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Energetic limits to brood care: influences on fertility, and longterm fitness consequences

Energetische Limitierung der Brutpflege: Einflüsse auf die Fertilität und langzeitige Fitneßkonsequenzen

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Summary

Physiology and ecology of animals set energetic limits to reproduction. The way in which these limits influence life histories of females is explored. Energetic limitations force trade-offs between the differing demands of self maintenance and growth (somatic effort) on the one hand, and reproduction (reproductive effort) on the other. The optimal strategy of parental investment is one which allocates the available resources such that maximal reproductive success is achieved at a minimal cost to the parent. Such trade-offs are difficult to measure since they can be hidden by variance in individual quality and allocation strategy. Experimental manipulations, however, demonstrate intra-individual trade-offs in which adult females trade present reproductive success against future survival (less frequently) or future fertility (more commonly). There is, however, also a more complex trade-off between generations. Here reduced reproductive effort of the parent may lead to reduced quality (fertility or survival chances) of offspring. The exact pattern of such trade-offs is adapted to the life-history of a species. Longterm maternal effects of this sort considerably complicate fitness measurement. The physiological mechanisms which lead to these trade-offs are largely unexplored, but ontogeny apparently plays a major role.

Introduction

Females increase reproductive success (RS) by garnering more resources whereas for males the best way to again additional RS is to get access to more mates (Bateman 1948, Trivers 1972, Clutton-Brock 1988). Through the process of selection, this leads to entirely different reproductive strategies of males and females, a fact which was recognized by Darwin and induced him (1871) to formulate his theory of sexual selection.

If the main avenue to increased RS for females is to acquire and convert resources then selection should make them particularly proficient at doing so. Nevertheless, during brood care, bird and mammalian females often work at the limits of their capacity (Drent and Daan 1980, Loudon and Racey 1987, Trillmich 1986) suggesting that energy and nutrient resources in the environment are limiting female reproductive output. Behavioral ecology tries to determine which strategies – within the limits of the organism's physiological capacity – permit an animal to achieve maximal RS under conditions of limited resources. Of course, males face the same kind of problem when competing for access to mates, but this problem will not be addressed here (see Kenagy et al. 1989).

Evidence for the limits on energy acquisition and use

An organism's capacity for acquiring and processing food is limited by physiological and ecological constraints. There are two kinds of physiological constraints:

1) Metabolizable energy intake is limited by the ability to process food (Kirkwood 1983).

Constraints on the digestion and uptake of food are mediated by limited gut length and by limited rates of food degradation und uptake into the system following digestion. This leads to an allometric formula for maximal metabolizable energy which Kirkwood (1983) gives as $ME_{max} = 1713 * \text{body mass}^{0.72}$ (KJ/day).

2) Energy output also is limited by the work capacity of an animal. Drent and Daan (1980; see also Masman et al. 1990) made a strong argument that parent animals cannot work continuously, i.e. over a period of days, with an energy output much beyond 3–4 times basal metabolic rate, a work load which for man corresponds to heavy wood cutting.

In addition to the phsyiological constraints on energy use there are also ecological limits. In most environments, food is not available in unlimited quantity. Under conditions of ecological stress it may even become so short in supply that parents abandon their breeding attempts and are forced to channel all available energy into selfmaintenance. This became evident with particular clarity during the 1982–83 El Niño event in the eastern Pacific where pinnipeds and sea birds experienced a severe food shortage leading to complete abandonment of breeding and sometimes severe adult mortality (review in Arntz and Fahrbach 1991, Trillmich and Ono 1991 in press). Furthermore, parent animals work under constraints of limited time for gathering food in the natural environment (e.g. Meijer et al. 1989, Trillmich 1990).

