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How Reliance on Allomaternal Care Shapes Primate Development

With Special Reference to the Genus *Homo*¹

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Abstract

According to the Cooperative Breeding Hypothesis, slow maturing apes with the life history attributes of those in the line leading to the genus *Homo* could not have evolved unless male and female allomothers had begun to help mothers care for and provision offspring. The unusual way

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hominins reared their young generated novel phenotypes subsequently subjected to Darwinian social selection favoring those young apes best at monitoring the intentions, mental states, and preferences of others and most motivated to attract and appeal to caretakers. Not only were youngsters acquiring information in broader social contexts than other apes, but they also would have been emotionally and neurophysiologically different from other apes in ways relevant to how humans learn. Contingently delivered rewards to dependents who attracted and ingratiated themselves with allomothers shaped their behaviors and vocalizations and transformed the way developing youngsters learned from others and internalized their preferences.

1 Setting the Plio-Pleistocene Stage

Apes with the life history attributes of *Homo sapiens* could not have evolved unless male and female allomothers had helped mothers care for and provision their exceedingly costly, slow-maturing offspring born after relatively short inter-birth intervals. We refer to this as the *Cooperative Breeding Hypothesis* (Hrdy, 2009, 2016a). Across the animal world, breeding systems characterized by female or male group members other than parents (alloparents) helping parents to care for and provision offspring have evolved many times in social insects, in 9% of 10,000 species of birds (Cockburn, 2006), and in perhaps 3% of 4,500 species of mammals. The prevalence of allomaternal care tends to be higher among social carnivores (Clutton-Brock, 2016). The prevalence of shared care is higher still among primates where females or males other than the mother care for and *at least minimally provision* offspring in more than 30% of species in the Order Primates (Isler & van Schaik, 2012a; Perry, 2020). However the only primates with

extensive alloparental provisioning involving group members definitely known not to be the genetic parents as well as parents, occur among humans and in a distantly related subfamily of New World monkeys, the Callitrichidae, containing marmosets and tamarins.

Various circumstances conducive to the evolution of cooperative breeding pertained among hominins in Plio-Pleistocene Africa (Meindl, Chaney, & Lovejoy, 2018). These included: cohesive social groups containing close relatives; production of increasingly costly, slower maturing young; increasing reliance on hunting and extractive foraging such that immatures began to depend on adults to acquire or process food for them and to facilitate their learning appropriate skills (Clutton-Brock, 2016; Emlen, 1991; Hawkes, 2020; Hrdy, 2009; Jaeggi & van Schaik, 2011; Langen, 2000; O'Connell et al., 2002), and importantly, ecological instability (Burkart, van Schaik, & Griesser, 2017; Jetz & Rubenstein, 2011).

Unpredictable rainfall against a background of increasing aridity rendered the emergence of shared provisioning more and more critical for the survival of dependent hominin offspring (Anton, Potts, & Aiello, 2014; Magill, Ashley, & Freeman, 2013; Morgan, 2020; O'Connell et al., 2002; Richerson, and Boyd 2020). In spite of recurring periods of food shortage accompanied by high child mortality, hominin mothers in the line of bipedal apes leading to *Homo sapiens* were producing slower maturing, increasingly large-brained, energetically more costly offspring, yet also beginning to produce infants after shorter intervals. How? Along with others, we have hypothesized that by 2 million years ago with *Homo erectus*, hominin mothers increasingly relied on assistance from other group members to supplement offspring who even after weaning still remained years from nutritional independence (Burkart, Hrdy, & van Schaik 2009; Hawkes 2020; Hawkes et al., 1998; Hrdy, 1999; Konner, 2010; Meehan & Crittenden, 2016). (Figure 6. 1).

FIGURE 6.1 HERE

It's not easy to date gradual, often subtle, life history changes from the fossil record. This unusual combination of prolonged nutritional dependence accompanied by earlier weaning permitting mothers to resume cycling, conceive again, and reproduce faster, would almost certainly have required some type of allomaternal assistance. In our previous work we have tentatively tied these life history changes to the early Pleistocene with the emergence of somewhat larger brained *Homo erectus*. However, some paleontologists hypothesize that slower development, and with it, longer dependence and allomaternal assistance, were already getting underway with *Australopithecus* by 3 million or so years ago (De Silva, 2011; Gunz et al., 2020). A few researchers push allomaternal assistance (involving fathers) back even earlier to *Ardipithecus* (Raghanti et al., 2018).

Over time, stacking of closely spaced dependent offspring would further intensify reliance on allomaternal provisioning. By the Pleistocene we suspect that hominins were adopting even more flexible residence patterns than those found in the other Great Apes (Koenig & Borries, 2012), with “multilocal” residence patterns beginning to resemble those typical of twentieth-century hunter-gatherers (Hill et al., 2011; Marlowe, 2010). Greater female autonomy of movement and the emergence of pair-bonds (why they emerged being a topic still debated), would increase chances that probable fathers and matrilineal kin resided nearby (Behar et al., 2008).

Greater postpartum tolerance on the part of ordinarily possessive ape mothers coevolved with increasing, albeit still facultative, neurophysiological responsiveness on the part of fathers and other allomothers increasingly motivated to care for immatures (Abraham et al., 2014; Numan, 2014; Raghanti et al., 2018). The more dependent upon allomaternal assistance primate mothers are, the more sensitive they become to cues of social support, especially postpartum (Hrdy, 1999, 2016b). Compared with the reflexive protectiveness and possessiveness typical of all

but the most stressed or inexperienced Great Ape mothers, postpartum commitment of these hominins would likely have been more conditional. Across traditional societies, mothers are known to abandon at birth infants considered defective as well as adjust parental investment in line with social and ecological circumstances (Hrdy, 1999, chapters 12 and 13; Konner 1972; Scrimshaw 1984; see Salmon & Hehman, Chapter 4, this volume).

Infants who could no longer count on being the sole priority of a single-mindedly dedicated mother had to elicit and maintain maternal commitment while also attracting and ingratiating themselves with others. Rewarded when they succeeded, over the course of development infants learned to express otherwise latent sociocognitive potentials. As we use the term, “ingratiating behaviors” refer to anything an infant does to increase his or her chances of being chosen as the object of beneficent attention (including provisioning) where offspring best at ingratiating themselves with others would be most likely to survive. Over the course of development, these youngsters learned to monitor and be interested in the intentions, thoughts, and feelings of others, even internalizing their preferences. Over generations, youngsters best at doing so would be more likely to survive, resulting in populations of apes emotionally very different from their ancestors (Figure 6.2).

