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Variation in the Social Systems of Extant Hominoids: Comparative Insight into the Social Behavior of Early Hominins

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Abstract The observed social systems of extant apes and humans suggest that the common ancestral state for Miocene hominoids was living in multimale–multifemale groups that exhibited a tendency to fission and fusion in response to ecological and/or social variables. The Hominoidea share a set of social commonalities, notably a social niche that extends beyond kin and beyond the immediate social group, as well as extensive intraspecific flexibility in social organization. We propose that an essential feature of hominoid evolution is the shift from limited plasticity in a generalized social ape to expanded behavioral plasticity as an adaptive niche. Whereas in most nonhominoid primates variability and flexibility take the shape of specific patterns of demographic flux and interindividual relationships, we can consider behavioral flexibility and plasticity as a means to an end in hominoid socioecological landscapes. In addition, the potential for innovation, spread, and inheritance of behavioral patterns and social traditions is much higher in the hominoids, especially the great apes, than in other anthropoid primates. We further suggest that this pattern forms a basis for the substantial expansion of social complexity and adaptive behavioral plasticity in the hominins, especially the genus *Homo*. Our objectives in this article are threefold: 1) summarize the variation in the social systems of extant hominoid taxa; 2) consider the evolutionary processes underlying these variations; and 3) expand upon the traditional socioecological model, especially with respect to reconstructions of early hominin social behavior. We emphasize a central role for both ecological and social niche construction, as well as behavioral plasticity, as basal hominoid characteristics. Over evolutionary time these

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characteristics influence the patterns of selection pressures and the resulting social structures. We propose that a mosaic of ecological and social inheritance patterns should be considered in the reconstruction of early hominin social systems.

Keywords Ecological and social niche construction · Evolution · Hominin social organization · Hominoidea

Introduction

Socioecological studies of nonhuman primates attempt to explain the mechanisms by which variation in ecological factors, such as the abundance, quality, and distribution of food, as well as predation pressure, influence demography and social relationships within and between groups (Clutton-Brock 1974; Sterck *et al*. 1997; van Schaik and van Hoof 1983; Wrangham 1979, 1980). This approach is often invoked to help explain and/or model the evolution of specific components of social systems. In applying this classic theoretical framework, researchers primarily search for the social and behavioral manifestations of sensitivity to ecological variables. Broad quantitative analyses seeking to document correlations between behavioral and ecological variables have historically been accomplished by comparing data from closely related taxa living in different environments, distantly related taxa living in similar environments, and more recently among populations within the same taxa (Clutton-Brock 1974; Clutton-Brock and Harvey 1977; Kamilar and Ledogar 2011; Strier 2003). As we refine our research methods, and the overall number of studies increases, we are faced with both a broad range of social-system-wide variants between taxa, and also increasingly prevalent within-taxa "variations on a theme" (Strier 1994; Thierry 2008). Bernard Thierry (2008) goes as far as to suggest that we should consider discarding the current socioecological approach and its expectation that a single comprehensive model will be able to accurately describe, and predict, primate social systems. We might not take it quite this far (Koenig and Borries 2009) but we do suggest that the implication of the ubiquitous nature of variaion within social systems is that our interpretations are simultaneously more informed yet less absolute. We attempt to ameliorate this paradox in the hominoids by considering the evolutionary processes underlying these variations, especially as they apply to the reconstruction of hominin social systems (Alexander 1990; Flinn *et al*. 2005; Potts 1998). Specifically, we suggest that much variation in extant hominoid social behavior reflects epiphenomenal adaptive response (plasticity in expressed social behavior) to local environmental and social conditions, and not optimally fixed behavioral patterns produced by selection.

Social systems, both within and between taxa, within the superfamily Hominoidea (comprising the families Hominidae and Hylobatidae) are complex and diverse with respect to the organization and structure of social groups and individual relationships (Brockelman *et al*. 1998; Doran and McNeilage 1998; Malone and Fuentes 2009; Potts 1998; Stumpf 2007; van Schaik 1999; White 1996a). Do certain patterns of sociality transcend this diversity? van Schaik *et al*. (2004) outline four realms of social commonalities among the great apes (hominids): 1) a tendency toward fission–fusion social organization (or at least toward facultative

social units); 2) relatively high subordinate leverage; 3) intrasexual bonds among nonrelatives are as common, or more so, than bonds among relatives; and 4) remarkably extensive intraspecific flexibility in social organization and affiliation. In addition, Reichard and Barelli (2008) summarized small ape (hylobatid) social systems within the aforementioned schema and conclude that *all apes* demonstrate this sort of variation, and are indeed unified by behavioral and demographic social flexibility. If these commonalities among extant apes, in addition to slow life histories (Kelley 1997), are indeed reflective of ancestral adaptive patterns, then it is highly likely that significant variability in social organization and affiliation is a core facet of the hominoid adaptive niche.

The traditional socioecological model does not, inherently, incorporate substantial variation and social flexibility as core features of social systems. If we are to merge this perspective into such approaches we will have to consider alternative evolutionary pathways in addition to standard trait selection of clearly defined social states (Foley and Lee 1989; Thierry 2008). This can lead to a more dynamic process that incorporates and better explains the observed variation and flexibility in extant ape societies. Rather than assuming a drive toward optimal solutions, with a group of finite and specific social phenotypes competing in a population, we suggest that the interface between organisms and their environments should also be viewed as historical, population-level processes. This perspective involves a dynamic evolutionary process that incorporates forces *in addition* to the action of natural and sexual selection. Population level processes are inherently complex as they encompass a host of factors including environmental conditions, historical contingencies, density-dependent effects, and stochastic processes (such as genetic drift and some behavioral innovation). Such processes involve the potential for evolutionarily relevant, but nongenetically determined, insertions of pertinent behavioral, and even physiological patterns (Jablonka and Lamb 2005; West-Eberhardt 2003). As such, they do not necessarily result from optimal adaptive trajectories as measured by models of reproductive fitness, but rather in broader behavioral potentials and social systems that diminish the pressure for, and impact of, individual strategies of cost minimization and benefit maximization. Considering the social commonalities of the Hominoidea, e.g., a social niche that extends beyond kin and beyond the immediate social group, our overarching goal is to develop a conceptual model capable of explaining the shift from limited plasticity in a generalized social ape to expanded behavioral plasticity as an adaptive niche, especially in the hominins. Our model attempts to illustrate unifying processes underlying the social systems of early hominins. We begin by highlighting salient data from a review of published studies on extant hominoid socioecology. Next we summarize emergent perspectives in evolutionary theory including a focus on phenotypic plasticity, social and ecological inheritance, and especially, niche construction (Fuentes 2009; Jablonka and Lamb 2005; Odling-Smee *et al*. 2003). The core point of niche construction theory is that although genetic variation is subject to natural selection via differential survival and reproductive success, the very selective environments themselves are also engaged and structured by modifications made by niche constructing organisms, and this process is especially salient when considering hominin evolution (Kendal *et al*. 2011). We conclude by considering the applicability of these perspectives in relation to hominoid evolution.

