

APPENDIX I — 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* (2009), posted on line by Sarah B. Hrdy June 23, 2010, at www.citrona.com

Background

When I began to write *Mothers and Others*, it was still widely assumed among Developmental Psychologists, Attachment Theorists, Neuroscientists and many others, that exclusive care of infants by their mothers was the primate norm, a generalization which I knew to be incorrect. "In fact," as I wrote in the book "this continuous-care-and-contact mothering characterizes only about half of the roughly 276 species of living primates . . ." (2009:68) Even as I wrote this, I was aware that the taxonomy I had relied on was being expanded. The current version of Noel Rowe's encyclopedia of living primates encompasses closer to 413 species. Furthermore, in the book I had written that half of all primate species exhibited some form of allomaternal infant care (p. 84) and that some 20% of all primates would exhibit both alloparental care and at least minimal provisioning of young (p. 92). But these are almost certainly low estimates. Until recently fieldworkers have simply not been specifically on the look-out for allomaternal involvement in infant care. Often, it was just taken for granted that the individual holding the baby must be the parent even when she (or he) was actually not.

As I neared completion of the book, in August of 2008, I attended the Symposium on *Cooperative Breeding in primates: Expanding our Perspectives on Taxonomic Distribution and Mechanisms* convened by Anita Ginther and Stacey Tecot held at the International Primatological Society meetings in Edinburgh. During her summation of the Ginther and Tecot session, Patricia Wright (2008) mentioned her "eyeball" estimate that perhaps as many as 19% of all primates were cooperative breeders. At the time most biologists and social scientists—if they thought about the topic at all—would have considered her estimate implausibly high. Yet Pat's eyeball estimate was remarkably close to my own estimate independently arrived at. Shortly afterwards, together with Stacey Tecot, and with input from Patricia Wright, and essential logistical assistance from Noel Rowe who provided us with the in-progress and much expanded taxonomy for the new edition of *The Pictorial Encyclopedia of Living Primates* (hopefully accessible on line soon at All the World's Primates), we embarked on a preliminary classification of infant care across primates. Our aim was to make a more accurate classification of infant care among primates available at the All The World's Primates website. It was an ongoing project, part of Noel Rowe's ambitious plan to make comprehensive, up-to-date information from primate field studies more widely accessible. We also hoped to alert fieldworkers to the need for more precise information on exactly which individuals care for and provision primate infants. Beyond that, I had a more specific and personal aim, to pin down Pat's and my estimates and to document the claims I was making in the book.

Not only was I convinced that shared care was far more widespread in primates than researchers in many fields realized, but I also believed that cooperative breeding (simply defined as alloparental care plus alloparental provisioning) was more prevalent in the Order Primates than in mammals generally. Some three percent of mammals are estimated to breed cooperatively—a crude assessment now several decades old, in desperate need of reassessment. Nevertheless the 3% estimate for mammals generally is still widely cited for lack of any more accurate estimate (e.g. Russell 2004). For birds, fortunately, we do have an up-to-date and highly authoritative calculation thanks to Alexander Cockburn. Cockburn (2006) estimates that around 9% of birds (852 of 5,143 species) breed cooperatively. It would appear then that cooperative breeding evolves more readily in the Order primates than in most other mammals, and that as an Order, primates are pre-adapted to evolve a breeding system which if not exactly rare, at least is fairly uncommon breeding system. My goal became to try to understand what must have been the quite profound sociocognitive implications for apes with such a breeding system evolving in the genus *Homo* (Hrdy 2009; see also Burkart et al. 2009).

I suspected that maternal tolerance of other group members post-partum was a crucial precondition for the evolution of shared care, and that this variable would turn out to be important for understanding the evolution of

shared care and cooperative breeding in primates. But were shared care and cooperative breeding as prevalent in primates as I assumed? And exactly what conditions are conducive to post-partum tolerance in primates? I needed answers to these questions.

