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Behavioral endocrinology of mammalian fatherhood

Katherine E. Wynne-Edwards and Catharine J. Reburn

Upon first exposure to a newborn, male rats (*Rattus norvegicus*) attack and consume them. However, repeated exposure to young pups elicits parental behavior (e.g. licking, retrieval and a nursing posture over the pups) over a period of several days. During this transformation from killer to caregiver, hormones involved in maternal behavior do not change and endocrine manipulations, including castration, have little effect. Thus, initially, hormones did not appear to be involved in mammalian paternal behavior[1].

Instead, evidence supporting a role for hormones in both the onset and the maintenance of male parental behavior has come consistently, but slowly, from studies of naturally paternal species. Direct paternal care is rare in mammals but is found in some species; for example, callitrichid primates that bear twin offspring (*Callithrix* and *Saguinus* spp.), and rodents, including prairie voles (*Microtus ochrogaster*), California mice (*Peromyscus californicus*), Mongolian gerbils (*Meriones unguiculatus*) and Djungarian hamsters (*Phodopus campbelli*). In each case, both field and laboratory data support a reproductive payoff to the paternal male, in terms of increased female fertility

Mammalian fatherhood involves a muted version of the maternal experience. In spite of previous assumptions to the contrary, hormones influence mammalian paternal behavior. Naturally paternal males experience dynamic changes in the same hormones involved in maternal behavior and these hormones have access to the same brain pathways. Men becoming fathers for the first time are similar to their female partners too. These recent studies are still correlational, but promise to illuminate maternal behavior and to biologically validate the experiences of involved fathers.

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and improved offspring survival and/or growth[2,3]. Paternal behavior includes all aspects of maternal behavior except lactation (and at least one bat species is capable of lactation[4]) and can include midwifery during the birth[5] (Fig. 1). It also appears to involve activating existing neural circuits leading to maternal behavior.

Sexual dimorphism?

Hormones, including estradiol, progesterone, testosterone, cortisol, prolactin, vasopressin and oxytocin, are involved in the onset and maintenance of mammalian maternal behavior (Table 1). Except for a small number of genes on the Y chromosome, male and female mammals have the same DNA. Sexual dimorphism in neuroendocrine and endocrine pathways is usually minimal[6], except for neuroendocrine circuits leading to stereotypical sexual behavior. Thus, rather than selecting for novel pathways to elicit paternal behavior, laws of parsimony suggest that natural selection should activate pre-existing maternal neural and endocrine circuits. Current hypotheses assume that this homology will extend to neuroendocrine circuits involved in paternal and maternal behavior[6–8].

Hormone changes associated with paternal behavior

No current studies provide causal proof of hormone–behavior relationships in the control of natural paternal behavior (Box 1). However, causal proof has been offered in the rat and correlational evidence for homology with maternal behavior in naturally paternal species is strong (Fig. 2). Male laboratory rats are not normally parental and are not descended from naturally parental ancestors. Nevertheless, the castrated male rat has been successfully used as a model for maternal behavior in the absence of pregnancy and lactation. Lesions in key hypothalamic nuclei (e.g. the medial preoptic area) disrupt, and hormone implants elicit, male maternal behavior[7,9]. Unfortunately, neither estradiol nor progesterone concentrations have been reported for males of any naturally paternal species.

In Mongolian gerbils and Djungarian hamsters, testosterone concentrations rise before the birth (presumably associated with the postpartum mating), decline sharply by the day after the birth and recover over the next few days[8,10]. In female mammals, testosterone concentrations also increase soon after the birth and are associated with the onset of maternal aggression to defend her newborn offspring[11].

