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Maternal Influences on Development, Social Relationships, and Survival Behaviors

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INTRODUCTION

As a naturalist, Darwin (1859) made two observations that were particularly important for the development of his theory of natural selection—that there is significant phenotypic variation among individuals of a species, including artificially selected or domesticated species, and that offspring resemble their parents. Since the Modern Synthesis (see Fisher 1930; Wright 1931; Haldane 1932), with our growing understanding of genes and inheritance, significant advances have been made in identifying the genetic processes responsible for individual differences and family resemblance. It is now well established that phenotypes of developing young can be influenced by parents through the transfer of genetic material. However, parents can also influence the traits of their young by rearing them in particular microhabitats, providing them with food and other resources, and protecting them from predators or parasites. Until recently, scant attention has been paid to these parental effects, or the ways in which a parent's phenotype or environment influence the phenotype of its offspring. Parental effects are of special relevance to the fields of evolutionary biology and ecology for several reasons. First, they can maintain and magnify heritable individual differences across generations and thus have potent effects on the speed, strength, and direction of natural selection (see also Wade et al., McAdam, this volume). Second, parental effects lead to parent-offspring resemblance, which can be

adaptive if offspring encounter similar social and environmental features as adults (assuming parents themselves were successful in that environment). Third, parental effects provide a rich source for phenotypic plasticity, including anatomical, physiological, and behavioral traits, because parents respond to dynamic cues in their environment (e.g., reduced food availability or current photoperiod) and can influence offspring accordingly. Because these intergenerational changes are plastic, parents can respond rapidly to changing environments and produce offspring whose phenotypes are well suited for current conditions, more rapidly than change based on evolution through natural selection (see also Cairns et al. 1990; Mousseau & Fox 1998). However, it should be noted that dynamic responses to environmental changes can result in negative maternal effects, such as when offspring exhibit foraging strategies similar to their mother's, yet these strategies are not longer effective in the current environment.

One of the hallmarks of mammalian behavioral development is its sensitivity to the social and physical environments provided by mothers during gestation and lactation. Therefore, opportunities for maternal effects on offspring phenotypes—morphological, physiological, and behavioral—can be particularly robust (see Reinhold 2002). A mother's set of social partners, her habitat, her physiology, her diet, and even her daily activity rhythms can have profound and lasting effects on offspring phenotypes. From a functional perspective, these effects make adaptive sense when offspring develop in similar social and physical environments as their mothers. They also contribute to individual differences within a population, with alternative phenotypes being favored by selection depending on spatial and temporal changes in social environmental conditions (reviewed in Stamps 2003; see also Mateo 2007a).

In this chapter I will present an overview of potential maternal effects on behavioral development, including pre- and postnatal effects of social experiences, stress, and seasonality on the expression of developing phenotypes. I will also discuss in detail, from a comparative approach, how maternal effects mediate the development, plasticity, and functional significance of a suite of social and survival behaviors. Examples will be drawn from studies of both captive and free-living mammals, with a focus on comparative research with ground-dwelling squirrels. Treatment of maternal effects in other contexts can be found throughout this volume, including dominance hierarchies, nutritional status, natal dispersal, intrauterine position, and population cycles. I focus on both proximate and ultimate levels of analysis

of the interplay between developmental processes and their social and environmental contexts.

PROCESSES AND OUTCOMES OF MATERNAL EFFECTS

Any treatment of maternal effects should consider both the processes and the outcomes of these effects. For example, the outcome of behavioral development in species with parental investment often results in juvenile social behavior resembling parental repertoires (Bateson 1982). The process of this parental influence on the development of offspring social behavior, or any other behavioral repertoire, can range along a continuum from direct to indirect (reviewed in Mateo & Holmes 1997). Parents have a direct influence when they orient their behavior toward their young, such as by leading their young to a food source or preventing them from interacting with particular conspecifics. For a parent's influence to be considered direct, its behavior must change qualitatively or quantitatively as a function of its offspring's presence. At the other end of the continuum, parents have an indirect influence when their normal behavior inadvertently affects juvenile behavior, but is not directed specifically towards their young. Adults are thus incidental models of behavior and juveniles are inadvertent observers, and a parent's behavior is not contingent on the presence of its offspring. Examples of indirect influences include parents' own antipredator responses, their food preferences, and their reactions to territorial intrusions. Production of alarm calls (vocal signals emitted in response to predators) by adults can be an example of a direct or indirect influence depending on whether the likelihood of calling is contingent on the presence of the adults' young (e.g., Cheney & Seyfarth 1990; Hoogland 1995). Note that the effects on offspring do not necessarily differ if parental influence is direct or indirect.

