Paternal Behavior and Aggression: Endocrine Mechanisms and Nongenomic Transmission of Behavior

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I. INTRODUCTION

Paternal behavior is often ignored in mammals, in part because, for many mammals, male contributions to parental behavior are not crucial to offspring survivorship. Recent studies, however, have begun to reevaluate the importance of paternal behavior, and to identify components of its physiological control. In mammalian species with high levels of paternal care, the male can increase survivorship of offspring (e.g., Snowdon, 1996; McInroy et al., 2000) and this has been most clearly demonstrated in the California mouse, Peromyscus californicus, through both laboratory and field studies (Dudley, 1974a; Gubernick et al., 1993; Cantoni and Brown, 1997; Gubernick and Teferi, 2000). Hormonal control of paternal behavior has also become a topic of interest (see Wynne-Edwards, 2003; this volume). The most extensively studied hormone influencing paternal care is testosterone (T), a steroid hormone currently most noted for its negative effects on paternal behavior, along with its positive effects on aggression. Here, however, we review evidence across a variety of species that T is not always negatively associated with paternal care and that, in fact, T can promote paternal care in some species, including California mice. The neuropeptide arginine vasopressin (AVP) is also positively associated with both aggression and paternal behavior. We review studies examining the

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relationship between AVP and these social behaviors in rodent species, including California mice. For both T and AVP, we describe the results in the context of the evolution of hormone–behavior relationships.

In addition to influencing offspring survival, paternal behavior also may influence offspring behavior once those individuals become adults. We describe evidence that both paternal and maternal behavior may have nongenomic effects on aggression and paternal behaviors that are transferred across generations. For this plasticity in behavior to occur, there must be plasticity in the underlying endocrine and/or neurobiological mechanisms. We present evidence that AVP may be a critical neuro-chemical underlying this nongenomic transfer of behavioral patterns. Finally, we conclude with an integration of the different sections of the review and a discussion of plasticity in behavior and the underlying physiological mechanisms.

A. Classic Viewpoint of the Relationship among Testosterone, Aggression, and Paternal Behavior

It is widely accepted that T is positively associated with aggression (Nelson, 2000). For example, the role of T in the expression of aggression in a number of songbirds is well established (reviewed by Beletsky et al., 1995). There are also a variety of studies demonstrating links between T and aggression in mammals, although the putative association has been refined, at least in primates, to suggest that T is more likely to be linked with competitive aggression and less with aggression or violence resulting from the increased impulsivity associated with changes in serotonin levels (reviewed by Higley et al., 1996a). Testosterone levels appear to fluctuate extensively when males experience a social challenge in a variety of species (Wingfield et al., 1990, 2001; Mazur and Booth, 1998). For example, in California mice, T levels in males increase after winning an encounter with a conspecific male (T. Oyegbile and C. A. Marler, unpublished data; T. Oyegbile, B. C. Trainor, and C. A. Marler, unpublished data). Similarly, in human males, decisive winners of tennis matches show elevations of T levels in comparison to losers (Mazur and Lamb, 1980). This elevation in T may be related to the effort involved in the social challenge of the tennis match because winning a lottery does not alter T levels (Mazur and Lamb, 1980). Together, these studies suggest an association between competitive aggression and changes in T levels.

In contrast to this positive association between plasma T levels and aggression, negative associations between plasma T levels and paternal behavior are found across numerous species in a wide variety of taxa

(reviews: mammals—Brown, 1985; Brown et al., 1995; Wynne-Edwards, 2001; fish—Brown, 1985; Knapp et al., 1999; Kishida and Specker, 2000; birds—Collias, 1950; Ketterson and Nolan, 1994; Beletsky et al., 1995; Buntin, 1996; anurans—Townsend and Moger, 1987). The most extensive studies compare North American temperate zone passerine birds, in which T levels and competitive aggression decrease as paternal care, such as feeding behavior, increases (Wingfield, 1994b; Ketterson and Nolan, 1994; Beletsky et al., 1995). Testosterone levels are thought to be maintained at higher levels in polygynous species as compared with monogamous species because polygynous males allocate more time and energy to male–male aggression and attracting mates and less to parental care (Wingfield et al., 1990). In many songbird species, if the higher T levels observed early in the breeding season are extended into the parental phase with silastic implants, paternal care decreases, largely supporting a cause-and-effect relationship (Hegner and Wingfield, 1987; Ketterson et al., 1992; Saino and Møller, 1995; Beletsky et al., 1995; Moreno et al., 1999; De Ridder et al., 2000). The idea that T increases competitive aggression, but decreases paternal care, is an intuitively satisfying one, on first inspection, because paternal behavior involves nurturing behavior, whereas competitive aggression often involves offensive attacks with the risk of injury.

B. Evidence of Plasticity in Hormone–Behavior Relationships across Species

Despite the strong evidence from songbirds, there are reasons to be cautious about the broad applicability of the classic avian model for the association between T and paternal care. Many studies demonstrate species differences in behavioral relationships and in hormone–behavior relationships (e.g., Crews, 1983; Crews and Moore, 1986). Three examples are as follows. First, many female mammals are capable of exhibiting heightened levels of maternal aggression while simultaneously showing high levels of maternal nurturing behaviors (e.g., Svare and Gandelman, 1976; Gleason et al., 1981; Garland and Svare, 1988; Mayer et al., 1990). Estrogen, which can promote maternal nurturing behaviors, can also promote maternal aggression (e.g., Rosenblatt et al., 1994), suggesting that the expression of high levels of aggression need not prevent the expression of high levels of parental care.

Second, behaviors associated with T in one species may occur independently of T in another species. Crews (1984) presented a classic example of variation in hormone–behavior relationships by examining variation in the association among gamete production, sex hormone

secretion, and mating behavior (i.e., courtship). The three are often temporally linked. Testosterone is required for gametogenesis to occur. Thus, if mating behavior is stimulated by T, T can link mating behavior with gametogenesis. In contrast, there are species such as the male red-sided garter snake (*Thamnophis sirtalis*) (Camazine *et al.*, 1980; Crews *et al.*, 1984; Garstka *et al.*, 1982) and some mammalian species (Clemens *et al.*, 1988; Mendonça *et al.*, 1996) in which mating behavior may occur at a different time from gamete production and thus courtship behavior occurs independently of sex hormone secretion. These studies demonstrate species variation in hormone–behavior relationships.

Finally, while the positive association between T and aggression occurs in a variety of avian species, suggesting that paternal care should decrease when aggression is high (Nelson, 2000), this positive association does not occur universally. For example, aggression levels are less dependent on, or even independent of, T levels in some Arctic and tropical species (reviewed by Wikelski *et al.*, 1999a; Wingfield *et al.*, 2001; Hau *et al.*, 2000). Territorial aggression during the nonbreeding season can also be T independent (e.g., Wingfield, 1994a). In several of these bird species (reviewed by Canoine and Gwinner, 2002), even when basal levels of T are maintained, T can increase in response to an aggressive encounter (e.g., Wikelski *et al.*, 1999b).

There is also evidence of dissociation of T and aggression in mammals. For example, in year-round territory holders such the wood rat (*Neotoma fuscipes*; Caldwell *et al.*, 1984) and the California mouse (Trainor and Marler, 2001), castration does not reduce aggression. However, in the California mouse, male T levels increase in response to winning an encounter (T. Oyegbile and C. A. Marler, unpublished data). Castrated males do not adjust their aggression levels in response to winning a previous encounter (Trainor and Marler, 2001), whereas intact males become more aggressive (Trainor and Marler, 2001; T. Oyegbile and C. A. Marler, unpublished data). In species such as these, in which aggression and T levels are sometimes associated and sometimes not associated, there may be more plasticity in how T influences paternal care than is observed in the traditional avian model. We have provided only a few examples here, but clearly there can be considerable variation in hormone–behavior relationships.

We need to be cautious about generalizing about the relationship between T and paternal behavior, particularly in species in which only correlational studies have been conducted. There are exceptions to the hypothesis that heightened T levels decrease paternal care. The two are not always related and there are examples in which T and parental care are, in fact, positively related.

II. TESTOSTERONE: AN AGGRESSION HORMONE, A NURTURING HORMONE, OR BOTH?

In this section we compare and contrast the association between androgens and paternal care in birds, amphibians, fish, rodents, nonhuman primates, and primates (see Table I for a review of species referenced in text, except for birds). A strong emphasis is placed on the dynamic changes in T in response to life history changes associated with parenting, with a focus on manipulative studies where available.

We propose that some of the variation observed between species may be explained by species differences in behavioral ecology, specifically whether conspecific aggression needs to be expressed at the same time as paternal behavior. A study examining baseline T levels in several species of *Peromyscus* mice is also included because it is tempting to suggest that species with high levels of paternal care may have low species baseline T levels because of the incompatibility of high T with paternal care. We conclude that when comparing baseline levels of T across species it is critical to take into account not only the behavioral ecology, which we emphasize here, but also the phylogenetic relatedness and the habitat of the species. Our primary focus is on the direction of the dynamic changes in T that frequently occur with the expression of paternal behavior.

A. TESTOSTERONE AND PATERNAL CARE: BIRDS

The role of T is well established within several species of temperate zone, seasonally breeding birds. Administration of exogenous T results in decreased paternal care in a number of avian species (reviewed by Ketterson *et al.*, 1992; Beletsky *et al.*, 1995). One important characteristic of these birds that might account for the negative effect of T on paternal behaviors is that paternal behaviors are expressed much later in the breeding season compared with aggressive and mating behaviors (Ball, 1992). Thus, in monogamous species that exhibit high levels of paternal behavior, T may drop, not simply because it has a negative effect on paternal behavior, but also because once a territory has been formed and mating has occurred, T becomes less important for attracting new mates, aggression used in male–male competition to obtain mates, and mate guarding of receptive females.

Despite general evidence in support of a negative relationship between T and paternal care there is nonetheless variation in this response in birds and there are examples in which the negative effect of T on paternal care is either limited or absent. Artificially increasing T initially reduced

TABLE I

POSITIVE AND NEGATIVE ASSOCIATIONS BETWEEN PATERNAL CARE AND ANDROGEN/TESTOSTERONE LEVELS[a]

	Association/correlation			Manipulation		
	Positive	Negative	No association	Positive	Negative	No effect
Amphibians		Puerto Rican frog (Townsend and Moger, 1987)				Puerto Rican frog (Townsend et al., 1991)
Fish	Marine garibaldi (11-KT) (Sikkel, 1993) Peacock blenny (Oliveira et al., 2001) Black-chinned tilapia (Kishida and Specker, 2000)	Bluegill sunfish (Kindler et al., 1989) Black-chinned tilapia (Kishida and Specker, 2000) Plainfin midshipman (Knapp et al., 1999)	Plainfin midshipman (Knapp et al., 1999)	Three-spined stickleback (Smith and Hoar, 1967; Borg, 1987) Blue gourami (Johns and Liley, 1970) Bluegill sunfish (Smith, 1969; Kindler et al., 1991)		
Rodents	California mouse (Trainor and Marler, 2001)	California mouse (B. C. Trainor and C. A. Marler, unpublished data)	California mouse (Gubernick and Nelson, 1989)	California mouse (Trainor and Marler, 2001, 2002)	Mongolian gerbil (Clark and Galef, 1999)	Prairie vole (Lonstein and De Vries, 1999)

	Djungarian hamster (Reburn and Wynne-Edwards, 1999)	Djungarian hamster (Reburn and Wynne-Edwards, 1999) Mongolian gerbil (Brown et al., 1995; Clark and Galef, 2000)	Common marmoset (Dixson and George, 1982)	Prairie vole (Wang and De Vries, 1993; Lonstein et al., 2002)
Primates	Cotton-top tamarin (Zeigler and Snowdon, 2000; Zeigler et al., 2000)	Black tuft-eared marmoset (Nunes et al., 2000, 2001) Humans (Storey et al., 2000; Berg and Wynne-Edwards, 2001)		

Abbreviation: 11-KT, 11-Ketotestosterone.

[a]See text for reviews of avian studies. In the category of association/correlation, associations include species that display a decrease or increase at the same time that paternal behavior changes. Some studies can support either a positive or negative association. Experimental studies are emphasized wherever possible.

paternal care, but this effect disappeared when nestlings reached 4–5 days of age in Lapland longspurs (*Calcarius lapponicus*), and there was no significant effect of paternal T on number and mean body mass of offspring fledged (Hunt et al., 1999). While T implants significantly increased singing behavior, there was no effect on male provisioning of nestlings in either male great tits (*Parus major*) or male chestnut collared longspurs (*Calcarius ornatus*) (Van Duyse et al., 2000; Lynn et al., 2002). In great tits, T implants also had no effect on nestling development or survival (Van Duyse et al., 2000). Lapland longspurs and chestnut collared longspurs have relatively short breeding seasons and male paternal care may have a more important impact on lifetime reproductive success than in other avian species in which T suppresses paternal care. Thus, there are avian species that do not display a decrease in paternal behavior in response to increased levels of T, possibly because of environmental factors such as a short female receptivity period (Hunt et al., 1999; Williamson, 1968) or abundant food resources that may reduce the benefits of defending territories (Hunt et al., 1997; Tyron and MacLean, 1980).

Although the effects of elevated T levels on paternal behavior have been well studied in birds, relatively little is known about the role of baseline T levels. In the polygynous spotless starling (*Sturnus unicolor*), the antiandrogen cyproterone acetate increased paternal care of young as compared with controls and T-implanted males (Moreno et al., 1999). However, T replacement treatment in gonadectomized ring doves (*Streptopelia risoria*) enhanced the positive effects of progesterone on paternal behavior (Stern and Lehrman, 1969). This suggests that lower T levels could have important effects on paternal behavior that cannot be deduced from the traditional paradigms of increasing T levels with implants.

Summary

We conclude that for birds there is strong evidence that increased T can result in a decrease in paternal care, but there is also variation between species. In many species there is a temporal separation of mating behaviors and paternal behaviors and T mediates an important trade-off between mating and paternal behaviors. However, when breeding seasons are compressed and paternal behaviors are critical for offspring survival, this inverse relationship appears to be weaker. In most studies, the theoretical framework (e.g., life history evolution) has led investigators to primarily use implants to increase T levels to peak levels. However, to understand how T modulates paternal behavior, it would be useful to know more about the role of baseline T levels.

B. Testosterone and Paternal Care: Amphibians

Studies on taxonomic groups other than birds have often depended on correlations. A dependence on correlations can be problematic, as can be seen in the Puerto Rican frog (*Eleutherodactylus coqui*). Male Puerto Rican frogs display prolonged paternal care for eggs including egg-brooding behavior and defense of nests against egg cannibalism (Townsend *et al.*, 1984). Androgen levels are high when males call to attract females (Townsend and Moger, 1987) and possibly to repel males from their territories. Males typically cease calling when they obtain a clutch of eggs and their androgen levels also drop. On the basis of the behavior and T associations, this example first appears to support a negative association between T and paternal care. However, Townsend *et al.* (1991) proceeded to increase T levels and found no effect on paternal care. T levels above baseline are not negatively associated with paternal behavior, as was suggested by the natural changes in T in male Puerto Rican frogs. However, decreasing T levels via castration may still influence paternal behavior in this species. Although androgen levels may drop after males obtain a clutch of eggs, to reduce costs associated with higher androgen levels (reviewed by Wingfield *et al.*, 2001), those costs do not include reduced paternal care. Thus, increased T does not result in decreased parental care, despite correlational data suggesting otherwise.

From an evolutionary perspective it is not clear why T is not involved in trade-offs between parental care and calling behavior in the Puerto Rican frog, but the answer may reside in the underlying physiological mechanisms that activate calling behavior in anurans. The relationship between variation in androgens levels and calling behavior is unclear, although baseline androgen levels appear to be needed across the breeding season. While T and dihydrotestosterone appear necessary for calling behavior (e.g., reviewed by Houck and Woodley, 1995; Emerson and Hess, 1996; Marler and Ryan, 1996; Solis and Penna, 1997), these androgens alone are not sufficient to activate calling behavior (e.g., Wada and Gorbman, 1977; Wetzel and Kelley, 1983; Burmeister and Wilczynski, 2001). Activation of calling behavior instead may depend significantly on the neuropeptide arginine vasotocin (reviewed by Boyd, 1997; Semsar *et al.*, 1998; Tito *et al.*, 1999; Klomberg and Marler, 2000). An investigation into the relationship between arginine vasotocin and paternal care in anurans would be of interest because arginine vasotocin may prove to be important for linking paternal care with calling behavior and aggression. Also, these studies remind us that experimental manipulations are essential for investigating these relationships between social behavior and the underlying physiological mechanisms.

Summary

The one set of studies with the Puerto Rican frog demonstrates the value of conducting hormone manipulations because interpretations drawn from the correlations between androgens and paternal care may not be correct. This point is raised again in the discussion of paternal care and T in the California mouse (Section II.D).

C. Testosterone and Paternal Care: Fish

The frequency of paternal care in fishes is relatively high compared with other nonavian vertebrate groups. We first discuss correlational studies and follow this with experimental studies. We show that the two types of studies indicate a differing role for androgens in the regulation of paternal care in these fish studies compared with the bird studies.

1. Correlational Studies

In some species of fish there is a tight coupling between territorial aggression and paternal behavior that complicates the study of paternal behavior in fishes, making it difficult to manipulate paternal behavior without affecting territorial aggression. For example, in centrarchid fish, including bluegill sunfish (*Lepomis macrochirus*) and small-mouth bass (*Micropterus dolomieui*), males build nests that are aggressively defended (Gross, 1984; Wiegmann and Baylis, 1995). Males fan the eggs and try to deliver oxygen and protect them from other predators, usually conspecifics (Gross and MacMillan, 1981). Nonetheless, correlational studies have examined how androgens such as T and the nonaromatizable androgen 11-ketotestosterone (11-KT) are associated with paternal care when territorial behavior occurs at the same time as paternal behavior. In both the male bluegill sunfish and the marine garibaldi (*Hypsypops rubicundus*), T and 11-KT levels appear to be negatively associated with paternal care: they rise during the prespawning phase when males are establishing their territories, fall after spawning, and remain low while guarding eggs at the nest (Kindler *et al.*, 1989; Sikkel, 1993). However, in marine garibaldi 11-KT levels were significantly higher during nest guarding than after the breeding season, suggesting that, while 11-KT levels were considered low during nest building, the levels were nonetheless above baseline levels observed during the breeding season. This indicates that higher T levels are not incompatible with paternal care.

Other correlational studies have also indicated that low androgen levels are not a prerequisite for paternal care. In male plainfin midshipman fish (*Porichthys notatus*) there was no significant difference in 11-KT levels

between males without eggs and those that were guarding eggs, although males guarding embryos had significantly lower 11-KT levels than males without eggs (Knapp *et al.*, 1999). Male peacock blennies (*Salario pavo*) guarding nests expressed higher 11-KT levels later in the breeding season compared with earlier (Oliveira *et al.*, 2001), although sneaker male intrusions also increase late in the breeding season. Both of these examples suggest that high paternal investment may occur in the presence of high 11-KT levels. However, as indicated earlier, one difficulty in interpreting the changes in androgen levels across the breeding season is that paternal behaviors are often confounded with territorial behaviors. Thus, changes in androgen levels could be associated with paternal behavior, aggression, or both.

