive. First, milk composition, milk quantity, and consequently maternal energy output vary during the lactation period (Oftedal, 1980, 1984) and this may drastically affect perceptions of efficiency and investment (Glazier, 1985b). Thus, data from studies not controlling for lactation stage are difficult to evaluate. Second, because significant increases occur during lactation in various behaviors (*e.g.*, activity cycle, nest building, huddling, aggression, licking: see Ewer, 1973; Leuthold, 1977;

Galef, 1981; Clutton-Brock *et al.*, 1982; Ostermeyer, 1983; Gittleman, 1988*b*) and in anatomical weight (*e.g.*, mammary tissue, gut, heart; see Williamson, 1980; Sampson and Jansen, 1984), it is difficult to tease apart the relative energetic costs of lactation (milk production) *versus* these other factors. Future studies should include measurements of energy use in various aspects of lactation, not only those associated with milk production. Third, considerable variation in lactation costs may be associated with intra-litter variation. Recent empirical data and theoretical models show that in some species mothers differentially invest in males and females (see, *e.g.*, Maynard Smith, 1980; Clutton-Brock and Albon, 1982; Lee and Moss, 1986), with increased investment in the sex which has the more variable reproductive success (in most mammals, males) *and* is influenced by parental investment. As Clutton-Brock *et al.* (1984) illustrate in red deer (*Cervus elaphus*), indicators of a female's energetic capacity (body weight, dominance) appear to be good predictors of differential investment. Physiologists should, therefore, incorporate this evolutionary approach in estimating costs of lactation.

#### *Post-lactational parental care*

Despite an explosion of studies examining the ecological and evolutionary features of parental care in mammals (see, *e.g.*, Eisenberg, 1981; Gubernick and Klopfer, 1981; Elwood, 1983; Taub, 1984; Gittleman, 1985), no study has directly measured the metabolic costs of parental care, either in a male or female. This is a glaring omission given repeated observations showing the presumed costly increase in food provisioning, den site defense, infant carrying behavior, and teaching duties. Take, for example, the energetic costs of carrying an infant by a male primate, a common feature in monogamous species (see Hamilton, 1984; Altmann, 1986). Increases in energy costs of transporting a mass are directly proportional to the relative mass of the transported object and the lean body mass of the carrier (Taylor *et al.*, 1980).

Transporting an infant weighing 1.5 kg when six months old will increase the energy cost of locomotion to a 15 kg male by 10% for the interval of carrying while eliminating the added cost of locomotion to the infant. Energy cost to such a male carrier will involve an increased metabolic cost of 5.6% of his energy expenditure during a 12 hr day if an infant is carried over an all day route and 2.8% for a half day route. Alternatively, many female mammals show significant weight loss during lactation and often display maternal weight at weaning that is lower than that before mating. The cost of reattaining that initial body mass may be significant, and yet it is altogether unstudied.

#### SYNTHESIS

Several implications derive from this discussion for future studies of mammalian reproduction. First, most studies have considered gestation and lactation as *the* most important reproductive events with respect to energy expenditures. In this perspective, about 20% of the energy is allocated to gestation, 80% to lactation (*e.g.*, Oftedal, 1985; see Table 1). However, the variation in this allocation should be substantial and almost certainly is a function of the relative allocation of time to gestation *vs.* lactation; thus, as reflected by the predominance of question marks in Table 1, the use of one variable (*e.g.*, gestation length) as an index of energetic cost (or parental investment) is likely to lead to erroneous explanations of reproductive strategies, sexual selection, and sex allocation. Second, behavioral compensation is potentially the most important tactic for minimizing additional energy requirements during reproduction. The complexity of this strategy is such that attention need be given to changes in maternal time/energy budgets from mating through weaning; without this information, the costs of reproduction may be seriously underestimated. Related to this are potential problems of presumed energetic costs of behavior; every attempt should be made to determine that, for



TABLE 1. Relative energy allocation for mammalian reproduction.

Reproductive event	% increase	% total costs	Efficiency
Mate access	?	?	?
Mating and courtship	?	?	?
Gestation	20-30	20	10-15%
Lactation	35-149	80	15-45%
Parental care/recovery	?	?	?

example, suckling frequency and duration actually reflect energy transfer.

