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The Ecology of Weaning

Parasitism and the Achievement of Independence by Altricial Mammals

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1. An Overview of Weaning

At birth and for some time thereafter altricial mammals are, by definition, almost totally dependent on their parents or other caretakers for provision of many of the necessities of life. Although many mammals are born relatively helpless, none continue to depend on conspecifics for sustenance throughout their life cycles. Prior to reaching reproductive age each altricial mammal must become competent to acquire directly from the environment those goods and services which it previously acquired only indirectly as the result of interaction with conspecific caretakers. This transition from an infantile dependence on others for transduction of environmental resources to an adult mode of independent acquisition of necessities is in two senses a gradual process. First, independence with respect to any single need is rarely achieved suddenly; most often a series of graded transitional stages intervene between total dependence on caretakers for supply of a given resource and independent acquisition of that resource. The developing rat pup, for example, moves successively from *in utero* total dependence for nutrition on mother's blood, to postparturient total dependence on mother's milk, to a mixed diet of mother's milk and solid food, to a diet of solid food transported to the home burrow by adult conspecifics, to feeding trips with adult conspecifics, to independent acquisition of solid food. Second, the juvenile may exhibit adultlike behavior in meeting each of its various needs at different ages. The rat pup, for example,

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initiates endogenous thermoregulatory behavior some time before it initiates independent feeding on solid foods.

Thus, while weaning in the dictionary sense of "accustoming an organism to the loss of mother's milk" frequently occurs during a fairly restricted period during ontogeny, weaning in the broader sense implied above (i.e., achievement of the adult degree of independence of conspecifics in the acquisition of the necessities of life) is an ongoing process extending from birth (after which oxygen is acquired independently) to shortly prior to reproductive maturity, when, for example, independent construction of harborage sites may be initiated. It is the latter broad view of the weaning process with which I will be concerned here.

The extended period during which weaning in this sense occurs has been studied in detail by psychologists with two distinct goals: first, to determine the factors mediating observed changes in the form of mother–young interaction during the weeks following parturition, and second, to elucidate the processes underlying the development of behavior.

In the present paper I will discuss the possibility that consideration of parental investment theory (Trivers, 1974) suggests the necessity of a change in theoretical orientation with respect to the selection pressures responsible for the apparent complementarity between the time course of maternal behavior of the dam and the changing requirements of her developing young. I will further argue that this change in orientation concerning the behavioral synchrony of the mother–young dyad suggests the need for a broadening of the range of factors considered as important in determining the time course of behavioral development in altricial mammals (see Hofer, this volume, for a related view). Last, I will propose that understanding of both behavioral development and mother–young interaction depend in some measure on interpretation of the process of weaning. I will draw an analogy between various stages in the weaning process and various types of parasitism. And, to illustrate the implications of the theoretical position suggested above, I will use this analogy to interpret the time course of behavioral development in rat pups during the weaning period.

1.1. Mother–Young Interaction

Maternal behavior during the period of mother–young interaction has been described as "changing in ways which are correlated with changes in the needs of the developing young" (Rosenblatt and Lehrman, 1963, p. 8). While such a statement of correlation is descriptive and does not imply that adjustments in the behavior of mothers are caused by changes in the need states of their young, it does focus attention on one possible cause of the synchrony in the behavior of mothers and their young (i.e., infant needs) at the expense of others. One could as easily describe the behavior of the young as changing in ways which are correlated with changes in the willingness of the dam to provide them with resources (i.e., parentally regulated). Or, more equivocally, one could describe the behavior of both dam and young as changing so as to correlate changes in the resource contribution of the dam with changes in the needs of the young (i.e., mutually adjusted). The three different statements of correlation suggest three different hypothetical histories of the evolution of the observed synchrony of mother–young interaction as well as three different general models of the proximate causation of changes in the behavior of mothers and young during their period of interaction.

There is little question that each of the three correlational statements mentioned above points to an important feature of the evolution of the behavior of mother and young. Clearly, during evolutionary time, the needs of the young have become adapted to the willingness and ability of their dam to provide them with resources, just as the willingness of the dam to invest in her offspring has become adapted to the needs of the young for energy inputs to assure adequate growth. Given the partial communality of reproductive interests of parent and young, such co-evolution is inevitable.

It has, however, recently been pointed out that the reproductive interests of parent and offspring are not identical (Trivers, 1974). To a certain extent a mother and her young are competing, each seeking to maximize its own inclusive fitness, even if such individual maximization is achieved at the expense of the other member of the parent–offspring pair. To put the matter simply, there is reason to believe that offspring should be selected to attempt to acquire more parental investment* than parents will be selected to give (Trivers, 1974). This is because the young of a given litter show only reproductive profit from parental investment in them, while the dam has to consider both the costs and benefits of continuing to transduce energy to a given litter rather than saving it for investment in future litters.

Trivers' (1972, 1974) discussions of parental investment and parent–offspring conflict have several possible implications for the study of the proximal causation of the behavior of both mother and young during their period of interaction. First, Trivers' model implies that the conflict between mother and young evolves to a situation in which it is the reproductive interests of the mother which set the upper bound on the amount and duration of her investment in any given litter of young. The irreducible needs of the young may set a lower bound on maternal investment, but this lower limit is probably seldom arrived at in a successful reproductive effort. The observation that the willingness of the dam to invest in a given litter sets the upper limit on energy flow to the young suggests that it might be more useful, in discussions of parent–young interaction, to treat the dam as providing the environment to which the young must respond rather than to treat the young as presenting needs which the dam must meet.

Second, in psychological discussions of parent–offspring interactions, as in classical evolutionary theory, the parent is frequently treated as the active partner.

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*Parental investment in an offspring is defined as "anything done by the parent for the offspring that increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring" (Trivers, 1974, p. 249).

The current approach in evolutionary theory, briefly described above, is to view dependent young as relatively equiactive participants in a parent–offspring conflict. Such a theoretical position suggests that at the level of mechanism it might be fruitful to treat the neonate as acting to acquire investment from the dam rather than as a passive recipient of the dam's beneficence (see Bell and Harper, 1977, for a related view).

Third, in both the psychological and biological literature the neonate is often treated as to some extent inefficient, inept, and inadequate. Trivers' position suggests that it might be more valid to treat neonates as exhibiting behaviors and physical characteristics adapted to acquiring parental investment and thus maximizing survival, growth, and, ultimately, inclusive fitness of the young within the environmental niche defined by their parents.

In the present paper I will, therefore, treat dependent young as acting so as to maximize net energy gain within the constraints imposed by their dam's limited willingness to invest in them.

1.2. Development of Behavior

The progressive increase over time in the apparent complexity of the behavior of mammalian neonates is generally viewed as resulting from two factors and their interaction. First, maturation in the complexity and sophistication of the neural and muscular structures underlying behavior is treated as necessary for increased behavioral complexity. Second, experiences of the neonate in interaction with the physical and social environment early in development are treated as necessary conditions for the organization of behavior appearing later in development (Schneirla, 1957).

Lehrman and Rosenblatt's (1971, p. 10) description of the development of feeding behavior in kittens provides an elegant example of this point of view:

> . . . although we see the same relationships between sucking and food intake during the whole period through weaning, the internal relationships between the animal's behavior and the needs which it serves are constantly changing through some interaction between the growth of the infant and the experience it has in the interaction with its mother made possible by that growth. At first the sucking behavior is reflexly initiated by stimuli offered by the initiative of the mother, or simply by the proximity of the mother to the infant. The growth of the infant and its experience in the situation described by this interaction lead to the emergence of an internal connection between (a) the sucking behavior by which the infant gets food, (b) the felt need for food, and (c) the external source of food, so that the infant becomes able to perceive the source of food as such, to orient to it at its own initiative, and to learn to distinguish many subtle details of the food source.