Direct and indirect parental influences on the process of behavioral development share several characteristics. First, influence can have an immediate effect, such as when the response of an adult to a predator evokes almost simultaneously a response by a juvenile, or it can have a delayed effect, such as when an immature animal observes an adult's response to an alarm call but does not show its own responses until it can locomote independently. Second, neither process of influence implies complex mental states or awareness of juveniles' traits by parents (cf. Cheney & Seyfarth 1990). Third, juveniles can be passive observers or recipients of adult actions; that is, young need not seek out adults and copy their behavior. Fourth, as

noted above, "direct" and "indirect" describe *processes* rather than *outcomes* of influence, and do not necessarily differ in the importance they play in juvenile behavioral development (Mateo & Holmes 1997). These processes of parental effects on juvenile ontogeny are potentially common among mammals, particularly those with extended maternal care.

MATERNAL EFFECTS ON SOCIAL DEVELOPMENT

Prenatal Environmental and Social Effects

Among mammals, development starts at conception, and because sensory and perceptual development begins in utero, the uterine environment of developing fetuses can affect their later morphology, physiology, and behavior. The onset of sensory function during development is remarkably consistent in birds and mammals, with the perceptual senses showing the following order of onset: tactile, vestibular, chemical, auditory, and visual. In altricial rodents, the latter two systems may not be functioning until after birth, and all systems continue to develop and form cortical connections during postnatal life (Gottlieb 1981; Alberts 1984; see also Alberts & Ronca 1993). Thus maternal effects can begin prenatally through a variety of sensory experiences, with fetuses moving when the mother grooms, travels, or sleeps, "smelling" what the mother eats, and experiencing changes in stress hormones when the mother experiences an agonistic social interaction, a predation attempt, or chronic food shortage. As a result of early perceptual development, therefore, experiences prior to birth can have enduring effects. For instance, fetuses can experience odors in the amniotic fluid that can later influence food preferences or social recognition of kin (Hepper 1987; Porter et al. 1991; Terry & Johanson 1996; Hudson et al. 1999; Galef, this volume). Mothers can therefore indirectly guide their offspring toward safe food items or amiable conspecifics. In summary, prenatal perceptual experiences can have long-lasting effects on offspring phenotypes (Alberts 1984; Smotherman & Robinson 1988; Grubb & Thompson 2004).

One of the best-known maternal effects in birds and mammals involves variation in the exposure of offspring to gonadal hormones (Schwabl 1999; Ryan & Vandenbergh 2002). In some mammals, exposure to gonadal hormones during gestation can have profound effects on adult morphology, physiology, and behavior, particularly among polytocous (litter size > 1) species. For example, individuals gestating between two males experience higher androgen levels than those between two females, and these intrauterine position (IUP) effects have consequences in adulthood, including

variation in rates of sexual maturation, fecundity, aggressive tendencies, parental behaviors, territoriality, and sexual attractiveness. IUP can also affect sex ratios of future litters, thereby creating intergenerational transmission of IUP effects (see Vandenbergh, this volume). Observations of laboratory-born animals with known IUPs released into the wild suggest that early exposure to gonadal hormones can affect reproductive and social behaviors (Zielinski et al. 1992).

Maternally mediated gonadal-hormone exposure can have adaptive or functional effects as well. For example, females may experience higher fitness if their litters are male-biased, such as when the local breeding population is female-biased (short-term sex-ratio biasing; Fisher 1930; e.g., Creel et al. 1998; Allainé 2004) or when a female in a polygynous species is in exceptionally good condition and would be favored to overproduce sons (Trivers & Willard 1973; e.g., Clutton-Brock et al. 1984; Meikle et al. 1993; Hewison & Gaillard 1999). In such situations, daughters would more often gestate between males and be partially masculinized as adults. Those daughters may also overproduce sons themselves (as females gestating between two males tend to produce male-biased litters), and if that daughter is in exceptionally good condition herself, this would be beneficial, but if she is in moderate or poor condition, then selection would not favor her sons over her daughters, and she would experience a fitness loss. Thus the maternal effects via IUP can, over time, influence secondary sexual characteristics, sex ratios, and reproductive success depending on original maternal condition and local demographics.

Steroidal hormones can exert other effects on offspring during gestation, although some effects have not been well studied in mammals. For example, elevated maternal glucocorticoids can have negative effects on offspring morphology, development and survivability (e.g., tropical damselfish, *Pomacentrus amboinensis*: McCormick 1998; common shrew, *Sorex cinereus*: Badyaev et al. 2000; lizards, *Lacerta vivipara*: Meylan & Clobert 2004; root voles, *Microtus oeconomus*: Bian et al. 2005; barn swallows, *Hirundo rustica*: Saino et al. 2005; but see Uller & Olsson 2006 on lizards). Thus the impact of social or environmental stressors experienced by one generation can have effects on their reproductive success as well as on the phenotypes of the next generation. In addition, in quail pre-laying maternal corticosterone is correlated with female-biased clutches (Pike & Petrie 2006). Among most birds natal dispersal is female-biased, and thus if the mother experiences crowding or food shortages, for example, she would benefit from producing daughters that will leave the natal area and, perhaps, settle in less competitive environ-

