AMER. ZOOL., 36:197–204 (1996)

Trade-offs in Energy Allocation During Lactation[1]

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SYNOPSIS. During lactation, mothers require energy to meet both maternal and offspring requirements. If a mother exports too much energy to dependent offspring (in milk), her weight loss may be excessive and maternal risk may increase. Conversely, too little energy allocation to offspring may reduce the growth rate or induce mortality of dependent offspring. This paradigm was evaluated in cotton rats (*Sigmodon hispidus*) supporting small (3 pup) and large (6 pup) litters from early to late lactation. Several types of evidence indicate that physiological constraints limit the ability of mothers with large litters to provide resources to offspring. Mothers with large litters produced a dilute, energy-poor milk and their rates of food intake, weight loss and energy export per litter appeared to approach physiological maxima. Whereas the energy exported to pups in small litters increased from early to late lactation, the energy flow per pup in large litters was consistently low; consequently, offspring in large litters had low growth rates. An increase in either maternal food intake or weight loss (catabolism of maternal tissue) could have provided additional energy to offset the low growth rate of pups in large litters. However, mothers with large litters did not substantially increase their food intake or weight loss compared with mothers supporting small litters. These results indicate that the maternal support of offspring in large litters is limited. The pattern of energy allocation shown by cotton rats with large litters likely reflects a compromise between meeting maternal and offspring energy requirements (*cf.*, Parker and Macnair, 1979). The energy flow is greater than optimal for the parent but less than optimal for the offspring. Less maternal-offspring conflict occurs in small than large litters because offspring in small litters maintain a high growth rate at a relatively low maternal cost. Yet, under favorable environmental conditions, the reduction in maternal-offspring conflict has no apparent fitness benefit.

INTRODUCTION

Mammals experience unique types of developmental, physiological and environmental constraints, yet their patterns of maternal investment are in many ways analogous to those of other taxa. Thus, several papers in the symposium demonstrate the importance of the environment, maternal size and ontogenic (age-related) effects in evaluating maternal-offspring interactions. These sources of variation also are critical in evaluating maternal effects of mammals (*e.g.*, Pond, 1977; Martin, 1984; Oftedal, 1984; Bronson, 1985; Kurta and Kunz, 1987; Gittleman and Thompson, 1988). Mammalian species are particularly well-suited for the study of maternal effects because the time period of mother-offspring interactions is protracted. Maternal influence occurs during three major phases: gestation, lactation and the post-weaning period of development. Nutrient and energy flow between the mother and offspring are important during gestation and lactation;

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[1] From the symposium *Maternal Effects on Early Life History: Their Persistence and Impact on Organismal Ecology*, presented at the Annual Meeting of the American Society of Zoologists, 29–30 December 1993, at Los Angeles, California.

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parental care and training of the offspring are crucial during later stages of development. Maternal effects on mammalian young can last several years, particularly in taxa such as primates that have an extended period of juvenile dependence (*e.g.*, Altmann, 1983).

Maternal effects are frequently evaluated by examining variables at one point in time (*e.g.*, maternal weight; ova weight at a specific stage; neonate weight at birth or weaning), rather than time-dependent variation (*e.g.*, the rate of weight gain by ova or neonates). However, an emphasis on rates of change provides more detailed information to evaluate ongoing maternal-offspring interactions. For instance, the rate of maternal food intake can affect the mother's ability to export nutrients and energy to dependent offspring during pregnancy and lactation, which in turn can influence rates of prenatal and postnatal growth.

One indicator of the magnitude of maternal effort is the extent to which a mother's rate of food intake increases during periods of maternal effort (compared with periods when no offspring are supported). Investigations of small mammals indicate that the average rate of food intake increases by 9–32% during gestation and 66–146% during lactation (Kaczmarski, 1966; Migula, 1969; Randolph *et al.*, 1977; Millar, 1978), and that peak rates during lactation are even higher (Hammond and Diamond, 1992). These results illustrate that lactation imposes a far greater energetic burden on mothers than does gestation (comparative data are not available for the post-weaning period). Thus, many researchers interested in evaluating reproductive effort have focused on examining interactions during lactation.