There is a second view of the developmental process, complementary to the first, which has been largely ignored by psychologically oriented students of behavior. In discussing the ontogeny of regulatory mechanisms in the rat pup, Adolph (1957, p.131) has clearly described that view.

> We tend to speak as though the regulations with which the adult is endowed are the only adequate ones, superior to those of infants. In doing so, we recognize that they are in use longer than those of infants. Actually we are not justified in believing that adult regulations could successfully be imposed on infants. *As far as we know, each stage of development is functionally complete in its own right,* and the common supposition that the adult stage enjoys special advantages cannot rigorously be sustained, because we have no criterion of advantages and disadvantages other than the frequency of survival in natural circumstances. (Emphasis added)

Williams (1966, p. 71) makes the same point somewhat more succinctly:

> The succession of somata in the life cycle of an organism must provide an adjustment of each stage to the one before and the one after in addition *to an adaptive selection of environmental niches and precise adaptation to each niche.* (Emphasis added)

Although considerable attention has been paid to the development of structures underlying behavior and the role of experience in the achievement of the adult behavioral phenotype, little attention has been paid to the fact that the organism at every point in development is a functional entity, adapted to the environment in which it finds itself. The reason for the inattention paid to this view by comparative psychologists, with at least a secondary interest in using the study of animal development to understand human development, is not difficult to surmise. But there is some reason to question whether the role of experience in the development of adult behavior in nonprimate mammals is nearly so great as in primates. The human juvenile clearly requires specific experiences during the period of dependence on its parents to acquire the language, social, and motor skills necessary to develop a successful adult behavioral phenotype. Nonhuman primates may exhibit an analogous dependence on experience during ontogeny for the development of important aspects of their adult social behavior (H. F. Harlow and M. K. Harlow, 1965).

Recent technical innovations (Hall, 1975) have made it possible to rear rat pups both in isolation from all conspecifics (including their dam) and without the opportunity to experience oral ingestion from days 2–18 postpartum. Pups raised in this fashion exhibit essentially normal patterns of feeding when they reach weaning age and do not exhibit detectable deficits in food recognition, patterns of ingestion, or response to various nutrient stresses at the time of introduction to solid food (Hall, 1975). Thoman and Arnold, (1968) similarly found relatively small effects of hand rearing of rat pups on subsequent reproductive behaviors. While I would most certainly not wish to argue that experiences unique to the juvenile period, such as suckling from a dam, play no role in the development of their adult behavioral analogues, findings such as those of Hall and of Thomas suggest that engagement in some juvenile patterns of behavior are not necessary conditions for the emergence of a normal adult behavioral phenotype. If this is so, then understanding of the function of the behavior of juveniles must to some extent be sought in other factors in addition to their contribution to the development of later behavior.

The argument that the development of behavior must await the development of supporting neural coordinating centers and muscular strength also has obvious validity, but it does not contribute to understanding why neural substrates sufficient for some behaviors (e.g., nipple attachment, suckling, and huddling) are present at birth, while substrates sufficient for the support of other behaviors are absent (Darwin, 1877). Further, it is difficult to determine whether the failure to observe a given behavior pattern in a neonate is due to the absence of the necessary neural and muscular substrate for that behavior. The fact that an organism fails to exhibit some pattern of behavior early in life can surely not be taken as evidence that the underlying structures necessary to support that behavior are absent, or the explanation becomes circular. It is always possible either that the necessary supporting structures are present but their expression is actively inhibited at some points during development (Bower, 1976; Graham *et al.,* 1978) or that the external conditions necessary for the expression of a behavior in the neonate have not been identified. For example, Hall (1979) has recently found that rat pups as young as 3 days of age are capable of feeding independently of the mother by lapping milk, but only if they are both deprived of food and placed in a warm environment, (see also Smith and Spear, 1978).

I would suggest that consideration of the behavioral adaptations required by the environment in which the neonate finds itself at each point in development may provide some insight into the observed course of development. The remainder of the present chapter is, in essence, an examination of the heuristic value of treating the neonate as exhibiting behavioral adaptations necessary for survival and growth within the ecological niche defined by its caretaker at each point in its life cycle.

1.3. Parasitism: An Analogy to the Life Strategy of the Altricial Juvenile Mammal

In attempting to understand the relationship between the juvenile mammal and the environment provided by its dam I was struck by the parallels between the mother–young relationship and the host–parasite relationship. In the present section I will develop the analogy between host–parasite and parent–young interactions, which I will use to interpret the process of weaning and the time course of development in later sections.

Parasitism is usually defined as an intimate relationship between two heterospecific organisms during which the parasite, usually the smaller of the two partners, is metabolically dependent on the host. I will simply broaden the definition by considering metabolically dependent members of the same species to be parasites on their source of nutrition. The analogy between dependent neonates and parasites is surely appropriate in terms of the somatic relationship of the young to their dam and may even be justified to some extent in terms of their genetic relationship. So long as there is not genetic identity between the investing dam and her dependent offspring (as is always the case in sexually reproducing species), the foreign genes of the young are in fact parasitic on the genes of the investing parent.

A broadening of the definition of parasitism to include members of the same species is not unique to the present discussion. For example, the males of a number of species of angler fish (*Ceratiidae, Linophrynidae,* and *Photocorynidae*) spend much of their lives attached to the much larger females. The males have their own gills and respiratory system, but their food is obtained directly from the bloodstream of the female. They may be completely dependent on the female for nourishment and they often exhibit specializations to their parasitic mode of life, including reduced dentition and a simplified intestinal tract. Such relations between members of the same species have been labeled "sexual parasitism" (Villwock, 1973; Kikkawa and Thorne, 1971) for much the same reasons that I would propose to treat altricial mammals as "reproductive parasites" of their dam.

Parasitic relationships in nature are of many different kinds. The parasite may be internal to its host (an *endoparasite*) or attached to its exterior (an *ectoparasite*). It may be completely dependent on its host metabolically (an *obligate parasite*) or only partially dependent (a *facultative parasite*). The parasite may be *active* in seeking its host or may *passively* await the arrival of its host in a fixed location. It may be continuously (a *constant parasite*) or intermittently (a *periodic parasite*) in contact with its host. Clearly different modes of parasitic interaction with a host require different sensory, motor, somatic, and behavioral adaptations on the part of the parasite if it is to succeed in its parasitic way of life.

The older view of parasitic animals is that they are degenerate because many have lost some if not all of the organs that their nonparasitic relatives have. However, such alterations in phenotype can be, perhaps, more profitably viewed as adaptive specializations for the particular mode of life parasites have adopted and the particular ecological niche they occupy than as the result of degeneracy (LaPage, 1963; Bates, 1961). As Bates (1961, p. 180) has proposed, "The degeneracy of parasitism is specialization involving the loss of structures and functions that are no longer needed." Similarly, altricial mammals are sometimes described as "helpless and poorly developed" (Vaughan, 1972, p. 363). Again there might be something to gain from viewing altricial mammals as adapted to the particular ecological niches which they occupy.

Part of the usefulness of the parasitism analogy is that it makes clear the fact that as the young mammal increases in age, both its means of utilizing the dam as a host and its degree of dependence on the mother as a resource base change. The young mammal moves through a series of ecological niches with movement from niche to niche required by changes in the energy resources provided by the dam. In many invertebrate parasites one sees similar changes in host exploitation during the life cycle or ontogeny of the organism and correlated changes in phenotype associated with the particular niche exploited in each life stage (see footnote on page 236 for an example). Further, the parasitism analogy makes explicit the point that the young are to some extent exploiters of their dam rather than cooperative partners in their interaction with her.*

In terms of the present analogy, prior to parturition the fetal mammal is functionally an obligate, constant endoparasite. At parturition it becomes an ectoparasite, obligate, periodic, and passive. As it increases in age it moves from a passive to an active mode of interaction with its host, and the interaction moves from an obligate to a facultative parasitism. Once milk delivery from the dam ceases, the juvenile may becomes a commensal of its host dam. In succeeding sections I will use this parasitic analogy to discuss the series of ecological niches which the dam provides for her young and the behavioral and phenotypic adaptations which the young exhibit to the succession of niches made available to them by their caretaker.

