



CURRENT TOPICS IN PRIMATE SOCIOENDOCRINOLOGY

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■ **Abstract** Socioendocrinology is the study of the effect of the social environment on the interactions between hormones and behavior. Individuals have evolved a physiological flexibility that enables them to respond to their social surroundings in a manner that maximizes reproductive success. We present evidence that (a) males who have evolved to participate in infant care have different endocrine profiles around offspring from males who have not evolved to regularly participate in infant care, (b) the energetic costs of reproduction in both males and females creates conditions conducive to elevated levels of both stress and sex hormones, (c) adolescent subfecundity among females evolved as a mechanism fostering mate choice, (d) some primate species are probably facultative ovulators, and (e) endocrine suppression of subordinate males probably does not contribute to delayed onset of reproduction but does contribute to reduced access to females, which hampers progeny production. Hormones and behavior are inextricably intertwined in a feedback relationship that regulates each other.

INTRODUCTION

Socioendocrinology is the study of the effect of the social environment on the interactions between hormones and behavior (Figure 1). Understanding the dynamic interactions that link the social environment with neuroendocrine mechanisms and behavior provides a foundation for determining factors regulating differential reproductive success among individuals. Socioendocrine factors construct ontogenetic trajectories beginning in utero and operating until death. For example, neuroendocrine feedback mechanisms achieve a prominent role in mediating reproductive processes in postpubescent animals, but differences in fetal and neonatal development influence adult neuroendocrine profiles. Prenatally stressed rhesus macaques (*Macaca mulatta*) develop different neuroendocrine feedback

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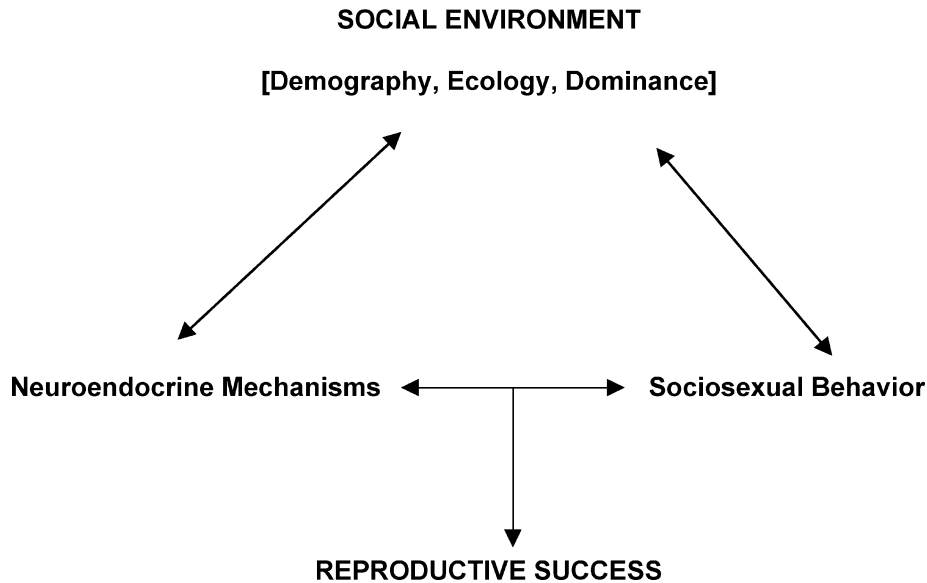


Figure 1 The basic paths of socioendocrinology. Modified from Bercovitch & Ziegler 1990 and Dixson 1998.

sensitivities compared with control subjects (Clarke et al. 1994), and blockage of elevated neonatal testosterone levels in male common marmosets (*Callithrix jacchus*) results in attenuation of the pubertal rise in testosterone (Lunn et al. 1994).

One fundamental tenet of socioendocrinology is that individuals have evolved an adaptive flexibility enabling them to adjust both mating effort and parental effort according to social surroundings, which yields alternative mating strategies promoting individual reproductive success. All animals need not continually strive to achieve the alpha slot in a hierarchy in order to maximize their chances of contributing to subsequent generations. Animals respond to their social surroundings in a manner that balances the benefits of current reproduction against the costs of future reproduction, even if such a calculation involves retarded reproductive maturation or reproductive restraint. A socioendocrinological perspective provides a framework for connecting reproductive endocrinology with evolutionary biology.

Rather than give an extensive review of the literature, this contribution provides a critical assessment of four key topics: (a) associations between male parental care, paternity, and endocrine state, (b) relationships among stress, social strategies, and reproduction, (c) the socioendocrinology of reproductive maturation in females, and (d) the socioendocrinology of reproductive maturation in males. These five subjects were chosen because they are some of the most active and controversial areas posing challenges for future research projects in the field of primate socioendocrinology.

ASSOCIATIONS AMONG MALE PARENTAL CARE, PATERNITY, AND ENDOCRINE STATE

Direct male parental care is rare in mammals. Only 10% of mammalian species exhibit some type of paternal care, but male care of infant primates occurs in approximately 40% of primate genera (Kleiman & Malcom 1981). Among nonhuman primates, extensive paternal care is most often associated with monogamous, or polyandrous, species such as siamangs (*Symphalangus* spp.), owl monkeys (*Aotus* spp.), titi monkeys (*Callicebus* spp.), goeldii's monkeys (*Callimico goeldii*), marmosets (*Callithrix* spp.), and tamarins (*Saguinus* spp.), with several cercopithecine species also displaying strong male-infant bonds (Whitten 1987, Smuts & Gubernick 1992). The evolutionary explanation(s) for paternal care are controversial; the leading contenders are protection from nonparental infanticidal males (van Schaik & Paul 1997, van Schaik & Janson 2000), care of probable offspring that enhances survivorship prospects (Bernstein 1976, Bercovitch 1995), sharing the energetic burden of raising descendants because of metabolic constraints of lactation (Heymann 2000), and using infants as devices to increase prospects for future matings (Price 1990, Smuts & Gubernick 1992).