FIGURE 6.2 HERE

In this contribution, we reconstruct how growing up in such a social environment may have impacted dependent immatures along with the cascading consequences this would have had on uniquely human forms of learning and language. We start by asking: How would dependent immatures respond to the challenges of eliciting vital, but facultatively proffered, maternal and allomaternal attentions? What would this little ape need to do? Because none of us can go back in time to observe how early hominin infants would have behaved, we draw on evidence for how

nonhuman ape and modern human babies responded in “virtual” experiments with and without allomaternal care to test assumptions made here about how hominin infants would have behaved with allomaternal care (Hrdy, 2016a), as well as on evidence from other primate infants reared in contexts where they had to rely on allomaternal care and provisioning. Although inevitably speculative, this reconstruction is informed by both comparative evidence and a growing understanding of the survival challenges hominin infants must have confronted.

2 Growing up as a Cooperative Breeder – Callitrichid-Hominin Parallels

As our point of departure we begin with callitrichid monkeys (comprising marmosets and tamarins), the only extant primates besides humans with *extensive* alloparental in addition to parental care and provisioning of infants. Even though not all elements of human cooperative childcare are also present in callitrichids, they nevertheless face many similar challenges and thus share some critical proximate mechanisms of helping, including hormonal regulators and psychological predispositions (Burkart et al., 2017).

Callitrichids face similar challenges to those hominin infants would have faced, although they do so endowed with far smaller brains. Callitrichid mothers customarily give birth to twins, and due to post-partum oestrus are immediately pregnant again (Erb & Porter, 2017; Garber, 1997). They are thus lactating and gestating at the same time, and the new set of offspring is born before the previous one is fully independent. This costly reproduction is only possible because other group members help by carrying infants, protecting them, and substantially provisioning them (Guerreiro Martins et al., 2019). Like human mothers, callitrichid mothers are highly tolerant towards other group members interested in carrying their babies, and they adjust their maternal investment relative to how much help is available (Bardi et al., 2001; Fite et al., 2005;

Hrdy, 1999). Helpers provisioning immatures exhibit highly prosocial motivations (Brügger et al., 2018; Guerreiro Martins et al., 2019). Callitrichid twins are thus confronted with challenges similar to youngsters born to hominin mothers who, when conditions permitted, similarly produced more closely spaced young (in “as-if” litters)

A system reliant on allomaternal care is only feasible if mothers are willing to allow access to their infants and if other group members are interested in caring for offspring that are not their own (Snowdon, 2001; Burkart et al., 2009; Burkart, Martins et al., 2018). Among cooperatively breeding primates such as callitrichids, caretaking includes carrying, feeding, and protecting the infants. Infant carrying requires not only high tolerance by mothers, but also among all other group members because vulnerable neonates are handed over from one caregiver to the next in coordinated joint actions. Since only mothers lactate, others feed immatures by sharing and actually proffering palatable foods, unusual behaviors among primates. Since immatures are not always close to adults who find food, adults even offer it proactively with food-offering calls. This requires a high level of donative intent. Finally, group members have to coordinate and take turns in activities such as infant transport, vigilance, and protection.

To fulfill these tasks, high levels of social tolerance among adults during everyday life is mandatory. Moreover, a predisposition to not only care about one’s own well-being but also about that of others and to be willing to help them, are essential for proactive provisioning and the coordination of cooperative activities (Figure 6. 3).

FIGURE 6.3 HERE

So is it the case that primate species exhibiting extensive levels of shared care tend to be more cooperative and prosocial than other species? Group Service experiments estimating cooperation in 24 groups belonging to 15 different primate species, including humans, suggests that both

social tolerance and proactive prosociality are indeed correlated with the amount of allomaternal care (Burkart et al., 2014, Figure 6.4).

FIGURE 6.4 HERE

The coordination of these cooperative activities, and figuring out who is willing to take over an infant to carry it, is smoother if individuals are constantly monitoring the whereabouts, activities, and intentions of their group members. This attentional predisposition toward monitoring others in a relaxed way is evident in the lack of gaze aversion in callitrichid monkeys and has recently been documented with gaze tracking studies comparing active vision in the cooperatively breeding marmoset and the independently breeding macaque monkeys. The marmosets had longer inspection times for faces, and looked at them directly more frequently compared to the macaques (Nummela et al., 2019). Together, these predispositions per se can already facilitate performance in socio-cognitive tasks such as social learning or cooperative problem solving (Burkart & van Schaik, 2010), and impact the development of youngsters born into such groups.

In addition, however, immatures face an additional set of specific challenges in such a social environment, and those best at mastering them have increased fitness. Most importantly, immatures have to appeal to and solicit succor from allomothers as well as mothers. Human infants and infants in the distantly related callitrichids appear to have converged on some similar modes of doing so. So how might such solutions be extended and transformed if dependent immatures were endowed with much more powerful ape cognitive systems to begin with? And what might have been the cascading consequences for uniquely human forms of learning and language? It's time to look at little apes reared under the novel circumstances pertaining among Pleistocene hominins.

3 The Hominin Infant's To-Do List

3.1 First Order of Business: Appeal to Mother

Although born with open eyes, able to blurrily seek the eyes of someone else, all newborn apes are otherwise altricial, utterly dependent on others for warmth, protection, locomotion, and food (Bard, 2012; Tomonaga et al., 2004). Fortunately, apes enjoy the built-in mammalian advantage of being born to a mother who during gestation was suffused by hormones lowering her threshold for responding to sounds and smells of a warm, wriggling, fluid-covered baby. If only the newborn can make it to maternal nipples, root, suck, and stimulate lactation, ensuing surges in oxytocin and prolactin, further enhancing her nurturing impulses. With lactation underway, even an inexperienced first-time ape mother becomes increasingly bonded to this newcomer. But over the course of hominin evolution, increasing maternal reliance on allomaternal assistance would have rendered mothers increasingly sensitive to cues of available social support. In the absence of social support, the commitment of even the most experienced human mother falters (see especially Bugos & McCarthy, 1984; Hrdy, 1999, 2016b).

Over evolutionary time, more contingent commitment preadapted human mothers to become more discriminating than other apes. In addition to their parity, prior experience, physical condition, and likely social support, mothers began to respond to specific physical attributes of each infant. Consciously or not, each costly infant was in competition not only with still nutritionally dependent older siblings, but also with subsequent infants a mother might bear under ecologically more opportune conditions if only she retrenched upon investment in this one, or bailed out altogether, and resumed cycling sooner. Over the course of the Pleistocene (perhaps earlier?), hominin babies came under increasing pressure to look good and sound vigorous right at

birth, advertising that they were full-term, robust, good bets for survival, worth further investment. This challenge may help explain why, over the course of hominin evolution, fetuses began to stockpile adipose tissue at an unlikely time, just prior to squeezing through increasingly narrow birth canals. By now, human neonates are born much fatter than other apes (ca.10–14% body fat contrasted with 3–4% for chimpanzees). No doubt, an extra dollop of energy was initially beneficial for thermoregulation and fueling fast-growing brains, contributing to the emergence in mothers of sensory biases favoring plump babies (Kuzawa et al., 2014). Over time, plumpness may also have come to serve as an infantile equivalent of sex appeal seducing mothers into embarking on a long, exorbitantly costly, endeavor (Hrdy, 1999, chapter 21).