2. The Rat Pup as Parasite

Energy passes from mother to young in three forms: (1) as calories in milk, (2) as heat conducted from mother to young during periods of contact, and (3) as mechanical energy utilized in physical movement of the young, nest or burrow construction, or transport of food. In the following sections I will describe the willingness of the dam to commit resources of each type to her young as changing over time and the young as exhibiting compensatory adjustments in their physical characteristics and behavior. Such an analysis clearly requires rather detailed knowledge of the energy commitment of the dam and of the development, both somatic and behavioral, of the young. To my knowledge such information is available at the present time only for rats *(Rattus norvegicus)*, and my discussion will therefore be focused on the interaction of rat dams and their litters.

2.1. The Environment Provided by the Host: Parental Investment by the Dam

Because the dam provides the environment to which the young must adapt, it is necessary to first consider the changes over postpartum time in the willingness of the dam to invest in her offspring.

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*One might well argue that the analogy between the relationship of parasite and host and that of mother and young is inappropriate in that hosts are typically adversely affected by interaction with their parasites while dams benefit from interaction with their offspring. Whether one considers the young as beneficial or harmful to the parent depends on the level of analysis employed. In genetic terms, offspring are clearly beneficial to their dam in that they provide a potential medium for replication of the dam's genetic compliment. In physiological terms the offspring are, of course, a considerable burden to her. Thus, the parasitism analogy, while failing to reflect important positive aspects of the relationship of mother to young, calls attention to the metabolic costs associated with parental investment and is useful in that regard.

2.1.1. Milk Flow from from Mother to Young

Figure 1 presents data on the amount of milk flow from a lactating rat to her litter of 8 pups as measured by rate of ^{85}Sr transfer (Babicky *et al.*, 1970). The important findings (confirmed by Ostadalova *et al.*, 1971) are (1) that there is a gradual increment in milk transfer which reaches a maximum on day 15 postpartum, and (2) that milk transfer declines gradually from day 15 until is ceases on days 27–28 postpartum. Variation in litter size (3, 8, or 15 sucklings) has been found to effect the total amount of milk transferred but not the day of peak transfer or the day of termination of milk delivery (Ostadalova *et al.*, 1971).

2.1.2. Conductance of Heat from Mother to Young

The cost to the mother of maintaining contact with her young, and thus conducting heat to them, is less obvious than the cost to her of provision of milk or mechanical energy (Pond, 1978); the mother exhibits a rise in body temperature at the same time that the pups gain heat from her, because the mother–young huddle reduces the surface to volume ratio of all participants and is energy conserving (Leon *et al.*, 1978). The cost to the mother of prolonged periods of contact with her offspring is probably twofold: First, it reduces her potential foraging time, and second, it results in the dam suffering hyperthermia (Leon *et al.*, 1978; Woodside, 1978).

Figure 2 presents data describing the percentage of the day which the dam spends in contact with her offspring (Grota and Ader, 1969). As contact is both a necessary and sufficient condition for heat transfer, the data provide a rough indication of the mother's contribution of heat to her young during the first three postpartum weeks. The data indicate (1) a steady decrease in contact time from parturition to day 17 postpartum (see also Leon *et al.*, 1978; Woodside, 1978) and (2) a subsequent low but constant level of contact.

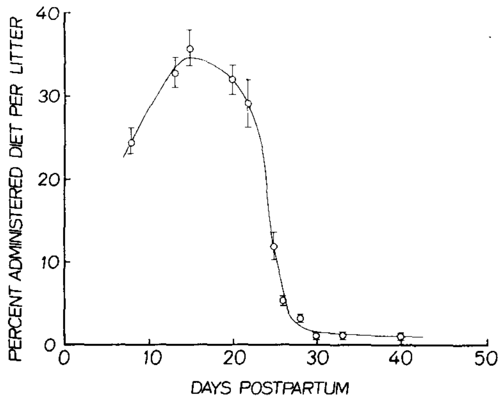

Figure 1. Percentage of labeled $SrCl_2$ injected into the dam appearing in pups 48 hr following injection, as determined by whole-litter radiation counts (adapted from Babicky *et al.*, 1970).

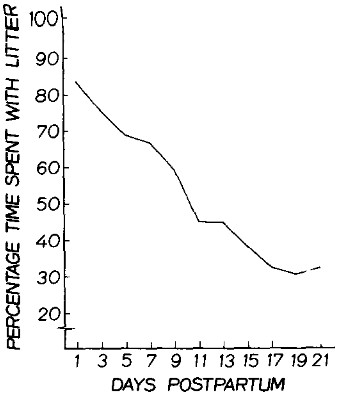

Figure 2. Percentage of time lactating rats spent with their litters during 21 days postpartum (adapted from Grota and Ader, 1969).

2.1.3. Mechanical Energy Provided by the Dam

2.1.3a. Movement of Pups. Figure 3 presents data indicating the probability of dams retrieving entire litters of pups during the 30 min subsequent to the displacement of the pups from the nest site and the probability of the mother transferring her entire litter to a new nest site during the 3 hr following destruction of her original nest (Brewster, unpublished data). The data indicate (1) a high probability of movement of the young to a place of safety from parturition to day 14, (2) followed by a gradual decline in willingness to move pups, (3) ending with a total unwillingness to move pups by day 22. (See also Grota and Ader, 1969; Rosenblatt and Lehrman, 1963.) That such changes in the dam's probability of moving young are due in some measure to changes in her internal condition rather than changes in the movement eliciting properties of the young is strongly indicated by the finding of Rosenblatt and Lehrman (1963) that 4-day

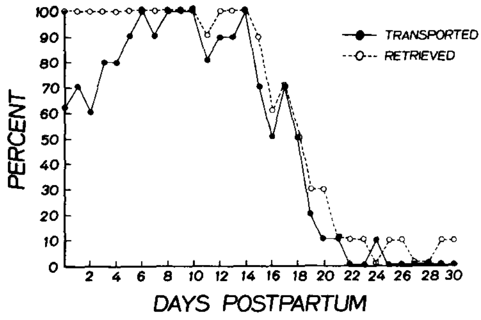

Figure 3. Percentage of females retrieving entire litters or transporting entire litters to new nests during test periods (Brewster, unpublished).

postpartum females will retrieve 19-day-old pups, while 19-day postpartum females will not.

2.1.3b. Nest Building and Burrow Construction. As can be seen in Fig. 4, the willingness of the mother to engage in nest-building behavior (Rosenblatt and Lehrman, 1963) shows a similar pattern to that of pup movement: (1) A period of high levels of nest-building activity, (2) a period of gradual waning of investment beginning on day 13 or 14, and (3) a total cessation of activity on day 17 or 18.

Little is known of maternal investment in burrow construction or food transport to the nest site, but Calhoun (1962, pp. 29, 33–38) reports that just prior to weaning of the young (postpartum day 17 or 18), lactating females enlarge their burrows and form a food cache.

2.1.4. Discussion

There are two general features of the changes in maternal investment over the period of mother–young interaction of particular importance to subsequent discussions. First, the energy transfer from mother to young in each category wanes prior to day 22 postpartum. Second, in each case the energy input by the dam to the young decreases gradually rather than ending abruptly. It cannot be determined from the data presented in Figs. 1–4 whether this gradual waning in energy investment by dams is an individual or group phenomenon, but both published data (Grota and Ader, 1969) and personal communications indicate that at least in the cases of retrieval, transport, nest building, and contact time individual dams exhibit a gradual reduction in investment (Brewster, personal communication; Croskerry, personal communication; Leon, personal communication).

