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Persistence of maternal effects in baboons: Mother's dominance rank at son's conception predicts stress hormone levels in subadult males

Patrick Ogola Onyango [a,b,*], Laurence R. Gesquiere [a], Emmanuel O. Wango [b,d], Susan C. Alberts [c,d], Jeanne Altmann [a,b,d]

[a] *Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA*
[b] *Department of Animal Physiology, University of Nairobi, Chiromo Campus, P.O. Box 30197 00100, Nairobi, Kenya*
[c] *Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338, USA*
[d] *Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya*

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ABSTRACT

Dominance status and reproductive experience are maternal characteristics that affect offspring traits in diverse taxa, including some cercopithecine primates. Maternal effects of this sort are widespread and are sources of variability in offspring fitness. We tested the hypothesis that maternal dominance rank and reproductive experience as well as a male's own age and dominance rank predicted chronic fecal glucocorticoid (fGC) concentrations in 17 subadult wild male baboons, *Papio cynocephalus* (median age 6.5 years), in the Amboseli basin, Kenya. Among these variables, maternal dominance rank at a subadult male's conception was the sole significant predictor of the male's fGC and accounted for 42% of fGC variance; sons of lower ranking mothers had higher fGC than did those of high-ranking mothers. This result is striking because subadult male baboons are approximately 4–6 years past the period of infant dependence on their mothers, and are larger than and dominant to all adult females. In addition, many males of this age have survived their mothers' death. Consequently, the influence of maternal dominance rank persisted well beyond the stage at which direct maternal influence on sons is likely. Persistence of these major maternal influences from the perinatal period may signal organizational effects of mothers on sons' HPA axis. Although short-term, acute, elevations in GC are part of adaptive responses to challenges such as predators and other emergencies, chronically elevated GC are often associated with stress-related pathologies and, thereby, adverse effects on fitness components.

Introduction

Non-genetic parental effects, usually known as maternal effects, occur in many taxa (reviewed in Bernardo, 1996; Kirkpatrick and Lande, 1989; Mousseau and Fox, 1998; Wolf et al., 1998). These effects often arise from parents' social environment and from the parent's exposure to psychosocial stressors or access to essential resources, which may in turn impact offspring fitness (e.g., in dung beetles, Hunt and Simmons, 1997; cleaning gobies, Whiteman and Côté, 2004; savannah baboons, Altmann and Alberts, 2005; black lemurs, Bayart and Simmen, 2005; spotted hyenas, Dloniak et al., 2006; bluegill sunfish, Neff and Lister, 2006; dark-bellied brent geese, Poisbleau et al., 2006; mandrills, Setchell et al., 2006; mountain gorillas, Scott and Lockard, 2006; lizards, Warner et al., 2007). Maternal effects on offspring phenotype may also arise from maternal reproductive experience or age because of age-related changes in maternal condition and reproductive investment strategies (Curio, 1983; Förslund and Pärt, 1995; Stearns, 1992; Williams, 1966).

Maternal effects have been demonstrated to impact several fitness components of offspring in a range of species, including effects on birth weight or egg size (e.g., humans and chimpanzees, Fessler et al., 2005; zebra finch, Gilbert et al., 2006; rove beetle, Kyneb and Toft, 2006; soil mites, Plaistow et al., 2006; fish, Taborsky, 2006; lizards, Warner et al., 2007), growth rate and age at maturity (e.g., mandrills, Setchell et al., 2002; savannah baboons, Altmann and Alberts, 2005; beetles, Kyneb and Toft, 2006; mites, Plaistow et al., 2006), and longevity or probability of survival (e.g., mandrills, Setchell et al., 2006; fruit flies, Priest et al., 2002; herring gulls, Bogdanova et al., 2006; turtles, Paitz et al., 2007). These effects also impact the development of competitive traits such as aggression and mounting behavior (Dloniak et al., 2006; Forstmeier et al., 2004; Royle et al., 2005), and both song rate and mate choice (Forstmeier et al., 2004). In the baboon population that is the focus of the present study, both maternal dominance status and parity have maternal effects; one or both predict offspring growth, dominance status of daughters, and age at maturity of both sons and daughters (Alberts and Altmann, 1995b; Altmann and Alberts, 2003, 2005).

