



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 carnivores 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 carnivores, 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.

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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 polygyny 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 Szathmari, 2011; Bunn and Gurtev, 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 carnivores 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 carnivore 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 carnivores). 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 carnivores, 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 (Cowlshaw, 1994; Stanford, 1998), which should not be confused with mobbing (e.g., Gursky, 2006; Tórriz 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 carnivores, 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-

attacks open up the novel (and among primates unique) niche of opportunistic social carnivore through confrontational scavenging, with all its implications for the further social evolution of *Homo* (Bickerton and Szathmari, 2011).

In this study, we will test the predictions described above. In a first series of comparative analyses, we ask whether a primate species' lifestyle (which we shall define below as the unique combination of habitual substrate use and preferred habitat type) affects modal group size and/or the absolute and relative number of males in the modal group, as well as the degree of sexual dimorphism. We next examine whether males are indeed the more active sex in primate counter-attacks against predators and whether terrestrial carnivores elicit more counter-attacks in which these males work together. Finally, we will ask whether the two primate taxa that most frequently engage in counter-attacks and that are arguably most relevant to unravelling the human condition, *Pan* and *Papio* (i.e., through homology and homoplasy, respectively), exhibit larger group sizes in open than in closed habitats. We will use the outcome of these comparative analyses to infer additional, derived features of the social organization of *H. ergaster*.

2. Material and methods

2.1. Cross-species comparisons

Two different datasets were compiled for two series of inter-specific analyses. First, we collated data from the literature and online sources (for details see: Willems et al., 2013, 2015; Willems and van Schaik, 2015) on modal group size, group composition, and degree of sexual dimorphism for a large number of social primate species. Taxa were characterized by lifestyle, which we defined as comprising both the predominant mode of substrate use ([semi-] terrestrial or arboreal) and the preferred habitat type (wooded or more open vegetation, the latter allowing for a woody vegetation cover of up to 25%; cf. Edwards, 1983) of a species. This classification resulted in three broad lifestyle categories: 1) terrestrial species that live in relatively open habitats, 2) terrestrial species that live in wooded habitats, and 3) arboreal species that live in wooded habitats.

Second, we surveyed the literature for reports on counter-attacks by primate prey against confirmed predator species. We included any report of proactive or reactive aggression that involved chases and/or physical contact, and thus also considered rescue attempts by group members in which a chase or physical contact with the predator was initiated by an individual that was not the victim of the initial predator attack. Importantly, however, we did not consider mobbing events *sensu stricto* (Crofoot, 2012). For each counter-attack, we recorded among others: the species of both primate and predator, the age-sex class and number of individuals involved, and—if known—whether or not the predator was killed or died as a consequence of the counter-attack.

2.2. Within-species comparisons

In addition to the two interspecific datasets described above, we also compiled two datasets to compare foraging group sizes across populations of chimpanzees (*Pan troglodytes* subspp.) and non-hamadryas savanna baboons (*Papio* spp.). Both taxa are large-bodied and terrestrial (in fact, size and weight of either fall within the range of estimates for those of early *Homo*: Antón et al., 2014), and therefore capable of counter-attacking a wide range of potential predators, but different populations live in either more wooded or open environments, allowing for within-taxon analyses of the potential effect of habitat type on group size.

2.3. Statistical analyses

Where feasible, we controlled cross-species comparisons for the potentially confounding effect of phylogenetic relatedness using Phylogenetic Generalized Least Squares (PGLS) analyses, implemented in the “Caper” package (Orme et al., 2013) for R version 3.3.0 (R Core Team, 2016). To most appropriately incorporate the magnitude of the phylogenetic signal in model residuals due to common ancestry (Pagel's λ : Pagel, 1999; Freckleton et al., 2002), we used maximum likelihood estimation. A phylogenetic Bayesian consensus tree comprising 156 species was downloaded from the 10 k Trees Project website (Arnold et al., 2010) and extended with more recent phylogenies available for *Presbytis* spp. and the *Saguinus nigricollis* group (following Matauschek et al., 2011; Meyer et al., 2011; van Woerden et al., 2012).

In the first series of cross-species comparisons, we investigated possible differences in modal group size, group composition, and degree of sexual dimorphism, associated with a species' lifestyle. Where required, variables were transformed prior to analysis to ensure normality of model residuals. We specified non-orthogonal contrasts a priori to tease apart the confounded effects of substrate use and habitat type, and thus tested: i) whether among species living in wooded habitats, differences in the response variable were apparent between the two modes of substrate use (arboreal or terrestrial), and ii) among terrestrial taxa, whether differences existed between species from different habitat types (wooded or open).

The second series of cross-species comparisons focused on our survey of primate counter-attacks. Given the small sample size and pronounced taxonomic bias in this dataset, we could not correct for phylogenetic dependencies and therefore opted for non-parametric, more descriptive analyses instead. We used: i) a goodness of fit test to establish whether reports on counter-attacks were proportionally distributed over the three lifestyle categories as expected from their relative abundance among species in our large comparative dataset, ii) exact binomial tests to assess whether males and females participated in counter-attacks as frequently as expected based on the adult sex-ratio in the group, and iii) the Fisher's exact test to look for a difference in the number of individuals involved in counter-attacks against different predator types.

Lastly, in the within-taxon comparisons for *Pan* and *Papio*, we utilized Wilcoxon rank sum tests to establish for each taxon whether there was a difference in foraging group size (i.e., party size and group size, respectively) between populations exploiting wooded or open habitats.