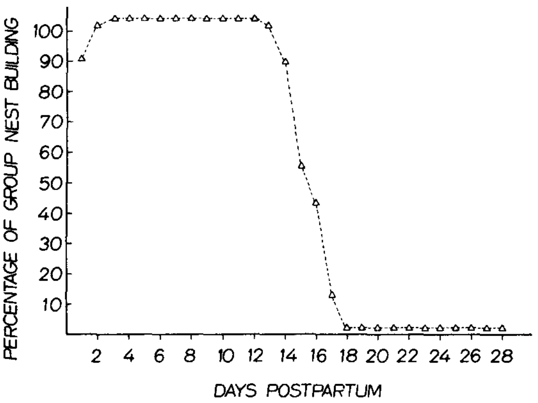

Figure 4. Percentage of mothers building nests on each of 28 days postpartum (adapted from Rosenblatt and Lehrman, 1963).

The fact that investment by the dam changes gradually, suggests that the pups are not exposed to sudden shifts in their environment, and one would therefore expect an absence of abrupt transitions in pup behavior or morphology over the course of development. By contrast, invertebrate parasites often undergo abrupt transitions from one ecological niche to another (i.e., from one host to the next, or from a parasitic to independent mode of existence) and their morphology and behavior exhibit discrete, clearly identifiable stages correlated with the succession of clearly defined niches they occupy. The absence of such abrupt niche shifts in altricial mammals makes the identification of moments of transition difficult and consequently makes it difficult to identify well-defined stages in the development of the young. Therefore, rather than attempting to identify and discuss stages in pup development, I have chosen to describe behavior of the young at three representative points in development: (1) in infancy, when the pup is totally dependent on the dam (day 5), (2) during the transition from dependence to independence (day 18), and (3) when independent existence is a possibility (day 40). The goal of each discussion will be to see if some sense can be made of the pup's succession of phenotypes, when those phenotypes are considered in relation to the successive environments dams provide.

In effect, my approach will be a comparative one, seeking to understand the adaptations of a series of closely related phenotypes in terms of the environment to which each must adapt. In this model the study of the same organism over developmental time is a comparative enterprise, in that although the underlying genotype remains constant, aspects of the genotype expressed in the phenotype change as a function of age.

2.2. The Rat Pup as Obligate, Passive Ectoparasite—Day 5 Postpartum

During the days immediately following birth the altricial mammal has available to it an ecological niche which it is uniquely adapted to exploit and in which competition for resources is at a minimum. The recently parturient dam is both able and willing to provide energy in all forms sufficient for pup growth, and competition for the energy resources of the dam is limited (from the point of view of any single pup) to the dam herself, contemporaneous siblings, and any fetuses the dam may be carrying in a postpartum pregnancy. At this time the juvenile rat exhibits a phenotype highly adapted to the function of exploitation of the dam as an energy source.*

*The functional significance of neonatal phenotypes as releasers of parental investment is clearly illustrated by the young of Estrilid finches and their brood parasites, various species of widow bird. Food-begging behavior by the young is very highly specialized in both the finch young and the mimetic young of the widow-bird parasite. "The Estrilid finches have highly specialized gape patterns. . . . The [food] begging gape presented to the parents is characterized by black spots on the palate, tongue, and lower mandible. In addition, the greatly thickened outgrowths on the upper and

As one might expect, given the total dependence of the 5-day-old pup on resources obtained from the dam and the pup's consequent need to exploit the dam in an efficient fashion, the 5-day-old pup gives every indication of being an optimal eliciter or releaser of maternal investment. Replacing a dam's pups every 5 days with neonates results in the maintenance of the high levels of suckling behavior characteristic of the early stages of mother–young interaction. Replacing 5-day-old pups with those 12 days of age results in a rapid decline in suckling time (Grosvenor and Mena, 1974; see also Grota, 1973).

The efficiency of neonatal rat pups as releasers of nurturent behavior by conspecifics is further exemplified by their ability to cause even nonreproductives exposed to them to behave "maternally" (Rosenblatt, 1967). The high level of specialization of the neonate for the elicitation of nurturance is suggested by the finding that exposure to 1- to 2-day-old pups induces "maternal" behavior in nonreproductive conspecifics both more reliably and more rapidly than exposure to older pups (Stern and MacKinnon, 1978).

As discussed in the preceding section, the pup cannot continue indefinitely to depend totally on the dam for energy inputs. As the pup changes phenotype to begin exploitation of energy sources other than the dam, it apparently must sacrifice some of those characteristics which optimize its exploitation of the dam. The nature of the resulting compromises in the phenotype of the young which result in the deterioration of pups' ability to elicit maternal investment are of considerable interest within the present conceptual framework.

2.2.1. Thermoregulation

The exothermic or poikilothermic characteristic of rat pups and other altricial mammals is often treated as resulting from the poor state of development of the young. However, it is important to keep in mind that homoiothermy or endothermy is not the goal or end point of a progressive phylogenetic evolution. Rather, it is one solution to the challenges posed by sets of environmental conditions. Most of the adult members of existing species are, in fact, successful exotherms, and their ability to become inactive during periods of stress in temporarily unsuppor-

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lower mandible carry one or two rounded papillae, which are usually white, or blue in some species. . . . The number and position of spots vary [among species], they may be lost from the tongue or the lower beak, or fuse to form arches. . . . The parents pump food only into the right pattern and ignore young with an incompatible pattern which are smuggled into the nest. Such young would rapidly die, and so it is easy to predict the appearance of the beaks of the young widow birds [the brood parasites]. As expected, the nestlings of the different widow-bird species are found to possess gape patterns indistinguishable from those of the host's young. The Estrilid finches exhibit a number of additional important signals contributing to the overall begging signal. The nestlings utter specific begging calls and rotate the head in an unusual manner while begging. Both these features are copied exactly by the widow birds. Finally, the coloration of the plumage of the parasite is identical to that of the host. Distinct differences can only be observed in the adults" (Wickler, 1968, pp. 196–197).

tive environments can be viewed as an advantage rather than a disadvantage (Schall and Pianka, 1978). The neonatal rat exists in an ecological situation totally different from that of the adult of its species, and it is at least possible that the exothermy of the pup represents an adaptation to its niche rather than a failure to achieve the endothermic mechanisms of the adult.

Because of the great ratio of surface area to body weight of the neonatal rat pup the energy expenditure required for homoiothermy would be great (Conklin and Heggeness, 1971). In order to maintain a constant body temperature, a pup would have to use an additional 4 cal/10 g per day for every 1°C it elevated its body temperature above ambient (Hahn *et al.,* 1961). Energy used for thermal homeostasis would be a cost to be subtracted from the energy inputs acquired by the pup from its dam. Thus maximization of net energy gain and, hence, growth by infant rats is facilitated by limiting the energy expended on endogenous heat production (Hopson, 1973) and dependence on exogenous sources of thermal energy.

