

# Primate Allomaternal Care

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## Abstract

Allomaternal care (AMC) (i.e., infant care that is provided by group members other than an infant's mother) is a rare, although phylogenetically widespread, mammalian infant care strategy. In primates, however, AMC occurs at unusually high frequencies, particularly among several haplorhine (monkey and ape) taxa. In fact, AMC is present in every major primate radiation and has been described in 74% of 154 species for which data are available. Its widespread presence in the Order Primates suggests that there may have been strong selective pressure for AMC early in primate evolution, but it is currently unknown why these behaviors are so common in primates. Research focused on captive callitrichids (tamarins and marmosets) has contributed greatly to our understanding of the potential causes and consequences of highly derived forms of AMC (i.e., cooperative breeding). Recent efforts have shifted focus to understand the selective pressures leading to the expansion and diversification of AMC throughout the Primate Order, thus expanding research to investigate the causes and consequences of less derived forms of AMC. Here we review the broad-scale patterns observed in primates and outline innovative and exciting avenues of research moving forward.

## INTRODUCTION

Allomaternal care (AMC) is infant care provided by individuals other than the genetic mother (e.g., fathers, siblings, aunts, uncles, or unrelated individuals, termed *helpers*), including several seemingly altruistic behaviors such as babysitting, carrying, nursing, crèching, or huddling for thermoregulation. Although AMC has been observed in several taxonomically diverse species (e.g., birds, social insects, and mammals), mammalian mothers are typically the sole providers of infant care and AMC is uncommon. However, recent research indicates that AMC is notably abundant in primates, suggesting that relatively strong selective pressures helped shape this behavior early in our evolution.

AMC was the likely evolutionary antecedent to cooperative breeding—a more derived form of AMC including infant provisioning, that evolved in only a few species including the callitrichids (tamarins, marmosets)

and humans. Cooperative breeding is ubiquitous among humans, and proposed to have been profoundly important during human evolution: Mothers and offspring gained significant energetic benefits, enabling higher maternal fertility, protracted infant development, and less costly brain growth, which ultimately led to emotionally modern brains (Hrdy, 2009). It is thought that when the cognitive abilities shared by apes and our earliest human ancestors merged with these underlying prosocial motivations, “shared intentionality”—a social disposition identified as the source of many uniquely human traits, such as culture and language—emerged (Burkart, Hrdy, & van Schaik, 2009). These traits allowed our ancestors, and eventually modern humans, to forge deeper social relationships, and cooperate on an unparalleled level. In short, prosocial behaviors associated with ancestral forms of shared infant care (i.e., AMC) paved the way for us becoming human.

## FOUNDATIONAL RESEARCH

### WHO CARES?

The study of primate AMC has traditionally focused on New World and Old World monkeys. Until recently, AMC in primates was viewed as exceptional, and thought to be entirely absent in one of the two primate suborders (strepsirrhines, i.e., lemurs, lorises, galagos). As data have accumulated, scientists have been surprised to discover that primate AMC is both widespread and common. Nearly 75% of primate species display some type of AMC (Table 1). By suborder, AMC is present in 61% of strepsirrhines, and 76% of haplorhines (monkeys, apes including humans) for which there are data.

Currently, it is difficult to make many meaningful statements about the abundance of AMC because (i) we lack solid empirical data for many species; (ii) estimates are heavily impacted by the number of species in the given taxonomic group; and (iii) these broad-scale analyses do not consider intra-specific variation. However, it is notable that AMC is present in 100% of callitrichids (tamarins, marmosets). Perhaps even more remarkable, because AMC was thought to be absent in strepsirrhines until just recently, is the frequency at which AMC occurs in several of the nocturnal, solitary and pair-living cheirogaleids (dwarf lemurs, mouse lemurs). Pair-living males babysit (Fietz & Dausmann, 2003), and although solitary species were once thought to have “little or no opportunity for nonmaternal care” (Ross & MacLarnon, 2000, p. 94), ‘solitary’ females communally nest their infants and share in allomaternal suckling (Eberle & Kappeler, 2006). It should be noted, however, that we lack data for three of five cheirogaleid genera, reinforcing the fact that more information is still needed. Both callitrichids