Methods and Sources of Bias

Tecot, Wright, Rowe's and my classification was undertaken with the help of dozens of fieldworkers who generously responded to queries we sent out. Their personal communications along with published references and details about study sites will be posted along with information on many other aspects of primate taxonomy, behavior and natural habitats at <http://www.awpdb.com>. The infant care portion remains a work-in-progress that will need to be expanded, revised and up-dated as new or better information becomes available. Although that infant care classification project has no fixed endpoint, some readers of *Mothers and Others* might want to know exactly which species I was counting as well as which cases I did not yet know about, or which I misclassified. Readers may also want to know more about possible sources of bias shaping the classification. *Mothers and Others* focused on the psychological implications of humankind's deep history of cooperative breeding, and a strict contractual word limit meant that I could not detail the comparative data on primate infant care there. This is why I am posting the tallies I had in hand at the time the book was published in April of 2009 here on [my website](#). Readers are referred to [All the World's Primates' website](#) for further details, references and updates.

By April 2009 Stacey Tecot and I had been able to locate information on infant care for 105 species, about a quarter of the 413 species of primates that will ultimately be included on the [All the World's Primates website](#), and not necessarily a random sample. For one thing, my special interest in the *Callitrichidae* meant that species in that family were over-represented. That said, there is no reason to suppose that the surprisingly large number in the sample of species with shared suckling was anything other than representative. All the same, I should emphasize that in addition to over-representation of callitrichids, the 25% estimate for cooperative breeding may have been inflated by including species where alloparental provisioning amounted to nothing more than shared suckling. At present we simply do not have quantitative studies which allow us to evaluate the frequency of alloparental suckling, much less information on the nutritional value or fitness consequences of sporadic suckling by allomothers. Readers should attend therefore to the wording of the definition of cooperative breeding that we applied: alloparental care plus *at least minimal* alloparental provisioning. That provisioning may often be very minimal, but just how important or unimportant alloparental provisioning is remains to be determined. (In fairness, it should be noted that estimates of the prevalence of cooperative breeding in birds and other taxa suffer from similar limitations even though beak to beak provisioning is definitely easier to quantify than suckling).

The specific criteria we used to classify infant care are repeated below but need some explanation. It was because we wanted to include as broad a spectrum of the primate order as possible that we focused on the weeks and months right after birth, the period for which field reports were most likely to specify just who was interacting with immatures. Nevertheless quantitative information on which individuals hold and carry infants, and for how long, etc. was rarely recorded. Even though our classification focused on early life, we were acutely aware that growth stages in different species are far from standardized. We also realize that a great deal of parental and alloparental investment in primates extends far beyond early infancy and may include behaviors other than direct care (e.g. protection or resource defense). For a few species we actually have detailed information on this already. Wild siamangs and Hamadryas baboons provide two of the best documented cases in point. In many groups of wild siamang, the probable father assumes the role of primary caretaker, but not before the infant is 12-18 months of age and no longer nursing during daytime. The mother is the exclusive carrier and provisioner of the infant prior to that point (Lappan 2009). Among Hamadryas baboons, an adult male may "kidnap" and rear an older infant. Even among savanna baboons males can be especially attentive to particular infants (often infants born to females they recently mated with) and long after that maturing infant begins to spend more time off his or her mother, the male may intervene to protect or socially support him or her (Buchan et al. 2003). Hopefully better data, and also information on just "who cares" during later stages of development, will be fleshed out in future editions of the website at [All the World's Primates](#). For this first effort however, we focused on early infancy.

Tentative Conclusions

As laid out in Table 1 below the estimate for primates that bred cooperatively was based on the inclusion of many species with nothing more than alloparental care plus suckling (Ss) as well as species with alloparental care plus provisioning where food was actually transferred from an alloparent to an infant (Sp and Ssp). Of the sample of 105 species, only 38 (some 36%) were characterized by exclusive maternal care of infant where no individual other than the mother held or carried the baby. Obviously though, other group members may contribute to infant survival through their vigilance or territory defense. Thirty six of the 105 species in the sample (34%) had some form of shared care. Only five species (5% of the sample) had paternal care plus provisioning. Another 13 species exhibited shared care plus allomaternal suckling of some other female's baby (12%), 7 (7%) exhibited shared care plus provisioning with food transfers, and 6 (6%) exhibited alloparental care plus suckling and provisioning with food transfers. It was on the basis of these last three categories that I calculated that some 25% of primates in our sample exhibited alloparental care plus at least minimal provisioning, and thus qualify as "cooperative breeders".