At day 5 postpartum the dam may spend as much as 80% of the day in contact with her young and during periods of contact simultaneously provides warm milk and, by conduction, an exogenous source of thermal energy. An exothermic pup can reduce its metabolism during periods when it is unable to acquire nutrients (i.e., when its mother is absent) and have its body temperature and metabolic rate raised passively only during periods when the opportunity for food acquisition exists. This ability of the pup to allow its body temperature and, consequently, its metabolism to fall during periods in which the opportunity for food acquisition is absent (see Fig. 5) results in very considerable energy saving. For example, the total caloric requirement of a 1-day-old pup maintained in 33°C ambient is 47 cal/10 g per day, while its requirement at 20°C ambient is only 37 cal/10 g per day (Hahn and Koldovsky, 1960). Hahn *et al.* (1961) have estimated that if a rat pup kept at 20°C both maintained its body temperature at 33°C by endogenous heat production and continued normal growth it would have to consume more than twice as much milk as an exothermic pup. Clearly exothermy and the consequent ability to allow body temperature and metabolic rate to fall

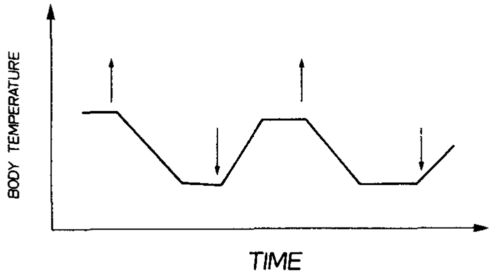

Figure 5. Schematic representation of infant rat body temperature in the presence or absence of the dam. Upward arrows indicate the mother's leaving and downward ones the mother's returning to the nest (adapted from Hahn *et al.*, 1961).

during periods when food acquisition is impossible provide important benefits to the obligate, parasitic neonatal rat.

The minimization of endogenous heat production in the neonate may have an additional important effect. Leon *et al.* (1978) have provided evidence consistent with the view that the duration of maternal nesting bouts is limited by the rate of maternal temperature increment during her periods of contact with the young in the nest. To the extent that pups can decrease their rate of endogenous heat production, they can increase the duration of periods of contact with the dam and, thereby, their access to the energy the dam provides. Blackmore (1972) has reported increasing rates of pup growth from days 2–8 postpartum as a function of increasing hours of pup contact with their dam. While it cannot be determined from Blackmore's data whether increased pup stimulation of the dam results in increased milk letdown or increased pup suckling time results in increased milk delivery from a constant supply, it is clear that pups can increase their net energy gain by maximizing their duration of contact with the dam.* To the extent that pup endothermy would decrease mother–young contact time it would decrease the rate of energy acquisition by the pups.

Increased access to the dam not only increases potential feeding time for the young rat but also increases the amount of stimulation which the pups may provide to the dam. There is strong evidence that stimulation of the dam by the young is necessary both to maintain the rat dam's willingness to invest in them and to prevent her initiation of investment in future litters. Removal of pups from their mother for 2–4 days immediately following parturition results in the gradual disappearance of maternal behavior in the dam (Rosenblatt and Lehrman, 1963). Further, removal of pups from their mother results in her ovulating three days later, permitting her reimpregnation (Van der Schoot *et al.,* 1978).

2.2.2. Feeding Behavior

The neonatal rat pup is totally dependent on the dam to provide nutrients and waits passively in the nest for her arrival. Active pursuit of food is, in normal circumstances, limited to searching, rooting, nipple attachment, and sucking behaviors necessary for milk acquisition. Though different from the feeding behavior of adults, the ingestive behavior of the young (described in detail in Hall and Rosenblatt, 1977) is both highly complex and specifically adapted to the exploitation of the dam. While the neonate lacks the dentition necessary for the mastication of solid food it does have an enzyme, lactase, which permits it to absorb and utilize lactose, a source of carbohydrates and calories in maternal milk.

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*This statement is an oversimplification. There must be an upper limit to mother–young contact time beyond which additional suckling of the pups by the dam would reduce the time available to her for foraging to the point where she could no longer support herself and her young.

High levels of lactose activity in the small intestine of rat pups are initiated just prior to birth and terminate at 21–22 days postpartum. As Alvarez and Sas (1971, p. 827) have proposed, "the physiological immaturity of the newborn seems to be in this case rather a physiological adaptation (in a broad sense) to a milk diet."

The young depend on their mother not only for the gathering and preliminary processing of food but for regulation of intake as well. Pups exhibit a willingness to attach to their dams' nipples independent of nutritional deprivation state, will remain attached to the teats so long as they are available, and will ingest whatever milk is ejected from the nipples until the pups are on the verge of drowning in milk overflow from their stomachs (Hall and Rosenblatt, 1977). Thus, within broad limits (Friedman, 1975) the food intake of the infant rat is a function of food delivery by the dam.

The regulatory behavior of the rat pup with respect to food intake can, like its thermoregulatory behavior, be viewed as a "primitive analogue of adult behavior" (Hall *et al.,* 1977, p. 1141) or as a sophisticated means of exploiting the host dam. Because the net energy acquisition and growth rate of the pup are determined in the main by the amount of milk it can acquire from a single dam unwilling or unable to supply all the milk the pup could potentially utilize, the pup has nothing to gain from refusing or delaying nipple attachment regardless of its internal state. Because continued investment by the dam is dependent, at least in part, on nipple stimulation by the pups, attachment and suckling may provide important long-term benefits to the young as well as the immediate benefit provided by direct milk acquisition. For example, suckling stimulation provided by the rat pup has been demonstrated to stimulate prolactin release by the dam (Grosvenor *et al.,* 1970). High circulating levels of prolactin in turn stimulate both future lactation and the elevated levels of food intake by the dam which allow nursing rats to feed their young without depleting their own energy reserves (Fleming, 1976, 1977; Tucker, 1974; Cotes and Cross, 1954).

I have placed considerable emphasis in the preceding discussion on the importance of direct pup stimulation of its mother in the elicitation of continued parental investment. My underlying assumption has been that the greater the stimulation by the litter the greater the investment by the dam. There are unfortunately relatively few data to support such an assumption. The present approach to mother–young interaction points to the need for further work on the extent to and means by which the parasite pup may affect the behavior of the host dam and modify it to the pup's own advantage during periods of contact with her.*

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*The ability of parasites to manipulate the behavior of hosts to their own advantage is certainly not unique to the mother–infant relationship. To take a spectacular example, the lancet fluke *(Dicrocoelium dentriticum),* which encysts in the suboesophogeal ganglia of host ants, changes the behavior of the ant host so that instead of returning to its nest during the cooler parts of the day the ant clings to the top of a blade of grass. This parasite-induced pattern of behavior keeps the infected ant exposed to accidental ingestion by the crepuscular grazing ungulates which are the next host of the lancet fluke (Holmes and Bethel, 1972).

2.2.3. Locomotory Behavior

The neonatal rat depends on its dam not only for energy in the form of milk and conducted heat and for energy conservation provided by the dam in the form of insulation provided by the nest and burrow, but also for physical transport from one point to another. The locomotory capacity of the pup is limited to the ability to move in an oriented fashion only the very short distances necessary to modify the surface to volume ratio of the huddle for purposes of thermoregulation (Alberts, 1978 *a, b*) or to orient to the nest over distances of a few centimeters (Cornwell-Jones and Sobrian, 1977). In general, rat pups expend little energy on locomotion and, instead, both induce the dam to retrieve them to the nest site if they are displaced more than a short distance from it, or to move them to a new nest site should the original nest lose its insulating properties as a result of flooding or disturbance (Brewster and Leon, 1980*a;* Sturman-Hulbe and Stone, 1929). Again one could consider the lack of independent locomotory capacity of rat pups as evidence of their poor state of physical development or as an elegant means of reducing energy expenditure.

Although the young depend almost totally on the dam for the mechanical energy required for locomotion, they are capable of increasing the probability that the dam will move them, should they require movement, by emitting ultrasonic vocalizations (Allin and Banks, 1971; Brewster and Leon, 1980, *a*) and are also capable of assuming a special curled posture which facilitates their movement by the mother (Brewster and Leon, 1980 *b*). In one sense, arguing that the locomotory capacity of the pup is primitive in comparison with that of the adult, is like arguing that horseback riding is a primitive form of locomotion in comparison with walking. Although the locomotory behavior of the adult may be behaviorally or psychologically more complex than that of the juvenile, the behavior of each is functionally adaptive within its niche and neither is simple or primitive in that respect. Because human psychological and behavioral functioning is the most complex of that of any species, we tend to attribute superiority to complex behavioral mechanisms, though there is no good reason to do so. It is surely equally reasonable to consider simple solutions to a problem as more elegant and sophisticated than complex ones. In this perspective the neonatal pup is seen as the near-perfect parasite able to exploit its dam for its caloric, thermal, and mechanical energy needs while conserving its own energy for growth.