Finally, our knowledge of reproductive energetics is limited to domesticated mammals, cricetine rodents, murine rodents, bats, pinnipeds, and a few wild ungulates. Given the variability in energy use and allocation within these few species (see Nicoll and Thompson, 1987), phylogenetic constraints on life history patterns (Gittleman, 1986) make it imperative that we increase the breadth of our knowledge by examination of reproductive energetics in more distantly related taxa.

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#### REFERENCES

- Altmann, J. 1983. Costs of reproduction in baboons. In W. P. Aspey and S. I. Lustick (eds.), *Behavioral energetics: The costs of survival*, pp. 67-88. Ohio State University Press, Columbus, Ohio.
- Altmann, J. 1986. Parent-offspring interactions in the Anthropoid primates: An evolutionary perspective. In M. H. Nitecki and J. A. Kitchell (eds.), *Evolution of behavior: Paleontological and field approaches*, pp. 161-178. Oxford University Press, Oxford.
- Anthony, E. L. P. and T. H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* 58:775-786.
- Bartholomew, G. A. 1952. Reproductive and social behavior of the northern elephant seal. *Univ. Cal. Publ. Zool.* 47:369-472.
- Beach, F. A. 1965. Retrospect and prospect. In F. A. Beach (ed.), *Sex and behavior*, pp. 535-568. Wiley, New York.
- Beach, F. A. and L. Jordan. 1956. Sexual exhaustion and recovery in the male rat. *Q. Rev. Biol.* 8: 121-133.
- Bell, D. J. 1983. Mate choice in the European rabbit. In P. Bateson (ed.), *Mate choice*, pp. 211-233. Cambridge University Press, Cambridge.
- Bell, D. J. 1986. Social effects on physiology in the European rabbit. *Mammal Rev.* 16:131-137.
- Bennett, A. F. 1986. Measuring behavioral energetics. In M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships*, pp. 69-81. University of Chicago Press, Chicago.
- Berger, J. 1986. *Wild horses*. University of Chicago Press, Chicago.
- Bonner, W. N. 1984. Lactation strategies in pinnipeds: Problems for a marine mammal. *Symp. Zool. Soc. London* 51:253-272.
- Bowen, W. D., O. T. Oftedal, and D. J. Bonness. 1985. Birth to weaning in four days: Remarkable growth in the hooded seal, *Systophora cristata*. *Can. J. Zool.* 63:2841-2846.
- Brockway, J. M., J. D. Macdonald, and J. D. Pullar. 1963. The energy cost of reproduction. *J. Physiol.* 167:318-327.
- Brody, S. 1945. *Bioenergetics and growth, with special reference to the efficiency complex in domestic animals*. Reinhold, New York.
- Bronson, F. H. 1979. The reproductive ecology of the house mouse. *Q. Rev. Biol.* 54:265-299.
- Bronson, F. H. and E. F. Rissman. 1986. The biology of puberty. *Biol. Rev.* 61:157-195.
- Calder, W. H., III. 1984. *Size, function, and life history*. Harvard University Press, Cambridge, Massachusetts.
- Calow, P. 1981. Resource utilization and reproduction. In C. R. Townsend and P. Calow (eds.), *Physiological ecology*, pp. 245-270. Sinauer, Sunderland, Massachusetts.

