

*Symbiosis in
Parent-Offspring
Interactions*

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CHAPTER 11

*Costs and Benefits of Mammalian
Reproduction*

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**Parasitism and Symbiosis: Metaphors of Mammalian
Mother-Young Interaction**

The relationship between parent and offspring is only one type of intimate association between living organisms observed in nature. Infants, parasites, symbiotes: all participate in relationships characterized by metabolic dependence between participants. This multiplicity of naturally occurring dependent relationships is useful in the study of parental behavior because an analysis of one type of intimate association can provide insight into others. For example, viewing the developing mammal as a parasite of its mother¹, as a metabolically dependent active exploiter of its dam, can suggest ways of analyzing parent-offspring relationships not apparent from more traditional perspectives (Galef, 1981).

Parasitism is only one type of intimate association which could serve as a metaphor for the association between mother and young (see Alberts & Gubernick, Chapter 2). The defining characteristics of a parasitic relationship

¹ The relationship between dam and young is analagous to that between host and parasite only at a somatic or phenotypic level of analysis. The presence of maternal genes in a dam's offspring and the absence of a host's genes in its parasite makes the analogy unworkable at the genetic level (see Galef, 1981, for further discussion). As I am concerned in the present chapter with the effects of reproduction on the soma of dams, the analogy may be useful.

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are injury inflicted by the parasite on its host and absence of benefits returned to the host by its dependent (LaPage, 1963). In other types of intimate association such as symbiosis² or mutualism, each participant provides the other with benefits. Thus the appropriateness of the terms *symbiosis* or *parasitism* as metaphors of the phenotypic relationships between mammalian mothers and altricial young depends on whether the dam suffers somatic costs in bearing and rearing offspring and whether the young return benefits to their dam. If juveniles deplete their dam or place their dam at risk, reducing her chances of subsequent reproduction, a parasitic metaphor of the mother–young relationship would seem appropriate. If on the contrary, rearing a litter enhances or leaves unchanged a parent’s future reproductive potential, the interaction between mother and young is more akin to a symbiotic than a parasitic relationship.

For reasons both theoretical (see below) and intuitive, I and many others have assumed that the demands made on a dam by a litter considerably reduced her future fecundity. The pertinent literature search convinced me that this matter is not as straightforward as I had thought. Reproductively active mammals have behavioral and physiological strategies that may negate the potential costs and risks associated with reproduction. Further, reproductively active individuals can garner phenotypic benefits from their grown offspring, benefits that may outweigh any residual reproductive costs. Consequently, young mammals may act as phenotypic symbiotes rather than phenotypic parasites of their dams.

Parental Investment and Life History Tactics: Theories and Data

Trivers (1972) has defined parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the expense of the parent’s ability to invest in other offspring” (p. 139). The “other offspring” in Trivers’s definition could be either contemporaries of the individual receiving parental investment or products of reproductive episodes subsequent to that in which the individual under consideration was born. Trivers’s model is clearly suitable for discussing the relationship among individuals born in a single reproductive episode. However, even if resources can be provided to one

² There is some inconsistency in the biological literature concerning the use of the term *symbiosis* (Whitfield, 1979). Some authors employ *symbiosis* as a generic term to refer to any intimate association of animals or plants of different species regardless of whether the metabolic dependence is unilaterally or mutually beneficial. In this case *mutualism* is used to specify an association in which the interactants benefit one another. I have used *symbiosis* in the dictionary or ordinary sense to refer to an association advantageous to both participants and not harmful to either.

member of a litter only by denying resources to others, engaging in a reproductive episode does not necessarily lessen the ability of reproducers to provide resources for future offspring.

It is frequently postulated that engaging in a reproductive episode compromises an individual's probability of future successful reproduction. Bell (1980, p. 47), for example, suggested that any increase in fecundity is attained only at the expense of adding to the mortality risk. Similarly, Schaffer (1974) and Charlesworth and Leon (1976) hypothesized that reproduction is costly because it involves a commitment of available resources to reproduction, rather than to self-maintenance and growth. Assertions that reallocation of resources or increased mortality are phenotypic costs of reproduction are useful because they raise significant empirical issues. Is it the case, as Bell suggested, that reproductively active females have a reduced probability of survival? Do females, in fact, allocate resources necessary for their own growth and maintenance to their young?

While answers to these questions may seem obvious, they are not. For example, the hypothesis that reproduction necessarily involves allocation by a dam to her young of resources that she would otherwise utilize for self-maintenance or growth assumes that the resources exploited by an individual are environmentally limited. If, to the contrary, resource acquisition by reproductively inactive individuals living in adequate environments is self-limited rather than environmentally limited, then it would not be necessary for reproductively active individuals to sacrifice growth or self-maintenance to reproductive activity. Reproductively active individuals might simply devote more time to resource acquisition than reproductively inactive individuals. There is no *a priori* reason that the reproductively active individual need make phenotypic sacrifices during reproduction.

The need for empirical verification of hypotheses concerning the somatic costs of reproduction has been recognized, but the confirming evidence is surprisingly weak. Bell (1980) referred readers to Stearns (1976) and Calow (1977) for examples of reproduction increasing mortality. Examination of Stearns's original sources regarding increased mortality in reproductively active female mammals generally either provides no support for the hypothesis that fertility increases mortality or is irrelevant to it. Among those cited in Stearns (1976, p. 17) or Calow (1977, p. 569), Geist (1971, p. 300) only suggested that barren female mountain sheep may have a better chance of survival than those pregnant or suckling. He called for empirical investigation of that hypothesis, rather than presenting evidence to support it. Berger (1972, p. 162) suggested that increased mortality in olive baboon females at the "assumed" beginning of the adult stage (47–52 months) "may represent mortality incurred during the first pregnancy or birth," but he provided no evidence that

this is so.³ Numerous studies showing that “half-starved domestic animals are relatively infertile” (Maynard & Loosi, 1962, p. 434) do not directly support the hypothesis that fertility increases mortality. In fact, such evidence suggests that animals do not attempt to reproduce if reproduction would be phenotypically costly.