2.3. The Rat Pup as Facultative, Active Ectoparasite—Day 18 Postpartum

Two events occur on or about day 17 postpartum which require rat pups to abandon once and for all their obligate, passive parasitic niche. First, as can be seen in Fig. 6, adapted from Babicky *et al.* (1973), the energy delivered by the dam via her milk begins to drop precipitously in the face of steadily increasing

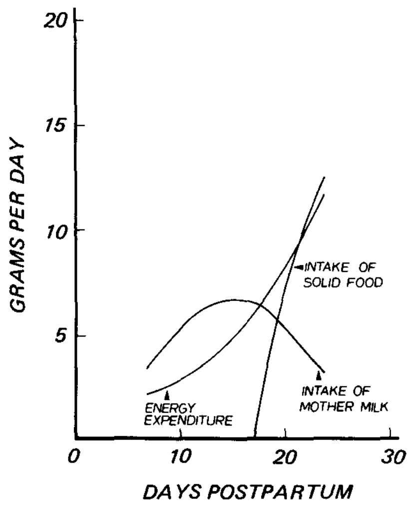

Figure 6. Schematic representation of the energy balance of litters of 8 rat pups (adapted from Babicky *et al.*, 1973).

energy demands by the young. Although the minimal metabolism of the pups at neutral temperature (as measured by oxygen consumption per kilogram per minute) remains essentially constant from birth to maturity (Taylor, 1960), the body weight of each pup and, consequently, its energy requirements grow rapidly. Even if the dam were to maintain her day 15 postpartum peak level of milk production indefinitely, by the time her pups reached 18–19 days of age, they would still either have to abandon growth or seek alternative sources of nutrition. In order to maintain a net positive energy flow the pups are obliged to begin ingesting solid food and to make the consequent transition from obligate to facultative dependence on the dam for nutrition. Second, as indicated in Fig. 7, adapted from Rosenblatt (1965), at about the same time that the dam reduces her nutritional contribution to her young she becomes increasingly unwilling to return to the nest site to initiate nursing bouts and, on occasion, even actively avoids her young when they attempt to suckle from her (Rosenblatt, 1965). The pups are thus forced to become active rather than passive in their exploitation of their dam as an energy source.

Whether the failure of the milk supply of the dam and her unwillingness to suckle play a role as proximal stimuli for initiation of feeding on solid food or whether the pups are endogenously driven to initiate ingestion of solid food is not clear. It is, however, clear that to continue to show a positive net energy flow in the face of a falling commitment by the dam the pup must begin to exploit alternative resources. The active, facultative parasitic niche of the 18-day-old obviously requires a markedly different phenotype for success than the passive, obligate parasitic niche of the 5-day-old, and in fact, the young pup has undergone a major metamorphosis in the intervening weeks. It has acquired an adult coat of fur, its ears and eyes have opened, giving it the full range of sensory systems, and its bodily proportions and musculature have altered so as to permit independent locomotion. As discussed below, the behavior of the pup has undergone changes as profound as its morphology.

2.3.1. Thermoregulation

In order either to actively seek the dam outside the nest site or to independently acquire solid foods in the general environment, the pup must be capable of activity even when out of contact with the dam, its major exogenous source of heat. According to Hahn (1956) and Hahn *et al.* (1956), chemical thermoregulation as well as insulation from the fur reach full development when the animals open their eyes at approximately 16 days of age (Croskerry, 1974). Thus, the 18-day-old rat can maintain constant colonic temperature over a fairly broad range of ambient temperatures, though even the 21-day-old pup does not possess the full adult capacity for maintaining a stable body temperature (Conklin and Heggeness, 1971). It should be kept in mind, however, that in the natural environment the rat pup does not leave the thermally protected environment of the burrow for extended periods of time until it reaches approximately 34 days of age (Boice, 1977; Calhoun, 1963). Prior to this time, movement by the pup is confined to explorations within the insulating burrow or brief trips on the surface in the vicinity of the burrow entrance. The microenvironment of the pup, even at 18 days of age, is thus not so thermally stressful as that of the adult.

2.3.2. Feeding Behavior

Perhaps the most marked behavioral changes associated with the change from obligate to facultative and from passive to active dependence on the dam as a

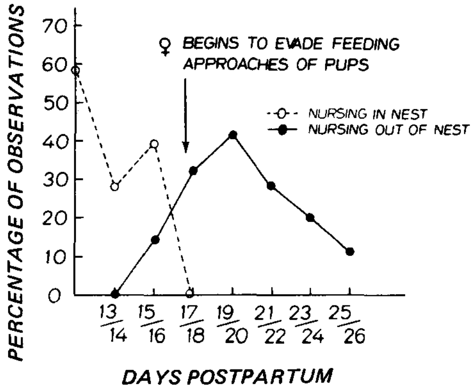

Figure 7. Percentage of observations of rat dams nursing in and out of the nest during the later stages of lactation (adapted from Rosenblatt, 1969).

source of energy are concerned with the control of feeding. Again the observed behavioral phenotype appears appropriate for the expanded niche of the 18-day-old. Whereas the neonate incurs little cost in attempting to feed and has access only to the finite supply of food provided directly by the dam, the 18-day-old must expend energy (in pursuit either of the dam or of solid food) in order to eat and has access to the functionally infinite supply of food available in the real world as well as to the declining energy supply of the dam's milk. Thus, the 18-day-old faces many of the same cost–benefit decisions concerning when and where to eat as do conspecific adults. One would expect, therefore, to see the emergence of adult patterns of control of feeding at about the time when facultative parasitism is imposed on the young by the failure of the milk supply of the dam. It has recently been reported (Hall and Rosenblatt, 1977, 1978) that whereas 15-day-old pups do not show increased ingestion with increasing deprivation, 20-day-old pups do and that nutritive preloads reduce intake of milk in 20-day-olds but not in 10-day-olds. Similarly, Hall *et al.* (1977) have found a dramatic increase in the latency of nondeprived pups to attach to the dam's nipple in 14- to 16-day-old young but not in 11- to 13-day-old young. Further, Hall *et al.* (1977) have found that pups at 15–17 days of age sucking on a dry nipple begin to exhibit a tendency to abandon that nipple and transfer attachment to another. Thus, the rat pup becomes sensitive both to its own internal state and to the nutritive return from its ingestive activity only when it has options other than mother's milk to satisfy its nutritive requirements.

Whether the absence in the obligate, parasitic neonate of the behaviors appropriate for multisource feeding are the result of an absence of appropriate neural structures to support those behaviors or are the result of an active inhibition of existing structures is open to question. The results of a recent series of studies by Martin and Alberts (1979) suggest that in at least one case it is inhibition of a developed neural mechanism rather than a failure of development which is responsible for the absence of a behavior during the obligate, parasitic state which emerges in the facultative, parasitic stage. Martin and Alberts have found that 15- to 16-day-old rat pups receiving flavored milk via a tongue cannula learn to avoid the flavor introduced into the milk only if milk delivery occurs while the pups are not attached to the nipple. Littermates treated identically while attached to the nipple fail to form the aversion. In contrast, nipple attachment fails to inhibit taste aversion learning in pups 21–22 days old at training. I would suggest that obligate, parasitic 15-day-olds cannot afford to learn an aversion to the taste of their dam's milk, experienced while suckling, and that the lack of capacity to learn aversions while attached to the nipple is thus an adaptation to the obligate, parasitic mode of life. Facultative parasites can learn to avoid the flavor of mother's milk and still survive, and such learning may play an important role in inducing pups to abandon mother's milk and find other sources of nutrition.