All analyses were conducted in R version 3.3.0 (R Core Team, 2016), with statistical significance set at $\alpha_{2\text{-tailed}} < 0.05$. Where required, however, we applied Bonferroni corrections to control the family-wise error rate across multiple comparisons.

3. Results

3.1. Cross-species comparisons

Information on modal group size, the absolute and relative number of males in the modal group, and sexual dimorphism was collected for a total of 171 species, representing all major primate radiations (three Tarsiiformes, 18 Lemuriformes, 56 Platyrrhini, and 94 Catarrhini). Given previously reported phylogenetic differences in predator response (Crofoot, 2012) and our primary interest in Old World Primates (i.e., the Catarrhini, to which our own lineage belongs), we conducted our first set of analyses across the entire taxon and across Catarrhini only.

3.2. Modal group size

A highly significant PGLS model ($n_{\text{species}} = 171$, $\lambda_{\text{ML}} = 0.931$, $F_{(2, 168)} = 6.36$, $R^2_{\text{Adj.}} = 0.059$, $p < 0.005$; Fig. 1A), expressing total group size as a function of lifestyle, revealed that: i) among species living in a wooded habitat, terrestriality is associated with larger group sizes than arboreality ($B \pm SE = 0.38 \pm 0.12$, $p < 0.005$), and ii) among terrestrial taxa, no difference exists between species from wooded and more open habitats ($B \pm SE = 0.07 \pm 0.16$, $p = 0.657$). This pattern was also found when the analysis was restricted to diurnal Catarrhini only ($n_{\text{species}} = 93$, $\lambda_{\text{ML}} = 0.758$, $F_{(2, 90)} = 4.57$, $R^2_{\text{Adj.}} = 0.072$, $p < 0.05$; Supplementary Online Material [SOM] Table S1).

3.3. Absolute and relative number of males in the species' modal group

A subsequent analysis across all taxa for which data were available ($n_{\text{species}} = 137$, $\lambda_{\text{ML}} = 0.919$, $F_{(2, 134)} = 10.36$, $R^2_{\text{Adj.}} = 0.121$, $p < 0.001$; Fig. 1B) indicated that: i) among species living in a

wooded habitat, terrestriality is associated with more males in the modal group than arboreality ($B \pm SE = 0.31 \pm 0.12$, $p < 0.05$), and ii) among terrestrial taxa, no difference exists between species from wooded and more open habitats ($B \pm SE = 0.15 \pm 0.16$, $p = 0.346$). The same pattern emerged when the analysis was conducted on diurnal Catarrhini only ($n_{\text{species}} = 77$, $\lambda_{\text{ML}} = 0.901$, $F_{(2, 74)} = 7.07$, $R^2_{\text{Adj.}} = 0.138$, $p < 0.005$; SOM Table S2).

In addition, two nested models were constructed to investigate the number of males in a species' modal group in relation to lifestyle and the number of females. The first of these (PGLS_{interaction}: $n_{\text{species}} = 135$, $\lambda_{\text{ML}} = 0.762$, $F_{(5, 129)} = 40.23$, $R^2_{\text{Adj.}} = 0.594$, $p < 0.001$) revealed that: i) the number of males across all lifestyles is significantly and positively associated with the number of females ($B \pm SE = 0.58 \pm 0.12$, $p < 0.001$), ii) among species living in a wooded habitat, the strength of this association (i.e., the slope of the linear model) is the same for terrestrial and arboreal species ($B \pm SE = 0.07 \pm 0.13$, $p = 0.591$), and iii) among terrestrial species, there is no difference in this respect either between species from a wooded or more open habitat ($B \pm SE = 0.34 \pm 0.22$, $p = 0.118$). The second, more parsimonious model (PGLS_{main effects only}:

