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ADOLESCENT PREGNANCIES IN NON-HUMAN PRIMATES: AN ECOLOGICAL AND DEVELOPMENTAL PERSPECTIVE

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INTRODUCTION

From the standpoint of natural selection, reduction in age of first reproduction potentially will have major advantages, both by increasing the number of offspring and by reducing generation time. All other things being equal, we would expect any heritable trait that reduced age of first reproduction to spread in a population over successive generations. What, we might then ask, limits the reduction of reproductive onset in primates, human and non-human, and why might "all other things" not be equal? Anthropoid primates, monkeys and apes, have an unusually long prereproductive period for mammals of their size and there is higher mortality risk for first offspring than for ones born later. These facts suggest that primates may be pushing the limits of the cost/benefit balance of accelerating reproductive onset. Our recognition among humans of a category of pregnancies that we refer to as "adolescent pregnancies" suggests that there are some special characteristics of pregnancies that occur to unusually young females. I shall focus, below, on the thesis that adequate adult functioning, including successful reproduction, depends on maturation of a number of different somatic and behavioral systems and that these various systems differ in the conditions and degree to which they are subject to acceleration. Whether reproductive acceleration is advantageous or disadvantageous will depend on the extent to which other critical developmental processes are also accelerated under those conditions that accelerate attainment of reproductive maturity.

What do we mean by adolescent pregnancies? Do they exist in non-human primates? Most people agree on what pregnancies fall within the category of adolescent pregnancies—at least while we restrict our discussion to humans, to our own culture, and to recent times. As soon as we expand our perspective, however, we suddenly realize that our intuitive idea rests on a number of implicit assumptions about the time course of normal development and the potential consequences of deviation. We find that these assumptions may be difficult to explicate and that they may be more culturally, historically, and species bound than we thought (see Chapter 2 by Lancaster, Chapter 3 by Eveleth, Chapter 6 by Worthman, Chapter 14 by Whiting et al., and Chapter 15 by Vinovskis). By expanding our time frame and the populations that we examine, we are forced to consider what the basic issues are that lead us to single out, and be concerned about, adolescent pregnancy.

Researchers have always categorized as an adult any monkey female who has given birth to an infant. In fact, the presence of a pregnancy that has been carried to term is taken as prima facie evidence that the female is no longer just an adolescent who is experiencing menstrual cycles, but rather that she is an adult. We might note that the other monkeys seem to make the same distinction as the human observers do. That is, there seems to be an implicit assumption that reproductive maturity is appropriately coupled with other aspects of physical maturity and with psychological and social maturity as well, and that a monkey has completed the essential aspects of her "school of life" as well as having achieved internal maturation by the time she gives birth to her first infant.

It is the assumption of this synchrony of development that seems to be at the core of any consideration of adolescent pregnancy. Adolescent pregnancies are those that occur as a result of some degree of developmental dyssynchrony, those pregnancies that occur before other aspects of development are as complete as usual, or as is considered to be desirable for both the parent and the infant. What, then, do we know of normal developmental synchrony in non-human primates; what are the conditions under which reproduction is accelerated; and what are the consequences of this acceleration and of any developmental dyssynchrony or new synchronies that result? These are the questions explored in the several sections below, starting first with a brief overview of patterns of maturation and reproduction in anthropoid primates.

REPRODUCTION AND PREADOLESCENT MATURATION

Relative to other mammals of comparable size, anthropoid primates might be considered as poor reproducers: in ecological jargon they are characterized as K-selected (Mc Naughton and Wolf, 1973). That is, monkeys and apes have relatively long gestations and long infant and juvenile stages, small litter size (usually only one), and a long interval between successive births (Sacher and Staffeldt, 1974; Western, 1979; Eisenberg, 1981). Although these reproductive deficits, both later onset of reproduction and lower rate of reproduction, may be partially compensated for by a somewhat longer adult span (Sacher, 1978), the primary compensation probably must occur through mortality reduction at earlier life stages. Infancy is the period of highest mortality in non-human primates as it is in humans and most other mammals (Caughley, 1966). Features of a parent's physical, psychological, and social condition may be particularly important to offspring survival in primates.