In subsequent sections, I have reviewed literature relevant to the costs and benefits resulting from female mammalian reproduction, particularly in rodents. The questions I have addressed are whether and how reproductive episodes affect future fecundity. I have focused attention on rodents because of the wealth of laboratory data on reproduction in that order and the necessity of experimentation under controlled conditions to evaluate the costs of engaging in many reproductive activities.

It might be argued that data collected in the laboratory are inadequate for appraising the effects of reproduction on survival or fecundity, because laboratory-maintained subjects are protected from a variety of factors that affect the costs and risks incurred by females engaging in reproduction in natural circumstances. Unfortunately, studies in nature can rarely be sufficiently well controlled to permit unequivocal determination of the causes of any observed changes in mortality or fecundity associated with reproduction. Reproductively active and inactive members of free-living populations surely differ prior to self-assignment to the two reproductive states. In consequence, interpretation of field studies of reproductive effects on future fitness is difficult. For example, Richdale (1957) found that 3-year-old penguins that had previously reproduced (in their second year) lost only 18% of their eggs prior to hatching, while penguins reproducing for the first time in their third year lost 30% of their eggs during incubation. While these data have been interpreted as demonstrating a “negative cost” of reproduction in 2-year-old

³ I have not had the opportunity to examine in detail all the references cited by Calow and Stearns regarding the cost of reproduction in iteroparous species. However, in each case that I have examined, the data have not carried the message attributed to them. Two further examples will suffice: (1) Clough (1965) found no effects of reproductive activity on resistance to starvation in voles (*Microtus pennsylvanicus*) but did find that reproducing females had a significant “slightly lower resistance,” as measured by survival time in 9.5°C water, than nonbreeding females of similar weight; (2) barnacles lose weight following reproduction, either as the result of expulsion of egg masses (Crisp & Patel, 1961) or as the result of a reduction of feeding activity (Barnes, 1962). However, the effects of loss of weight on future fecundity are not established. Williams (1962) stated that curtailed growth “would mean lowered fecundity in the next breeding season” (p. 172). Daly and Wilson (1978) suggested that “reproducers are more apt to be squeezed out by their neighbors and to lose the chance to reproduce again” (p. 129). Neither cited any reference to support these notions. The inconsistency in interpretation suggests that these are hypotheses concerning, not empirical observations of, effects of reproduction on future fecundity.

penguins (Bell, 1980), they are also consistent with the hypothesis that only the most reproductively capable penguins breed in their second year. Such confounds, while unavoidable, are the curse of unobtrusive field studies.

On the other hand, the generality of laboratory findings is open to question. They may provide an accurate description and a causal analysis of events unique to the laboratory itself and of little relevance to more general issues. Furthermore, in standard laboratory situations, many of the factors are absent that might differentially affect reproductively active and inactive individuals (e.g., predators, disease-bearing organisms, fluctuations in food supply and temperature, and social interaction with conspecifics). While it might be possible to introduce such variables into controlled settings, there will always be uncertainty about whether any controlled situation adequately reflects the challenges that organisms face in natural habitats.

In ideal circumstances, it would be possible to determine under controlled conditions both the magnitude of each cost and benefit (in terms of future fecundity) associated with reproduction, and the environmental range in which those costs and benefits influence reproducers. Such laboratory data could be used to model reproductive histories of natural populations subject to particular environmental pressures. Field data could determine the adequacy of laboratory results to account for observed breeding histories in the natural environment. The data necessary even to approach the ideal situation are simply not available for any species.

Bioenergetics of Pregnancy and Lactation

Potential Costs of Pregnancy and Lactation

The demand for nutrients that embryos and suckling young make on their dam certainly has the potential to reduce her capacity for self-maintenance. Individual offspring may grow to more than one-third their adult weight while still dependent on their dam for nutrition (guinea pigs; Paterson, 1967), and litters of suckling young may approach twice the weight of their dam before they wean (bank voles; Kaczmarski, 1966).

To provide for the growth of young, reproducing rodents require from 166% to 234% of the calories needed by reproductively inactive controls (Millar, 1979). Lactating rats and mice, respectively, contribute the equivalent of 44% and 110% of the calcium in their skeletons to their offspring (Simkiss, 1967). More generally, the requirements of lactating rats for the majority of essential dietary components are from 2 to 10 times the amounts needed by nonlactating individuals (Nelson & Evans, 1961).

Reducing Costs of Reproduction

The demand for nutrients that young place on their dam can be met in either of two ways: (1) the dam can increase her rate of ingestion and alter her selection of nutrients to meet the needs of her young, or (2) she can catabolize her own tissues for substances needed by her young (e.g., elephant seals). Some mammals (e.g., humans—Hyttén & Thompson, 1961; cotton rats—Randolph, Randolph, Mattingly, & Foster, 1977) employ a mixed strategy, increasing nutrient intake during pregnancy beyond the immediate needs of developing fetuses and self-maintenance, storing the surplus, and then catabolizing that surplus and passing it on to neonates during the nursing period, when the nutrient needs of the mother–young aggregate are greatest.

The first strategy, increasing nutrient intake, may be universal in rodents under laboratory conditions. It probably occurs whenever food is continuously available throughout pregnancy and lactation. Cotton rats (*Sigmodon hispidus*), for example, increase their food intake by 25% during pregnancy and 65% during lactation (Randolph *et al.*, 1977). In the laboratory rat, food intake increases 60% during pregnancy and from 180% to 250% during lactation (see Randolph *et al.*, 1977, p. 40, for further examples).

Reproductively active female rats (*Rattus norvegicus*) also increase their relative intake of specific nutrients, especially sources of protein, fat and calcium, if given the opportunity to do so (Richter, 1942). This increase mitigates the potential depletion of their reserves in meeting offspring demands.

