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# The social organization of *Homo ergaster*: Inferences from anti-predator responses in extant primates

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ABSTRACT

Patterns of primate socioecology have been used to suggest that the first truly savanna-dwelling hominin, *Homo ergaster*, lived in sizeable groups. Here, we revisit these estimates and infer additional features of the social organization of these early hominins based on anti-predator responses observed across the primate taxon. We first show that the effect of habitat on primate group size, composition, and sexual dimorphism is negligible after controlling for substrate use and phylogeny: terrestrial species live in larger groups with more and bigger males than arboreal taxa. We next hypothesize that groups can only survive in open habitats if males are able to engage in joint counter-attacks against the large carnivorans typical of such environments. To test this, we analyze reports on primate counter-attacks against known predators and find these are indeed disproportionately frequent in terrestrial taxa living in open habitats, sometimes even involving the use of tentative weapons. If we subsequently only examine the taxa that are particularly adept at this (chimpanzees and baboons), we find an effect of habitat type on group size: groups on the savanna are larger than those in the forest. We thus infer that *H. ergaster* lived in very large groups with many males that jointly defended the group against carnivorans, and argue that these counter-attacks will readily have turned into confrontational scavenging and cooperative hunting, allowing *Homo* to move into the niche of social carnivore. These two features (life in very large multi-male groups and a switch to persistent carnivory) shaped the evolution of our lineage to such an extent that the social organization of *H. ergaster* may already have contained many key elements characterizing modern day foragers: male bonding, incipient male–female friendships with food sharing, a tendency toward endogamy, and the presence of large communities that eventually turned into the ethno-linguistic units we can still recognize today.

## 1. Introduction

The social organization of mobile hunter-gatherers, or foragers, shows the uniquely human combination of complex fission-fusion and pair bonding (Hill et al., 2011; Layton et al., 2012; Kelly, 2013). First, mobile foragers form three-level fission-fusion societies, composed of party-band-society. They live in bands of on average 30 individuals that jointly occupy a camp. However, there are contacts between bands: individuals may move between them and a particular set of bands occasionally comes together for social events. Thus, these bands together form the macro-band or community, whose members share the same language and societal labels (Moffett, 2013). Moreover, within a band, during their day-to-day activities, individuals move in highly variable parties, i.e., bands show high fission-fusion dynamics (Aureli et al., 2008). Second, men and women form pair bonds, although on average these bonds are neither long-term stable, nor exclusive, nor necessarily monogamous.

An important unresolved question is how this social organization evolved, and two main models have recently been proposed (Chapais, 2013; van Schaik, 2016b). The first assumes that early hominin groups lived in single-male or multi-male social units that gradually formed associations, thus forming large multi-level societies, somewhat like geladas, hamadryas and guinea baboons, or Asian colobines (Grueter et al., 2012; Swedell and Plummer, 2012; Patzelt et al., 2014). The second model assumes early hominins lived in chimpanzee-like fission-fusion societies with a large number of bonded males and immigrant females. According to either scenario, male–female bonding arose at one stage, but whereas the first suggests that monogamous pair bonds arose early

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on (Chapais, 2013), the latter sees them as clearly derived, less exclusive, and much more recent (van Schaik, 2016b).

Any such comparison based reconstructions are inevitably speculative. Moreover, they do not always specify which hominin species had which kind of social organization, or whether they model the band or the community. The only semi-hard evidence we have are estimates of sexual dimorphism and their correlations with social organization among extant species (Plavcan and van Schaik, 1997; Plavcan, 2001), but in this respect we only know that *Australopithecus* was more dimorphic than *Homo*, especially because of the increased body size of the latter species' females (Antón et al., 2014). The moderate dimorphism in the latter is compatible with various social systems, though most likely with fission-fusion polygynandry and less so with multi-level societies consisting of one-male units (Plavcan and van Schaik, 1997).

Here we intend to pursue an alternative approach. Both anatomy (Bramble and Lieberman, 2004) and archeology (Plummer, 2004) leave little doubt that by circa 2.0 Mya *Homo ergaster* (cf. Klein, 2009; but elsewhere also *Homo erectus* sensu stricto) spent a considerable proportion of its time on open, grassland-dominated terrain (Plummer et al., 2009), where it routinely engaged in carnivory (Ferraro et al., 2013). This meat was most probably acquired by a combination of confrontational scavenging and active hunting from ambush (Bickerton and Szathmary, 2011; Bunn and Gurtov, 2014), both subsequently bolstered by endurance running (Bramble and Lieberman, 2004). Regardless of the method of acquisition, these hominins must have been able to defend themselves and their prey carcasses against a variety of large carnivorans that roamed these landscapes at the time (Van Valkenburgh, 2001; Lewis and Werdelin, 2007; Treves and Palmqvist, 2007). The effectiveness of this defense is apparent from a reduced life history pace relative to their ancestors (Antón et al., 2014), indicative of a reduced risk of extrinsic mortality, which had reached levels comparable to that of arboreal orangutans (Schwartz, 2012). Moreover, the precipitous drop in African carnivoran species richness after approximately 1.5 Mya has been ascribed to fierce interference competition from opportunistically carnivorous hominins (in particular through confrontational scavenging and intra-guild killing: Van Valkenburgh, 2001) that pushed other members of the carnivore guild to extinction (Lewis and Werdelin, 2007).