- Calow, P. 1984. Economics of ontogeny—adaptation aspects. In B. Shorrocks (ed.), *Evolutionary ecology*, pp. 81–104. Blackwell, Oxford.
- Charnov, E. L. 1982. *The theory of sex allocation*. Princeton University Press, Princeton, New Jersey.
- Cheal, P. D., A. K. Lee, and J. L. Barnett. 1976. Changes in the haematology of *Antechinus stuartii* (Marsupialia), and their association with male mortality. *Aust. J. Zool.* 24:299–311.
- Clutton-Brock, T. H. 1985. Birth sex ratios and the reproductive success of sons and daughters. In P. J. Greenwood, P. H. Harvey, and M. Slatkin (eds.), *Evolution—essays in honour of John Maynard Smith*, pp. 221–236. Cambridge University Press, Cambridge.
- Clutton-Brock, T. H. and S. D. Albon. 1982. Parental investment in male and female offspring in mammals. In King's College Sociobiology Group (eds.), *Current problems in Sociobiology*, pp. 223–247. Cambridge University Press, Cambridge.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308:358–360.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red deer: Behavior and ecology of two sexes*. University of Chicago Press, Chicago.
- Costa, D. P. and R. L. Gentry. 1986. Free-ranging energetics of northern fur seals. In R. L. Gentry and G. L. Kooyman (eds.), *Fur seals*, pp. 79–101. Princeton University Press, Princeton, New Jersey.
- Costa, D. P., B. J. Le Boeuf, A. C. Huntley, and C. L. Ortiz. 1986. The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. *J. Zool.* 209:21–33.
- Daly, M. 1979. Why don't male mammals lactate? *J. Theor. Biol.* 78:325–345.
- Dauphine, T. C. 1976. Biology of Kamanurik population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. *Can. Wild. Serv. Rep. Ser. No. 38*.
- Davies, J. L. 1949. Observations on the grey seal (*Halichoerus grypus*) at Ramsey Island, Pembrokeshire. *Proc. Zool. Soc. London* 119:673–692.
- Denenberg, V. H., D. R. Ottinger, and M. W. Stephens. 1962. Effects of maternal factors upon growth and behavior of the rat. *Child Develop.* 33:65–71.
- Dewsbury, D. A. 1982. Ejaculate cost and mate choice. *Am. Nat.* 119:601–610.
- Dewsbury, D. A. and D. K. Sawrey. 1984. Male capacity as related to sperm production, pregnancy initiation, and sperm competition in deer mice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* 16:37–47.
- Diakow, C. 1974. Male-female interactions and the organization of mammalian mating patterns. *Adv. Study Behav.* 5:227–268.
- Dunbar, R. I. M. 1984. *Reproductive decisions*. Princeton University Press, Princeton, New Jersey.
- Duncan, P., P. H. Harvey, and S. M. Wells. 1984. On lactation and associated behaviour in a natural herd of horses. *Anim. Behav.* 32:255–263.
- Eisenberg, J. F. 1981. *The mammalian radiations*. University of Chicago Press, Chicago.
- Elwood, R. W. (ed.) 1983. *Parental behaviour in rodents*. John Wiley and Sons, New York.
- Elwood, R. W. and D. M. Broom. 1978. The influence of litter size and parental behaviour on the development of the Mongolian gerbil pups. *Anim. Behav.* 26:438–454.
- Ewer, R. F. 1973. *The carnivores*. Cornell University Press, Ithaca, New York.
- Farr, L. and R. V. Andrews. 1978a. Rank-associated differences in metabolic rates and locomotor activity of dominant and subordinate *Peromyscus maniculatus*. *Comp. Biochem. Phys.* 61A:401–406.
- Farr, L. and R. V. Andrews. 1978b. Rank-associated desynchronization of metabolic and activity rhythm of *Peromyscus maniculatus* in response to social stress. *Comp. Biochem. Phys.* 61A:539–542.
- Fedak, M. A. and S. S. Anderson. 1982. The energetics of lactation: Accurate measurements from a large mammal, the Grey seal (*Halichoerus grypus*). *J. Zool.* 198:473–479.
- Fleming, M. W., J. D. Harder, and J. J. Wukie. 1981. Reproductive energetics of the Virginia opossum compared with some Eutherians. *Comp. Biochem. Physio.* 70B:645–648.
- Friedman, M. I. and J. P. Bruno. 1976. Exchange of water during lactation. *Science* 197:409–410.
- Frisch, R. E. 1984. Body fat, puberty and fertility. *Biol. Rev.* 59:161–188.
- Fuchs, E. and S. Kleinknecht. 1986. The influence of chronic social confrontation on oxygen consumption of *Iupia belangeri* under resting conditions. *Z. Sauget.* 51:57–59.
- Galef, B. G., Jr. 1981. The ecology of weaning. In D. J. Gubernick and P. H. Klopfer (eds.), *Parental care in mammals*, pp. 211–241. Plenum, New York.
- Gibson, R. M. and F. E. Guinness. 1980. Behavioural factors affecting male reproductive success in red deer (*Cervus elaphus* L.). *Anim. Behav.* 28:1163–1174.
- Gittleman, J. L. 1985. Functions of communal care in mammals. In P. J. Greenwood, P. H. Harvey, and M. Slatkin (eds.), *Evolution: Essays in honour of John Maynard Smith*, pp. 187–205. Cambridge University Press, Cambridge.
- Gittleman, J. L. 1986. Carnivore life history patterns: Allometric, phylogenetic and ecological associations. *Am. Nat.* 127:744–771.
- Gittleman, J. L. 1988a. The comparative approach in ethology: Aims and limitations. In P. P. G. Bateson and P. H. Klopfer (eds.), *Perspectives in ethology*, Vol. 8, Plenum Press, New York.
- Gittleman, J. L. 1988b. Behavioral energetics of lactation in a herbivorous carnivore, the red panda (*Ailurus fulgens*). *Ethology*. (In press)
- Gittleman, J. L. and O. T. Oftedal. 1987. Comparative growth and lactation energetics in carnivores. In A. Loudon and P. A. Racey (eds.), *Reproductive energetics in mammals*, pp. 41–77. Oxford University Press, Oxford.
- Glazier, D. S. 1985a. Energetics of litter size in five