Introduction to the Model

The basic premise of our model is that the early- to mid-Miocene hominoids exhibited a limited social plasticity relative to modern hominoids, but, like most anthropoid primates, had an emphasis on social bonding between select individuals and the creation of social networks within groups as core facets of their basic socioecology. Over the course of the Miocene we suggest that variability in social and ecological selection pressures favored those individuals who were able to exhibit increased behavioral and demographic plasticity (short term and long term) in behavioral response to ameliorate external pressures. This selection for plasticity in behavioral response, combined with slowed maturation and increased pressure for maintenance of complex social relationships in a fission–fusion context, would have enabled expansion in neurological elements, such as von Economo and mirror neurons (Allman *et al*. 2010; Ramachandran 2011) that facilitate a wider range of potential behavioral response without requiring the selection of specific behavioral patterns. With increased social and ecological complexity, social groups, and the individuals within them, experienced more evolutionarily relevant nongenetic inheritance (ecological and social). This, combined with expanded abilities to respond to selection pressures via relatively plastic behavioral responses or innovations, increased the role of a feedback system between niche construction and selection pressures favoring continued expansion in social plasticity via behavioral and neural expansion (Fig. 1) (MacKinnon and Fuentes 2011). We suggest that it is in the hominins that this processes has had the most substantive expansion and that specific ecological and structural pressures have had a more constraining effect on the other hominoids. Previous models emphasize an intensification of selective pressure via conspecific "social competition" proceeding from a diminished intensity of extrinsic pressures, i.e., hominins became "ecologically dominant") (Alexander 1989, 1990; Flinn *et al*. 2005), or adaptive flexibility in reposnse to environmental fluctuation (Potts 1998). We do not envision that hominins achieve a "dominance" over ecological pressures through social competiton, or that ecological instability/unpredictability is the core driver of evolutionary change. Rather, we seek to meld these perspectives into one wherein social and ecological niches are seen as wholly integrated, and inherited, with a dynamic mutual mutability between organisms, groups, and their ecologies.

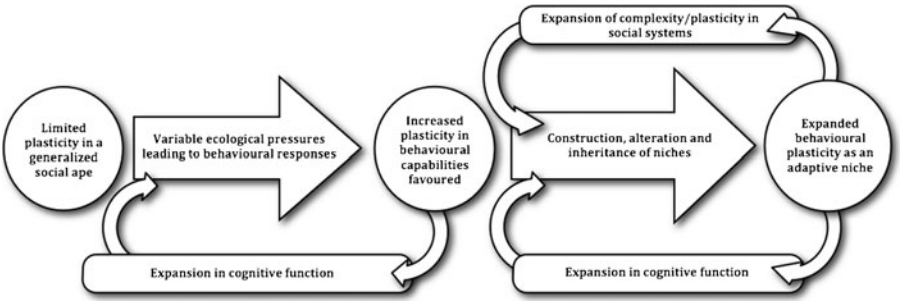


Fig. 1 Simple trajectory for expanding social plasticity. Specific aspects of cognition, especially those related to behavioral plasticity, evolved largely in response to the increasingly challenging demands of a social life that includes the construction, alteration, and inheritance of social and ecological niches.

For this model to be valid, the following premises must hold true: 1) evidence for multiadult grouping pattern and social context in the early hominoids; 2) evidence for growth in areas of the brain that facilitate enhanced flexibility not contingent on specific trait function in the hominoid lineage; 3) substantive variability in social association patterns within and between living taxa, and between individuals and groups, in the hominoid lineage; 4) observed innovative flexibility in behavioral response to ecological pressures in extant taxa; 5) significant inheritance of social and ecological variables in extant hominoid groups; and 6) all of these patterns are more robust in the hominin lineage and especially in modern humans.

It is highly likely that mid- and late-Miocene hominoids occurred largely in mixed-sex groups (expectation 1) (Conroy 1990; Strier 2007), and there is no debate that brain size and neurological complexity increased in the hominoid lineages relative to other anthropoids (expectation 2). In this article we address the other expectations to provide support for the proposed model.

Overview of Nonhuman Hominoid Social Diversity

In this section, we summarize published data on hominoid ecology and social behavior to elucidate the commonalities and differences among taxa. We briefly review salient data on variability from each of the extant hominoid genera (Table I). We partition

Table I Taxonomy of the living hominoids (including extinct hominins)

Superfamily Hominoidea
Family Hylobatidae
Genus *Hoolock* (2 species)
Genus *Hylobates* (7 species)
Genus *Nomascus* (7 species)
Genus *Symphalangus* (1 species)
Family Hominidae
Subfamily Ponginae
Genus *Pongo* (2 species)
Subfamily Homininae
Tribe Gorillini
Genus *Gorilla* (2 species)
Tribe Hominini
Subtribe Panina
Genus *Pan* (2 species)
Subtribe Australopithecina
Genus *Ardipithecus* (2 extinct species)
Genus *Australopithecus* (5 extinct species)
Genus *Kenyanthropus* (1 extinct species)
Genus *Paranthropus* (3 extinct species)
Subtribe Hominina
Genus *Homo* (7 extinct and 1 extant species)

Taxonomy adapted from Wood and Richmond (2000) and reflective of anatomical and molecular evidence (Brandon-Jones *et al*. 2004; Geissmann 2007; Groves 2001; Ruvolo 1997; Wood and Lonergan 2008)

superfamily-wide variation in this manner, i.e., by genus, for organizational purposes and our rubric should not be mistaken for an assumption of intragenus homogeneity with regard to feeding and socioecology. We also consider the evolutionary implications of the expression of individual variation and behavioral plasticity for the emergent relationships among individuals and groups.

Family Hylobatidae

A mid-Miocene date of 15.0–18.5 million years ago (mya) is estimated for the gibbon-great ape (here Hylobatidae–Hominidae) divergence (Raaum *et al*. 2005; Tyler 1993), followed by the commencement of diversification into the four extant generic lineages *ca*. 10.5 mya (Chatterjee 2006, 2009). In spite of controversial (but informative) fossil evidence, the family is distinguished from the great apes by a suite of niche-specific synapomorphies related to their highly mobile and energetically efficient mode of overhead suspensory locomotion, as well as small body size, small group size, and territorial behavior (Jablonski and Chaplin 2009). Although not fully resolving all ongoing debates, the recent publication of Lappan and Whittaker's (2009) edited volume elevates our understanding of the hylobatids, especially with respect to evolutionary relationships, biogeography, socioecological flexibility, and the importance of a population-level perspective. Long considered to exhibit relatively uniform social structures, we now appreciate the patterns of variation both within and between gibbon genera. The recognition of such variation, in light of the highly specialized morphological characters that unify the hylobatids (and arguably constrain certain aspects of behavior and ecology), underscores important evolutionary lessons for our discussion herein, and therefore warrants the brief summary that follows (Brockelman 2009; Malone and Fuentes 2009).