Our approach here is to ask whether extant nonhuman primates show patterns of anti-predator responses that can be used to infer key aspects of the social organization of *H. ergaster* and derive predictable secondary consequences. Primates broadly respond to predators in two distinct ways (Fichtel, 2012). The first is early detection and flight to refuges in the landscape or safe microhabitats, such as dense vegetation (against raptors) or high in trees (against large carnivorans). The second is confronting the predator and if need be to counter-attack. Given their larger body size and more elaborate weaponry in most taxa, this response is especially expected from males (Hall and DeVore, 1965; Cheney and Wrangham, 1987; Crofoot, 2012). Although some species use both strategies, the majority rely mainly or exclusively on the first, including some of the species that venture into open terrain. Thus, although patas monkeys and vervet monkeys spend time in open areas, they do so in ways that minimize the (perceived) risk of predator encounter (Willems and Hill, 2009; Burnham and Riordan, 2012) and, when meeting dangerous carnivorans, run to the safety of the trees rather than confront them (Enstam and Isbell, 2002).

Species following the “detection-and-flight” strategy will nonetheless benefit from living in larger groups, such as when these groups detect predators from a larger distance, giving them more time to withdraw to the safety of the trees, dense foliage, or the fine branches of the canopy (van Schaik, 1983). There is extensive evidence that larger groups are more effective at detecting predators before they can attack and may also discourage attacks in other ways (e.g., by confusing the predator: Caro, 2005). Thus, an important variable in relation to predation risk, regardless of behavioral response, is group size (Cheney and Wrangham, 1987; Isbell, 1994; Fichtel, 2012).

Early comparative work (Clutton-Brock and Harvey, 1977) showed that terrestrial primates live in far larger groups than arboreal primates. The general interpretation was that species living in open terrain, away from the safety of the trees, had to live in larger groups (Clutton-Brock and Harvey, 1977; Foley, 1987). When applied to hominin evolution, this meant that moving into open vegetation was accompanied by a major increase in group size (Foley, 1987). These studies, however, did not explicitly tease apart the possible effects of substrate use (terrestrial or arboreal) and habitat type (wooded or open), making it difficult to interpret the pattern of correlations and thus of responses to selective pressures; nor did they control for phylogenetic non-independence. Now that much more empirical information has accumulated and more powerful comparative methods are available, we can re-examine this conclusion and, if found wanting, develop another explanation.

There is a rich literature on social primates suggesting that at higher predation risk, male representation in groups is higher, which leads to better survival of immatures as expressed in a greater proportion of immatures per adult (Treves, 2001). Indeed, among arboreal folivorous primates, groups are more likely to contain more than one adult male where monkey-eating eagles occur (van Schaik and Hörstermann, 1994). More generally, it has been suggested that the proportion of males among adults is higher where predation risk is higher (Anderson, 1986; Hill and Lee, 1998), although this could not be confirmed in a study that controlled for phylogenetic dependencies (Nunn and van Schaik, 2000). Thus, it is possible, though not certain, that species living in open terrain have a higher absolute and relative number of adult males in their groups than those living in closed habitats.

Finally, it has been suggested that in species living on the open savanna, sexual dimorphism is more extreme because males take on a special role in anti-predator defense (DeVore and Washburn, 1963). Again, however, the comparative evidence accumulated so far remains ambiguous (Plavcan, 2001).

These proposed patterns in social organization and morphology are consistent with behavioral observations that females and immatures seek the company of adult males when perceived predation risk is high, such as when crossing open areas (in chimpanzees: Tutin et al., 1983) or in the simulated presence of a predator (a harpy eagle in spider monkeys: Symington, 1987). This greater male involvement as perceived predation risk increases is consistent with a special role for males in group defense through vigilance (van Schaik and van Noordwijk, 1989), but also through mobbing and actual attacks on predators (Stanford, 1998).

Counter-attack may be the only effective anti-predator strategy on the treeless parts of the savanna; even if species spend only part of their time far enough on the open plains to make fleeing to trees unfeasible, they must be able to deal with predators when they do. The second distinct anti-predator strategy, therefore, is to confront the predator, usually communally (Fichtel, 2012). There are few reports on actual counter-attacks against predators (Cowlishaw, 1994; Stanford, 1998), which should not be confused with mobbing (e.g., Gursky, 2006; Tórrez et al., 2012). Here, we will ask which species counter-attack, whether the expected bias toward males as attackers is confirmed, and whether certain predators (in particular terrestrial carnivorans, characteristic of the African savanna) elicit more collaborative counter-attacks than others. If a clear pattern is detected, this will inform the hominin situation, especially given that once established, effective joint counter-