**Table 1**  
Phylogenetic Distribution of Allomaternal Care in the Order Primates

Source	N			AMC excluding protection (%)	AMC		Carrying		Notes
	Species	Strep	Hap		Strep (%)	Hap (%)	Strep (%)	Hap (%)	
Isler and van Schaik (2012)	98	20	78	72.00	65.00	74.36	45.00	58.97	445 mammals
Hrdy (2010)	120	27	93	68.33	48.15	75.27	N/A	N/A	Primates
Tecot <i>et al.</i> (2012, 2013)	23	23	0	65.22	65.22	N/A	34.78	N/A	Lemurids
Combined dataset: Isler and van Schaik (2012), Tecot <i>et al.</i> (2012, 2013)	109	78	31	71.50	64.52	74.36	48.39	58.97	—
All datasets combined	154	31	123	74.03	61.29	76.42	N/A	N/A	—

Combining databases by Hrdy and Tecot (unpublished data, available in All the World's Primates Database), Isler and van Schaik (2012), Tecot *et al.* (2012), and Tecot, Baden, Romine, and Kamilar (2013). Strep, strepsirrhines; Hap, haplorhines.

and cheirogaleids comprise several litter-bearing species for which helpers alleviate maternal energetic burden and increase infant survival (Bales, Baker, Miller, & Tardif, 2000; Fietz & Dausmann, 2003). Despite the fact that the majority of the remaining primates bear singletons, AMC by fathers, other relatives, and unrelated individuals occurs throughout the Order.

AMC by adult males is generally strongest in species where paternity is certain. Male care is most common among pair-living taxa, including at least two lemur species (mongoose lemurs, red-bellied lemurs; Figure 1), several New World monkeys (tamarins, marmosets, titis, owl monkeys), and some apes (siamangs, humans). In cases where females are not monopolizable and males can maximize their reproductive success by living with a pair-mate rather than seeking out multiple females, the benefits of paternal care are clear. However, even resident males who are unrelated to the mother and infant will sometimes provide care to extra-pair young (fat-tailed dwarf lemurs, Fietz *et al.*, 2000).

In group-living species with AMC, some adult males also provide infant care, and not necessarily more often to their own genetic offspring (Ménard *et al.*, 2001). More often, nulliparous females (i.e., females who have not borne offspring) provide care. Juvenile helpers of both sexes are generally older



**Figure 1** Red-bellied lemur (*Eulemur rubriventer*) male carrying an infant while traveling in Vatoharanana, Ranomafana National Park, Madagascar. *Source:* Photo credit Lahitsara Jean Pierre.

siblings, but help is not always directed towards relatives (Fairbanks, 1990), and cannot be explained entirely by kin selection. Although AMC among adult females is most common in female bonded species (i.e., those with little female emigration and high female relatedness), allomothering also occurs in species in which both sexes emigrate (capped langurs, Stanford, 1992), although to a much lesser degree (Bennett & Davies, 1994). Despite this, AMC is never prevalent in species characterized by male philopatry (i.e., where males remain in their natal groups), except perhaps in anomalous cases of maternal death.

### WHY HELP? ADAPTIVE VALUE OF AMC

Traditionally, studies of AMC have focused on the benefits to caregivers because helping and cooperation seemed paradoxical in light of evolutionary theory: Why should fathers invest in one infant when they can produce several progeny by mating with additional females? Why should individuals invest in infants who are not their own, sometimes foregoing their own reproduction to do so? While several forms of AMC may not be costly (e.g., huddling with infants for thermoregulation), contributing time and energy to infants can be (Heinsohn & Legge, 1999). Babysitters can suffer drastic reductions in body mass by sacrificing time normally allocated to foraging and feeding (Clutton-Brock *et al.*, 1998), carrying infants makes travel more energetically expensive and awkward (Altmann & Samuels, 1992), and in extreme cases, one's own reproduction may be suppressed (Solomon & French, 1997). Despite the associated costs of AMC, studies have revealed that helpers can gain direct benefits by, for example, learning to parent and subsequently increasing their own offspring's survival (vervet monkeys, Fairbanks, 1990), or by securing an infrequently available breeding position (marmosets, Abbott, Digby, & Saltzman, 2009). They can also benefit indirectly by providing care to related offspring and increasing their inclusive fitness (Briga, Pen, & Wright, 2012; Hamilton, 1964), and even by caring for unrelated individuals via mutualism (black-and-white ruffed lemurs, Baden, Wright, Louis, & Bradley 2013), or reciprocal altruism (capuchins, O'Brien & Robinson, 1991). Thus, AMC may represent an optimal reproductive strategy, yielding relatively higher fitness pay-offs to caregivers than alternative scenarios.