Optimal allocation and trade-offs in energy use

How then are brood care strategies of females organized to make the best use of limited resources of energy and nutrients? Given all the afore mentioned limitations the conclusion becomes inevitable that animals are faced with an allocation problem (Williams 1966), i.e. they cannot simultaneously use the available resources to support the needs of (i) self maintenance, (ii) growth of the parent, and (iii) reproduction. If not all of these demands can be fully satisfied trade-offs among the different functional needs have to be made (Sibly and Calow 1986). Trivers (1972) first formalized this idea in his theory of parental investment following the logic of Fisher's (1930) definition of reproductive value. Parental investement is defined by Trivers as all effort expended on offspring which increases their fitness at the expense of the parents fitness (Fig. 1 a). Decreases in parental fitness can derive either from a decrease in parental survival or a decrease of its fertility in future reproductive episodes. The best brood care strategy then is one which produces maximal gain in offspring fitness at a minimal loss to the parent's ability for future reproduction (Fig. 1 b).

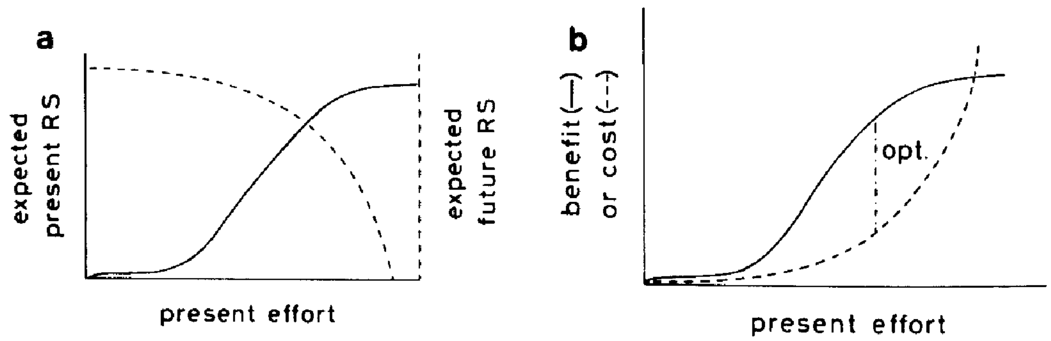

Fig. 1: A graphical model of parental investment. a – Costs to parents and benefits to offspring (measured as reduced/increased expected future survival and fertility) increase with increasing parental effort. b – The optimal strategy results in the maximal net fitness gain to parents. It is located where the difference between the cost of a given parental effort and the benefit (reproductive success) achieved by expending that effort is maximal.

Methodological problems in the demonstration of trade-offs

Can such trade-offs actually be shown? Assuming that parental effort can be measured adequately in terms of the number of offspring reared to independence one would predict that parents which reared most offspring should survive less well or show lower fertility in the next reproductive period than parents which expended less effort. When I measured survival in relation to breeding effort in the European Starling *(Sturnus vulgaris)* the prediction of a trade-off was not upheld (Fig. 2). Local survival, as measured by females' return rate to the breeding colony in the next year, correlated positively with the number of young reared to independence in the previous year.

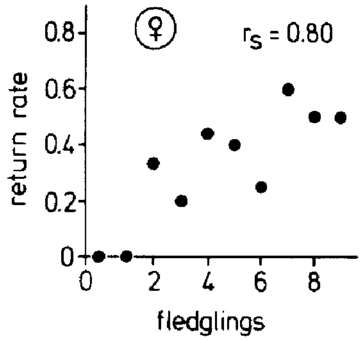

Fig. 2: Local survival of female Starlings is positively correlated with the number of fledglings reared in the previous year (Trillmich unpubl. data).

Why does this simple test not produce the expected result? The measurement makes the hidden naive assumption that all animals are equal in their foraging and parenting abilities. It thus ignores the fact – well established by Darwin and basic to selection theory – that variability in the quality of individuals is ubiquitous and is the raw material of selection. If some individuals are more efficient at gathering and using resources then they may well expend more on somatic effort (i.e. self maintenance) as well as reproductive effort than less efficient parents. This idea which says that resource availability differs among individuals is graphically presented in Fig. 3 (van Noordwijk and de Jong 1986). If individuals dispose of varying amounts of resources, but allocate these resources in a similar manner then a positive correlation between somatic and reproductive effort must be found in the population (Fig. 3a). On the other hand, with similar resource levels but varying allocation a negative correlation between the two measures will be found (Fig. 3b) (van Noordwijk and de Jong 1986).