Once increasingly discriminating hominin mothers began to notice associations between birth weight and later outcomes, one of evolution's more consequential self-reinforcing feedback loops would be underway. With runaway social selection for neonatal plumpness underway, extra energy stores became available for brain development, in turn rendering allomaternal provisioning even more essential. Over generations, allomothers as well became attuned to cues of neonatal viability, adjusting levels of commitment accordingly (Hrdy, 2016b).

This brings us to the hominin infant's *second order of business*.

3.2 Attract Others

Because hominin mothers as well benefitted from allomaternal assistance, it behoved females to reside near trusted others, matrilineal kin and/or adult males who were probable fathers. Unlike exceedingly possessive Great Ape mothers, mothers in traditional human societies not only tolerate, but often encourage postpartum contact with infants. Whether this shift was due to innately more tolerant temperaments, to greater autonomy in selecting who to live among, or both,

is not clear. In any event, maternal tolerance facilitated intimate exposure of trusted group members to infantile smells and sounds, generating maternal-like affiliation-promoting neurophysiological transformations in male and female allomothers alike (Abraham et al., 2017; Bales et al., 2004; Carter & Perkeybile, 2018; Hrdy, 2009). Among humans, only a few hours of intimate contact with grandparents can be sufficient to produce surges in oxytocin and reorder priorities (Hrdy, 2019). (Among marmosets, similar oxytocin increases are found not only in mothers, but in all group members after the birth of new babies; Finkenwirth et al., 2016.)

But other factors also enter in, including the allomother's own physical condition and past caretaking experiences, alternatives available, as well as the infant's vulnerability and level of need. Facing this uncertainty, cues from infants themselves to elicit allomaternal involvement would again be paramount. Over time, human allomothers become sensitive to the same viability cues that mothers respond to. Magnetic resonance images of modern human brains reveal that even nulliparous women find the faces of plump, healthy-looking (read full-term) babies "cuter" and more rewarding to look at (Glocker et al., 2009). Not only physical viability cues, but also behavioral interactions will attract caregivers. Humans are born with neurological capacities comparable to those of other apes, but differences soon emerge (Lonsdorf et al., 2010). At birth, both chimpanzee and human newborns seek out eyes, are capable of mutual gazing, and caught just right, may imitate someone else's outstretched tongue or other facial expressions (Myowa-Yamakoshi, 2010). Both species exhibit reflexive "fairy smiles," soon to be replaced by more open-eyed "social smiles" in response to someone else. Among newborn chimpanzees, that someone else would always be their own mother (Matsuzawa, 2010). In traditional human societies, however, bearily gazing newborns engage a wider audience (Konner, 1972, 2010). Over time as infants grow accustomed to and learn to trust specific allomothers, the sorts of

emotional bonds primate infants forge with mothers prove sufficiently elastic to encompass multiple attachment figures, an average of six attachment figures among the Central African Aka hunter-gatherers Courtney Meehan studied (Meehan & Hawks, 2013). It is not known whether human infants are more prone to forge multiple attachments than are other apes if cared for by both mothers and others because nonhuman apes virtually never are.

A challenge unique to immatures of cooperatively breeding primates is that they are not in continuous contact with their caregiver. This can be buffered by proactive caregiving motivations by adults as in callitrichids where group members monitor babies on carriers eager to take over when necessary (Yamamoto & Box, 1997), or proactively announce that they have found food and are ready to share it. Such provisioning is different from food sharing patterns in other primates, where at most, immatures are passively tolerated when taking their mother's food (Brown et al., 2004; Jaeggi et al., 2010). Nevertheless, without being in constant body contact with a single caregiver, cooperatively breeding immatures face the chronic risk of being overlooked.

Among apes such as chimpanzees, gorillas, or orangutans, newborns constantly held by mothers in direct skin-to-skin contact have less need to smile or vocalize. Calling would only be useful if separated, or later, at weaning, as youngsters object to maternal rejections. Otherwise, low, scarcely audible sounds make more sense than loudly advertising to predators, "vulnerable baby here!" Among primates with shared care, life tends to be noisier. Infants need to stay "in touch without touch" and may complain to prompt maternal retrievals. Infant langur monkeys spend up to 50% of their first day of life being held and carried by females-other-than-mothers, calling incessantly (Hrdy, 1977).

Life is even noisier in animals with biparental and alloparental provisioning where babies beg for treats. This correlation is best documented in birds (Leighton, 2017), but it also holds for callitrichids and humans who fall among the most voluble of primates (Burkart, Martins et al., 2018). Vocalizing starts early in marmosets and tamarins, becoming more frequent and specialized over the course of development. Begging calls spike around weaning when allomaternal provisioning is most critical (Brown et al., 2004; Rapaport & Brown, 2008). But these infants not only are noisy beggars, but also engage in babbling-like behaviors, by producing repetitive, random-sounding streams of elements of adult vocalizations that can last for more than a minute. This babbling-like behavior comes with likely cost because it is noisy and makes infants conspicuous to predators. It peaks around weaning when allomaternal provisioning is most critical and turns out to be an effective attention getter as adults are more likely to approach and interact with immatures that are babbling (Elowson, Snowdon, & Lazaro-Perea, 1998).

Something similar goes on in humans. The onset of babbling roughly coincides with the time hunter-gatherers allomothers begin providing edible treats (discussed below). Within weeks of birth, human infants emit engaging noises. Learning progresses more rapidly if infants notice others reacting. By ten weeks some actually take turns vocalizing. The sound of a baby laughing generates an especially powerful stimulus, audible at some distance and signaling emotional engagement (Parsons et al., 2013; Riem Madelon et al., 2017). As babies put two and two together, conditioning plus early glimmerings of intersubjectivity (Trevarthen & Aitken, 2001) encourage them to incorporate sensory biases and preferences of potential caretakers into their own expanding repertoires for ingratiating themselves with others (Gopnik, 2020). By nine months, little humans go out of their way to be helpful (Warneken & Tomasello, 2006). By 19 months, infants readily share, even offer delectable food items to someone else (Barragan et al.,

2020). These human youngsters also care about what others think of their performance (Engelmann et al., 2012; Reddy, 2003).