ments. The costs and benefits of maternal effects can depend on the ecological and demographic patterns of a species. For instance, adult female spotted hyenas (*Crocuta crocuta*) are behaviorally dominant over males, due in part to prenatal androgenization. This dominance allows females with cubs to compete for scarce food resources (carcasses), and females with higher circulating androgens during gestation produce cubs with high levels as well. These androgens increase aggressive behaviors in cubs, which may have fitness consequences for offspring if it helps them to compete at kills (Dloniak et al. 2006; see also Holekamp & Dloniak, this volume).

Perinatal environmental and social effects

Maternal traits mediated by the external environment can also be transmitted nongenetically to offspring. Most altricial mammalian young are reared in nests, burrows, or dens and are not directly exposed to the same range of physical and social environments that the mother experiences. However, a young animal can experience the effects of food availability, climate changes (temperature, day length), or social instability before leaving the natal nest. One of the most salient perinatal maternal effects is the influence of a mother's physical condition and body weight on her offspring, with heavier females producing heavier young at birth and/or investing more in those young than females in poor condition (Boonstra & Hochachka 1997; Hansen & Boonstra 2000; see also Bowen, Cheverud & Wolf, Wilson & Festa-Bianchet, this volume). In many mammals, body weight at birth or during the juvenile period predicts adult mass (e.g., Birgersson & Ekvall 1997; Festa-Bianchet et al. 2000) or survival probability (e.g., Trombulak 1991; Neuhaus 2000), which in turn can have important consequences for adult fitness and lifetime reproductive success (Atkinson & Ramsay 1995; Festa-Bianchet et al. 2000; Wilson et al. 2005). Furthermore, positive maternal effects may be more potent for the sex that benefits most from philopatry, such as female offspring among mammals (e.g., Rieger 1996; but see Baker & Fowler 1992), and male offspring among birds (e.g., Visser & Verboven 1999), whereas poor maternal condition can have more of an effect on the sex that disperses (e.g., Labov et al. 1986; Meikle et al. 1995).

In addition, the optimal time to reproduce may be population-specific rather than species-specific, particularly when species are found along latitudinal or elevational gradients. Photoperiodic cues (day length) can be important indicators of upcoming seasonal changes and signal appropriate times for reproductive efforts. The photoperiod experienced by females during pregnancy is relayed to young during gestation and lactation through the

hormone melatonin. In rodents, maternal melatonin can influence offspring growth rate, fat deposition, pelage, and sexual maturation. Young born in the spring or early summer mature quickly and can start breeding that year, but those born in the late summer remain prepubertal often until the following spring, reducing energetic demands until the reproductive season begins again. Thus perinatal melatonin from mothers adaptively primes young for somatic and reproductive growth appropriate for the time of year in which they are born (reviewed by Lee & Gorman 2000). Photoperiodic cues are not the only mechanism that can trigger breeding condition; social and dietary cues experienced by mothers can also influence development or regression of reproductive organs (Goel & Lee 1996; Demas & Nelson 1998; Lee & Gorman 2000; Ergon et al. 2001). That is, a mother can guide her offspring to partition their somatic and reproductive efforts to best suit their future fitness potential, accelerating puberty and mating if conditions are favorable, or delaying sexual maturation until breeding conditions are appropriate, in turn increasing the mother's own lifetime fitness.

If a pregnant female experiences an unstable social environment, high predation pressure, or unpredictable adverse climatic conditions, her adrenalhormone responses can affect the hypothalamic-pituitary-adrenal (HPA) functioning of her developing offspring (e.g., Maccari et al. 1995; Barbazanges et al. 1996). For example, offspring of mothers experiencing stressors can have heightened acute stress responses compared with young of nonstressed females. In some laboratory rodents early postnatal stress decreases HPA activity and reactivity to novel objects and facilitates some forms of learning (Levine 1994; Maccari et al. 1995). However, severe exposure to stressors results in maladaptive HPA axes, with animals exhibiting inappropriate responses to novel or stressful situations, impaired learning and altered social behaviors (e.g., McEwen & Sapolsky 1995; Lupien & McEwen 1997). Thus, perinatal exposure to stress hormones, during either gestation or lactation, can fine tune sensitivity and efficacy of the HPA axis and the behaviors relating to it, producing, for example, animals with more neural receptors, lower responsiveness to stressors, and improved learning capabilities (Lupien & McEwen 1997; Catalani et al. 2002; Joëls et al. 2006; Yang et al. 2006; see also Champagne & Curley, this volume). If a mother experiences chronic stress during gestation or lactation, then this fine-tuning of her offspring's HPA axes can help them to manage similar experiences if they remain in that environment. I note, however, that there is little empirical evidence that this maternal effect operates among free-living mammals (but see below).