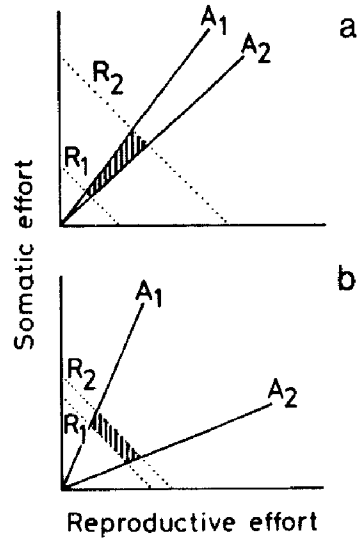

Fig. 3: Measured correlations between reproductive and somatic effort depend on relative variances in resource availability (or quality of individuals) (a), and variance of resource allocation to different functions within a population (b). Various combinations of the two factors can produce everything from positive, over zero, to negative correlations making experimental investigation of trade-offs necessary (after van Noordwijk and de Jong 1986).

Intra-individual trade offs

A situation of near identical resources but varying allocation can be created experimentally if clutch or brood size is manipulated up and down from its natural size. By such a manipulation, birds of a given quality – judged by their self-selected clutch size – can be forced to expend more or less of their energy on parental effort. In effect, the experimental manipulation artificially creates more variance in allocation of available resources to reproduction than is found under natural circumstances. This leads to the kind of increased variance in allocation assumed in Fig. 3b. Now the effect of deviations from the natural brood size on fertility and survival of parents can be tested.

A study by Gustafsson and Sutherland (1988) on the collared flycatcher *(Ficedula albicollis)* in Gotland, Sweden, provides an excellent example. The authors manipulated clutch size by increasing or decreasing it one or two eggs and comparing the breeding success, survival, and fertility of the parents with those of control animals whose clutches were not manipulated. No decrease in survival of adult birds was noted, but fertility of females decreased in the year following the rearing of an increased clutch and furthermore, even though more young were fledged in increased clutches, recruitment of such young to the breeding population showed a marked peak at the natural clutch size (Fig. 4).