Increased transduction of resources needed to meet nutrient requirements of a developing litter might appear to press a dam's capacity to process ingesta. However, reproductively active females are anatomically and physiologically quite different from nonreproductives. Pregnant or lactating laboratory rats, for example, exhibit increase in the length, weight, and absorptive capacity of their small intestine (Fell, Smith, & Campbell, 1963); increase in liver, kidney, stomach, and cecum weights (Fell *et al.*, 1963; Peter & Krynen, 1966; Souders & Morgan, 1957); and changes in blood hemoglobin (Bond, 1958; see Pond, 1978, and Widdowson, 1976, for further examples of reproduction-associated changes in morphology). Consequently, reproductively active females are able to process twice-normal quantities of food without sacrificing the efficiency with which they metabolize nutrients (Kaczmariski, 1966; Randolph *et al.*, 1977).

Some morphological alterations that accompany pregnancy and lactation are permanent. For example, the increase in liver size in rats results from increases in both the size and the number of liver cells. Following reproduction, the cell size returns to normal, while the cell number remains elevated, so rats that have reared litters have more cellular livers than those that have not

lactated (Kennedy, Pearce, & Parrott, 1958). Other morphological alterations caused by reproduction are relatively temporary. For example, the bone erosion that occurs in all parts of the skeleton during lactation, irrespective of dietary calcium level, is repaired whether the female becomes pregnant again immediately or not (Ellinger, Duckworth, Dalgarno, & Quenouille, 1952). As Widdowson (1976) has stated, "whether permanent or temporary, there is no evidence that any of the changes [in the structure of the dam's body] do her any ultimate harm" (p. 11).

Evidence of Success

That rodent dams maintained in the laboratory with *ad libitum* access to food, nesting material, and warmth transduce to their young considerably more energy than is required for their growth and development, while continuing self-maintenance and normal growth, is strongly indicated by a variety of findings.

First, female laboratory rats allowed to reproduce continuously grow *more* rapidly than controls maintained without access to males, as indicated by reproductively induced increase in tibia length and body weight (the latter corrected for increased weight of uteri, ovaries, and mammary glands) (Bogart, Sperling, Barnes, & Asdell, 1939). Cotton rats in laboratory settings show positive energy balance throughout pregnancy and lactation (Randolph *et al.*, 1977).

Second, females of a variety of rodent species (rat, mouse, gerbil, old-field mouse, etc.) can become sexually receptive shortly following parturition and consequently (at least under laboratory conditions) nurse one litter while gestating a second. If either pregnancy or lactation pressed the females' capacity to transduce nutrients, one would expect females simultaneously pregnant and lactating to have difficulty in caring for both litters. To the contrary, Bruce and East (1956) found no difference between the weight of mouse pups weaned by female mice impregnated in a postpartum estrus and those weaned by nonpregnant females. Furthermore, and surprisingly if one assumes that reproduction stresses the energy transduction capacity of the mouse dam, impregnated lactating females reared a greater percentage of litters and as many pups per litter as nonpregnant individuals. Also, removal of the senior litter from a lactating and impregnated dam *decreased* her success with the litter initiated in postpartum estrus from an average of 8.0 to 6.5 pups per litter (Bruce & East, 1956).

The picture in rats is similar. Lactating and impregnated females produce litters of the same size and growth rate as females caring for only a single litter. Removal of the senior litter has no effect on either the number of young rats per junior litter at birth or the growth rate and weaning success of

the junior litter (Babcock, Bogart, Sperling, & Asdell, 1940; Woodside, Wilson, Chee, & Leon, 1981). In the laboratory, lactating and nonlactating collared lemmings have litters of equal size (Hasler & Banks, 1975).

Such data do not suggest that laboratory reproduction is achieved at the expense of self-maintenance, and they are not consistent with the notion that reproductive females are pushed to the limits of their capacity to transduce nutrients. Rather, in supportive environments, females can both increase the resources they exploit, without sacrificing utilization efficiency, and select a modified spectrum of nutrients to meet the specific demands of reproduction. Thus, in energy-rich environments, they are able to maintain both themselves and a large number of offspring without deleterious consequences. Of course, females reproducing in natural circumstances may face environmentally imposed limits on resource transduction. (A discussion of strategies for coping with such environmental stress is on page 270.)

While field data on the effects of reproduction on survival in rodents are both difficult to collect and rare, Dapson (1979) has provided useful information on the old-field mouse (*Peromyscus polionotus*). He found, in general, that survival over two-month periods during the breeding season was independent of age even though the youngest age class was nulliparous, and the older classes contained many pregnant and many lactating females. The only exception was a disproportionate loss in the oldest age cohort in a population in which that cohort exhibited a high frequency of postpartum impregnation. While there is clearly a variety of interpretations of such correlational data, they do suggest that in free-living old-field mice, no cost is associated with simple reproduction, and some degree of risk is associated with simultaneous pregnancy and lactation.

Costs of Pregnancy and Lactation

Costs of Reproduction Per Se

Evidence that female rodents may be able to reproduce without incurring any obvious phenotypic cost by increasing both their capacity to transduce resources and their exploitation of external resources bears only indirectly on the question of the effects of one reproductive episode on subsequent ones.

If engaging in a reproductive episode reduces subsequent reproductive capacity in females, one would expect females to show decreased reproductive success with increasing parity. In the case of those mammalian species in which females deliver litters, loss of reproductive capacity might be reflected in either reduced litter size at birth or at weaning over successive parities.