The most extensive studies on the socioendocrinology of paternal care in primates have been conducted on cotton-top tamarins (*Saguinus oedipus*) (Figure 2, see color figure). Cotton-top tamarins are cooperative breeders, with the entire family participating in caring for the twin infants. Tamarin fathers begin carrying their young on the day of birth and spend as much time as do mothers with their infants during the first five days after birth (Ziegler & Snowdon 2000; Ziegler et al. 2000a,b). Sons and daughters delay their emigration from the family to help rear younger brothers and sisters. In captivity, both experienced fathers and their sons show elevated levels of prolactin following the birth of infants compared with nonfather tamarins (Ziegler et al. 1996).

Although prolactin is often thought of as a "female" hormone associated with lactation, blood concentrations in men and women are comparable, and newborn infants have higher prolactin levels than do nursing mothers (Norman & Litwack 1997). Evidence that prolactin was involved in male parenting behavior in primates initially emerged from studies of the common marmoset and the cotton-top tamarin. Marmoset males have elevated prolactin concentrations following the birth of infants (Dixson & George 1982, Torii et al. 1998, Mota & Sousa 2000), which was thought to be related to infant contact because prolactin levels were higher in males carrying infants than in males not carrying infants. Lowering endogenous prolactin in young, inexperienced marmosets, using bromocriptine, caused an increase in the time to retrieval of marmoset infants, compared with control subjects, which suggests that prolactin promotes responsiveness to infants (Roberts et al. 2001).

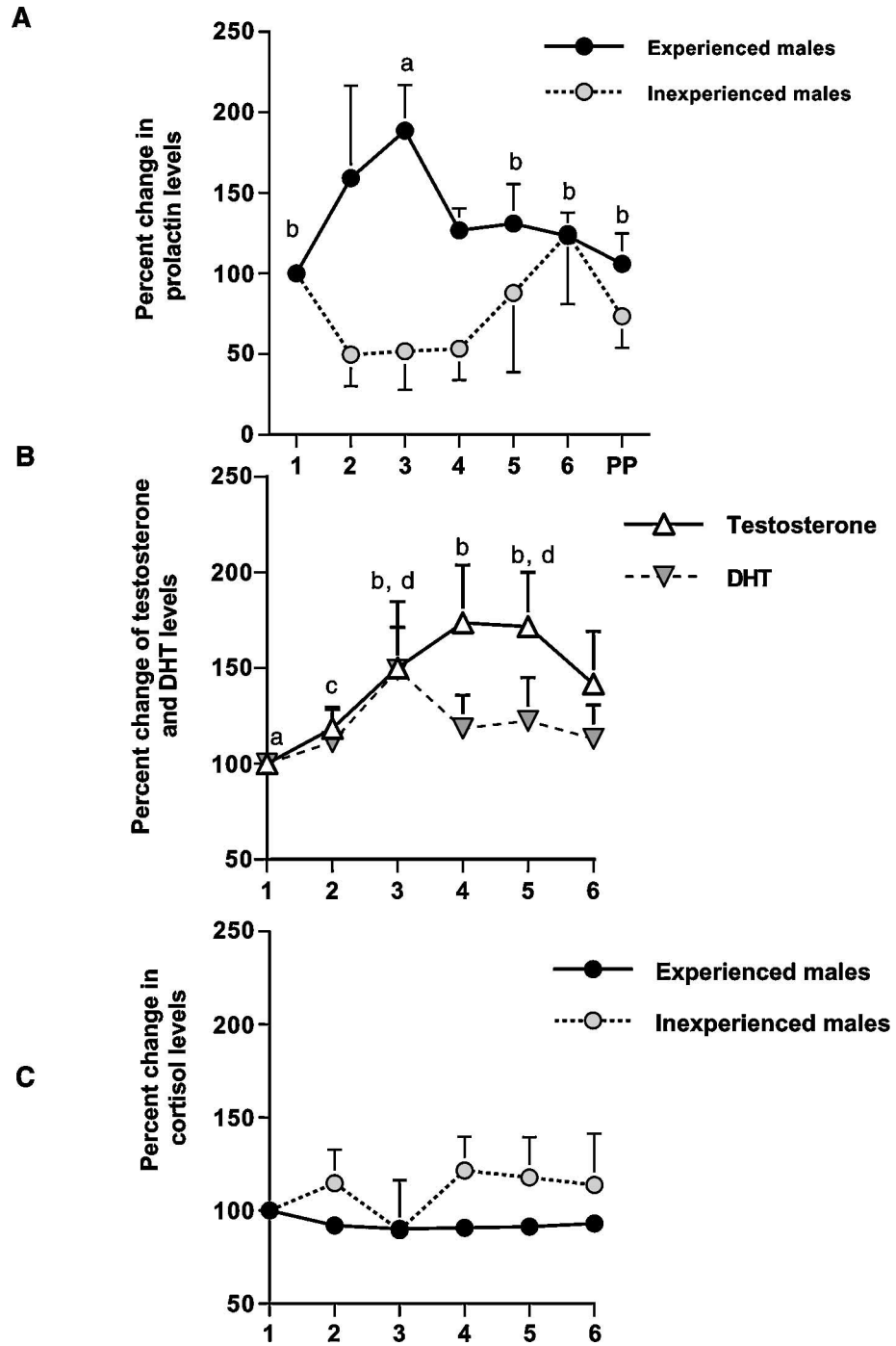
Prolactin levels are elevated in cotton-top tamarin fathers throughout the first six weeks following the birth of their infants, whereas elevated prolactin in mothers is dependent on viable nursing infants (Ziegler et al. 2000a). Prolactin levels are positively correlated with the number of previous births with which a male

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has been involved. Although hyperprolactinemia suppresses testosterone concentrations in men (Norman & Litwack 1997), and many biparental birds display inverse relationships between prolactin and testosterone (Ziegler 2000), prolactin and testosterone levels do not change significantly from pre- to postpartum in cotton-top tamarin fathers. Figure 3 shows levels of prolactin, testosterone, and dihydrotestosterone (DHT), a potent androgenic metabolite of testosterone) among cotton-top tamarin males under a variety of conditions. Mean prolactin levels by month of gestation (6-month gestation period for the cotton-top tamarin) reveal a difference in prolactin for experienced and inexperienced father tamarins (Ziegler & Snowdon 2000). For experienced fathers, a significant rise in prolactin occurs during the second and third gestational month, whereas inexperienced fathers show elevated prolactin levels during the last month prior to birth. Cortisol levels show little change in males throughout pregnancy of mate, regardless of level of experience of the father, but cortisol levels are elevated in new, inexperienced fathers (Ziegler et al. 1996). Tamarins have a postpartum ovulation that occurs within a couple of weeks following parturition and, therefore, have a simultaneous period of parenting and breeding. In fact, testosterone levels are significantly elevated in male tamarins around the time of the postpartum ovulation (Ziegler et al. 2000a).