In contrast to centrarchid fish, some cichlid fish present examples in which T and estradiol levels decrease at the onset of paternal behavior in the absence of the confounding factor of nest defense. These cichlid fish, including the black-chinned tilapia (*Sarotherodon melanotheron*), express paternal behavior mainly in the form of mouth brooding and do not exhibit nest defense. Male black-chinned tilapia carry fertilized eggs after spawning for several days and continue to incubate hatched embryos for about 1 week (Trewavas, 1983). T and estradiol levels decreased 6 days after spawning, but both hormones then increased during the remaining incubation and peaked on the day that fry were released (Kishida and Specker, 2000). A similar increase in androgens during the end of the egg incubation period was observed in female mouth-brooding tilapia (*Oreochromis mossambicus*) (Smith and Haley, 1988). The decrease in T during the early portion of the egg incubation period is probably caused by the brooding of eggs, because egg removal blocked the initial drop in androgens (Specker and Kishida, 2000). Although low androgen levels are associated with paternal behavior in these cichlids during the brooding of eggs, Specker and Kishida (2000) dismiss the hypothesis that a decrease in T is the causal mechanism for paternal behavior because T levels are high at spawning when paternal behavior commences. The evidence from these correlational studies indicates that androgens decrease during periods of paternal care, but they also suggest that higher androgen levels may not be incompatible with paternal care. Androgen manipulations in mouth-brooding cichlids could prove useful in teasing apart the roles that androgens play in regulating nest guarding and paternal care.

2. Hormone Manipulation Studies

In contrast to the correlational experiments just described, most experimental studies of fishes that are castrated have found that androgens promote paternal behavior. Fanning behavior in male three-spined

sticklebacks (*Gasterosteus aculeatus*) with fertilized eggs was reduced after castration and then restored by T replacement injections (Smith and Hoar, 1967). Similarly, exogenous treatment with 11-KT, the predominant androgen secreted by stickleback testes (Borg *et al.*, 1989), maintained nest-building, spawning, and paternal behaviors in castrated males (Borg, 1987). Castration also reduced paternal behavior in male blue gouramis (*Trichogaster trichopterus*) (Johns and Liley, 1970) and inhibited nesting behavior in sunfish (Smith, 1969). Treatment with the antiandrogen cyproterone acetate also inhibited nesting behavior (Kindler *et al.*, 1991). However, as castration also interfered with spawning in these latter two studies, it is unclear whether this effect is specific to paternal behavior or is a more general effect on sexual behavior. In summary, androgens appear to promote paternal behavior, although in some cases this relationship may be complicated by corresponding changes in sexual behavior and aggression.

Summary

Correlational studies of fish have identified cases in which males express paternal behaviors when androgens are relatively high, and hormone manipulation studies have found that androgens can promote paternal behaviors. In most of these species, aggression is an essential component of paternal behavior, as nest and/or egg guarding is often an essential activity. Thus, it is possible that aggression and some aspects of paternal behavior have become positively linked through androgens. This point is further discussed in relation to the California mouse.

D. TESTOSTERONE AND PARENTAL CARE: RODENTS

In rodents there are both correlational and manipulative studies examining the association between T and paternal care. We focus primarily on species displaying high levels of paternal care [see Brown (1985) and Brown *et al.* (1995) for reviews on house mice and rats]. One important feature of most paternal rodent species is the presence of a postpartum mating period (California mice: Gubernick, 1988; Djungarian hamsters: Parkening and Collins, 1991; prairie voles: Richmond and Conaway, 1969). In these species, there is a conspicuous lack of separation between mating behaviors/aggression and parental behaviors. Thus when females are receptive, males may be expressing both mate-guarding aggression and paternal care. On the basis of our studies with the California mouse, we hypothesized that this overlap between mating/aggression and parental behaviors increases the probability that T will be positively associated with paternal care (Trainor and Marler, 2001), as was

found in some fish species. Here we summarize correlational data that suggest that high T levels are not incompatible with aspects of paternal care. In the manipulative studies there is support for our hypothesis, but there is considerable variation between studies. We propose potential explanations for some of this variation based on methodology (i.e., sexual and paternal experience) and on species differences in the onset of paternal care.

1. Correlational Studies

Male T levels change in association with a mate's pregnancy in several species of rodents. As in many avian field studies, when measured across the breeding cycle, T levels decline after the birth of a male's offspring (Brown *et al.*, 1995; Reburn and Wynne-Edwards, 1999). Similarly, we have found that fathers have significantly lower levels of T than do mated males in California mice (B. C. Trainor and C. A. Marler, unpublished data; but see Gubernick and Nelson, 1989, for a similar but nonsignificant trend). These decreases in T typically have been interpreted in a similar manner as those of temperate zone birds; T inhibits paternal behavior.

However, the decrease in T is anticipated by a surge in T at parturition, coinciding with a postpartum estrus. Is this surge in T related to paternal behavior? At the time of this T surge, first-time Mongolian gerbil (*Meriones unguiculatus*) fathers avoid their pups during the 24-h period after parturition (Clark and Galef, 2000), suggesting that there is a negative relationship between T and paternal behavior. In contrast, first-time Djungarian hamster (*Phodopus campbelli*) fathers experience a T surge around the time of parturition (Reburn and Wynne-Edwards, 1999) and actually assist with parturition and consume the placenta with the mother (Jones and Wynne-Edwards, 2000). This indicates the opposite, that is, a possible positive relationship between T and paternal behavior. In addition, T levels in Djungarian hamster males increase again 5 days after parturition. Thus while correlational data again indicate that T levels may decline when paternal behavior is expressed, high T levels are not necessarily incompatible with paternal care, a pattern similar to that found in some fish.

In addition to examining the dynamic changes in T and its association with paternal behavior, we also examined correlational data between paternal care and T levels in *Peromyscus* from a slightly different angle. Baseline T levels can also be examined across species and associated with behaviors or morphological traits (e.g., Emerson *et al.*, 1993). Because baseline T levels are low in California mice as compared with other species, we speculated that this is related to their monogamous mating system and high levels of paternal behavior. We examined the association
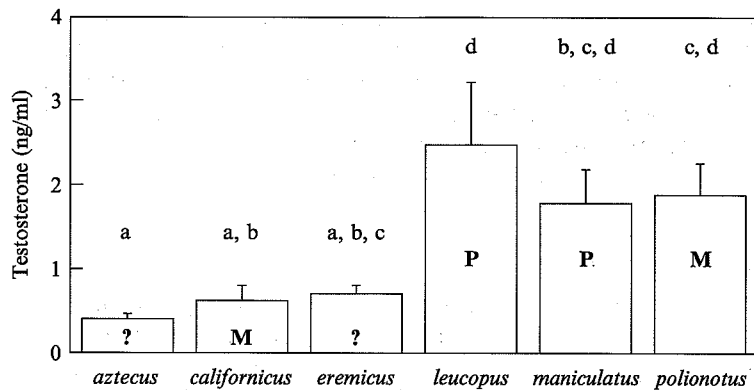
FIG. 1. Testosterone levels in laboratory-housed male mice representing six species of *Peromyscus*. Differences between groups are marked with different lower-case letters (Duncan's multiple range test, $p < 0.05$). Mating systems are indicated as follows: M, monogamous; P, polygynous; ?, unknown.

between baseline T levels and paternal behavior in a small subset of *Peromyscus* mice (Fig. 1; B. C. Trainor and C. A. Marler, unpublished data). For a rough estimate of variability in T levels across closely related species of *Peromyscus*, we obtained blood samples from six species of *Peromyscus* and measured T, using an assay previously validated for California mice (Trainor and Marler, 2001). We sampled cactus mice (*P. eremicus*), Aztec deer mice (*P. aztecus*), California mice (*P. californicus*), white-footed mice (*P. leucopus*), deer mice (*P. maniculatus*), and oldfield mice (*P. polionotus*) from individuals housed within our own colony and from the *Peromyscus* Stock Center at the University of South Carolina. Aztec deer mice, California mice, and deer mice had mean T levels similar to those reported in other studies (Klein and Nelson, 1997; Demas and Nelson, 1998; Bester-Meredith and Marler, 2001). There were significant differences in T levels across species (Fig. 1, $F_{5,44} = 4.39$, $p = 0.002$). As predicted, the highly paternal California mouse had lower levels of T compared with the less paternal white-footed mouse (Duncan multiple range test, $p < 0.05$). We previously also found a nonsignificant trend ($p = 0.07$) for a lower level of T in California mice as compared with white-footed mice (Bester-Meredith and Marler, 2001). However, the oldfield mouse is also monogamous (Foltz, 1981) and highly paternal (Margulis, 1998), but had male T levels that were not significantly different from those of the white-footed mouse or the deer mouse ($p > 0.05$), species with polygynous mating systems (Birdsall and Nash, 1973; Xia and Millar, 1991) and low levels of paternal behavior

(Wolff and Cicirello, 1990; Schug et al., 1992; Bester-Meredith et al., 1999). The variation in T levels across Peromyscus species may be more likely due to phylogenetic or ecological constraints, as the white-footed mouse, deer mouse, and oldfield mouse are more closely related to each other than to the other three species examined (Avise et al., 1974; Stangl and Baker, 1984; Kass et al., 1992), and all three species with lower T levels live in desert habitats in the southwestern United States and Central America (Baker, 1968; Sullivan et al., 1997). Our results indicate that high baseline T levels are not incompatible with a monogamous, highly paternal mating system. In addition, the variation in T levels across Peromyscus species is more likely due to phylogenetic or ecological constraints, rather than to the species typical mating system. These results highlight the complexity of the relationships between hormone levels, phylogeny, ecology, and behavior and, as in some of the bird studies, suggest that habitat may affect the function of T. Future T manipulations in Peromyscus species other than the California mouse (as discussed below) may prove to be illuminating.

2. Hormone Manipulation Studies

Testosterone manipulations have been performed in the California mouse, the prairie vole, and the Mongolian gerbil. We have investigated experimentally how baseline T levels affect paternal behavior in the California mouse. The birth of pups in California mice is associated with a significant decrease in male T levels. Male California mice show high levels of paternal behavior starting on the day of parturition (Gubernick and Alberts, 1987b), and continue to care for pups throughout their development until weaning (Bester-Meredith et al., 1999). Interestingly, the onset of expression of paternal behavior coincides with the postpartum estrus (Gubernick, 1988). The California mouse therefore may be similar to the fish species referenced earlier because high aggression levels associated with mate-guarding behavior may occur during the same time frame that paternal care is expressed. Most males undergo a transition from attacking or ignoring pups to exhibiting paternal behavior immediately after the birth of their own pups (Gubernick and Nelson, 1989).

We manipulated baseline T levels in the California mouse to examine the effects on paternal behavior (Trainor and Marler, 2001, 2002; K. Cravens, B. C. Trainor, and C. A. Marler, unpublished data). We observed castrated males with their own pups from their second litter; castrations or sham manipulations were performed after the postpartum mating period following the birth of their first litter. Castration decreased paternal behavior whether males were observed with their own pups or with foster pups. Castration combined with T replacement therapy restored paternal behavior in males observed interacting with foster pups (Trainor and
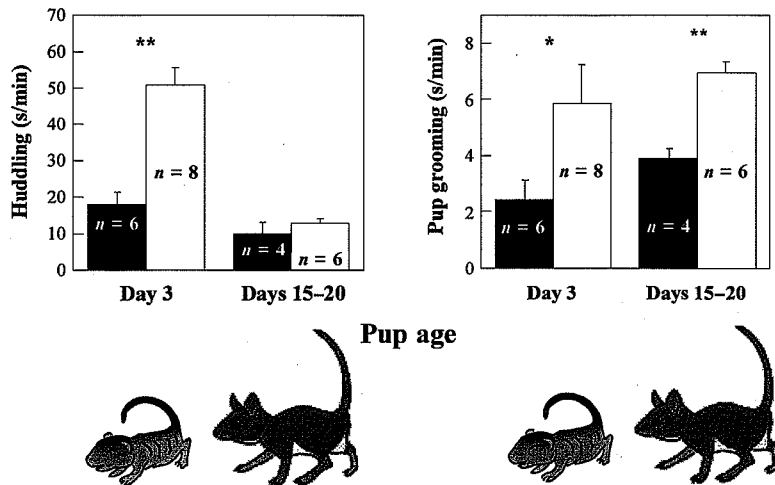
FIG. 2. Huddling and pup-grooming behavior of castrated (solid columns) and intact male California mice (open columns) at different stages in the development of their pups. Castration reduced both huddling and pup grooming on day 3 (modified from Trainor and Marler, 2001), but only pup grooming on days 15–20 (K. Cravens, B. C. Trainor, and C. A. Marler, unpublished data). **$p < 0.001$; *$p < 0.05$.

Marler, 2001). The effect of T on paternal behavior can, however, vary with different stages of pup development. In Fig. 2, we summarize data from two studies. In the first study, males were observed for 30 min with their mate and pups 3 days after parturition (Trainor and Marler, 2001). In a second study, males were observed for eight 10-min observation periods spaced throughout the dark phase between days 15 and 20 after parturition (K. Cravens, B. C. Trainor, and C. A. Marler, unpublished data). To facilitate comparisons between the two studies, analyses were conducted on rates of behavior during observations.

Castration reduced pup-grooming rates both on day 3 and during days 15–20 after birth, but only huddling on day 3. However, examination of huddling rates across the studies shows that on days 15–20 both castrated and intact males huddled less frequently than did castrated males on day 3. This is not surprising as male huddling behavior steadily decreases as pups mature (Fig. 3; Bester-Meredith *et al.*, 1999) and are able to thermoregulate more efficiently. Although pup grooming responded to T across different stages of pup development, the functional basis of this behavior may change. Even though the overall rate of pup grooming changes little over time (Fig. 3; Bester-Meredith *et al.*, 1999), males decrease the amount of time spent grooming the anogenital region of pups 2 weeks after
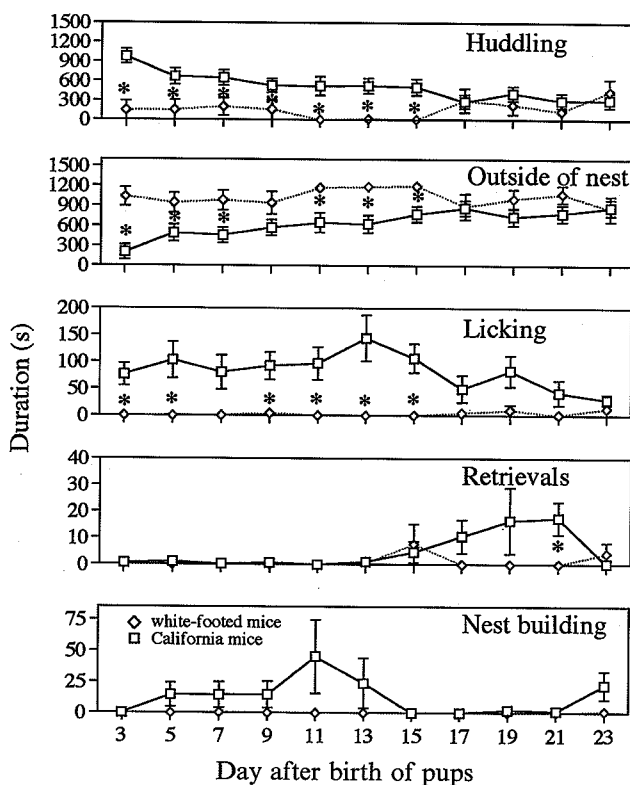
FIG. 3. Amount of time spent huddling with pups, outside of the nest, licking/grooming pups, retrieving pups, and nest building by male white-footed mice (*P. leucopus*) and California mice (*P. californicus*) during 1200-s observation periods beginning on day 3 and ending on day 23 after the birth of pups (from Bester-Meredith *et al.*, 1999). Data are presented as means $\pm$ standard errors. $*p < 0.05$.

parturition (Gubernick and Alberts, 1987a). As the pups mature, the function of pup grooming may change from stimulating the development of the anogenital tract (Moore, 1984, 1992) to other functions such as coat maintenance or possibly social functions.

Testosterone also mediates the effect of exposure to pups on paternal behavior. When castrated males with T implants were tested with foster pups on consecutive days, males showed significantly higher levels of pup grooming (paired $t_{12} = 2.24$, $p = 0.04$) and tended to show higher levels of huddling (paired $t_{12} = 1.99$, $p = 0.06$) on the second day compared with the first (Trainor and Marler, 2002). This effect was absent for pup grooming (paired $t_{12} = 0.86$, $p = 0.4$) and huddling (paired $t_{12} = 1.02$, $p = 0.32$) in

castrated males without T replacement. Thus, higher T levels were associated with higher levels of paternal care.

The reported variability in the effects of T on male parental behavior in other rodent species may reflect species differences or, as we discuss below, variation in methodology (i.e., social experience). When virgin adult male prairie voles were castrated and exposed to pups, they displayed either a decrease in paternal behavior (Wang and De Vries, 1993), which was restored with T implants, or no change (Lonstein and De Vries, 1999). However, T can act early during postnatal development in prairie voles to promote the expression of parental behavior after maturation (Lonstein et al., 2002), although apparently not prenatally (Roberts et al., 1996; Lonstein et al., 2002). This effect of T during early development may be related to social structure because the prairie vole is a cooperative breeder (Getz et al., 1990) and can express parental behaviors before acquiring reproductive experience (Lonstein and De Vries, 1999). In such species, the positive influence of T on paternal behavior may occur early during development, before expression of paternal behavior. The role of T may also be related to territorial aggression levels because male prairie voles display a high degree of home range overlap, in contrast to the fairly exclusive territories maintained by California mice (review by Goodson and Bass, 2001). Overall, T is not negatively related to paternal behavior in prairie voles and, in fact, there is evidence that T may be positively associated with paternal behavior. It also demonstrates, however, how variation in the timing of paternal behavior and aggression might affect how T influences these behaviors.

In contrast to California mice and prairie voles, an increase in paternal behavior followed castration in Mongolian gerbils (Clark and Galef, 1999). Methodological differences may explain why these results differ. The male gerbils were sexually inexperienced, but had cohabitated for 10 days with a female already inseminated by a male. Males therefore lacked the normal sequence of stimuli typically experienced before having pups (i.e., mating, cohabitation, birth of pups). These additional stimuli may initiate paternal behavior, whereas T may maintain paternal behavior and the effect of T on parental behavior may change after the onset of paternal behavior. The initiation of paternal behavior may be more strongly associated with other steroid and peptide hormones. For example, correlational studies have documented that steroid and peptide hormones such as prolactin change before parturition (Brown et al., 1995; Gubernick and Nelson, 1989; Reburn and Wynne-Edwards, 1999). These changes could play an important role in priming males to exhibit paternal behaviors in response to changes in T. It will therefore be important to examine the role of T in maintaining paternal behavior in male gerbils.

Summary

In rodents, there does not seem to be a simple relationship between T levels and paternal behavior. Across species of *Peromyscus*, low T levels are not a prerequisite for paternal behavior as seen with high baseline T levels measured in the monogamous *P. polionotus*. Within rodent species, in almost every case, male T levels peak at parturition and decline shortly afterward. There is substantial variation in the timing of the onset of paternal behavior across species, although the onset of paternal behavior usually appears after a period of increased T levels. In Djungarian hamsters, Mongolian gerbils, and California mice, the onset of paternal behavior follows the high T levels preceding parturition while in the prairie vole the onset of male parental behavior occurs postnatally. This raises the possibility that the increased T levels observed before the onset of paternal behavior are more important than the decreased T levels that have been observed after parturition. Again, high T levels are not incompatible with some aspects of paternal behavior.