Prolactin has been studied in males because of its role in mammalian maternal behavior and its importance for the expression of paternal behavior in birds (Box 2). In 1982, Dixson and George reported that male common marmosets (*Callithrix jacchus*) carrying their twin offspring had prolactin concentrations that were fivefold higher than concentrations in males without offspring[12]. Seven years later, Gubernick and Nelson reported that male California mice had prolactin concentrations as high as their lactating female partners soon after the birth[13]. In recent years, prolactin concentrations have been shown to increase between pairing and early fatherhood in the Mongolian gerbil[10], the Djungarian hamster[8] and the
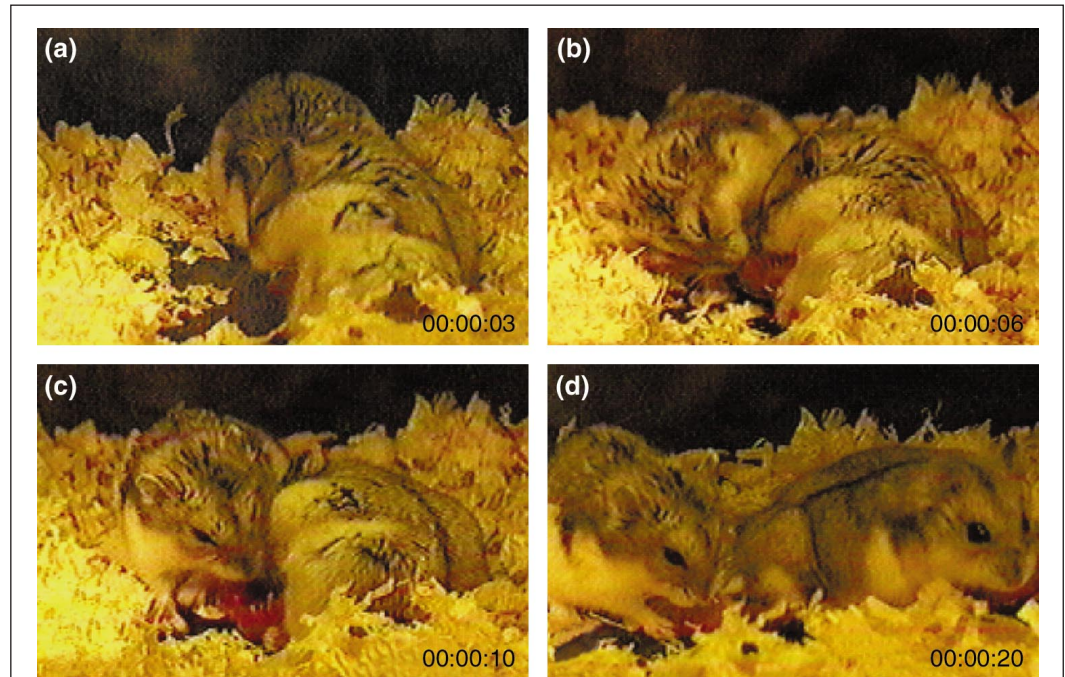

Fig. 1. Male midwifery in Djungarian hamsters (*Phodopus campbelli*). A sequence of four images drawn from a 20 s sequence (times are shown on each frame) during the birth of the second pup in a Djungarian hamster litter. In each image, the male is on the left and the female is on the right. (a) The pup has crowned and is being licked by the female; it is still dark purple in color and does not have an open airway. The first pup in the litter is visible in the foreground, partially covered by bedding. The male is approaching from the rear. (b) The male is tugging on the head of the crowned pup and is thus mechanically assisting in the birth. (c) The pup is born and the male is clearing the nares of membranes. The pup has just flushed to the bright red color that indicates hemoglobin oxygenation. The female is engaged in anogenital grooming and pulling on the umbilicus. (d) The female leaves the nest area as she pushes to deliver the placenta. The male is left alone with the neonate and continues to lick and sniff it, removing all membranes, blood and amniotic fluid. *Photograph by J. Jones and K.E. Wynne-Edwards.*

Table 1. Hormones involved in mammalian maternal behavior

Hormone	Effects on maternal behavior	Measurements in paternal males	Refs
Testosterone	An increase following parturition facilitates maternal aggression.	Mongolian gerbil, Djungarian hamster and human	8,10,11,22
Estradiol	Rises to a peak at parturition then sharply declines following birth. The prepartum rise is important for the onset of maternal behavior.	None	34,35
Progesterone	Withdrawal before the birth facilitates the onset of maternal behavior.	None	34,35
Cortisol	Decreases with pair bond formation and increases before the birth. Its function is not known.	Djungarian hamster, cotton-top tamarin and human	8,14,16
Prolactin	Production and release are facilitated by other hormones implicated in control of parental care (eg. estradiol, oxytocin and vasopressin). Hypothalamic administration before the birth facilitates the onset of maternal behavior.	California mouse, Mongolian gerbil, Djungarian hamster, cotton-top tamarin, common marmoset and human	8,10,13–15, 22,36–38
Vasopressin	Increases social affiliation. Facilitates prolactin release.	Prairie voles and deermice	16–18,39,40
Oxytocin	Facilitates prolactin release. Intracerebral ventricular injections facilitate, and agonists delay, the onset of maternal behavior.	Not correlated in California mice and prairie voles	16,17,20

cotton-top tamarin (*Saguinus oedipus*)[14]. In the tamarin, prolactin concentrations in experienced fathers never return to the lower concentrations typical of inexperienced males[14]. In the marmoset, alloparents have similar prolactin increases[15]. This pattern is not seen in Siberian hamsters[8] (*Phodopus sungorus*), which only interact with young pups late in the breeding season and are not paternal in the laboratory[3,5].