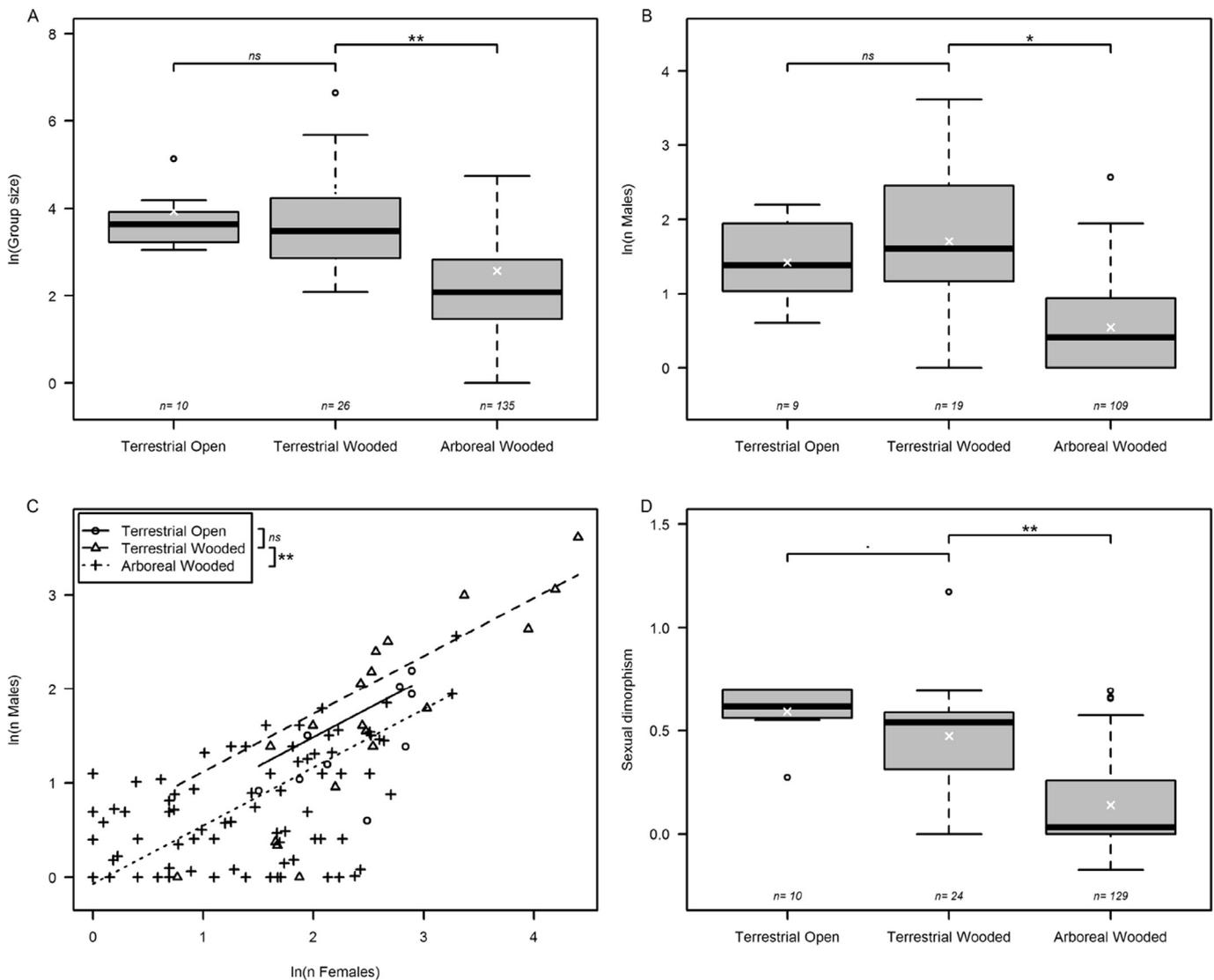


Figure 1. Results from a series of comparative (Phylogenetic Generalized Least Squares) analyses. Among species living in a wooded habitat, terrestrial species aggregate in larger groups (A) with more (both absolute [B] and relative to the number of females [C]) males that are more sexually dimorphic (D) than in arboreal species. In contrast, among terrestrial species, no significant differences in these respects were found between species from different habitat types, although sexual dimorphism showed a statistical trend ($p = 0.056$) for males being relatively larger in species living in an open environment than those living in a wooded habitat.

$n_{\text{species}} = 135$, $\lambda_{\text{ML}} = 0.795$, $F_{(3, 131)} = 54.41$, $R^2_{\text{Adj.}} = 0.545$, $p < 0.001$, $\Delta \text{AIC} = 10.82$; Fig. 1C), moreover, showed that: i) again, the number of males across all lifestyles is significantly and positively associated with the number of females in the group ($B \pm \text{SE} = 0.63 \pm 0.09$, $p < 0.001$), ii) among species living in a wooded habitat, the number of males per female (i.e., the intercept of the linear model) is significantly higher (i.e., more males) in terrestrial than arboreal species ($B \pm \text{SE} = 0.29 \pm 0.09$, $p < 0.005$), and iii) among terrestrial species there is no difference in intercept between species from a wooded or a more open habitat ($B \pm \text{SE} = 0.02 \pm 0.06$, $p = 0.837$). The exact same pattern was found when restricting these analyses to diurnal Catarrhini (PGLS_{interaction}: $n_{\text{species}} = 75$, $\lambda_{\text{ML}} = 0.712$, $F_{(5, 69)} = 22.12$, $R^2_{\text{Adj.}} = 0.588$, $p < 0.001$; PGLS_{main effects only}: $n_{\text{species}} = 75$, $\lambda_{\text{ML}} = 0.708$, $F_{(3, 71)} = 29.25$, $R^2_{\text{Adj.}} = 0.534$, $p < 0.001$, $\Delta \text{AIC} = 7.60$).

3.4. Degree of sexual dimorphism

A final PGLS analysis across all taxa specified the degree of sexual dimorphism as a function of a species' lifestyle ($n_{\text{species}} = 163$, $F_{(2, 160)} = 7.96$, $R^2_{\text{Adj.}} = 0.079$, $p < 0.001$; Fig. 1D) and showed that i) among species living in a wooded habitat, terrestriality is associated with a higher degree of male-biased sexual dimorphism than arboreality ($B \pm \text{SE} = 0.11 \pm 0.03$, $p < 0.005$), while ii) among terrestrial taxa, there is a statistical trend for species from more open habitats to exhibit a more pronounced male-biased sexual dimorphism than species from wooded habitats ($B \pm \text{SE} = 0.07 \pm 0.04$, $p = 0.056$). When considering diurnal Catarrhini only, the exact same results were obtained ($n_{\text{species}} = 86$, $F_{(2, 83)} = 5.15$, $R^2_{\text{Adj.}} = 0.089$, $p < 0.01$; SOM Table S3).

3.5. Counter-attacks against known predators

For our second set of cross-species analyses, we turned to our survey of primate counter-attacks. A total of 40 reports were located in the literature comprising 16 species from 13 different genera, retaliating against four broadly defined types of predator: raptors, reptiles (overwhelmingly constricting snakes), carnivorans (i.e., Felidae, Canidae and Hyaenidae), and other primates (i.e., chimpanzees). Well over half ($n = 24$) of these reports were on either *Pan* or *Papio*, and although this disproportional representation partly reflects a taxonomic bias in research effort, it is likely to also be due to the relatively large body size and terrestrial substrate use of these two genera, predisposing them to the effective use of counter-attacks against a wide range of predators (Crofoot, 2012).