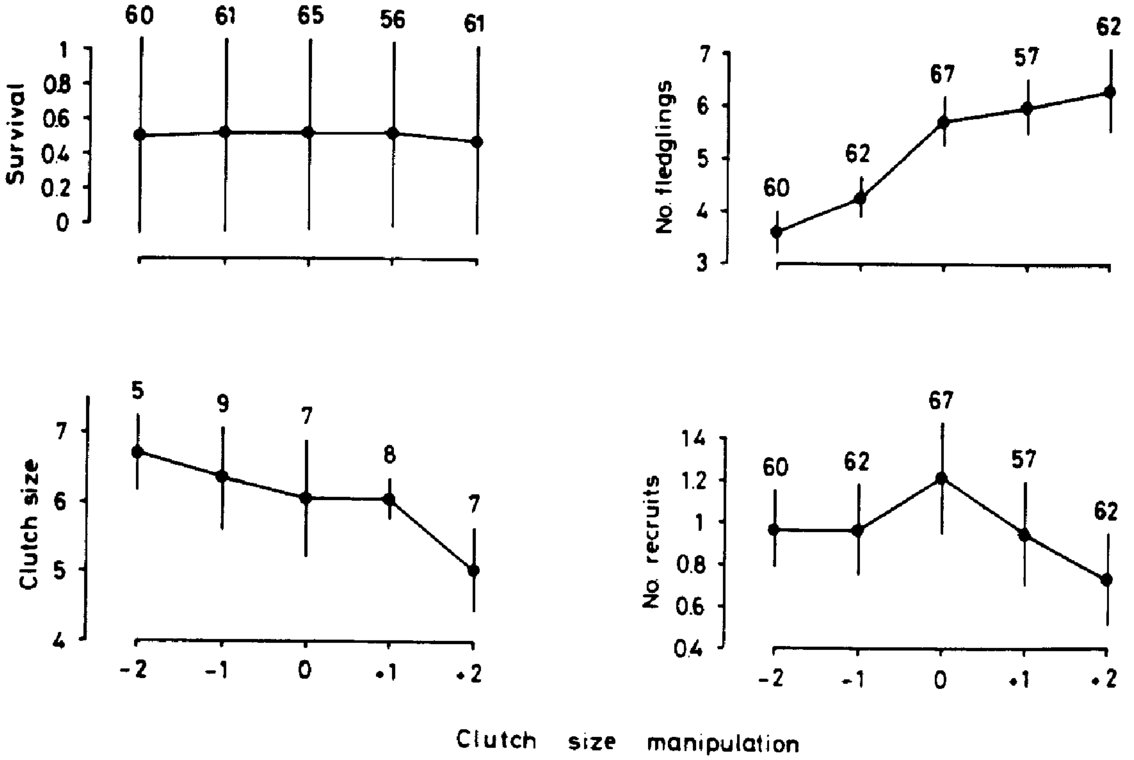

Fig. 4: The effects of clutch size manipulation on life history parameter in collared flycatchers *(Ficedula albicollis)*. Upper left panel: adult female survival is unaffected by clutch size manipulations. Upper right: Larger clutches produce more fledged young. Lower left: female fertility correlates negatively with the extent of clutch size manipulation. Lower right: Production of recruits to the population peaks at natural clutch size and decreases in reduced and enlarged clutches (from Gustafsson and Sutherland 1988).

Survival and recruitment of young greatly depends on fledgling mass. Fledgling mass is largest in smallest clutches, which however, cannot contribute very many fledglings because numbers are limited. Mass is intermediate in normal sized broods which produce most recruits, but the many young of enlarged broods leave the nest at low body mass such that survival is compromised to the extent that it leads to lower overall recruitment to the breeding population than at the natural brood size.

In birds, fertility trade-offs as demonstrated in the example of the collared flycatcher are generally more common than survival trade-offs (Lindén and Moller 1989). This makes intuitive sense since passerine adult birds have much better survival chances than recently fledged young and, therefore, can expect higher future reproductive success than their young. In other words, selection is expected to act on life histories so that parents are less likely to trade their own survival and probability of future reproduction against the much lower chances of survival and reproduction of their young. Such an interpretation is supported by the fact, shown before in the collared flycatcher example, that the probability of recruitment of young to the breeding population is much lower than survival chances of the parents (Fig. 4; see also Tinbergen and Daan 1990).

Trade-offs across generation boundaries

The previous example already showed a trade-off across generations in enlarged broods of the collared flycatcher: not only did maternal fertility decrease the year after rearing an increased brood (intra-individual trade-off), but young of enlarged broods also suffered reduced recruitment to the breeding population. We observed an inter-generation trade-off in which part of the cost of reproduction are transferred to the offspring. Such inter-generational trade-offs can be structured in many ways which appear to be adapted to the life history of the species concerned. Perrigo (1987, 1990) provided a particularly striking example of the contrasting ways in which parent-offspring conflict (sensu Trivers 1974) about maternal investment is resolved in house mice *(Mus musculus)* versus deer mice *(Peromyscus maniculatus)* (Fig. 5). When mice were experimentally food limited during lactation female house mice reduced the number of young (usually by cannibalizing young), but maintained weaning mass and weaning age, whereas deer mice weaned almost the same number of young but at much reduced weaning mass and opted to extend the lactation period often much beyond normal weaning. Perrigo (1990) interpreted this difference by suggesting that house mice are opportunistic breeders which breed year round. For them, a life history strategy which produces large young rapidly is more adaptive since population density is almost always relatively high and only large young have a high probability to survive to breeding age and establish in the population. Once established they can breed immediately because the environment is largely aseasonal.