- species of *Peromyscus* with generalizations for other mammals. *J. Mamm.* 66:629-642.
- Glazier, D. S. 1985b. Relationship between metabolic rate and energy expenditure for lactation in *Peromyscus*. *Comp. Biochem. Physiol.* 80A:587-590.
- Goldstein, D. L. 1988. Estimates of daily energy expenditure in birds: The time-energy budget as an integrator of laboratory and field studies. *Amer. Zool.* 28:829-844.
- Gubernick, D. J. and P. H. Klopfer. (eds.) 1981. *Parental care in mammals*. Plenum, New York.
- Halliday, T. R. 1987. Physiological constraints on sexual selection. In J. W. Bradbury and M. B. Andersson (eds.), *Sexual selection: Testing the alternatives*, pp. 247-264. John Wiley & Sons, New York.
- Hamilton, W. J., III. 1984. Significance of paternal investment by primates to the evolution of adult male-female associations. In D. M. Taub (ed.), *Primate paternalism*, pp. 309-335. Van Nostrand Reinhold, New York.
- Hanwell, A. and M. Peaker. 1977. Physiological effects of lactation on the mother. *Symp. Zool. Soc. London* 41:297-311.
- Harvey, P. H. 1986. Energetic costs of reproduction. *Nature* 321:648-649.
- Harvey, P. H. and T. H. Clutton-Brock. 1985. Life history variation in primates. *Evolution* 39:559-581.
- Havera, S. P. 1979. Energy and nutrient costs of lactation in fox squirrels. *J. Wild. Mgt.* 43:958-965.
- Kaczmarek, F. 1966. Bioenergetics of pregnancy and lactation in the bank vole. *Acta Theriol.* 11:409-417.
- Kenagy, G. J. 1987. Energy allocation for reproduction in the golden-manteled ground squirrel. In A. Loudon and P. A. Racey (eds.), *Reproductive energetics in mammals*, pp. 259-273. Oxford University Press, Oxford.
- Kenagy, G. J. and G. A. Bartholomew. 1985. Seasonal reproductive patterns in five coexisting California desert rodent species. *Ecol. Mon.* 55:371-397.
- Kendeigh, S. C. 1969. Tolerance of cold and Bergmann's rule. *Auk* 86:13-25.
- Kihlström, J. P. 1972. Period of gestation and body weight in some placental mammals. *Comp. Biochem. Physiol.* 43A:673-679.
- Kleiber, M. 1961. *The fire of life. An introduction to animal energetics*. Wiley, New York.
- Klein, D. R. and R. G. White. 1978. Parameters of caribou population ecology in Alaska. *Biol. Pap. Univ. Alaska Spec. Rep.* No. 3.
- Knapton, R. W. 1984. Parental investment: The problem of currency. *Can. J. Zool.* 62:2673-2674.
- Kunz, T. H. 1987. Post-natal growth and energetics of suckling bats. In M. B. Fenton, P. A. Racey, and J. M. V. Rayner (eds.), *Recent advances in the study of bats*, pp. 395-420. Cambridge University Press, Cambridge.
- Kunz, T. H. and K. A. Nagy. 1987. Methods of energy budget analysis. In T. H. Kunz (ed.), *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C.
- Kurta, A. 1986. Factors affecting the resting and postflight body temperature of little brown bats, *Myotis lucifugus*. *Phys. Zool.* 59:429-438.
- Kurta, A. and T. H. Kunz. 1987. Size of bats at birth and maternal investment during pregnancy. In A. Loudon and P. A. Racey (eds.), *Reproductive energetics in mammals*, pp. 79-106. Oxford University Press, Oxford.
- Lee, A. K. and A. Cockburn. 1985. *The evolutionary ecology of marsupials*. Cambridge University Press, Cambridge.
- Lee, P. C. and C. J. Moss. 1986. Early maternal investment in male and female African elephant calves. *Behav. Ecol. Sociobiol.* 18:353-361.
- Leitch, I. F., F. F. Hytten, and W. Z. Billewicz. 1959. The maternal and neonatal weights of some Mammalia. *Proc. Zool. Soc. London* 135:11-28.
- Leuthold, W. 1977. *African ungulates*. Springer-Verlag, Berlin.
- Lindstedt, S. L. and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* 125:873-878.
- Lindstedt, S. L. and W. A. Calder. 1981. Body size, physiological time, and longevity of homeothermic animals. *Q. Rev. Biol.* 56:1-16.
- Loudon, A. and P. A. Racey. (eds.) 1987. *The reproductive energetics of mammals*. Oxford University Press, Oxford.
- Mattingly, D. K. and P. A. McClure. 1982. Energetics of reproduction in large-littered cotton rats (*Sigmodon hispidus*). *Ecology* 63:183-195.
- Mattingly, D. K. and P. A. McClure. 1985. Energy allocation during lactation in cotton rats (*Sigmodon hispidus*) on a restricted diet. *Ecology* 66:928-937.
- Maynard Smith, J. 1977. Parental investment—a prospective analysis. *Anim. Behav.* 25:1-9.
- Maynard Smith, J. 1980. A new theory of sexual investment. *Behav. Ecol. Sociobiol.* 7:247-251.
- McC. Graham, N. 1964. Energy exchanges of pregnant and lactating ewes. *Aust. J. Agric. Res.* 15:127-141.
- McClure, P. A. 1987. The energetics of reproduction and life histories of cricetine rodents. In A. Loudon and P. A. Racey (eds.), *The reproductive energetics of mammals*, pp. 241-258. Oxford University Press, Oxford.
- McClure, P. A. and J. C. Randolph. 1980. Relative allocation of energy to growth and development of homeothermy in the eastern wood rat (*Neotoma floridana*) and hispid cotton rat (*Sigmodon hispidus*). *Ecol. Mon.* 50:199-219.
- McCullough, D. R. 1969. *The tule elk: Its history, behavior and ecology*. University of California Press, Berkeley, California.
- McNab, B. K. 1980. Food habits, energetics, and the population biology of mammals. *Am. Nat.* 116:106-124.
- Merson, M. H. and R. C. Kirkpatrick. 1981. Relative sensitivity of reproduction activity and body-fat level to food restriction in white mice. *Am. Midl. Nat.* 106:305-312.