### WHAT ABOUT MOTHERS? ADAPTIVE VALUE TO MOTHERS AND THEIR OFFSPRING

Many primate females are "continuous care and contact" mothers (Hrdy, 2009), who prohibit others from interacting with their offspring, presumably because of potential threats such as negative infant handling and infanticide that can severely and directly impact infant survival. But mothers who allow others to help them rear their young can benefit in dramatic ways. In cooperative breeders, relatively greater AMC can increase an infant's quality of care, health, and survival, and a mother's reproductive rate (humans, Egeland & Hiester, 1995; Sear, Mace, & McGregor, 2000; callitrichids, Bales *et al.*, 2000). Broad, comparative analyses determined that haplorhine mothers receiving help reproduce faster than mothers without help and may ultimately experience relatively higher reproductive success (Mitani & Watts, 1997). However, these effects on fertility are absent in lemurids (Tecot *et al.*, 2012) and nonprimate mammals (Isler & van Schaik, 2012). These divergent results may indicate distinctive selective pressures for haplorhines, or reflect

the very strong influence of callitrichids on these analyses. As cooperative breeders, litter-bearing callitrichids have a highly derived form of AMC that includes infant provisioning, and that potentially allows offspring to grow quickly and at less of an energetic cost to mothers, who often resume cycling soon after birth. It appears that this extensive form of AMC largely drove the positive relationship between AMC and fertility in haplorhines (Isler & van Schaik, 2012). At the same time, fetal and infant growth rates for strepsirrhines are only available from provisioned, captive animals, which may result in overestimated growth rates in species lacking AMC. Data on more taxa will help determine whether these relationships hold true for noncooperatively breeding haplorhines, and whether the benefits to strepsirrhines have been underestimated.

Additional hypotheses for the evolution of AMC in primates have been tested using broad-scale comparative analyses, but caution should be used in interpreting such studies. Comparative meta-analyses fail to consider inter-individual variation and/or the fluctuating selection pressures at the intraspecific level under which primate sociality has evolved (Strier, 2009). Therefore, they may not provide the level of resolution needed to determine the adaptive benefits of AMC in species where individual care is facultative (i.e., can but does not always occur), or the selective pressures leading to the expression of AMC. For example, in testing whether maternal energetic stress favors the evolution of AMC (owing to energetic savings afforded mothers), Ross and MacLarnon (2000) were limited in using species dietary categories as proxies for nutritional stress. Because species have evolved adaptations to successfully extract nutrients from their dietary items, an ideal test of the relationships between energetic stress and AMC might be one that is conducted among species sharing a dietary guild. Individual-level investigations within a single species might be most informative in helping to address what internal states and social and physical environments select for AMC, and whether and how the quality and quantity of AMC influences reproductive success (Mitani & Watts, 1997).

#### PROXIMATE MECHANISMS PROMOTING AMC

Individual variation can help identify environmental pressures selecting for and prohibiting AMC. Maternal size, litter size, and group size are all associated with variation in AMC (Bales, French, & Dietz, 2002), indicating that AMC can release individuals from certain reproductive constraints. It is also possible that energetic need drives maternal tolerance of AMC (Ross & MacLarnon, 2000), such that lower-ranking mothers, mothers bearing twins, or mothers with older dependent offspring would allow AMC to a greater

extent than higher-ranking mothers, mothers bearing singletons, or mothers who recently gave birth.