Genus Hylobates Gibbon species within the genus *Hylobates* are the most studied of hylobatid taxa. Over a period of four decades, comparative data on the feeding ecology of several species of *Hylobates* have been published (Bartlett 1999, 2007, 2009; Brockelman *et al*. 1998; Ellefson 1974; Gittins 1982; Kappeler 1984; Leighton 1987; MacKinnon and MacKinnon 1980; Palombit 1997; Raemaekers 1979; Reichard 2009; Srikosamatara 1984; Suwanvecho 2003; Whitten 1984). Unfortunately, the dispersal patterns, pair formation/maintenance processes, and intra- and intergroup social organization of most members of the genus have been little studied. However, the white-handed gibbon (*Hylobates lar*) is especially well known from two sites: Khao Yai National Park in Thailand (Brockelman *et al*. 1998; Reichard 1995, 2003, 2009) and Ketambe Research Station in the Gunung Leuser National Park, Sumatra (Palombit 1992, 1994, 1996). Detailed observations of reproduction, natal dispersal, pair formation, and group structure in the Khao Yai population, from 1978 to the present, represent the largest data set available with which to address questions about hylobatid social organization. Specifically, the static model of highly territorial, monogamous pairs living in nuclear family groups can be assessed with data encompassing the life histories for individuals in several neighboring social groups. A genetic relationship between adults and immatures in social groups is usually assumed in the nuclear family model. The findings of the many researchers at Khao Yai raise questions about these assumptions (Brockelman *et al*. 1998; Reichard 2009).

Although knowledge of life histories and familiarity with migrating individuals are rare, as are actual genetic data, genetic relatedness in hylobatid social units may also be assessed by comparing estimated ages of offspring to a known interbirth interval (IBI). Brockelman *et al*. (1998) and others, based on long-term observation at Khao Yai, indicate a minimum IBI of *ca*. 3 yr. Data from a sample of 64 white-handed gibbon groups at Khao Yai reveal that 33 % of the groups contained young estimated to be <2 yr apart in age (Brockelman *et al*. 1998). These data, in combination with relatively short dispersal distances, suggest that it is not uncommon for groups to contain young from more than one family, and that related individuals, e.g., siblings, cousins, may frequently reside in neighboring territories. The potentially large number of non-nuclear families in this population stands in stark contrast to the conclusions of earlier researchers (Leighton 1987) as to the invariably monogamous social and reproductive behavior of hylobatids (Fuentes 2000). Further challenges to the nuclear family model come from direct observation of partner turnover and extrapair copulations (EPCs), reported to comprise up to 12 % of all copulations (Reichard 1995, 2009). The implications of these observations for the nature of intergroup interactions are great. Given the potential interrelatedness of gibbon groups, aggressive interactions with neighbors may in fact be detrimental to an individual's own fitness. Indeed, Bartlett (2003) reports that although a majority of intergroup encounters were considered agonistic, 20 % consisted of vocal exchanges only, 6 % were neutral, and 17 % included affiliation. Data such as these emphasize the importance of conceptualizing the gibbon "group" to be intimately interconnected to "rich networks of genetic and social ties" at the community level (Whittaker and Lappan 2009, p. 5; see also Brockelman *et al*. 1998).

Genus Symphalangus Siamang (*Symphalangus syndactylus*) are relatively well known from Sumatra, as well as the Malay Peninsula. The siamang is the largest of all gibbon species and is found in primary and secondary, lowland and montane forests up to 3800 m. Long considered to be the true folivores of the family, Elder (2009), based on a larger sample of diets, fails to discriminate between siamang and the small-bodied hylobatids (*Hylobates*, *Hoolock*, and *Nomascus*) on several key dietary variables and concludes that there is no significant relationship between body mass and folivory among the four hylobatid genera. Further, general patterns of dietary and behavioral variation, consistent with those found among species within the genus *Hylobates*, are evident between the insular (Sumatran) and mainland subspecies of siamang (Chivers 1974; Lappan 2005; MacKinnon and MacKinnon 1980; Palombit 1992; Raemaekers 1979).

Palombit (1996) uses quantitative measurements of social interactions and spatial relationships of adult pairs to make interspecific comparisons between pair-bonding behavior in siamangs and white-handed gibbons at Ketambe. Analyses of close proximity and (nongrooming) physical contact are used to evaluate time spent in affiliation by males and females, and to compare the male and female investment in social relationships with opposite-sex adults. The results indicate that siamang pairs demonstrate greater spatial cohesion than do pairs of white-handed gibbons. Further, interspecific differences in the contributions of the sexes toward maintenance of the male–female social relationship suggest the presence of differing selective pressures affecting the importance of these relationships in different social and ecological contexts.

A recent long-term study of siamang groups at the Way Canguk Research Station in southern Sumatra provides new insight into the social complexity of siamang populations (Lappan 2005, 2007). The occurrence of cohesive, greater-than-two-adult groups (multimale/unifemale composition) in four of the five of the focal groups, and the observation of polyandrous mating patterns in three of the four groups with more than a single adult male, provided an opportunity for the examination of male–infant, male–male, and male–female relationships (Lappan 2007). Lappan's conclusions are relevant to our discussion as they provide potential for insight into underlying ecological factors, i.e., distribution of resources, that are predicted, by current models of hylobatid social organization, to ultimately result in the evolution of gibbon pair bonds. In the multimale groups at Way Canguk, Lappan (2007) reports low rates of overall aggression, mutual tolerance among males, and variability in the strength and signaling of male–female bonds. Further, Lappan's analyses of both genetic and behavioral data indicate that genetic relatedness cannot always be predicted from observable social relationships (Lappan 2005, 2007).

Genus Hoolock Western and Eastern hoolock gibbons (*Hoolock hoolock* and *H. leuconedys*, respectively) inhabit rainforests and semideciduous forests in tropical and subtropical areas of India, Burma, China, and Bangladesh. Very little is known about the behavioral ecology of this genus. Hoolock gibbons are relatively large among hylobatid taxa, and are the only gibbons that range substantially outside of the tropics (Das and Biswas 2009; Mootnick *et al*. 1987). A predicted dietary response to a seasonal environment might include increased reliance on leaves as fruit availability decreases. However, Gittins and Tilson (1984), studying at a subtropical locale, reported a stable consumption of fruit throughout the year at a level comparable to gibbon species of the genus *Hylobates*.