- Migula, P. 1969. Bioenergetics of pregnancy and lactation in European common vole. *Acta Theriol.* 14:167-179.
- Millar, J. S. 1977. Adaptive features of mammalian reproduction. *Evolution* 31:370-386.
- Millar, J. S. 1978. Energetics of reproduction in *Peromyscus leucopus*: The cost of lactation. *Ecology* 59:1055-1061.
- Millar, J. S. 1981. Pre-partum reproductive characteristics of eutherian mammals. *Evolution* 35:1149-1163.
- Millar, J. S. 1984. The role of design constraints in the evolution of mammalian reproduction. *Acta Zool. Fennica* 17:133-136.
- Mitchell, B., D. McCowen, and I. A. Nicholson. 1976. Annual cycles of body weight and condition in Scottish red deer. *J. Zool.* 180:107-127.
- Morton, J. R. C., V. H. Denenberg, and M. X. Zarrow. 1963. Modification of sexual development through stimulation in infancy. *Endocrinology* 72:439-442.
- Myrcha, A., L. Ryszkowski, and W. Walkowa. 1969. Bioenergetics of pregnancy and lactation in the white mouse. *Acta Theriol.* 12:161-166.
- Nagy, K. A. and G. G. Montgomery. 1980. Field metabolic rate, water flux, and food consumption in three-toed sloths (*Bradypus variegatus*). *J. Mamm.* 61:465-472.
- Nagy, K. A., R. S. Seymour, A. K. Lee, and R. W. Braithwaite. 1978. Energy and water budgets in free-living *Antechinus stuartii* (Marsupialia: Dasyuridae). *J. Mamm.* 59:60-68.
- Nicoll, M. and S. D. Thompson. 1987. Basal metabolic rates and energetics of reproduction in eutherian mammals: Marsupials and placentals compared. In A. Loudon and P. A. Racey (eds.), *Reproductive energetics of mammals*, pp. 7-27. Oxford University Press, Oxford.
- Oftedal, O. T. 1980. Milk and mammalian evolution. In K. Schmidt-Nielson, L. Bollis, and C. R. Taylor (eds.), *Comparative physiology: Primitive mammals*, pp. 31-42. Cambridge University Press, Cambridge.
- Oftedal, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: A comparative review. *Symp. Zool. Soc. London* 51:33-85.
- Oftedal, O. T. 1985. Pregnancy and lactation. In R. J. Hudson and R. G. White (eds.), *Bioenergetics of wild herbivores*, pp. 215-238. CRC Press, Boca Raton, Florida.
- Ortiz, C. L., B. J. Le Boeuf, and D. P. Costa. 1984. Milk intake of elephant seal pups: An index of parental investment. *Am. Nat.* 124:416-422.
- Ostermeyer, M. C. 1983. Maternal aggression. In R. C. Elwood (ed.), *Parental behaviour of rodents*, pp. 151-179. John Wiley and Sons, New York.
- Partridge, G. G., G. E. Loble, and R. A. Fordyce. 1986. Energy and nitrogen metabolism of rabbits during pregnancy, lactation, and concurrent pregnancy and lactation. *Br. J. Nutr.* 56:199-207.
- Pond, C. M. 1977. The significance of lactation in the evolution of mammals. *Evolution* 31:177-199.
