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The Role of Maternal Effects in Mammalian Evolution and Adaptation

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THE ROLE OF MATERNAL EFFECTS IN EVOLUTION

Offspring phenotype is, in part, the result of the genes they inherit from their parents. In sexually reproducing animal species, offspring inherit half of their genes from their mothers and half from their fathers. Therefore, both parents are equally likely to affect their offspring's phenotype through direct genetic effects. Offspring phenotype can also be affected by the parental phenotype. These parental phenotypic effects on the offspring's phenotype can have a significant impact on the offspring's survival and reproduction and therefore have important consequences for evolution and adaptation. In evolutionary biology, they are referred to as "maternal effects," perhaps because in many of the organisms in which they have been demonstrated they are more likely to originate from mothers than from fathers.

Maternal effects can result in phenotypic similarities between mothers and offspring. For example, in many mammalian species, large mothers in good body condition can produce large offspring by virtue of the fact that they can transfer to them large amounts of nutrients during pregnancy and lactation. Cross-fostering studies in rodents and nonhuman primates have shown that there is a strong resemblance between the parental care patterns of mothers and those of their adopted daughters (Francis et al. 1999; Maestripieri et al. 2007). When maternal effects result in phenotypic similarities between mother and offspring, they essentially represent a mechanism for

nongenetic transmission of traits from one generation to the next. Correlations of traits between mothers and offspring due to maternal effects can significantly bias estimates of additive genetic variance and genetic correlations. Therefore, knowledge of maternal effects is required to understand the genetic basis of traits and their potential for evolutionary change.

Although it has long been known that maternal effects can complicate our ability to estimate the genetic basis of traits, the adaptive ecological and evolutionary significance of maternal effects has only recently been appreciated (Cheverud 1984; Kirkpatrick & Lande 1989; Cheverud & Moore 1994; Bernardo 1996; Mousseau & Fox 1998a, b; Wolf et al. 1997; 1998; 2002; Wolf & Wade 2001). When individual variation in the maternal phenotypic traits that affect the offspring's phenotype has a significant genetic basis, this variation can be subject to natural selection. In other words, natural selection can favor the evolution of maternal genes whose effects are expressed in the offspring's phenotype, i.e., "maternal-effect genes." Genetic maternal effects can play an important role in evolutionary dynamics. For example, theoretical studies have demonstrated that maternal effects can dramatically affect the strength and direction of evolution in response to selection (e.g., Kirkpatrick & Lande 1989; Wade 1998). They can slow down or accelerate the rate of evolution of a character and, in some cases, also lead to evolution in the opposite direction to selection (Kirkpatrick & Lande 1989; Qvarnström & Price 2001). Therefore, knowledge of maternal effects is required to fully understand the evolution of traits by natural selection. Accordingly, maternal effects have been the focus of intense scrutiny in recent evolutionary-biology research.

The source of variation in some maternal phenotypic traits that have the potential to affect offspring phenotype may be largely environmental rather than genetic. Given the high degree of phenotypic plasticity in many vertebrate taxa, mothers can adjust their phenotype in response to their environment and shape their offspring's phenotype accordingly. By doing so, mothers are in effect transferring information about the environment to their offspring. If the mothers' adjustments to the environment are adaptive and if the environment is stable across generations, that is, if the cues from the mother's environment are a good predictor of the environment in which offspring will find themselves, then the offspring's phenotypic adjustments are also adaptive. Therefore, nongenetic maternal effects provide a mechanism for cross-generational phenotypic plasticity and make a significant contribution to an organism's fit with the environment (Bernardo 1996; Mousseau & Fox 1998a, b). By modifying the offspring's phenotype or inducing the

expression of new phenotypic traits, nongenetic maternal effects can also allow offspring to colonize new ecological niches and be exposed to new selective pressures. This, in turn, may result in the expression of previously unexpressed genes in the offspring that have significant phenotypic effects on their fitness. Therefore, nongenetic maternal effects can play an important role not only in promoting adaptation to local environmental conditions but, more generally, in evolutionary change in the population. A high degree of phenotypic plasticity may also imply that some individual responses to the environment can be maladaptive. If a mother's responses to the environment are maladaptive, maternal modifications of the offspring phenotype may be maladaptive as well. Therefore, maternal effects may also provide a mechanism by which maladaptive phenotypic traits are transmitted across generations (e.g., Maestripieri 2005a).