We shall take as our baseline, or norm, the patterns of reproduction and development that are found in wild, unprovisioned animals that are living with a sufficiently normal complement of predators or other natural hazards that the population is approximately stable in age-sex distribution and stationary in total size. We shall then explore conditions that diverge from this and consider the developmental consequences of the divergence. The available data for these explorations are predominantly from the larger, primarily ground-dwelling monkeys, the macaques of Asia, and the baboons of Africa, and, to a lesser extent from chimpanzees. Because the author's work is on savannah baboons, Papio cynocephalus, and because some of the most extensive available developmental data are for this species, these animals will be used for illustration.

Baboons and macaques, like most anthropoids other than the small, monogamous monkeys who provide extensive paternal care, give birth to a single offspring (Schultz, 1948; Leutenegger, 1979). In Amboseli National Park where we have conducted a longitudinal study of baboons since 1971, over one-hundred pregnancies have resulted in only one instance of live-born twins and one other of stillborn twins. The single primate young has a tenacious grip (Hines, 1942) that enables it to ride close against its mother's ventrum. There, a baboon infant obtains warmth, access to the nipple, and transportation as its mother spends three-quarters of the daytime walking and feeding to obtain nutrition for them both (Altmann, 1980). Among savannah baboon species, an adult male, usually the one within the multi-male social group who is likely to be the infant's father, will probably provide some active as well as passive care for the infant (see e.g., Altmann, 1978; Packer, 1979; Stein, 1984). However, the burden of most care falls to the mother in this as well as other nonmonogamous species.

Possible maternal weight loss during the months of infant care (e.g., Whichelow, 1976, for humans and a review for several mammalian species in Widdowson, 1976) and effects of nursing on prolactin levels

(Konner and Worthman, 1980, for humans), results in a prolonged postpartum amenorrhea, which lasts anywhere from 6 to 18 months in Amboseli baboons. Thereafter, the infant or young juvenile still depends on individuals and on the group as a whole for occasional care, warmth at night, learning opportunities, and predator warning and defense. By 1–1½ years of age a youngster can obtain its own nutrition (S. Altmann, unpublished data) and has a fairly good chance of survival without maternal care (J. Altmann, 1980). A long juvenile period follows—a fascinating developmental stage for which there has been a paucity of research (but for illuminating exceptions see Lancaster, 1971 for vervet monkeys; Owens 1975a,b and Pereira 1984 for baboons). Although mortality remains high for young juvenile baboons, the later juvenile years, from about age 3–5 for females and 5½ or 6 for males is one of low mortality, relative independence, much play, and changing dominance relationships accompanied by relatively frequent aggressive interactions (Altmann, 1980; Pereira, 1984; Altmann et al., unpublished data).

ADOLESCENCE

The transition from the juvenile period to that of adolescence is delineated in many species by the presence of externally visible indicators of reproductive maturation. For females this usually means presence of sex skin swellings or particular other skin swellings or coloration, externally visible menstruation, or onset of estrous behavior. For males, descent or enlargement of testes or changes in skin coloration are diagnostic features of adolescence or "subadulthood."

In seasonally breeding macaques, the females usually first become pregnant in the breeding season the year after the one in which they first exhibit estrous behavior, coloration, and swelling (see review in Lancaster, Chapter 2, this volume). In savannah baboons, in which breeding is not restricted to a single season, first pregnancy occurs 6–15 months after the first menstrual cycle (Altmann et al., 1977, 1981; Scott, 1984). This is approximately four cycles after the components of the female's menstrual cycle (Altmann et al., unpublished data), and other characteristics of the cycle (Scott, 1984) are the same as those for fully adult females. In the great apes, too, there is a period of adolescent subfertility; 2–3 years elapse between onset of cycles and first pregnancy in wild chimpanzees (Tutin and McGinnis, 1981) and gorillas (Harcourt et al., 1980; Fossey, 1982). The duration of adolescent subfertility among baboon and macaque females is at least partially physiological. In addition, there may also be a social component because fully adult males do not form consorts with these adolescents until their cycles are indistinguishable, by our external daily observations (Alt

mann et al., unpublished data), from those of adults (see also similar results in Scott, 1984).