The observed occurrence of lifestyles across reported counter-attacks deviated significantly from the expected occurrence, based on the representation of lifestyles across species in our large comparative dataset (Goodness of Fit test: $\chi^2_{\text{Monte Carlo}} = 111.9$, $p < 0.001$). Following the post hoc procedure of Neu et al. (1974), we found that reports on counter-attacks by terrestrial taxa from open habitats were more common than expected, those by arboreal taxa living in wooded habitats less common than expected (both: $p_{\text{Bonferroni}} < 0.017$; Table 1), while those by terrestrial species in wooded habitats occurred as expected. In addition, counter-attacks by arboreal taxa involved more rescue attempts and were generally

more reactive, while those by terrestrial species were often unprovoked and proactive, and may therefore have been more effective as prevention.

Figure 2A shows that in the 36 counter-attacks for which information on participation by the two sexes was available, males were much more frequently involved than females. Assuming a highly conservative adult sex ratio of 1:1 (i.e., the most male-biased sex ratio in the social unit of any taxon in our survey), Bonferroni corrected comparisons revealed that males participated significantly more often than expected (exact binomial test: $n_{\text{participation}} = 34$, $n_{\text{total}} = 36$, $p < 0.001$), while females did so significantly less often than expected (exact binomial test: $n_{\text{participation}} = 9$, $n_{\text{total}} = 36$, $p < 0.01$). In fact, males were about four times more likely to be involved in counter-attacks than females.

We further noted that in about half (47.1%) of the counter-attacks in which males participated, they did so together with at least one other male. Given that we were primarily interested in the effect of predators typical of the African savanna some 2.0 Mya, we contrasted terrestrial carnivorans against all other predator types in our sample. Estimation of the (conditional maximum likelihood) odds ratio showed that males were about 6.4 times more likely to jointly counter-attack carnivorans than all other predator types combined (Fisher's exact test: 95% CI = 1.17–48.02, $p < 0.05$; Fig. 2B). In fact, males were only reported to jointly counter-attack carnivorans or chimpanzees, and did so even in taxa without male bonding.

In eight out of 36 (25.0%) reported counter-attacks in which the fate of the predator was known, the predator was killed. For six of these documented kills information on participation was available, which showed that one ($n = 2$) or more ($n = 4$) males were always involved in such lethal counter-attacks. Lastly, the use of physical objects such as sticks or stones (i.e., “weapons”) during counter-attacks was observed in three genera: *Pan*, *Papio*, and *Cebus* (Kortlandt, 1967; Hamilton et al., 1975; Boinski, 1988).

3.6. Within-species comparisons

3.6.1. Foraging group sizes in *Pan* and *Papio* Given that we found chimpanzees and baboons to be the primate taxa that most frequently counter-attacked their known predators, we looked whether their foraging group sizes increased in areas of higher predation risk. In a comparison across 14 populations of chimpanzee, party size was indeed found to be significantly larger in more open (median = 11.0) than in wooded habitats (median = 4.8; $W = 5.00$, $r = 0.549$, $p < 0.05$; Fig. 3A). A similar result was found across 35 populations of non-hamadryas savanna baboon, as total group size was larger in more open (median = 55.5) than wooded habitats (median = 37.0; $W = 74.00$, $r = 0.438$, $p < 0.01$; Fig. 3B). These results were confirmed by spatially explicit analyses, accounting for the relative geographic location of populations (see SOM), and represent medium to large effect sizes. This is seemingly in contrast with the cross-species comparisons reported above, in which no such effect of habitat type on modal group size was found among terrestrial taxa (Fig. 1A); yet these apparently conflicting results merely underline the importance of

Table 1

A comparison of the frequency of occurrence of the different lifestyles in our survey on primate counter-attacks.

Lifestyle	Observed	Expected ^a	Expected proportion	Observed proportion (95% CI _{Bonferroni})	Occurrence
Terrestrial open	18	10	0.058	0.262–0.638	More than expected
Terrestrial wooded	8	26	0.152	0.049–0.351	As expected
Arboreal wooded	14	135	0.789	0.169–0.531	Less than expected

^a Expected values were set as the frequency of each lifestyle in an independently constructed comparative dataset comprising 171 taxa used in the previous set of analyses.

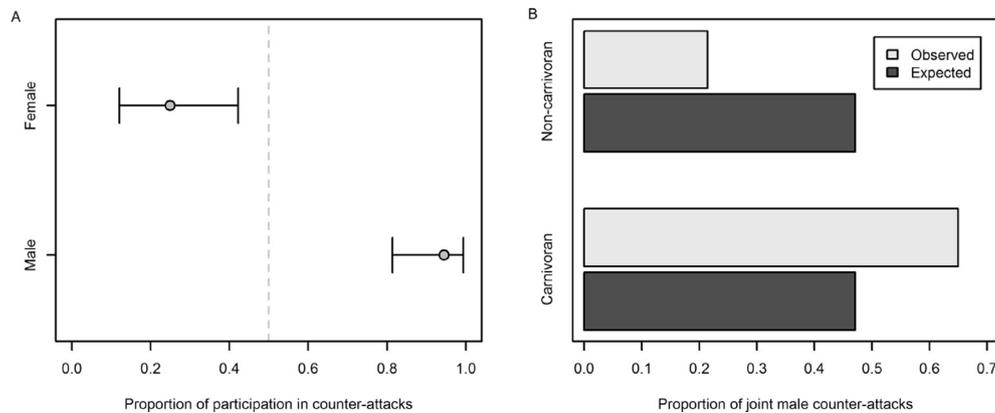


Figure 2. A survey of the primatological literature on primate counter-attacks against locally confirmed predators. Males were found to be far more often involved than expected, while females were less often involved than expected (A, gray dotted line represents the expected rate of participation assuming a conservative adult sex ratio of 1:1). In addition, males were more likely to engage in joint counter-attacks against carnivorous than against all other predator types combined (B).

behavioral plasticity within a lineage, about which PGLS analyses cannot inform.