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* Corresponding author. Fax: +1 609 2580 2712.
E-mail address: pogola@princeton.edu (P.O. Onyango).

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Although maternal effects are widespread, their role in the production of physiological traits, and the mechanisms by which they are mediated, are less well understood (but see Walker et al., 2004 for a recent review of the experimental findings for rodents and implications for humans, and Sanchez, 2006 for a review of the impact on HPA axis development of experimentally manipulated adverse care in primates). One proposal is that social or nutritional stressors experienced by a mother impact her hypothalamic–pituitary–adrenal (HPA) pathway (e.g. social: Creel, 2001; Goymann and Wingfield, 2004; nutritional: Coplan et al., 2006, Lesage et al., 2001). Glucocorticoids (GC), which are one of the end-products of this HPA pathway, may then adversely impact the fetus or young infant through direct effects during gestation and/or lactation, or through indirect effects via change in maternal behavior. Short-term increases in the secretion of GC are adaptive and enable an individual to overcome stressful stimuli and meet acute challenges (Abbott et al., 2003; Romero, 2002, 2004; Sapolsky, 2005; Sapolsky et al., 2000). In the long term, however, chronically elevated levels of GC arise from a number of mechanistic failures, compromise major functions of the body including reproduction, immunity, and growth, and are associated with many pathological conditions (Sapolsky, 1992a).

Because maternal effects associated with either social or nutritional factors may impact offspring GC either through maternal physiology or behavior during the fetal or infant stages, concentrations of GC in offspring are particularly promising candidates for investigation of maternal effects. Moreover, persistence of maternal influences from the perinatal period into maturity may signal organizational effects of mothers on sons' HPA axis. According to the fetal programming hypotheses (e.g. Barker et al., 1993; Phillips, 2007), the extent to which such maternal effects impose fitness costs will depend on whether differences in lifetime experiences of sons match those of their perinatal period.

Current characteristics of an individual, such as age or dominance rank, regardless of genetic, maternal, or other contributions to these traits, also influence fitness components in most species (Abbott et al., 2003; Alberts et al., 2003; Alberts et al., 2006; Clutton-Brock, 1988; Côtè and Festa-Bianchet, 2001; Förslund and Pärt, 1995; Holand et al., 2004; Holekamp et al., 1996; von Holst et al., 2002; Packer et al., 2000; Romero, 2004; Sapolsky, 2005). Furthermore, differences in GC levels are also sometimes associated with these current characteristics of an individual (Creel, 2001; Goymann and Wingfield, 2004; Sapolsky and Altmann, 1991). In the present research, we sought to extend our prior investigations of maternal effects in wild baboons through evaluation of both maternal effects and current traits in older offspring (specifically subadult males) and by measurement of these males' glucocorticoids, a major component of response to challenge.

Table 1
Characteristics of 17 the subadult males in the present study (see text for details)

Male	Maternal characteristics		Offspring characteristics			
	Parity	Rank	Mean age	Mean rank	# months sampled	Mean fGC
Ced	4	6	7.17	10.40	17	42.33
Dyn	5	3	6.75	14.64	11	43.23
Elv	1	10	6.12	4.89	18	61.71
Fuz	4	13	7.11	11.43	14	60.05
Lat	3	3	7.03	7.64	11	33.23
Leb	1	7	6.97	12.13	8	51.41
Lui	1	5	6.48	12.86	15	52.20
Naw	2	6	5.83	14.89	9	49.67
Net	7	4	6.39	9.43	14	46.16
Nyl	4	7	6.95	11.67	15	39.61
Oce	6	9	6.81	2.73	15	77.89
Vap	2	7	6.29	7.40	15	43.20
Vaz	4	5	6.66	7.00	11	48.16
Vei	2	4	6.44	6.37	19	34.15
Voy	10	8	5.81	6.23	13	49.08
Wes	1	3	6.15	10.50	16	45.08
Weu	7	1	6.20	7.13	16	44.62

Table 2
Results of linear regression model predicting sources of variance in fecal glucocorticoids concentrations for 17 subadult male baboons

Predictor	Adjusted R^2	Std. beta	*F* statistic	*T* statistic	Significance
Whole model	0.298		2.701		0.082
Maternal rank		**0.642**		**2.968**	**0.012**
Parity		0.052		0.236	0.817
Male age		−0.100		−0.461	0.653
Male rank		−0.170		−0.756	0.464

Only maternal dominance rank predicted son's fGC concentrations.