3.3 Vocal Control and More Flexible Vocalizing

Old World monkeys and apes are sophisticated communicators. Vervet monkeys, for example, emit one kind of call to alert group-mates of raptors, a different alarm-call for terrestrial enemies. They are also sensitive to context, taking into account who is listening and who is out of range, modifying calls accordingly (Cheney & Seyfarth 1990). Apes, particularly chimpanzees and bonobos, also make extensive use of hands and arms to communicate what they want, extending an arm palm up when requesting something. Even so, their vocal repertoires never achieve the richness, sophistication, and flexibility of their gesturing (Pollick & de Waal, 2007). Rather, nonhuman apes seem surprisingly limited in the kinds of vocalizations they emit (Slocombe & Zuberbühler, 2010), a marked contrast with humans who early in development increase vocal control and start to build larger and more flexible vocal repertoires (Zuberbühler, 2011). So how did this get started?

One important element developed elsewhere concerns the challenges that adults, rather than the immatures of cooperative breeders, are confronted with (Burkart, Martins et al., 2018; Snowdon, 2001). They must increasingly coordinate their activities with others, as for when transferring infants back and forth. Their prosociality motivates them to not only share food with others, but also provides information useful to them. Vocal communication is a prime candidate to provide solutions to such challenges. In line with this proposal, the large vocal repertoires of cooperatively breeding birds are driven by an increase in contact and alarm calls (Leighton, 2017). A critical element is added by immatures who grow up in an increasingly voluble environment.

From a comparative perspective, it seems clear that shared care with babies carried by others increases vocalization frequency. Allomaternal provisioning and contingent reinforcement raises the stakes, with begging leading to more calling, especially if immatures have to compete for rewarding attentions (Goldstein, King, & West, 2003; Leighton, 2017). Through the expression of otherwise latent capacities and their subsequent shaping, attention-getting and begging set the stage for selection to favor enhanced vocal control accompanied by goal-oriented shaping of acoustic structure. Indeed, as in marmosets, vocal development in humans occurs earlier than motor development (Gustison et al., 2019). By contrast, infants in constant close contact with single-mindedly dedicated mothers (as in independently breeding species such as chimpanzees) would more often be called upon to cling than cry.

Experiments with marmosets undertaken by Asif Ghazanfar and his team demonstrate how contingent responsiveness by caretakers generates turn-taking and also speeds development of specialized, more mature-sounding calls (Takahashi, Fenley, & Ghazanfar, 2016). For 40 minutes a day during the first two months of life, each of a pair of marmoset twins was separated from their parents and allowed to call. Whereas one twin was provided consistent feedback from taped parental calls, the other twin received less consistent feedback. The more reliable the feedback, the more rapidly infants progressed from the coarse, random-sounding vocalizations typical of immatures to cleaner, more tonal, adult-like *phoe* calls (Takahashi et al., 2016; Takahashi, Liao, & Ghazanfar, 2017). By 2 to 3 months of age, their utterances resembled the turn-taking “conversations” human babies engage in with their caretakers. Chow et al. (2015) further showed that parents actively intervene when immatures make typical mistakes while learning to engage in turn-taking. If immatures get timing wrong and “interrupt” their parents, parents add an extra break before responding. When immatures respond with a wrong call type, the parents themselves

interrupt them with the correct *phoe* call. In another example of convergent evolution between human cooperative breeders and these tiny-brained, distantly related New World monkeys, Takahashi and colleagues (2017) noted that infant marmosets responding to contingent reinforcement rely on one of the same circuits to guide their *phoe* calls that humans use in speech. The patterning of FoxP2 expression in marmosets' cortico-striatal circuit turns out to be analogous to that in both humans and songbirds. Moreover, a role of oxytocin has recently been proposed for the social motivation and evolution of vocal learning and language (Theofanopoulou, Boeckx, & Jarvis, 2017), which is consistent with the increase of oxytocin in all group members after the birth of marmoset immatures (Finkenwirth et al., 2016) and its link with prosociality among group members (Finkenwirth & Burkart, 2017).

Observations of golden lion tamarins (*Leontopithecus rosalia*) in Brazil illustrate how these increasingly complex, two-way conversations function in natural habitats (Rapaport, 2011). Solitary adults traverse the treetops hunting for spiders, insects, and small frogs, prying prey from inside holes or tangled foliage. Youngsters learn to locate, stalk, and dexterously extract and dispatch struggling, sometimes biting or stinging, prey. Learning takes time and practice as immatures grow more adept at responding to adults volunteering prey. Deliveries peak near the end of weaning when up to 90% of their diets are provided by (mostly male) allomothers (Rapaport, 2011). Food transfers are often initiated by youngsters begging. But when adults locate food, provisioners too emit staccato "food-offering calls." Mothers, probable fathers, and other helpers extract the food and call the infant to come and get the food out of their hands. As prey-catching efficiency improves, but before youngsters reach adult proficiency, mentors switch from "come and get it" calls to "hey, look here!" calls. Adult calls direct older immatures' attention to a particular patch of substrate where prey have been detected. The finder then waits nearby while

the young locate and extract the prey for themselves. Such adjustment of adults to immature skill levels has also been found in other callitrichids in captive studies (cotton-top tamarins, Humle & Snowdon, 2008; common marmosets, Chow et al., 2015; Dell’Mour, Range, & Huber, 2009). As infants increasingly associate an allomother’s particular call with a particular reward, they register regularities in how others respond to particular sounds they themselves make.

Opportunities to link own vocal productions to regularities in how others respond to them are particularly evident for babbling (humans) or babbling-like behaviors (callitrichids). In humans babbling emerges spontaneously at around 5–7 months, about the same time as the emergence of milk teeth, which among hunter-gatherers often coincides with allomothers beginning to offer pre-masticated and other (sometimes “kiss-fed”) treats to infants (Hrdy, 2009). At some level (consciously or not) children recognize that babbling attracts rewarding attention. This may help explain why older children revert to “baby talk” after the birth of a younger sibling (S. Hrdy, personal observation 2019). Interestingly, babbling in marmosets not only attracts caregivers, but also speeds up the acquisition of adult-like forms of vocalizations. Moreover, babbling similarly can resume and spike among juvenile marmosets following the birth of new infants in their group (Snowdon & Elowson, 2001). Apparently the same message is being conveyed: “pay attention to *me!*”

“If babbling changes adult behavior in predictable, infant-oriented ways,” as Goldstein and colleagues propose, “infants should be able to recognize changes in others’ actions as a result of their vocalizations” (Goldstein et al., 2003, p. 8034), launching more goal-oriented vocal control. As with other apes, humans are born with limited motor control over articulation, but beginning around six months, humans gain increased vocal control, including more tongue involvement, with vocal tracts continuing to develop over the first 15 months, contributing to greater vocal

flexibility and larger vocal repertoires in humans than other apes (Zuberbühler, 2011). Impressed by the coincidence in timing between increased vocal control and the transition from baby-calls to babbling-like streams of consonants and vowels, Klaus Zuberbühler makes a compelling case that increased control derived from hominin infants' need to attract allomaternal attentions (Zuberbühler, 2011, pp. 71, 77–79). Although “babbling” is widely assumed to have first emerged in human children in preparation for the acquisition of spoken language – akin to Mother Nature adding training wheels on a bicycle – it makes more sense (and is far less teleological) to consider the initial emergence of traits like babbling as byproducts of infantile needs to attract caregivers. A key innovation here was increased motor control over articulation. Once vocalizations become subject to voluntary control they can be shaped via conditional reinforcement, critical preadaptations for the eventual evolution of spoken language.