Recent investigations confirm that lactation is energetically demanding, and indicate that the maternal energy requirement at peak lactation can approximate the maximum for sustained work (Kirkwood, 1983; Weiner, 1987, 1989; Peterson *et al.*, 1990). Mothers appear to approach an upper limit or "ceiling" to their rate of energy assimilation during lactation (Kenagy *et al.*, 1989, 1990; Mover *et al.*, 1989; Hammond and Diamond 1992, 1994). In an apparent response to the high rate of food intake during lactation, digestive accommodation can occur in which the gut expands and becomes more absorptive (Souders and Morgan, 1957; Fell *et al.*, 1963). However, the increase in nutrient uptake associated with gut hypertrophy may not keep pace with the increase in food intake at peak lactation (Hammond and Diamond, 1992). Thus, constraints on digestion and energy assimilation may occur.

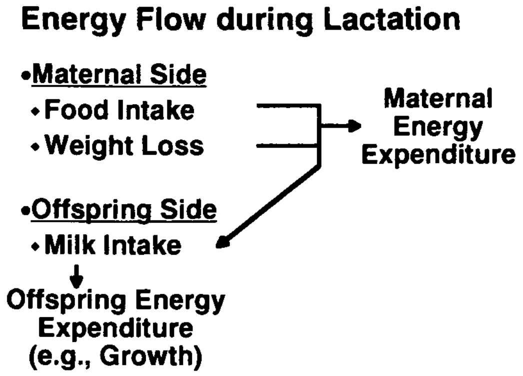

FIG. 1. Patterns of energy flow in mother-offspring groups during lactation. Maternal food intake and weight loss provide metabolizable energy that is allocated for maternal use or exported as milk to maintain offspring.

Energetic costs and benefits of lactation can be visualized by examining pathways of energy flow between the mother and offspring (Fig. 1). The mother obtains energy for metabolic processes either by increasing food intake or through weight loss (catabolism of body tissues). Part of the energy derived from these sources is allocated for maternal energy expenditures, and part is allocated as milk to support the growth and development of offspring. Although food intake often provides the major source of energy for lactating mammals (*e.g.*, Millar, 1975), catabolism of maternal body tissue also comprises an important energy source (Randolph *et al.*, 1977; Weiner 1987). For instance, many pinnipeds such as phocid seals fast during lactation. In these species the energy derived from maternal weight loss provides the sole source of chemical energy for milk provisioned to offspring (Bowen, 1991; Costa, 1991). Weaning (not shown in Fig. 1) commences near the end of the lactation period, and is typically a gradual process in which solid food eventually substitutes completely for the provided milk.

The patterns of energy flow illustrated in Figure 1 indicate that trade-offs and conflicts may occur during lactation. Benefits to offspring (*e.g.*, enhanced growth) have an associated maternal cost (*e.g.*, maternal weight loss). If the mother allocates too much of her resources to offspring by supplying an excess flow of nutrients and energy in milk, she may lose weight excessively and increase her risk of mortality. Conversely, an insufficient rate of energy export to young may decrease postnatal growth or cause offspring mortality. To what extent should the mother allocate her resources to offspring rather than conserve resources to meet maternal requirements? The decision may have important fitness consequences.

The idea that conflicts can occur between the mother and offspring has been in the literature for many years, and Trivers (1974) presents the first models that incorporate the important role of the offspring that stand to benefit from maternal resources. Trivers reasons that weaning is in the interest of a lactating mother, but not the suckling young; thus maternal-offspring conflict may be most intense near the time of weaning (late lactation). Other work has clarified and expanded arguments related to parent-offspring conflicts. For example, the expression of conflict may vary depending on whether the parental investment is derived from one or two parents (Parker and Macnair, 1979; Parker, 1985; Lazarus and Inglis, 1986 and others), and in sexually dimorphic species whether the parental resources are allocated to male or female offspring (Clutton-Brock, 1991; Redondo *et al.*, 1992).

Despite the rather extensive theory on trade-offs in parental effort, few investigations provide empirical data to test the theory (*cf.*, Fuchs, 1982). In his comprehensive review, Clutton-Brock (1991) points out specific areas where data are needed. One theory that has been examined to some extent is the potential trade-off between current and future parental investment (Williams, 1966; Trivers, 1972; Pianka and Parker, 1975). That theory predicts that the total parental investment in reproduction should vary depending on parental ability and environmental conditions; decreasing parental investment particularly during periods with adverse environmental conditions should permit an increase in a parent's future reproductive contribution. An implicit assumption of this theory is that the parent's investment into reproduction is inversely related to its investment in somatic tissue, hence a large parental investment would decrease a parent's ability to support future reproduction. However, parental investment into somatic and reproductive tissue is not always reciprocal, and investment into reproduction may not always occur at the expense of somatic tissue (Tuomi *et al.*, 1983). Indeed, parental investment during lactation occurs either by increasing food intake (no negative effect on parental somatic tissue), or by catabolizing maternal tissue (a short-term negative effect on somatic tissue offset by weight gain after the lactation period). Data are scarce, but neither type of investment may be sufficient to decrease a mother's future reproductive ability, unless food or other resources are limited (*cf.* Clutton-Brock *et al.*, 1989).