Hoolock gibbons have been observed to occur in greater-than-two adult groups, including two adult males and a female; two adult females and a male; and up to five adult males in a bachelor group in northeast India. Overall, 4 of the 34 hoolock groups on which studies have been published (12 %) had a composition that runs counter to the traditional view of hylobatid social organization (Ahsan 1995; Choudhury 1990; Mukherjee *et al*. 1991–1992; Siddiqi 1986; Tilson 1979).

Genus Nomascus Understanding the basic range of diversity within this genus is very much an ongoing affair, including the recent classification of a seventh species (Thinh *et al*. 2010). As such, relatively few studies of the genus *Nomascus* have been conducted (Bleisch and Chen 1991; Fan *et al*. 2006; Geissmann 2007; Haimoff *et al*. 1987; Jiang *et al*. 1999; Ruppell 2007; Sheeran 1993; Zhenhe *et al*. 1989). Species in this genus range in montane forests up to 2900 m. With the exception of the siamang, this represents the highest recorded altitude for a gibbon species (Bleisch and Chen 1991). The diet of the western black-crested gibbon (*Nomascus concolor*) has been reported to be more folivorous than those of other gibbons of similar size, and black-crested gibbons have been observed to come to the ground to forage on bamboo shoots. Early reports of group structure reported one male–multifemale groups of up to four females, and average group sizes of 5.25 individuals (Haimoff *et al*. 1987). Overall, published reports indicate that *ca*. 25 % of groups of *Nomascus* spp. have greater than two adults, including observations of groups of up to 10

individuals, groups with up to 4 adult females, and multiple females with dependent infants (Bleisch and Chen 1991; Haimoff *et al*. 1986; Lan and Sheeran 1995).

Bleisch and Chen (1991) report that western black-crested gibbon (*Nomascus concolor concolor* and *N. c. jingdongensis*) habitat in the Wu Liang Mountain and Ai Lao Mountain Natural Protected Areas in the center of the Yunnan Province, China consists of low-stature mixed broadleaf evergreen and deciduous trees. This seasonal subtropical habitat differs from the tropical forests usually associated with gibbons. Day range sizes are generally larger than those found for other gibbon species. Group size/composition was determined for seven groups. Groups were no larger than five individuals and well within the usual range for gibbons. Three groups consisted of a single male and multiple individuals that produced female vocalizations. The presence of multiple female singers in a single group is presented as evidence that these gibbons live in polygynous groups (Bleisch and Chen 1991). However, because immature individuals produce female songs in this species, this conclusion is tenuous. It is important to note that polygyny is one of many mating patterns that may exist within this particular social organization. Similarly, although monogamy is often assumed, in reality there is a wide range of diversity in mating patterns in primates whose grouping patterns is predominated by two-adult pairs (Fuentes 2000, 2002). Direct observations of mating behavior, genetic data, and long-term studies of this and other gibbon species are needed before interspecific comparisons can be considered complete.

Summary: Family Hylobatidae

This overview of socioecological studies clearly demonstrates the extent of interspecific variability within the family Hylobatidae. It is also increasingly understood that ecological pressures, in addition to intrasexual competition, drive core aspects of gibbon social systems, e.g., relatively small group sizes and close sociospatial proximity among gibbon pairs (Bartlett 2009; Malone and Fuentes 2009). This view of the variability within the Hylobatidae suggests that we need to envision a broader evolutionary scenario. Expanding the focus beyond mating monogamy, pair-bondedness, and territoriality, and incorporating theoretical toolkits that go beyond basic selection models we can realize that single explanations, e.g., infanticide, fail to predict the social variability in the Hylobatidae. There is an active and emergent relationship between individuals, groups, populations, and their environments. This perspective is compatible with an increasing acknowledgment in evolutionary biology that a mutually interactive relationship exists between organisms and their environment through niche construction (Kendal *et al*. 2011; Laland *et al*. 2001; Odling-Smee *et al*. 2003). Niche construction conceptualizes evolution of *both* populations of organisms and their environments. This perspective models niche construction as a mutually mutable function of organisms and environments with a dynamic interface affecting the shape and behavior of populations and the patterns and characteristics of selective pressures in ecosystems (Odling-Smee 2007).

In the case of gibbons, the construction of territories and territorial relationships among contiguous groups creates a social and ecological niche relationship via genetic and ecological inheritance systems. The ability of organisms to not only impact their environment, but also, in part, shape the selective forces that they face,

may result in more plastic or variable behavioral profiles (MacKinnon and Fuentes 2011; West-Eberhardt 2003). In addition to these ecological underpinnings, Reichard (2009) concluded, based on evidence of sociosexual flexibility, that hylobatids share with the great apes "a basic cognitive capacity for solving nonsocial problems with social solutions" (p. 371). Within the context of an individual gibbon's lifetime, their small focal group can consist of genetic kin or not, as well as more than one adult of the same sex (and therefore potential mating competitors) or not. In addition, the presence of genetic kin and/or extremely familiar individuals in neighboring groups can result in either strong, moderate, or low levels of feeding competition at overlapping feeding sites. Indeed, territories represent inherited social barriers to range expansion in most cases, and yet the hylobatids, via behavioral flexibility (including core aspects of their vocal repertoire) successfully accommodate both diverse and shifting demographic make-ups within both small focal groups and larger communities (or neighborhoods).

Family Hominidae

The extant nonhuman members of the family Hominidae can provide a comparative evolutionary perspective into the nature and structure of social variation and socioecological patterns in the human lineage. Human grouping patterns, sociality, and the relationships within and between groups might be reflective of shared patterns in the broader taxonomic group. Here we briefly summarize the current consensus view of the large-bodied hominoids, with respect to social and ecological variation. Of particular interest for our discussion of early hominin socioecology is the African hominoid subfamily Homininae especially with respect to the patterns of group cohesion and socialstructural variants. Although all large-bodied hominoids are united by morphological similarities and physiological profiles, a wide range of social and ecological niche space is occupied by species within this family. We begin with the Asian great ape subfamily Ponginae, and then proceed to review the Homininae.

Subfamily Ponginae Consensus puts orangutan (Ponginae) divergence from the African Ape clade at *ca*. 12 mya, although some support exists for both early (19–24 mya) (Easteal and Herbert 1997) and late (8–9 mya) (Arnason et al. 1996) divergence scenarios. Subsequent divergence into Bornean (*Pongo pygmaeus*) and Sumatran (*P. abelii*) species occurred *ca*. 2.7–5 mya (Steiper 2006). Further, some researchers recognize distinct lineages of Bornean orangutans at the subspecies or even subpopulation level (Groves 2001; Warren *et al*. 2001). Regardless of these ongoing taxonomic discussions, we can safely treat the genus *Pongo* with a general focus on the interaction among biological, ecological, and social variables.