Prepartum changes in male cotton-top tamarin endocrine profiles during their mate's pregnancy indicate how the social environment modifies the endocrine state. Cues emitted from the female mate could signal impending birth and provide an adaptive milieu for paternal care. Male cotton-top tamarins are known to receive arousal cues from female tamarins' periovulatory scent marks (Ziegler et al. 1993). Olfactory cues during pregnancy, stimulated by hormonal changes or produced by direct male-female contact, could regulate male parent endocrine state. Male tamarins have well-developed vomeronasal organs (Wysocki 1979) and female tamarins have well-developed scent glands (Epple 1986). Female tamarins scent mark substrates in their environment (Epple 1986, Savage et al. 1988) and are known to scent mark throughout pregnancy (Epple 1976). Social stimulus through increased contact time with the pregnant female can also initiate a cascade of hormonal events (Uvnas 1997), and these events might be important in initiating male parental behaviors. Although the physiological mechanism triggering pre- and postpartum endocrine changes in males is unknown, the socioendocrinology of cotton-top tamarin mating and rearing systems indicates a coordinated network that prepares the pair for parenthood and implicates multiple caregivers in the survival of offspring.

Figure 3 Mean + SEM percentage changes in urinary (A) prolactin, (B) testosterone and DHT, and (C) cortisol from the first month of gestation in experienced and inexperienced male cotton-top tamarins. Months with the same letters are not significantly different from each other, whereas months with different letters indicate statistically significant differences. Modified from Ziegler & Snowdon (2000).



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The socioendocrinology of parental care in cotton-top tamarins has many similarities to that of humans. For example, the endocrine changes associated with pregnancy and parturition not only prepare a mother for delivering an infant but also stimulate neurochemical changes within the brain to influence maternal behavior (Numan 1994, Bridges 1996). Similar life history stage-specific differences appear in some hormone levels for both females and males, e.g., higher concentrations of prolactin and cortisol in the period just before the birth of an infant are accompanied by lower levels of sex steroids postnatally (Storey et al. 2000). Additionally, men who experience more pregnancy-like symptoms (couvade) during their wife's pregnancy have higher mean prolactin levels than men with fewer symptoms. Testosterone levels in men appear to be lower following infant birth, whereas cortisol levels are higher prior to parturition (Berg & Wynne-Edwards 2001). Hormonal changes occur prior, and in response, to parturition in both mother and father in both cotton-top tamarins and people. Father participation in the direct care of his children has increased over the past 30 years in many areas of Europe and America (Lamb 1981, 1987), with research into the motivational factors and benefits of father participation receiving increasing attention. In both sexes, hormonal patterns may have evolved to facilitate infant care behaviors.

Children who have positive involvement with both parents throughout childhood are more likely to be confident, social individuals (Lieberman et al. 1999), and fathers are more likely to invest care in their biological children than in their step children (Daly & Wilson 1988). Cultural factors play a prominent role in shaping whether or not fathers are likely to be directly involved with their children (Hewlett 1992a). Since cultural factors are one component of the social environment, studying the relationship between cultural practices and the endocrinology of fatherhood falls within the domain of primate socioendocrinology. Even in societies where father participation is encouraged, considerable variation exists among fathers in patterns of paternal care. But, as with the cotton-top tamarins, some of the variability in human father responses to infants is associated with periparturitional hormonal changes within the father (Storey et al. 2000, Berg & Wynne-Edwards 2001).

We suggest that evolution has molded a malleable endocrine state among males that responds to the social environment by regulating internal milieu among fathers in a fashion that promotes the survival of their offspring. In species where male care of infants is crucial, we expect endocrine changes in males that will augment their parental roles, whereas in primate species in which male care is unimportant for infant survivorship, pre- and/or postpartum modifications in endocrine state are less likely to occur.

Continuing to examine socioendocrine influences on male parental behaviors in primates is important for understanding mechanisms involved in fostering male reproductive success. We propose that hormonal profiles will have co-evolved with social behavior during the evolution of breeding systems to ensure that patterns of parental investment maximize reproductive success. Therefore, studying the socioendocrinology of paternal care can provide insights into the evolutionary foundations of different mating systems.

STRESS, SOCIAL STRATEGIES, AND REPRODUCTION

Primates are often challenged by conspecifics or predators. The fight-or-flight response demands increased energy mobilization, which is achieved by activation of the endocrine stress response. The stress response is a biological mechanism that operates by dampening digestive, immune, and reproductive systems while stimulating cardiovascular and musculoskeletal activity (Sapolsky 1994, Norman & Litwack 1997). Glucocorticoids flood the circulatory system and mediate metabolic processes by converting amino acids to carbohydrates, which conserve glucose as an energy source. Elevated glucocorticoids, or corticosteroids, inhibit both antibody production and the inflammatory response, which is one reason why topical application of cortisone ointment alleviates itching. Cortisol is the major primate glucocorticoid and belongs to the same “superfamily” of hormones as the sex steroids because all are derived from cholesterol and all share similar receptor binding properties.