It might be argued that mother's milk is never toxic to young rats, so that the capacity to form aversions to flavor experienced while on the nipple is never of use. However, the development of lactase deficiency and consequent lactose intolerance in 21- to 22-day-old rats (Alvarez and Sas, 1961), taken together with the phenomenon reported by Martin and Alberts (1979), suggests that the combination of lactase disappearance in the pup and the emergence of the capacity to associate gastrointestinal distress with milk experienced while on the nipple may be an important proximal factor in motivating pups to seek food in the general environment. It has been argued (M. Lieberman and D. Lieberman, 1978; Rozin, 1976) that progressive lactase deficiency in young mammals and consequent experience of gastrointestinal distress in association with milk ingestion may be a mechanism regulating both the time and rate of abandonment of suckling in young mammals.* Of considerable interest with respect to this hypothesis the known temporal relationship in rats between the relative time of onset of (1) lactase deficiency [days 21–22 postpartum (Alvarez and Sas, 1961), (2) the ability to associate illness with cues experienced while suckling [between days 16 and 20 postpartum (Martin and Alberts, 1979)], (3) the failure of the milk supply of the dam to provide energy sufficient for continued pup growth [days 16–18 postpartum (Babicky *et al.,* 1973)], and (4) the onset of ingestion of solid food [day 17 postpartum (Galef, 1979; Babicky *et al.,* 1973)]. The findings presented above suggest that in rats, initiation of ingestion of solid food may result from failure of the dam's milk supply (see Davies, 1978), while the rate of transition to independent feeding may be accelerated by lactase deficiency and consequent learned aversions to mother's milk.

2.3.3. Locomotory Behavior

As mentioned above, the 19-day-old pup, while capable of rapid and efficient independent locomotion, is still an adequate stimulus for the elicitation of retrieval behavior in recently parturient dams (Rosenblatt and Lehrman, 1963). However, the pup's own mother at 19 days postpartum is no longer willing to engage in the physical movement of her young from one location to another. Eighteen-day-old pups must provide the mechanical energy to bring themselves in contact with their dam and other sources of nutrition. Although the mother is not willing to transport the young to resources, she does provide mechanical energy to transport resources to the young. Rat pups in the wild do not leave the natal burrow until 28 days of age, and there is some question as to where the solid foods which the pups could begin to utilize on day 17 (Galef, 1979; Babicky *et al.,* 1973) might come from. Rats are known to hoard food in their burrows (Barnett, 1975; Calhoun, 1962; Pisano and Storer, 1948), and it is likely that the food cache of the dam is the first

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*The role of lactase in the utilization of milk by neonatal rats and the role of lactase disappearance in the abandonment of mother's milk as a source of nutrition in weanling rats is probably less important than in other species. Whereas rat milk has only 5.9% of its calories in its carbohydrate fraction, the percentage of calories in carbohydrates in the milk of other species is far higher (cow milk, 29.5%; human milk, 45.1%) (Cox and Mueller, 1937).

solid food ingested by her young. While I know of no reports in the literature of laboratory studies of the time course of hoarding during the period of mother–young interaction, Calhoun (1962, p. 29) reports formation of a food cache by a lactating female rat in the wild immediately prior to weaning of her young. This observation suggests that although the dam will no longer physically move her young, and the young no longer elicit maternal locomotion by emitting ultrasonic vocalizations (Allin and Banks, 1970), the dam is still willing to invest mechanical energy in the young by transporting food to them. Investigations of postpartum hoarding by the dam is required to determine the extent of the dam's commitment of mechanical energy in this form.

2.4. The Juvenile Rat as Commensal—Day 40 Postpartum

In a commensal relationship the commensal is not metabolically dependent on its host; to the contrary, it is fully capable of independent survival. The spatial proximity of the participants in a commensal relationship does, however, allow the commensal to share resources (most frequently food and shelter) with its host without obvious detriment or benefit to the host. The success of the commensal, be it a pilot fish *(Naucrates ductor)* accompanying a shark or a rat living in a human dwelling and eating refuse, often depends in considerable measure on the tolerance of the host for the presence of the commensal.

The facultatively parasitic 18-day-old rat pup is already a commensal of its dam, sharing the food which she may transport to the home burrow and benefiting from the protection which that burrow provides against both extremes of temperature and humidity and the intrusion of predators.

On the 28th day postpartum, milk transfer from a rat dam to her young ceases (Ostadalova *et al.,* 1971; see also Fig. 1) and the young, which have been gradually increasing the proportion of energy they acquire from sources other than mother's milk (Babicky *et al.,* 1973; see also Fig. 6), can no longer directly exploit their dam as a source of nutrition. As discussed in the preceding section, a cache of food may be available in the burrow to sustain the pups for some time, but on about the 34th day of postpartum life rat pups (at least in seminatural environments) (1) begin to explore on the surface at some distance from the nest site, (2) begin to acquire food in the extra-burrow environment, and (3) undertake their first harboring with conspecifics other than their own mothers and siblings (Calhoun, 1962, p. 152). Thus, by 40 days of age the juvenile rat pup has extended its commensal relationships, with respect to both food and shelter, from its dam to others of its species. This new ecological situation places new demands on the pup and is reflected in changes in both its behavior and physiognomy.

2.4.1. Thermoregulation

The 40-day-old rat has the full adult capacity to maintain colonic temperature in the face of cold stress at least as severe as 5°C (Adolph, 1957). The final improvement in ability to control internal temperature, probably due to development of vascular mechanisms (Hahn, 1956; Hahn *et al.*, 1961, p. 134), is achieved at about day 30 postpartum, prior to the pup undertaking extended trips away from the thermal protection of its home burrow (Calhoun, 1962).

Although capable of maintaining independent thermal homeostasis, neither the juvenile 40-day-old nor the reproductively capable adult do so under normal circumstances. Both exhibit a tendency to huddle in groups in response to cold stress (Steiniger, 1950), as does the neonate. While the factors important in the control of huddling have been investigated in neonates (Alberts, 1978*a,b*), little is known of the factors affecting huddling in adults, though it has been suggested that huddling at later ages serves important, if unspecified, social functions (Barnett, 1975, p. 106) in addition to its thermoregulatory role.

The fact that juvenile rats, even those as old as 40 days, maintain a core temperature several degrees lower than that of adult conspecifics at any of a wide range of ambient temperatures (Adolph, 1957) suggests that the conductance of metabolic heat between fully and partially grown individuals may provide greater benefits to the latter animals than to the former. Full equivalence in heat transfer is not reached until the juvenile achieves adult size.

2.4.2. Feeding Behavior

Although both patterns of ingestion and the caloric regulatory behavior of 40-day-old rats are indistinguishable from those of adult conspecifics, selected aspects of feeding behavior in the juvenile remain distinctive. While adults independently select feeding sites and dietary items (Galef, 1977*a*), immature rats, even those as old as 40 days of age (Galef and Clark, 1971*a*; Galef and Heiber, 1976), are profoundly influenced in their selection of feeding sites and diets by the behavior of adults of their species (Galef, 1977*b*). The juvenile is guided by both visual and olfactory cues from adults in the selection of a location in which to feed and is guided in its selection of a diet by gustatory cues experienced both during ingestion of mother's milk and while feeding on solid food in the nest site (Galef and Sherry, 1973; Galef and Henderson, 1972; Clark and Galef, 1972). Although the 40-day-old rat has the full range of thermoregulatory, locomotory, and ingestive behaviors sufficient to permit independent acquisition of food, it lacks the experience of resource distribution possessed by adult colony members that have a history of food acquisition in the area in which the pup undertakes its first feeding trips outside the burrow. By approaching adults at a distance from the nest site (Galef and Clark, 1971*b*), by following adults as they move about the clan territory (Calhoun, 1962, p. 149), and by using residual olfactory cues deposited by conspecifics (Galef and Heiber, 1976; Telle, 1966) the juvenile rat can both reduce its probability of ingesting toxic substances (Steiniger, 1950) and reduce the time and energy it must spend in locating needed nutrients in the general environment (Galef, 1977*b*). Adult conspecifics, already familiar with the location and safety of the various potential ingesta to be found in their home range, have less need to attend to the behavior of conspecifics in their feeding site selection and, in fact, exhibit relatively little social influence on their feeding behavior (Galef, 1977*b;* Galef and Clark, 1971*a*).