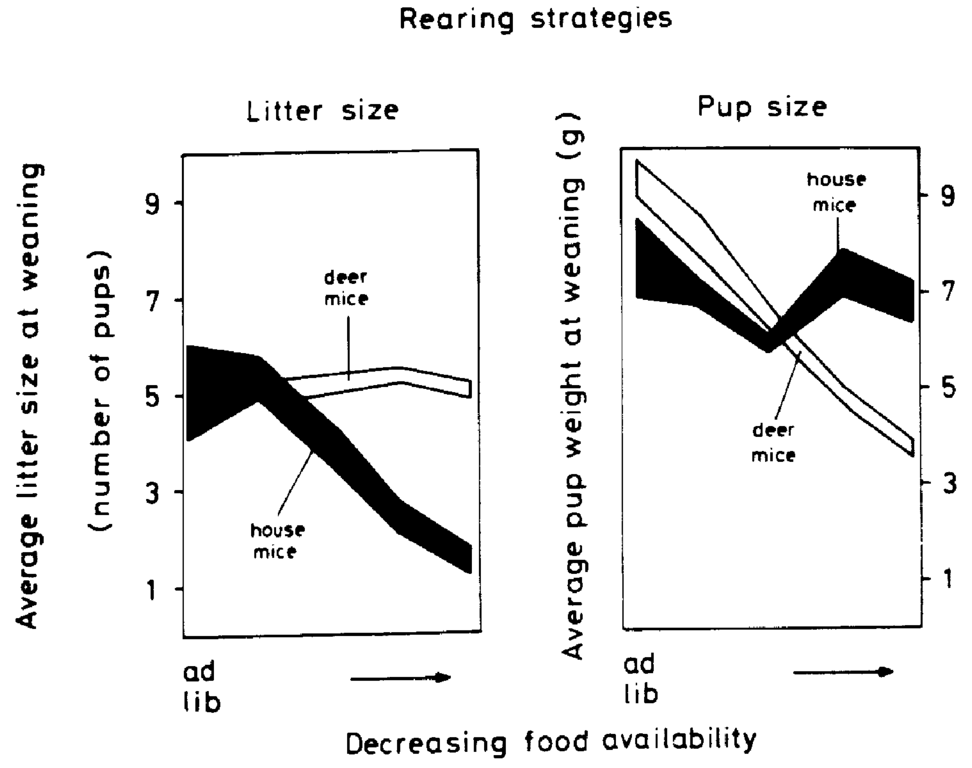

Fig. 5: Rearing strategies in house *(Musa musculus)* and deer mice *(Peromyscus maniculatus)*. For explanation see text (changed after Perrigo 1990).

In contrast, deer mice are seasonal breeders and most of their young will not breed before the spring following their birth. Because of a short breeding season, females have little chance to replace young which die during the lactation period. It may then be the better option to produce many small young because these young can grow throughout the winter, the non-breeding season, in effect catching up growth which they could not achieve during the rearing period. Such a reproductive strategy may contribute most young to the next generation or the next season when breeding will again become possible. In both these solutions the young incur the major cost of reproduction, in the case of the house mice these are survival costs that are borne by the young, not the mother, and in the case of the deer mouse young suffer from reduced body mass which may reduce survival through the winter and perhaps reduce fertility throughout the life of the young (see below). Clearly this interpretation is preliminary and needs more empirical research into the life history of these two species before it can be accepted without reservation.

Strategies of trade-off across generation boundaries can be very flexible. In the Galapagos fur seal *(Arctocephalus galapagoensis)* time to weaning of the single young varies greatly according to environmental circumstances, from one to three years. Fur seals have a post-partum estrus and delayed implantation which, in principle, would lead to a yearly cycle of pupping (Trillmich 1990). In years of high food abundance, young Galapagos fur seals can be weaned as yearlings whereas in poor years young remain with the mother and may be nursed until they are three years old. Even though they begin to forage independently of the mother at about 8 months of age, independent foraging apparently does not produce enough returns to support yearlings in poor years.