There is growing consensus that the physiological mechanisms promoting and maintaining maternal care may also facilitate AMC (Ziegler, 2000). Mothers undergo critical endocrine changes during pregnancy and lactation that have evolved to enhance responsiveness to offspring (Saltzman & Maestripieri, 2011). More recently, research examining the endocrinological profiles of fathers found that they respond to their mate's pregnancy (Ziegler, Washabaugh, & Snowdon, 2004) and to infants themselves, indicating that paternal hormonal changes can facilitate, maintain, or prime individuals for care. For example, there is abundant support for an inverse relationship between paternal care and testosterone, which may decrease the likelihood of infant-directed aggression, or reflect the trade-off between mating and parenting effort (Wingfield, Hegner, Dufty, & Ball, 1990). In humans, paternal testosterone decreases pre- to postpartum (Storey, Delahunty, McKay, Walsh, & Wilhelm, 2006), and after mating and siring offspring (Gettler, McDade, Feranil, & Kuzawa, 2011). Testosterone levels decrease once males become fathers, and are lower in those who invest more (Gettler *et al.*, 2011; Nunes, Fite, Patera, & French, 2001). The neuropeptide prolactin has several hundred biological actions, including stimulating female lactation, inhibiting male sexual behavior, and mediating parental behavior (Freeman, Kanyicska, Lerant, & Nagy, 2000). This hormone also responds to carrying/infant contact (cotton-top tamarins, common marmosets, Ziegler, 2000), infant cries, and play (humans, Fleming, Corter, Stallings, & Steiner, 2002) in fathers. Ziegler, Prudom, Zahed, Parlow, and Wegner (2009) found that prolactin elevations even buffered experienced fathers from weight loss associated with infant carrying, thus reducing energetic costs.

To our knowledge, very little research has examined the hormonal mechanisms underlying AMC in nonparental helpers (i.e., alloparental care), although help from these individuals is hypothesized to be essential (Hrdy, 2009). Higher levels of vasopressin (which promotes offspring care) in grandmothers than control women (Gray & Samms-Vaughan, 2009), and elevated prolactin levels in cooperatively breeding nonprimate babysitters that are otherwise absent in nonhelpers (meerkats, Carlson *et al.*, 2006) suggest that alloparental care also can have a hormonal basis. Variation in hormone levels can thus help explain variation in AMC, although this research is still in its infancy, particularly as it pertains to free-living individuals. Extending this research to nonparental helpers would provide a critical test of the importance of hormonal mechanisms for the expression of infant care. It is also essential to understand how different individuals have been shaped by natural selection to help, not only in nonhuman primates, but also in our own evolutionary history.

Because the observation that AMC is widespread in primates occurred recently, a disparity of appropriate models has resulted in a research focus on a very limited set of primate species: the callitrichids. Two species in particular (*Callithrix jacchus*, *Saguinus oedipus*) have contributed the vast majority of what we know of primate hormones facilitating AMC. Therefore, we still know very little about the role that hormones play in the expression of AMC in the majority of species. One recent study by Rafacz, Margulis, and Santymire (2012) of bi-parental and exclusively maternal hylobatids (siamangs and gibbons, respectively) suggests that the same mechanisms are at work in species with less specialized paternal care. Future research on these mechanisms in species with facultative AMC will be fundamental in determining how adaptable (and critical) these systems are, and whether all primate AMC is rooted in such adaptability.

### CUTTING EDGE RESEARCH

Outside of studies with humans, the bulk of the work described herein has been conducted in captivity, largely owing to the fact that, until relatively recently, noninvasive hormonal sampling was difficult, if not impossible (Ziegler & Wittwer, 2005). Experimental studies have been particularly influential on contemporary studies of hormone-behavior relationships. They identified several hormones of interest, partly through selectively blocking their expression and observing effects on behavior, or injecting exogenous hormone, and were at times able to determine cause and effect. It is now well recognized that fecal metabolites can provide reliable measures of steroids such as cortisol and androgens, they parallel serum levels, and have been used in numerous studies as long-term (i.e., not acute) measures of adrenal and gonadal axis activity (Tecot, 2013). Recent work indicates that not only steroids, but also oxytocin and vasopressin, bonding hormones of potential interest in AMC research, and prolactin can be measured reliably in urine (Seltzer & Ziegler, 2007; Soltis, Wegner, & Newman, 2005). Armed with the ability to make predictions about hormones and the expression of AMC in variable social and mating structures, and the logistical feasibility of extracting these hormones from noninvasively collected samples, we can now investigate the mechanisms involved in facilitating and maintaining AMC in the natural environments in which they evolved.

Recent work in the field of behavioral genetics has revealed that variation in behavioral style (i.e., personality) can be explained, in part, by variation at the genotypic level (Bradley & Lawler, 2011), opening new and exciting avenues of inquiry. Although few investigations have examined the genetic basis of parental care in primates, parental effort does appear to have a significant heritable component in other animals (Komdeur, 2006).