Figure 1 presents data from a variety of sources (see figure caption for references) describing the mean size at birth of successive litters in Norway rats (both wild and domesticated), house mice, golden hamsters, old-field mice, Mongolian gerbils, bandicoots (*Perameles gunni*), and domestic sows. The data do not support the hypothesis that fecundity decreases with increasing parity. In every case, there was either a slight increase or no change in litter size at birth with successive reproductive episodes. It should be pointed out that if one extends such curves out to the tenth or fifteenth litter, a dramatic decrease in litter size is invariably observed. The difficulties in determining whether this decrease in number of young following 10 or more parturitions is the result of the effects of previous parturitions or of increasing age make data from older females difficult to interpret. For example, Porter (1967), in his experiment of most extreme outcome, found that laboratory rats that were first bred at 90, 120, and 200 days of age had, respectively, 7.2, 6.3, and 2.8 young per successfully breeding female. However, one might well expect that if participation in reproductive episodes *per se* reduced litter size, the cumulative effects of five or six reproductive acts should be perceptible. The

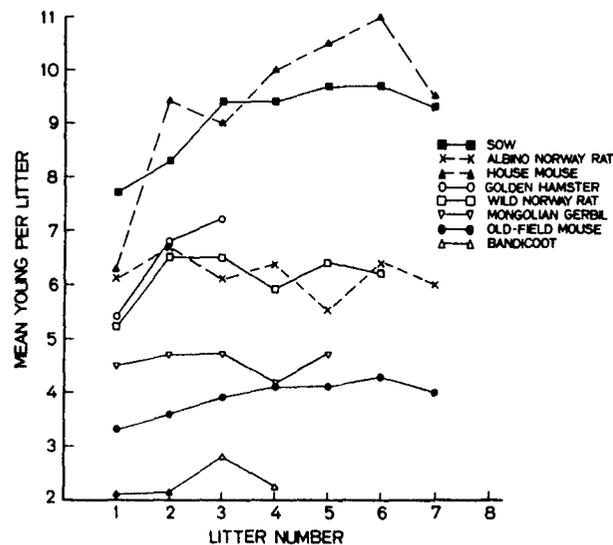


Figure 1. Number of young per litter at birth as a function of successive parturitions in the bandicoot (Heinshohn, 1966); the old-field mouse (Williams, Carmon, & Golley, 1965); the Mongolian gerbil (Marston & Chang, 1965; see also Tanimoto, 1943); the golden hamster (Day, 1976); the domesticated and wild Norway rat (King, 1924; see also Donaldson, 1924, p. 25); the house mouse (Biggers, Finn, & McClaren, 1962); and the domestic sow (Lush & Molln, 1942).

absence of such observable effect is not consistent with the hypothesis that reproductive effort reduces subsequent reproductive capacity.

It is interesting to note that in each case presented in Figure 1, as well as in a number of other data bases I have examined, the second litters were consistently larger than the first ones. It is also the case, at least in laboratory rats, that nearly 100% of females producing a first litter also produce a second (148 of 148; King, 1924), so the enhanced size of second litters cannot be due to differences in the sample of females producing first and second litters. The fact that increased size in second litters is found in female rats first bred at 306 days of age, as well as in those first bred shortly after puberty (Asdell, Bogart, & Sperling, 1941), indicates that the enhancing effects of a first parturition on a second are not simply the result of an age-related increase in litter size during the period immediately following the achievement of reproductive maturity. Taken together, the data suggest that first parturitions enhance second litter size and that subsequent parturitions have little effect on their successors.

In summarizing the results of what is, in my estimation, the most convincing study yet undertaken of breeding effects on future reproduction, Asdell *et al.* (1941) concluded that

1. Initiating breeding late in the life of a female rather than at the normal age *reduces* her reproductive ability by increasing the intervals between litters and reducing the size of litters.
2. The failure of females to give birth, with later resorption of fetuses, is *more* frequent in females first bred late in life than in those starting breeding early.
3. Virgin females show irregularities and cessation of estrus cycling earlier in life than do breeding females.
4. All females, regardless of their age at first breeding, produce more young and suckle them better after they have been reproducing "for a while" than they do in the first litter or two.

Such findings are consistent with the hypothesis that reproduction itself has a stimulative rather than an inhibitory effect on future reproduction. The only evidence presented by Asdell *et al.* (1941) of a reproductive cost involved females whose young were removed immediately following parturition. Females whose young were removed at birth produced subsequent larger litters than females suckling young. Unfortunately, Asdell *et al.* bred the females in the former group every 28 days and those in the latter group every 42 days (Babcock *et al.*, 1940), so one cannot tell whether there is a cost associated with lactation or a benefit associated with brief interpartum intervals. In either case, both females breeding and suckling young and those breeding and not suckling from 100 days of age had litters at 280 days of age as large as or larger than those beginning breeding and suckling at 280 days of

age, indicating that 180 days of reproduction (production of approximately four litters) had no adverse effect on future litter size.

The optimal, and rarely employed, experimental design for assessing the effects of previous reproduction on litter size involves matching females for breeding age and systematically varying their prior reproductive experience. I have been able to find only two studies using such a design, one by Day and Galef (unpublished observations), using golden hamsters as subjects, and one by Asdell *et al.* (1941), using rats. Both sets of data are presented in Figure 2. As is clear from an examination of the figure, in neither rats nor hamsters is there any sign of a previous breeding effect on the size of litters produced by females of a given age.

Data describing the effects of increasing parity on weaning success in rodents are far less common than those describing the effects of parity on litter size at birth. Asdell *et al.* (1941) found negligible effects of increasing parity in rats on either the percentage of young raised to 21 days of age or the weight of individual young at weaning. Marston and Chang (1965) reported no effect of successive litters on the number of pups weaned per litter by Mongolian gerbils, other than a tendency for mothers rearing first or second litters to be less successful in weaning young than those with greater reproductive experience.