The potential interpretations of the correlational and manipulative California mouse studies also demonstrate the difficulties of extrapolating a relationship between T and paternal behavior from only correlational studies, as described in the set of amphibian studies. While the correlational studies indicated a negative relationship between T and paternal behavior in California mice, the manipulative studies demonstrated a positive relationship between T and paternal care. While T levels were lower in fathers, it was these low T levels that maintained paternal care.

Two of the three biparental rodent species displayed a positive relationship between T and paternal behavior, although the timing of the effect may differ. Because of differences among the studies and because so few species have been studied, it is not yet possible to determine whether a positive association is more likely to be found in highly paternal species with a postpartum estrus. However, these studies, combined with the previously discussed fish studies, suggest that this is still a viable hypothesis. Future studies may find that there are common actions of T on paternal behavior across rodents, although the social system of each species is likely to play an important role in explaining interspecific variation in this relationship.

E. Testosterone and Paternal Care: Nonhuman Primates

Most studies examining hormones and paternal behavior in primates have documented the changes in male peripheral hormone levels across a

mate's pregnancy or in response to infants. Early studies on common marmosets (*Callithrix jacchus*) detected no changes in T levels (Dixson and George, 1982). However, more recent studies have found somewhat contrasting results. In cotton-top tamarins (*Saguinus oedipus*), gradual increases in male urinary T levels were observed across a mate's pregnancy regardless of previous reproductive experience (Ziegler and Snowdon, 2000). Testosterone levels remained high after parturition when males began infant-carrying behavior (Ziegler *et al.*, 2000). In contrast, urinary T levels in the related black tuft-eared marmosets (*Callithrix kuhlii*) were negatively correlated with paternal behavior. Male black tuft-eared marmosets with more parental experience, and fathers that spent more time carrying infants, had lower T levels (Nunes *et al.*, 2000, 2001). Currently it is unclear why T and paternal behaviors would be positively correlated in one tamarin species, but negatively correlated in a closely related marmoset. It is possible that methodological differences may have contributed to the contrasting results across species. Studies on the cotton-top tamarins reported T levels averaged across months whereas studies on the black tuft-eared marmosets reported T levels averaged across weeks. There is also variation in the onset of paternal behavior. Black tuft-eared marmoset fathers express their highest levels of infant-carrying behavior 3–4 weeks after parturition (Nunes *et al.*, 2000), whereas cotton-top tamarin fathers express their highest levels of carrying behavior immediately after parturition (Snowdon, 1996). The timing of the paternal behaviors, as well as the methodological differences, could contribute to the varying results between these related species.

Summary

Again, these studies indicate that high T is not incompatible with paternal care. As in the rodents, there is also a hint that the timing of the expression of paternal behavior may be important. The species that displayed the highest levels of paternal care immediately after parturition, cotton-top tamarins, also maintained high T levels during this time period. As in the rodents, there was also an elevation of T in males immediately before parturition.

F. TESTOSTERONE AND PATERNAL CARE: HUMANS

Studies on human participants found differences in testosterone levels between fathers after parturition and expectant fathers during pregnancy that are qualitatively similar to patterns observed in other paternal mammals (e.g., Wynne-Edwards and Reburn, 2000). Testosterone levels were lower in males sampled during the 3-week period after parturition, but

were not different from preparturition levels in a separate group of males sampled 4–7 weeks after parturition (Storey et al., 2000). Cortisol levels were increased during the 4 weeks before parturition and did not fully return to baseline until 4–8 weeks later. Especially interesting were behavioral observations, in which men were asked to hold a doll on their shoulder during a 30-min interview period. Men who held the doll on their shoulders for the full 30 min had significantly lower T levels and a higher prolactin response to a crying baby than did men who put the doll down before the 30-min interview was finished (Storey et al., 2000). In another experiment men responded to tapes of crying infants with an increase in T during the 3-week period after parturition, but not at other times. Although these findings do not involve actual paternal behaviors, such comparisons between hormone changes and behavior from the same individuals are relatively rare, even in the animal literature. Despite the small sample sizes, the results suggest that male hormonal changes may be associated with paternal behavior. In a more recent study, on average, male T levels declined on becoming fathers, but there was extensive variation in the pattern of T level changes surrounding parturition (Berg and Wynne-Edwards, 2001).

Summary

As in many other species, it is not clear whether human paternal behavior alters hormones levels or whether hormones are more important in regulating behavior. However, T levels appear to be associated with paternal behavior in human fathers.

G. Summary for Testosterone and Paternal Care

Across taxa there appears to be considerable variation in the association between androgens and paternal care (Table I), despite a general tendency to assume a negative interaction. For example, T was high, or at least above baseline, when paternal behavior was expressed in a variety of species. In several species, artificial increases in T did not always result in a large decrease in paternal behavior. Finally, artificial increases in T raised the level of paternal behavior in several fish and rodent species. One factor that may dictate some of the general effects of androgens on paternal behavior is the temporal association between aggression, mating, and paternal behavior. In temperate zone, seasonally breeding birds, mating and paternal behaviors are temporally dissociated and T inhibits paternal behavior. In contrast, in species in which mating behavior, paternal behavior, and aggression coincide, such as in a number of fish species and California mice, T can promote paternal behavior. This effect of temporal association or dissociation of behaviors and hormones on

behavior–hormone relationships may parallel the variation found in androgen control of mating behaviors mentioned earlier (e.g., Crews, 1984). It was proposed that testosterone control of mating behavior depends on the temporal association of mating behavior, gametogenesis, and high levels of T (Crews, 1984). More species using androgen manipulations must be further studied to determine the predictive power of the hypothesized relationship. At a minimum, however, this review demonstrates that there are a number of species that do not fit the generally held view that there is a negative association between paternal care and T.

III. Arginine Vasopressin: Functionally Similar to Testosterone?

The neuropeptide AVP and T are related both at a behavioral and a cellular level. Significant parallels can be drawn between the behavioral correlates of AVP and of T, including the diversity of social behaviors that they can influence. Arginine vasopressin and T may act in concert to shape sexually dimorphic behaviors such as aggression and may also function to make the two sexes more similar with respect to parental behaviors (reviewed by De Vries and Boyle, 1998). In this section, we describe the positive effects of AVP on aggression. We also describe how AVP can positively influence paternal care, despite evidence of a positive relationship between AVP and aggression. Thus, as in the relationship between T and social behaviors, we also find that AVP can have positive effects on both paternal behavior, and aggression.

A physiological relationship between T and AVP also has been demonstrated. For example, castration in rodents can cause a decrease in AVP immunoreactivity and receptors in the bed nucleus of the stria terminalis and amygdala (reviewed by De Vries and Boyle, 1998; Viau et al., 1999; Young et al., 2000). In addition, T can modify the behavioral response to central injections of AVP (e.g., Albers et al., 1988) and can accomplish this by altering densities of V_1 AVP receptors (Delville et al., 1996). Thus, levels of the two hormones (AVP is referred to as a hormone instead of a neurochemical in this review) are at least partially associated in a positive manner in rodents, and again both have the potential to positively influence aggressive as well as paternal behavior in some species.

A. Arginine Vasopressin: An Aggression Hormone, a Nurturing Hormone, or Both?

In this section, we discuss evidence that AVP has positive associations with both aggression and the nurturing behaviors found in paternal care,

thus further illustrating that the two categories of behavior can be positively associated with each other through linkage with the same underlying physiological mechanisms.

Because AVP is less well studied than T, we discuss the relationship between AVP and aggression in more detail than in the previous discussion of the relationship between T and aggression. Arginine vasopressin has been associated with aggression in mammals (reviewed by De Vries and Boyle, 1998; Koolhaas et al., 1998), while the nonmammalian homolog, arginine vasotocin (AVT), has similar effects in fish (e.g., Semsar et al., 2001), birds (reviewed by Goodson and Bass, 2001), and amphibians (e.g., Semsar et al., 1998; Klomberg and Marler, 2000). Within mammals, AVP has been associated with aggression in a number of species including house mice (e.g., Bluthe et al., 1993; Compaan et al., 1993), Rattus spp. (e.g., Everts et al., 1997), prairie voles (e.g., Winslow et al., 1993), golden hamsters (Mesocricetus auratus; reviewed by Ferris, 1992), California mice (e.g., Bester-Meredith and Marler, 2001), and humans (Coccaro et al., 1998). Variation in aggressive behavior has been correlated with AVP-immunoreactive cell and fiber characteristics, peptide and receptor mRNA, and AVP receptor binding (reviewed by Goodson and Bass, 2001). In mammals, attention has been focused primarily on the behavioral function of a sexually dimorphic AVP pathway originating in the bed nucleus of the stria terminalis and medial amygdala and projecting to the lateral septum (reviewed by De Vries and Miller, 1998). The density of AVP-immunoreactive staining in this sexually dimorphic pathway differs between strains of house mice bred for long and short attack latencies (Compaan et al., 1993). The medial amygdala, which provides input into this pathway and has extensive connections to the olfactory system and to other brain areas associated with social behavior, has been associated with aggression in rats (Koolhaas et al., 1990). In addition, evidence from the golden hamster suggests a behavioral role for AVP located within the hypothalamus, particularly in the anterior hypothalamus, a brain area associated with aggression (Delville et al., 1998, 2000). In the golden hamster, neuroanatomical tracing studies and comparisons of fos expression reveal connections between the anterior hypothalamus and the medial amygdala and the bed nucleus of the stria terminalis that are associated with offensive aggression (Delville et al., 2000). Interactions between the vasopressinergic neurons of this pathway and serotonergic neurons may be critical in the regulation of aggressive behavior in hamsters (Ferris and Delville, 1994; Ferris et al., 1997). Overall there is strong evidence for an association between AVP/AVT and aggression in these brain areas across a wide variety of species; we emphasize here

associations within three mammalian genera: *Mesocricetus*, *Microtus*, and *Peromyscus*.

For the relationship between AVP and paternal behavior we focus on *Microtus* and *Peromyscus*. Fewer studies have examined the relationship between AVP and paternal behavior. Nonetheless, an emerging picture from these two genera is that there are close links among aggression, paternal behavior, and, in some cases, pair bonding: three behavioral categories that appear to be positively associated in these species with each other, as well as AVP. Within brain areas where limbic system *fos* expression has been associated with paternal behavior in the prairie vole, including several areas connected to the medial amygdala such as the lateral septum and the bed nucleus of the stria terminalis (Kirkpatrick *et al.*, 1994a), AVP has been identified as a possible substrate of paternal behavior. Disruption of this system via removal of input from the olfactory bulb disrupts the expression of paternal care in prairie voles (Kirpatrick *et al.*, 1994b). The possible role of AVP in the lateral septum of prairie voles and in the bed nucleus of the stria terminalis in California mice is discussed in more detail later.

We also review the potential plasticity of the AVP neurochemical system in response to social conditions provided by conspecifics, with subsequent effects on aggressive and parental behaviors. The plasticity of the AVP neurochemical system becomes crucial when we later discuss the cross-generational effects of parental behavior and its interactions with aggression and AVP in California mice.

B. ARGININE VASOPRESSIN AND AGGRESSION: GOLDEN HAMSTERS (*Mesocricetus auratus*)

The most detailed studies that relate AVP to aggression have been performed with adult golden hamsters. In golden hamsters, rank and dominance behavior, as well as specific aggressive behaviors, have been linked to AVP in both group-housed and isolated individuals. Subordinate males have significantly lower levels of AVP immunoreactivity in the anterior hypothalamus as compared with dominant males (Ferris *et al.*, 1989). Manipulations of AVP also alter dominance and aggressive behaviors toward an intruder: AVP microinjections increase dominance behaviors, whereas AVP blockers decrease them (Ferris *et al.*, 1984, 1986, 1988, 1993, 1997; Ferris and Potegal, 1988). Arginine vasopressin receptor blockers also decreased the number of attacks and increased attack latency toward a conspecific male intruder (Ferris and Potegal, 1988; Potegal and Ferris, 1990). However, the social status of a male golden hamster can modify the effectiveness of AVP manipulations on aggression.

A subordinate male injected with AVP will increase flank-marking behavior and will become the dominant individual in a pair (Ferris *et al.*, 1986). Conversely, a dominant male treated with the AVP blocker dPTyr(me)AVP becomes the subordinate individual in a pair (Ferris *et al.*, 1986). This is accompanied by a decrease in flank-marking behavior. However, a dominant male will not increase flank-marking behavior in response to AVP injections, possibly because he has reached a maximum level of AVP-induced flank-marking behavior. In summary, the evidence of a contribution by AVP to the control of dominance and aggressive behaviors is extensive in golden hamsters.

As suggested indirectly by the studies described above, there is plasticity in the AVP neurochemical system in response to social conditions in adults (e.g., Ferris *et al.*, 1989), but plasticity can also occur during development in golden hamsters. Male golden hamsters exposed to aggressive adults shortly after weaning were less likely than control males to attack individuals of a similar size to themselves. In these socially subjugated males, AVP levels were also 50% lower in the anterior hypothalamus (Delville *et al.*, 1998; although it should be noted that these males were also more likely to attack intruders weighing 35–40% less). By altering the social conditions of these males during late development, adult neuro-transmitter levels and aggression levels were also altered. Overall, these studies on golden hamsters demonstrate that within a species, AVP can influence aggression and that changes in social conditions can alter both behavior and the AVP neurochemical system.

Summary

The studies with golden hamsters elegantly demonstrate a positive association between aggression and AVP in a mammal. In addition, these studies provide evidence that alterations in AVP can cause plasticity in competitive aggression and that changes in social condition can also alter AVP levels.

C. ARGININE VASOPRESSIN, AGGRESSION, PATERNAL BEHAVIOR, AND PAIR BONDING: VOLES (*Microtus*)

The formation of pair bonds in prairie voles coincides with an increase in aggression that may be associated with mate-guarding aggression or possibly with increased defense of pups against infanticide. In this section, we discuss how AVP is involved in these behaviors, as well as with paternal behavior, another behavior associated with mating. For example, AVP manipulations reveal that AVP can regulate both affiliative behaviors and the formation of pair bonds (Winslow *et al.*, 1993; Cho *et al.*, 1999; Young

et al., 1999; Pitkow *et al.*, 2001; Liu *et al.*, 2001). In addition, at the time of mating there is a significant change in AVP-immunoreactive staining in the lateral septum (Bamshad *et al.*, 1994) and an increase in AVP gene expression in the bed nucleus of the stria terminalis (Wang *et al.*, 1994b), suggesting that mating may trigger an AVP-induced increase in mate-guarding aggression. This onset of mate-guarding aggression can also be blocked through administration of an AVP antagonist (Winslow *et al.*, 1993). AVP injections also caused an increase in resident–intruder aggression in sexually experienced male prairie voles, although not in the promiscuous montane vole (Young *et al.*, 1997). Interestingly, AVP administered during development also increased adult aggression (Stribley and Carter, 1999), suggesting that the formation of AVP pathways earlier in development may shape adult levels of mate-guarding aggression. Therefore, in male *Microtus*, it has been hypothesized that AVP may regulate a variety of behaviors associated with pair bond formation that tie in with the increased aggression.

In addition to the role of AVP in mate-guarding aggression and the formation of pair bonds, it is also important for the regulation of paternal care, another behavior associated with pair bond formation in prairie voles. After young are born, male prairie voles display high levels of paternal care (reviewed by Wang and Insel, 1996). The onset of paternal behavior coincides with an increase in AVP gene expression in the bed nucleus of the stria terminalis and a decrease in AVP-immunoreactive staining in males, suggesting an increase in production and release of AVP as paternal behavior is initiated (Bamshad *et al.*, 1993, 1994; Wang *et al.*, 1994b, 2000). Castration eliminated AVP-immunoreactive staining in the lateral septum and caused a decrease in the expression of paternal behavior (Wang and De Vries, 1993). Furthermore, intracerebroventricular injections of AVP increased paternal behavior, whereas an AVP antagonist decreased paternal behavior (Wang *et al.*, 1994a). The effects of AVP on paternal behavior also are supported by the finding that AVP induced paternal behavior (an aggregate measure of pup grooming, huddling, and time spent in contact with the pup) in the facultatively paternal meadow vole (*Microtus pennsylvanicus*) (Parker and Lee, 2001). In this same species, AVP receptor-binding patterns are also altered by the experience of mating and raising their own pups (Parker *et al.*, 2001). Overall, there is considerable evidence that AVP promotes paternal care, suggesting that AVP is involved in the regulation of a suite of behaviors associated with pair bond formation, including mate-guarding aggression and paternal care.

These studies also provide evidence of plasticity in AVP within individuals. As previously mentioned, within *Microtus*, changes in AVP immunoreactivity and AVP receptor-binding patterns were induced by the

experience of mating and raising pups. This demonstrates that AVP may change in response to events, which in turn leads to a potential change in paternal behavior.

Summary

The *Microtus* studies do not demonstrate the association between aggression and AVP as strongly as in the golden hamsters; however, the positive association between AVP and paternal behavior emerges in these vole species. In addition, these studies provide further evidence of plasticity in the AVP neurochemical system in response to experience.

D. ARGININE VASOPRESSIN, AGGRESSION, AND PATERNAL BEHAVIOR: CALIFORNIA MOUSE (*Peromyscus californicus*) AND WHITE-FOOTED MOUSE (*Peromyscus leucopus*)

There is evidence of an association between AVP and both paternal and aggressive behaviors in *Peromyscus*, although the role of AVP in regulating affiliative behavior has not yet been examined. AVP may be associated with resident–intruder aggression in both unmated and mated individuals, similar to both prairie voles and golden hamsters. In this section, we discuss how two species of *Peromyscus* differ in several types of behavior and then describe the links between these behaviors and AVP.

1. Aggression and Paternal Behavior

California mice are monogamous, and perhaps even more strictly monogamous than prairie voles (Ribble and Salvioni, 1990; Ribble, 1991), and males display high levels of parental behavior (Fig. 3) equivalent to levels found in females (Dudley, 1974a,b; Gubernick and Alberts, 1987b; Gubernick and Teferi, 2000). The white-footed mouse provides a contrast to the California mouse because males are polygynous and display lower levels of facultative paternal care (Fig. 3) (Xia and Millar, 1988; Schug *et al.*, 1992). For example, male white-footed mice rarely retrieve pups during the third week after the birth of the pups and also show less huddling and licking behavior toward the pups (Bester-Meredith *et al.*, 1999).