4. Discussion

This study set out to investigate anti-predator responses in extant non-human primates to arrive at phylogenetically informed inferences concerning the social organization of *Homo*. Below, we first summarize and interpret the pattern across the primate taxon as revealed by our analyses, and next, discuss its implications for the social evolution of our own lineage up to the point of *H. ergaster*, the first mobile hominin forager.

4.1. The pattern among extant non-human primates

Our first series of analyses showed that, when explicitly differentiating between the effects of habitat type and substrate use and while controlling for phylogenetic dependencies, habitat type is neither associated with differences in species' modal group size, nor with the number of males in the group (Fig. 1A–C). Instead, we found that among primates living in wooded habitats, taxa that travel on the ground live in larger groups with more males (both absolute and relative to the number of females) than those that travel through the canopy. A tentative explanation for how they can afford to live in such large groups is that terrestriality reduces the energetic costs of travel associated with climbing in animals of this size range (Alexander, 2003), while making it easier to cover large distances by enabling straight line travel. This would allow individuals to tolerate the lower energy returns in larger groups per unit time or distance travelled due to more intense within-group feeding competition, and thereby reap the benefits of enhanced protection that such larger aggregations offer against the more substantial risk of predation associated with living on the ground (Caro, 2005; Shattuck and Williams, 2010). In addition, the greater size and spread of groups of terrestrial species makes it more difficult for dominant males to monopolize mating access to their group's females, which in turn makes it adaptive for additional males to bear the costs of settling in these groups (cf., Carnes et al., 2011). These extra males may subsequently offer additional anti-predation benefits, either through vigilance, mobbing, or (joint) counter-attack (Anderson, 1986; van Schaik and van Noordwijk, 1989; Hill and Lee, 1998; see below).

Similar to the pattern in social organization, differences in the degree of sexual dimorphism were primarily associated with substrate use, rather than habitat type (Fig. 1D): males in terrestrial species are relatively larger than those in arboreal species, most

likely because of the constraints on body size imposed by an arboreal lifestyle (Alexander, 2003). Nevertheless, among terrestrial taxa, male-biased dimorphism tended to be more pronounced in species living in open rather than wooded habitats, suggesting that larger males may confer additional benefits to females out on the open savanna (DeVore and Washburn, 1963). This latter finding could reflect female preferences to associate with males that are better protectors against predators through counter-attacks (cf., Plavcan and van Schaik, 1992).

The results of this first series of analyses would appear to counter the classic argument that moving out into the open savanna led to life in large groups, with relatively more adult males (Clutton-Brock and Harvey, 1977; Foley, 1987). However, previous interspecific comparisons did not account for the possibility of systematic differences in anti-predatory behavioral strategies. In retrospect, it is obvious that the predominant primate anti-predator strategy, refuge seeking (Fichtel, 2012), cannot work far away from trees on the open savanna. In such cases, the only effective behavioral strategy is active defense by counter-attacking the predator.

In our second set of analyses, we therefore turned to the literature on primate counter-attacks. We found that counter-attacks were reported far more frequently than expected for terrestrial species living in open habitats, and less frequently than expected for species living in the canopy (Table 1). Moreover, there were striking biases toward males being the main actors, and for them to work together more often against large carnivorous than against all other predator types combined (Fig. 2A and B). A critical precondition for any primate species to be able to truly live on the open savanna thus seems to be effective joint male counter-attack, which requires the presence of multiple large males that are able to work together, at least in high risk situations. That primate counter-attacks pose a real threat to the targeted predator is apparent from the observation that in our sample 25% of counter-attacks resulted in the death of the predator (a previous study on baboons reported an even higher predator mortality rate of 36%; Cowlshaw, 1994).

These findings may help resurrect an old, largely discarded idea: that males actively protect the group against predators (DeVore and Washburn, 1963). The reason the idea is now largely forgotten may be that it appears to imply biologically altruistic behavior on the part of the males involved. However, this need not be the case. First, males can gain indirect fitness benefits from defending kin (i.e., their likely offspring) and second, female preferences for vigilant and protective males may result in direct fitness benefits through enhanced mating access (van Schaik and van Noordwijk, 1989;

Arseneau et al., 2015). While currently the evidence for the latter idea is mainly observational, recent experimental work on birds has shown that males are more actively involved in risky anti-predatory behaviors when the size of a female audience is larger (Cunha et al., 2017). Moreover, only female preferences for valiant mates can explain why males that did not sire any offspring (e.g., because they only recently immigrated into the group) also participate in such protective actions.

Finally, we returned to the question of group size. Our third analysis was limited to intra-taxon variation in the two lineages that occasionally or routinely forage far away from the safety of trees and, perhaps as a consequence, are especially adept at proactive counter-attack, *Pan* and *Papio*. In both taxa, populations living in more exposed environments maintained larger foraging groups than those in more wooded habitats (Fig. 3), in line with the classic idea that moving out onto the savanna is associated with life in larger groups (Clutton-Brock and Harvey, 1977; Foley, 1987), but with the amendment that a switch in anti-predatory response from flight to confrontation is a prerequisite.