The flexible rearing strategy permits females to rear young under almost all conditions of food availability (but see Trillmich and Limberger 1985 and above for the rare food shortages during El Niño). There is, however, a price to be paid for this flexibility in time to weaning by both mother and young: when food conditions are poor pup growth rate is reduced and as a consequence the body mass of yearlings varies greatly from year to year (Trillmich 1990). This leads to variance in age at weaning and, therefore, age at first breeding, reducing the expected fertility of late weaned young which begin to reproduce a year later than early weaned young. On the other hand, there are also costs to the female. If a female has lactated in the year before the birth of her next young she is less fertile. Instead of a 90% birth rate as in non-lactating mothers, her probability of giving birth to a pup in the following year is reduced to about 33% (Trillmich unpublished data). This reduced fertility is decreased even more because small yearlings compete fiercly with a newborn for maternal milk. The newborn, even though it is defended by its mother against the aggression of the older sibling, loses in this competition and may starve to death. The probability of losing the newborn correlates negatively with the body mass of the yearling which accompanies its mother. Very heavy yearlings, reared in good years, will not compete with the newborn but forage on their own. Under those conditions, newborns can grow up just as if they had no older sibling. If, however, older (half-) silblings are small (≤ 10 kg) the newborns' probability to starve to death is close to one. Thus again part of the cost of reproduction is transferred to the young. In this case a large part of the trade-off is decided behaviorally between the young of two different cohorts with some mediating by the mother who usually initially defends the newborn against attacks by the previous young (Trillmich 1990 and unpubl. data).

Rearing decisions by the mother which affect the body mass of offspring can be considered maternal effects and are poorly explored. Such maternal effects were demonstrated to influence fitness for more than one generation. Huck and coworkers (Huck et al. 1986; Huck and Labov 1987) studied longterm maternal effects in the syrian hamster *(Mesocricetus auratus)*. They food restricted female hamsters during the period of lactation to about 70% of *ad libitum* food intake. Female offspring (the parental generation) were from then on always kept under ad libitum conditions.

Offspring of these females (F1) grew more slowly than young of control females which had been reared under ad libitum conditions (Huck et al. 1986). Moreover, the daughters (F2) in these litters which had never experienced food restriction reared fewer young, and produced