Orangutans are large-bodied, display a high degree of sexual dimorphism, and possess adaptations for a near-exclusively arboreal lifestyle characterized by quadrumanous clambering (Fleagle 1999, Knott and Kahlenberg 2007). Orangutan growth and development includes long life history phases, even relative to those of other hominoids, the ability to store excess energy as fat, and indeterminate growth and bimaturation in males, most likely a response to vigorous intrasexual competition (Galdikas and Wood 1990; Knott and Kahlenberg 2007; Leigh and Shea 1995; Maggioncalda *et al*. 2002).

As with the Hylobatidae, the backdrop of pronounced resource fluctuations in Southeast Asian forests is a cornerstone of rooting individual and group strategies in an ecological context. Southeast Asian rainforests are characterized by inter- and intra-annual variability in resource availability, driven in part by the interaction of climatic events (El Niño/Southern Oscillation) and mast fruiting by trees of the family Dipterocarpaceae (Ashton 1988; Curran *et al*. 1999; Fleming *et al*. 1987; Whitmore 1984). Fluctuations in the quantity and quality of available resources in Southeast Asian rain forests, including high variability in nutrient intake related to percentage of fruit in the diet, can substantially impact large-bodied, strictly arboreal mammals (Knott 1999a; Knott and Kahlenberg 2007). Orangutans occupy almost exclusively the high canopy of peat and freshwater swamps, extremely wet lowland forests, and mountainous slopes up to an altitude of 1200 m. The aforementioned morphological and physiological parameters, in combination with the ecology of their forested habitats, are central to explanations of orangutan social organization.

In addition to a semisolitary existence within highly overlapping ranges, orangutan females (and immature offspring) form social groupings that consist of travel bands, feeding aggregations, and consortships with individual males (Knott *et al*. 2008; Utami *et al*. 1997). Male ranges are large and overlap with both male and female ranges (Knott 1999a,b; van Schaik 1999). Perhaps this is best described as dispersed sociality, or individual based fission–fusion groupings. In addition, in areas of higher-than-usual/consistent productivity, e.g., Suaq Balimbing, Sumatra, as well as in captive and provisioned reintroduction sites, orangutans appear to be particularly gregarious. Especially relevant to our discussion here, habitual tool use in extractive foraging, as well as behavioral transmission and diffusion of social innovations throughout the population are associated with, and facilitated by, increased sociality (Fox *et al*. 1999, 2004; van Schaik 1999; van Schaik *et al*. 2003).

The flexibility inherent (and observed) in the dispersed sociality of orangutans is dramatic (especially if you include captive colonies). A core aspect of their behavioral response is the fact that in areas of high fruit density/low feeding competition they radically alter their behavioral profiles to engage in much higher rates of affiliation. Although the bimaturation strategies in males is partially a physiological response, one can see this pattern as potentially a long-term plastic adaptive response given the social structure (niche) of single adult males actively holding large territories as a response to both mating competition and the phenology of Southeast Asian forests. It may be that the behavioral patterns emerged first as plastic responses and that the endocrine functionality that facilitated the morphological shift followed the behavioral response. The current flexibility of this pattern in both behavioral and endocrine processes suggests that this is indeed a strong possibility. Also, the flexible use of tools in adaptive extrasomatic foraging also indicates the potential for particularly robust behaviorally flexible inheritances.

Subfamily Homininae: Tribe Gorillini The genus *Gorilla* is divided into eastern and western species (Vigilant and Bradley 2004). Eastern gorillas (*Gorilla beringei*) occupy limited portions of the mountainous and lowland forests of Rwanda, Uganda, and the Democratic Republic of Congo (DRC), while Western gorillas (*Gorilla gorilla*) occur over a broader distribution encompassing Nigeria, Cameroon, Equatorial Guinea, the Central African Republic, Angola, and the DRC. The two species

are broadly similar. Both species are very large and exhibit a strong degree of sexual dimorphism in both body mass and skeletal anatomy (Fleagle 1999). The nutritional requirements of large body size, in combination with a relatively generalized digestive anatomy and physiology, account for the primarily herbivorous diet of gorillas (Watts 1996). It is relevant to note that large body size likely acts to exert a wide array of specific constraints on gorillas, relative to the other hominoids.

Our understanding of gorilla socioecology is most informed by numerous studies of the mountain-dwelling populations of eastern gorillas (Doran and McNeilage 1998), although recent research is providing new insights into western gorilla sociality, diet, and ranging (Cipolletta 2004; Robbins *et al*. 2004; Rogers *et al*. 2004). Gorillas form stable, cohesive groups of 8–10 individuals, although much larger groups (>20 individuals, up to 40+) have been observed (Robbins 2007; Tutin 1996; Yamagiwa *et al*. 2003). Patterns of male and female philopatry, dispersal, and intergroup transfer are relatively complex in this genus. Female primary and secondary dispersal is the norm, while males may remain in their natal groups postmaturity, or disperse, either alone or with a subset of females, to join form their own group, join an all-male group, or become temporarily solitary (Caldecott and Ferriss 2005; Robbins 2007; Robbins *et al*. 2004). Owing to this complexity, gorillas can be characterized as exhibiting a continuum of grouping from cohesive one-male or multimale–multifemale groups to dispersed one-male or multimale subgroups (Doran and McNeilage 1998; Fuentes 2000). In addition, Goldsmith (1996) observed multimale–multifemale groups that fissioned into subgroups during times of low resource availability.

Intragroup social relationships among gorillas are most influenced by the aforementioned patterns of philopatry and dispersal, as well as the distribution of resources and the potential competition among females for male services, e.g., protection against extragroup males (Robbins 2007; Watts 2001). Abundant and evenly distributed resources, i.e., reduced levels of contest competition, are most likely the underpinnings of weak social bonds and/or dominance relationships among female gorillas (Harcourt 1979; Watts 2001), although Robbins *et al*. (2005) documents long-term stability in the female–female dominance relationships that do exist. In contrast, male–female relationships are the core of intragroup sociality and are characterized by high levels of affiliation, especially with respect to proximity maintenance, as well as the sustained, low-level agonistic behavior of males directed toward females (Robbins 2003, 2007; Sicotte 1994; Watts 1992). The nature of intergroup encounters ranges from aggressive to peaceful, with the degree of relatedness among males and number of potential migrant females accounting for much of the variance (Bradley *et al*. 2004; Sicotte 1993).

Although current body size and concomitant nutritional requirements of *Gorilla* spp. may be a signfiicant constraint on the types and patterns of behavioral plasticity exhibited, the range of variaition in grouping patterns, demography, and affiliation strategies suggests support for the argument of a core role for adpative plasticity in the taxa.

Subfamily Homininae: Subtribe Panina Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are studied at a variety of sites and to varying degrees of detail. Chimpanzees are now generally recognized as having four subspecies: western chimpanzee (*Pan troglodytes verus*) and the Nigerian-Cameroon chimpanzee

(*P. t. ellioti*) in West Africa; the central chimpanzee (*P. t. troglodytes*) in Central Africa; and the Eastern chimpanzee (*P. t. schweinfurthii)* in East Africa. The bonobo is confined to the central Congo basin in Central Africa, south of the Congo River. Studies of both bonobos and chimpanzees vary greatly in length, degree of habituation and history of provisioning, as well as the direct and indirect effects from local human populations, all of which may contribute to demographic differences between studies.