For example, variation in the arginine vasopressin 1a gene (*AVPR1a*) in prairie voles has been linked to the quality and quantity of paternal care (Hammock & Young, 2005). Although evidence from field studies are more tenuous (Ophir, Campbell, Hanna, & Phelps, 2008; Solomon *et al.*, 2009), together, captive and wild-based studies provide strong evidence indicating the importance of this gene region in mediating social behavior (Fink, Excoffier, & Heckel, 2006; Heckel & Fink, 2008).

In humans, *AVPR1a* variants have been linked to altruistic tendencies (Israel *et al.*, 2008) and the propensity for men to form long-term, content partnerships (Walum *et al.*, 2008). Recent surveys have identified significant intra- and interspecific *AVPR1a* sequence variation across nearly all major primate radiations (Anestis *et al.*, 2014; Babb, Fernandez-Duque, & Schurr, 2010; Hong *et al.*, 2009; Rosso, Keller, Kaessmann, & Hammond, 2008) but to date, researchers have been unable to link this variation to either social or mating system in primates (Hong *et al.*, 2009). However, recent studies have found links between microsatellite polymorphisms (i.e., repeating sequences of DNA) and various personality traits, including conscientiousness (Hopkins, Donaldson, & Young, 2012) and friendliness (Anestis *et al.*, 2014).

Although most work has focused on *AVPR1a*, several other promising candidate genes have also been linked to parental behavior. For example, more than 30 single nucleotide polymorphisms (i.e., DNA sequence variation occurring when a single nucleotide—A, T, C or G—differs among members of a population) are known in the *OXTR* gene region (Israel *et al.*, 2008). *OXTR* gene polymorphisms have been associated with several social behaviors, including empathy (Rodrigues, Saslow, Garcia, John, & Keltner, 2009), prosociality (Kogan *et al.*, 2011), and both maternal (Francis, Young, Meaney, & Insel, 2002) and paternal sensitivity (Bakermans-Kranenburg & van Ijzendoorn, 2008). While results from captive studies are intriguing, little if any work has focused on the links between *OXTR* variation and personality in the wild.

#### KEY ISSUES FOR FUTURE RESEARCH

Work in the last 4 years has substantially increased our understanding of how widespread AMC is, thus increasing (i) the power of comparative analyses, (ii) our ability to look for broad patterns of selection, and (iii) the availability of suitable species of study. However, we still lack complete data on the distribution of primate AMC, which can skew comparative analyses. We therefore encourage researchers to broaden their taxonomic focus and also report AMC behaviors whenever possible (and noting its absence in cases where AMC is

never observed). Furthermore, armed with increasingly sophisticated technologies, researchers can begin to address not only the AMC behaviors themselves, but also the endocrinological, molecular, and energetic underpinnings of AMC.

Finally, It is important to consider the delicate balance between generating high-resolution data (i.e., frequent, high intensity sampling) and large sample size (i.e., many individuals from several social groups). While studies of some species can easily meet both criteria (e.g., cercopithecids), many other species live in strikingly smaller social groups, particularly the strepsirrhines. Researchers are thus faced with the difficult trade-off between achieving fine-grained behavioral resolution and statistical power. This issue is further compounded in species with facultative AMC. This does not mean that studies aren't worthwhile. In these cases, collecting high-resolution data from a relatively small, hopefully representative sample of focal individuals is preferable to neglecting to study taxa at all.