Postnatal Environmental and Social Effects

Young mammals experience their broader physical and social environments more directly after birth, and social experiences with parents and siblings can have significant effects on development. In laboratory rats, the development of behavioral and physiological traits can be affected by variation in maternal behaviors, such as nursing postures and rates of licking and grooming of pups. For example, offspring of high licker/groomers are less fearful and have attenuated stress responses relative to those of low licker/groomers. Cross-fostering studies (in which animals are transferred from one mother to another shortly after birth; see Mateo & Holmes 2004 for a discussion of fostering designs) have shown that these effects on offspring are not genetic, but instead are due to postnatal maternal handling. In lab rats (*Rattus norvegicus*), daughters of high-licking and grooming mothers become high-licking and grooming mothers themselves, thereby transmitting variation in parental behavior nongenetically across generations (Meaney 2001; Champagne & Curley, this volume). Note that these long-term effects of handling and grooming result from the normal range of species-specific maternal care, rather than extreme versions of neglectful or attentive mothers. However, as yet it is not clear whether these licker/groomer phenotypes exist among free-living, outbred rodent mothers, or if the effects are found in other mammals.

Experience with mothers prior to dispersal can affect the social relationships that their offspring develop as adults. For instance, in large, group-living mammals, a mother's dominance rank within a hierarchy can be inherited by her offspring (Holekamp & Dloniak, Maestripieri, this volume). Transfer of dominance rank to offspring can be mediated by physical condition, such as when offspring of high-ranking females have larger body mass or greater competitive abilities and thus become high ranking themselves, but it can also arise through social dynamics, as when mothers intervene on the offspring's behalf to support them against lower-ranking conspecifics. Although the inheritance of a low rank, regardless of an individual's actual condition, might not be adaptive for that individual, social stability within a group because of these ranks can increase the fitness of all individuals in the group through access to food resources, defense of a territory, or detection of predators. This group benefit, however, is unlikely to compensate for an individual's low rank, and such individuals may attempt to rise in the hierarchy whenever the social context permits it. Mothers can also influence their offspring's choice of social partners, if young seek other adults that exhibit phenotypes similar to hers. For example, young can learn their mother's

odors, vocalizations, or pelage patterns, and preferentially interact with (or avoid) other conspecifics that exhibit similar traits. If these cues are heritable then such conspecifics would probably be kin; here learning about kin cues would likely be mediated through genetic effects, if offspring inherit both kin cues and preferences for those cues. However, preferences for kin can occur through nongenetic maternal effects if recognition cues are not heritable (e.g., Insley 2001; Sharp et al. 2005) or if learning about kin is mediated through interactions with the mother and unfamiliar kin (Holmes & Sherman 1983). Similar maternal effects can operate in mate-choice contexts, if young imprint on mother's cues and as reproductive adults avoid mating with individuals with similar cues (Dewsbury 1982; Bolhuis 1991; see also Vos 1995; Isles et al. 2002; Burley 2006; Maestripieri, this volume). Learning of maternal cues can also lead to maternal effects on sexually selected traits such as behavioral displays, as well preferences for those traits (Qvarnström & Price 2001).

MATERNAL EFFECTS ON SURVIVAL BEHAVIORS

Maternal effects can be important for the ontogeny of many adaptive behaviors, including those important for survival. This may seem counterintuitive at first, as survival behaviors might be expected to develop through a closed program (Mayr 1974). Some researchers have posited that survival behaviors, such as alarm calls or predator-avoidance tactics, are "preprogrammed" or "innate" so that the behaviors emerge independent of experiential input (Tinbergen 1953; Bolles 1970; Magurran 1990; Curio 1993). Others have proposed instead that these behaviors should be acquired or learned, through either direct or indirect experiences with predators and conspecifics (e.g., Vitale 1989; Cheney & Seyfarth 1990; Mateo 1996; Griffin 2004). Although this nature-nurture dichotomous approach is no longer formally endorsed, it still persists in the current literature despite acknowledgments by many that behavior is not innate or acquired per se, but instead develops epigenetically, through interactions between the organism and the series of environments it encounters throughout its life span (Lehrman 1970; Gottlieb 1976; Johnston 1987). For a developing mammal, one of the most salient aspects of its environment is its mother, who can have a significant influence on offspring acquisition of survival behaviors, such as antipredator strategies, foraging skills, and social acumen.

A behavioral system that required each juvenile to learn independently how to recognize and respond to predators would consume time and en-

ergy and be prone to fatal errors in learning (see Darwin 1859; Bolles 1970). Reliance on experience, whether it be practice or learning, may at first appear less than optimal, given the vulnerability of young to predators, but a flexible developmental program might be adaptive when predator contexts vary among age groups or among populations, favoring plasticity of species-typical behaviors (Johnston 1982; Shettleworth 1998; Richerson & Boyd 2001). In these instances, learning appropriate strategies from mothers would be beneficial.