MATERNAL EFFECTS IN MAMMALS

Maternal effects have been reported in a wide range of taxa but, until recently, most empirical research on adaptive maternal effects concentrated on plants and insects, and to a lesser extent fish, amphibians, reptiles, and birds (e.g., Mousseau & Fox 1998b). Maternal effects have long been known by breeders of domestic mammals (e.g., Bradford 1972; Koch 1972). Indeed, the covariation between maternal nutrition and offspring size and growth in domestic mammals is the system in which maternal effects were first recognized and studied (McLaren 1981; Bernardo 1996). Until recently, maternal effects in wild mammals received little systematic attention by evolutionary biologists. Yet maternal effects arguably play a larger role in the evolutionary dynamics and adaptation of mammals than in any other animal taxa (Reinhold 2002). Mammals are unique among vertebrates in that mothers and offspring have an intimate and extended association during gestation and lactation. This provides the opportunity for offspring size and growth to be influenced by maternal body condition. Aside from these nutritional maternal effects, other maternal effects involving physiological and behavioral mechanisms are also likely to be common. This is because of the extended period of maternal care and offspring dependence characteristic of many mammals, and therefore the many opportunities for interactions between mothers and offspring throughout their lifetime. For example, in some social mammals, offspring remain associated with their mothers through their entire lifetime and mothers continue to invest in them and influence their behavior and reproduction for many years after weaning.

In recent years there has been a dramatic increase in evolutionary studies of maternal effects in mammals. Maternal effects have been especially studied in wild populations of rodents (e.g., several genera and species of lemmings and voles, subfamily *Arvicolinae*: Boonstra & Hochachka 1997; Inchausti & Ginzburg 1998; Ergon et al. 2001; Oksanen et al. 2003; Ylonen et al. 2004; wild house mice, *Mus domesticus*: Nespolo et al. 2003; leaf-eared mice, *Phyllotis darwini*: Banks & Powell 2004; North American red squirrels, *Tamiasciurus hudsonicus*: McAdam et al. 2002; McAdam & Boutin 2003a, b) and wild ungulates (red deer, *Cervus elaphus*: Schmidt et al. 2001; mountain goats, *Oreamnos americanus*: Gendreau et al. 2005; Côté & Festa-Bianchet 2001; bighorn sheep, *Ovis canadensis*: Festa-Bianchet et al. 2000; Soay sheep, *Ovis aries*: Wilson et al. 2005). Many of these studies used data on nutritional maternal effects on offspring size and growth to test the predictions of evolutionary models. Nutritional maternal effects have also recently been studied in other groups of wild mammals such as pinnipeds and nonhuman primates (e.g., Ellis et al. 2000; Bowen et al. 2001; Altmann & Alberts 2005).

Nonnutritional maternal effects involving behavioral or physiological mechanisms are probably widespread in mammals but have only been investigated in a few mammalian groups, most notably rodents and primates. In these taxa, studies have also considered maternal effects on offspring phenotypic traits other than body size and growth rate. For example, field and laboratory studies of rodents have uncovered effects of maternal presence and behavior on a wide range of offspring phenotypic traits, including habitat selection, food preferences, antipredator behavior, and social preferences (e.g., Yoerg & Shier 1997; Mateo & Holmes 1997; 1999; Holmes & Mateo 1998; Galef 2002; Davis & Stamps 2004). Recent research with laboratory rodents has also elucidated the neuroendocrine and molecular mechanisms through which naturally occurring variations in maternal care affect the responsiveness to stress, and the behavior and reproduction of offspring, including the intergenerational transmission of maternal care (e.g., Francis et al. 1999; Meaney 2001; Champagne et al. 2003; Cameron et al. 2005). Maternal dominance rank in cercopithecine monkeys has long been known to affect a wide range of offspring phenotypic traits, including sex, growth rate, timing of first reproduction, and behavior (e.g., Silk 1983; Holekamp & Smale 1991; Berman & Kapsalis 1999; Altmann & Alberts 2005). Studies of primates have also addressed some of the physiological mechanisms underlying the influence of maternal behavior on offspring's reactivity to the environment as well as the intergenerational transmission of maternal behavior from mothers to daughters (Fairbanks 1989; Berman 1990; Chapais

& Gauthier 1993; Maestripieri 2005b; Maestripieri et al. 2007). Finally, interest in maternal effects is also growing among researchers studying human behavior, development, and cognitive evolution (e.g., Bjorklund & Pellegrini 2002; Bjorklund 2006).

The study of maternal effects in mammals is currently a highly heterogeneous area of research. In part, this is because these effects are of interest to and have been studied not only by evolutionary biologists but also by behavioral ecologists, biological psychologists, and anthropologists. As a result, there is notable heterogeneity in the use of concepts and definitions of maternal effects by different scientists. Research is also heterogeneous with regard to whether the focus is on the analysis at the level of the population versus the individual, whether the studies focus on genetic versus environmental maternal effects, whether these effects are quantified versus simply described, and whether the emphasis is on their evolutionary consequences versus their underlying mechanisms. For example, whereas studies focusing on maternal effects in wild rodents and ungulates have mostly focused on genetic maternal effects and their evolutionary consequences at the population level of analysis, studies of carnivores and nonhuman primates have mostly focused on environmental maternal effects and their underlying mechanisms at the level of the individual. Because of this heterogeneity, current research on maternal effects in mammals is not framed within a common body of theories and there is little communication between researchers working with different taxonomic groups. This volume reflects the variation in approaches to maternal effects that researchers have taken. We believe that it is premature to attempt a definitive synthesis of all of the research represented in this volume; rather, our goal is to integrate the conceptual and empirical studies of maternal effects in mammals, and hope that this will stimulate and direct the growth of this area of research. Moreover, a comprehensive and integrated elucidation of the role of maternal effects in the evolution and adaptation of mammals could enhance the understanding of these effects in other taxonomic groups as well.