Of course, parturitions could affect future fecundity not by reducing

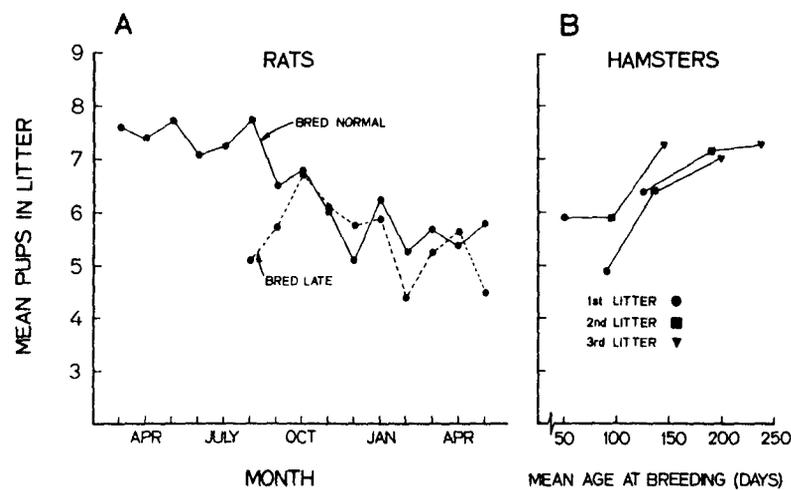


Figure 2. Panel A: Mean litter sizes of 50 female rats first bred either at 100 or 270 days of age (from Asdell, Bogart, & Sperling, 1941). Panel B: Mean litter sizes of 14 hamsters having first, second, and third litters at various ages (Day & Galef, unpublished observations).

litter size but by reducing the probability that a reproductively active female would survive or remain fertile. Babcock *et al.* (1940) determined the number of female rats either (1) first bred at the earliest possible date (approximately 65 days of age); (2) first bred at 100 days of age; or (3) first bred at 280 days of age still reproductively active after 365 days of age. They found no difference between the percentage of groups first bred at 100 and 280 days still breeding at 365 days, suggesting no effect of bearing from four to five additional litters on the survival or fertility in the group first bred at 100 days. It is relevant to note that the females bred as soon as they reached puberty (at approximately 65 days of age) exhibited almost twice the infertility rate at one year as did the females first bred at 100 and 280 days (13.5%), even though the females first bred at 65 days bore only one more litter, on average, than did the females in the 100-day group. Further, the per-female lifetime production of offspring was 10% less in the females first bred as early as possible than in those females first bred at 100 days of age. Taken together, these data suggest that reproduction does impose a reduction in survival or fertility on those female rats breeding prior to reaching full maturity, but not on those breeding in their prime.

In mice, there appear to be more important effects of breeding on future survival and fecundity. Suntzef, Cowdry, and Hixon (1962), for example, reported that the percentage of breeding female mice dying before 12 months of age (18%) is significantly greater than the percentage of breeding males or of virgin males or females dying in their first year (4%, 7%, and 6%, respectively). While providing clear evidence of a survival risk associated with reproduction, these data leave unresolved an important issue. It is, for example, possible that although engaging in a breeding episode carries a risk, that risk is reduced as a function of previous reproductive experience. Thus, although evidence of risk associated with reproduction is important, the effects of reproduction on that risk are equally so, and insofar as I know, there are no data available from which one can calculate the necessary conditional probabilities.

In sum, the extensive data available on rats suggest that the act of bearing and suckling a litter of young is more likely to augment than to reduce future fecundity. The limited data available on mice indicate an enhanced mortality resulting from reproductive effort *per se*.

Effects of Pregnancy and Lactation on Susceptibility to Infectious Disease

The data presented above, relevant to the question of the effects of reproductive episodes on their successors, offer relatively little support for the hypothesis that under laboratory conditions, each reproductive act carries an unavoidable cost in terms of future reproductive success. However, it is pos-

sible that a more focused examination of the specific potential costs associated with reproduction might provide a different picture. In the present section, I examine the possibility that reproductive activity increases the vulnerability of females to infectious disease.

A general review of the effects of pregnancy and lactation on immunological systems lies beyond both the scope of this chapter and the expertise of this author, and there is unfortunately no such review now available. However, even a superficial search of the literature reveals that changes in the endocrine system accompanying pregnancy and lactation have the potential to markedly alter the effectiveness of immunological defenses. Moderate levels of estrogen, for example, have been reported to increase body defenses by increasing phagocytic activity, raising serum γ -globulin levels, and increasing the rate of proliferation of antibody-producing cells (Kenny & Diamond, 1977; Nicol, Bilbey, Charles, Cordingly, & Vernon-Roberts, 1964). However, in large quantities estrogen is thymolytic and produces a depression in cellular immunity (Luz, Marques, Ayub, & Correa, 1975; Nelson, Hall, Manuel-Limson, Freidberg, & O'Brien, 1967). Thus, it is not easy to predict the net effects of reproductive activity on immunological defenses.

In those few studies in which the effects of pregnancy or lactation on response to artificially induced infection have been directly examined, the outcomes have been mixed. A number of investigators have reported increased susceptibility to disease in reproductively active animals. For example, both lactating and pregnant mice are more susceptible to foot and mouth disease than virgin controls (Campbell, 1960). There is also evidence of a pregnancy-associated depressed immunity to the rodent malarial parasite *Plasmodium berghei*, which results in a lethal recurrence of the disease during pregnancy in previously immunized mice (Van Zon & Eling, 1980).

The results of other studies indicate that susceptibility to disease varies as a function of the stage in pregnancy at which exposure to the infective agents occurs. Cotton rats (Weaver & Steiner, 1944) and possibly mice (Knox, 1950) are more resistant to murine poliomyelitic infection early in pregnancy than nonpregnant controls, but they are more susceptible to murine poliomyelitis and encephalomyocarditis virus late in pregnancy (Farber & Glasgow, 1968; Knox, 1950).

Pregnancy increases susceptibility to some strains of a virus but not others. Dalldorf and Gifford (1954) reported that mice become progressively more susceptible to severe infection with the pancreatic line of Coxsackie B-1 virus as gestation advances, but that neither the A-strain nor the brain line of the B-1 strain induces illness in pregnant animals.

Pregnancy can also change susceptibility to a disease by altering its portal of entry into the body. Thus, while pregnant mice are more susceptible to herpes simplex Type-2 virus introduced intravaginally (the normal route of

infection), they are less susceptible to the virus introduced intranasally (Overall, Kern, Schlitzer, Friedman, & Glasgow, 1975; Young & Gomez, 1979). Pregnant mice are less susceptible to influenza-A virus introduced intranasally (the normal route of infection) than nonpregnant controls (Young & Gomez, 1979).