A CASE STUDY: CONSTRAINTS ON LACTATION IN *SIGMODON HISPIDUS*

I reexamined results pertaining to energy flow during lactation in cotton rats (*Sigmodon hispidus*) (Rogowitz and McClure, 1995) to evaluate patterns of maternal investment and maternal-offspring conflict. Unlike altricial rodents, which are born naked and seemingly helpless, cotton rats are relatively precocial; they develop pelage, movement ability and thermoregulatory ability relatively early during ontogeny (Scheck, 1982). The maternal cost of lactation should be higher in cotton rats than in mothers supporting relatively altricial offspring because they require additional energy to support the thermoregulatory and activity costs of young.

I present data for F1 and F2 generations of field-caught cotton rats that were maintained in the laboratory with food and water available *ad libitum*. Males were removed

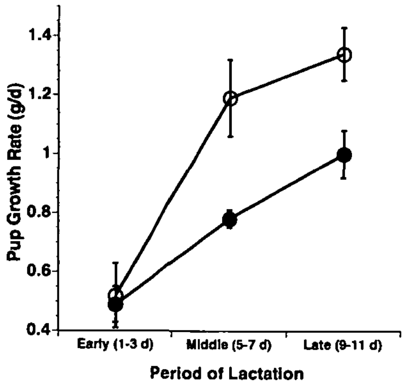

FIG. 2. Growth rates of cotton rat pups in small (3 pup, open circles) and large litters (6 pup, closed circles) during early, middle and late lactation (mean ± SE). Data are for both sexes; growth rates of male and female pups were similar (ANOVA, $P = 0.17$).

TABLE 1.. *Body weights and rates of food intake and weight loss in cotton rat mothers with small or large litters (mean ± SE).**

Variable	3-Pup Litters	6-Pup Litters	P
Body weight (g)	134 (4.5)	134 (4.4)	0.956
Food intake (g/d)	13 (0.6)	15 (0.6)	0.046
Weight loss (g/d)	3.3 (0.4)	3.4 (0.4)	0.961

* Probability values (P) for comparisons between small and large litters were derived by analysis of variance.

from the cages of females prior to parturition to insure that a new pregnancy did not occur during lactation. Maternal effort and its effect on offspring growth in small and large litters was examined during early (days 1–3), middle (days 5–7) and late lactation (days 9–11). The minimum age of weaning is 12 days in cotton rats (McClure, 1987).

Note that lactating cotton rats do not appear to invest resources preferentially into one sex. Male and female cotton rat pups have similar body weights (ANOVA, $F_{(1,133)} = 2.38$, $P = 0.12$) and daily growth rates (ANOVA, $F_{(1,133)} = 1.90$, $P = 0.17$) during the suckling period.

Consider the energetic costs and benefits of lactating mothers and their dependent offspring. In a situation in which the total energy requirement of offspring increases (*e.g.*, with a larger-sized litter), does the mother's export of chemical energy (in milk) increase in order to maintain a high rate of offspring growth, or is the allocation of maternal resources limited? If the energy allocation to pups is decreased, it may retard their growth or cause mortality, but on the positive side, it could reduce maternal risk, particularly if maternal ability to increase energy assimilation is limited (*cf.* Kenagy *et al.*, 1989, 1990; Mover *et al.*, 1989; Hammond and Diamond, 1992, 1994).

The variables of interest in this study included the mother's rates of food intake and weight loss (two sources of metabolizable energy), the rate of energy export in milk and the growth rate of suckling pups. All variables were measured gravimetrically, except energy export in milk (kJ/d), which was derived from the product of the energy content (kJ/g) and flow rate (g/d) of milk (for details, see Rogowitz and McClure, 1995). The energy content of milk was measured by combusting milk samples in a microbomb calorimeter. The flow rate of milk was determined from the fraction of water in milk, and the water influx to tritium-labeled pups after correcting for uptake of exogenous tritium (with unlabeled controls) and any intake of water from nonmaternal sources. Most (>95%) of the intake of suckling pups was from imbibed milk.