4.2. Social organization at the time of the emergence of Homo

Based on the pattern that emerged from our analyses, and given that during the early Pleistocene the expanding African savannas were inhabited by a far more formidable carnivoran community than at present (Van Valkenburgh, 2001; Lewis and Werdelin, 2007; Treves and Palmqvist, 2007), we can infer that coeval hominins could only have shifted to life on the savanna, even if part-time, once effective predator defense and joint male counter-attack had become well-established. Among extant primates, joint counter-attacks are most prevalent among chimpanzees and savanna baboons, two taxa that live in large, multi-male groups able to spend significant amounts of their activity period on the open savanna, far from the safety of trees, where they form larger foraging aggregations than in more wooded habitats. Joint counter-attacks against large carnivorans by *Pan* and *Papio* typically involve multiple adult males that effectively work together, even when not closely related, and occasionally involve the use of stones or sticks (Kortlandt, 1967; Hamilton et al., 1975).

These anti-predatory traits must also have characterized (and were further amplified in) the social organization of early *Homo*, as we know it spent a considerable amount of time on the open savanna (deMenocal, 2004; Plummer et al., 2009) and used stone, and presumably wooden, tools. In addition, groups were almost certainly male-bonded (Wrangham, 1987), given the male-bonded system of chimpanzees and bonobos and the clear tendency toward male bonding among extant mobile foragers (Murdock, 1967; Ember, 1978). We suspect that, in contrast, *Australopithecus* spp., being still somewhat tied to woody vegetation, may have largely

relied on flight and may therefore not have crossed the critical threshold to becoming systematic counter-attackers.

We cannot provide very accurate estimates of the modal group size for early *Homo*, apart from suggesting that it must have been large. Aiello and Dunbar (1993) inferred a group size of about 110, based on interspecific correlations between group size and neocortex ratio, which could be deduced from brain size. The validity of this inference depends critically on the correlation between group size and neocortex ratio, which although robust within lineages, does not hold across lineages (Barrett et al., 2003). This is important, given that it is not certain that *Homo* can be considered a great ape in this respect, and bipedal locomotion (being energetically cheaper than quadrupedal locomotion for primates of the same body size: Foley and Elton, 1998; Sockol et al., 2007) may have further increased the maximum ecologically tolerable group size. However, it seems fair to assume that minimal viable group sizes of early hominins venturing out onto the savanna must have been at least in the upper range of known chimpanzee communities or baboon groups, i.e., around 100 individuals or more (up to >140 for chimpanzees and ~200 for baboons: Stumpf, 2011; Swedell, 2011). In addition, early hominins may, at least initially, also have lived in more cohesive groups than extant chimpanzees, who on the open savanna increase not only group size but also cohesion (Pruetz and Bertolani, 2009).

To sum up, we can fairly safely infer the following features of the social organization of hominins at the time of the emergence of *Homo* (Fig. 4): i) very large (≥ 100 individuals) multi-male groups, most likely with initially somewhat reduced fission-fusion dynamics compared to the communities of forest chimpanzees, ii) socially tolerant (and presumably bonded) yet more sexually dimorphic males that are able to cooperate, at least under high risk conditions, and iii) male-biased predator defense in the form of joint counter-attacks, made more effective than in any extant non-human primate through the intelligent use of weapons. This suite of anti-predatory features was to serve as an important exaptation for the subsequent evolution of *H. ergaster* who, uniquely among primates, moved into the niche of social carnivore.

4.3. Implications for the social organization and evolution of *Homo ergaster*

Most of the evolutionary consequences of the anti-predatory traits derived above can be inferred with reasonable certainty. Others will, by necessity, be more speculative. Among the more certain inferences are two main side-effects of life in very large multi-male primate groups often reported in the literature: the formation of male-female friendships and increased philopatry of the sex that usually disperses (Fig. 4).

Stable male-female friendships that are not solely driven by shared parenthood were first described in baboons (Smuts, 1985),

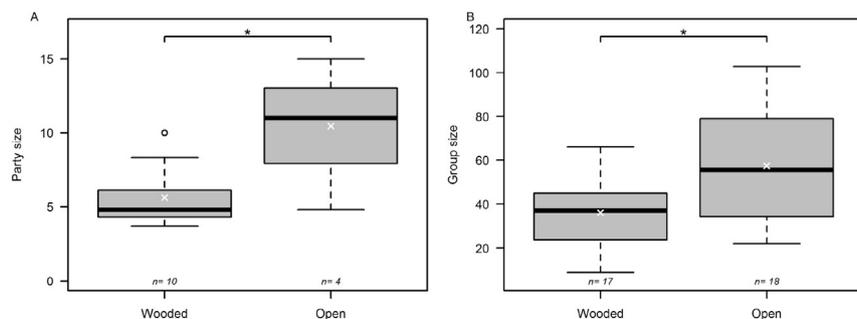


Figure 3. Within-taxon comparisons of foraging group size in open and wooded environments. For both *Pan troglodytes* spp. (A) and *Papio* (B), the average foraging group size was larger in populations living in more open than those living in wooded habitats.