A comparative study of antipredator behavior among species of ground-dwelling squirrels illustrates the potential for maternal effects on survival tactics. Ground squirrels are vulnerable to both aerial (e.g., hawks, eagles) and terrestrial (e.g., coyotes, weasels, martens, venomous snakes) predators, and most species produce vocal signals warning of danger from predators (reviewed in Owings & Hennessy 1984). Despite the obvious survival advantage of evading a hunting predator, young need to learn from which animals to flee, to which warning calls to respond, and in what manner. Belding's ground squirrels (*Spermophilus beldingi*) have two types of alarm calls that elicit two different behavioral responses by listeners. Whistles are elicited by fast-moving, typically aerial, predators and result in evasive behaviors such as running to or entering a burrow, and scanning the area only after reaching safety. Trills are elicited by slow-moving, primarily terrestrial, predators and usually cause others to post (a bipedal stance accompanied by visual scanning), with or without changing location (Mateo 1996). When juvenile *S. beldingi* first emerge aboveground at about one month of age, they do not discriminate behaviorally between these calls, or even among alarm calls and other conspecific and heterospecific vocalizations. It takes approximately one week for juveniles to learn to respond selectively to alarm calls and to show the correct response for each type of call; during this time up to 60% of juveniles disappear, many to predation (Mateo 1996).

By what processes do juveniles acquire their alarm-call responses? In *S. beldingi*, this learning is facilitated by experience hearing the calls as well as observations of adult reactions. Juveniles attend to and model adult responses, particularly those of their mother rather than those of other nearby females. Furthermore, juveniles adopt a response style similar to their mother's, remaining alert for extended periods if she does and showing more exaggerated vigilance responses if she does; these response patterns persist at later ages even when the mother is not visible at the time (Mateo 1996; Mateo & Holmes 1997). Adoption of maternal styles can be favored if mother's responses are locally adapted to the degree of predation threat in the natal

area. Mothers who locate their natal burrows at the edge of meadows are more reactive to alarm calls and remain alert longer than those from the center of a meadow (Mateo 1996), which can reflect increased vulnerability to predators near the edge (Elgar 1989). Mothers' reactions, which serve as models for juvenile responses, can reflect the mothers' own vulnerabilities (indirect maternal influence), or can be a form of maternal care, becoming more vigilant if they locate their natal burrow, and thus their offspring, in a dangerous area (edge) and less vigilant if in a safer region (center; direct maternal influences). [Note that parents can even teach appropriate responses to their offspring, adjusting their behaviors as the competency of their young improves (Caro & Hauser 1992).] Because *S. beldingi* juveniles model their responses after their mother's, they are also more alert if reared on the edge of a meadow than in the center (Mateo 1996). By acquiring responses that are appropriate for a given microhabitat, *S. beldingi* can optimize both their foraging and antipredator efforts, allowing juveniles (and adults) to gain adequate body weight before hibernation without expending energy on unnecessary vigilance (Mateo & Holmes 1999). In addition, females often nest near their mothers in subsequent years (J. M. Mateo, unpublished data), so adopting location-specific responses would be favored across generations. For example, long-term studies of rock and California ground squirrels (*S. variegatus, S. beecheyi*) demonstrate that animals sympatric with predatory snakes need to develop and maintain antisnake behaviors, whereas responses to snakes are no longer evident in the antipredator repertoires of animals living in habitats without snakes (Coss & Owings 1985; Coss et al. 1993; Owings et al. 2001). Such responses, then, would not necessarily be present upon first encounter with predators, but would be acquired rapidly with additional experience, perhaps through observational learning of their mother's responses (e.g., Swaisgood et al. 1999).

In addition to serving as a model for appropriate antipredator responses, a mother's physiological phenotype can affect her offspring's physiology, which in turn can modulate their behavioral responses to predators. First emergence of young ground squirrels from natal burrows is fairly synchronous, with most litters emerging within a ten-day period. This natal emergence draws predators, and direct encounters with predators, observations of sudden, rapid responses of nearby adults, and experience with hearing loud alarm calls likely cause changes in circulating glucocorticoids in adults and offspring alike. The range of cortisol responses depends on the particular stressor as well as an individual's HPA axis. As noted above, maternal stress responses can affect the HPA functioning of their offspring, and thus

a mother's hormonal patterns can have long-lasting effects on those of her young (Catalani 1997). This nongenetic transmission of adrenal functioning could have adaptive consequences for offspring. Mothers and their young that live near the edge of meadows are more vigilant and exhibit prolonged alarm-call responses, and they have lower basal cortisol levels than *S. beldingi* from the center of the meadow (J. M. Mateo, unpubl. data). This lower basal cortisol may allow animals to mount large acute responses, mobilizing energy for quick escapes from ambushing predators (Mateo 2007b).