3.4 Incorporate Others' Preferences

These novel capacities emerged within broader sociocognitive contexts where apes were already endowed with rudimentary Theory of Mind (Herrmann et al., 2007; Krupenye et al., 2016; Tomasello, 2019), already utilizing rich gestural repertoires (Pollick & de Waal, 2007), already employing tools and devising new modes of extracting food. At a social level, we suspect new modes of interpreting the preferences of others were also emerging, including new modes of emotional and perspective taking. This could help explain why even though locomotor abilities develop faster in chimpanzees and other extant apes, little humans are the precocious ones in terms of sociocognition and interactive communication. For example, even though chimpanzee infants are gamboling with others and playing much earlier than human children, human babies start to laugh much earlier, by four months of age compared to 12 months among wild chimpanzees. More complex social interactions, such as offering comfort, with one individual

consoling another with a hug, are seen as early as 13 months in human toddlers, not before 2.4 years in chimpanzees (Bründl, et al., 2020). In other words, human infants not only test better than other apes in sociocognitive realms (Herrmann et al., 2007), they develop these prosocial and subjectively interactive capacities early (Wobber et al., 2013), long before they could be any practical use in cooperative foraging or group defense (see Buttelmann, Chapter 13, this volume).

These are early days in the comparative study of anthropoid brain development, but in this context it is worth noting the unusually early development in human infants of brain areas implicated by inter-personal assessments and decision-making related to social interactions. Initial results from magnetic resonance imaging of developing chimpanzee and human brains suggest that when controlled for absolute size, white matter in the frontal cortex develops more rapidly in humans than in chimpanzees (Sakai et al., 2010, and especially Sakai et al., 2011). By the second half of the first year of life, this rapid trajectory of growth in parts of the brain linked to discriminating between or assessing others is already underway, continuing to expand to age three (see Wilder & Semendeferi, Chapter 8, this volume). Such precocity contrasts with slower maturation in other neural systems such as those controlling locomotion and physical coordination which proceed faster in infant chimpanzees who literally can run circles around their human counterparts. This raises the possibility that even though human infants are notably helpless at birth and through the first months of life, their altriciality is selective. Human infants develop at a slower pace than other primates in physical and locomotive domains, but their capacities for assessing motivations and preferences of others and for inter-subjective communication, mature faster (Hrdy, 2014).

By the Late Pleistocene, selection pressures from a range of new subsistence and socioecological challenges would have favored ever greater inter-individual coordination among

adults (Boehm, 2012; Tomasello, 2018; Tomasello, Kruger, & Ratner, 1993). But we propose that more other-regarding impulses provided the underpinnings for coordinated behaviors such as group hunting and were already present, having begun to emerge during childhood earlier in the Pleistocene. It is within this broader context that recent proposals linking cooperative breeding not only to the evolution of enhanced capacities for joint attention (Ben Mocha, Mundry, & Pika, 2019), but also for language, need to be understood (Burkart, Martins et al., 2018; Knight, 2016; Zuberbühler, 2011).

Social selection favoring more flexible communication coincided with other co-evolving feedback loops. But by themselves, neither larger brains nor increased uses for cooperation are sufficient to explain the evolution of language. As psychiatrist Peter Hobson reminds us “before language there (had to be) something else . . . that could evolve in tiny steps . . . that something else was *social engagement with each other*. The links that can join one person’s mind with the mind of someone else are, especially to begin with, emotional links” (Hobson, 2004, p. 2, emphasis in original). But what about the foundational steps? Klaus Zuberbühler’s speculations point us in a promising direction: “Once vocal control has evolved to help infants secure care, it is only a small step to producing utterances in context-specific ways” (Zuberbühler, 2011, p. 80). But, Zuberbühler adds, such a transformation “may only be possible against a background of other psychological skills, such as the ability to share intentions and attention (Tomasello, 2008), and well-developed comprehension” (Zuberbühler, 2011, p. 80). He expands on Tomasello’s insight regarding a “major difference” (Tomasello, 1999) between humans and other primates, involving (as Tomasello would later phrase it) capacities for “intersubjective sharing” (Tomasello & Carpenter, 2007, pp. 121–22).

Eagerness to ingratiate themselves with others would be enhanced by allomaternal care, an interpretation consistent with observations of captive chimpanzees who when co-reared by responsive human caretakers (allomothers of a different species) as well as their mothers, become more eager than wild chimpanzees are to engage in targeted helping of others (Bard, 2012; Yamamoto, Humle, & Tanaka, 2012; reviewed in Hrdy, 2016a). Even though human-tended chimpanzees do not acquire spoken language and other distinctively human traits, they nevertheless develop greater concern for the intentions and goals of others, learning the power that particular gestures, facial expressions, and utterances exert on others. For example, human-reared chimpanzees point to what they want in ways that wild apes almost never do (Tomasello, 2019). The expression of such interactive potentials in ape phenotypes would increase opportunities to share and increase effectiveness of helping. Over the course of human evolution, such opportunities may have increased selection favoring neuroendocrine systems conducive to prosocial responses including the increasingly “dopamine dominated” striatal systems being documented by paleontologists working in concert with neuroscientists (Raghanti et al., 2018). Interactions with processes that opened parental neural care systems to a wider range of social stimuli might have resulted in more unsolicited food sharing and general prosociality (Numan, 2014). Apes who needed to be more interested in the preferences of others would also find it more emotionally rewarding to do so. This chain of admittedly speculative reasoning brings us to a key component to the hominin infant’s to-do list.

3.5 Add Psychological Dimensions to *Kindchenschema*

Like all anthropoid primates, apes in the line leading to the genus *Homo* would grow up keenly aware of kin ties, alliances, statuses, and friendships. They would also be alert to competencies and reliability of group-mates (Cheney & Seyfarth, 2007; Perry, 2020). The quantitative skills and manipulative capabilities of a chimpanzee or orangutan fall in the same ballpark as those of two-and-a-half-year-old humans. They too exhibit rudimentary capacities for theorizing about what others know (Herrmann et al., 2007; Krupenye et al., 2016; Tomasello, 2020). Our Last Common Ancestors with these apes were already beginning to register what others intended or wanted.

