

Evolutionary strategies in lactation: nutritional implications

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The classical view of lactation is one of complete altruism. The mother devotes all her energies, except only those necessary to maintain her own life, to care for her young in order for the young to survive and reproduce. Mother bountiful gives her young the best of everything until they are old enough not to want any more milk. In this world, milk is available in virtually unlimited quantities and of a composition perfect for growth and development. Although lactation is recognized as an enormous drain on the mother, the emphasis is one of unstinting physiological and behavioural altruism. In this view of parental care, the young were seen as passive receivers of all their mother could provide.

This romantic view of lactation has been overturned mainly by Robert Trivers nearly 15 years ago in his analysis of the different selection pressures acting on parents and offspring (Trivers, 1974). Unfortunately, his work is not widely known amongst those whose interests in lactation lie in explaining how biological mechanisms work. This is a pity since the insights gained from such evolutionary analyses can throw much light on such topics as the control of the rate of milk secretion at different stages of lactation, mammary involution and milk composition.

The analysis of parental investment by Trivers (1974) was part of a re-emergence of evolutionary biology, from the doldrums of comparative anatomy and comparative physiology, as a dominant force in science. This re-emergence was at least in part due to W. D. Hamilton's masterly theory to explain the evolutionary basis of altruism on the basis of kinship. Hamilton's (1964) paper which picked up the thread from J. B. S. Haldane's writings on kinship and altruism in the 1950s is rightly regarded as a milestone in evolutionary theory on a par with the contributions of Darwin and Mendel.

Parent-offspring conflict

Trivers began his work because he observed for himself that relations between parents and offspring are not all sweetness and light, particularly at weaning. Conflict between offspring and parent can be intense, for example, in langur monkeys and baboons, the young becoming extremely aggressive to their mother when denied milk. Anyone who has kept a bitch with puppies will have seen the disdain and then outright aggression of the bitch to her young when they still try to suck at about 3 months of age. In other words, mothers do not care for their young for as long as the young wish to be cared for. This conflict, between the amount of maternal investment the mother is selected to give and the amount of maternal investment the young is selected to take, has been explained by Trivers from kinship theory. The key is that in most animals, including mammals of course, parent and offspring are not identically related: the offspring in an outbreeding system is related to the mother only by half. The interests of the mother are not therefore identical with the interests of the young. As Trivers (1985) puts it, 'there is an overlap of self-interest between parent and offspring but not an identity of self-interest'.

Cost-benefit analysis. Parental investment must be considered in two ways, on the one hand from the interests of the parent and on the other from the interest of the offspring. The selection on the parent has been to invest in its offspring to the extent of maximizing the number of offspring surviving to reproduce. The benefit in the analysis is therefore the extent to which the investment increases the survival of the present offspring, while the cost is the degree to which the investment decreases the parent's ability to invest in

other offspring, including those not yet born. Clearly, selection on the parent is to maximize the difference between benefit and cost. It is also evident that selection is strongly against over-investment in a particular offspring, since the parent's ability to produce further offspring would be impaired.

Selection pressure on the offspring is for it to devalue the cost it inflicts on its parents. In essence it is in competition with its siblings and potential siblings, and the extent to which it devalues the cost it inflicts depends on the degree of relatedness to its siblings, i.e. according to kinship theory. Selection would favour less devaluation of the cost to the mother with a closer degree of relatedness. Thus one would expect the young to be less demanding in, say, a species that is monogamous than one in which the father of the present offspring is less likely to be the father of future offspring (for example, in those monkeys in which the male is deposed at intervals). This aspect, of the effect of the degree of relatedness on the extent to which the young is selected to demand more than the mother is prepared to give, although crucial to the development of the theory, will not be explored further here. The key point is that because offspring are selected to devalue the cost of parental investment to the parent, the young demand more than the parent is selected to provide. It follows that the young will demand a longer period of parental investment than the parent is selected to give.