A standard paradigm has developed that assumes that low-ranking primates are subject to high levels of social or nutritional stress and, therefore, are characterized by higher cortisol levels and reduced reproductive success (e.g., Dunbar 1988). However, this scenario has proved increasingly inadequate among a number of species. We describe an alternative model that links reproductive activity to increased metabolic demands and elevated “stress.” We propose that animals have evolved a physiological flexibility enabling them to meet the energetic demands of mating activity by increasing in both adrenal and sex steroid concentrations without detriment to reproductive success. The effects of stress are modulated by positive social interactions among primates that decrease the potentially adverse impact of circulating glucocorticoids on reproductive processes.

Consider the situation among a number of nonprimate species. Breeding female green turtles (*Chelonia mydas*) have elevated levels of both corticosterone (the major glucocorticoid in most species) and progesterone; the catabolic properties of corticosterone probably facilitate the energetic demands associated with nest construction and egg laying (Jessop et al. 2000). In many passerine birds, such as the dark-eyed junco (*Junco hyemalis*), mating season elevations of both testosterone and corticosterone jeopardize immune function but are beneficial for shunting nutritional reserves into behavioral patterns and for exhibiting secondary sexual traits that promote reproductive success (Casto et al. 2001). Male copperhead snake (*Agkistrodon cantortrix*) fighting involves lots of physical contact without biting. Defeated males display significantly elevated corticosterone concentrations, but winners and losers have similar testosterone levels, which demonstrates a disconnect between the two hormones as well as shows how endocrine levels respond to social stimuli in snakes (Schuett et al. 1996). Finally, male marsupial mice (*Antechinus stuartii*), who all die after a one- to two-week mating season, are characterized by eightfold increases in testosterone and a doubling of cortisol levels, from the pre- to peak breeding period (McAllen 1998).

Among nonhuman primates, exposure to estrous females results in elevated concentrations of both testosterone and cortisol in long-tailed macaques (*Macaca*

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fascicularis) (Glick 1984), talapoins (*Miopithecus talapoin*) (Martensz et al. 1987), capuchins (*Cebus apella*) (Lynch et al. 2002), and squirrel monkeys (*Saimiri sciurius*) (Mendoza & Mason 1991). Among male rhesus macaques (*M. mulatta*), cortisol concentrations are neither related to social status nor negatively associated with testosterone concentrations (Bercovitch & Clarke 1995). Dominant male lesser mouse lemurs (*Microcebus murinus*) have significantly higher testosterone concentrations than do subordinate males, but the two classes of males do not differ in cortisol levels (Perret 1992), whereas dominant male squirrel monkeys have higher concentrations of both testosterone and cortisol than do subordinate males (Coe et al. 1979). Dominant male savanna baboons (*Papio cynocephalus*) have lower cortisol levels than subordinate males when the social hierarchy is stable, but low-ranking males who have extensive social affiliations and are adept at displacing aggression also have low cortisol concentrations (Sapolsky 1994). Male mountain gorillas (*Gorilla gorilla*) living in Rwanda show no evidence of rank-related differences in cortisol concentrations (Robbins & Czekala 1997), and rank effects on both cortisol and testosterone are absent among male muriquis (*Brachyteles arachnoides*) living in Brazil (Strier et al. 1999).

Social skills have a tremendous impact on male reproduction among primates (Strum 1987, Bercovitch 1991) and contribute to mitigating the expression of the endocrine stress response (Sapolsky 1994). Furthermore, among male primates, differences in reproductive success are more likely to arise from adoption of alternative reproductive strategies than from testosterone concentrations (Bercovitch & Goy 1990). Even under conditions of stress-mediated cortisol suppression of testosterone, spermatogenesis continues and males are capable of impregnating females. However, intense stress does interfere with the ability to achieve and sustain an erection (Sapolsky 1994, Bercovitch 1999).

Both nutritional and social stress operate along similar neuroendocrine pathways that can interfere with regular ovarian cyclicity and dampen female reproductive success (Bercovitch & Goy 1990, Bercovitch & Strum 1993). One might expect, therefore, a more pronounced connection between increased cortisol concentrations and reduced reproductive success in female compared with male primates. Semi-free-ranging female Barbary macaques (*Macaca sylvanus*) who are subjected to aggression from conspecifics excrete increased amounts of glucocorticoids (Wallner et al. 1999). In the same population, breeding lifespan accounts for 61% of the variance in female reproductive success, and low-ranking females initiate reproductive senescence at a younger age than high-ranking females (Paul & Kuester 1996). The detrimental consequences of stress in this population do not seem to modify reproductive rate but do appear to have negative consequences for life expectancy.

In captive long-tailed macaques, serum cortisol concentrations were not related to dominance rank under conditions of social stability (Stavisky et al. 2001), and limited evidence suggests that urinary cortisol is independent of female rank among wild long-tailed macaques (van Schaik et al. 1991). In female cotton-top tamarins, cortisol levels are higher during the periovulatory than the nonperiovulatory phase, with fertility suppression of postpubescent females not associated

with increased cortisol concentrations (Ziegler et al. 1995). The highest cortisol levels were documented for pregnant females, who also occupied the dominant position. Among female common marmosets, cortisol levels were higher in dominant, cycling females than in subordinate anovulatory females (Saltzman et al. 1994). Reproductive condition accounted for the elevated cortisol concentrations in dominant females in both species (Saltzman et al. 1994, Ziegler et al. 1995). The connection between high rank and high cortisol in these callitrichids was not a consequence of cooperative rearing and associated reproductive suppression because a similar pattern has been found among ring-tailed lemurs (*Lemur catta*), who reside in a different type of mating system.

Ring-tailed lemurs live in extremely seasonal habitats in Madagascar. They live in female-bonded social groups where the females are dominant to the males (Richard 1987, Gould 1999). Breeding seasonality is tightly constrained, with matings occurring during a one-month period. Toward the end of the dry season, when food resources are limited and predator pressure intensifies, cortisol concentrations of females increases slightly, but the best predictor of cortisol concentrations is female dominance status (Cavigelli 1999). Low-ranking females have low cortisol concentrations.