In addition to these species differences in mating system and in paternal investment, the monogamous California mouse and polygynous white-footed mouse also differ in levels of aggression. We investigated aggression in both *Peromyscus* species, using two types of tests, and, as is discussed later, these tests revealed two different types of aggression. In a resident–intruder aggression test, a male is placed in an observation cage 48–60 h before an encounter and, at the onset of the test, an intruder male is placed
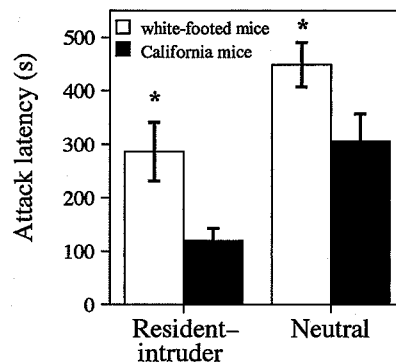
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FIG. 4. Attack latencies in resident–intruder and neutral aggression tests for male white-footed mice (*P. leucopus*) and male California mice (*P. californicus*) (from Bester-Meredith *et al.*, 1999). Data are presented as means ± standard errors. *$p < 0.01$.

into the smaller chamber of the observation cage. This testing paradigm gives males a resident advantage such that they are more likely to win an aggressive encounter (Archer, 1988) and is similar to territorial aggression because it involves defense of a familiar site. During a neutral aggression test, both animals are placed simultaneously in separate compartments of a novel observation cage. All tests were terminated as soon as an attack occurred and if no attack occurred, mice were separated after 10 min.

Using these two types of aggression tests, we confirmed field studies by other researchers that male California mice are highly territorial and aggressive (Fig. 4) and maintain exclusive territories (Ribble and Salvioni, 1990; Bester-Meredith *et al.*, 1999; Bester-Meredith and Marler, 2001), unlike male prairie voles, which display more overlap in their home ranges (Getz *et al.*, 1981). In contrast, white-footed mice are less aggressive than California mice and display territoriality only when population densities are high (Fig. 4) (Metzgar, 1971; Wolff and Cicirello, 1991; Bester-Meredith *et al.*, 1999; Bester-Meredith and Marler, 2001). Therefore, we found that these two species display different patterns of paternal care and aggression, two behaviors that have been linked with AVP. These two species also differ in AVP-immunoreactive staining, with California mice showing more extensive AVP immunoreactivity in the bed nucleus of the stria terminalis in addition to higher levels of aggression and paternal care (Bester-Meredith *et al.*, 1999).

2. Arginine Vasopressin, Aggression, and Paternal Behavior

As with golden hamsters and voles, the AVP neurochemical system may underlie the species-typical patterns of social behavior described above.

We examined the associations between neurochemical and behavioral patterns by using both between and within-genera comparisons.

We first compared AVP and behavioral patterns between *Microtus* and *Peromyscus* species. Specifically, we have hypothesized that species patterns of aggression in sexually inexperienced males are better predictors than paternal care of AVP-immunoreactive staining and receptor distribution at a species level (Bester-Meredith *et al.*, 1999). We rejected paternal behavior as a predictor of AVP-immunoreactive staining patterns in these broad species comparisons because of differences in patterns of AVP-immunoreactive staining between paternal and nonpaternal *Peromyscus* and *Microtus* species. Whereas the paternal *Microtus* species, the prairie vole, had lower levels of AVP-immunoreactive staining in the bed nucleus of the stria terminalis than the less paternal species, the polygamous and less paternal meadow vole (*M. pennsylvanicus*) (Wang, 1995), and fewer AVP receptors in the lateral septum than the polygamous and less paternal montane vole (*M. montanus*) (Insel *et al.*, 1994; Wang *et al.*, 1997; Young *et al.*, 1997), the opposite was true for *Peromyscus*. The more paternal California mouse had higher levels of AVP-immunoreactive staining in the bed nucleus of the stria nucleus and amygdala and higher receptor densities in the lateral septum as compared with the less paternal white-footed mouse (Bester-Meredith *et al.*, 1999). There is evidence, however, that the AVP-neurochemical patterns in these brain areas may be better explained by aggression and, as proposed by Goodson and Bass (2001), by social spacing patterns. Within these *Peromyscus* and *Microtus* species, those with higher levels of AVP-immunoreactive staining and AVP receptor density (California mice and meadow voles) may be more aggressive (*Microtus*: Hofmann *et al.*, 1982; Getz, 1962; Dewsbury, 1983; but see Colvin, 1973; *Peromyscus*: see above), and also maintain more exclusive territories (reviewed by Goodson and Bass, 2001). These results do not exclude AVP control of paternal behavior at a finer level of analysis (as described below) or address the question of plasticity in AVP response to experiences such as mating or raising pups, but do provide suggestive evidence that AVP-immunoreactive staining patterns in inexperienced male rodents could potentially be explained better by differences in aggression levels between species.

Within *Peromyscus* species there is further evidence linking AVP and aggression. When we cross-fostered between species of *Peromyscus* such that the more aggressive and paternal California mouse pups were raised by the less aggressive and less paternal white-footed mouse parents, and vice versa, we found changes in both aggression and AVP-immunoreactive
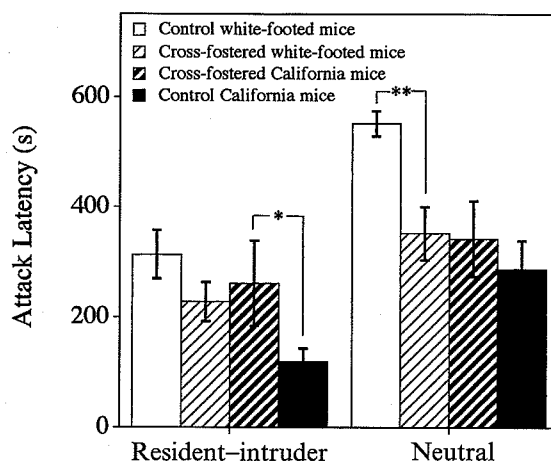
Fig. 5. Attack latencies in the resident–intruder test and test of aggression in a neutral arena for control white footed mice (resident–intruder, $n = 12$; neutral arena, $n = 13$), cross-fostered white-footed mice (resident–intruder, $n = 14$; neutral, $n = 13$), cross-fostered California mice (resident–intruder, $n = 10$; neutral, $n = 9$), and control California mice (resident–intruder, $n = 24$; neutral, $n = 23$) (from Bester-Meredith and Marler, 2001). A shorter attack latency indicates a higher level of aggression. Data are presented as means $\pm$ standard errors. $*p < 0.05$, $**p = 0.01$.

staining in the bed nucleus of the stria terminalis (Table II, Fig. 5, and Fig. 6).

However, there is an interesting interaction between the species and the two forms of aggression tests. While both species became more similar to their foster parents with respect to level of aggression, the two species differed in the type of aggression that changed (Fig. 5 and Table II). California mice raised by the less aggressive white-footed mice displayed a decrease in resident–intruder aggression, but no change in neutral aggression. In contrast, white-footed mice raised by the more aggressive California mice displayed an increase in neutral aggression, but no change in resident–intruder aggression.

It is important to note that changes in AVP in the bed nucleus of the stria terminalis appeared to be associated with resident–intruder aggression but not neutral aggression because changes in AVP immunoreactivity were observed only in California mice, the species displaying a change in resident–intruder aggression (Table II and Fig. 6).

Further evidence from manipulations and correlations strengthens the proposed association between AVP and resident–intruder aggression. In the case of resident–intruder aggression, an intracerebroventricular injection of 1 ng of an AVP V_{1a} receptor antagonist blocked resident–intruder

TABLE II

EFFECTS OF CROSS-FOSTERING ON AGGRESSION AND ARGININE VASOPRESSIN-IMMUNOREACTIVE STAINING IN CALIFORNIA MICE AND WHITE-FOOTED MICE[a]

| Species cross-fostered | Effect of cross-fostering on: | | | |
	R–I aggression	Neutral arena aggression	Paternal behavior	AVP-IR staining in the BNST
California mice	Control > cross-fostered	No effect	Control > cross-fostered	Control > cross-fostered
White-footed mice	No effect	Control < cross-fostered	No effect	No effect

Abbreviations: AVP, Arginine vasopressin; IR, immunoreactive.

[a]Effects of cross-fostering on aggression in the resident–intruder (R–I) test, aggression in the neutral arena, paternal behavior (retrievals), and AVP-IR staining in the bed nucleus of the stria terminalis (BNST) in male California mice (more paternal and aggressive species) raised by white-footed mice (less aggressive and paternal species) and male white-footed mice raised by California mice. The cross-fostered mice were compared with control mice. Summarized from Bester-Meredith and Marler (2001, 2003).

aggression, but not neutral arena aggression in California mice (J. K. Bester-Meredith, P. Martin, and C. A. Marler, unpublished data). In addition, in sexually experienced males, there is a direct association between levels of aggression and AVP-immunoreactive staining: resident–intruder aggression was positively correlated with optical density in the bed nucleus of stria terminalis (J. K. Bester-Meredith and C. A. Marler, unpublished data). Therefore, the association between AVP and aggression that is found in sexually inexperienced individuals remains present and perhaps even more potent in sexually experienced males.

A potential link between AVP and paternal behavior is also evident (Table II). California mice that were raised by the less parental and aggressive white-footed mice showed not only less aggression in the resident–intruder test, but also a decrease in paternal care when raising their own offspring (Table II). As adults, these cross-fostered male California mice displayed a decrease in pup retrievals, although no changes in nest building or in a composite score of time spent huddling, grooming, and in the nest (HGI score) (J. K. Bester-Meredith and C. A. Marler, 2003). Thus the decrease in AVP-immunoreactive staining in the bed nucleus of the stria terminalis found in the male California mice raised by white-footed mice is accompanied by both a decrease in resident–intruder aggression and a decrease in paternal behavior in the form of pup retrievals. In contrast, white-footed mice raised by California mice did not exhibit any change in resident–intruder aggression, paternal behavior, or
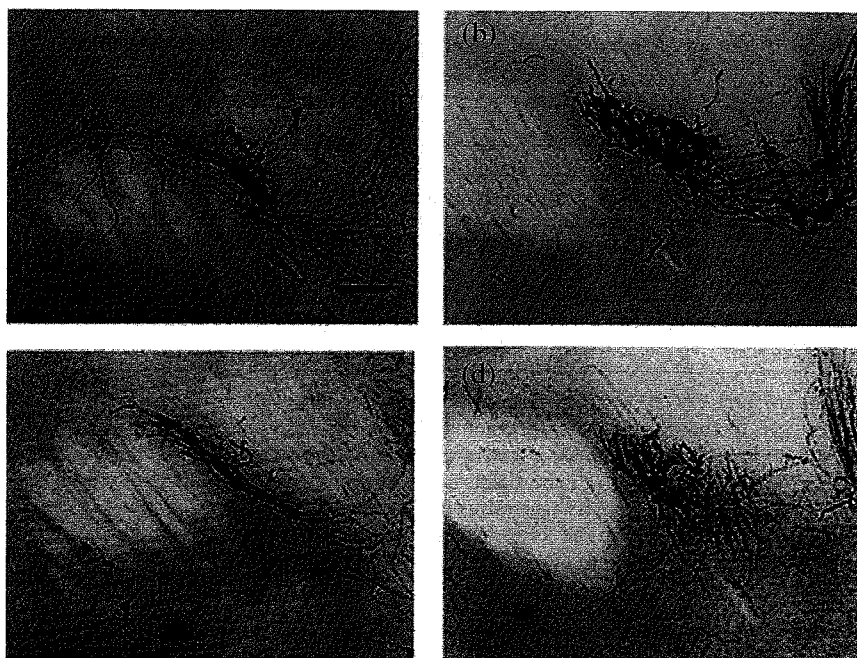
Fig. 6. Representative photomicrographs of AVP-immunoreactive staining in the bed nucleus of the stria terminalis, comparing sexually naive, male (a) control white-footed mice, (b) control California mice, (c) cross-fostered white-footed mice, and (d) cross-fostered California mice. Cross-fostered California mice had significantly less AVP-immunoreactive staining than the control California mice, but cross-fostering had no effect on AVP-immunoreactive staining in the white-footed mice (from Bester-Meredith and Marler, 2001). Bar: 100 μm.

AVP immunoreactivity in the bed nucleus of the stria terminalis. Therefore, only the species displaying a change in both paternal behavior and resident–intruder aggression after cross-fostering also exhibited a change in AVP immunoreactivity in the bed nucleus of the stria terminalis.

Similar to our findings with aggressive behavior, additional evidence from correlations strengthens the proposed association between AVP and paternal behavior. In the case of paternal behavior, examination of AVP levels in the bed nucleus of the stria terminalis in sexually experienced males showed that the degree of AVP-immunoreactive staining in the bed nucleus of the stria terminalis was positively correlated with a composite score consisting of huddling, grooming and time spent inside the nest when cross-fostered and control males were combined (Fig. 7; J. K. Bester-Meredith and C. A. Marler, 2003).
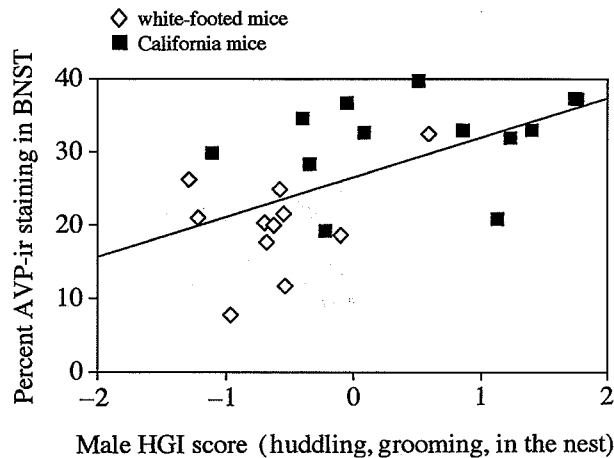
FIG. 7. Statistically significant correlation between maximum percent AVP-immunoreactive staining in the bed nucleus of the stria terminalis and Z-score composite scores of the average time spent huddling, grooming, and in the nest (HGI score) by in-fostered and cross-fostered white-footed (*P. leucopus*) and California mice (*P. californicus*) (J. K. Bester-Meredith and C. A. Marler, 2003).

In addition, AVP-immunoreactive staining was positively associated with retrievals: males that expressed retrieval behaviors during the observation periods had significantly higher levels of AVP-immunoreactive staining than did males that did not express retrieval behavior (Fig. 8; J. K. Bester-Meredith and C. A. Marler, 2003). Because our results rely on immunocytochemistry measurements, we cannot identify the direction of the relationship (i.e., amount of AVP produced or released) until we examine the effect of AVP manipulations on paternal behavior.

Our results suggesting an association between paternal behavior and AVP are consistent with the findings in *Microtus* that AVP can influence behaviors such as pup grooming, huddling, and time spent in contact with pups (Wang *et al.*, 1994a,b; Parker and Lee, 2001). However, because there was no effect of AVP on retrievals in the sexually inexperienced male *M. ochrogaster* and retrievals were not measured in the facultatively paternal *M. pennsylvanicus* (Parker and Lee, 2001), a critical future step is to examine the effects of AVP on retrievals in sexually experienced male California mice. Nevertheless, the correlations we found between AVP and the HGI score, along with retrievals, are generally consistent with the association found between AVP and paternal behavior in *Microtus* (see above). In addition, our cross-fostering studies again suggest that there is plasticity in both AVP and paternal behavior: this social manipulation
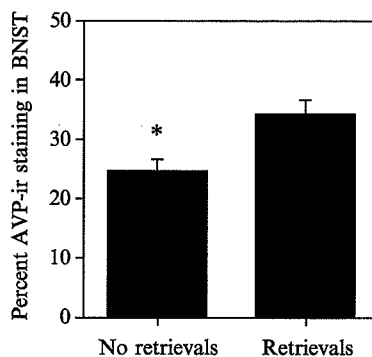
FIG. 8. Maximum percent AVP-immunoreactive staining in the bed nucleus of the stria terminalis of males that did not retrieve pups ($n = 20$) and males that did retrieve pups ($n = 4$) during the observation periods (J. K. Bester-Meredith and C. A. Marler, 2003). Data are presented as means ± standard errors. *$p < 0.05$.

modified both the intensity of AVP-immunoreactive staining in the bed nucleus of the stria terminalis and the degree of paternal behavior expressed by cross-fostered California mice.

Summary

As in golden hamsters and prairie voles, we also found in *Peromyscus* that AVP pathways can be associated with both aggression and paternal care and that there is plasticity in these AVP pathways. California mice and white-footed mice differ in both paternal care and aggression, with California mice showing more extensive paternal care, more aggression toward conspecifics, and higher AVP-immunoreactive staining in the bed nucleus of the stria terminalis. Cross-fostering studies indicate that AVP plays a role in aggression in sexually inexperienced California mice and it is possible that AVP modulates aggression even more strongly in mated individuals as indicated by the direct association between levels of AVP immunoreactivity and levels of aggression.

In these two *Peromyscus* species, we found that modifications may be made in the behavior and neurochemistry of future generations by exposing them to paternal behavior atypical for their own species. Cross-fostering between these two species produced a suite of behavioral changes that led fostered pups to adopt behavioral patterns typical of their foster parents, including a decrease in paternal care and resident–intruder aggression in cross-fostered California mice and an increase in neutral aggression in cross-fostered white-footed mice. Along with these behavioral changes, a reorganization of AVP pathways as typified by a

change in AVP-immunoreactive staining in the bed nucleus of the stria terminalis also occurred in California mice. The association between AVP and aggression is supported by other data in *Peromyscus*, including a decrease in resident–intruder aggression in California mice after intracerebroventricular injections of an AVP antagonist (Bester-Meredith and Marler, unpublished data). Although differences in paternal care cannot explain patterns of AVP-immunoreactive staining between rodent genera, plasticity in AVP pathways may be associated with changes in paternal care within individual rodent species. In support of this idea, we found a correlation between AVP immunoreactivity and two measures of paternal care when both species are combined.

Together with the previously discussed findings in golden hamsters and voles, these results indicate that AVP may be associated with both aggression and paternal care in rodents. In monogamous species, AVP also functions to modify affiliative behaviors, as in the prairie vole; however, this remains to be tested in *Peromyscus*. Finally, plasticity in AVP pathways may underlie plasticity in the expression of social behaviors in these species.

E. COMPARISON OF FUNCTIONS OF VASOPRESSIN AND TESTOSTERONE

Parallels can be drawn between the functions of AVP and T across species. The previous discussion indicates that both AVP/AVT and T have the potential to influence positively both aggression and paternal behavior. These hormones clearly have a significant impact on social behaviors. The association between each hormone and aggression can, however, vary between species (reviewed by Goodson and Bass, 2001; Canoine and Gwinner, 2002). It is not yet clear how the two hormones vary together across species and whether this relationship could be linked to the expression of paternal or other behaviors. For example, in the monogamous prairie vole, there is evidence that AVP can increase paternal behavior and aggression, as described earlier, but castration, which decreases AVP levels (Lonstein and De Vries, 1999; although note that time of the behavioral testing after castration may be important), does not decrease aggression (Demas *et al.*, 1999). Similar patterns occur in the monogamous California mouse: as described earlier, there is some evidence that AVP is associated with both paternal behavior and aggression and, in addition, castration also does not decrease aggression (Trainor and Marler, 2001). However, in California mice, T increases in response to winning an aggressive encounter (T. Oyegbile and C. A. Marler, unpublished data), and castration appears to inhibit the typical increase in aggression that occurs with increasing numbers of aggressive encounters (Trainor and

Marler, 2001). Therefore, while baseline levels of T may not influence aggression, transient T increases caused by social experience may have a significant impact on aggression. Within California mice, we are continuing to test whether T is positively associated with aggression and paternal care and have also initiated studies examining the role of progesterone (E. Davis and C. A. Marler, in press). We cannot rule out the possibility that T is less important in influencing aggression in monogamous species with high levels of paternal care compared with other species.