- Pond, C. M. 1984. Physiological and ecological importance of energy storage in the evolution of lactation: Evidence for a common pattern of anatomical organization of adipose tissue in mammals. *Symp. Zool. Soc. London* 51:1-32.
- Racey, P. A. 1973. Environmental factors affecting the length of gestation in bats. *J. Reproduct. Fert.* Suppl. 19:175-189.
- Racey, P. A. 1981. Environmental factors affecting the length of gestation in mammals. In D. Gilmore and B. Cook (eds.), *Environmental factors in mammal reproduction*, pp. 199-213. University Park Press, Baltimore, Maryland.
- Racey, P. A. 1982. Ecology of bat reproduction. In T. H. Kunz (ed.), *Ecology of bats*, pp. 57-104. Plenum Press, New York.
- Racey, P. A. and J. R. Speakman. 1987. The energy of pregnancy and lactation in heterothermic bats. In A. Loudon and P. A. Racey (eds.), *Reproductive energetics in mammals*, pp. 107-125. Oxford University Press, Oxford.
- Randolph, P. A., J. C. Randolph, K. Mattingly, and M. M. Foster. 1977. Energy costs of reproduction in the cotton rat, *Signodon hispidus*. *Ecology* 58:31-45.
- Reid, J. T. 1961. Nutrition of lactating farm animals. In S. K. Kon and A. T. Cowie (eds.), *Milk: The mammary gland and its secretion. II*. Academic Press, New York.
- Rosenblatt, J. S. and H. I. Siegel. 1983. Physiological and behavioral changes during pregnancy and parturition underlying the onset of maternal behavior in rodents. In R. W. Elwood (ed.), *Parental behavior in rodents*, pp. 23-66. John Wiley & Sons, New York.
- Rutberg, A. T. 1986. Dominance and its fitness consequences in American bison cows. *Behaviour* 96:62-91.
- Sadler, R.M.F.S. 1969. *The ecology of reproduction in wild and domestic mammals*. Methuen, London.
- Sadler, R.M.F.S. 1982. Energy consumption and subsequent partitioning in lactating black-tailed deer. *Can. J. Zool.* 60:382-386.
- Sampson, D. A. and G. R. Jansen. 1984. Protein and energy nutrition during lactation. *Ann. Rev. Nutr.* 4:43-67.
- Schmidt-Nielson, K. 1984. *Scaling: Why is animal size so important?*. Cambridge University Press, Cambridge.
- Short, R. V. 1985. Species differences in reproduction mechanisms. In C. R. Austin and R. V. Short (eds.), *Reproduction in mammals 4. Reproductive fitness*, pp. 24-61. Cambridge University Press, Cambridge.
- Slonaker, J. R. 1925. The effect of copulation, pregnancy, pseudopregnancy and lactation on the voluntary activity and food consumption of the albino rat. *Am. J. Physiol.* 71:362-394.
- Small, M. F. 1981. Body fat, rank, and nutritional states in a captive group of rhesus macaques. *Int. J. Primatol.* 2:91-95.
- Smith, B. W. and J. J. McManus. 1975. The effects of litter size on the bioenergetics and water requirements of lactating *Mus musculus*. *Comp. Biochem. Physiol.* 51A:111-115.
- Soholt, L. F. 1977. Consumption of herbaceous vege-