Chronic stress could decrease lifespan and thereby hinder reproductive output, but we suggest that the energetic costs of mating, especially among males, result in physiological adjustments that boost both sex and adrenal steroids. During the pre-mating season, male rhesus macaques accumulate substantial fat deposits that are drawn upon during the mating season as males decrease feeding time and increase time spent in sociosexual activities (Bercovitch 1997). Male rhesus macaques not only have elevated levels of testosterone and estrogen during the mating season (Bercovitch 1992), but cortisol concentrations among high-ranking males, who also have the greatest fat deposits (Bercovitch & Nürnberg 1996), are much higher during the peak mating season than during the postmating season (Bercovitch & Clarke 1995). Casto et al. (2001) have proposed that the breeding season elevations of testosterone and corticosterone in birds are costly in two ways: a high-energy reproductive behavior and a shorter life history, because the hormonal increases reduce survivorship prospects and suppress immune function. A similar life history profile might characterize males of many primate species, but whether longevity is reduced among the most reproductively active males has not yet been evaluated.

The situation among females is more complex, but it could be similar. A concurrent increase in glucocorticoids and ovarian steroids might reflect the energetic costs of mating among females. Although female savanna baboons in consort relationships with males do not travel more than nonconsort females, they significantly reduce feeding time (Bercovitch 1983), and estrogen has suppressive effects on appetite (Bielert & Busse 1983). Callitrichids have severe energy hurdles for raising twin offspring, and while the energetic costs of mating in captivity are not profound, the possibility remains that links between high rank and high cortisol are reflecting metabolic adjustments prior to gestation. We suggest that the energetic costs of reproduction in both males and females might create conditions conducive

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to elevations in both adrenal and sex steroids and that the role of cortisol and stress on reproductive suppression has been overestimated.

In conclusion, male reproductive strategies are stressful, and the metabolic challenges of mate guarding and mate acquisition require extensive energy use, which, in turn, demands the mobilization of glucocorticoids. Female reproductive strategies are more mysterious with respect to the role of adrenal steroids on reproductive processes. Evidence from field and laboratory studies demonstrate that fertility enhancement, not suppression, can be accompanied by high levels of glucocorticoids.

THE SOCIOENDOCRINOLOGY OF REPRODUCTIVE MATURATION IN FEMALES

Puberty begins with alterations in the hypothalamic GnRH pulse generator, a complex of neurons responsible for regulating the timing of release of gonadotropins (Terasawa et al. 1983, Norman & Litwack 1997, Plant 1999). Nocturnal outbursts of GnRH stimulate increased pulsatile secretion of LH, which triggers output of ovarian and testicular sex steroids, which drive development of reproductive potential and processes. Covert neuroendocrine adjustments prompting the transition from puberty to adulthood occur before outward manifestations of reproductive maturation. Ontogenetic physiological patterns bridging the period from pubescence to adulthood have been documented in detail, but primates are characterized by a fairly unique, and lengthy, phase of adolescent subfecundity (see Dixson 1998). Why a neuroendocrine system triggers gonadotropin pulsatility in the absence of concurrent and regular ovarian changes resulting in ovulation is unclear. We explain how social factors are partially responsible for regulating this life history stage, and suggest that prosimians, and possibly other primates, are facultatively reflex ovulators.

One resolution to the riddle of adolescent subfecundity might reside in female choice operating via two different pathways. One mechanism is reflex ovulation as a form of cryptic female choice (Eberhard 1996). Cryptic female choice occurs when females control sirehood in such a way that the rate at which they mate with a given partner is not correlated with the rate at which they co-reproduce with them. The other mechanism is neophyte mate choice designed to patiently adjudicate potential partners, given the costs of mating and producing offspring.

Primates are spontaneous ovulators, but reflex ovulation and spontaneous ovulation are not two discrete species-specific traits in mammals (Zarrow & Clark 1968, Conaway 1971, Jöchle 1975, Milligan 1982, Martin 1990). Rats ovulate spontaneously, but cervicovaginal stimulation increases output of eggs (Zarrow & Clark 1968), whereas camels are reflex ovulators, with about 5% of females ovulating spontaneously (van Tienhoven 1983). Coitus-induced ovulation has been reasoned to represent the primitive (Zarrow & Clark 1968) and the derived (Weir & Rowlands 1973) state, with the variety of ovarian dynamics across mammals failing to follow phylogenetic, ecological, or social classification (Conaway 1971,

van Tienhoven 1983). Some animals are considered “facultative reflex ovulators” (Jöchle 1975), where exposure to a male or coital activity can trigger the LH surge responsible for ovulation.

Prosimians and New World monkeys are the most likely candidates for facultative reflex ovulation. Reflex ovulation predominates in nongregarious mammalian species with penile spines (Zarrow & Clark 1968). Most prosimians live in non-gregarious mating systems (Bearder 1987, Dunbar 1988, Nash 1993) and possess prominent penile spines (Dixson 1987, 1998; Harcourt & Gardiner 1994). Among primates, penile spines and dispersed mating systems tend to coincide (Dixson 1987, Harcourt & Gardiner 1994). Although New World monkeys generally reside in large social configurations, some species have extensive penile spines. Regardless of the form of the mating system, the presence of penile spines in Primates suggests that facultative reflex ovulation might contribute to delayed first pregnancy following onset of ovarian processes. Sexually attracting, and mating with, an adult male establishes a necessary, but not sufficient, condition for reflex ovulation among adolescents.

Both Prosimians and New World monkeys transmit chemosignals that alter the reproductive endocrinology of conspecifics, providing a second clue to how social factors regulate the timing of adolescent subfecundity. Among cotton-top tamarins, exposure to a novel male facilitates onset of ovarian cyclicity but does not influence the maintenance of ovarian function (Ziegler et al. 1987, Savage et al. 1988, Widowski et al. 1992). Pairing lesser galagos with an adult male accelerates onset of first estrus (Izard 1990), whereas introduction of an adult male to group-living squirrel monkeys results in elevated estradiol output within 24 h (Mendoza & Mason 1991). Copulation in squirrel monkeys intensifies the midcycle estradiol surge, which could ensure ovulation, facilitate gamete transport, promote luteal function, or enhance implantation prospects (Yeoman et al. 1991). In common marmosets, young postpubescent females are significantly more likely to ovulate when living with an unrelated male than when living with their father (Saltzman et al. 1997). In peer groups of common marmosets, subordinate females, who tended to copulate with subordinate males, did not ovulate, whereas the dominant female, who copulated mostly with the dominant male, became pregnant (Abbott & Hearn 1978), indicating that facultative reflex ovulation might be stymied by low social status. Among nonprimates, a wealth of data reveals that chemical, tactile, and auditory cues from male mice modify the reproductive status of females by inhibiting or potentiating ovulation, as well as by interfering with implantation (Bronson 1989, Vandenberg 1994), despite classification as spontaneous ovulators (see Weir & Rowlands 1973; van Tienhoven 1983). Male induction of ovulation and female suppression of ovarian function represent a continuum of socioendocrine processes that regulate reproductive success. Reproductive development can be either accelerated or decelerated as a function of social stimuli.