Less direct tests of susceptibility to immunologically active agents than measures of survival in pregnant and nonpregnant mammals reveal evidence of no effects of pregnancy (Merritt & Galton, 1969); enhanced resistance in pregnant animals (Fabris, 1973; Kenny & Diamond, 1977; Mitchell, McRipley, Selvaraj, & Sbarra, 1966; Nicol *et al.*, 1964); and depressed resistance in pregnant subjects (Exon & Dixon, 1972; Rangnekar, Rao, Joshi, Virkar, Kora, & Dikshit, 1974). Such data are both contradictory and difficult to extrapolate to the effects on survival of exposure to disease-causing organisms.

Though there does seem to be a tendency for reproductively active females to be more susceptible than controls to viral agents, the effects of pregnancy on disease susceptibility seem to depend on the disease in question, the route of its entrance into the body, and the stage in pregnancy when exposure occurs. It should also be kept in mind that the selection of disease-causing agents for test in pregnant animals has been guided by clinical observations suggesting that pregnant human females suffer more severely from certain diseases than do nonpregnant women, for example, poliomyelitis (Pridelle, Lenz, Young, & Stevenson, 1952); pandemic influenza (Freeman & Barns, 1959); herpes simplex Type-2 (Young, Killam, & Greene, 1976); and malaria (Gilles, Lawson, Sibelas, Voller, & Allan, 1969). Evidence of enhanced resistance of pregnant women to other diseases, such as syphilis (Mitchell & Sbarra, 1965), is not of such practical importance and receives less mention in the literature and no experimental study.

The fact that experimental evidence of pregnancy-associated reduced resistance is mixed in a class of diseases generally selected for study on the basis of clinical indications that they are more virulent in pregnant than in nonpregnant women suggests that reduced resistance to disease during reproduction may not be a general phenomenon. However, available evidence does suggest a marginally enhanced susceptibility to disease in gravid animals.

In order for an organism to become ill, it must not only be susceptible to disease, but it must also be exposed to disease-causing agents. Even if reproductively active females are more susceptible to infection, they could reduce their probability of succumbing to illness by reducing their encounters with disease-bearing conspecifics. The tendency of pregnant or lactating females of many rodent species to isolate themselves and respond aggressively to the approach of conspecifics (Crowcroft, 1966; Gandelman, 1972; King, 1955; Hoogland, 1981a; Sherman, 1980a) might reduce exposure to contagious disease. While I do not think that there is any reason to suppose that

the antisocial behaviors observed in pregnant or lactating mammals have evolved specifically in defense against infection, it is reasonable to suppose that behaviors that isolate reproductively active females serve such a secondary function. It is not known whether in natural circumstances the net effect of changes in susceptibility to disease and changes in exposure to disease resulting from reproductive activity is to increase or to decrease the probability of illness.

Risk of Predation during Pregnancy and Lactation

The data discussed in preceding sections were derived primarily from laboratory studies in which females were protected from the need to expose themselves to the increased risk of predation while attending their young or acquiring nutrients to be transduced to their young. It is not, however, necessarily the case that the behavioral changes associated with pregnancy and lactation involve enhanced predation risks. In the laboratory, domesticated female rats exhibit marked decrements in running wheel activity 24 hr after impregnation. Throughout pregnancy and lactation, they are less than one-third as active as they were prior to impregnation (Sloanaker, 1924). Such reduced activity is, perhaps, more likely to reduce predation risk than to enhance it. In a study of mouse killing in rats, Galef (unpublished observations) established colonies of wild *mus musculus* separated from colonies of wild *Rattus norvegicus* by semipermeable barriers through which mice, but not rats, could pass. In each of three replications, the order of capture of mice by rats was the same: males were killed before nonreproductive females, which were killed in turn before pregnant or lactating females. Attachment of lactating females to their nest sites reduced their rate of exploration and preserved many lactating females for some days after the last of their nonreproductive colony-mates had departed.

In the field, Madison (1978a,b) found no changes in the activity of pregnant voles, but a sharp reduction in activity during lactation. This reduction in activity was accompanied by enhanced predation on lactating voles by snakes, which took significantly more vole dams (together with their litters) than nonreproductively active females (Madison, 1978a). However, as snake predation accounted for only 20% of the total reported instances of predation on subjects during the three-year course of the study (Madison, 1979), the overall reproduction effects on predation susceptibility cannot be determined.

In other rodent species that have been intensively studied, the observed predation rates have generally been too low to permit an estimation of the predation impact on reproductively active females, as compared with inactive ones. During seven years of observation of prairie dog colonies, Hoogland

(personal communication, 1980a) observed only eight instances of predator success: the capture of seven juveniles and one lactating female, which was also the most peripherally located animal in its colony. Sherman (1977, 1980a,b) similarly observed only one successful predatory attempt for each 347 hr of observation of Belding's ground squirrels. In the 14 instances in which adults were predation victims (of badger, coyote, and marten), 8 females and 6 males were taken. The data are simply too sparse to permit an assessment of the effects of prey reproduction on predator success. Because of the small size and the frequently nocturnal and fossorial habits of rodents, predation on them is not easily seen. There is, however, considerable discussion in the literature of factors enhancing predation on ungulate species in which predation is relatively easy to observe. These data are reviewed briefly below.

Mech (1970, pp. 246-263) devoted a chapter of his monograph on wolves to factors influencing prey selection: prey inexperience, prey malformation, illness, age, youth, injury, crippling, stupidity, abnormality in behavior, reduced sensory capacity, parasites, congenital disorders, diseases of the jawbone, rundown condition, infection with tape worm cysts, flesh wounds, bacterial infection, broken limbs, and a variety of other factors that may predispose deer, moose, and Dall sheep to fall prey to wolves. Pregnancy and lactation are conspicuous by their absence.

Schaller (1967, pp. 316-331) both reviewed the earlier literature on factors predisposing ungulates to predation (reaching conclusions similar to those of Mech) and reported his own findings on prey selection by tigers. The results varied markedly from one prey species to another. In the sambar, for example, yearling and adult males were taken four times more often than one would expect on the basis of their frequency in the population. On the other hand, female barashinha in late pregnancy were particularly susceptible to tigers.