CONTENT OF THE VOLUME

Maternal Effects in Mammals aims to provide a comprehensive representation of maternal-effects research in different mammalian groups, with a balanced emphasis between theory and data, genetic and environmental effects, evolutionary approaches and studies of mechanisms, field and laboratory approaches, and analyses at the populational, organismal, and molecular level.

The first two invited chapters provide the theoretical background necessary for those unfamiliar with the study of genetic maternal effects. The following chapters summarize the relevant work in mammals, sometimes in a topic-oriented perspective and sometimes in a taxon-oriented perspective.

Cheverud and Wolf (Chapter 2) and Wade et al. (Chapter 3) review recent theoretical advances in our understanding of maternal effects and their role in evolution. Their chapters mainly focus on genetic maternal effects and illustrate some experimental approaches with which these effects can be studied in the laboratory and in the field. McAdam (Chapter 4) and Wilson and Festa-Bianchet (Chapter 5) also focus on the evolutionary significance of genetic maternal effects, but the emphasis of their chapters is on the measurement of these effects, particularly nutritional maternal effects on offspring growth, in wild mammalian populations. McAdam draws examples from his research with wild red squirrels while Wilson and Festa-Bianchet review studies of wild ungulates. Chapters 6–13 largely focus on the study of individuals and their behavior rather than on population-level processes, and address both the ecological-evolutionary significance of maternal effects and the social, physiological, molecular, and cognitive mechanisms through which these effects may operate. Bowen (Chapter 6) discusses nutritional maternal effects on offspring size and development in pinnipeds, within the context of the ecological adaptations and the maternal investment strategies of these animals. In Chapter 7, Mateo provides an overview of behavioral and physiological maternal effects on a wide range of offspring fitness-related traits such as social relationships, reproduction, habitat use and dispersal, antipredator behavior, and reactivity to the environment in wild rodents and other mammals, with a special emphasis on seasonally breeding animals. Galef (Chapter 8) discusses the behavioral and cognitive mechanisms through which mammalian mothers may influence the development of food preferences and feeding behavior of their offspring, drawing from experimental studies of laboratory rodents as well as observations of free-ranging animals. Champagne and Curley (Chapter 9) review a large body of recent research showing that variations in maternal care patterns of laboratory rats and mice can alter the behavior, reproductive development, neuroendocrine responsiveness to stress, and maternal care patterns of the offspring, as mediated by alterations in gene expression. Vandenbergh (Chapter 10) reviews evidence that hormones from the mother, from exogenous hormone mimics, and from adjacent fetuses in the uterus can have profound effects on the behavior and physiological development of offspring. The most compelling evidence of these prenatal hor-

mone effects results from studies of rodents in which the postnatal development of fetuses adjacent to other males and exposed to their testosterone is compared to that of fetuses that lack this androgenic exposure. In Chapter 11, Holekamp and Dloniak describe a wide range of maternal effects on offspring development in fissiped carnivores, with particular emphasis on the influence of maternal social rank on offspring status, play behavior, reproductive development, association patterns, growth, survivorship, and dispersal patterns in spotted hyenas, *Crocuta crocuta*. The mechanisms underlying some of these effects are also discussed, including androgenic hormones, insulin-like growth factors, stress hormones, nutritional variables, and differential maternal care. Well-known examples of maternal effects in nonhuman primates, reviewed by Maestripieri in Chapter 12, include the maternal inheritance of dominance rank and its effects on reproduction in cercopithecine monkeys, the influence of maternal social networks and behavior on the social development, kin preferences, and social networks of the offspring, the effects of maternal behavior on the offspring's fearfulness, tendency to explore, and responsiveness to stress, the effects of maternal behavior on female reproductive maturation, and the nongenetic cross-generational transmission of maternal styles. Bjorklund et al. (Chapter 13) discuss the many ways in which maternal characteristics in humans can affect children's social, emotional, and cognitive development. Emphasizing the plasticity of human development and the contribution of variation in maternal behavior to epigenetic inheritance, Bjorklund et al. suggest that developmental processes driven by maternal effects may have played an important role in the evolution of human intelligence. Finally, in Chapter 14, Mateo and Maestripieri synthesize and integrate the conceptual and empirical information provided in the other chapters and discuss future directions for research on maternal effects in mammals and other taxa.

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