In addition, maternal glucocorticoids can affect the rate at which young learn important survival behaviors. In laboratory rodents the influence of glucocorticoids on learning and memory has an inverted-U-shaped function. Very low or very high levels of corticoids can lead to hypo- or hyper-arousal and poor selective attention to input and thus impair consolidation of new memories. Moderate levels of corticoids are optimal for attention to stimuli and consolidation of memories (reviewed in Lupien & McEwen 1997). Maternal glucocorticoids transmitted to offspring during gestation or lactation can have long-term effects on offspring hormones, and this "set point" may promote learning of antipredator responses, particularly in animals inhabiting areas with high predation pressure. Indeed, experiments in which maternal cortisol was manipulated during lactation show that juvenile *S. beldingi* with moderately elevated cortisol after emergence acquire spatial and associative-learning tasks faster than those with low or very high basal cortisol (Mateo, 2008).

Despite interacting with their offspring for just a few weeks after natal emergence, ground-squirrel mothers can also have a significant influence on the development of food preferences. Juvenile *S. beldingi* prefer foods that their mother consumed over food that she did not eat (Peacock & Jenkins 1988; see also Galef, this volume, for a review of maternal effects on food preferences). Maternal effects on food preferences might be especially evident in species that are active year round and for whom food availability changes with seasons. Maternal effects on kin preferences are well documented in ground squirrels. The most common social behavior among juveniles is play, and young prefer to play with littermates and other kin over non-kin; this discrimination among juveniles is typically mediated by odor cues (*S. columbianus*: Waterman 1986; *S. beldingi*: Holmes 1994; *S. lateralis*: Holmes 1995; Mateo 2003). In *S. beldingi*, mothers are important for the development and crystallization of these kin preferences. Juveniles reared in a seminatural enclosure without their mothers fail to develop play-partner preferences. However, when mothers are present but unable to intervene

in social interactions, littermate preferences still develop, suggesting that a mother's role is indirect. Indeed, it is a mother's presence at night in the burrow system that attracts her offspring to sleep together, which results in the formation of kin preferences (Holmes & Mateo 1998). Play is thought to lay a foundation for adult kin preferences and nepotism, and therefore is expected to vary with kinship (Michener 1983; Holmes 1994). In some sciurids, however, juveniles develop kin-recognition abilities and kin biases but there is no evidence of nepotism among adults (e.g., *S. columbianus, S. lateralis*); note, though, that kin recognition in sciurids might also function for inbreeding avoidance (Michener 1983; Mateo 2002).

MATERNAL EFFECTS AND HABITAT SELECTION

In most mammalian species, one or both sexes of offspring disperse from the natal area sometime after the age of independence from the mother. Although considerable empirical and theoretical work has focused on the proximate and ultimate explanations for natal dispersal (e.g., Greenwood 1980; Dobson 1982; Holekamp 1983; Dobson & Jones 1985; Pusey & Wolf 1996), fewer studies have considered how animals decide *where* to settle and what role, if any, parents play in this decision. Maternal effects can operate on habitat selection when offspring "imprint" or develop preferences for features of their natal habitat and settle in an area with similar features after dispersal. Davis and Stamps (2004) term this "natal habitat preference induction," and suggest that such preferences can be adaptive for offspring because settling in the first area that resembles the natal habitat reduces the energy expended, the search time and the exposure to potential predators while searching for a place to settle. In addition, if mother and offspring have similar phenotypes and the mother was successful in the natal area, then her offspring would do well in similar areas (see also Fowler 2005; Stamps & Davis 2006). Similar phenotypes could arise because they are heritable, or because both generations were affected by their immediate environments, affecting traits such as foraging styles or antipredator strategies, and thus natal habitat preference induction can result in nongenetic transmission of traits from mothers to offspring (e.g., Dittman & Quinn 1996; Olson & Van Horne 1998; Arvedlund et al. 1999; Vogl et al. 2002).