Two other life history traits of Prosimians and New World monkeys intimate facultative reflex ovulation as a reproductive strategy. New World monkeys tend to display relatively short estrous cycles, which are common among species where

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formation of a functional corpus luteum requires a mating stimulus (Martin 1990). Reflex ovulation and coitus-induced luteinization often co-occur. Second, postpartum estrus is frequently exhibited by reflex ovulators and is common among small-sized prosimians (e.g., mouse lemurs, lesser galagos) and Callitrichids (e.g., common marmosets, cotton-top tamarins), who reproduce aseasonally (Martin 1990, Ziegler et al. 1990).

In both Prosimians and New World monkeys, morphological characteristics and male modification of female reproductive endocrinology establish a foundation for possible facultative reflex ovulation. In these species, adolescent subfecundity could be adaptive by postponing initial ovulation until females are presented with appropriate socioecological conditions favoring offspring survival. Prosimians are ideal candidates for further investigation of facultative reflex ovulation because they share many traits with reflex ovulators: They often live in dispersed social systems, display brief periods of sexual receptivity, scent mark in accordance with stage of ovarian cycle, attract multiple males while in estrus, alter reproductive endocrinology as a function of social cues, and have spiny penises, elongated os baculum, and engage in prolonged intromission (Dixson 1998).

Another means by which female choice could account for adolescent subfecundity is to enable neophyte females the opportunity to hone mate selection judgement capabilities prior to first conception. Appraising suitable sires is facilitated by proceptive behavior, but maintaining a constant follicular state for this purpose is not physiologically feasible. Continuous high estradiol levels interfere with development of the feedback relationship required to stimulate a sharp spike triggering the gonadotropin surge responsible for ovulation (Bercovitch et al. 1987). Retaining high gonadotropin levels would facilitate downregulation of receptor quantity and reduce subsequent gonadotropin output. Therefore, prolonged proceptivity is not an option due to physiological constraints imposed on reproductive cycles, but anovulatory cycles provide an opportunity for proceptive behavior without risking impregnation. Among cercopithecines, female body mass at puberty is significantly less than at adulthood (Bercovitch 2000), and, among captive pigtailed macaques, *M. nemestrina*, infant mortality due to dystocia is more pronounced among primiparous than multiparous mothers (Dazey & Erwin 1976). Primates tend to have longer follicular stages than other mammals (Zelevnick & Fairchild-Benyo 1994), and multiple nonovulatory cycles increase female chances for scrutinizing males. Across Primates, the span of adolescent subfecundity is extraordinarily variable but tends to be longest among females residing in multimale mating systems and shortest among those living in paired mating systems (Figure 4).

Adolescent subfecundity could be a nonadaptive consequence of the evolution of an exceedingly fine-tuned neuroendocrine system that requires a lengthy interval to coordinate the various components. It could be a “physiological atavism” that has not been removed from Primates during evolution (Zarrow & Clark 1968). It could be adaptive by postponing first conception until socioecological conditions are favorable for induced ovulation and subsequent pregnancy. Or it could be adaptive by permitting females time to imbibe male traits as a precursor to mate selection. Adolescent female sexuality in Primates has received little systematic

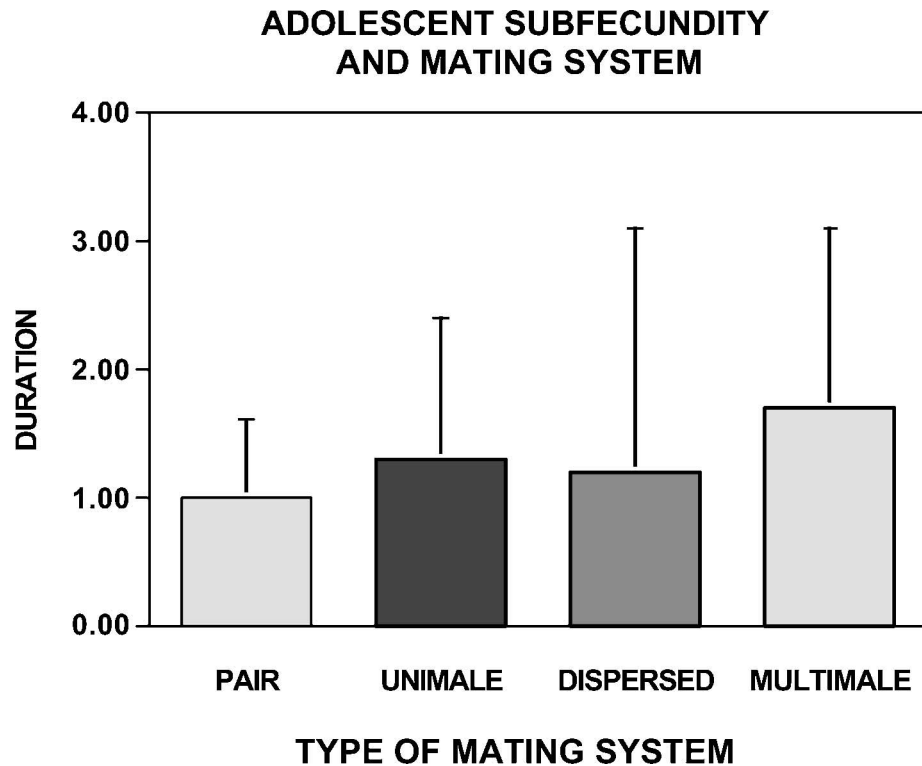


Figure 4 The relationship between duration of adolescent subfecundity and structure of the mating system. Histogram bars plot the mean plus standard deviation. Classification of mating systems follows Dixson (1991, 1995) and Harcourt et al. (1995). Differences in duration of adolescent subfecundity are absent when the four mating systems are compared (Kruskal-Wallis = 5.794, $P > 0.10$) but nearly significant when weight is held constant (ANCOVA: $F(3,35) = 2.780$, $P = 0.055$, multiple $r = 0.737$). The length of the adolescent subfecundity stage in multimale mating systems is significantly longer than that of the other systems combined (Mann-Whitney $U = 105$, $P = 0.03$).