For the time being, then, it is interesting to note that AVP can influence resident–intruder aggression in both prairie voles (Young et al., 1997) and California mice (J. K. Bester-Meredith and C. A. Marler, unpublished data), two species that display paternal care; but current evidence suggests that AVP may not influence aggression in either montane voles (Young et al., 1997) or white-footed mice (J. K. Bester-Meredith and C. A. Marler, unpublished data), two species that do not display high levels of paternal care during early development. So far, these comparisons of closely related species reveal that aggression of the more paternal species is characterized by being less influenced by baseline levels of T and perhaps more by variation in AVP, although changes in T in response to social experience may still prove to be important. Currently, however, we propose that these two neurochemicals can act in concert to regulate levels of aggression and paternal care within the same individuals under varying social conditions.

IV. Cross-Generational Transmission of Aggression through Behavioral Mechanisms and the Role of Arginine Vasopressin

Up to this point, we have established that AVP and T can be positively associated with both aggression and paternal behavior in some species. As we describe in this section, these characteristics make AVP and T ideal candidates for involvement in the behavioral transmission of aggression and paternal behavior across generations that we have identified in *Peromyscus*. We describe how a change in paternal retrievals in one generation can be transmitted to influence future levels of paternal retrievals in later generations. Furthermore, we suggest that this plasticity in paternal retrievals is a behavioral mechanism for transmitting resident–intruder aggression across generations in *Peromyscus*. A positive relationship between paternal retrievals and resident–intruder aggression is an integral component of this cascade of behavioral traits across generations.

While there is extensive literature examining the relationship between parental behavior and offspring aggression in humans, there is surprisingly little nonhuman research, despite the limitations inherent in research using humans. We therefore review existing animal studies (rodents and nonhuman primates) and a subset of the human studies. The focus is expanded to encompass different types of parental behaviors that might influence offspring aggression and two types of parental behavior that begin to emerge from some of these studies.

Finally, in Section V, we examine whether behavioral traits could pass beyond two generations in *Peromyscus* and address the role of AVP in this behavioral transmission of paternal and aggressive behaviors across generations. We have not yet extensively examined the role of T in this process, although our studies of AVP indicate that AVP is a likely mechanism for the observed behavioral plasticity.

A. PARENT–OFFSPRING INTERACTIONS: NONGENOMIC TRANSMISSION OF AGGRESSION ACROSS GENERATIONS

Thus far, we have focused primarily on hormone–behavior interactions, specifically the relationships between aggressive and paternal behaviors and the endocrine compounds T and AVP. A further complexity can be added to the interactions by focusing on how the two categories of behavior can interact. We have already described how an increase in adult aggression does not necessarily exclude an increase in paternal behaviors. Interactions between these two behavioral categories can also occur between parents and offspring during development. These interactions are potentially important because they provide a nongenomic mechanism for transmission of behaviors across generations. The effect of parental behavior on offspring aggression is likely to vary significantly depending on both the quantity and characteristics of parental care, but may also vary depending on the type of aggression that is measured. In this section, we review interactions between parental behavior and offspring aggression. In the following section we examine how parental behavior of the parents might influence parental behavior of the offspring when they become adults.

1. Parent–Offspring Interactions: Rodents

More manipulations have been performed with rodents than with other taxa, although research in this area is still limited, and focuses especially on the effects of father removal and cross-fostering. When fathers are removed early during development in rodents, there is typically a decrease in offspring adult aggression (house mice: Mugford and Nowell, 1972;

Wuensch and Cooper, 1981; southern grasshopper mouse [*Onychomys torridus*]: McCarty and Southwick, 1977; California mouse: Wallace *et al.*, 1998). Unfortunately, the effects of these studies on offspring aggression could be the result of either direct effects of the father on the pups, or indirect effects via changes in the mother. Cross-fostering studies represent a more sophisticated manipulation, but do not directly manipulate single behaviors. In one set of studies, a low-aggression line of house mice (*Mus musculus*) was cross-fostered with a high-aggression line that also displayed more maternal huddling, grooming, nursing, and retrieving (Mendl and Paul, 1990; Benus and Röndigs, 1997). Despite the many behavioral differences between these two lines, there was no effect of this manipulation on resident–intruder aggression. It is important to note that the role of the father was not tested in these studies because fathers provided little paternal care in either strain.

We have examined correlations between parental behaviors and offspring aggression in *Peromyscus* studies and found different associations between parental behavior and offspring aggression, depending on the sex of the parent and the type of aggression tested in the offspring. Our cross-fostering studies indicated that high maternal HNGI scores (indicating high levels of huddling, nursing, grooming, and time spent in the nest) were associated with lower levels of aggression expressed by male offspring in a neutral arena (J. K. Bester-Meredith and C. A. Marler, unpublished data). Aggression in a neutral arena was not associated with paternal HGI scores (huddling, grooming, and time spent in the nest) or pup retrieval behavior displayed by mothers or fathers. The suggested association between maternal HNGI scores and offspring aggression was somewhat unexpected because, as described above, house mice that are cross-fostered between highly aggressive and less aggressive strains that also differ in maternal care do not show changes in aggression. However, these previous studies concerned house mice, not *Peromyscus*, and males were tested in resident–intruder aggression tests and not neutral aggression tests (Mendl and Paul, 1990; Benus and Röndigs, 1996). Therefore, it is possible that an association between HNGI scores and offspring aggression may be revealed in house mice under other testing conditions.

In addition to this role for maternal behavior in regulating offspring aggression in the neutral arena, paternal behavior in the form of pup retrievals may serve a critical function in the development of resident–intruder aggression. We found that, in offspring raised by foster parents of the same or another species, the duration of paternal retrievals was positively associated with their aggression as adults in the resident–intruder test (J. K. Bester-Meredith and C. A. Marler, unpublished data). This positive association between male retrievals and offspring aggression in the

resident–intruder test seems to be independent of other factors including weight gain during development. In addition, the association between male retrievals and offspring aggressiveness was not driven by a single species or fostering group: all four groups (in-fostered California mice, cross-fostered California mice, in-fostered white-footed mice, cross-fostered white-footed mice) showed a similar pattern of association between retrievals and resident–intruder aggression. Thus some aspect of paternal retrieval behavior may influence pups and cause long-term changes that are revealed through resident–intruder aggression tests as adults.

Retrieving behavior and the more "nurturing" parental behaviors are associated differently with aggression in *Peromyscus*. Retrieving behavior in California mice may be fundamentally different from huddling and grooming. Huddling and grooming typically occur within the nest and can be considered "nurturing" behaviors. In contrast to the retrieving behavior most often observed in female rodents (Felton *et al.*, 1998; Gammie and Nelson, 1999), retrieving behavior in California mice occurs most frequently when pups are old enough to be active and locomote independently and at a time when huddling behavior occurs less frequently (Fig. 3; Bester-Meredith *et al.*, 1999). Retrieving behavior is sometimes preceded by a variety of grabbing and pulling behaviors by the parent, in which pups appear to resist retrieval. When the parent retrieves the pup, it grabs the pup just posterior to the forelegs. When the parent lifts the pup up, the pup is motionless and turned sideways. The parent usually places the pup back in the nest, after which the pup usually remains motionless for a short period of time. In contrast to pup-grooming behavior, castration did not affect pup retrieval behavior ($t_7 = 0.83$, $p = 0.44$; K. Cravens, B. C. Trainor, and C. A. Marler, unpublished data), suggesting another difference between the two types of behavior. Finally, although huddling, nursing, pup grooming, and time spent in the nest were significantly correlated with each other, retrieval behavior was statistically independent from the other parental behaviors in both males and females (J. K. Bester-Meredith and C. A. Marler, unpublished data). Thus, pup retrieval behavior may represent a different style of parental behavior. It is also possible that the different types of parental behavior may be controlled by slightly different mechanisms.

The effect of cross-fostering on resident–intruder aggression in California mouse pups is consistent with the proposed positive association between paternal retrievals and resident–intruder aggression. These pups displayed a decrease in resident–intruder aggression when raised by white-footed mice. To be consistent with the proposed relationship between retrievals and resident–intruder aggression, one would also have predicted an increase in resident–intruder aggression in the white-footed mouse pups

raised by the more paternal California mice. There was, however, no change in resident–intruder aggression in these cross-fostered white-footed mice. The answer to this seeming inconsistency may lie in a change in the retrieval behavior of California mouse fathers when raising white-footed mouse pups: the fathers decreased their rate of retrievals to a level similar to those typically displayed by white-footed mouse fathers. The characteristics of the white-footed mouse pups that caused this change in retrievals is unknown, but nonetheless resulted in a change in male California mouse retrieval behavior.

Within *Peromyscus*, we have identified two classes of parental behavior that are associated with two different types of aggression. Higher levels of the more nurturing maternal behaviors composing the HNGI score were associated with a decrease in neutral arena aggression, whereas higher levels of the "rougher" retrieval behavior by fathers was associated with increased resident–intruder aggression. We are currently in the process of manipulating paternal huddling and pup-grooming behaviors by castrating males. Preliminary evidence indicates that retrieval behavior is not influenced by castration ($t_8 = 0.51$, $p = 0.62$), so we are independently manipulating pup retrievals to examine the effects on resident–intruder aggression (K. Cravens, B. C. Trainor, and C. A. Marler, unpublished data).

In rodents, it appears that paternal behavior can have a significant impact on the behavior of male offspring, although further manipulations are needed. As more studies are performed with paternal rodents, we hope to identify more clearly the differential effects of maternal and paternal behavior and to continue to isolate specific paternal behaviors that influence offspring aggression.

2. Parent–Offspring Interactions: Nonhuman Primates

Few studies have examined the potential nongenomic effects of parental behavior on offspring aggression toward conspecifics in nonhuman primates. As a first approach, nonhuman primates have been removed from their mothers and raised in different environments, such as with peers present or absent. This manipulation in rhesus macaques, thought to provide a model of maternal neglect, resulted in increased aggression, accompanied by lower serotonin metabolites in a study by Higley et al. (1996b). In another study involving social separation, serotonin metabolite levels were higher in the peer-reared individuals than in mother-reared individuals (Higley et al., 1991). It is difficult to ascertain what component of the altered environment caused the changes in aggression and neurochemicals. However, it is possible that they are due to the presence or absence of the mother. When bonnet macaque (*Macaca radiata*)

mothers were exposed to a more unpredictable feeding regimen, there were lower levels of social interaction of any type between mothers and their offspring. These lower interaction levels were accompanied by decreased aggression and higher levels of serotonin metabolites (Andrews and Rosenblum, 1994; Rosenblum and Andrews, 1994; Coplan *et al.*, 1998). In a third species, the Japanese macaque (*Macaca fuscata*), neither maternal protectiveness nor maternal rejection was correlated with intensity or frequency of aggressive interactions (Schino *et al.*, 2001). The variability in the results obtained with these nonhuman primate models of maternal neglect suggests that the relationship between maternal behavior and offspring aggression needs to be further investigated. It is not clear whether the variation in results reflects species differences, parental effects, social interactions eliciting aggression, or other factors such as nutrition. There is also a need to examine whether offspring aggression is correlated with the different maternal styles of parenting that have been identified (e.g., Altmann, 1980; Fairbanks, 1996).

3. Parent–Offspring Interactions: Humans

The most extensive research on associations between parental and offspring behavior is found in humans, with the strongest emphasis on maternal behavior. There are some fairly consistent findings regarding the relationship between both child abuse and neglect with offspring aggression. Both child abuse and neglect are generally found to be associated with higher levels of aggression (reviewed by Widom, 2000). A number of researchers have reported a positive association between aggressive behavior in children and adults, and parental behaviors such as physical abuse, harsh discipline, restrictive discipline, and lack of warmth/rejection (e.g., Pettit and Bates, 1989; Weiss *et al.*, 1992; Travillion and Snyder, 1993; Dodge *et al.*, 1995; Scerbo and Kolko, 1995; Pettit *et al.*, 1996; Raine *et al.*, 1997; Schwartz *et al.*, 1997; Widom, 2000; Barnow *et al.*, 2001). In comparison, a more responsive or "warm" style of mothering can be associated with lower levels of aggression/misbehavior toward peers in boys (e.g., Chen and Rubin, 1994; Mize and Pettit, 1997). In the studies above, maternal and paternal effects appear similar in that warmth/affection and positive involvement with the child are negatively associated with misbehavior (including aggression). Studies have, however, revealed differences in the associations for fathers and mothers. For example, fathers, who responded to their children's negative affect, such as anger or pouting and whining during a physical play paradigm, with a similar negative affect response of their own, were more likely to have children that were physically and verbally aggressive toward peers, but this was not true of mothers (Carson and Parke, 1996). Other differences in

associations between the parenting styles of mothers and fathers and offspring behavior have been found, although not related to aggression (Kahen et al., 1994). Overall, negative associations are typically found between aggression and positive affect, whereas positive associations are found between aggression and harsh or restrictive discipline.

B. SUMMARY OF PARENT–OFFSPRING INTERACTIONS

The potential nongenomic effects of parental behavior on offspring aggression toward conspecifics have been the focus of considerable attention in humans and to a lesser extent in nonhuman primates and rodents. Thus far, it appears that *Peromyscus* may provide a rodent model system for examining parent and offspring interactions that are similar to humans. Unlike many other mammalian species but like humans, male California mice provide extensive paternal care toward offspring that may make critical contributions to the development of normal patterns of adult social behavior. Our *Peromyscus* studies suggest that, while human studies sometimes focus more on extreme parental behaviors such as child abuse or harsh discipline, more subtle parental behaviors may also influence offspring aggression. Retrievals, in particular, appear to represent a rougher type of parental care that may cause adaptive changes in aggression, and there may be equivalent behaviors with potent effects in humans that are less extreme than overt physical abuse. The advantage of this animal model system is that we can use an experimental approach to both behavior and the associated endocrine mechanisms. In *Peromyscus*, the rearing environment and neurochemicals, including AVP and T, can be manipulated under controlled conditions to pinpoint how specific factors influence offspring development. In both humans and *Peromyscus*, nurturing parental behaviors may produce effects on offspring aggression that are different from those produced by rougher forms of parental behavior. Manipulations in *Peromyscus* of parental behavior and other relevant variables, including AVP and T, may provide valuable insights into how human behavior is shaped by the conditions under which a child is raised.

V. ROLE OF PLASTICITY IN PATERNAL BEHAVIOR AND ARGININE VASOPRESSIN IN THE NONGENOMIC TRANSMISSION OF AGGRESSION ACROSS MULTIPLE GENERATIONS IN *Peromyscus*

We have described how *Peromyscus* fathers can potentially influence the aggressive behavior of their offspring, with a negative association between

paternal retrievals and resident–intruder aggression in the offspring. We have not yet asked, however, whether paternal behavior of the parents influences paternal behavior of their adult offspring. For aggression to pass on to future generations via nongenomic mechanisms (by behavioral processes), offspring displaying a change in resident–intruder aggression as adults must also alter their interactions with their own pups, that is, there is likely to be plasticity in their parental behavior. For example, cross-fostering from the less paternal meadow vole to the more paternal prairie vole increased paternal huddling behavior with pups (McGuire, 1988), although no changes in time spent in the nest occurred when white-footed mice and the more parental deer mice (*P. maniculatus*) were cross-fostered (Hawkins and Cranford, 1992). In this section we discuss evidence in *Peromyscus* that specific paternal traits may link generations through nongenomic effects on behavior.

An additional important question that we will be addressing concerns the physiological bases for the maintenance of these interactions across generations. Evidence for the effect of maternal traits on physiological traits of successive generations of offspring is more extensive than for paternal traits. Studies with female rats have found suites of neurochemical and behavioral traits linking generations through maternal effects (e.g., Francis *et al.*, 1999; Gonzalez *et al.*, 2001; Lovic *et al.*, 2001). In an interesting parallel to our studies, higher amounts of maternal licking/grooming behaviors alter the maternal behaviors of future generations (Caldji *et al.*, 1998; Francis *et al.*, 1999; Liu *et al.*, 1997; Boccia and Pederson, 2001). The hypothalamic–pituitary–adrenal (HPA) axis is a critical component in these cross-generational effects because individuals exposed to a higher level of maternal licking/grooming behavior are less fearful and have weaker HPA responses to stress (Liu *et al.*, 1997; Caldji *et al.*, 1998). Boccia and Pederson (2001) have also proposed plasticity in the density of oxytocin receptors as a potential mechanism. It will be valuable to examine whether huddling and grooming behaviors could also result in a decrease in neutral arena and/or resident–intruder aggression. In this section we discuss how a different physiological mechanism, AVP, may underlie the transfer of resident–intruder aggression and paternal behavior across generations in *Peromyscus* mice.

In California mice, paternal behavior seems to produce nongenomic effects on the behavior of future generations. We investigated whether cross-fostered California mice displayed any changes in paternal behavior in addition to the previously described aggressive behaviors. As adults, these male California mice raised by the less parental white-footed mice parents displayed a decrease in pup retrievals, although we found no changes in nest building or a composite score of time spent huddling,
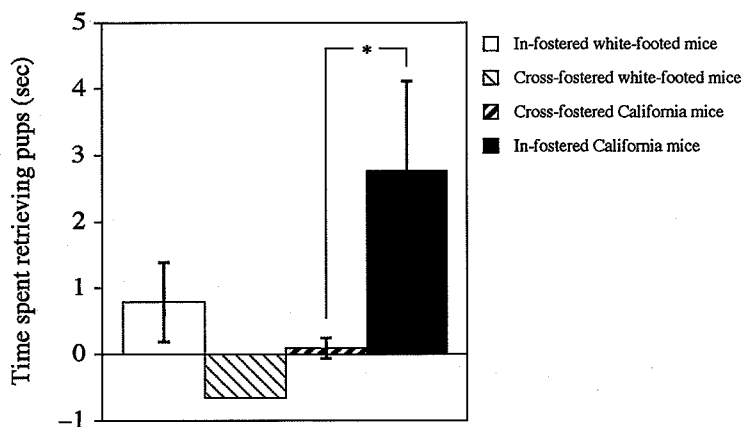
FIG. 9. Average time spent retrieving pups by male in-fostered and cross-fostered white-footed (*P. leucopus*) and California mice (*P. californicus*) (modified from J. K. Bester-Meredith and C. A. Marler, 2003). Data are presented as adjusted means ± standard errors. *$p < 0.05$. $n = 9$ per group for cross-fostered California mice, in-fostered California mice, and cross-fostered white-footed mice; $n = 4$ for in-fostered white-footed mice.

grooming, and in the nest (Fig. 9; J. K. Bester-Meredith and C. A. Marler, unpublished data).

Therefore, paternal retrievals appear to be especially important for transferring both paternal behavior and aggression traits across generations. Maternal retrievals may also prove to be important in influencing aggression, but we have yet to find a consistent effect (J. K. Bester-Meredith and C. A. Marler, unpublished data). Within house mice, a relationship between high levels of maternal aggression and maternal pup retrieval behavior has been found within a single generation, indicating that the two could be linked (Meek *et al.*, 2001), as they both serve to protect offspring. Our results provide new evidence that, at least in a highly biparental species, mothers may not be the only individuals that have nongenomic effects on the behavioral traits of their offspring. It appears that fathers play a larger role in offspring aggression than previously thought. The link between retrievals and aggression may prove to have interesting parallels with the positive relationship between harsher discipline/physical abuse and aggression described for humans. In rodents, the effect of natural variation in paternal retrievals on aggression may result in adaptive changes in aggression. It is also possible that this parallels the "less warm" parenting styles described earlier for humans.