For adolescent males, social factors appear to be even more important in preventing reproduction. Macaques and baboons, like most primates, are sexually dimorphic and to some extent polygynous. Males are in competition with each other for access to fertile females. Adolescent males are appreciably smaller than adult males, have not yet fully developed secondary sexual characteristics, and are subordinate to the adult males in the dominance hierarchy. Although juvenile males occasionally mate briefly with fertile adult females without much reaction from adult males, for the most part adolescent males are actively prevented from mating. In Amboseli, it is not until the end of adolescence, when the male is within the size range of fully adult males, has fully developed canines, and achieves a rapid rise in dominance, that he can successfully compete with adult males for reproductive access to fertile adult females (Altmann et al., in press). Before that time, his matings are almost exclusively with females who are also adolescents (see also Rostal and Eaton, 1983, for captive macaques and Scott, 1984, for another population of baboons) or with adult females at times that they are not likely to conceive.

Adolescence, then, encompasses an extended period that spans the transition from partial to complete reproductive competence. In addition, it is also a period during which other aspects of maturation proceed. For both males and females it is a period of continued growth (Watts and Gaven, 1982). It is during adolescence that most of the sexual dimorphism in weight develops. Apparently this is partially due to steeper weight velocity curves in males, but is also as a result of weight gain that continues until age 8–10 among baboon males, for example, and only until about age 6 or 7 for baboon females.

Adolescence, like the late juvenile period, is one of high survivorship. Adolescent males and females probably continue to acquire knowledge and skills during this period, the benefits of which may not be seen until several years later when females must simultaneously care for themselves and a neonate and when young males of most species leave their natal group to survive alone, if sometimes only briefly, and to make their way into a new group where they will live and reproduce as an adult.

Social maturation also proceeds during adolescence. Some data are available regarding attainment of dominance relationships in wild baboons. For baboon males, adolescence may be a period of temporary stability in dominance relationships. Baboon males are dominant to most or all adult females by the onset of adolescence, and they do not challenge adult males until the end of the period (Hausfater et al., unpublished data). Among females, during adulthood, dominance re

lationships change only rarely and, during maturation, daughters achieve dominance over members of families to whom their mothers were dominant (Hausfater et al., 1982). Most of this transition occurs before the onset of menstrual cycles (Walters, 1980; Scott, 1984), but some relationships remain unstable until the end of adolescence.

In a number of species, it has been reported that older juvenile and adolescent females play and fight less than do their male peers and interact with infants more than do the males (e.g., Lancaster, 1971; Pereira and Altmann, 1985, and references therein). However, major questions about adolescent behavior remain unanswered. For no wild primates do we have measures of the magnitude, sources, or consequences of the variability in performance of these behaviors, either among individuals, between sexes, or among populations or species; the data for provisioned and captive animals also remain limited (see review in Caine, 1985).

In summary, the period of adolescence in anthropoid primates is one of growth and maturation, physical and behavioral. Although the very limited available behavioral data pertain to social interactions, there is every reason to believe that individual skill attainment and other aspects of behavioral development are as important a feature of this period as those more obvious characteristics that have been reported.

REPRODUCTIVE ACCELERATION

It has recently become well-documented, particularly for savannah baboons and for Japanese macaques, that captivity, or even artificial food provisioning in the wild, results in greater weight gains throughout maturation, in lower age of onset of adolescence, and in earlier age of first reproduction (Altmann et al., 1977, 1981; Coe et al., 1979; Mori, 1979; Harcourt et al., 1980; Sugiyama and Ohsawa, 1982; Nicolson, 1982). In addition, interbirth intervals (essentially the duration of infancy) are shorter, and average annual survivorship for both infants and adults is increased. For baboons, a schematic diagram of these dramatic differences appears in Fig. 12.1.