For the time being however, I still prefer to use the conservative 20% estimate published in the book and simply say that the prevalence of alloparental care and at least minimal provisioning of infants (if only shared suckling) is likely to characterize at least a fifth of all primate species. That said, I would not be surprised if defined that way, the proportion turns out to be closer to a quarter of all primates.

The 40-50% figure for species exhibiting some type of shared care (referred to in the section on "How The Other Half Lives", pp. 87-92) is also a conservative estimate. If we add up the tallies for columns S + Ss + P + Sp + Ssp, shared care characterizes some 64% of the sample of 105 species, and this was relying on information that in many cases was gathered before researchers became alerted to the significance of allomaternal care. In the end, looking over this classification also strengthened my conviction that with some very intriguing exceptions (so far, *Trachypitecus phayrei* and perhaps other lutongs, Borries et al 2010) primate mothers only tolerate other group members taking, holding or carrying their new infants in two contexts: 1) when mothers reside with their mate in a monogamous pair, that is with the father on hand and in position to be relatively certain of paternity, or 2) when mothers had trusted matrilineal kin close by. I was particularly struck by the contrast between female philopatric species like *Colobus guereza* with extensive shared care and the total absence of shared care in male philopatric relatives such as *Procolobus badius*. Because strict (both social and reproductive) monogamy and extensive and exclusive paternal care is rare among primates, as it is among mammals generally, the availability of matrilineal kin looked to me to be the most likely pre-condition for the evolution of shared infant care.

Acknowledgements

I remain deeply indebted to all the primatologists who generously sent in information for the AWP website, and especially to Stacey Tecot for her hard work and thoughtful comments.

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DEFINITIONS AND CRITERIA FOR INFANT CARE CLASSIFICATION:

allomother - any group member other than the mother and including the father.

alloparent - any group member other than the genetic parents. Unless otherwise specified, allomaternal and alloparental behaviors are assumed to be benevolent (as in allomaternal care or allomaternal provisioning) or at worst neutral.

cooperative breeder - any species with alloparental care and provisioning of young. This definition is adopted from ornithology, the discipline which to date has provided most of the theory guiding our understanding of the evolution of cooperative breeding.

M – Exclusive maternal care, where mother is very possessive and is the only one to hold and carry her infant. In the case of apes and Old World monkeys the relevant period is between birth and the time when the infant begins to move off of its mother or other caretaker on its own. This assessment is complicated among prosimians and New World monkeys because even very young infants may play active roles in transferring themselves off their mother to another caretaker. In such cases the relevant period is between birth and the time when the infant can locomote off the caretaker and spend time off any caretaker.

S – Shared care, where mother is tolerant and allows allomothers to take and carry her infant within 3 weeks of birth.

P – Paternal care, where mother allows male she is paired with to take and carry infant and he is eager to do so. In New World monkeys, infant may actually take the initiative in transferring to “father”. Typically, the mother's mate is the main caretaker, and alloparents are rarely involved. Note that our classification system does not take into account potentially important roles played by the father later in infant development, as for example male care of year old infants in *Symphalangus*, or protective “baby-sitting” by male savanna baboons or the kidnapping of weaned infants by male *Papio hamadryas*. As more information becomes available it may be useful to create a separate classification focusing on paternal care rather than (as we have done here) maternal tolerance.

Pp – Paternal care with provisioning of older infants, approaching or just past age of weaning.