The first major pattern that emerged was a significant difference in the growth rate of offspring in small (3 pup) and large (6 pup) litters (Fig. 2). This pattern did not occur due to differences in maternal size; body weights of mothers supporting large and small litters were similar (Table 1). The cause of the low growth rate of pups in large litters was a low rate of energy transfer in milk (Fig. 3A). The energy flow to individual pups in large litters was consistently low during lactation. In comparison, the energy flow to pups in small litters was higher and accelerated from early to late lactation. Individual growth rates of pups varied depending on the rate of energy flow in milk (Fig. 4). On average, individual pups in large litters obtained 73.7% of the energy flow and grew at 71.2% the rate of pups in small litters. Despite the low rate

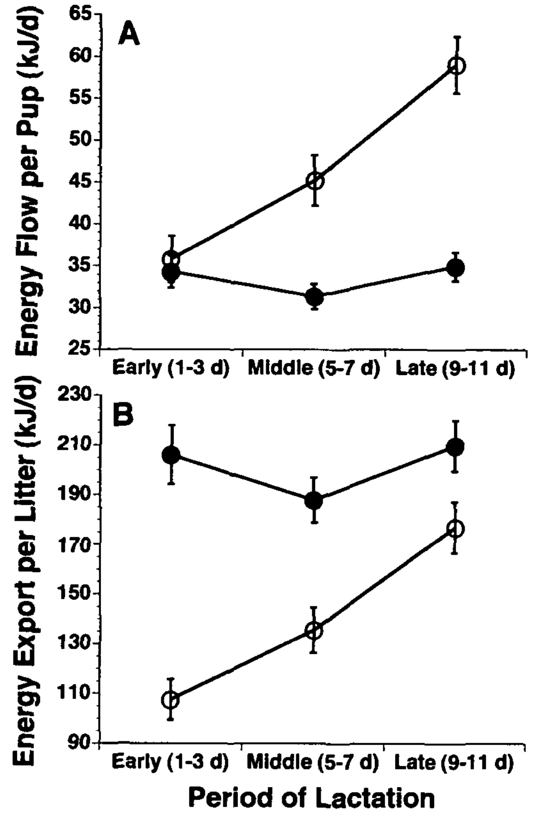

FIG. 3. Rates of energy export (in milk) to cotton rat pups in 3-pup (open circles) and 6-pup litters (closed circles). Energy export per offspring (A) and per entire litter (B) are shown (mean ± SE).

of energy transfer to individual pups in large litters, no mortality occurred.

Why were mothers with large litters exporting less energy to individual offspring and hence producing pups with relatively low growth rates? *A priori* one would expect mothers to nourish their young to the best of their ability in order to maximize their fitness. Several results indicate that physiological constraints limited the ability of mothers with large litters to export additional energy (see Rogowitz and McClure, 1995). Compared with mothers supporting small litters, mothers with large litters produced milk with a low energy content per dry mass throughout lactation. They also produced a dilute milk (with a low percent of solids) during mid- to late lactation. Third, their milk transfer to individual pups was less than that exported to pups in small litters, which may be caused by increased competition among offspring for a limited milk supply. Fourth, their rate of energy export to entire litters of 6 pups was higher than that of mothers supporting 3 pups (Fig. 3B), and it remained high from early to late lactation (max. = 280 kJ/d), further suggesting that an upper limit for energy export had been reached. This limit likely depends on factors such as maternal body size and ambient conditions, and is estimated here for mothers with a mean weight of 134 g maintained at 23–26°C.

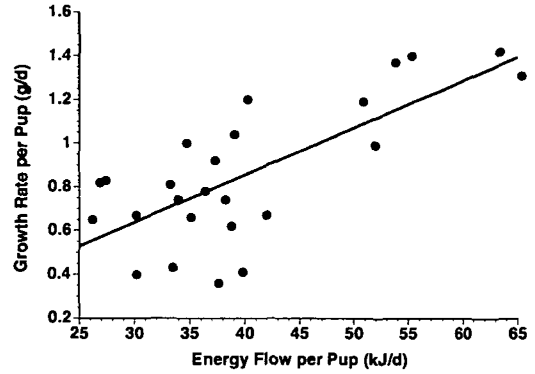

FIG. 4. Influence of energy flow in milk (X) on individual growth rates of cotton rat pups (Y): $Y = -0.009\ (0.175) + 0.022\ (0.004)\ X$ ($r = 0.73$, $P < 0.001$).

