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PHYSIOLOGICAL CONSTRAINTS ON LIFE HISTORY PHENOMENA: THE EXAMPLE OF SMALL BEAR CUBS AT BIRTH

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Attempts to explain ecological phenomena generally rely on simple optimality criteria involving limited sets of variables. Bounds on the adaptive responses available to meet particular ecological challenges are often not considered, and discrepancies between empirical observations and model predictions are frequently attributed to lack of model resolution (Pyke 1984). It is becoming clear, however, that the processes of adaptation are closely linked to important physiological constraints on the ability of organisms to achieve global ecological optima (Gould and Lewontin 1979). This study examines how such physiological constraints may have influenced an important life history characteristic of the eutherian mammals, namely, weight at birth.

A log-linear relationship between litter weight and weight of parturient mother has been documented for the eutherian mammals (Leitch et al. 1959; McKeown et al. 1976). Bears (Ursidae), which give birth to relatively small litters of tiny, immature neonates, display, among the eutherians, the most extreme deviations from the regression of litter weight on maternal weight (Leitch et al. 1959; Frazer and Hugget 1974; McKeown et al. 1976; Pond 1977; Case 1978). Depending on the regression formula used, litter weights for bears are from $\frac{1}{3}$ to $\frac{1}{10}$ of that predicted for female mammals of comparable size (Leitch et al. 1959; McKeown et al. 1976). Such anomalous exceptions to generalized allometric relationships are, by definition, rare (Calder 1984), but they are of particular importance to general ecological theory because of the insight they may provide into constraints bounding life history phenomena. In this paper we propose that the altricial ursid pattern of producing small neonates, and the consequent switch from transplacental to mammary nourishment, is an adaptive response to physiological constraints associated with supporting fetal development while in a state of hibernation and without access to food.

* Sequence of authors determined by the flip of a coin.

A brief overview of bear natural history is germane to our hypothesis. Because data on other species are so sparse, this review focuses on the Holarctic bears: the American black bear (*Ursus americanus*), the brown bear (*U. arctos*), and the polar bear (*U. maritimus*). Bear litter sizes vary from one to four with a modal litter size of two for most populations (Craighead et al. 1969). Bears breed in the spring, but implantation is obligately delayed until autumn in all species examined (Wimsatt 1963). A pregnant female enters a winter maternity den close to the time of implantation, giving birth there approximately 50 days after implantation (Wimsatt 1963; Hensel et al. 1969). The length of time spent in winter dens varies with species and location, and it is generally longer for more northerly populations (Johnson and Pelton 1980). The winter den of a bear is thermally insulated, making the microclimate of an occupied polar bear den even in the High Arctic relatively benign (Blix and Lentfer 1979). Cubs are nursed huddled within their mother's fur until the family emerges in the spring, by which time the cubs have reached the weight for mammalian neonates predicted by regression (Leitch et al. 1959). Thus, for bears the maternity den performs a protective function partially analogous to that of the uterus.

During winter dormancy, a female bear neither eats nor drinks, maintaining herself entirely through the metabolism of fat stores (Nelson 1980). A bear in winter dormancy is not simply a starving bear. Rather it is in a physiological state similar to that of hibernation but without the marked reduction in body-core temperature displayed by classical hibernating mammals (Folk et al. 1980; Lyman 1982). Body protein is protected, except when it is used to meet the growth and metabolic requirements of the developing fetuses and nursing neonates, and no urine is voided (Nelson et al. 1973; Lundberg et al. 1976; Nelson 1980). No other mammals, except some of the large Mysticeti cetaceans, go without food and water for extensive periods during active gestation (Frazer and Huggett 1973); and only bears, some cetaceans, and some phocid pinnipeds fast through part or all of the lactation period (Lockyer 1981; Fedak and Anderson 1982).

PHYSIOLOGICAL CONSIDERATIONS

Mammals exhibit a number of physiological responses to the problems of supplying sufficient metabolites to body tissues and coping with intermediary metabolic products and wastes while fasting. The primary metabolic response to the low blood-glucose levels that accompany extended fasting is the release of triglycerides and free fatty acids (FFA) from adipose tissue as alternative substrates of oxidation. This in turn leads to an increase in the rate of ketone-body formation in the liver (Krebs et al. 1971). Ketone bodies are required by the central nervous system, which can use only these or glucose, but not FFA, as oxidative substrates (Cahill and Aoki 1980). The use of FFA and ketone bodies during fasting, in lieu of glucose, serves to spare body protein that would otherwise be broken down in gluconeogenesis.

For pregnant females the problems associated with fasting are compounded, since both nutrient supply and waste clearance for fetuses must be mediated by

the mother across the placenta (Felig and Lynch 1970; Freinkel et al. 1972). Not surprisingly, the metabolic responses of gravid females to fasting are more rapid and markedly more extreme than those observed in non-gravid conspecifics (Freinkel et al. 1972; Girard et al. 1977). Although these responses are well documented for a number of mammalian species, the details of the metabolic interrelationships between mother and fetus during fasting are less well understood and have not been described for any of the Ursidae. In reviewing the data available for other mammalian species, we have assumed that the metabolic processes involved are not qualitatively different in bears (Battaglia and Meschia 1981).