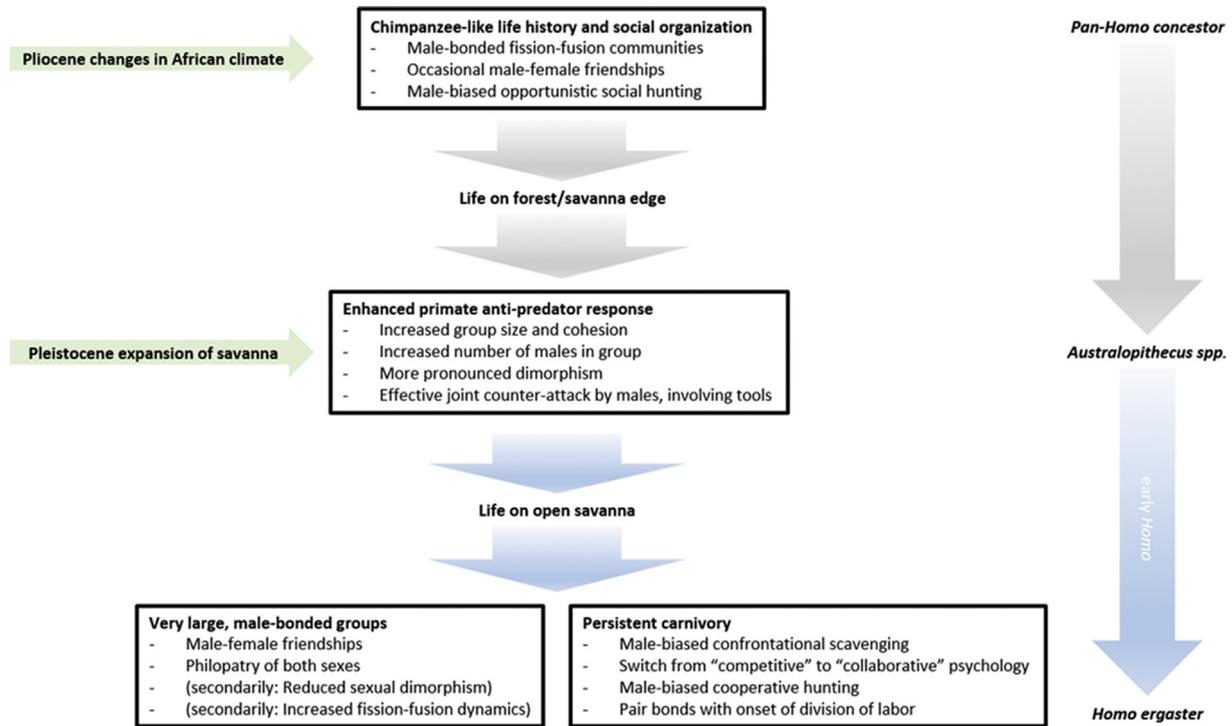


Figure 4. Schematic representation of the evolution of key elements in the social organization of *Homo ergaster* as reconstructed in this paper. Note that we only assume a chimpanzee-like *Pan-Homo* ancestor (i.e., last common ancestor) and a suite of primate typical anti-predator responses (as derived here) that were to serve as important exaptations for *Homo*'s colonization of the open savannas of the African Pleistocene. Time progresses from top to bottom.

and have since been reported in various other species living in large multi-male groups, including chimpanzees (Takahata, 1982; Chapais, 1983; Huffman, 1991; Manson, 1994; Ménard et al., 2001; Gomes and Boesch, 2009; Langergraber et al., 2013; Ostner et al., 2013). All cases concern unusually large groups for the species involved, with smaller groups not exhibiting this phenomenon. The most commonly proposed proximate mechanism is that the reduced ability of dominant males to monopolize access to females creates opportunities for other males to secure matings through means other than dominance. In the evolutionary trajectory of *Homo*, this reduced monopolization by dominants was probably further increased by active concessions (as also found in chimpanzees: Nishida et al., 1992; Duffy et al., 2007) made necessary by the vital fitness impact of effective male cooperation on the carnivorous African savannas of the Pleistocene. Because females benefitted more from such friendships than in most other primates, given the opportunities for acquiring access to meat (see below), selection will have further eroded the monopolization potential of dominant males by favoring an increase in the duration of the females' sexually active period and greater unpredictability of ovulation toward bonobo levels (van Schaik, 2016a). Reduced monopolization potential leads to reduced male competitive tendencies, which are reflected in the reduction in sexual dimorphism of *Homo* relative to *Australopithecus*.

Note that from studies on extant primates there are no indications that male-female friendships are anywhere near exclusive, nor does it appear that a single male or female necessarily maintains friendships with only one opposite-sex partner (e.g., Ostner et al., 2013). Because extant mobile foragers also have pair bonds that lack complete exclusiveness or long-term stability, and occasionally show polygyny (Marlowe, 2010; Layton et al., 2012), such heterosexual friendships may have continued to characterize the hominin line for a long time, arguing against the idea that

monogamous pair bonds are an ancient feature of our genus (contra Chapais, 2011, 2013).