Kruuk's (1972, pp 89-102) brief discussion of the characteristics of hyena prey shows that adult female wildebeests run the highest risk (and males the lowest) during the calving season, probably because of the female's reduced mobility prior to and while giving birth. However, hyenas, like wild dogs, leopards, and lions, take male gazelles more frequently than females. Although hyenas take female zebras more frequently than male zebras, Kruuk did not mention reproductive activity as significant in this differential mortality.

Schaller's monograph on prey selection (1972, pp. 221-232) in lions does not suggest that they are more likely to kill reproductively active female wildebeest, zebra, Thomson's gazelle, or buffalo. In fact, in each case, lions are more likely to kill adult males than females.

Considered together, the data are equivocal. Although in two cases, those

of hyena predation on wildebeest and tiger predation on barasingha, pregnancy seems to be an important factor in vulnerability, pregnancy may not have the same deleterious effect on other ungulate prey. It is, of course, possible that the metabolic demands of pregnancy and lactation make reproductively active females more susceptible to starvation, disease, parasites, etc., and hence to predation. If this were the case, one might expect females to be more frequent prey than males, which, as indicated above, is not generally true.

Benefits of Reproduction

During the period in which altricial young are dependent on their dam, they acquire substantial resources from her, while she receives relatively little in return. Huddling with pups may save mothers some of the energy normally used for thermoregulation (Leon, Croskerry, & Smith, 1978), and mothers may recover some of the resources provided to their offspring by ingesting the placenta (Ewer, 1968) or the urine and feces of their young (Baverstock & Green, 1975; Friedman & Bruno, 1976). Still, there can be little question that if one restricts attention to the period prior to weaning, dams contribute far more to the well being of their young than they receive in return. However, if the time frame is expanded to include the total period of interaction between a dam and her young, the young of a given reproductive episode may eventually contribute substantial resources to their dam and her future offspring. Resources invested in offspring are frequently returned, possibly with interest.

Overt Benefits

Perhaps the clearest cases of return on parental energy transduced to offspring is to be found in social insect species, in which each new colony is founded by a solitary queen. To quickly summarize Oster and Wilson's (1978) description of the colony foundation process in such species; the solitary founding queen, inseminated during her nuptial flight, locates a suitable nest site, constructs the first nest cell, and then rears a first brood of workers herself, feeding larvae on her own tissue reserves. When the first workers eclose as adults, the queen reverts to egg laying, and the workers forage for food, feed and care for the young and the queen, enlarge the nest site, and provide all the resources required for continued colony growth. Once the colony reaches mature size, it begins to produce queens and males, thus continuing the cycle. Early brood production is essential for the production of later ones, and the energy that the queen invests in her first broods is returned many times.

If such a positive return on the maternal transduction of resources to offspring were limited to the social insects, it would be of little relevance to the energy exchange between mammalian mothers and young. There is, however, evidence of similar relationships in mammalian species, though in mammalian cases, early litter production facilitates future litter production, rather than being a necessary precursor to future reproduction.

Moehlman (1979), for example, has reported that the reproductive success of pairs of black-backed jackals in a given season can be significantly enhanced by the attendance of their young of a preceding year. Such "helpers" contribute food directly to the pups, regurgitate food to the lactating mother, guard the pups during periods of parental absence, groom the pups, etc. On average, each helper adds 1.5 surviving pups to the litter it attends. Thus, helper individuals increase their dam's success in future reproductive episodes well beyond the investment that the dam made in them. While it is true that only a small percentage of young produced by any pair return to help with subsequent litters, only previously reproductively active pairs have potential access to helpers, which increase later reproductive potential.

Black-backed jackals are not the only canid groups in which females can expect returns from their weaned offspring. Lactating Cape hunting dogs and their pups solicit regurgitated food from other closely related members of their pack (vanLawick & vanLawick-Goodall, 1971; Schaller, 1972, p. 325). That these older relatives of later young is suggested by the observation that following their mother's death, young can be successfully maintained by pack members from 5 weeks of age to weaning at 10 weeks (Schaller, 1972, p. 332).

Similarly, in dwarf mongoose packs, in which only the dominant female successfully produces young, the young are frequently suckled by the dominant female's grown daughters, whose own breeding is suppressed (Rood, 1980; see also Rasa, 1977; Ewer, 1973).

In wild house mice (*Mus musculus*) and, to a lesser extent, deer mice (*Peromyscus maniculatus bairdii*) females impregnated within a few days of one another may combine their young in a communal nest, often sharing the rearing with mature daughters from previous parturitions (Crowcroft & Row, 1963; King, 1963; Saylor & Salmon, 1969). Young house mice of a domesticated strain reared in a communal nest have been shown to exhibit enhanced rates of growth relative to young raised by individual females, when the number of young per dam is kept constant (Saylor & Salmon, 1969; Werboff, Steg, & Barnes, 1970). In the laboratory, wild rats (*Rattus norvegicus*) maintained in matrilineal groups similarly pool their litters (author's observation), though the effects of this communal rearing on the growth of the young is not known.

Covert Benefits

While the instances of return of maternal resources to the dam by her grown young described in the preceding section are particularly straightforward examples of ways in which engaging in open reproductive effort may increase future reproductive success, they may represent obvious cases of a commonly more subtle class of interactions between mothers and their grown offspring.

The potential for future return on maternal transduction of energy to young exists in those species in which (1) at least some grown young are matrilocal; (2) the dams are reproductively active over a sufficient period of time to allow a first litter to wean while the mother is still engaging in reproduction; and (3) individual species members gain reproductive potential from the presence of conspecifics.