So imagine such an ape growing up *reliant on* the competencies and motivations of others. If contingent reinforcement from allomothers encourages turn-taking and speeds up acquisition of adult vocalizations in tiny-brained marmosets with only minimal awareness of what another marmoset knows (Burkart & Heschl, 2007; Burkart, Martins et al., 2018), how much more sensitive to the thoughts and preferences of others would apes already attuned to the thoughts and intentions of others become? Contingent allomaternal responses generate new psychological dimensions to *Kindchenschema* as apes growing up this way are conditioned to become more aware that others have preferences worth appealing to.

Youngsters would be conditioned to not only monitor the intentions of others, but increasingly to probe their thoughts and feelings so as to better conform to their preferences. Over time, learning which facial expressions, sounds, or conversational rhythms result in solicitude would mature into more sophisticated understanding of how others perceived their own intentions, behaviors, and thoughts and to begin to care about their “reputations.”

4 New Dimensions to Social Learning

4.1 *Expanded Avenues*

All apes are endowed with inordinate behavioral flexibility along with aptitudes for manipulating objects and imitating others. In the case of chimpanzees and orangutans, knowledge about what to eat, where to find and how to process it, is transmitted vertically during 5–8 years of intimate association with one other trusted individual, their mother. Mothers set the stage for socially induced independent practice (Jaeggi et al., 2010; Schuppli & van Schaik, 2018; Whiten, 1999) or, as in the case of chimpanzee nut-cracking, very occasionally make helpful adjustments (Boesch, 2012; Matsuzawa, 2010). The processes by which little apes copy and learn from others are, however, primarily self-initiated (Humble, Snowdon, & Matsuzawa, 2009). Provisioning and shared care broadens this initial context for social learning.

From an early age, youngsters with shared care observe a wider range of role models. For example, cooperatively breeding magpie jays with many helpers become more adept at harvesting arthropods than jays growing up with few helpers (Langen & Vehrencamp, 1998). Furthermore, demonstrators among cooperative breeders tend to be more prosocial, even deliberately helpful (Burkart et al., 2009; Burkart & van Schaik, 2010). Recall that golden lion tamarin allomothers (often probable or possible progenitors), provide the majority of food for nearly weaned infants. Adults call when they have food to offer, but with older immatures, they call them to places where prey is hidden and then immatures have to extract it for themselves. As performance levels plateau, food calls cease. Rapaport (2011, p. 746) compares this progressive, developmentally sensitive behavior coupled with vocalizations that track the needs and skills of youngsters, to “teaching-like” behavior on the part of allomothers providing foraging assistance to youngsters (cf. Thornton & McAuliffe, 2006 for cooperatively breeding meerkats).

Incorporating situation-dependent vocalizations enhances effectiveness of these demonstrations while contingently delivered edible rewards rivets the attention of mentees. Anyone who has ever tried to habituate wild creatures, or even skittish domestic ones, knows that food rewards provide the quickest short-cut to taming or training them. Now add to this prosocial-provisioning-vocalizing mix mentalizing mentees eager to accommodate their mentors. Possibilities for information transfer expand exponentially.

4.2 *Emotionally Modern and Mentalizing Mentees*

Even in the absence of detectable Theory of Mind, tiny-brained marmosets prove remarkably prosocial, sharing food or rushing to assist others. Marmosets coordinate with others to crack open tough fruits. They take babies from mothers then voluntarily return them for nursing (Burkart et al., 2009, 2014; Garber, 1997). Tamarins even use guided demonstrations accentuated by vocalizations to transmit age-appropriate information (Rapaport, 2011). In this respect, tiny-brained callitrichids converge on something close to what ethnographers studying hunter-gatherers term “natural pedagogy” (Hewlett, Fouts, & Boyette, 2011). Yet even as tamarins adjust demonstrations to the skill level of pupils, they do so without mentalizing what another knows. Marmosets who readily follow the gaze of another individual do so without registering *what* that individual is seeing (Burkart & Heschl, 2007).

So what would happen if instead of the reflexive responsiveness of marmosets, the primates undertaking shared care and provisioning of young were already larger-bodied, bipedal, tool-users possessed of rudimentary Theory of Mind, with brains in the process of doubling from the 400 cc of chimpanzees or australopiths to the more expansive brains typical of *Homo erectus*? And what if novel contexts for social development coincided with new foraging tactics, more

valuable food packets, and with these, a raised “grey ceiling” so that over time whenever—and for whatever reasons—they became favored, even costlier brains could evolve (Isler & van Schaik, 2012a, 2012b)? Little hominins growing up as cooperative breeders would have opportunities to observe group members of different ages and sexes (Deffner & McElreath, 2020; Gurven, 2020; Hawkes, 2020), trust them as their mothers do, gauge their competencies and intentions, decide who was likely to be helpful or not—something modern humans begin to do from as early as three months old (Hamlin, Wynn, & Bloom, 2007, 2010). And what if at the same time these infants were beginning to monitor the intentions of others, seeking to conform to their preferences, even beginning to internalize their preferences and at the same time also developing larger and more flexible vocal repertoires?

Many factors were involved in the evolution of language (see Locke & Bogin, Chapter 10, this volume). Some clearly had to do with the unusual way apes in the line leading to *Homo sapiens* were reared. Learning language is a highly social endeavor. Anyone who has ever spent time with babies knows that their mother is not the only person who speaks to them in high-pitched “motherese.” It is from eagerly listening to others that youngsters acquire new phonemes and words. Immatures learn new sounds better in the presence of someone else than when by themselves. As young as nine months, babies watching instructive videos more readily discriminate sounds and learn foreign phonemes if another child is present (Lytle, Garcia-Sierra, & Kuhl, 2018).

Not only current interactions but also past experiences with others influence children’s readiness to mentalize what someone else knows. When experimenters set up a computer game where 5-year-olds must explain to someone else where to collect a digital prize, they were told that the unseen other (really the experimenters’ confederate) was either a toddler or another 5-

year-old. Subjects adjusted instructions accordingly. When told their partner was a toddler, subjects spent longer explaining the game than when they assumed the other child was older. The more days between birth and age four that the subject had spent with others in daycare, the readier that child was to take the other's level of understanding into account, mentalizing what they were likely to already know (Stolk et al., 2013).