## REFERENCES

- Abbott, D., Digby, L., & Saltzman, W. (2009). Reproductive skew in female marmosets. In R. J. C. Hager (Ed.), *Reproductive skew in vertebrates* (pp. 337–368). Cambridge University Press: Cambridge, England.
- Altmann, J., & Samuels, A. (1992). Costs of maternal care: Infant-carrying in baboons. *Behavioral Ecology and Sociobiology*, *29*, 391–398.
- Anestis, S., Webster, T., Kamilar, J., Fontenot, M., Watts, D., & Bradley, B. (2014). AVPR1A variation in chimpanzees (*Pan troglodytes*): Population differences and association with behavioral style. *International Journal of Primatology*, *35*, 305–324.
- Babb, P., Fernandez-Duque, E., & Schurr, T. (2010). AVPR1A sequence variation in monogamous owl monkeys (*Aotus azarai*) and its implications for the evolution of platyrrhine social behavior. *Journal of Molecular Evolution*, *71*, 279–297.
- Baden, A., Wright, P., Louis, E., & Bradley, B. (2013). Communal nesting, kinship, and maternal success in a social primate. *Behavioral Ecology and Sociobiology*, *67*, 1939–1950.
- Bakermans-Kranenburg, M., & van Ijzendoorn, M. (2008). Oxytocin receptor (*OXTR*) and serotonin transporter (*5-HTT*) genes associated with observed parenting. *Cognitive and Affective Neuroscience*, *3*, 28–134.
- Bales, K., Baker, A., Miller, K., & Tardif, S. (2000). Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, *71*, 27–38.
- Bales, K., French, J., & Dietz, J. (2002). Explaining variation in maternal care in a cooperatively breeding mammal. *Animal Behaviour*, *63*, 453–461.
- Bennett, E., & Davies, A. (1994). The ecology of Asian colobines. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution* (pp. 129–171). Cambridge University Press: Cambridge, England.
- Bradley, B., & Lawler, R. (2011). Liking genotypes, phenotypes, and fitness in wild primate populations. *Evolutionary Anthropology*, *20*, 104–119.

- Briga, M., Pen, I., & Wright, J. (2012). Care for kin: Within-group relatedness and allo-maternal care are positively correlated and conserved throughout the mammalian phylogeny. *Biology Letters*, *8*, 533–536.
- Burkart, J., Hrdy, S., & van Schaik, C. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, *18*, 175–186.
- Carlson, A., Russell, A., Young, A., Jordan, N., McNeilly, A., Parlow, A., & Clutton-Brock, T. (2006). Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers. *Hormones and Behavior*, *50*, 94–100.
- Clutton-Brock, T., Gaynor, D., Kansky, R., MacColl, A., McIlrath, G., Chadwick, P., ... , Skinner, J. (1998). Costs of cooperative behaviour in suricates (*Suricates suricatta*). *Proceedings of the Royal Society London, B*, *265*, 185–190.
- Eberle, M., & Kappeler, P. (2006). Family insurance: Kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, *60*, 582–588.
- Egeland, B., & Hiester, M. (1995). The long-term consequences of infant day-care and mother-infant attachment. *Child Development*, *66*, 474–485.
- Fairbanks, L. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, *40*, 553–562.
- Fietz, J., & Dausmann, K. (2003). Costs and potential benefits of parental care in the nocturnal fat-tailed dwarf lemur (*Cheirogaleus medius*). *Folia Primatologica*, *74*, 246–258.
- Fietz, J., Zischler, H., Schwiegk, C., Tomiuk, J., Dausmann, K., & Ganzhorn, J. (2000). High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behavioral Ecology and Sociobiology*, *49*, 8–17.
- Fink, S., Excoffier, L., & Heckel, D. (2006). Mammalian monogamy is not controlled by a single gene. *Proceedings of the National Academy of Sciences*, *103*, 10956–10960.
- Fleming, A., Corter, C., Stallings, J., & Steiner, M. (2002). Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*, *42*, 399–413.
- Francis, D., Young, L., Meaney, M., & Insel, T. (2002). Naturally occurring differences in maternal care are associated with the expression of oxytocin and vasopressin (*v1a*) receptors: Gender differences. *Journal of Neuroendocrinology*, *14*, 349–353.
- Freeman, M., Kanyicska, B., Lerant, A., & Nagy, G. (2000). Prolactin: Structure, function, and regulation of secretion. *Physiological Reviews*, *80*, 1523–1631.
- Gettler, L., McDade, T., Feranil, A., & Kuzawa, C. (2011). Longitudinal evidence that fatherhood decreases testosterone in human males. *Proceedings of the National Academy of Sciences*, *108*, 16194–16199.
- Gray, P., & Samms-Vaughan, M. (2009). Investigating potential hormonal associations of grandmaternal care in Jamaica. *International Journal of Biological Anthropology*, *4*(1).
- Hamilton, W. (1964). The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology*, *7*, 1–52.
- Hammock, E., & Young, L. (2005). Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science*, *308*, 1630–1634.