In contrast to a pregnant female, which can readily catabolize FFA during fasting, dependence on fatty acids as an energy source by the mammalian fetus has not been observed (Roux and Yoshioka 1970; Girard et al. 1979; Hahn 1979; Warshaw 1979). Appreciable transplacental transfer of FFA does occur in some species, especially during fasting when maternal plasma FFA levels are elevated, but these appear to be deposited in fetal adipose tissue or used for structural requirements (Edson et al. 1975; Elphick et al. 1975; Girard et al. 1977). Although some increase in enzymatic activity for FFA oxidation occurs in fetal tissue during maternal fasting, the increases are significantly lower than those that occur postpartum (Kimura and Warshaw 1983). *In vitro* analyses also indicate that fetal tissues have little or no ability to use FFA for meeting energy requirements (Roux and Myers 1974; Freund et al. 1984).

The reason for the lack of FFA catabolism in the mammalian fetus is puzzling (Hochachka and Somero 1984), especially considering that the neonate can catabolize fatty acids as the primary source of energy within a few hours of birth (Hahn 1979). Although the details of the transfer process are not fully understood, it is clear that FFA do not cross the placenta as readily as glucose or ketone bodies (Dancis et al. 1976; Robinson and Williamson 1980), possibly limiting their availability as a fetal substrate. Glucose and FFA also differ in relative oxygen requirements during catabolism, with FFA requiring more oxygen per molecule of ATP produced than does glucose (Hahn 1978). Although fetal metabolism is fully aerobic under most conditions (Harned 1978), it is nonetheless very high and relatively constant per kilogram of fetal weight (Battaglia and Meschia 1978, 1981), in marked contrast to postnatal mammals, in which oxygen consumption is inversely related to body mass. Additionally, fetuses exist in a state of relatively low oxygen availability because of the lack of direct atmospheric exchange with their circulatory system. The total oxygen stores of a near-term fetus are probably less than 1–2 min (Longo and Power 1976), and a reduction in maternal oxygen supply rapidly leads to fetal hypoxia and associated intrauterine growth retardation (Van Geijn et al. 1981). Furthermore, unlike glucose, the catabolism of FFA is strictly aerobic in all eukaryotes (Lehninger 1975). Therefore, a fetus may be constrained from large-scale dependence on FFA as an energy source because this would increase both the potential for limitation of its growth rate and its vulnerability to energy shortages and tissue damage during periods of oxygen stress. These problems may be of particular relevance for a fetus developing

within a hibernating bear because oxygen concentrations in the den are reduced by the limited exchange of gas with the external atmosphere (Withers 1978).

Although maternal fat stores may not be directly available to supply the energy requirements of the developing fetus, they could, in theory, be converted to ketone bodies for subsequent use as the principal oxidative substrate (Cahill 1972). However, the extent to which fetuses metabolize ketone bodies as an energy source, in lieu of glucose, during long-term maternal starvation has not been determined. The sustained maternal levels of circulating ketone bodies that would be required to produce substantially larger fetuses than those typical of bears may lead to ketonemia, consequently interfering with the physiological adaptations required for survival under conditions of no available food or water (reviewed in Nelson 1980).

The alternative to the direct or indirect use of maternal fat stores to supply fetal energy demands is a reliance on maternal amino acids for gluconeogenesis throughout gestation. However, this might deplete maternal body protein so as to jeopardize survival. Thus, it seems clear that a considerable selective advantage would accrue to any adaptation making maternal fat stores available to developing young. Although there appear to be constraints on this adaptation in utero, these stores can be directly incorporated into milk, the sole source of neonatal nourishment. In contrast to fetuses, early neonates have a rapidly rising capacity for oxidizing FFA and may meet most or all of their energy requirements from fatty acid oxidation (Hahn 1979), while limiting gluconeogenesis, a major pathway for energy acquisition in the fetus (Miller 1969; Snyderman 1978; Snell 1982). Bear milk is higher in total solids, fat, and protein, and lower in carbohydrates, than that of other carnivores and of most other terrestrial mammals; it more closely resembles that of pinnipeds and cetaceans (Jenness et al. 1972; Jenness 1974). More than 50% of these total solids consist of fatty acid chains of 16 carbon atoms or more, probably mobilized directly from adipose tissue (Jenness et al. 1972). By nursing small neonates instead of maintaining developing fetuses, a fasting female could thus use her fat stores and avoid the loss of body protein resulting from gluconeogenesis, simultaneously eliminating the potential problem of pH imbalance from ketoacidosis that could accompany high rates of fetal ketone-body utilization. Furthermore, the potential problem of extreme ketonemia would not be simply passed on to her neonate. Even a neonate depending on FFA as an energy source would be constrained to use ketone bodies only in its central nervous system. Other tissues could catabolize FFA, and high levels of circulating ketone bodies are common in all mammalian neonates because of the ketogenic nature of their diets (Warshaw 1979).