   Among territorial mammals, a mother with good foraging skills can improve the physical condition and chances of survival of her offspring not just during gestation and lactation, but after offspring dispersal as well. If mothers acquire ample food resources and defend these caches from others,

then as young become independent, these caches can be transferred to them as a form of parental investment. Desert-dwelling bannertail kangaroo rats (*Dipodomys spectabilis*) cache large quantities of seeds in mounds, which are defended from conspecifics through scent marking and foot drumming (Randall 1993). These mounds are valuable resources and are maintained over many generations, with some mothers "bequeathing" the mounds to their offspring (Jones 1986). Female Columbian ground squirrels (*S. columbianus*) move their nest sites more often when their yearling daughter is present, with those daughters typically settling into the mother's old territory (Harris 1984). Prior to mating and giving birth, female red squirrels (*Tamiasciurus hudsonicus*) start building food caches that they leave for their independent offspring months later (Boutin et al. 2000). Such transfer of food resources likely benefits the inheriting offspring, although there are no long-term empirical data documenting increased lifetime reproductive success as a result of bequeathals. Related to this, some mothers, particularly older ones, will shift their territories to make room for their reproductive daughters, occasionally moving to territories that are less optimal (Sherman 1976; Berteaux & Boutin 2000; pers. obs.). However, unlike bestowal of food caches, there is little evidence that "territory bequeathal" affects offspring survival or reproductive success (Lambin 1997).

OTHER MATERNAL EFFECTS ON OFFSPRING PHENOTYPES

Timing of birth and offspring survival

In many taxonomic groups, individuals that mate early often produce offspring that are higher quality (e.g., higher body weight) and/or more likely to survive than those of parents that mate later in the breeding season (e.g., side-blotched lizards, *Uta stansburiana*: Sinervo & Doughty 1996; greater snow goose goslings, *Anser caerulescens atlantica*: Lepage et al. 1998; pink salmon, *Oncorhynchus gorbuscha*: Dickerson et al. 2002; Verreaux's sifaka, *Propithecus verreauxi*: Lewis & Kappeler 2005; tree swallows, *Tachycineta bicolor*: Nooker et al. 2005; but see Alaskan moose, *Alces alces*: Bowyer et al. 1998). Species that experience seasonal fluctuation in resources often constrain reproductive efforts so that offspring are born during peak food availability and nutritional value. This maximizes the opportunity for young to grow during times of abundance, improving their body condition and likelihood of future survival and reproductive success. Thus timing of reproduction represents a potential maternal effect. Mothers that mate earlier in the season, and thus give birth earlier in the period of resource abundance, will

likely have greater reproductive success than those that mate later and give birth to young that must forage during the seasonal decline in food items and/or their nutritional value prior to independence or dispersal (Dobson & Michener 1995; Sedinger et al. 1997; Millesi et al. 1999; Réale et al. 2003). Because offspring condition can affect their future reproductive success, these offspring can also mate earlier than those born to later breeders, thus transmitting the trait over generations nongenetically (but see Sinervo & Doughty 1996 for possible genetic effects on timing of reproduction). Note, however, that there can be a trade-off between somatic investment and reproductive investment by females, particularly if they are young or are in poor condition and need access to those resources themselves before bearing the costs of gestation and lactation (e.g., Dobson et al. 1999; Millesi et al. 1999). Related, the timing of reproduction can be associated with increasing the female's future reproductive success, such as attempting to breed early so as to gain sufficient weight prior to the next breeding period (e.g., synchronous fawning among roe deer [*Capreolus capreolus*] because of the impending rut: Gaillard et al. 1993; see also Price & Boutin 1993).

Highly seasonal species, such as obligate hibernators, illustrate the potential importance of reproductive timing and maternal effects. Some ground-squirrel species have extremely short active seasons, being awake and socially active for just a few months each year. Females mate shortly after emerging from hibernation and rear their young for about a month in an underground natal burrow. The combined needs for young to develop in the relative safety of the natal burrow and to emerge above ground and begin foraging constrain the timing of natal emergence. Overwinter survival in some ground-dwelling squirrels is dependent upon the acquisition of adequate body fat prior to hibernation, and more than 60% of juveniles do not survive their first winter (Barash 1973; Murie & Boag 1984; Sherman & Morton 1984; J. M. Mateo, unpubl. data). Thus offspring born to females that mate earlier in the short breeding season are often heavier and have a greater chance of surviving than those that emerge later in the summer. In European ground squirrels (*S. citellus*), early-born litters are often larger and are nursed longer than later-born juveniles. Females that enter hibernation at a heavy weight emerge in the spring earlier and mate earlier than those that hibernate at lower weights (Millesi et al. 1999). Thus, although females can pay an energetic cost for early reproduction and prolonged lactation (weighing less at hibernation), their daughters can reap those energetic benefits and reproduce earlier the following spring themselves. In Richardson's ground squirrels (*S. richardsonii*), females that mate early have heavier offspring that

also have more time to forage during the active season (Dobson & Michener 1995), and thus are more likely to survive hibernation. Among Uinta ground squirrels (*S. armatus*), females born early in the summer are more likely to survive their first hibernation than those born later in the season (Rieger 1996). Indeed, in *S. beldingi*, those surviving at least one year are born significantly earlier in the season than those that die or disappear (J. M. Mateo, unpubl. data). The same is true for *S. columbianus* offspring, although litter size is a greater predictor of survival than is date of birth (Dobson et al. 1999), perhaps because this species tends to have smaller litters than other species. Note, however, that very early mating can be risky if mothers experience adverse environmental conditions (e.g., Morton & Sherman 1978; Inouye et al. 2000; Farand et al. 2002) or if earliest emerging young suffer high mortality due to less dilution of predation risk. Future work could focus on similar interspecific comparisons, as well as search for sex differences in maternal effects as a function of timing of reproduction.