- Heckel, G., & Fink, S. (2008). Evolution of the arginine vasopressin 1a receptor and implications for mammalian social behavior. In I. D. Neumann, R. Landgraf & B. V. Elsevier (Eds.), *Progress in brain research: Advances in vasopressin and oxytocin—from gene to behavior* (pp. 321–330). Elsevier: Philadelphia, PA.
- Heinsohn, R., & Legge, S. (1999). The cost of helping. *Trends in Ecology and Evolution*, 14, 53–56.
- Hong, K., Matsukawa, R., Hirata, Y., Hayasaka, I., Murayama, Y., Ito, S., & Inoue-Murayama, M. (2009). Allele distribution and effect on reporter gene expression of vasopressin receptor gene (AVPR1a)-linked VTNR in primates. *Journal of Neural Transmission*, 116, 535–538.
- Hopkins, W. D., Donaldson, Z., & Young, L. J. (2012). A polymorphic indel containing the RS3 microsatellite in the 5' flanking region of the vasopressin V1a receptor gene is associated with chimpanzee (*Pan troglodytes*) personality. *Genes, Brain and Behavior*, 11, 552–558.
- Hrdy, S. (2010). *Estimating the prevalence of shared care and cooperative breeding in the Order Primates, an appendix to mothers and others: the evolutionary origins of human understanding*. Retrieved from <http://www.citrona.com/hrdy/documents/AppendixIa.pdf>
- Kogan, A., Saslow, L., Impett, E., Oveis, C., Keltner, D., & Rodrigues Saturn, S. (2011). Thin-slicing study of the oxytocin receptor (OXTR) gene and the evaluation and expression of the prosocial disposition. *Proceedings of the National Academy of Sciences USA*, 108, 19189–19192.
- Komdeur, J. (2006). Variation in individual investment strategies among social animals. *Ethology*, 112, 729–747.
- Ménard, N., von Segesser, F., Scheffrahn, W., Pastorini, J., Vallet, D., Gaci, B., . . . , Gautier-Hion, A. (2001). Is male–infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie*, 324, 601–610.
- Mitani, J., & Watts, D. (1997). The evolution of non-maternal caretaking among anthropoid primates: do helpers help? *Behavioral Ecology and Sociobiology*, 40, 213–220.
- Nunes, S., Fite, J., Patera, K. J., & French, J. (2001). Interactions among paternal behavior, steroid hormones, experience. *Hormones and Behavior*, 39, 70–82.
- O'Brien, T., & Robinson, J. (1991). Allomaternal care by female wedge-capped capuchin monkeys: Age, rank, relatedness. *Behaviour*, 119, 30–50.
- Ophir, A., Campbell, P., Hanna, K., & Phelps, S. (2008). Field tests of cis-regulatory variation at the prairie vole avpr1a locus: Association with V1aR abundance but not sexual or social fidelity. *Hormones and Behavior*, 54, 694–702.
- Rafacz, M., Margulis, S., & Santymire, R. (2012). Hormonal correlates of paternal care differences in Hylobatidae. *American Journal of Primatology*, 74, 247–260.
- Rodrigues, S., Saslow, L., Garcia, N., John, O., & Keltner, D. (2009). Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proceedings of the National Academy of Sciences USA*, 106, 21437–21441.
- Rosso, L., Keller, L., Kaessmann, H., & Hammond, R. (2008). Mating system and avpr1a promoter variation in primates. *Biology Letters*, 4, 375–378.