Sp – Shared alloparental and parental care plus provisioning, where provisioning ranges from minimal to extensive. To date, there is very limited information on the timing, frequency and nutritional content of food delivered by allomothers and it is hoped that more information on this topic will be forthcoming.

Ss – Shared allomaternal care plus suckling. Group members other than the mother care for infants, and if the allomother is lactating, she allows an infant other than her own to suckle. Allomaternal suckling may range from occasional and brief access (e.g. in some cebus monkeys) to more sustained access, as in species where two mothers share a nest. At present, little information is available on the duration or nutritional significance of allomaternal suckling.

Ssp – Alloparental care plus allomaternal suckling and provisioning

Table 1. Infant Care Classification of 105 Species for *All the World's Primates*
(See <http://www.awpdb.com> for further details and references.)

M - maternal care	S - shared care	Ss - care w/suckling
Allenopithecus nigrovi	Alouatta guariba	Saimiri boliviensis
Cercopithecus diana	Alouatta palliata	Cercopith. ascanius
C. ascanius	Alouatta pigra	Cercopithecus mitis
C. cambelli	Alouatta senicula	Erythrocebus patas
C. hamlyni	Ateles geoffroyi	Lemur catta
C. mona	Brachyteles hypoxanth	Microcebus murinus
C. neglectus	Saguinus labiatus	Galago senegalensis
C. nictans	Saguinus nigricollis	Propithecus candidus
Macaca fuscata	Saguinus albifrons	Propithecus diadema
M. mulatta	Cebus apella	Propithecus edwardi
M. nemestrina	Saimiri sciureus	Varecia rubra
M. radiata	Cercopith. aethiops	Varecia variegata
Mandrillus leucophaeu	Colobus guereza	Trachypithecus johnii
Papio anubis	Colobus polykomos	
P. cynocephalus	Macaca arctoides	
P. hamadryas*	Macaca hecki	
P. ursinus	Macaca ochreata	
Procolobus badius	Macaca pagensis	
Theropithecus gelada	Macaca sylvanus	
Cheirogaleus medius	Macaca thibetana	
Gorilla beringei	Macaca tonkeana	
Gorilla gorilla	Miopithecus talapoin	
Pan paniscus	Nasalis larvatus	
Pan troglodytes	Pygathrix nemaesus	
Hylobates lar	Rhinopithecus roxella	
Symphalangus syndac*	Semnopithecus entellu	
Avahi laniger	Simias concolor	
Indri indri	Trachypithecus cristat	
Loris lydekkerianus	T. delacouri	
Loris tardigradus	T. francoisi	
Cacajao melanocephal	T. obscurus	
Chiropotes satanus	T. phayrei	
Chiropotes utahickae	T. pileatus	
Pithecia pithecia	Eulemur mongoz	
Pongo abelii	Eulemur rubriventer	
Pongo pygmaeus	Hapalemur griseus	
Tarsius bancanus		
Tarsius syrichta		
n=38	n=36	n=13

P-pat. care (provis.*)	Sp-Shared care+prov	Ssp- Care+milk+prov
Mico humeralifer	Callimico goeldi	Cebuella pygmaea
Aotus azarae*	Callithrix aurita	Saguinus mystax
Aotus trivirgatus*	Callithrix jacchus	Cebus capucinus
Leontopithecus rosalia*	Callithrix kuhli	Cebus nigrurus
Callicebus moloch*	Leonto. chrysomelas	Cebus olivaceus
	Saguinus fuscicollis	Homo sapiens**
	Tarsius spectrum	
n=5	n=7	n=6
Older P. hamadryas		
Older S. syndactylis (see text)		

*Species with both paternal care and provisioning. Since provisioning is largely by males very likely to be the genetic father, these species are not included among cooperative breeders.

**Although it is not usual to include Homo sapiens among cooperatively breeding mammals (e.g. Solomon and French 1997; Russell 2004; Vasey 2007), based on evidence from hunter-gatherer and other traditional societies, clearly this is where they belong (Hrdy 2009 and references therein).

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