In mammals, glucocorticoid hormones are involved in the establishment of social bonds in mated pairs and might sensitize females to stimuli involved in maternal imprinting (bonding to the infant)[16]. In male Djungarian hamsters, but not Siberian hamsters, cortisol concentrations are

Fig. 2. Schematic endocrinology of fatherhood. Changes in the concentration of hormones implicated in the control of mammalian paternal behavior (Table 1). The generalized pattern represents results from studies in naturally paternal species and our assumption that the underlying neuroendocrine control of parental behavior will be homologous in males and females. Changes are relative to unpaired adult males. Question marks (?) indicate gaps in our current understanding.

elevated on the day immediately before the birth[8]. In cotton-top tamarins, cortisol is also elevated in first-time fathers relative to experienced fathers[14]. In tamarins, in both species of hamster and in monogamous prairie voles, pairing reduces circulating corticosteroid concentrations[8,14,16].

Oxytocin and vasopressin are intimately involved in affiliative behaviors, such as pair-bond formation[16,17]. They also inhibit other behaviors, such as infanticide, that are inappropriate in a family group. Social affiliation is probably a prerequisite for paternal behavior in mammals. As such, oxytocin and vasopressin are candidates for priming and/or facilitating social interactions with offspring. However, at present, neither appears to play a direct role in the initiation of paternal behavior. Vasopressin is broadly correlated with the extent of paternal behavior in deermice (*Peromyscus* spp.)[18] and voles (*Microtus* spp.)[17], but immunoreactive vasopressin fibers are not essential for paternal behavior in adult prairie voles[19]. Oxytocin is correlated with sociality[16] but peripheral oxytocin concentrations are unchanged in California mice before and after becoming fathers[20].

Other hormones are likely to join this list in the near future. For example, prostaglandin F2 alpha elicits the full range of stereotypical birth behaviors in both the male and the female tammar wallaby (*Macropus eugenii*)[21].

Men becoming fathers
Recent data suggest that there will also be a biological basis for 'involved' fatherhood in men[22] (Box 3). Both men and women had significantly higher prolactin and cortisol concentrations before the birth, and lower sex steroid concentrations immediately after the birth. Men reporting pregnancy symptoms or reporting strong emotional responses to standardized stimuli from neonates also had significantly higher prolactin concentrations. Further studies investigating the changes within individual men, the effects of circadian rhythm disruption and the role of prolonged physical contact during pregnancy (see later) are indicated.

Ecologically relevant stimuli
It is possible that males in species with highly developed paternal repertoires offer paternal behavior indiscriminately to all dependent young animals, but it is unlikely. In recent years, evidence that behavioral fathers are often not the genetic father of the offspring they nurture and protect has stimulated discussion about the conditions essential for the expression of paternal care, and the probable evolution of mechanisms to detect cuckoldry[23]. Social and environmental stimuli involved in the timing and expression of parental behavior should be sensitive to the behavioral ecology of each species.

For females, offspring might be born at a time of social upheaval, when their survival prospects are extremely limited; they might compromise the ability of a female to continue reproductive investment in older offspring; they might have poor health; or they might be born into an environment where food is suddenly scarce[24]. For males, the absence of stimuli from the pregnant female (= failure of mate guarding[25]) should decrease the probability of male paternal behavior. Cues from the female are important for the onset and maintenance of paternal care in California mice[26], although considerable interindividual variability in the expression of paternal behavior remains[27].

Chemical signals from the pregnant female, whether transmitted by air, physical contact or ingestion, are obvious candidates that could influence the later expression of paternal behavior – the same might also be true for
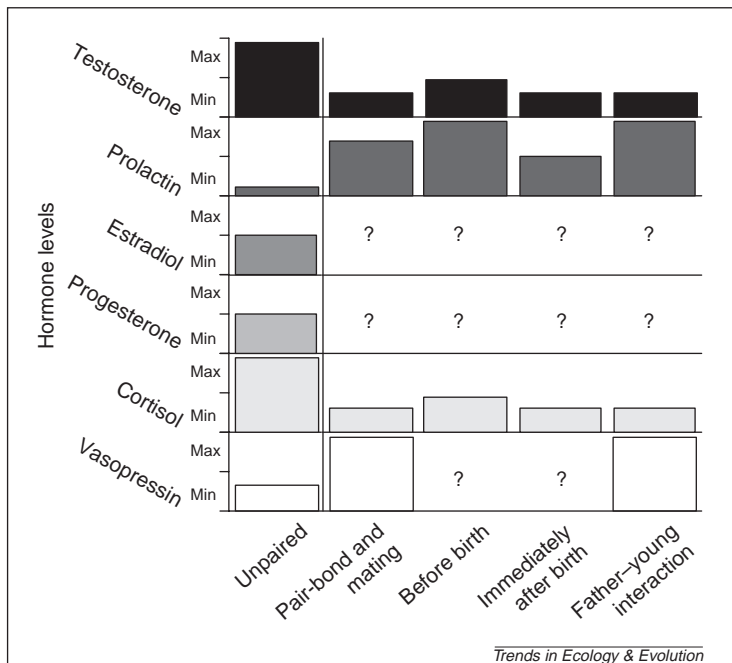
Box 2. The role of prolactin