While it is true that colonial lifestyles entail both costs and benefits (Hoogland & Sherman, 1976), it seems likely that in group-living species, the net benefits of social living outweigh the net costs (Bertram, 1978). In matrilocal species, an individual's own offspring obviously contribute their numbers to their dam's social groups and become potential sources of social benefits. Although the literature on the degree of consanguinity in rodent populations is far from complete, it does seem to be generally the case that in colonial rodents (for example, Norway rats, roof rats, Mongolian gerbils, prairie dogs, and Belding's ground squirrel), the basic social group consists of senior individuals and their offspring of several years (Crowcroft, 1966, p. 29; Gromov & Popov, 1979; Hoogland, 1981b; King, 1955; Sherman, 1977, 1980a; Telle, 1966). Thus, in many rodent species, a female's previous successful reproduction can increase the size of her group and thus increase her access to the benefits of group living. It is probably the case that the social benefits of reproduction are greater in small groups than in large ones, for as group size increases, the relative contribution of a single reproductive episode to group size decreases. Further, as population density or number increases beyond some optimum, the costs of group living may begin to outweigh the benefits.

Laboratory experiments on the effects of increasing population size on the reproductive success of female population members received considerable attention in the 1950s and 1960s. The study of the mechanisms underlying the regulation of population sizes in nature below the apparent carrying capacity of the environment focused attention on falling birthrates and infant survival rates in confined populations approaching asymptotic size. Data describing the typical results of such a study in house mice (Figure 3; Christian, Lloyd, & Davis, 1965) illustrate the well-known finding of decreased infant survival and

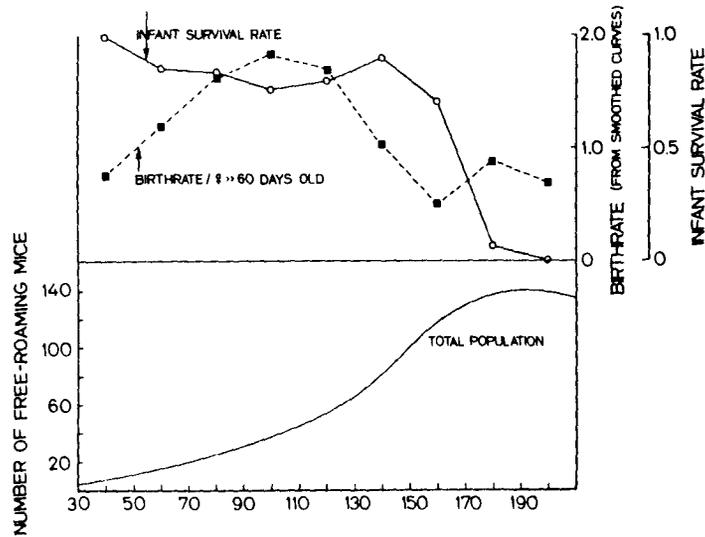


Figure 3. Demographic data from a freely growing confined population of house mice (*Mus musculus*) indicating the nursing survival rate and the birthrate per female over 60 days of age in two-day intervals. Also shown is the total population size over days. (From Christian, Lloyd, & Davis, 1965.)

female fecundity with increasing population size. The figure also reveals an equally robust, but generally ignored, phenomenon: an increase in individual female fecundity correlated with the growth of the population to moderate size. Unfortunately, the factors responsible for such an increase in reproductive efficiency have not been explored.

The clearest evidence of particular benefits of sociality in rodents is found in field studies of two highly matrilineal species, Belding's ground squirrel and the black-tailed prairie dog. In the latter species, Hoogland (1981b, p. 7) reported that he has not detected a single case in which a black-tailed female emigrated from her natal territory on her own apparent initiative. Similarly, "female Belding's ground squirrels mature and breed near their birth places until they die or disappear" (Sherman, 1977, p. 1248). Clearly, in such instances, daughters have the opportunity to provide social benefits to their dam and her subsequent offspring.

Both Belding's squirrels and black-tailed prairie dogs engage in complex antipredator behaviors, and the role of social life in predator defense has received the greatest attention. In black-tailed prairie dogs, increasing coterie size correlates with decreased latency in predator detection (Hoogland,

1981a); decreased time scanning for predators (Hoogland, 1979); and increased time feeding (Hoogland, 1981b). The fact that individuals living on the periphery of wards spend more time watching for predators than those living centrally, and that birth is synchronized in neighboring burrows, suggests that individuals living in groups may also benefit from "selfish herd" effects (Hamilton, 1971; Hoogland, 1979b) resulting from conspecific proximity.

Belding's ground squirrel adult females—and yearlings living near relatives—alarm-call in response to the appearance of predators, while juveniles do not, and juveniles frequently flee into burrows other than their home burrow (Sherman, 1977). There is thus a tendency for juveniles to gain protection from their older sisters, who provide both places of refuge and warning of potential danger.

Life in social groups may provide benefits other than enhanced protection from predation. Wild Norway rats, for example, eat foods brought to the home burrow by those conspecifics successful in foraging (Barnett & Spencer, 1951), and food caches are communally created and exploited resources (Calhoun, 1962, p. 109). Rats, both wild and domesticated, can also influence one another's food selection, providing some degree of protection against the ingestion of toxic foods, and reducing the time spent, especially by juveniles, in searching for food (Galef, 1976, 1977; Galef & Clark, 1971; Lavin, Freise, & Coombes, 1980; Steiniger, 1950). Trails from one place of safety to another and from refuges to feeding sites are cleared and maintained by the combined action of numerous animals (Calhoun, 1962, pp. 54–70; Telle, 1966). Matrilocal grown young provide food caches, refuges, trails, and information to their younger siblings and may thus increase their dams' reproductive success.

Similarly, nonbreeding adult and yearling black-tailed prairie dogs assist breeders in defense of the coterie territory, on which both they and the breeding adults and their young feed (Hoogland, 1981a; King, 1955). They also maintain the mounds around burrow entrances, carry nesting material into burrows other than those in which they sleep, and reduce the heat loss of conspecifics by huddling with them (Hoogland, 1981a,b).

While the data provide no unequivocal evidence of reproductive benefits to a dam resulting from the immediate presence of her sons or daughters, they are certainly consistent with such a view.

Discussion

The apparently straightforward argument that females engaging in reproduction must suffer reduced future reproductive potential ignores the fact that natural selection has been acting for millennia, both to weed out those