There are numerous potential mechanisms through which aggression may be transmitted nongenetically from parents to offspring, but all, alone or together, must satisfy three critical components for a mechanism or

mechanisms involved in this transfer: the ability to influence paternal behavior, the ability to influence aggression, and, last, the potential for plasticity in response to the social environment. Currently, we have no evidence that T is involved in these cross-generational effects. Radio-immunoassay of plasma samples collected from California mice and white-footed mice that were not exposed to aggressive or sexual encounters revealed no differences in T levels between cross-fostered and control animals (Bester-Meredith and Marler, 2001). However, variation in these adult T levels may have varied depending on other factors such as social experience. The absence of differences between cross-fostered and control animals in adult T levels also does not exclude the possibility that T levels could have been critical during development in shaping future aggressive-ness. Because T can significantly influence paternal huddling and pup-grooming behaviors (Trainor and Marler, 2001), and we have evidence that these paternal behaviors are associated with variation in offspring neutral aggression, it is worth studying further the possibility that T is involved in some cross-generational effects.

Arginine vasopressin currently appears to be the best candidate for satisfying the requirements mentioned above. As described earlier, AVP is known to be positively associated with aggression and paternal care in rodents and is plastic in response to changing social conditions. In California mice, AVP was associated with variation in paternal care and was positively associated with resident–intruder aggression. In addition, also as described earlier, exposure to variation in paternal care also altered both AVP in the bed nucleus of the stria terminalis and resident–intruder aggression. We propose that AVP provides a link between aggression and paternal behavior so that these behaviors can be changed in concert and also be plastic in response to social interactions. Thus, AVP is currently a primary candidate for mediating this transfer of resident–intruder aggression and paternal care across generations.

VI. Summary of Nongenomic Transmission of Aggression and Paternal Behavior across Generations and the Role of Arginine Vasopressin

The last two sections suggest that both paternal and maternal effects may play a role in the nongenomic transfer of behavior. Evidence is building that parents can have a significant impact on the social behaviors of their offspring. Paternal effects may be particularly important in highly paternal species and may also play a significant role in the transfer of resident–intruder aggression across generations. As suggested by the data

in Fig. 9, paternal effects can potentially influence several future generations given the dramatic effect of cross-fostering on the subsequent retrieval behavior of offspring. In rodents and other species there may be a greater degree of responsiveness to the social environment during development than previously believed.

Arginine vasopressin is a likely candidate for part of the mechanism underlying this transfer of behaviors between generations because it has been positively linked with both aggression and paternal behavior and appears to be plastic in response to the social environment. The studies described in the last two sections provide additional support for a positive association between paternal behavior and resident–intruder aggression, as found in some of the T studies described earlier. The behavioral and neurochemical links further suggest that aggression and paternal care may interact across several generations.

VII. Conclusions

Our review reveals a number of important points about paternal behavior with respect to both behavior and physiology. First, there is a tendency to overestimate the negative effect of male aggression on the ability to provide paternal care and the negative relationship between T and paternal behavior. While it is often assumed that high levels of male aggression are incompatible with paternal behavior, we found several lines of evidence suggesting otherwise, including the research on the California mouse. There is considerable plasticity in the relationship between aggression and paternal behavior across species and, as in maternal aggression and maternal behavior, high levels of aggression can be expressed while individuals are also caring for young. It appears that in some species (and sexes), mating behavior, parental behavior, and aggression may coincide, in response to a variety of ecological pressures. For example, in some rodent species postpartum estrus may allow females to produce a larger number of litters during their lifetimes and allow these females to be pregnant with one litter while still nursing another litter. If a male of such a species provides parental care and defends a territory, as in the case of the California mouse and some fish species, then males must be able to express both aggression and paternal behavior in the same general time frame. This behavioral overlap could also occur in species in which there is a shorter breeding season and the behaviors need to be expressed in a shorter time frame, such as in Arctic species. This contrasts with the majority of avian studies that have involved species with longer breeding seasons. In these species, aggression and courtship may be temporally

separated from the expression of paternal behavior. Thus there may be environmental and social conditions that change the probability that aggression and paternal behavior will overlap and be positively associated.

Consistent with this plasticity in behavioral relationships, the relationship between T and paternal behavior can also vary across species. While there are several bird studies indicating a negative relationship between T and paternal care, there are also studies across taxa suggesting that T can also be positively associated with paternal behavior. In the example described above with Arctic avian species, where paternal care, aggression, and courtship may be more temporally compressed, these species must be capable of showing paternal behaviors in spite of high T levels. In the case of the California mice and some fish species among which the behaviors also overlap, T manipulations have demonstrated a positive association between T and paternal care. As more manipulative studies are conducted across species, this positive relationship between T and paternal care may prove to be important in more species, depending on a variety of costs and benefits of higher T levels that vary from species to species. However, as in the case of the behavioral associations, there may be general conditions that increase the probability that high T levels are compatible with paternal behavior, as well as cases where increased T can actually increase levels of paternal care in species with higher levels of temporal overlap between aggression, paternal care and courtship behavior.

We also described examples where T levels decreased, but nonetheless there was a positive causal relationship between T and paternal care in some species of fish and mammals. We have evidence that one mechanism that may allow this to occur, at least in the California mouse, is the conversion of T to estradiol via the enzyme aromatase (Trainor and Marler, 2002). Thus, plasticity in the relationship between T and paternal behavior could be partially controlled by levels of the aromatase enzyme in specific brain areas associated with paternal care. A drop in T during paternal care may therefore still be compatible with a positive relationship between T and paternal behavior because of changing levels of aromatase. The positive relationship between AVP and paternal behavior is also potentially compatible with this scenario. Aromatase may modulate effects of T on AVP, as T could increase AVP levels via conversion of T to estrogen (De Vries et al., 1994).

A second important point revealed by this review is that behavioral variation across species could also be influenced by the responsiveness or plasticity of the species to the social environment provided by the parents (and likely other individuals in the environment), and that includes both

maternal and paternal effects. The nongenomic effects across generations may be important only for some mammalian species. We found that cross-fostering between California mice and white-footed mice changed only resident–intruder aggression in California mice and only aggression in a neutral arena in white-footed mice. Further studies will be necessary to determine whether white-footed mice failed to display changes in resident–intruder aggression because they were not exposed to significant variation in paternal retrieval behavior or whether they are less responsive to variation in paternal behavior. Because male white-footed mice typically display less paternal care early during development, it is possible that offspring are less responsive to variation in paternal care. A point not mentioned earlier is that, while an AVP blocker significantly decreased resident–intruder aggression in California mice, it had no effect on resident–intruder aggression in white-footed mice (J. K. Bester-Meredith, P. Martin, and C. A. Marler, unpublished data). Thus, there may be variation across species regarding plasticity in offspring aggression in response to paternal behavior, as well as in the physiological mechanisms underlying the plasticity in behavior. There are so few studies examining how parental care in general can influence offspring aggression through nongenomic mechanisms that it is difficult to draw generalities from the studies presented. Nonetheless, studies in these *Peromyscus* species provide a starting point for examining how paternal behavior can influence aggression and paternal behavior of offspring. The power of the effect of paternal behavior on the aggression and paternal behavior of offspring may have been significantly underestimated. We have evidence that this effect could potentially continue on to future generations.

It is also worth noting that the type of paternal behavior studies we have described may be crucial for revealing paternal effects on the aggression of offspring. Retrievals are more rarely expressed than other parental behaviors, but may have a significant impact on resident–intruder aggression. In contrast, other paternal behaviors such as huddling and grooming may act to reduce aggression, although the type of aggression may differ. Studies into the physiological bases of these different types of paternal behavior (as well as different types of aggression) may help to reveal potential differences in the functions of these behaviors.

This review, combined with others such as that of Goodson and Bass (2001), continues to support the idea that AVP can be plastic in response to social conditions, both in developing individuals and in adults. Variation in certain types of aggression, such as resident–intruder aggression, may be strongly influenced by AVP. Plasticity in T levels during development could also contribute to variation seen in aggressive behavior, but more studies need to be performed in which the roles of the two hormones are

compared. It may be that AVP and T perform in concert to influence plasticity in aggressive behavior.

Finally, this review is a reminder of the plasticity in the relationship between behavior and hormonal mechanisms both within and across species, as discussed at the beginning of the chapter. Both the AVP and T studies provided examples of the dynamic variation that can exist in these relationships. The AVP and behavior studies demonstrated that the social environment can modify individual hormone levels and this can, in turn, modify that individual's behavior. The degree of plasticity for specific behaviors can vary even among closely related species, perhaps as a reflection of their behavioral ecology, including the degree to which they display territorial behavior and the timing of paternal behavior. Hormones may have evolved, in part, to link together certain behaviors in a variety of ways, influenced by such traits as the timing of different social behaviors. Our studies support the generality of concepts that relate the evolution of plasticity in behavior to hormone–behavior relationships across species.

VIII. SUMMARY

Aggression and paternal behavior can be linked in a variety of ways, and the relationship between hormones and these social behaviors may be equally variable. We have illustrated how high levels of aggression can be compatible with high levels of paternal care. Under such conditions, T may be positively associated with paternal care and aggression, even in species in which a decrease in T occurs with the onset of paternal care. Similar to T, AVP also can be positively associated with both aggression and paternal care. Individual variation in paternal care and aggression may be mediated by variation in AVP and T levels and receptors. This physiological variation could in turn be important for survival of offspring and also for shaping variation in paternal behavior and aggression of those offspring. Behavioral and endocrine changes may be passed on to multiple generations. The degree of plasticity in these relationships remains to be elucidated, but our results suggest that variation in AVP and T may be important for altering paternal and aggressive behaviors in response to the social environment.

References

Albers, H. E., Liou, S. Y., and Ferris, C. F. (1988). Testosterone alters the behavioral response of the medial preoptic–anterior hypothalamus to microinjection of arginine vasopressin in the hamster. *Brain Res.* **456,** 382–386.

Altmann, J. (1980). "Baboon Mothers and Infants." University of Chicago Press, Chicago, IL.

Andrews, M. W., and Rosenblum, L. A. (1994). The development of affiliative and agonistic social patterns in differentially reared monkeys. *Child. Dev.* **65,** 1398–1404.

Archer, J. (1988). "The Behavioral Biology of Aggression." Cambridge University Press, Cambridge.

Avise, J. C., Smith, M. H., and Selander, R. K. (1974). Biochemical polymorphism and systematics in the genus *Peromyscus.* VI. The *boylii* species group. *J. Mammal.* **55,** 751–763.

Baker, R. H. (1968). Habitats and distribution. *In* "Biology of *Peromyscus* (Rodentia)" (J. A. King, Ed.), pp. 98–126. American Society of Mammalogists, Stillwater, OK.

Ball, G. F. (1992). Endocrine mechanisms and the evolution of avian parental care. *In* "Proceeding of the XXth International Ornithology Congress," pp. 984–991.

Bamshad, M., Novak, M. A., and De Vries, G. J. (1993). Sex and species differences in the vasopressin innervation of sexually naïve and parental prairie voles, *Microtus ochrogaster* and meadow voles, *Microtus pennsylvanicus. J. Neuroendocrinol.* **5,** 247–255.

Bamshad, M., Novak, M. A., and De Vries, G. J. (1994). Cohabitation alters vasopressin innervation and paternal behavior in prairie voles (*Microtus ochrogaster*). *Physiol. Behav.* **56,** 751–758.

Barnow, S., Lucht, M., and Freyberger, H. J. (2001). Influence of punishment, emotional rejection, child abuse, and broken home on aggression in adolescence: An examination of aggressive adolescents in Germany. *Psychopathology* **34,** 167–173.

Beletsky, L. D., Gori, D. F., Freeman, S., and Wingfield, J. C. (1995). Testosterone and polygyny in birds. *In* "Current Ornithology" (D. M. Power, Ed.), Vol. 12, pp. 1–41. Plenum Press, New York.

Benus, R. F., and Röndigs, M. (1996). Patterns of maternal effort in mouse lines bidirectionally selected for aggression. *Anim. Behav.* **51,** 67–75.

Benus, R. F., and Röndigs, M. (1997). The influence of the postnatal maternal environment in accounting for differences in aggression and behavioural strategies in *Mus domesticus. Behaviour* **134,** 623–641.

Berg, S. J., and Wynne-Edwards, K. E. (2001). Changes in testosterone, cortisol, and estradiol levels in men becoming fathers. *Mayo Clin. Proc.* **76,** 582–592.

Bester-Meredith, J. K., and Marler, C. A. (2001). Vasopressin and aggression in cross-fostered California mice (*Peromyscus californicus*) and white-footed mice (*Peromyscus leucopus*). *Horm. Behav.* **40,** 51–64.

Bester-Meredith, J. K., and Marler, C. A. (2003). Vasopressin and the transmission of paternal behavior across generations in mated cross-fostered *Peromyscus* mice. *Behav. Neurosci.* (In press.)

Bester-Meredith, J. K., Young, L. J., and Marler, C. A. (1999). Species differences in paternal behavior and aggression in *Peromyscus* and their associations with vasopressin immunoreactivity and receptors. *Horm. Behav.* **36,** 25–38.

Birdsall, D. A., and Nash, D. (1973). Occurrence of multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). *Evolution* **27,** 106–110.

Bluthe, R. M., Gheusi, G., and Dantzer, R. (1993). Gonadal steroids influence the involvement of arginine vasopressin in social recognition in mice. *Psychoneuroendocrinology* **18,** 323–335.

Boccia, M. L., and Pederson, C. A. (2001). Brief vs. long maternal separations in infancy: Contrasting relationships with adult maternal behavior and lactation levels of aggression and anxiety. *Psychoneuroendocrinology* **26,** 657–672.

Borg, B. (1987). Stimulation of reproductive behaviour by aromatizable and nonaromatizable androgens in the male three-spined stickleback, *Gasterosteus aculeatus* L. *In* "Proceedings of the 5th Congress of European Ichthyologists" (S. O. K. Kullander and B. Fernholm, Eds.), pp. 269–271. Swedish Museum of Natural History, Stockholm, Sweden.

Borg, B., Schoonen, W. G. E. J., and Lambert, J. G. D. (1989). Steroid metabolism in the testes of the breeding and nonbreeding three-spined stickleback, *Gasterosteus aculeatus*. *Gen. Comp. Endocrinol.* **73,** 40–45.

Boyd, S. K. (1997). Brain vasotocin pathways and the control of sexual behaviors in the bullfrog. *Brain Res. Bull.* **44,** 345–350.

Brown, R. E. (1985). Hormones and paternal behavior in vertebrates. *Am. Zool.* **25,** 895–910.

Brown, R. E., Murdoch, T., Murphy, P. R., and Mojer, W. H. (1995). Hormonal responses of male gerbils to stimuli from their mate and pups. *Horm. Behav.* **29,** 474–491.

Buntin, J. D. (1996). Neural and hormonal control of parental behavior in birds. *In* "Advances in the Study of Behavior" (C. T. Snowdon and J. S. Rosenblatt, Eds.), Vol. 25, pp. 161–213. Academic Press, San Diego, CA.

Burmeister, S. S., and Wilczynski, W. (2001). Social context influences androgenic effects on calling in the green treefrog (*Hyla cinerea*). *Horm. Behav.* **40,** 550–558.

Caldji, C., Tannenbaum, B., Sharma, S., Francis, D., Plotsky, P. M., and Meaney, M. J. (1998). Maternal care during infancy regulates the development of neural systems mediating the expression of fearfulness in the rat. *Proc. Natl. Acad. Sci. USA* **95,** 5335–5340.

Caldwell, G. S., Glickman, S. E., and Smith, E. R. (1984). Seasonal aggression independent of seasonal testosterone in wood rats. *Proc. Natl. Acad. Sci. USA* **81,** 5255–5257.

Camazine, B., Garstka, W., Tokarz, R., and Crews, D. (1980). Effects of castration and androgen replacement on male courtship behavior in the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Horm. Behav.* **14,** 358–372.

Canoine, V., and Gwinner, E. (2002). Seasonal differences in the hormonal control of territorial aggression in free-living European stonechats. *Horm. Behav.* **41,** 1–8.

Cantoni, D., and Brown, R. E. (1997). Paternal investment and reproductive success in the California mouse, *Peromyscus californicus*. *Anim. Behav.* **54,** 377–386.

Carson, J. L., and Parke, R. D. (1996). Reciprocal negative affect in parent–child interactions and children's peer competency. *Child Dev.* **67,** 2217–2226.

Chen, X., and Rubin, K. H. (1994). Family conditions, parental acceptance, and social competence and aggression in Chinese children. *Soc. Dev.* **3,** 269–290.

Cho, M. M., De Vries, A. C., Williams, J. R., and Carter, C. S. (1999). The effects of oxytocin and vasopressin on partner preferences in male and female prairie voles (*Microtus ochrogaster*). *Behav. Neurosci.* **113,** 1071–1079.

Clark, M. M., and Galef, B. G., Jr. (1999). A testosterone-mediated trade-off between parental and sexual effort in male Mongolian gerbils (*Meriones unguiculatus*). *J. Comp. Psychol.* **113,** 388–395.

Clark, M. M., and Galef, B. G., Jr. (2000). Effects of experience on the parental responses of male Mongolian gerbils. *Dev. Psychobiol.* **36**, 177–185.

Clemens, L. G., Wee, B. E. F., Weaver, D. R., Roy, E. J., Goldman, B. D., and Rakerd, B. (1988). Retention of masculine sexual behavior following castration in male B6D2F1 mice. *Physiol. Behav.* **42**, 69–76.

Coccaro, E. F., Kavoussi, R. J., Hauger, R. L., Cooper, T. B., and Ferris, C. F. (1998). Cerebrospinal fluid vasopressin levels: Correlates with aggression and serotonin function in personality-disordered subjects. *Arch. Gen. Psychiatry* **55**, 708–714.

Collias, N. E. (1950). Hormones and behavior with special reference to birds and the mechanisms of hormone action. *In* "A Symposium on Steroid Hormones" (E. S. Gordon, Ed.), pp. 277–329. University of Wisconsin Press (Business Press), Lancaster, PA.

Colvin, D. V. (1973). Agonistic behaviour in males of five species of voles *Microtus. Anim. Behav.* **21**, 471–480.

Compaan, J. C., Buijs, R. M., Pool, C. W., de Ruiter, A. J. H., and Koolhaas, J. M. (1993). Differential lateral septal vasopressin innervation in aggressive and nonaggressive male mice. *Brain Res. Bull.* **30**, 1–6.

Coplan, J. D., Trost, R. C., Owens, M. J., Cooper, T. B., Gorman, J. M., Nemeroff, C. B., and Rosenblum, L. A. (1998). Cerebrospinal fluid concentrations of somatostatin and biogenic amines in grown primates reared by mothers exposed to manipulated foraging conditions. *Arch. Gen. Psychiatry* **55**, 473–477.

Crews, D. (1983). Diversity of hormone-behavior controlling mechanisms. *BioScience.* **33**, 545–566.

Crews, D. (1984). Gamete production, sex hormone secretion, and mating behavior uncoupled. *Horm. Behav.* **18**, 22–28.