Chimpanzees live in a wide diversity of habitats encompassing the complete range from highly productive lowland rain forests (Boesch and Boesch-Achermann 2000; Tutin and Fernandez 1993), to moist forest habitats (Reynolds 2005; Watts and Mitani 2002; Wrangham *et al*. 1996), to montane and bamboo forests (Yamagiwa and Basabose 2006), and to dry savanna or savanna mosaic (Hunt and McGrew 2002; Pruetz 2006). Extensive data on chimpanzees have come from long-term studies in mosaic habitats with grassland, forest, and woodland, most notably Gombe (Goodall 1986) and Mahale (Nishida 1990). Bonobos, in contrast, are confined to the Congo Basin, but are also found in a diversity of habitats, from polyspecific evergreen rain forest with little human disturbance (White 1992), to mixed primary and secondary forest with close association with human populations (Kano 1992), to mosaic of forest and savanna (Hohmann and Fruth 2003) and to dry forest and savanna mosaic (Myers Thompson 2002). Seasonality varies marked between species and sites, with seasonality being less marked at many bonobo sites than chimpanzee sites (Doran *et al*. 2002). With such a large diversity of sites and conditions, it is not surprising that the behavior of chimpanzees or bonobos vary among sites (White 1996a). In addition, cultural differences among different chimpanzee populations add to the diversity of observed behavior (Whiten *et al*. 1999).

Chimpanzees and bonobos at all sites are highly frugivorous, supplemented with leaves, flowers, pith, insects, and meat (Nishida and Hiraiwa-Hasegawa 1987; White 1996b). Not surprisingly with such a wide variety of habitats, chimpanzees and bonobos diets vary in content and diversity between sites. In general, highly productive sites are associated with more fruit consumption and more diverse diets (Stumpf 2007). There is also considerable variation among study populations in the amount of meat eating, hunting, and tool-use to obtain insects and other food items. Both chimpanzees (Boesch 1994; Goodall 1968; Nishida *et al*. 1979; Watts and Mitani 2002) and bonobos (Badrian and Malenky 1984; Hohmann and Fruth 2008; White 1994) take animal prey, although there is considerable variation in hunting or capture behavior as well as prey species taken among study populations. The manufacture and/or use of tools to obtain food is more commonly observed in chimpanzee studies (McGrew 1992) but is also known for bonobos (Badrian *et al*. 1981; White 2008).

Both bonobos and chimpanzees can be broadly defined as showing fission–fusion social systems with communities of multiple males and females with male philopatry. Chimpanzees are male-bonded with strong social ties among usually related males. Chimpanzee communities can vary from small stable units with only one male as at Bossou, albeit under uncommon conditions (Sugiyama 2004; Sugiyama and Koman 1979), to large units of 150 individuals (Watts 2008). Bonobo communities in contrast show strong relationships among females as well as between males and females (Furuichi 1987; White 1989). As in chimpanzees, bonobo communities also vary from those with smaller membership numbers (referred to as “splinter groups”)

centered around immigrating females that persist for between 2 and 3 yr (White 1996b) to larger long-term, stable communities of up to 50–120 individuals (Furuichi 1989; White 1996b). As to be expected with the wide range of ecological conditions both among sites as well as seasonally within sites, party composition varies greatly and can often correlate to food availability, distribution of estrus females, or demographics. In general, chimpanzee sociality reflects great male–male affiliation among often somewhat related males with usually low but varying amounts of female cohesion, and bonobo sociality is based more on female–female affiliation among less related females (Doran *et al*. 2002; Furuichi *et al*. 1998; Hohmann *et al*. 1999; Inoue *et al*. 2008; Kano 1992; Lehmann and Boesch 2008; Morin *et al*. 1994; White 1986, 1996b; Wrangham 1986). The greater female affiliation in bonobos may be possible through reduced feeding competition through more use of terrestrial herbaceous vegetation (Wrangham 1986) or larger food trees associated with the more productive habitat (Malenky 1990; White 1986; White and Wrangham 1988). Under these conditions female sociality may be an evolutionary selective advantage because of increased ability to negate male aggression (Wrangham 1986) or from cooperative alliances among females for the defense of monopolizable food sources (White 1986; White and Lanjouw 1992).

Within this subtribe, we find the clearest evidence for the presence of social and ecological niche construction in the nonhominin Hominoids. Indeed, "cultural traditions," boundary patrols, tool creation/use, and the varied nature of intersexual relationships, set within complex fission–fusion communities, demonstrate that in this taxa most ecological challenges are tackled behaviorally, innovatively and with substantial flexibility. It is reasonable to attribute such clearly maniftested behavioral patterns to a ratcheting up of the roles for niche construction and mulitiple modes of inheritance in the Hominini, i.e., Panina, Australopithecina, and Hominina, since a divergence from the Gorillini.

Summary: Family Hominidae

The great apes are characterized by several morphological, physiological, and social characteristics, including an extension of life history phases and varied patterns of complex social relationships that extend beyond biological kin, beyond reproductive relationships, and beyond the immediate social group. In addition, our understanding of intraspecific variation suggests an evolutionary history of expanding behavioral plasticity in response to variable ecological and social selection pressures. Protracted life histories, coupled with social complexity and encephalization in the lineaage produces a ratcheting effect that forms the core of the hominid niche. Variation in social systems is simultaneously related to resource distribution, population density, and individual social relationships both within and between social groups (Fuentes 2009, 2011, Thierry 2008). Orangutans, although generally occurring in small groups or as individuals, do form larger aggregations at particularly resource-rich sites. The African hominoids, more reliant on terrestrial locomotion and interaction patterns, can best be described as occurring primarily in some variant of multimale–multifemale groups that exhibit variable cohesion and group/subgroup size along a continuum. It is possible, therefore, that all current hominid grouping patterns are derived from a more gregarious multiadult group composition in the past (Fuentes 2000;

Strier 2007). If the current assumption of White *et al*. (2009) about hominin ancestry emerging from a late-Miocene hominid group is correct, then the composite descriptions (locomotor, dietary, and social systems) of extant hominoids represent derivations from this generalized ancestor. This makes it difficult to infer early-hominin social characteristics from any particular living hominoid, e.g., chimpanzees, and increases the likelihood that shared general patterns of social organization, i.e., multimale–multifemale groups and expanded social networks, are basal for any hominoids. These general patterns are likely to be upheld regardless of any inferred mating system variants; i.e., monogamous mating does not preclude the presence of expanded social networks.