There appear to be no fundamental physiological or developmental constraints to the production of extremely small neonates that undergo considerable development while nursing. All metatherian mammals at birth are tiny relative to their mother and in an extremely immature state (Tyndale-Biscoe 1973), but they begin suckling almost immediately and continue their development, until independence, solely on a diet of maternal milk. The duration of lactation in metatherians is 5–10 times longer than in eutherians of similar adult body size (Green 1984).

EVOLUTIONARY CONSIDERATIONS

Fossil records of the evolutionary development of a behavioral trait such as denning are necessarily scarce. However, denning is believed to have occurred in early Miocene Amphicyonidae carnivores, suggesting a long evolutionary history in the Ursidae and their relatives (Hunt et al. 1983). Denning probably arose in response to food supplies that fluctuated with seasonal environmental changes. Under such conditions it might be more cost-effective for a large well-armed omnivore, with no need to remain lean for either rapid escape from danger or for capture of prey, to deposit fat stores during periods of food abundance and reduce energy expenditures through inactivity and fasting during subsequent periods of food scarcity. The seasonal nature of these fluctuations, however, may have resulted in the period of food abundance being too short to support the full-term development of large, mature neonates, while still allowing these young the time necessary to deposit sufficient fat stores of their own to support winter hibernation. Because of the allometric nature of metabolic processes (Kleiber 1975), ursids, by virtue of their large size, have relatively low energy demands per unit of body weight and therefore require less depression of normal metabolic functions in order to survive a winter's fast than do smaller mammals with proportionately similar fat stores (Morrison 1960; Lindstedt and Boyce 1985). This may have given bears the evolutionary option of supporting developing offspring while fasting, thus allowing them to adopt denning behavior.

The evolutionary radiation of bears and their relatives has resulted in at least some species living in habitats with sufficient food to allow year-round foraging. Polar bears feed primarily on seals on the arctic sea ice through winter, and most do not den for extended periods. However, pregnant females do den in the autumn and, like other ursids, remain without food or water for many months during pregnancy and lactation. At birth the ratio of litter weight to maternal weight is typically low (Kleiman 1983). Giant pandas (*Ailuropoda melanoleuca*) are closely related to modern bears (O'Brien et al. 1985) and also give birth to relatively small neonates, usually singletons (Kleiman 1983), but unlike temperate and arctic ursids, giant pandas do not spend an extended period in their den after parturition. Instead, the female carries the tiny neonate with her as she forages for bamboo (Schaller et al. 1985). Perhaps because of phylogenetic constraints, female polar bears and giant pandas have not adopted a more typical eutherian gestation length and birth weight, although high-quality food is apparently available to allow foraging before and immediately after parturition.

Physiological constraints on fetal nutrition, as outlined, could have wider ecological implications. For example, when access to carbohydrates is phylogenetically constrained, then shortened gestation, smaller neonates, and a longer period of lactation would be favored. This may explain why insectivores and carnivores, which subsist on carbohydrate-poor diets, give birth to relatively smaller and less mature neonates than do other orders of mammals (McKeown et al. 1976; Martin 1984). Similarly, different requirements for fats, carbohydrates, and proteins between pregnant and nonpregnant animals could lead to spatial

segregation of individuals by reproductive status at times of feeding (see, e.g., Watson and Staines 1978). Thus, physiological constraints might play as large a role in determining more-general trends in neonatal weight as those that have been suggested for mechanical-design constraints (Millar 1981), and they may have important consequences for optimal foraging theory.

SUMMARY

Bears give birth to tiny, immature neonates and, for eutherian mammals, display the most extreme deviations from the regression of litter weight on mother weight. This may reflect physiological constraints on the ability of a pregnant female to meet the requirements of fetal metabolism while in a state of winter dormancy and without access to food or water. Although all postnatal mammals can use body-fat stores to supply energy during fasting, the mammalian fetus does not appear to have the capacity for catabolizing significant quantities of free fatty acids. Instead, it requires glucose as the principal oxidative substrate. However, a fasting female could continue to supply glucose to a developing fetus through gluconeogenesis only by using her body protein, eventually jeopardizing her own survival. By shortening the period of gestation and giving birth to very small, immature neonates, a female would shift from transplacental to mammary nourishment of her offspring. Fatty acids from maternal lipid stores could then be incorporated into milk and used directly for nourishing the offspring, thereby sparing maternal body protein. At the same time, the female would avoid elevated levels of ketone bodies, which might interfere with the maintenance of winter dormancy. The virtual absence of fatty acid catabolism by mammalian fetuses, even in species with an appreciable level of placental transfer of free fatty acids, is in striking contrast to the predominant use of lipids as an energy source by neonates. This notable absence of an energetic pathway in fetuses has never been adequately explained.

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