Materials and methods

Subjects

The research was conducted in a well-studied natural population of baboons in the Amboseli/Longido basin, 2° 40'S, a semi-arid short grass savannah ecosystem located at the foot of Mt. Kilimanjaro in southern Kenya (Behrensmeyer and Boaz, 1981; Western and van Praet, 1973). The subjects were 17 pre-dispersal subadult male baboons, *Papio cynocephalus*, that were born into five wild-feeding groups monitored by the Amboseli Baboon Research Project (ABRP). In baboon males the transition to subadult from the juvenile stage is marked by rapid testes enlargement, which is associated with production of viable sperm and occurs at a median age of 5.7 years in Amboseli (Alberts and Altmann, 1995b). After about 2–3 years spent as subadults, males achieve a size and competitive ability that enables them to defeat some adult males in fights, thereby accomplishing the transition to adulthood and gaining potential access to fertile females (Alberts and Altmann, 1995a; Alberts et al., 2006). Samples for GC analysis were collected across the 20 months prior to the males' natal dispersal, another major male maturational milestone, one that usually occurs during subadulthood or early adulthood (Alberts and Altmann, 1995b). In other words, we focused on males during an important, relatively narrow life-history stage, circumscribed on the lower end by testicular enlargement and on the upper end by natal dispersal (both of which occur throughout the year, as do conception and birth in females). We included all natal males that were subadult for an appreciable period of time between September 2000 and May 2005, the period for which fecal hormone samples were available for subadults across many pre-dispersal months.

ABRP research has been ongoing for over three decades. All members of study groups are individually identifiable, and each group is the focus of detailed observations several days each week. Consequently, ages of all males born into ABRP study groups are known to within a few days. Because the study subjects and their mothers were part of this long-term research project, we had data on the focal male subjects in the months prior to their natal dispersal (their age, fGC profiles, dispersal dates, and dominance rank), as well as on their mother's dominance rank and reproductive experience at the time of the male's conception, approximately 6 years prior to average age at hormone sampling for the current project.

Dominance rank

Dominance ranks are assigned based on outcomes of pair-wise agonistic encounters by creating a dominance matrix from these outcomes (win/loss) with rank orderings that minimize entries below the main diagonal (Hausfater, 1975). All subadult and adult males rank above all adult females, enabling us to readily assign dominance ranks that reflect ordinal rankings of individuals within each sex. The highest ranking individual of each sex is ranked 1, the next 2, and so on. In Amboseli, rank assigned in this way predicts rates at which females are spatially supplanted (Altmann, 1980 p.98), access of adult males to estrous females (Alberts et al., 2006; Hausfater, 1975), growth rates of sexually immature offspring (Altmann and Alberts, 2005), adult rank of daughters, age at sexual maturity of sons and daughters (Alberts and Altmann, 1995b), and female reproductive rates (Altmann and Alberts, 2003, Davidson, in revision).

Female dominance rank in baboons is highly stable throughout adulthood (Pereira, 1995; Walters and Seyfarth, 1987), with the major exception that older mothers sometimes cede rank to mature daughters (Combes and Altmann, 2001); because mothers and daughters occupy adjacent ranks, however, even these rank changes are relatively small. A female's dominance rank at her offspring's conception has been predictive of a number of offspring characteristics; here we term this the male's maternal dominance rank (Altmann, 1980; Altmann and Alberts, 2005). Among the subjects in this study, maternal dominance rank ranged from 1 to 13 (median 6); see Table 1. Not only are ranks of mature females highly stable in general, but on the average, the rank positions of mothers in this study changed by less than one from a son's conception through the end of his first year of life, i.e. the 18-month period of gestation and infant dependence, and no mother changed more than two rank positions during this period.