The main comparative studies of Japanese macaques are a result of different amounts of food provisioning, or absence of provisioning, in otherwise either wild or at least free-ranging animals (e.g., Mori, 1979; Sugiyama and Ohsawa, 1982). These authors have usually studied the effects of different feeding regimes on the same groups of animals. Additional data are available from captive animals. The data for baboons result from comparisons of wild savannah baboons with those in captivity (e.g., Snow, 1967; Altmann et al., 1977, 1981; Nicolson, 1982; Coehlo, 1985). Limited data are also becoming available for ba-
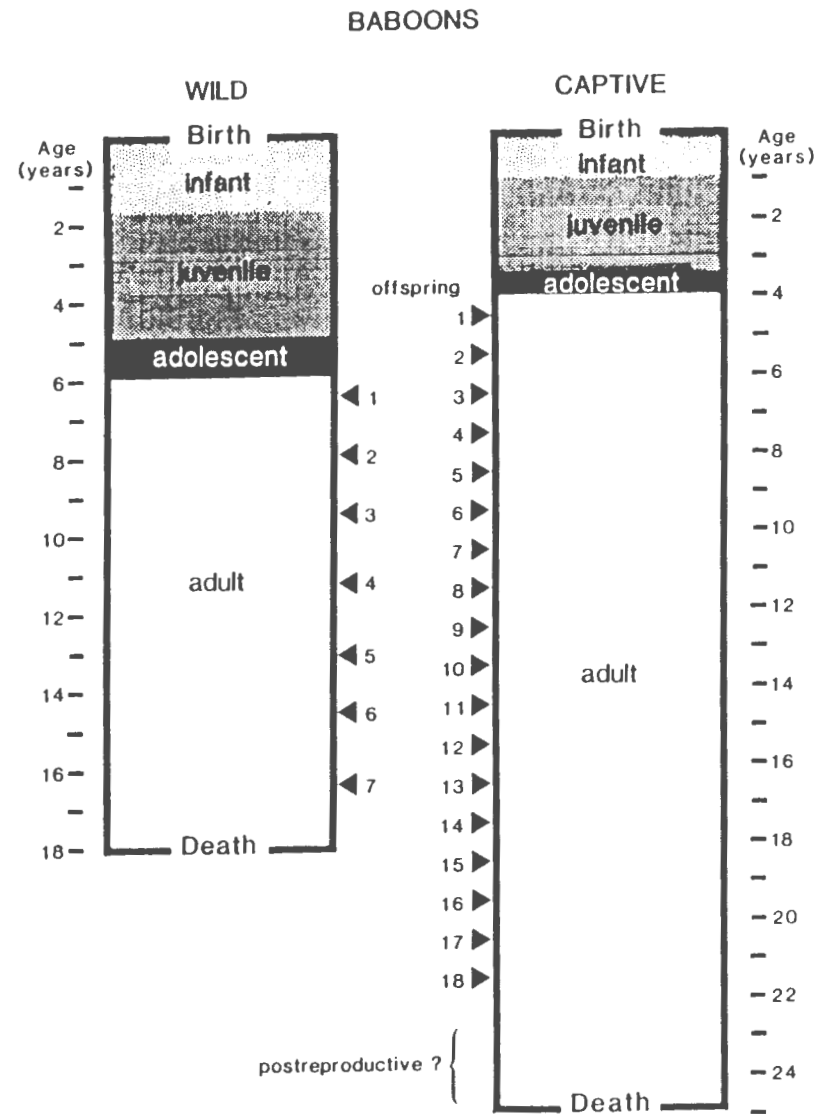
BABOONS

FIGURE 12.1. Schematic diagram of differences in reproductive patterns between wild and captive baboons.

boons under conditions of varying food availability, natural or human-produced, in the wild (Strum and Western, 1982; Altmann et al., unpublished data). The data for chimpanzees come from wild animals with limited and varying amount of food provisioning and from captive animals (Coe et al., 1979; Tutin and McGinnis, 1981, Pusey, 1983). It is often the case that data pertaining to a particular issue or to changes in a certain variable are not available for each species. Where comparable data are available for several species, they are in at least qualitative agreement, with the exception that Chism et al. (1984) found no difference in reproductive parameters between captive and wild patas monkeys, *Erythrocebus patas.*

Below, is constructed a tentative scenario for the effects of food provisioning or a high nutritional plane on the time course of development. This has been done by pooling and piecing together data for these various species and conditions and by making extrapolations and predictions from the limited data base.

1. *From birth, weight gain is greater in food supplemented conditions than otherwise and the difference in weight between the two conditions increases with age.* This has been a consistent finding, for several taxa, of the many studies that have been previously cited. Anatomical and physiological constraints on prenatal development and parturition probably limit the possible variability in birth weight itself (see Schultz, 1969, and Napier and Napier, 1970, for anatomical constraints, and Riopelle and Hale 1975 for reduction in gestation length when full-term weight is reached earlier).

2. *Weight is more accelerated than skeletal growth and skeletal growth more than tooth eruption* (Mori, 1979; Altmann et al., 1981; Sigg et al., 1982).