attention, and understanding the evolution of this life history period requires more detailed investigations.

THE SOCIOENDOCRINOLOGY OF MALE REPRODUCTIVE MATURATION

Neuroendocrine pathways guiding male reproductive maturation are identical to those of females, except that instead of fine-tuning pulsatile GnRH discharges into a cyclical pattern regulating ovulation, males develop a more stable rhythmicity that fosters continuous sperm production. Social stimuli retarding or accelerating

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reproductive maturation in males have not been scrutinized as solidly as those in females. Most information comes from papionins (i.e., macaques, mandrills, baboons, and mangabeys), but social factors have also been identified as promoting alternative paths of reproductive development in orangutans (*Pongo pygmaeus*). One difficulty encountered in studying the socioendocrinology of male reproductive maturation is that the most likely candidates are species that live in multimale-multifemale social systems, yet, in these same systems, females regularly mate with multiple partners, so evaluating the reproductive consequences of suppressed or accelerated maturation requires genetic analysis of sirehood. In addition, as noted earlier, thwarted reproductive endocrinology among males need not have negative repercussions on spermatogenesis and reproductive success.

Spermatogenesis occurs in the seminiferous tubules of the testes, with follicle stimulating hormone (FSH), the key hormone regulating spermatogenesis in primates (Sharpe 1994, Norman & Litwack 1997, Jones 1997). Testosterone exerts a secondary influence on sperm production. Circulating androgen concentrations are not correlated with rates of spermatogenesis (Johnson & Everitt 1984, Rommerts 1988), and testicular androgen concentrations do not correlate with sperm count (Weinbauer & Nieschlag 1991). Sperm production is related to testis size, but sperm output depends on ejaculatory frequency, epididymal efficiency, sperm storage capacity, and degree of precopulatory stimulation (Bercovitch 1989, Johnson 1989). Male cotton-top tamarins residing in their cooperative breeding family group are not developmentally suppressed but require exposure to an unrelated female in order to initiate their reproductive careers (Ginther et al. 2002). Hence, reproductive suppression among males involving endocrine profiles is unlikely to hamper sperm production, and, even in the presence of diminished sperm production, the fundamental factor promoting paternity is access to females and not sperm count (see Bercovitch 1989).

The most detailed information about the socioendocrinology of male reproductive maturation comes from studies of rhesus macaques. Among adolescent males within a cohort, higher ranking animals and those whose mothers are dominant tend to have elevated testosterone concentrations and larger testicles than lower ranking peers or those whose mothers are subordinant (Bercovitch & Goy 1990, Bercovitch 1993, Dixson & Nevison 1997). Among adult male rhesus macaques, a cluster of traits, including high dominance status, large body mass, relatively large testes, and good body condition are associated with actual progeny production (Bercovitch & Nürnberg 1996). Sons of high-ranking mothers are heavier than peers from one year of age (Figure 5) through adulthood, and infant weight accounts for a small fraction of the variance in adult male reproductive success (Bercovitch et al. 2000). High-ranking young males are more likely to sire offspring in their natal troop than are low-ranking peers (Bercovitch et al. 2000).

Dominant male rhesus macaques tend to remain in their natal troop longer than subordinate males (Colvin 1986), and some evidence implicates neuroendocrine factors as a variable influencing the timing of natal dispersal. Males who disperse at relatively young ages tend to have lower levels of cerebrospinal fluid concentrations of 5-hydroxyindoleacetic acid (CSF 5-HIAA), a serotonin metabolite, with low

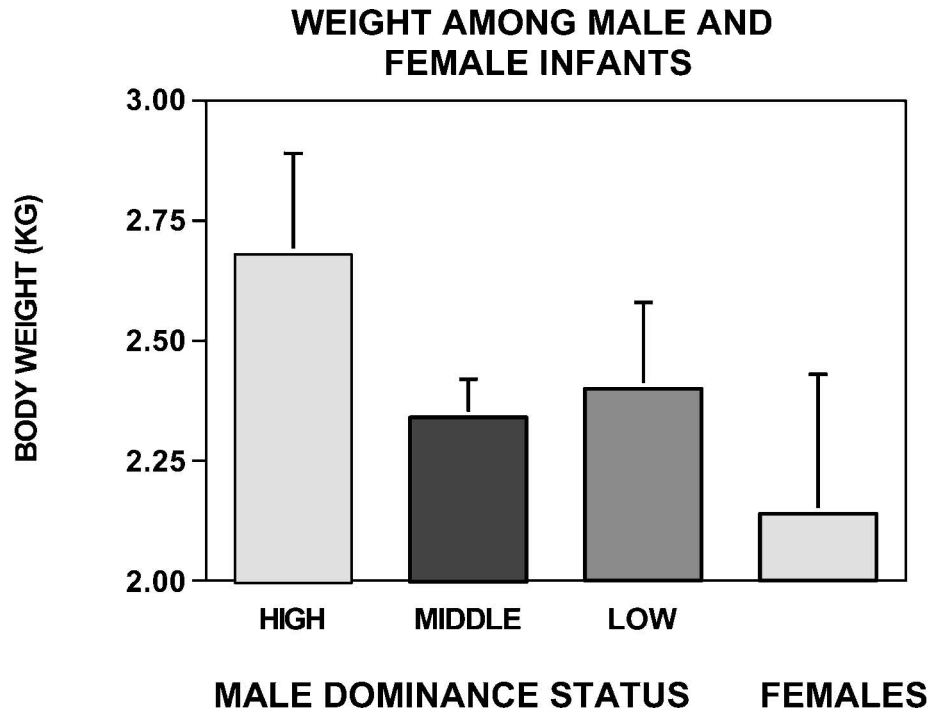


Figure 5 The influence of dominance rank on male mass at one year of age. Histogram bars plot the mean plus standard deviation. High-ranking males weigh significantly more than lower ranking peers (ANOVA: $F(2,8) = 4.823$, $P = 0.04$), and females weigh significantly less than males ($t = -3.329$, $df = 26$, $P < 0.01$). Modified from Bercovitch et al. 2000.