Crews, D., and Moore, M. C. (1986). Evolution of mechanisms controlling mating behavior. *Science* **231**, 121–125.

Crews, D., Camazine, B., Diamond, M., Mason, R., Tokarz, R. R., and Garstka, W. R. (1984). Hormonal independence of courtship behavior in the male garter snake (*Thamnophis sirtalis parietalis*). *Horm. Behav.* **18**, 29–41.

Davis, E. S., and Marler, C. A. (2003). Progesterone challenge in female *Peromyscus* mice. *Horm. Behav.* (In press.)

Delville, Y., Mansour, K. M., and Ferris, C. F. (1996). Testosterone facilitates aggression by modulating vasopressin receptors in the hypothalamus. *Physiol. Behav.* **60**, 25–29.

Delville, Y., Melloni, R. H., Jr., and Ferris, C. F. (1998). Behavioral and neurobiological consequences of social subjugation during puberty in golden hamsters. *J. Neurosci.* **18**, 2667–2672.

Delville, Y., De Vries, G. J., and Ferris, C. F. (2000). Neural connections of the anterior hypothalamus and agonistic behavior in golden hamsters. *Brain Behav. Evol.* **55**, 53–76.

Demas, G. E., and Nelson, R. J. (1998). Short-day enhancement of immune function is independent of steroid hormones in deer mice (*Peromyscus maniculatus*). *J. Comp. Physiol. B* **168**, 419–426.

Demas, G. E., Moffatt, C. A., Drazen, D. L., and Nelson, R. J. (1999). Castration does not inhibit aggressive behavior in adult male prairie voles (*Microtus ochrogaster*). *Physiol. Behav.* **66**, 59–62.

De Ridder, E., Pinxten, R., and Eens, M. (2000). Experimental evidence of a testosterone-induced shift from paternal to mating behaviour in a facultatively polygynous songbird. *Behav. Ecol. Sociobiol.* **49**, 24–30.

De Vries, G. J., and Boyle, P. A. (1998). Double duty for sex differences in the brain. *Behav. Brain Res.* **92**, 205–213.

De Vries, G. J., and Miller, M. A. (1998). Anatomy and function of extrahypothalamic vasopressin systems in the brain. *Prog. Brain Res.* **119,** 3–20.

De Vries, G. J., Wang, Z., Bullock, N. A., and Numan, S. (1994). Sex differences in the effects of testosterone and its metabolites on vasopressin messenger RNA levels in the bed nucleus of the stria terminalis of rats. *J. Neurosci.* **14,** 1789–1794.

Dewsbury, D. A. (1983). A comparative study of rodent social behavior in a seminatural enclosure. *Aggress. Behav.* **9,** 207–215.

Dixson, A. F., and George, L. (1982). Prolactin and parental behaviour in a male new world primate. *Nature* **299,** 551–553.

Dodge, K. A., Pettit, G. S., Bates, J. E., and Valente, E. (1995). Social information-processing patterns partially mediate the effect of early physical abuse on later conduct problems. *J. Abnorm. Psychol.* **104,** 632–643.

Dudley, D. (1974a). Contributions of paternal care to the growth and development of the young in *Peromyscus californicus. Behav. Biol.* **11,** 155–166.

Dudley, D. (1974b). Paternal behavior in the California mouse, *Peromyscus californicus. Behav. Biol.* **11,** 247–252.

Emerson, S. B., and Hess, D. L. (1996). The role of androgens in opportunistic breeding, tropical frogs. *Gen. Comp. Endocrinol.* **103,** 220–230.

Emerson, S. B., Rowsemitt, C. N., and Hess, D. L. (1993). Androgen levels in a Bornean voiceless frog, *Rana blythii. Can. J. Zool.* **71,** 196–203.

Everts, H. G. J., De Ruiter, A. J. H., and Koolhaas, J. M. (1997). Differential lateral septal vasopressin in wild-type rats: Correlation with aggression. *Horm. Behav.* **31,** 136–144.

Fairbanks, L. A. (1996). Individual differences in maternal style: Causes and consequences for mothers and offspring. *In* "Advances in the Study of Behavior," Vol. 25 (C. T. Snowdon and J. S. Rosenblatt, Eds.), pp. 579–611. Academic Press, San Diego, CA.

Felton, T. M., Linton, L., Rosenblatt, J. S., and Morrell, J. I. (1998). Intact neurons of the lateral habenular nucleus are necessary for the nonhormonal, pup-mediated display of maternal behavior in sensitized virgin female rats. *Behav. Neurosci.* **112,** 1458–1465.

Ferris, C. (1992). Role of vasopressin in aggressive and dominant/subordinate behaviors. *Ann. N. Y. Acad. Sci.* **652,** 212–226.

Ferris, C. F., and Delville, Y. (1994). Vasopressin and serotonin interactions in the control of agonistic behavior. *Psychoneuroendocrinology* **19,** 593–601.

Ferris, C. F., and Potegal, M. (1988). Vasopressin receptor blockade in the anterior hypothalamus suppresses aggression in hamsters. *Physiol. Behav.* **44,** 235–239.

Ferris, C. F., Albers, H. E., Wesolowski, S. M., Goldman, B. D., and Luman, S. E. (1984). Vasopressin injected into the hypothalamus triggers a stereotypic behavior in golden hamsters. *Science* **224,** 521–523.

Ferris, C. F., Meenan, D. M., Axelson, J. F., and Albers, H. E. (1986). A vasopressin antagonist can reverse dominant/subordinate behavior in hamsters. *Physiol. Behav.* **38,** 135–138.

Ferris, C. F., Singer, E. A., Meenan, D. M., and Albers, H. E. (1988). Inhibition of vasopressin-stimulated flank marking behavior by V1-receptor antagonists. *Eur. J. Pharmacol.* **154,** 153–159.

Ferris, C. F., Axelson, J. F., Martin, A. M., and Roberge, L. F. (1989). Vasopressin immunoreactivity in the anterior hypothalamus is altered during the establishment of dominant/subordinate relationships between hamsters. *Neuroscience* **29,** 675–683.

Ferris, C. F., Delville, Y., Grozonka, Z., Luber-Narod, J., and Insel, T. R. (1993). An iodinated vasopressin (V1) antagonist blocks flank marking and selectively labels neural binding sites in golden hamsters. *Physiol. Behav.* **54,** 737–747.

Ferris, C. F., Melloni, R. H., Koppel, G., Perry, K. W., Fuller, R. W., and Delville, Y. (1997). Vasopressin/serotonin interactions in the anterior hypothalamus control aggressive behavior in golden hamsters. *J. Neurosci.* **17,** 4331–4340.

Foltz, D. W. (1981). Genetic evidence for long-term monogamy in a small rodent, *Peromyscus polionotus. Am. Nat.* **117,** 665–675.

Francis, D., Diorio, J., Liu, D., and Meaney, M. J. (1999). Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science* **286,** 1155–1158.

Gammie, S. C., and Nelson, R. J. (1999). Maternal aggression is reduced in neuronal nitric oxide synthase-deficient mice. *J. Neurosci.* **19,** 8027–8035.

Garland, M., and Svare, B. (1988). Suckling stimulation modulates the maintenance of postpartum aggression in mice. *Physiol. Behav.* **44,** 301–305.

Garstka, W. R., Camazine, B., and Crews, D. (1982). Interaction of behavior and physiology during the annual reproductive cycle of the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Herpetology* **38,** 104–123.

Getz, L. L. (1962). Aggressive behavior in meadow and prairie voles. *J. Mammal.* **43,** 351–358.

Getz, L. L., Carter, C. S., and Gavish, L. (1981). The mating system of the prairie vole, *Microtus ochrogaster*: Field and laboratory evidence for pair-bonding. *Behav. Ecol. Sociobiol.* **8,** 189–194.

Getz, L. L., McGuire, B., Hofmann, J., Pizzuto, T., and Frase, B. (1990). Social organization and mating system of the prairie vole, *Microtus ochrogaster. In* "Social Systems and Population Cycles in Voles" (R. H. Tamarin, R. S. Ostfeld, S. R. Pugh, and G. Bujalska, Eds.), pp. 69–80. Birkhauser Verlag, Basel, Switzerland.

Gleason, P. E., Michael, S. D., and Christian, J. J. (1981). Prolactin-induced aggression in female *Peromyscus leucopus. Behav. Neural Biol.* **33,** 243–248.

Gonzalez, A., Lovic, V., Ward, G. R., Wainwright, P. E., and Fleming, A. S. (2001). Intergenerational effects of complete maternal deprivation and replacement stimulation on maternal behavior and emotionality in female rats. *Dev. Psychobiol.* **38,** 11–32.

Goodson, J. L., and Bass, A. H. (2001). Social behavior functions and related anatomical characteristics of vasotocin/vasopressin systems in vertebrates. *Brain Res. Brain Res. Rev.* **35,** 246–265.

Gross, M. R. (1984). Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. *In* "Fish Reproduction: Strategies and Tactics" (G. Potts and R. Wootton, Eds.), pp. 55–75. Academic Press, New York.

Gross, M. R., and MacMillan, A. M. (1981). Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). *Behav. Ecol. Sociobiol.* **8,** 163–174.

Gubernick, D. J. (1988). Reproduction in the California mouse, *Peromyscus californicus. J. Mammal.* **69,** 857–860.

Gubernick, D. J., and Alberts, J. R. (1987a). "Resource" exchange in the biparental California mouse (*Peromyscus californicus*): Water transfer from pups to parents. *J. Comp. Psychol.* **101,** 328–334.

Gubernick, D. J., and Alberts, J. R. (1987b). The biparental care system of the California mouse, *Peromyscus californicus. J. Comp. Psychol.* **101,** 169–177.

Gubernick, D. J., and Nelson, R. J. (1989). Prolactin and paternal behavior in the biparental California mouse, *Peromyscus californicus. Horm. Behav.* **23,** 203–210.

Gubernick, D. J., and Teferi, T. (2000). Adaptive significance of male parental care in a monogamous mammal. *Proc. R. Soc. Lond. B Biol. Sci.* **267,** 147–150.

Gubernick, D. J., Wright, S. L., and Brown, R. E. (1993). The significance of father's presence for offspring survival in the monogamous California mouse, *Peromyscus californicus. Anim. Behav.* **46,** 539–546.

Hau, M., Wikelski, M., Soma, K. K., and Wingfield, J. C. (2000). Testosterone and year-round territorial aggression in a tropical bird. *Gen. Comp. Endocrinol.* **117,** 20–33.

Hawkins, L. K., and Cranford, J. A. (1992). Long-term effects of intraspecific and interspecific cross-fostering on two species of *Peromyscus. J. Mammal.* **73,** 802–807.

Hegner, R. E., and Wingfield, J. C. (1987). Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* **104,** 462–469.

Higley, J. D., Suomi, S. J., and Linnoila, M. (1991). CSF monoamine metabolite concentrations vary according to age, rearing, and sex, and are influenced by the stressor of social separation in rhesus monkeys. *Psychopharmacology.* **103,** 551–556.

Higley, J. D., Mehlman, P. T., Poland, R. E., Taub, D. M., Vickers, J., Suomi, S. J., and Linnoila, M. (1996a). CSF testosterone and 5-HIAA correlate with different types of aggressive behaviors. *Biol. Psychol.* **40,** 1067–1082.

Higley, J. D., Suomi, S. J., and Linnoila, M. A. (1996b). Nonhuman primate model of type II alcoholism? 2. Diminished social competence and excessive aggression. *Alcohol. Clin. Exp. Res.* **20,** 643–650.

Hofmann, J. E., Getz, L. L., and Klatt, B. J. (1982). Levels of male aggressiveness in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus. Can. J. Zool.* **60,** 898–912.

Houck, L. D., and Woodley, S. K. (1995). Field studies of steroid hormones and male reproductive behavior in amphibians. *In* "Amphibian Biology" (H. Heatwole and B. K. Sullivan, Eds.), pp. 677–703. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.

Hunt, K. E., Hahn, T. P., and Wingfield, J. C. (1997). Testosterone implants increase song but not aggression in male Lapland longspurs. *Anim. Behav.* **54,** 1177–1192.

Hunt, K. E., Hahn, T. P., and Wingfield, J. C. (1999). Endocrine influences on parental care during a short breeding season: Testosterone and male parental care in Lapland longspurs (*Calcarius lapponicus*). *Behav. Ecol. Sociobiol.* **45,** 360–369.

Insel, T. R., Wang, Z. X., and Ferris, C. F. (1994). Patterns of brain vasopressin receptor distribution associated with social organization in microtine rodents. *J. Neurosci.* **14,** 5381–5392.

Johns, L. S., and Liley, N. R. (1970). The effects of gonadectomy and testosterone treatment on the reproductive behavior of the male blue gourami *Trichogaster trichopterus. Can. J. Zool.* **48,** 977–987.

Jones, J. S., and Wynne-Edwards, K. E. (2000). Paternal hamsters mechanically assist the delivery, consume amniotic fluid and placenta, remove fetal membranes, and provide parental care during the birth process. *Horm. Behav.* **37,** 116–125.

Kahen, V., Katz, L. F., and Gottman, J. M. (1994). Linkages between parent–child interaction and conversations of friends. *Soc. Dev.* **3,** 238–254.

Kass, D. H., Berger, F. G., and Dawson, W. D. (1992). The evolution of coexisting highly divergent LINE-1 subfamilies within the rodent genus *Peromyscus. J. Mol. Evol.* **35,** 472–485.

Ketterson, E. D., and Nolan, V., Jr. (1994). Male parental behavior in birds. *Annu. Rev. Ecol. Syst.* **25,** 601–628.

Ketterson, E. D., Nolan, V., Jr., Wolf, L., and Ziegenfus, C. (1992). Testosterone and avian life histories: Effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *Am. Nat.* **140,** 981–999.

Kindler, P. M., Philipp, D. P., Gross, M. R., and Bahr, J. M. (1989). Serum 11-ketotestosterone and testosterone concentrations associated with reproduction in male bluegill (*Lepomis macrochirus*: Centrarchidae). *Gen. Comp. Endocrinol.* **75,** 446–453.

Kindler, P. M., Bahr, J. M., and Philipp, D. P. (1991). The effects of exogenous 11-ketotestosterone, testosterone, and cyproterone acetate on prespawning and parental care behaviors of male bluegill. *Horm. Behav.* **25,** 410–423.

Kirkpatrick, B., Kim, J. W., and Insel, T. R. (1994a). Limbic system *fos* expression associated with paternal behavior. *Brain Res.* **658,** 112–118.

Kirkpatrick, B., Williams, J. R., Slotnick, B. M., and Carter, C. S. (1994b). Olfactory bulbectomy decreases social behavior in male prairie voles (*M. ochrogaster*). *Physiol. Behav.* **55,** 885–889.

Kishida, M., and Specker, J. L. (2000). Paternal mouthbrooding in the black-chinned tilapia, *Sarotherodon melanotheron* (Pisces: Cichlidae): Changes in gonadal steroids and potential for vitellogenin transfer to larvae. *Horm. Behav.* **37,** 40–48.

Klein, S. L., and Nelson, R. J. (1997). Sex differences in immunocompetence differ between two *Peromyscus* species. *Am. J. Physiol.* **273,** R655–R660.

Klomberg, K. F., and Marler, C. A. (2000). The neuropeptide arginine vasotocin alters male call characteristics involved in social interactions in the grey treefrog, *Hyla versicolor.* *Anim. Behav.* **59,** 807–812.

Knapp, R., Wingfield, J. C., and Bass, A. H. (1999). Steroid hormones and paternal care in the plainfin midshipman fish (*Porichthys notatus*). *Horm. Behav.* **35,** 81–89.

Koolhaas, J. M., van den Brink, T. H. C., Roozendaal, B., and Boorsma, F. (1990). Medial amygdala and aggressive behavior: Interaction between testosterone and vasopressin. *Aggress. Behav.* **16,** 223–229.

Koolhaas, J. M., Everts, H., de Ruiter, A. J. H., de Boer, S. F., and Bohus, B. (1998). Coping with stress in rats and mice: Differential peptidergic modulation of the amygdala–lateral septum complex. *Prog. Brain Res.* **119,** 437–448.

Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., Sharma, S., Pearson, D., Plotsky, P. M., and Meaney, M. J. (1997). Maternal care, hippocampal glucocorticoid receptors, and hypothalamic–pituitary–adrenal responses to stress. *Science* **277,** 1659–1662.

Liu, Y., Curtis, J. T., and Wang, Z. X. (2001). Vasopressin in the lateral septum regulates pair bond formation in male prairie voles. (*Microtus ochrogaster*). *Behav. Neurosci.* **115,** 910–919.

Lonstein, J. S., and De Vries, G. J. (1999). Sex differences in the parental behavior of adult virgin prairie voles: Independence from gonadal hormones and vasopressin. *J. Neuroendocrinol.* **11,** 441–449.

Lonstein, J. S., Rood, B. D., and De Vries, G. J. (2002). Parental responsiveness is feminized after neonatal castration in virgin male prairie voles, but is not masculinized by perinatal testosterone in virgin females. *Horm. Behav.* **41,** 80–87.

Lovic, V., Gonzalez, A., and Fleming, A. S. (2001). Maternally separated rats show deficits in maternal care in adulthood. *Dev. Psychobiol.* **39,** 19–33.

Lynn, S. E., Hayward, L. S., Benowitz-Fredericks, Z. M., and Wingfield, J. C. (2002). Behavioural insensitivity to supplementary testosterone during the parental phase in the chestnut-collared longspur, *Calcarius ornatus. Anim. Behav.* **63,** 795–803.

Margulis, S. W. (1998). Relationships among parental inbreeding, parental behaviour and offspring viability in old field mice. *Anim. Behav.* **55,** 427–438.

Marler, C. A., and Ryan, M. (1996). Energetic constraints and steroid hormone correlates of male calling behaviour in the tungara frog. *J. Zool. Lond.* **240,** 397–409.

Mayer, A. D., Monroy, M. A., and Rosenblatt, J. S. (1990). Prolonged estrogen–progesterone treatment of nonpregnant ovariectomized rats: Factors stimulating home-cage and maternal aggression and short-latency maternal behavior. *Horm. Behav.* **24,** 342–364.

Mazur, A., and Booth, A. (1998). Testosterone and dominance in men. *Behav. Brain Sci.* **21,** 353–363 [discussion, pp. 363–397].

Mazur, A., and Lamb, T. A. (1980). Testosterone, status and mood in human males. *Horm. Behav.* **14,** 236–246.

McCarty, R., and Southwick, C. H. (1977). Paternal care and the development of behaviour in the southern grasshopper mouse, *Onychomys torridus. Behav. Biol.* **19,** 476–490.

McGuire, B. (1988). Effects of cross-fostering on parental behavior of meadow voles (*Microtus pennsylvanicus*). *J. Mammal.* **69,** 332–341.

McInroy, J. K. E., Brousmiche, D. G., and Wynne-Edwards, K. E. (2000). Fathers, fat, and maternal energetics in a biparental hamster: Paternal presence determines the outcome of a current reproductive effort and adipose tissue limits subsequent reproductive effort. *Horm. Behav.* **37,** 399–409.

Meek, L. R., Dittel, P. L., Sheehan, M. C., Chan, J. Y., and Kjolhaug, S. R. (2001). Effects of stress during pregnancy on maternal behavior in mice. *Physiol. Behav.* **72,** 473–479.