3. *Menarche occurs earlier in food-enriched situations, perhaps as a result of greater weight or of body fat accumulation but age, or some other physical variable that is less food-sensitive than weight, is also a factor in determining age of menarche, resulting in attainment of reproductive functioning at a lower weight in low nutrition than in high-nutrition animals.* Among primates, the importance of minimal weight or fat accumulation has been best studied for humans (e.g., Frisch and Revelle, 1969, and sequelae; see also discussion in Lancaster, this volume, Chapter 2). The non-human evidence comes primarily from the studies of Mori (1979) and of Sugiyama and Ohsawa (1982) on Japanese macaques. Mori discusses the fact that older low-weight females for whom menarche has been delayed do reach menarche after a few years delay, despite low weight.

4. *Age of first conception is also accelerated in food enriched situations (references as previously noted). However, this seems to be pri*

marily a result of earlier attainment of menarche, that is, the length of adolescent subfertility is less reduced than is the age of menarche. The data are primarily the same as those for menarche but the period of subfertility is not itself usually reported. It appears that the duration of subfertility is at least partially a function of the time needed for full hormonal developmental and coordination which is not food limited in the ecological sense (e.g., McNaughton and Wolf, 1973). See, for example, Reiter, Chapter 4 this volume, for a review of the human data.

5. *If the food enrichment is through provision of a concentrated source, social differences favoring early and more successful reproduction in high-ranking animals are exaggerated relative to their occurrence in unprovisioned, lower-nutrition conditions.* The evidence for this is primarily from the work on Japanese macaques cited above. An important point for future research is the need to distinguish the effects of food enrichment at the group level and the extent to which food enrichment is equally available to all members of the group. This distinction is important whether the enrichment is human-produced or otherwise. Some natural foods may be readily monopolizable, such as fruiting trees; others such as grass corms are not (e.g., Wrangham, 1980). Likewise, although human-produced food enrichment usually results in concentrated resources to which high-ranking animals have greater access, this need not necessarily be the case. One would expect these two types of changes in overall food abundance to have different effects on social-class differences in reproduction.

6. *Food provisioning or other human-enrichment situations tend to produce higher survival rates as well as high reproductive rates, population growth, a larger proportion of immature animals in the population, at least in the short run, and larger kin groups and maturing age cohorts* (e.g., Altmann and Altmann, 1979; Southwick et al., 1980; Berman, 1980). These social factors may interact with the direct nutritional effects, perhaps magnifying them through social facilitation (e.g., Vandenbergh and Drickamer, 1974; Vandenbergh, 1977; models in Silk and Boyd, 1983). However, at high animal densities the social effects may produce reproductive delay or other suppression, particularly for low-dominance status animals (e.g., Dunbar and Dunbar, 1977; Dunbar, 1984; see also review of reproductive facilitation and suppression in McClintock, 1981).

7. *Infant survivorship may not be as great for first born infants in high-nutrition situations as would be predicted based on the improved survival for later-born offspring* (see review in Lancaster, this volume, Chapter 2). The data are, as yet, quite inadequate on this point but it may be that there is higher risk from inadequate skeletal development and from the greater social pressures that occur particularly for low-

ranking females in the high-density, often captive, situations in which high nutrition studies have been conducted.

As tentative or speculative as some of the preceding conclusions are, most arise fairly directly from existing data, albeit limited in some cases. In the next section, however, it will be necessary to move further from existing data as we consider potential consequences of differential changes in developmental rates.

DEVELOPMENTAL DYSSYNCHRONY AND ADOLESCENT PREGNANCIES

If all aspects of physical, psychological, and social development occurred apace, population biologists, cross-cultural anthropologists, and students of historical change would still surely find the acceleration of interest, but the question of adolescent pregnancies would not arise. It is the situation of differential effects on aspects of development, in particular the situation in which first pregnancies occur at an earlier stage relative to other aspects of development, that leads us to consider some mothers as still being adolescents and to speculate on the possible detrimental consequences for them and for their offspring.

With respect to dyssynchrony of physical development, the data suggest that under conditions of food enrichment a monkey female will give birth to her first infant not only at a younger age but at a smaller skeletal size and less complete dental development than she would otherwise. Consequently, although a higher nutritional plane could result in less competition between a mother and her fetus or offspring for nutrients, and probably does for older mothers, adolescent mothers and their offspring may be in greater competition over nutrients, particularly those nutrients, such as calcium, that are in high demand for skeletal growth. Thus, food enrichment probably results in better nutrition and better health for both high parity mothers and their infants but it may put adolescent primiparous females at higher risk. One would expect this relationship to be some U-shaped function of nutrition rather than a linear one.