- tation and water during reproduction and development of Merriam's kangaroo rat, *Dipodomys merriami*. *Am. Midl. Nat.* 98:445-457.
- Speakman, J. R. and P. A. Racey. 1987. The energetics of pregnancy and lactation in the brown long-eared bat, *Plecotus auritus*. In M. B. Fenton, P. A. Racey, and J. M. V. Rayner (eds.), *Recent advances in the study of bats*, pp. 367-393. Cambridge University Press, Cambridge.
- Stack, H. 1985. The energetics of reproduction in *Eptesicus fuscus*, the big brown bat. Ph.D. Diss., Boston University.
- Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41:173-187.
- Stebbins, L. L. 1977. Energy requirements during reproduction in *Peromyscus maniculatus*. *Can J. Zool.* 55:1701-1704.
- Stewart, R. E. A. 1986. Energetics of age-specific reproductive effort in female harp seals, *Phoca groenlandica*. *J. Zool.* 208:503-517.
- Struhsaker, T. T. 1967. Behavior of elk (*Cervus canadensis*) during the rut. *Z. Tierpsychol.* 24:80-114.
- Studier, E. H. 1979. Bioenergetics of growth, pregnancy and lactation in the laboratory mouse, *Mus musculus*. *Comp. Biochem. Physiol.* 64A:473-481.
- Studier, E. H., V. L. Lysengen, and M. J. O'Farrell. 1973. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). II. Bioenergetics of pregnancy and lactation. *Comp. Biochem. Physiol.* 44A:467-471.
- Taub, D. M. (ed.) 1984. *Primate paternalism*. Van Nostrand Reinhold, New York.
- Taylor, C. R., N. C. Heglund, T. A. McMahon, and T. R. Looney. 1980. Energetic cost of generating muscular force during running. *J. Exp. Biol.* 86:9-18.
- Thomas, D. C. 1982. The relationship between fertility and fat reserves of Peary caribou. *Can. J. Zool.* 60:597-602.
- Thompson, S. D. and M. E. Nicoll. 1986. Basal metabolic rate and energetics of reproduction in therian mammals. *Nature* 321:690-693.
- Tiefer, L. 1969. Copulatory behavior of male *Rattus norvegicus* in a multiple-female exhaustion test. *Anim. Behav.* 17:718-721.
- Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell (ed.), *Sexual selection and the descent of man, 1871-1971*, pp. 136-179. Aldine, Chicago.
- Vernon, R. E. and D. J. Flint. 1984. Adipose tissue: Metabolic adaptation during lactation. *Symp. Zool. Soc. London* 51:119-140.
- Wang, G. H. 1925. The changes in the amount of daily food-intake of the albino rat during pregnancy and lactation. *Am. J. Physiol.* 71:736-741.
- Widdowson, E. M. 1981. The role of nutrition in mammalian reproduction. In D. Gilmore and B. Cook (eds.), *Environmental factors in mammal reproduction*, pp. 145-159. University Park Press, Baltimore, Maryland.
- Williamson, D. H. 1980. Integration of metabolism in tissues of the lactating rat. *FEBS Lett.* 117: k93-k105.