Emerging Perspectives from Contemporary Evolutionary Theory: The Ecology of Early Hominin Social Diversity

Selection and other evolutionary factors mould aspects of the genetic, morphological, and behavioral variation in primate populations, but the day-to-day behavioral interactions among primates also actively shape the social environment. The variation we see in the structures of ape societies lends itself to a diverse array of social bonds and networks. The nonkin alliances that are important for chimpanzees, the homo- and heterosexual bonding in gorillas, and the potential community level associations across gibbon groups are all indicators of patterns and potentials of structural plasticity in behavioral systems in the hominoids. In fact, this is likely an ancestral pattern in the hominoids, and thus a baseline for the hominins. The ability of all hominoid groups to fission and fusion temporally and spatially and yet maintain social cohesion across a range of ecological circumstances suggests that the shape and structure of interindividual relationships and its inherent flexibility might reflect an adaptive pattern in the hominoids (Fig. 2). This is different from such basic demographic flexibility in the macaques, for example, as the hominoids exhibit variance in the patterns and structures of social relationships and their

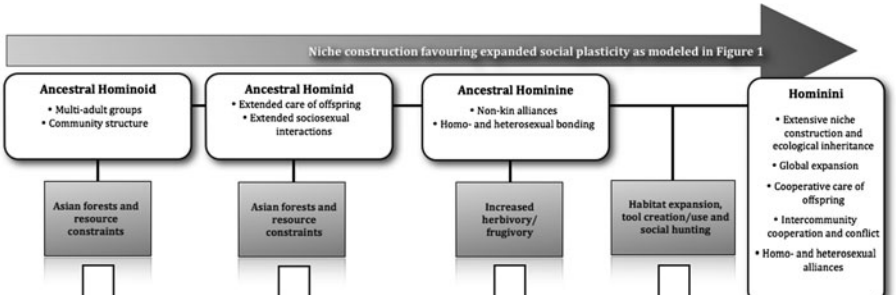


Fig. 2 Basal characteristics and expansion via niche construction in hominoids.

ecological interfaces, not merely variance in group demographic variables. In addition, the potential for innovation, spread, and inheritance of behavioral patterns and social traditions is much higher in the hominoids, especially the great apes, than in other anthropoid primates. Although in most nonhominoid primates, variability and flexibility take the shape of specific patterns of demographic flux and interindividual relationships, such as basic alliances and coalitions, we can consider behavioral flexibility and plasticity as means to an end in hominoid socioecological landscapes.

There is an emerging recognition in evolutionary theory that phenotypic plasticity; continuous and reversible transformations in behavior, physiology, and morphology in response to rapid environmental fluctuations; and epigenetic inheritance are important for many organisms, and may be the result of evolutionary processes and be characterized as adaptations (Jablonka and Raz 2009; West-Eberhardt 2003). Piersma and Drent (2003, p. 28) suggested that "when environments change over shorter timescales than a lifetime, individuals that can show continuous, but reversible, transformations in behavior, physiology or morphology, might incur a selective advantage." It is also the case that organisms are not only impacted by their immediate environments, but also in part shape those environments, and thus the selection pressures that they face. Further, organisms potentially pass along these altered environments to subsequent generations. In a sense, we see that many organisms displaying such plasticity in responses are engaged in some level of niche construction (Odling-Smee *et al*. 2003; Stamps 2003). However, in the hominin lineage this capacity for flexible responses to shifting environmental pressures, via both behavioral plasticity and the ability to modify extrasomatic material, underwent further selection in the late Pliocene and early Pleistocene favoring enhanced plasticity relative to other hominoid forms (Dunbar *et al*. 2010; Potts 1998, 2004).

Niche construction is the building and destroying of niches by organisms and the mutual dynamic interactions between organisms and environments (Odling-Smee *et al* 2003). Organisms engaged in niche construction significantly modify the selection pressures acting on them, on their descendants, and on unrelated sympatric populations. Odling-Smee *et al*. (2003) identified four major consequences of niche construction and their resultant, prime implications. Niche construction:

1) Impacts/alters energy flows in ecosystems through ecosystem engineering;
2) Demonstrates that organisms modify their, and other, organisms' selective environments;
3) Creates an ecological inheritance, including modified selection pressures, for subsequent populations; and
4) Is a process, in addition to natural selection, that contributes to changes over time in the dynamic relationship between organisms and environments (niches).

Ecological inheritance and niche construction in general can occur via behavioral action, and we suggest that the hominoids lay a baseline for such action through their socially and ecologically flexibile responses to selective pressures. We propose that this creates a form of socio-ecological inheritance resulting in social niche construction in the hominoids, which in turn forms the baseline for a feedback system facilitating the hominin expansion on these themes (MacKinnon and Fuentes 2011; Sterelny 2007).

Niche construction is occurring in the hominoids (and at some level in many primates for that matter, Fuentes 2011) so we can envision the plasticity present at the group and population levels as a major component of the hominoid niche, and an even more important component of the hominin niche (Kendal *et al*. 2011). For example, Flack *et al*. (2006) argued for social niche construction in anthropoid primates in which social networks constitute the essential social resources in gregarious primate societies. They posited that "the structure of such networks plays a critical role in infant survivorship, emergence and spread of cooperative behavior, social learning and cultural traditions." If Flack *et al*. (2006, p. 426) are correct (Fuentes 2011, MacKinnon and Fuentes 2011), we can view hominoid individuals engaging in social niche construction and thus individuals in hominoid groups negotiate these social networks modifying their boundaries and internal landscapes in the context of changing social relationships, demographics and, potentially, ecological variables. The flexible (within certain boundaries) social and ecological characteristics of the hominoids can act as a niche constructing process that both maintains flexibility and modifies selection pressures that then feedback on the system modifying the patterns that the variation takes.

Odling-Smee *et al*. (2003) stated that humans are the "ultimate niche constructors," and suggest that niche construction in general, and ecological inheritance in particular, is likely to be very important in understanding human evolution (Dunbar *et al*. 2010; Kendal *et al*. 2011). What then can understanding the variation in extant hominoids tell us about hominin evolution? First it gives us a phylogenetic baseline: the earliest hominins already existed in multiadult groups with a high degree of social complexity, patterned but flexible social bonding between individuals within the group and a level of interindividual cooperation and competition at least equal to that found in modern ape societies. Individuals exhibited substantial behavioral flexibility and a repertoire of vocal and gestural communication. Rudimentary tool use and manipulation of the environment was present, as was sexual dimorphism in size. The early hominins shared with the other hominoids an acute type of "social intelligence" (Dunbar and Shultz 2007). This suggests that specific aspects of cognition, especially those related to behavioral plasticity, evolved largely in response to the increasingly challenging demands of a complex social life of constant competition and cooperation with others in the social group (Herrmann et al. 2007) in addition to the external ecological pressures (Fig. 2). Recent overviews of niche construction in human prehistory demonstrate the pattern of flexibility in response to selection pressures via behavioral shifts resulting in rapid gene–culture coevolution, and this can be seen as directly emerging for the kind of socioecological inheritance we posit here (Dunbar *et al*. 2010, Fuentes *et al*. 2010; Gintis 2011; Kendal *et al*. 2011). Understanding shared (and likely ancestral) behavioral and socialecological patterns in the hominoids provides insight into the structures of initial variation necessary for the development of the hominin evolutionary niche.