4.3 Concern for Reputation and Learning

Within the first year of life, hominins approaching this level of emotional modernity would, like behaviorally modern humans today, actively seek to become the object of someone else's attention, feel at least a glimmer of pride when approved of, shame when disapproved of (Reddy, 2003; Trevarthen & Aitken, 2001). After a year or so these youngsters may have already been disposed to spontaneously offer something interesting or desirable to someone else, the way 14-month-old behaviorally modern humans do today, even proffering an item differing from their own preference (Repacholi & Gopnik, 1997). Although it has long been assumed that the ability to reason about what others are thinking (Theory of Mind, TOM) does not develop until around age 4, as early as 2.5 children clearly have learned how to conform to the preferences of others. Capacities for intuiting the perspectives and preferences of others appear to be supported by different, independently maturing, brain networks. Recent research using magnetic resonance imaging points to different areas of the brain involved in later developing more verbal and explicit TOM. These largely preverbal capacities involved in "implicit theory of mind" emerge earlier in development than do verbal capacities (Wiesmann et al., 2020).

In any event, today's behaviorally modern Western children readily absorb and follow normative rules (Gopnik, 2010, pp. 224–25), expect others to do so, and care desperately about

their own reputations (Engelmann, Herrmann, & Tomasello, 2012). When someone is trying to teach them something children not only feel pride at success, but want others to know “I did it!” Experiments comparing preschool children with chimpanzees show that the former are far more concerned with managing their reputations. Children, for example, are more likely to share, less likely to steal, if they are being watched by a peer. In contrast, chimpanzees behave the same way whether observed by a groupmate or not (Engelmann et al., 2012).

Equipped with sophisticated language, behaviorally modern children employ flattery to cultivate the goodwill of others as early as three or four years of age (Fu & Lee, 2007). By early adulthood, behaviorally modern humans in developed countries today find it so pleasurable to talk about themselves that it stimulates the same neural regions as anticipating something delicious to eat would (Tamir & Mitchell, 2012). This concern with presentation of self, reputation, and impressing others may fuel tendencies to register the intentions and preferences of others who are modeling behavior and then conform. This may explain why human children, but not other apes, don’t just imitate, they often “over-imitate.” Children add all the same ritualized bells and whistles as a demonstrator used even if these are far in excess of procedures needed to accomplish the task (Gopnik, 2010; Nielsen et al., 2014; Whiten et al., 2009). Acute sensitivity to the intentions, thoughts, and preferences of others, eagerness for their approval and a rush of dopamine and other neurochemical rewards when sensing approval, add new dimensions to social learning.

Primatewide, youngsters learn to conform to social rules while growing up. Monkeys and children alike internalize proper etiquette for approaching a dominant group member. But human youngsters display a special eagerness to ingratiate themselves with others and internalize their preferences, adding subjective dimensions to this quest. Evolutionary psychiatrist Randolph Nesse

hypothesizes that runaway social selection favoring self-consciousness and concern with reputation in creatures already interested in mentalizing what others think, helps to explain why our ancestors evolved the internal self-monitoring we call “a conscience” (Nesse, 2007, 2019).

Whether or not such ingratiating tendencies encourage humans to behave in fair, generous, or civic-minded rather than more self-serving ways, is another matter. It probably depends more on socioecological contexts and immediate goals than on what are sometimes taken to be hard-wired moral sensibilities (Bloom, 2013; Hamlin & Wynn, 2011; Hamlin et al., 2010). As early as six months, long before language, infants exhibit preferences for helpful versus hurtful others (Hamlin & Wynn, 2011). However, it is unclear how prosocial versus self-interested such preferences are. In experiments simulating *voir dire* in an imaginary courtroom, Melnikoff and Bailey (2018) asked adult subjects who they would prefer in the jury, depending on whether they served as lawyer for the defense or for the prosecution. The researchers were struck by how conditional on peoples’ current goals their preferences for moral vs. immoral actors could be.

Whatever standards prevail, quests to demonstrate mental and behavioral responses conforming to others’ preferences pave the way for internalizing group norms (Gavriletes & Richerson, 2017) and for behavior that group members consider “moral” (Boehm, 2012; Tomasello, 2016). It is exactly this third-party perspective that is so strikingly deficient in nonhuman primates (Burkart, Brügger, & van Schaik, 2018), absent in creatures who otherwise exhibit many critical building blocks for morality (de Waal, 2006; Silk & House, 2016). Other primates may conform to local traditions, but they don’t seem to care much if *others* do so or not, and even unusually prosocial primates such as marmosets do not manage their reputations by increasing their helpfulness when observed by others (Burkart, Brügger, & van Schaik, 2018). But like great apes, early hominin would almost certainly have been able to theorize about what others

knew (Krupeye et al., 2016) and over the course of human evolution became distinctively motivated to care about their reputations. This same aptitude would presumably have been advantageous for cooperatively breeding marmosets as well, but they may have simply lacked the cognitive infrastructure to register how they appear to others.

5 Conclusions

Across taxa, earlier weaning, shorter inter-birth intervals, and longer spans of post-weaning (or in the case of birds, post-fledging) dependence are predictable corollaries of cooperative breeding. In the case of the cooperatively breeding apes in the line leading to the genus *Homo*, reliance on care and provisioning from alloparents as well as parents, conditioned dependent immatures to develop an un-ape-like eagerness to monitor and care about the intentions of others, mentalize what they were thinking and feeling, and seek to ingratiate themselves with them leading to the expression and refinement of otherwise latent ape potentials. This novel context for development and social learning coincided with directional social selection (West-Eberhard, 1983, 2003) favoring youngsters best at ingratiating themselves with protectors, mentors, and providers. By two million years ago this combined process of development-plus-social selection was already contributing towards the emergence of cognitive and emotional phenotypes in hominins that were very different from those among our Last Common Ancestors with chimpanzees and other great apes.

Without any foresight on Mother Nature's part concerning how important questing for intersubjective engagement and escalating concerns with reputations would eventually turn out to be, *Homo erectus* infants would have been conditioned to monitor and care about what others were thinking, including thinking about them. They would have been rewarded for internalizing their preferences in ways others apes are not. Resulting concerns with reputation make having a

conscience increasingly useful. Long before the emergence of *anatomically modern* big-brained humans by 300,000 years ago (Hublin et al., 2017), or before behaviorally modern humans with symbolic thought and language, these emotionally different apes were already eager to appeal to and help others. Although activities such as group hunting or inter-group warfare are frequently cited as the contexts in which greater inter-individual cooperation, communication skills, and helpfulness evolved, such explanations do not fit with the observation that helpful tendencies emerge early and in both sexes, with girls if anything better able to interpret others' expressions and feelings than boys (Geary, 2018).