- Saltzman, W., & Maestriperi, D. (2011). The neuroendocrinology of primate maternal behavior. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *35*, 1192–204.
- Sear, R., Mace, R., & McGregor, I. (2000). Maternal grandmothers improve the nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society B*, *267*, 461–467.
- Seltzer, L., & Ziegler, T. (2007). Non-invasive measurement of small peptides in the common marmoset (*Callithrix jacchus*): A radiolabeled clearance study and endogenous excretion under varying social conditions. *Hormones and Behavior*, *51*, 436–442.
- Solomon, N., & French, J. (1997). *Cooperative breeding in mammals*. Cambridge, England: Cambridge University Press.
- Solomon, N., Richmond, A., Harding, P., Fries, A., Jacquemin, S., Schaefer, R., ... , Keane, B. (2009). Polymorphism at the *avpr1a* locus in male prairie voles correlated with genetic but not social monogamy in field populations. *Molecular Ecology*, *18*, 4680–4695.
- Soltis, J., Wegner, F., & Newman, J. (2005). Urinary prolactin is correlated with mothering and allo-mothering in squirrel monkeys. *Physiology and Behavior*, *84*, 295–301.
- Stanford, C. (1992). Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behavioral Ecology and Sociobiology*, *30*, 29–34.
- Storey, A., Delahunty, K., McKay, D., Walsh, C., & Wilhelm, S. (2006). Social and hormonal bases of individual differences in the parental behaviour of birds and mammals. *Canadian Journal of Experimental Psychology*, *60*, 237–245.
- Strier, K. (2009). Seeing the forest through the seeds. *Current Anthropology*, *50*, 213–228.
- Tecot, S. (2013). Variable energetic strategies in disturbed and undisturbed rain forest habitats: Fecal cortisol levels in southeastern Madagascar. In J. Masters, M. Gamba, F. Génin & R. Tuttle (Eds.), *Leaping ahead: Advances in Prosimian Biology* (pp. 185–195). Springer: New York, NY.
- Tecot, S., Baden, A., Romine, N., & Kamilar, J. (2012). Infant parking and nesting, not allomaternal care, influence Malagasy primate life histories. *Behavioral Ecology and Sociobiology*, *66*, 1375–1386.
- Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J., Reiss, D., Igl, W., ... , Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor 1a gene (AVPR1A) associates with pair-bonding behavior in humans. *Proceedings of the National Academy of Sciences*, *105*, 14153–14156.
- Wingfield, J., Hegner, R., Dufty, A., Jr., & Ball, G. (1990). The “challenge hypothesis”: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*, 829–846.
- Ziegler, T., & Wittwer, D. (2005). Fecal steroid research in the field and laboratory: improved methods for storage, transport, processing, and analysis. *American Journal of Primatology*, *67*, 159–174.
- Ziegler, T., Washabaugh, K., & Snowdon, C. (2004). Responsiveness of expectant male cotton-top tamarins to mate’s pregnancy. *Hormones and Behavior*, *45*, 84–92.

Ziegler, T., Prudom, S., Zahed, S., Parlow, A., & Wegner, F. (2009). Prolactin's mediative role in male parenting in parentally experienced marmosets (*Callithrix jacchus*). *Hormones and Behavior*, *56*, 436–443.

#### FURTHER READING

- Chism, J. (2000). Allocare patterns among cercopithecines. *Folia Primatologica*, *71*, 55–66.
- Donaldson, Z., & Young, L. (2008). Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, *322*, 900–904.
- Emlen, S. (1991). Evolution of cooperative breeding in birds and mammals. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (3rd ed., pp. 301–335). Oxford, England: Blackwell Scientific.
- Fernandez-Duque, E., Valeggia, C., & Mendoza, S. (2009). The biology of paternal care in human and nonhuman primates. *Annual Review of Anthropology*, *38*, 115–130.
- Hrdy, S. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge, MA: Belknap Press of Harvard University Press.
- Isler, K., & van Schaik, C. (2012). Allomaternal care, life history and brain size evolution in mammals. *Journal of Human Evolution*, *63*, 52–63.
- Israel, S., Lerer, E., Shalev, I., Uzefovsky, F., Reibold, M., Bachner-Melman, R., ... , Ebstein, R. (2008). Molecular genetic studies of the arginine vasopressin 1a receptor (*AVPR1a*) and the oxytocin receptor (*OXTR*) in human behavior: From autism to altruism with some notes in between. *Progress in Brain Research*, *170*, 435–449.
- Ross, C. (2003). Life history, infant care strategies, and brain size in primates. In P. M. Kappeler & M. E. Pereira (Eds.), *Primate life histories and socioecology* (pp. 266–284). Chicago, IL: University of Chicago Press.
- Ross, C., & MacLarnon, A. (2000). The evolution of non-maternal care in anthropoid primates: A test of the hypotheses. *Folia Primatologica*, *71*, 93–113.
- Tecot, S., Baden, A., Romine, N., & Kamilar, J. (2013). Reproductive strategies and infant care in the Malagasy primates. In K. Clancy, K. Hinde & J. Rutherford (Eds.), *Building babies: Primate development in proximate and ultimate perspective*. Developments in primatology: Progress and prospects (pp. 321–359). New York, NY: Springer.
- Whitten, P., Brockman, D., & Stavisky, R. (1998). Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*, *27*(Suppl.), 1–23.
- Ziegler, T. (2000). Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica*, *71*, 6–21.

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