Mendl, M., and Paul, E. S. (1990). Parental care, sibling relationships and the development of aggressive behaviour in two lines of wild house mice. *Behaviour* **116,** 10–41.

Mendonça, M. T., Chernetsky, S. D., Nester, K. E., and Gardner, G. L. (1996). Effects of gonadal sex steroids on sexual behavior in the big brown bat, *Eptesicus fuscus,* upon arousal from hibernation. *Horm. Behav.* **30,** 153–161.

Metzgar, L. H. (1971). Behavioral population regulation in the woodmouse, *Peromyscus leucopus. Am. Midl. Nat.* **86,** 434–448.

Mize, J., and Pettit, G. S. (1997). Mothers' social coaching, mother–child relationship style, and children's peer competence: Is the medium the message? *Child Dev.* **68,** 312–332.

Moore, C. L. (1984). Maternal contributions to the development of masculine sexual behavior in laboratory rats. *Dev. Psychobiol.* **17,** 347–356.

Moore, C. L. (1992). The role of maternal stimulation in the development of sexual behavior and its neural basis. *Ann. N. Y. Acad. Sci.* **662,** 160–177.

Moreno, J., Veiga, J. P., Cordero, P. J., and Minguez, E. (1999). Effects of paternal care on reproductive success in the polygynous spotless starling *Sturnus unicolor. Behav. Ecol. Sociobiol.* **47,** 47–53.

Mugford, R. A., and Nowell, N. W. (1972). Paternal stimulation during infancy: Effects upon aggression and open-field performance of mice. *J. Comp. Physiol. Psychol.* **79,** 30–36.

Nelson, R. J. (2000). "An Introduction to Behavioral Neuroendocrinology." Sinauer Associates, Sunderland, MA.

Nunes, S., Fite, J. E., and French, J. A. (2000). Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Anim. Behav.* **60,** 857–865.

Nunes, S., Fite, J. E., Patera, K. J., and French, J. A. (2001). Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets (*Callithrix kuhlii*). *Horm. Behav.* **39,** 70–82.

Oliveira, R. F., Almada, V. C., Goncalves, E. J., Forsgren, E., and Canario, A. V. M. (2001). Androgen levels and social interactions in breeding males of the peacock blenny. *J. Fish Biol.* **58,** 897–908.

Parkening, T. A., and Collins, T. J. (1991). Reproduction, pregnancy, and circulating reproductive hormones in the lactating Siberian hamster (*Phodopus sungorus*). *J. Exp. Zool.* **257,** 401–407.

Parker, K. J., and Lee, T. M. (2001). Central vasopressin administration regulates the onset of facultative paternal behavior in *Microtus pennsylvanicus* (meadow voles). *Horm. Behav.* **39,** 285–294.

Parker, K. J., Kinney, L. F., Phillips, K. M., and Lee, T. M. (2001). Paternal behavior is associated with central neurohormone receptor binding patterns in meadow voles (*Microtus pennsylvanicus*). *Behav. Neurosci.* **115,** 1341–1348.

Pettit, G. S., and Bates, J. E. (1989). Family interaction patterns and children's behavior problems from infancy to four years. *Dev. Psychol.* **55,** 729–739.

Pettit, G. S., Clawson, M. A., Dodge, K. A., and Bates, J. E. (1996). Stability and change in peer-rejected status: The role of child behavior, parenting, and family ecology. *Merrill-Palmer Q* **42,** 267–294.

Pitkow, L. J., Sharer, C. A., Ren, X., Insel, T. R., Terwilliger, E. F., and Young, L. J. (2001). Facilitation of affiliation and pair-bond formation by vasopressin receptor gene transfer into the ventral forebrain of a monogamous vole. *J. Neurosci.* **21,** 7392–7396.

Potegal, M., and Ferris, C. F. (1990). Intraspecific aggression in male hamsters is inhibited by intrahypothalamic vasopressin-receptor antagonist. *Aggress. Behav.* **15,** 311–320.

Raine, A., Brennan, P., and Mednick, S. A. (1997). Interaction between birth complications and early maternal rejection in predisposing individuals to adult violence: Specificity to serious, early-onset violence. *Am. J. Psychiatry.* **154,** 1265–1271.

Reburn, C. J., and Wynne-Edwards, K. E. (1999). Hormonal changes in males of a naturally biparental and a uniparental mammal. *Horm. Behav.* **35,** 163–176.

Ribble, D. O. (1991). The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* **29,** 161–166.

Ribble, D. O., and Salvioni, M. (1990). Social organization and nest co-occupancy in *Peromyscus californicus*, a monogamous rodent. *Behav. Ecol. Sociobiol.* **26,** 9–16.

Richmond, M., and Conaway, C. H. (1969). Management, breeding, and reproductive performance of the vole, *Microtus ochrogaster*, in a laboratory colony. *Lab. Anim. Care* **19,** 80–87.

Roberts, R. L., Zullo, A., Gustafson, E. A., and Carter, C. S. (1996). Perinatal steroid treatments alter alloparental and affiliative behavior in prairie voles. *Horm. Behav.* **30,** 576–582.

Rosenblatt, J. S., Factor, E. M., and Mayer, A. D. (1994). Relationship between maternal aggression and paternal care in the rat. *Aggress. Behav.* **20,** 243–255.

Rosenblum, L. A., and Andrews, M. W. (1994). Influences of environmental demand on maternal behavior and infant development. *Acta Paediatr. Suppl.* **397,** 57–63.

Saino, N., and Møller, A. P. (1995). Testosterone-induced depression of male parental behavior in the barn swallow: Female compensation and effects on seasonal fitness. *Behav. Ecol. Sociobiol.* **36,** 151–157.

Scerbo, A. S., and Kolko, D. J. (1995). Child physical abuse and aggression: Preliminary findings on the role of internalizing problems. *J. Am. Acad. Child Adolesc. Psychol.* **34,** 1060–1066.

Schino, G., Speranza, L., and Troisi, A. (2001). Early maternal rejection and later social anxiety in juvenile and adult Japanese macaques. *Dev. Psychobiol.* **38,** 186–190.

Schug, M. D., Vessey, S. H., and Underwood, E. M. (1992). Paternal behavior in a natural population of white-footed mice (*Peromyscus leucopus*). *Am. Midl. Nat.* **127,** 373–380.

Schwartz, D., Dodge, K. A., Pettit, G. S., and Bates, J. E. (1997). The early socialization of aggressive victims of bullying. *Child Dev.* **68,** 665–675.

Semsar, K., Klomberg, K., and Marler, C. A. (1998). Arginine vasotocin increases calling-site acquisition by nonresident male grey treefrogs. *Anim. Behav.* **56,** 983–987.

Semsar, K., Kandel, F. L., and Godwin, J. (2001). Manipulations of the AVT system shift social status and related courtship and aggressive behavior in the bluehead wrasse. *Horm. Behav.* **40,** 21–31.

Sikkel, P. C. (1993). Changes in plasma androgen levels associated with changes in male reproductive behavior in a brood cycling marine fish. *Gen. Comp. Endocrinol.* **89,** 229–237.

Smith, C. J., and Haley, S. R. (1988). Steroid profiles of the female tilapia, *Oreochromis mossambicus*, and correlation with oocyte growth and mouthbrooding behavior. *Gen. Comp. Endocrinol.* **69,** 88–98.

Smith, R. J. F. (1969). Control of prespawning behavior of sunfish (*Lepomis gibbosus* and *L. megalotis*). I. Gonadal androgen. *Anim. Behav.* **18,** 575–587.

Smith, R. J. F., and Hoar, W. S. (1967). The effects of prolactin and testosterone on the parental behaviour of the male stickleback *Gasterosteus aculeatus. Anim. Behav.* **15,** 342–352.

Snowdon, C. T. (1996). Infant care in cooperatively breeding species. *In* "Advances in the Study of Behavior," Vol. 25 (C. T. Snowdon and J. S. Rosenblatt, Eds.), pp. 643–689. Academic Press, San Diego, CA.

Solis, R., and Penna, M. (1997). Testosterone levels and evoked vocal responses in a natural population of the frog *Batrachyla taeniata. Horm. Behav.* **31,** 101–109.

Specker, J. L., and Kishida, M. (2000). Mouthbrooding in the black-chinned tilapia, *Sarotherodon melanotheron* (Pisces: Cichlidae): The presence of eggs reduces androgen and estradiol levels during paternal and maternal parental behavior. *Horm. Behav.* **38,** 44–51.

Stangl, F. B., Jr., and Baker, R. J. (1984). Evolutionary relationships in *Peromyscus*: Congruence in chromosomal, genetic and classical data sets. *J. Mammal.* **65,** 643–654.

Stern, J. M., and Lehrman, D. S. (1969). Role of testosterone in progesterone-induced incubation behaviour in male ring doves (*Streptopelia risoria*). *J. Endocrinol.* **44,** 13–22.

Storey, A. E., Walsh, C. J., Quinton, R. L., and Wynne-Edwards, K. E. (2000). Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evol. Hum. Behav.* **21,** 79–95.

Stribley, J. M., and Carter, C. S. (1999). Developmental exposure to vasopressin increases aggression in adult prairie voles. *Proc. Natl. Acad. Sci. USA* **96,** 12601–12604.

Sullivan, J., Markert, J. A., and Kilpatrick, C. W. (1997). Phylogeography and molecular systematics of the *Peromyscus aztecus* species group (Rodentia: Muridae) inferred using parsimony and likelihood. *Syst. Biol.* **46,** 426–440.

Svare, B., and Gandelman, R. (1976). Postpartum aggression in mice: The influence of suckling stimulation. *Horm. Behav.* **7,** 407–416.

Tito, M. B., Hoover, M. A., Mingo, A. M., and Boyd, S. K. (1999). Vasotocin maintains multiple call types in the gray treefrog, *Hyla versicolor. Horm. Behav.* **36,** 166–175.

Townsend, D. S., and Moger, W. H. (1987). Plasma androgen levels during male parental care in a tropical frog (*Eleutherodactylus*). *Horm. Behav.* **21,** 93–99.

Townsend, D. S., Stewart, M. M., and Pough, F. H. (1984). Male parental care and its adaptive significance in a neotropical frog. *Anim. Behav.* **32,** 421–431.

Townsend, D. S., Palmer, B., and Guillette, L. J., Jr. (1991). The lack of influence of exogenous testosterone on male parental behavior in a neotropical frog (*Eleutherodactylus*): A field experiment. *Horm. Behav.* **25,** 313–322.

Trainor, B. C., and Marler, C. A. (2001). Testosterone, paternal behavior, and aggression in the monogamous California mouse (*Peromsycus californicus*). *Horm. Behav.* **40,** 32–42.

Trainor, B. C., and Marler, C. A. (2002). Testosterone promotes paternal behaviour in a monogamous mammal via conversion to oestrogen. *Proc. R. Soc. Lond. B Biol. Sci.* **269,** 823–829.

Travillion, K., and Snyder, J. (1993). The role of maternal discipline and involvement in peer rejection and neglect. *J. Appl. Dev. Psychol.* **14,** 37–57.

Trewavas, E. (1983). "Tilapine fishes of the genera *Sardotherodon, Oreochromis* and *Danakilia*." Cornell University Press, Ithaca, NY.

Tyron, P. R., and MacLean, S. F. (1980). Use of space by Lapland longspurs breeding in arctic Alaska. *Auk* **97,** 509–520.

Van Duyse, E., Pinxten, R., and Eens, M. (2000). Does testosterone affect the trade-off between investment in sexual/territorial behaviour and parental care in male great tits? *Behaviour* **137,** 1503–1515.

Viau, V., Chu, A., Soriano, L., and Dallman, M. F. (1999). Independent and overlapping effects of corticosterone and testosterone on corticotropin-releasing hormone and arginine vasopressin mRNA expression in the paraventricular nucleus of the hypothalamus and stress-induced adrenocorticotropic hormone release. *J. Neurosci.* **19,** 6684–6693.

Wada, M., and Gorbman, A. (1977). Mate calling induced by electrical stimulation in freely moving leopard frogs, *Rana pipiens. Horm. Behav.* **9,** 141–149.

Wallace, H., Meredith, C., and Marler, C. A. (1998). Effect of father's presence on offspring's aggression and vasopressin levels in the mouse *Peromyscus californicus. Soc. Neurosci. Abstr.* **24,** 1440.

Wang, Z. X. (1995). Species differences in the vasopressin-immunoreactive pathways in the bed nucleus of the stria terminalis and medial amygdaloid nucleus in prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*). *Behav. Neurosci.* **109,** 305–311.

Wang, Z. X., and De Vries, G. J. (1993). Testosterone effects on paternal behavior and vasopressin immunoreactive projections in prairie voles (*Microtus ochrogaster*). *Brain Res.* **631,** 156–160.

Wang, Z. X., and Insel, T. R. (1996). Parental behavior in voles. *In* "Advances in the Study of Behavior," Vol. 25 (C. T. Snowdon and J. S. Rosenblatt, Eds.), pp. 643–689. Academic Press, San Diego, CA.

Wang, Z. X., Ferris, C. F., and De Vries, G. J. (1994a). Role of septal vasopressin innervation in paternal behavior in prairie voles (*Microtus ochrogaster*). *Proc. Natl. Acad. Sci. USA* **91,** 400–404.

Wang, Z. X., Smith, W., Major, D. E., and De Vries, G. J. (1994b). Sex and species differences in the effects of cohabitation on vasopressin messenger RNA expression in the bed nucleus of the stria terminalis in prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*). *Brain Res.* **650,** 212–218.

Wang, Z. X., Young, L. J., Liu, Y., and Insel, T. R. (1997). Species differences in vasopressin receptor binding are evident in early development: Comparative anatomic studies in prairie and montane voles. *J. Comp. Neurol.* **378,** 535–546.

Wang, Z. X., Liu, Y., Young, L. J., and Insel, T. R. (2000). Hypothalamic vasopressin gene expression increases in both males and females postpartum in a biparental rodent. *J. Neuroendocrinol.* **12,** 111–120.

Weiss, B., Dodge, K. A., Bates, J. E., and Pettit, G. S. (1992). Some consequences of early harsh discipline: Child aggression and a maladaptive social information processing style. *Child Dev.* **63,** 1321–1335.

Wiegmann, D. D., and Baylis, J. R. (1995). Male body size and paternal behaviour in smallmouth bass, *Micropterus dolomieui* (Pisces: Centrarchidae). *Anim. Behav.* **50,** 1543–1555.

Wetzel, D. M., and Kelley, D. B. (1983). Androgen and gonadotropin effects on male mate calls in South African clawed frogs, *Xenopus laevis. Horm. Behav.* **17,** 388–404.

Widom, C. S. (2000). Motivation and mechanisms in the "cycle of violence." *Nebr. Symp. Motiv.* **46,** 1–37.

Wikelski, M., Hau, M., Robinson, W. D., and Wingfield, J. C. (1999a). Seasonal endocrinology of tropical passerines: A comparative approach. *In* "Proceedings of the 22nd International Ornithological Congress, Durban" (N. J. Adams and R. H. Slotow, Eds.), pp. 1224–1241. BirdLife, Johannesburg, South Africa.

Wikelski, M., Hau, M., and Wingfield, J. C. (1999b). Social instability increases plasma testosterone in a year-round territorial neotropical bird. *Proc. R. Soc. Lond. B Biol. Sci.* **266,** 551–556.

Williamson, F. S. L. (1968). Common Lapland longspur. *In* "Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies" (O. L. Austin, Jr., Ed.), US National Museum Bulletin 237, Part 3, Smithsonian Institute, Washington, D. C. pp. 1597–1608. .

Wingfield, J. C. (1994a). Regulation of territorial behavior in the sedentary song sparrow, *Melospiza melodia morphna. Horm. Behav.* **28,** 1–15.

Wingfield, J. C. (1994b). Hormone–behavior interactions and mating systems in male and female birds. *In* "The Differences between the Sexes" (R. V. Short and E. Balaban, Eds.), pp. 303–330. Cambridge University Press, Cambridge.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr., and Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* **136,** 829–846.

Wingfield, J. C., Lynn, S. E., and Soma, K. K. (2001). Avoiding the "costs" of testosterone: Ecological bases of hormone–behavior interactions. *Brain Behav. Evol.* **57,** 239–251.

Winslow, J. T., Hastings, N., Carter, C. S., Harbaugh, C. R., and Insel, T. R. (1993). A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature* **365,** 545–548.

Wolff, J. O., and Cicirello, D. M. (1990). Mobility versus territoriality: Alternative reproductive strategies in white-footed mice. *Anim. Behav.* **39,** 1222–1224.

Wolff, J. O., and Cicirello, D. M. (1991). Comparative paternal and infanticidal behavior of sympatric white-footed mice (*Peromyscus leucopus noveboracensis*) and deermice (*P. maniculatus nubiterrae*). *Behav. Ecol.* **2,** 38–45.

Wuensch, K. L., and Cooper, A. J. (1981). Preweaning paternal presence and later aggressiveness in male, *Mus musculus. Behav. Neurol. Biol.* **32,** 510–515.

Wynne-Edwards, K. E. (2001). Hormonal changes in mammalian fathers. *Horm. Behav.* **40,** 139–145.

Wynne-Edwards, K. E. (2003). From dwarf hamster to daddy. *In* "Advances in the study of Behavior" (P. J. B. Slater, Ed.), pp. 207–261. Academic Press, San Diego, CA.

Wynne-Edwards, K. E., and Reburn, C. J. (2000). Behavioral endocrinology of mammalian fatherhood. *Trends Ecol. Evol.* **15,** 464–468.

Xia, X., and Millar, J. S. (1988). Paternal behavior by *Peromyscus leucopus* in enclosures. *Can. J. Zool.* **66,** 1184–1187.

Xia, X., and Millar, J. S. (1991). Genetic evidence of promiscuity in *Peromyscus leucopus. Behav. Ecol. Sociobiol.* **28,** 171–178.

Young, L. J., Winslow, J. T., Nilsen, R., and Insel, T. R. (1997). Species differences in V_{1a} receptor gene expression in monogamous and nonmonogamous voles: Behavioral consequences. *Behav. Neurosci.* **111,** 599–605.

Young, L. J., Nilsen, R., Waymire, K. G., MacGregor, G. R., and Insel, T. R. (1999). Increased affiliative response to vasopressin in mice expressing the V_{1a} receptor from a monogamous vole. *Nature* **400,** 766–768.

Young, L. J., Wang, Z., Cooper, T. T., and Albers, H. E. (2000). Vasopressin (V_{1a}) receptor binding, mRNA expression and transcriptional regulation by androgen in the Syrian hamster brain. *J. Neuroendocrinol.* **12,** 1179–1185.

Young, L. J., Lim, M. L., Gingrich, B., and Insel, T. R. (2001). Cellular mechanisms of social attachment. *Horm. Behav.* **40,** 133–138.

Ziegler, T. E., and Snowdon, C. T. (2000). Preparental hormone levels and parenting experience in male cotton-top tamarins, *Saguinus oedipus. Horm. Behav.* **38,** 159–167.

Ziegler, T. E., Wegner, F. H., Carlson, A. A., Lazaro-Perea, C., and Snowdon, C. T. (2000). Prolactin levels during the periparturitional period in the biparental cotton-top tamarin (*Saguinus oedipus*): Interactions with gender, androgen levels, and parenting. *Horm. Behav.* **38,** 111–122.