From ring doves to passerine birds, an important role for prolactin in avian parental behavior is well established[45]. In female mammals, altered pituitary prolactin release is the functional end-point of many pheromonal inputs to reproduction (e.g. puberty onset and pregnancy interruption[46]), including maternal care[36].

In males, as well as females, prolactin has access to receptors and functions in key target areas of the brain involved in maternal behavior[9]. Null mutation of the prolactin receptor also impairs maternal behavior[36].

In naturally paternal species, prolactin correlates with the expression of paternal behavior[8,10,13–15]. In the same way that paternal responsiveness is prolonged following parental experience, prolactin concentrations in experienced fathers remain elevated[14].

In spite of this evidence, little comparative endocrinology of mammalian prolactin is available. The primary barrier to this research is the extent of interspecific diversity in prolactin sequence. Antibodies rarely crossreact in distantly related species and antagonists are controversial[47].

Currently, mammalian studies are restricted to rats, hamsters, sheep and humans, whereas chicken prolactin has been widely useful in avian species. Efforts to overcome these technical barriers should yield exciting new insights into the neuroendocrinology of social behavior.

Box 3. Men becoming fathers

Recently, the first study of hormone changes in men becoming fathers (Fig. I) was published[22]. It firmly placed those highly motivated 'dads' in the 'naturally paternal' hormone responsiveness category.

Methods: Canadian couples were recruited from prenatal classes and were visited at home either before or after the birth. Blood was sampled twice. During the 30 minutes between samples, the man held a soft doll wrapped in a soiled receiving blanket from the neonatal nursery, while the couple listened to unconsoled baby cries recorded in the neonatal unit and watched a video clip about breastfeeding a newborn. Each adult then completed a brief questionnaire inquiring about male pregnancy symptoms[48] and emotional responses to the stimuli.

Results: prolactin and cortisol concentrations were higher in men sampled during the final three weeks of pregnancy than in men sampled earlier in the pregnancy. Testosterone concentrations were lower in men sampled in the three weeks after the birth than in men sampled before the birth.

The difference between the first blood sample and the second blood sample (called the 'situational reactivity') also varied relative to the birth. Just before the birth cortisol decreased between samples, whereas soon after the birth testosterone increased between the two samples.

Hormone concentrations also varied relative to emotional and physiological responsiveness of individuals. Men reporting pregnancy symptoms and men reporting strong emotional responses to the stimuli had significantly higher prolactin concentrations and experienced a significantly larger testosterone decrease between the two blood samples than men without these responses.

Overall, hormone concentrations in men were substantially lower than in women, but patterns of change were similar[34] and were correlated within couples. *Photograph by K.E. Wynne-Edwards.*

humans. Human cultures with extensive paternal care also have prolonged contact within a pair-bond[28], hormone concentrations within couples are correlated[22] and at least one human pheromone has been found[29].

Close proximity between a male and a pregnant female creates additional opportunities to evoke hormonal changes in the male. For example, when male Djungarian hamsters midwife the delivery of their young they consume amniotic fluid and at least 50% of the placental tissue[5]. Both amniotic fluid and placenta are potent sources of hormones[30], and they function in individual recognition and mother–infant bonding[31].

Of course, it is also possible that the stimuli needed for the onset of paternal behavior are temporally displaced from the birth. Appropriate reduction in infanticidal behavior of male mice involves an interval timer activated during mating[32], many of these species have opportunities for alloparental experiences with siblings born while they are still juveniles[15,33], and pair-bond formation has neural and endocrine consequences that might facilitate paternal behavior[16]. Experimental tests of causal hypotheses linking hormonal changes (including temporally displaced hormonal changes) to paternal behavior are urgently required.

Conclusions

Recent progress in understanding the behavioral endocrinology of mammalian fatherhood embraces the hypothesis that naturally occurring paternal behavior will be homologous with maternal behavior. It is anticipated that a wide variety of hormones are involved in paternal behavior. Early results show great promise that a biological basis for involved fatherhood will be found and that including the human animal will capture a wide audience. We see this potential as an opportunity to better understand maternal behavior, by studying parental behavior in the absence of pregnancy and lactation; an opportunity to explore the modulatory interactions between hormones and behavior in a relevant social context; and an opportunity to biologically validate the experiences of involved fathers.

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