The 40-day-old rat, usually treated as already weaned, is thus both dependent on food resources shared with adult conspecifics and on information acquired from conspecifics for its sustenance.

2.4.3. Locomotory Behavior

As mentioned above, the 40-day-old pup is influenced in its movements about its home range by the chemical cues deposited by adult conspecifics as well as by the physical paths which adults create through snow, dense grass, and other barriers to locomotion (Calhoun, 1962, p. 54–84; Telle, 1966). Both of these patterns of behavior, like thermoregulatory huddling, extend into adulthood and therefore cannot be considered behavioral adaptations specific to the juvenile period.

Young rats do, however, exhibit a pattern of locomotory behavior which is observed at its highest frequency during the same period when the ability to share resources both with the dam and other adult conspecifics is of greatest importance (Baenninger, 1967). Such behavior patterns are frequently described as "play behavior," and while no satisfactory definition of such activities exists, their functional significance has been an active area of discussion. It is generally assumed that the benefits of play are delayed rather than immediate (Fagan, 1974), and result from the opportunity to practice, acquire, or develop motor and social skills, thus affording some as yet undemonstrated benefit in later life (Fagan, 1976). Interpretations of the functions of play behaviors are thus congruent with interpretations of the function of many of the other activities of juvenile organisms, which are similarly treated as necessary precursors of the emergence of a successful adult phenotype. It is, of course, possible that the distinctive locomotory patterns of juveniles serve a function at the time of their expression rather than (or in addition to) any delayed beneficial effects which they might produce. As mentioned in the introduction to the present section, the success of the commensal juvenile rat depends in large measure on the tolerance of conspecific adults for its presence at feeding sites and in burrows, in that the young rat is incapable of defending itself successfully against sustained attack by older and, therefore, larger conspecifics. Both informal description (Steiniger, 1950) of the interaction of juveniles and adults at feeding sites and experiments in which foreign juveniles were introduced into established wild rat colonies (Barnett, 1975, p. 121) suggest that adult rats are surprisingly tolerant of the presence of juveniles. Either the phenotype of the commensal juvenile is not such as to elicit aggression from adult conspecifics or the young exhibit types of behavior which actively inhibit aggression. It seems possible that the distinctive gait and "playful" mode of social interaction of the juvenile serve either to conceal from adult conspecifics aggression eliciting patterns of movement (Alberts and Galef, 1973) or to inhibit tendencies to attack, normally elicited by the presence of unfamiliar conspecifics (Galef, 1970; for a similar view see Ghiselin, 1974, p. 261).

In either case, the determination of the properties of juveniles which inhibit aggression during their period of commensalism with adults requires further investigation as it is one of the more important features of the success of juvenile rats.

2.4.4. Sequela

As suggested in the immediately preceding discussions, the dependence of rats on conspecifics for a variety of the necessities of life never ceases. To carry the parasitism analogy to its inevitable and somewhat overdrawn conclusion, most adult rats are in many ways symbiotes of their fellows, exchanging thermal energy by huddling in cold temperatures, exchanging physical energy in the joint construction of burrows and trails and defense of the clan territory, and feeding off one another's food caches (Calhoun, 1962). It is only those individuals which leave the home range of their natal clans to establish new colonies that are faced with the need to acquire independently all the necessities of life.

3. Conclusion

Within the Aristotelian philosophical system each "type" or species was considered to begin life as simple, undifferentiated matter endowed with the "potentiality" or capacity for "realizing" the adult "form" of its species. The process of development was viewed as fundamentally one of achieving this adult form. While contemporary students of development would feel uncomfortable with the teleological implications of the Aristotelian position, the notion that the adult form is in some sense more realized than antecedent somas is an intuitively comfortable one. The existence of a developmental analogue of the *scala naturae* with the fetus or newborn infant at its base and the reproductively active adult at its apex is often assumed in discussions of ontogeny; the adult phenotype is treated as a goal toward which antecedent somas progress. While it is true both that interactions of the environment and organism early in life may affect later development and that interactions of environment and organism late in life cannot affect early development, it cannot be inferred from these observations that the organism's development has evolved with the production of the adult phenotype as its end point. At a genetic level of analysis the adult is as much a precursor of the fetus as the fetus is of the adult.

The intuitively appealing notions that some stages of development are better adapted than others and that the adult phenotype is the end point or goal of the life cycle tend to lose their appeal when one examines the life histories of species which, unlike most vertebrate species, do not move from a protected to an unprotected environment as they mature. The message implicit in such life histories is that the life cycle is, in fact, a cycle without definable end point. While the life history of a species such as the liver fluke, *Fasciola hepatica,** is more easily seen as a series of adapted phenotypes, each meeting the criterion of gene maintenance, than is the life history of a mammalian species such as *R. norvegicus,* the function of the developmental succession of somas is identical in the two cases. The maturing or weaning mammal moving through its life cycle is not *progressing* from a dependent to an independent state; rather, as the individual grows older, it *changes* both its behavior and the ecological niche it occupies so as to maximize its probability of maintaining the genes it temporarily houses.

One can conceive of each point in the life cycle as having two theoretically discriminable functions. First, it has to be adequate to deal with the challenges to survival posed at that point. Second, any given stage (whether fetus or adult) must produce the next succeeding stage, if the genes which it contains are to be maintained (Williams, 1966, p. 44). It is the underlying thesis of the present paper that too little attention has been directed to the study of the first of these functions of the early stages of the life cycle of mammalian organisms and that there has been a consequent overemphasis on the second. The resulting imbalance in perception of the nature of the phenotypes expressed prior to the emergence of the adult form has resulted in a failure within the psychological tradition to explicitly consider the behavioral and somatic adaptation of nonadult phenotypes to their environment.

The two views of development, one stressing the contribution of a given stage to its successors and the other the interaction of each stage with its environment, are clearly complementary. Each has its contribution to make to the understanding of the organism during the nonadult period of its life. The preceding pages are intended to suggest that there may be heuristic value in treating the organism as adapted to the succession of environments in which it must survive and grow in order to insure the protection of its genetic complement for future generations.

There is, of course, a danger inherent in interpretations of behavior and morphology deduced from their hypothetical functions. Such explanations are no more

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*The liver fluke *(F. hepatica),* for example, develops from a zygote into a first larval stage, the miracidium, that lives independently in an aquatic environment about which it swims by means of a covering of cilia. It has the neuromuscular machinery to identify, approach, and burrow into a particular species of aquatic snail. Inside the snail the miracidium metamorphoses into a second larval stage, the sporocyst, which reproduces by internal budding to produce the third larval stage, the redia. Rediae migrate within the snail and are capable of producing other rediae asexually and of metamorphosing into the last of the larval stages, the cercaria, which are provided like the earlier miracidia with a means of migrating to a new host. The cercaria burrows out of its snail host, swims by wiggling its tail to a blade of grass, attaches itself to the plant, casts off its tail, and encloses itself in a protective membrane. Inside the membrane the cercaria changes into a more or less amorphous mass, the metacercaria, which when ingested by a sheep or other herbivore hatches out as a young fluke. The immature fluke in time develops into a hermaphroditic adult capable of laying fertilized eggs, which continue the cycle (LaPage, 1963, p. 32).

than working hypotheses, and their value is dependent on the interest of the empirical investigations which they may generate.

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