In this article we posit a central role for social and ecological inheritence and established a set of distinct criteria with which to asses this possibility (expectations 1–6). In the previous sections we've presented a series of taxonomic overviews and theoretical enhancements relevant to our inferences about social behavior in the early hominins. These taxonomic overviews demonstrate that there is evidence to support our model of expanding social plasticity as a means to an end in hominoid social

systems. Specifically, substantive variablity in social association patterns, innovative flexibility in behavioral response to ecological pressures, and significant inheritence of social and ecological variables are found in all extant hominoid taxa, especially so within the Hominini.

Conclusion

> Hominin evolution is hominin response to selective environments that earlier hominin have made. Incontrast to social intelligence models, I have argued that hominins have both created and responded to a unique foraging mode, a mode that is both social in itself and which has further effects on hominin social environments." (Sterelny 2007, p. 728)

Kim Sterelny eloquently highlights the role of social plasticity, intelligence, and intragroup cooperation in the hominin history of exploiting and manipulating extrasomatic means to engage, and alter, local selective ecologies. Richard Potts made a similar argument positing that the fluctuating and complex environments faced by early hominins favored an extensive suite of flexible behavioral traits as an adaptive response (Potts 1998). R. D. Alexander (1989, 1990) and Flinn *et al*. (2005) posited that dominance over ecological pressures led to the prominence of a social selective enviroment in hominin evolution. Here we have argued that the baseline for these patterns of hominin evolution lie in hominoid wide trends.

Among taxa with similar physiological and ecological profiles, we are faced with not only a broad range of social-system-wide variants *between* taxa, but also *within-taxa* "variations on a theme." The former can be exemplified by reflecting on the broad spectrum of social organizations of the hominoids, from that of the orangutan (permitting description as semisolitary with occasional aggregations), to the centrality of the hylobatid pair bond (albeit variable in several key aspects including formation and stability), to the fission–fusion societies of the panins. The latter, or intrataxa variation, can be exemplified by considering the presence of one-male–multimale, or all-male groups—each relatively stable and cohesive—within species of gorillas. In regard to our own genus, a strengthening of male kin relationships, including the potential for greater levels of kin-biased recognition over temporal, i.e., generational, and spatial, e.g., intergroup relationships, as well as associations between specific males and females, are the major trends in the divergence from the African hominoids. Modern humans, constructing social relationships in response to a myriad of interacting social, economic, political, and ecological factors, exhibit an unparalleled range of complexity and flexibility in social organization (Kendal *et al*. 2011).

Given our emergent understanding of the social organizations of extant apes, whether "solitary" or any iteration of multiadult structure, extragroup social relationships are prominent in all taxa. It is possible, given this superfamily level analysis, that such extragroup social relationships are both basal for this clade, and indicative of enhanced flexibility and responsiveness to novel conditions, as articulated in Potts' (1998) concept of variability selection and Sterelny's (2007) positing of human

evolution as a niche constructive trajectory. Therefore, recognizing the implications of such social systems and structures in hominoids, i.e., the immediate, small, social group is NOT the exclusive venue for understanding and assessing the social system, we predict this general pattern of multimale–multifemale social structure, coupled with the dynamics of extragroup interactions in the context of a community structure, to be important in the elaboration of social and cognitive "hominoid themes" in early hominin social systems.

Extant hominoid taxa display specific types of variation in grouping patterns, and we contend that this emerges from an ancestral multiadult social system. This broad theme of plasticity in group composition and social dynamics is a phylogenetic heritage of the hominoids and its elaboration and modification is a major element in the trajectory of hominin evolution. The split between hominins and the other hominoids lies between 7 and 10 mya and resulted in expanded changes in behavioral patterns and neurological systems. In the hominin lineage these include ubiquitous and complex tool use (including compound tools), social sharing of prized resources, dynamic communities as a social baseline with hyper-cooperation within groups, extreme behavioral tradition inheritance within and between populations, complex coordination and materially dense communication, and habitual appearance of complex social relationships that cross generational, biological kinship, and sex boundaries. However, given our current understanding of the strong similarities in both morphological and genetic structures across at least the African hominid clade (*Pan*, *Gorilla*, and *Homo*), and largely across hominoids in general, these significant changes in behavior did not necessarily involve *de novo* evolutionary innovations, but rather they were enhancements and modifications of preexisting patterns; specifically those patterns of plasticity and behavioral complexity noted as shared among the hominoids above. Our model suggests that intrataxa variation in group demography coupled with a degree of flexibility in the formation of social bonds and relationships, across ecological constraints, is the baseline niche that hominins exploited and expanded on. The implication for the study of hominins is that while other hominoids can be of use in understanding the shared underpinnings for hominin evolutionary trajectories and broader phylogenetic processes in the hominoid (or even hominine) lineage, the use of specific extant analogues (bonobo vs. chimpanzees vs. gorillas) as representative models of hominin behavior and social systems will give us limited, or erroneous, outcomes.

Critical to our perspective is elevating the importance and centrality of the social niche in hominin evolution. As previously mentioned, we are not the first to suggest this (Alexander 1989, 1990; Flinn *et al*. 2005; Sterelny 2007). Although acknowledging some similarities, we emphasize the construction and alteration of social and ecological niches, in concert with behavioral plasticity, functioning in a more dynamic system of inheritances. In particular, our perspective is complementary to, but differentiated from, the Ecological Dominance and Social Competition model (Alexander 1989, 1990; Flinn *et al*. 2005) by specifically incorporating niche construction, and by moving beyond interindividual competition as the core selective element.

Nearly 2 mya members of our genus expanded their ability to exploit physiological and behavioral processes to negotiate increasingly complex and information-rich social and ecological networks. In the genus *Homo* we see extreme use of temporally and spatially complex coalitions and alliances; inter- and intragroup social

negotiations involving symbolic, somatic, and material components; and a level of social and material reciprocity not seen in other lineages. These have become the primary hominin avenues for achieving social and reproductive success (Dunbar *et al*. 2010; Nowak and Highfield 2011; Sussman and Cloninger 2011). If our model is accurate, and the available evidence provides some support for it, our goals for understanding human and other hominoids' behavioral patterns and processes need to follow the broader trends in evolutionary theory and ecology and include a more diverse suite of approaches, placing niche construction and behavioral plasticity alongside natural and sexual selection as viable explanatory mechanisms.

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