Time-course and termination of parental investment. Early in the period of parental investment, the benefit:cost ratio is high. But as lactation, now using lactation as an example of parental investment, continues, the offspring grows and the demands increase. Maternal resources for the future are decreasing, either because reserves used to fuel the early part of lactation need to be replenished, or because reserves are being drawn on increasingly to support milk secretion. Therefore, the cost of lactation, in terms of production of future offspring, increases and the benefit:cost ratio falls. When this ratio reaches unity, the mother is selected to terminate investment because beyond this point her overall reproductive success will suffer. Incidentally, from kinship theory, the offspring are selected to demand continued investment until the benefit:cost ratio equals the degree of relatedness of the siblings (half if full siblings or one-quarter if half-siblings) (for explanation, see Trivers, 1985).

Those who are accustomed to seeing animals in well-fed and housed conditions are sometimes tempted to forget the costs of lactation to the mother. But in the wild food may be hard to find and, in many species from a variety of habitats, breeding does not occur at the frequency achieved by well-fed, captive animals. For example, red deer '... are frequently in such poor condition at the end of the summer's lactation that they fail to conceive at the rut and so breed only in alternate years, recovering body condition in yeld years and losing body condition in calving years' (Loudon & Kay, 1984).

Trivers's (1985) analysis showed that it is the mother who sets the overall strategy of parental investment in terms of both quantity and time-course. While the overall strategy may be modulated by the young, there is ample evidence that the time-course of lactation is programmed genetically. During the period of marked parent-offspring conflict at weaning, the young may, of course, try a whole range of psychological tricks to induce its mother to continue investment. In some species (the horse and man are two examples) sucking may be permitted on occasions after weaning. The cost to the mother may well be negligible but the benefit to the offspring and to the mother's overall reproductive success may be high. In this case the transfer of anti-bacterial substances to young susceptible to infection may account for this continuation of low-cost parental care.

General features and adaptive strategies. While Trivers's (1985) analysis provided the broad outline of the selection pressures operating in parental investment, there are a

number of related aspects, litter size for example, that cannot be pursued here. But within this broad framework, different animals in different environments have evolved a range of adaptive strategies of reproduction. Since lactation is part of the whole reproductive process, it cannot be dealt with in isolation from the rest of the reproductive strategy. For example, it is self-evident that lactation must form the major part of parental investment in mammals which bear altricial young. Nevertheless general relationships have started to emerge both with respect to other aspects of reproductive strategy and to metabolic body size.

The recognition of general features and specific strategies is being helped greatly by allometric analysis of characters between species. Improvements in mathematical methodology and in reliable data bases are both important developments which have allowed the preliminary studies of Brody (1945), Payne & Wheeler (1968) and Hanwell & Peaker (1977) to be developed much further (see Martin, 1984; Oftedal, 1984). A great problem in such comparative studies is unreliable information, both for milk yield and composition (Peaker, 1977; Oftedal, 1984). For example, milk composition changes during lactation in many species; few reports of milk composition include the stage of lactation. In some species the milk removed from the mammary gland at the end of milk removal is richer in fat than that removed earlier; single small samples of milk may therefore yield meaningless information. Oftedal (1984) has drawn up a list of criteria for the inclusion of information on milk composition in allometric analyses. Information on milk composition has been published for about 200 species; but only in about one-quarter of these can the information be said to be reliable. Information on milk yield, other than in farm and laboratory animals, is difficult and expensive to obtain, so comparative studies of this type, needing large data bases, present a particular problem in the present climate for funding science. Whilst information gathering can be condemned in terms of Medawar's aphorism, 'Since Newton we need no longer record the fall of every apple', or as an indulgence in *aardvarkism* (i.e. repeat all your observations in every species and eventually get to the aardvark), there is still a genuine need for more reliable information from a number of mammalian phylogenetic lines.

An important grade shift in maternal investment has become evident from allometric studies (Martin, 1984; Oftedal, 1984): primates produce less milk of lower energy and protein contents than other mammals of similar body-weights. Grade shifts such as this can be seen in log-log plots of milk energy output, for example, *v.* body-weight. Points for the primates form a line below that for other mammals, while both lines have a similar slope of approximately 0.75, i.e. like metabolic rate varies with body-weight. Primates are therefore characterized by a low parental investment per unit time. Similarly, ungulates which normally bear one young have lower investments per unit time than animals which bear many young.