Laboratory data suggest that first-born infants have a lower birth weight than infants born later (e.g., Broadhurst and Jinks, 1965; see also Lancaster, Chapter 2, this volume). Although this may put the infants at greater risk as in humans (Van Valen and Mellin, 1967; also see Garn, this volume), low birth weight may also have the positive effect of facilitating parturition in a mother whose skeletal development is less complete. If one were able to increase infant birth weight it might be at the cost of greater problems at parturition, at least in many of the monkeys which, like humans, have potential problems of infant

"fit" during birth, and in contrast to the great apes that do not (Schultz, 1969). These birth and infant survival problems would be greatest for those monkeys, such as squirrel monkeys, that naturally have the greatest birth-proportion problems. Moreover, anthropoid species seem to vary in the stage of growth at which they reach menarche and at which they first reproduce (Rowell, 1977; Watts, 1985). Cross-species predictions and comparative studies should be highly informative for understanding the range of physical developmental synchrony and its consequences.

As little as is known about dyssynchrony in physical development, it is still greater than the information available on factors that accelerate behavioral development, both individual and social, and the potential dyssynchronies that might arise when reproductive maturation is accelerated. One obvious concern is whether the time needed for learning about foods and the home range, and the time necessary for development of foraging skills, and social skills used in grooming, aggression, mating, and care of infants can be reduced, and whether it is reduced under conditions that accelerate reproductive maturation. It is quite possible that learning can be, and is, appropriately accelerated because abundant food supply reduces the time spent foraging and frees more time for leisure activities (Altmann, 1980; Lee, 1984; Brennan et al., 1984; Altmann et al., unpublished data), but this has not been studied.

Another potentially important kind of dyssynchrony arises when we consider the attainment of adult dominance rank. As discussed above, for example, Amboseli baboons have attained their usually permanent dominance rank by the time they conceive their first infant. If reproductive maturation is accelerated, is attainment of dominance rank comparably accelerated? If not, does this result in detrimental levels of stress and disruption for the female and her infant if these rank-change interactions occur after reproduction begins? It is unknown.

Two factors appear to be potentially important in determining whether a consequential dyssynchrony results from reproductive acceleration. The first is related to the reduction in time needed to obtain and process food that usually occurs in high nutrition situations. If this time is used to increase the rate and time spent in social and other behavioral activities whose development would otherwise be relatively retarded, and if an increased density of these activities within a shorter period and at an earlier age can result in the same level of maturation, then dyssynchrony may not occur; otherwise it probably will. Second, there is probably a range of synchrony, not just a particular set amount, that is within the animals' range of response without any detriment to functioning. The amount of reproductive acceleration or variability that normally occurs as a result of temporal and spatial variability in food

available to different groups or populations or to successive age cohorts may well be within the animals' range of response; that due to major upheavals or change such as coming in contact with human-provided food sources may not be. An understanding of both of these factors would contribute considerably to a basic understanding of developmental plasticity as well as to the specific questions of interest here.

CONCLUSION

An exploration of issues involved in adolescent pregnancies in non-human primates raises many questions about the meshing of developmental events. These have not been the subject of investigation in primate studies, neither for normal development nor with respect to situations that change the developmental time course. This is an example of a situation in which study of an important human problem leads us to interesting basic questions about non-humans. However, the benefit is potentially in the other direction as well. The very fact that this sometimes culture-bound and emotional topic contains elements that are of general developmental importance across species, suggests that non-human primates might also provide useful animal models for the study of adolescent pregnancies, with contributions both from comparative studies of well-chosen contrasting primate species and from in-depth investigations of developmental variability within a single species or even population.

Finally, we should bear in mind that we have considered only one situation in which *relative* acceleration of reproduction can occur, albeit probably the one most common in human and non-human primates. Reproductive maturation will also occur early in the life cycle relative to other aspects of maturation if there is delay of other aspects of physical, or, more likely behavioral maturation, for example, by increasing demands for skills that a functioning adult needs in a complex society. The dyssynchronies that result are likely to have some, but not all, features in common with those that have already commanded our attention.

ACKNOWLEDGMENTS

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