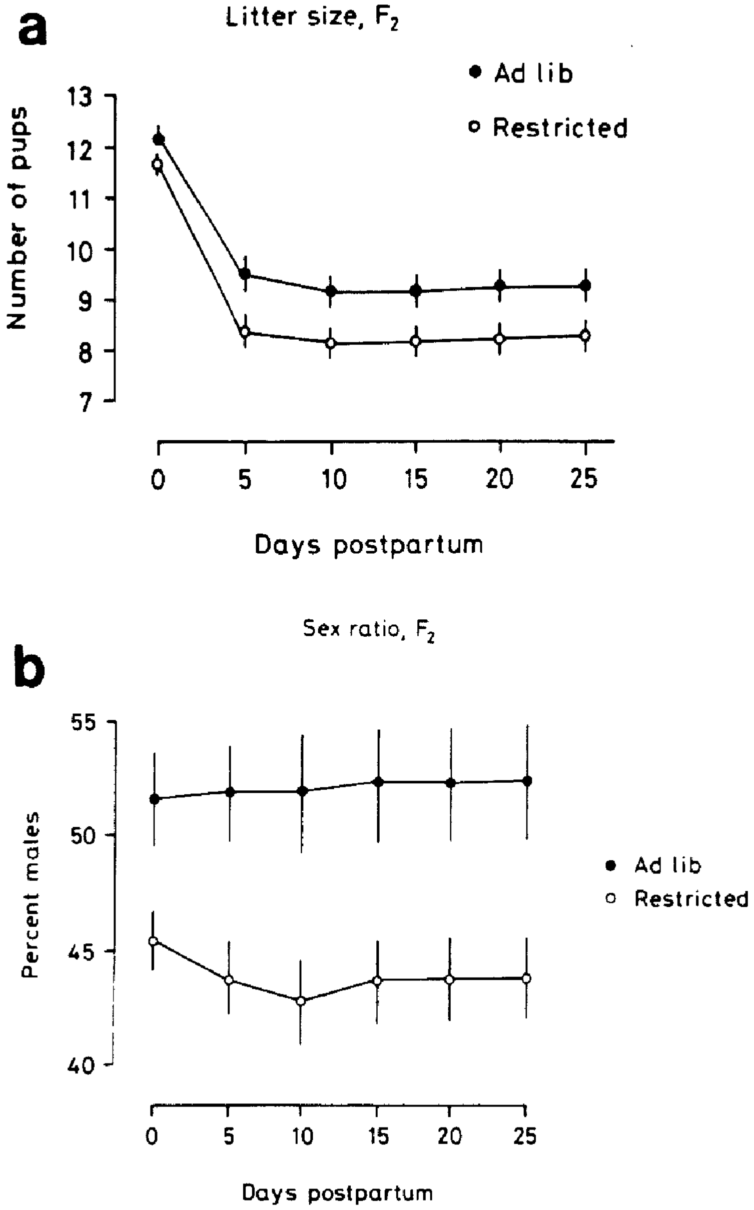

Fig. 6: The effects of food limiting females (F1) during the time when they were nursed by their mothers on reproductive properties of their daughters (F2). a – number of young reared by females whose mothers had been food restricted during their ontogeny in comparison to control females reared under ad libitum conditions. b – the same for the sex ratio in litters of F2 – and control females (changed after Huck and Labov 1987).

fewer and lighter male pups in their litters (Huck and Labov 1987) (Fig. 6). Similar effects were found in house mice by Christian and Lemunyan (1958) indicating that longterm maternal effects may occur in many species, and that inter-generational trade-offs (Stearns 1989) are perhaps more commonly employed for the solution of energy allocation problems in animal reproduction. It is not at all clear which physiological mechanisms create the observed longterm maternal effects on offspring-female fertility across generational boundaries.

Conclusion

Energetic limitations have serious implications for the reproductive strategy of animals. This is made abundantly clear by the examples described. Necessarily, limitations of energy and nutrients lead to trade-offs which are a characteristic feature of reproductive strategies.

Even though such trade-offs were frequently shown, however, the exact form of the trade-off curves is generally unknown because they are exceedingly difficult to measure given all the biological variability among individuals of a species and among their environments. Knowledge of such a trade-off curve is, however, necessary to determine if allocation is really optimal. Physiological mechanisms which lead to the observed trade-offs are generally unexplored. One of them might operate during the ontogeny of young. When rearing conditions are suboptimal young may grow up to become low quality individuals which throughout their life can never compete very successful or can never command as many resources as young having grown up under more favourable circumstances. Thus maternal effects may provide the basis for some of the differences between individuals in their resource acquiring abilities postulated by van Noordwijk and de Jong (1986). We need to pay more attention to the measurement of trade-offs across generations and to the physiological mechanisms involved.

A crucial premise for the argument of selection producing better adapted phenotypes is the inheritance of characters. If non-inherited traits (maternal effects) influence competition between individuals this complicates our measurement of fitness considerably. Under those conditions the outcome of competition has a strongly attenuated effect on the character state in the population because selection will be less direct. If inter-generational trade-offs are common and have strong, longterm influences on the fitness of individuals we will have to measure fitness effects across a number of generations and cannot be content with the usual counting of young weaned/fledged or even of young recruited which is difficult enough. Intergenerational trade-offs thus add a further dimension of complexity to the theoretical and empirical determination of optimal allocation of resources to reproduction. The research program addressing this problem necessarily demands longterm research of the life history strategy of individuals and of the consequences for offspring. Such longterm research is, however an absolute requirement if we are to understand the complexity of the adaptations in life history strategy.

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