By the Late Pleistocene as cooperative hunting of big game, division of labor, and sharing of food became more important, hominins of both sexes must *already* have become predisposed to read the intentions of others in order to coordinate with and help them (Hawkes, 2014; Hrdy, 2009, 2016a; Tomasello & Gonzalez-Cabrera, 2017). By the time coordinated hunting of large animals was established in the human repertoire—whether by 400,000 years ago as in Tomasello's reconstruction or closer to Chris Boehm's "magic number" (Boehm, 2012, p. 313) of 250,000 years ago—it was probably accompanied by "punitive social selection" against stingy or overly domineering men as documented for hunter-gatherer societies (Boehm, 2012, p. 164; Tomasello, 2016, 2018). If so, these members of the genus *Homo* would have already become motivationally very different from their more self-centered, solipsistic ape ancestors. In Boehm's account, sanctions against bullies could extend to exile or even execution of offenders, pressuring them to conform to and adopt group norms, behave in a "moral" way. We suggest that with internalization of norms underway, archaic humans would already have been, from an early age, sensitive to what others felt and thought about them, concerned about personal reputations, and

eager to cooperate. Hominins were preadapted to internalize ways of behaving and expressing themselves that others preferred.

Higher-quality food sources and multiple provisioners continuing to buffer weanlings from recurring shortages in the Late Pleistocene was lifting the grey ceiling that limits energy available for brains. The stage was set for these *emotionally modern* early humans to meet new social and ecological challenges in ways that would favor the evolution of even more costly, *anatomically modern*, brains. Expanding social networks and accompanying motivations would also encourage the emergence of more sophisticated modes of vocal communication that would vastly expand both the ability to learn from multiple others (via gossip and teaching) and expand the reach and importance both of normative ways of doing things (Richerson and Boyd 2020) and of reputations. Such processes would stress conformity and further favor the internalization of group norms and human indoctrinability, hallmarks of *behaviorally modern* humans.

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Figure Captions

Figure 6.1. We hypothesize that by two million years ago, with the emergence of *Homo erectus*, mothers were already beginning to wean infants somewhat earlier than among other apes. Earlier weaning and shorter inter-birth intervals were only feasible because alloparents (group members other than genetic parents) as well as parents, helped to care for and provision nutritionally dependent, slow maturing hominin young. (“The real Pleistocene family” as reconstructed by artist Viktor Deak, copyright SbhLit).

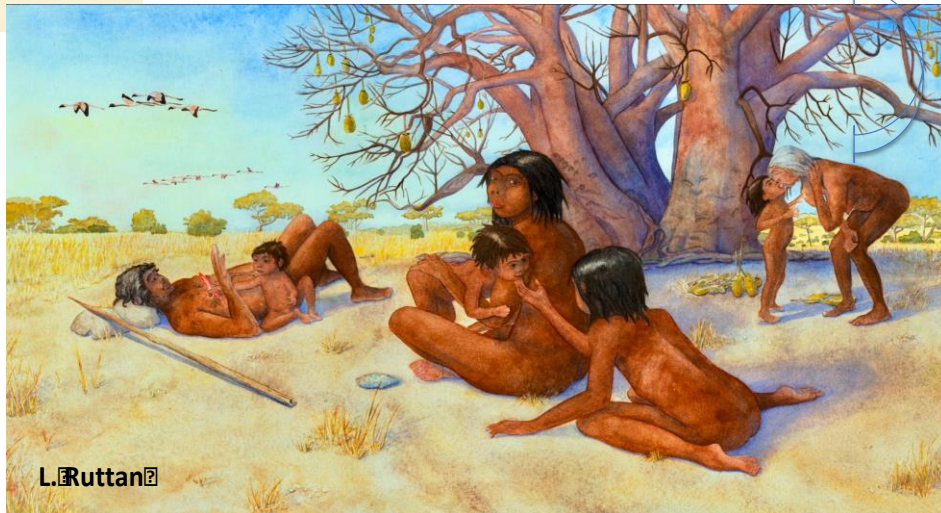


Figure 6.2. This thought experiment traces dual ontogenetic and evolutionary processes set in motion when mothers in the line leading to the genus *Homo* began to rely on alloparental care and provisioning to rear increasingly costly, sometimes more closely spaced, offspring. Intermittent behavioral conditioning would encourage youngsters to repeat and refine facial expressions, attitudes, and vocalizations most likely to appeal to potential caretakers. This would lead to the expression of otherwise latent potentials and the formation of novel neural networks. Over generations, these quite novel ape phenotypes would be exposed to directional social selection favoring youngsters best at ingratiating themselves with others, setting in motion a causal chain of adaptive evolution that began with development (West Eberhard, 2003).

MOTHERS & OTHERS? THOUGHT EXPERIMENT:



What would happen if you took a lever, a manipulative, tool-using ape possessing rudimentary theory of mind and reared them in a novel context where infants had to elicit contingently provided care and provisioning from ~~all~~ allomothers as well as mothers...?

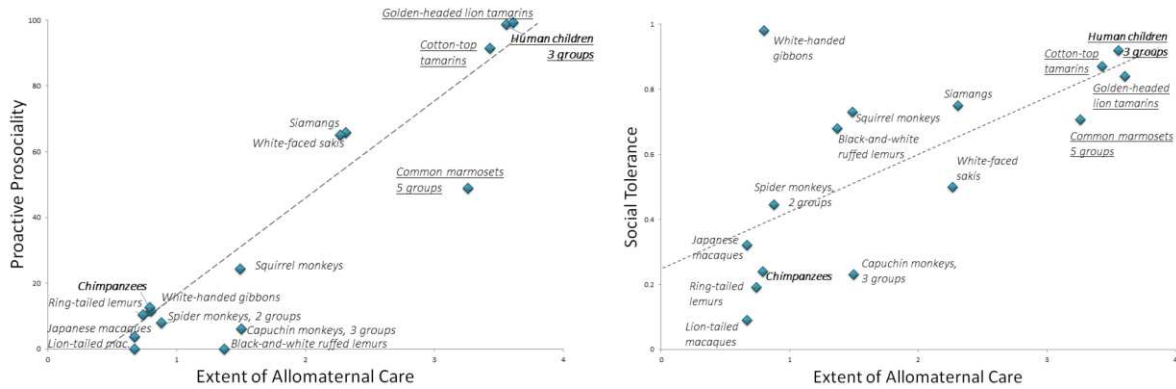


...so developing immatures learned to be more other-regarding, resulting in novel ape phenotypes? Over generations, directional social selection would favor those best equipped to ingratiate themselves with others (Art courtesy L. Ruttan)

Figure 6.3. Cotton-top tamarins in a group service experiment. The individual on the right-hand side pulls the food reward to within reach of its group members, without being able to get anything for itself. To assess group level proactive prosociality, the percentage of food items made available to the group is measured.



Figure 6.4. Results from group service experiments described in Burkart et al. (2014). The amount of allomaternal care directly predicts proactive prosociality (left-hand side; % of food items made available to group members) and social tolerance (right-hand side; 1 = high, 0 = low) across primate species, including humans. Great apes are highlighted in bold, cooperatively breeding primates are underlined.



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