Two other indications that mothers with large litters approached a limit for energy allocation were that they did not substantially increase their rates of food intake or weight loss over levels shown by mothers with small litters. Their food intake was marginally higher than that of mothers with small litters, and their weight loss was equivalent to that of mothers supporting small litters (Table 1).

EVALUATING TRADE-OFFS IN ENERGY ALLOCATION

Do lactating mammals put themselves at risk to provide resources for their offspring, or do they limit their allocation of energy resources to young in favor of self-preservation? Results for cotton rats suggest that the latter is true. Cotton rat pups in large litters obtained much less energy and consequently grew much less rapidly than did pups in small litters, yet mothers supporting large litters did not counteract this by increasing their per capita energy allocation to offspring. Indeed, several types of evidence such as their production of dilute milk and the plateau in energy flow to litters (Fig. 3B) indicate that mothers with large litters reached an upper limit for energy export to offspring. A significant increase in either maternal weight loss or maternal food intake could have supplied additional energy to compensate for the low growth rates of pups in large litters. However, mothers with large litters did not risk excessive weight loss in order to provide additional energy for offspring growth (they lost weight at a rate similar to that of mothers with small litters), and their rate of food intake also was insufficient to offset the slow growth of their offspring.

These results suggest that under conditions of maternal exertion, self-maintenance of the mother takes precedence over the maintenance of individual offspring. Published information for other mammals supports this hypothesis. For example, dependent neonates often die (due to abandonment or cannibalism) or have low growth rates under cold or stressful conditions, particularly in large litters, whereas their mothers usually survive and can subsequently reproduce (Cameron, 1973; Fuchs, 1982; Heasley, 1983; Myers and Master, 1983; Kaufman and Kaufman 1987; Perrigo 1987; Rogowitz, unpublished data). Mothers with large litters presumably do not make a conscious decision to limit maternal care under suboptimal conditions. It is more likely that their limited maternal support comprises an evolved energy-sparing mechanism, which permits self-preservation and a chance of future reproduction.

The reproductive tactic of cotton rats supporting large litters seems to involve maintaining a level of energy allocation to suckling young as high as possible without exceeding physiological limits. Several types of evidence described above indicate that mothers with large litters approached their upper limit for energy export. Providing additional chemical energy to offspring could have put them at risk. Mothers with only three pups were able to steadily increase their energy export per pup during lactation, consequently the growth rates of their pups accelerated from early to late lactation. In contrast, mothers supporting six pups never provided sufficient energy to permit the rapid growth of pups. Studies of Knight *et al.* (1986) and König *et al.* (1988) also indicate that milk flow constrains offspring growth in large litters.

The low maternal investment of cotton rats into offspring in large litters was not a response to adverse environmental conditions. All mother-offspring pairs, with large or small litters, obtained food and water *ad libitum*, and encountered the same moderate conditions. Instead, the pattern of investment likely reflects a physiological compromise between providing for maternal and offspring requirements, similar to the "pro-rata" model of Parker and Macnair (1979) in which the parent is sensitive to offspring demands but supplies only a portion of those demands. That model predicts that a parent will supply more energy than its optimum, but less than the optimum for offspring. In the case of cotton rats supporting large litters, the rate of energy export was not optimal but closer to maximal for the mother, and it also was much lower than the optimum for offspring growth. Nonetheless, all of the slow-growing offspring in large litters survived to weaning under the favorable environmental conditions of the study. Thus, by maintaining maternal integrity, *e.g.*, not losing too much body weight while attempting to meet offspring needs (albeit not fully), mothers with large litters still achieved a high fertility. In contrast, the lactation effort of mothers with small litters favored increased offspring growth. Their allocation of energy during lactation was closer to the optima for both the mother and offspring because the pups achieved a high growth rate at a relatively low maternal cost until late lactation (when the maternal cost approached that of mothers supporting large litters). Although the conflict between meeting parental and offspring energy requirements was less in small than large litters, all offspring survived to weaning regardless of litter size. Thus, the reduction in maternal-offspring conflict associated with supporting a smaller-sized litter under favorable conditions provided no immediate fitness benefit. A delayed effect on fitness also was unlikely because mothers that supported small or large litters were observed to reproduce again without a significant time lag, and offspring from small and large litters rapidly attained reproductive maturity under the favorable study conditions. These results suggest that a reduction in maternal-offspring conflict may enhance fitness only under adverse environmental conditions.

ACKNOWLEDGMENTS

I thank Joe Bernardo for the invitation to share my perspectives on maternal effort and maternal-offspring conflict in this symposium, and Indiana University for providing intramural support.

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