Length of Maternal Dependence

Among mammals, offspring are dependent on their mother at least until weaning, yet across species there is variation in the duration of care and protection afforded by mothers. This variation is, in part, correlated with the length of time young remain with their mothers. In species with extended dependency on parental care, there may be repeated opportunities for young to observe and learn from their parents' behaviors (e.g., foraging, spatial, antipredator, and social behaviors). Conversely, in species with little or no parental care after weaning, individuals often acquire behavior without assistance from adults. Thus, the length of dependence on adults provides another opportunity for a maternal effect, as it will influence the developmental process of the offspring's behavioral repertoires, and extended maternal care may allow for variable pathways of behavioral development, including social facilitation of responses (Heyes & Galef 1996; Reinhold 2002). For example, experiences with their mothers can significantly modify the responses of young vervet monkeys (*Chlorocebus aethiops*) to predators and alarm calls warning of predators, as they maintain close proximity to their mothers for at least 2 years (Cheney & Seyfarth 1990; for other species see also Yoerg & Shier 1997; White & Berger 2001; Swaisgood et al. 2003) In fish, Brown (1984) studied the development of antipredator behavior in two bass species differing in the length of time the male parent guards his young. Recently hatched young of a species with limited paternal care (*Ambloplites rupestris*) showed predator-avoidance behavior sooner than young of a species with extended

care (*Micropterus salmoides*). Mexican jays (*Aphelocoma ultramarina*) with prolonged associations with experienced adults exhibit mobbing behavior at a later age than less social scrub jays (*A. coerulescens*) that fledge at an earlier age (Culley & Ligon 1976).

Comparisons among animals that differ in active-season lengths, growth rates, or periods of dependence upon mothers provide an opportunity to examine maternal effects on offspring behavioral repertoires. For instance, juveniles of some nonhibernating species, which have slower growth rates than those that hibernate (e.g., Clark 1970; Morton & Tung 1971; Pizzimenti & McClenaghan 1974; Maxwell & Morton 1975) and subsequently longer associations with their mothers, can exhibit more social facilitation of behavioral development than juveniles with limited growth periods. Depending on their latitude and elevation, *S. beecheyi* can have long active seasons and extended co-occurrence of mothers and their young (up to 12 months; Dobson & Davis 1986), and thus maternal behavior can directly or indirectly influence the behavior of *S. beecheyi* juveniles more so than responses of *S. beldingi* juveniles, which have only a 3–4 month developmental period prior to autumnal immergence into hibernacula (pers. obs.). In addition to physiological (Morton & Tung 1971; Maxwell & Morton 1975) and social (Armitage 1981) adaptations to the length of the growing period, then, selection can favor more maternal effects in slowly maturing species than in species with accelerated growth. Likewise, lengthy associations between mothers and their young might permit maternal effects to play a larger role in generating heritable trait variation, which can then be operated upon by natural selection. Interspecific differences in developmental rates as a function of ecological conditions could have significant effects on mother-offspring interactions and social development. Studies of free-living mammals therefore present a unique opportunity to examine in detail how the intertwining effects of latitude, elevation, and climate on active-season length and pre- and postweaning growth rates influence behavioral development.

SUMMARY

Mammalian behavioral development is exquisitely tuned to the physiological, environmental, and social contexts in which ontogeny occurs. The various maternal effects described in this chapter, including prenatal hormonal effects, modeling of appropriate survival behaviors, and timing of reproduction, are amenable to examination from both proximate and ultimate levels of analysis. As described above, we are beginning to understand how

maternal physiology affects offspring phenotype, such as the effects of gonadal hormones, glucocorticoids, and melatonin. Much of this work has focused on laboratory rodents, but as evidenced throughout this volume, similar work is now being done with mammals in other orders and in the field. From a functional perspective, maternal effects will have a selective advantage when they increase the survival and reproductive success of offspring, but of course can have negative consequences if a mother is in poor condition or if she faces adverse conditions during reproduction. In general, maternal effects will be favored when mothers and their offspring experience similar social and physical environments and thus similar resource availability, predation pressure, and social dynamics. In concluding this chapter, I emphasize the need for more behavioral studies integrating levels of analysis as well as levels of biological organization. In addition, future work could take advantage of groups of closely related mammalian species with contrasting life-history parameters, preferred habitats, or degrees of sociality. Recent interdisciplinary research offers encouraging signs that we will soon identify and understand the links between mechanisms and functions of maternal effects.

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