levels of CSF 5-HIAA associated with reduced social competence, excessive aggression, and increased mortality risks (Mehlman et al. 1995, Higley et al. 1996).

Delayed dispersal among male rhesus macaques is therefore linked with reduced mortality risks, high dominance rank, accelerated reproductive development, and earlier onset of reproductive career. However, the primary determinant of short-term reproduction in males is not body condition or status, but the number of females with which they have mated (Bercovitch & Nürnberg 1996). Dominant males not only mate with more females than subordinate males, they also have longer mount series (Carpenter 1942, Kaufmann 1965). The longer mount series is accompanied by a greater number of thrusts per intromission, or mounts before ejaculation, which should maximize the number of sperm delivered into a female (Bercovitch & Nürnberg 1996). In summary, dominant males appear to have a reproductive edge in rhesus macaques because they are characterized by a number of social, sexual, and physiological traits that foster mating with multiple females, but subordinate males do adopt surreptitious tactics that have been linked with actual reproductive success (Berard et al. 1994).

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Patterns documented in rhesus macaques have been found in other papionins. Sons of high-ranking female savanna baboons undergo accelerated reproductive maturation (Alberts & Altmann 1995), and evidence that high-ranking young natal males have sired offspring in their troop of birth has been reported from a number of study sites (Packer 1979, Smuts 1985, Bulger & Hamilton 1988, Altmann et al. 1996). Alpha male mandrills (*Mandrillus sphinx*) have more pronounced secondary sexual developments, higher testosterone concentrations, and greater reproductive success than subordinate males (Wickings & Dixson 1992, Dixson et al. 1993), with abrupt changes in social status associated with changes in physical appearance and reproductive activity (Setchell & Dixson 2001). Subordinate male mandrills develop more slowly than do dominant conspecifics (Setchell & Dixson 2002). Young sons of high-ranking Barbary macaques (*M. sylvanus*) have a higher mating success than sons of low-ranking females (Paul & Kuester 1990), and mating success is strongly tied to actual reproductive success in this population (Paul et al. 1993).

Orangutans (*P. pygmaeus*) are unusual among primates because the socioendocrinology of male development results in the co-existence of two “morphs”: those with or without secondary sexual traits (Kingsley 1982, Graham & Nadler 1990). Suppression of endocrine levels is associated with failure to develop secondary sexual traits but not with reduced fertility (Maggioncalda et al. 1999, 2000; Dixson et al. 1982). Development of secondary features, such as cheek flanges, enlarged laryngeal sacs, and lengthy beards, seems suppressed under conditions of high male density and is possibly in the wild a response to the negative effects of vocal signals, i.e., male loud calls (Maggioncalda et al. 1999). Whether the alternative developmental strategies have comparable reproductive success among orangutans in the wild is unknown.

Male access to females is not only a consequence of agonistic competition among some primate species but is also related to the adoption of complex social strategies (Strum 1987, Bercovitch 1991). Among cercopithecines, male reproductive maturation begins significantly later in life, lasts for a longer period of time, and is more variable in duration than it is among females (Bercovitch 2000). A lengthy period of development permits males the opportunity to boost body mass prior to engaging in costly male competition, as well as reducing susceptibility to predators and buffering against feeding uncertainties during dispersal. Large size enhances endurance rivalry, or the ability to withstand long periods of feeding deprivation while mate guarding (Andersson 1994, Bercovitch 1997). A long life history stage devoted to male reproductive maturation also allows males the opportunity to learn complex social skills, which could be quite important in troop integration following dispersal and in forming nonkin alliances (see Bercovitch 1988, Silk 1993, Widdig et al. 2000). In some cercopithecines, new male migrants enter a troop at the lower echelons of the dominance hierarchy, while in other species, males enter at the upper echelons of the status structure; but in both types of cercopithecine primates, sexually receptive females actively solicit newcomers (Berard 1999). Female mate choice for novel males provides a

genetic hedge against inbreeding, as well as diversifying genetic composition of offspring (Bercovitch 1997). The advantage of selecting novel males is unclear, but the behavior conforms with Darwin's (1882) observation that "... females often prefer strangers to their old companions." Translating sexual invitations into reproductive opportunities in the face of resident male competition probably requires brains as well as brawn.

In summary, we suggest that socioendocrine factors play a substantial role in regulating male reproductive development. Although a direct connection between suppressed endocrine status and sperm production is lacking, males with retarded physiological development appear to be at a disadvantage compared with peers in terms of social behaviors related to obtaining and maintaining access to sexually receptive females. Therefore, males with accelerated sexual maturation probably sire offspring at earlier ages than their peers with retarded sexual maturation, but the differences are more likely to be due to social skills than a direct consequence of endocrine suppression of fertility, as is the case with females.

CONCLUSION

Primate socioendocrinology is a challenging field. The growing use of noninvasive methods for determining endocrine profiles, as well as genetic relationships, provides multiple opportunities to advance our understanding of primate socioendocrinology. One of the hallmarks of primates is their extensive ability to establish and maintain complex social relationships. This capacity has undoubtedly been constructed during evolution by developing a flexible physiological system responsive to the social environment. Hormones and behavior are inextricably intertwined in a feedback relationship that regulate each other.

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