A general feature of milk composition is that both the total energy and protein contents of milk are negatively correlated with body-weight. But carnivores appear to be an exception. In those species studied so far, the larger ones (for example, the brown bear) have more concentrated milks than the smaller ones like the fox. Such information is useful since it indicates the specific need for related studies. More recent work in carnivores (see Gittleman & Oftedal, 1987) is uncovering layers of complexity of adaptation in life-history, metabolic rate and lactation. Many large members of the Carnivora are herbivorous-folivorous and it appears that their adaptive strategy is related to this diet.

While some general relationships and strategic adaptations like the ones described can be gleaned from allometric studies between species, other adaptive strategies may first become evident from observation and experiment. For example, some features of the

control of lactation in mice suggest that they may have been selected to suckle the young of close relatives in communal nests (see Knight & Peaker, 1982). Such an altruistic strategy may not be unexpected where kinship is close, especially since in times of nutritional plenty (the conditions such *r*-selected small mammals exploit by a rapid increase in reproduction) the cost of lactation to future reproductive potential appears to be relatively low (see findings of Fuchs, 1982).

In an article such as this it is impossible to describe the range of strategies that have evolved; the reader is referred to recent symposia (Peaker *et al.* 1984; Loudon & Racey, 1987).

Plasticity of adaptive strategies and the role of nutrition. The main part of this article has been concerned with genetically determined strategies and their evolution. A major question concerns the degree of plasticity of a strategy with changes in the environment. Natural selection would obviously militate against the evolution of a rigid strategy that could not exploit sudden natural benefits or cope with moderate natural shortages of resources. This is certainly the case with lactation, and everybody knows that nutrition affects the rate of milk secretion. The duration of lactation in a number of species also varies with nutrition, but all aspects of lactation do not show the same degree of plasticity: nutritional effects on milk composition are relatively minor. Trivers (1985) defined parental investment as anything done for the offspring, including building it, which increases the offspring's reproductive success at a cost to the remainder of the parent's reproductive success. Thus, lactation can be considered subject to proximate investment analysis by the maternal organism against the background of the genetically determined strategy. When nutrition is not limiting and breeding does not have to be fitted into a tight seasonal window, clearly the investment analysis will come out in favour of the young. When food is short the outcome of the investment analysis is more complicated. In animals like man with long gestation periods and considerable investment needed over many years, the outcome may favour the offspring. At the other extreme, small rodents may kill some or even all their litter when the investment analysis indicates an unfavourable outcome to the present lactation. Incidentally, investment analysis has been introduced recently into the Civil Service in Britain as a means of appraising purchases; its introduction was regarded as a great step forward by government. It may be new to government but it has been around for a good few million years!

The questions for the nutritionists with interests in lactation are how and when investment analysis in lactation is carried out. Although we have a great deal of information on the proximate factors (for example, type, quantity, periodicity of food) that affect the quantity of milk secreted and the duration of lactation, and we know how the final hormone signals to the tissues involved are made, we know very little of how control is integrated. It would seem likely from studies on nutrition during pregnancy that a major investment analysis is made at about the time of parturition and involves the state of body reserves; the outcome of this analysis appears to set the, later, maximum rate of milk secretion, and indeed may also largely determine the duration of lactation. While enormous advances have been made in the understanding of biological control mechanisms operating within organisms, there are still many unanswered questions which evolutionary considerations can pinpoint and show the direction for future work. As a further example, there is substantial evidence that mothers can invest differentially in male and female offspring (males often need to be bigger to achieve reproductive success). How is this differential investment achieved?

Finally, lest the reader receives the impression that the writer is falling into the trap of believing every observation can be explained as adaptive if only one thinks long and hard enough, there are still simple findings that seem hard to explain. For example, if a goat

receives no food for more than a few hours (a short period of starvation for a ruminant), the rate of milk secretion falls precipitously, but is restored a few hours after food is restored (Linzell, 1967). There appears to be no fail-safe mechanism to protect the offspring. However, in early lactation milk yield bounces back fully after starvation; in late lactation it does not. At least that effect could be predicted from the general strategy of parental investment!

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