A second upshot from life in very large multi-male groups is that individuals can find potential (i.e., sufficiently unrelated) mating partners within their social unit, so that strict dispersal of at least one sex as typical in primates (Schülke and Ostner, 2012) is no longer observed. In primate species with male dispersal, males become increasingly more likely to remain in their natal group when groups contain more females (van Noordwijk and van Schaik, 2004). A broader comparative analysis across birds and mammals confirmed that in groups containing 15 or more individuals of the philopatric sex, mean relatedness among group members drops to the population average (Lukas et al., 2005), reducing the need for systematic dispersal to avoid inbreeding. We suspect that this tendency toward philopatry of both sexes arose early on in the evolutionary trajectory of *Homo*. Groups may have met quite rarely, due to the unusually large home ranges accompanying a more specialized feeding niche (see below) and living in open habitats with low food density (Layton and O'Hara, 2010), and encounters with other communities will have been largely hostile. Thus, transfer during intergroup encounters may not have been an option. However, the alternative found in *Pan*, solo dispersal by females, may have been prohibitively costly in the high predation risk environment of the African Pleistocene. This lack of dispersal may have persisted for a very long time in our lineage as suggested by recent evidence for consistent endogamy in the post-marital residence patterns of prehistoric hunter-gatherers (Brewer, 2016).

The third, somewhat more speculative, corollary of life in large groups is that, once predator defense and counter-attack had become sufficiently effective (through the ever more sophisticated use of tools and even defensive structures: Leakey, 1971), the very large groups of early *Homo* would have been increasingly able to fission into bands to enhance foraging efficiency (Aureli et al.,

2008). The pattern of keeping one's main social and sexual bonds within the same community (as described above), however, may have simply persisted across bands. This idea contrasts with the traditional notion that the forager band is the equivalent of the primate group, and thus arose from it (e.g., Johnson and Earle, 2000). The bands of modern mobile-foragers regularly exchange members, occasionally come together, and speak the same language; most members who leave end up staying in the same community, which constitutes the ethno-linguistic unit (Moffett, 2013). The band is therefore homologous with the fission-fusion party found in certain primate communities, whereas the ethno-linguistic unit is homologous to the very large, male-bonded group that arose from the primate typical anti-predator responses described here. It is thus most parsimonious to assume that the large *H. ergaster* group or community was the evolutionary precursor to the ethno-linguistic unit of modern human foragers. These modern communities often became far larger than the original *H. ergaster* groups, but this is consistent with bands becoming essentially modular units that maintained social relations and exchanged members (Foley and Lee, 1989; Rodseth et al., 1991). Of course, when communities became too big and social contact between the most distant bands became ever more sporadic, they would split permanently.

We also note another major consequence of the suite of anti-predator responses derived in this study, which concerns subsistence ecology rather than social organization (Fig. 4). In the scarce and variable environment of the early Pleistocene, joint counter-attacks (that initially served a purely defensive purpose) would readily have found a novel application in the context of competition over highly nutritious food with social carnivores at kill sites or other animal carcasses (Van Valkenburgh, 2001). Such confrontational scavenging probably arose early on (Leakey, 1967; Blumenschine et al., 1987) out of joint defense and, together with the kind of opportunistic hunting observed in *Pan* (which most parsimoniously was already present in the last common ancestor of *Pan* and *Homo*: Stanford, 1995; Newton-Fisher, 2007; Surbeck and Hohmann, 2008), allowed early *Homo* to move into the niche of social carnivore. This switch to persistent carnivory by male alliances triggered a cascade of other, and among primates unique, evolutionary changes in the further evolution of *Homo* (e.g., Stanford and Bunn, 2001).

Given that predator defense, confrontational scavenging, and opportunistic social hunting were all inherently polyadic cooperative behaviors in which joint, coordinated actions were critical for survival, a gradual yet fundamental transition in hominin psychology must have been favored by natural selection, moving away from the primate typical "competitive cooperation" mindset to increasingly more prosocial tendencies (Bickerton and Szathmari, 2011; Herrmann and Tomasello, 2012; Tomasello et al., 2012). This will have led to hunting becoming a truly collaborative effort, not only in the sense that individuals perform coordinated and complementary actions to capture prey (Boesch and Boesch, 1989), but also in that carcasses are jointly (and thus efficiently) processed and meat is actively shared. Confrontational scavenging and truly cooperative hunting thus significantly strengthened already existing bonds between males.

Confrontational scavenging and cooperative hunting may also have favored the development of male-female friendships into opportunistically monogamous pair bonds (Crick et al., 2013; Goffe and Fischer, 2016). Because of the historical male bias in joint counter-attacks against predators, meat acquisition was (and still is, see Marlowe, 2007) a predominantly male activity, and female mating preferences will have adapted to this by not only rewarding good protector males, but also successful and generous scavengers

and hunters. Sexual selection will thus have further reinforced male cooperative behaviors (a suggestion recently also made to explain public good production by male vervet monkeys: Arseneau et al., 2015; Arseneau-Robar et al., 2016), and may have provided a first evolutionary incentive for males to proactively start provisioning females, most probably at safe and central locations close to established sleeping sites (Leakey, 1971). The foundation for monogamous pair bonds within a network of large male-bonded fission-fusion groups, along with central place provisioning of females (and likely offspring) by males, as well as the first elements of a tentative sexual division of foraging labor (Marlowe, 2007), may thus already have been laid in the social organization of *H. ergaster*.

A final consequence may concern the rearing system. As meat procured by males and foraged resources procured by females became more important, and the techniques required for this ever more complicated and locally specialized, weaned immatures will have found it increasingly difficult to sustain themselves. This development may have favored active provisioning by the mothers and older immature kin (Hawkes, 2003), but also incited a shift from passive meat sharing by males with female friends and their offspring toward active provisioning. Meanwhile, the trend toward specialization of female foraging niches and the increased yields this engendered would over time lead to a two-way exchange of commodities between friends: the sexual division of labor (Marlowe, 2007). This division of labor, based ultimately on the economics of reproduction, may not only have favored more exclusive mating relationships in spite of frequent spatial separation, but also the evolution of menopause, as females with declining reproductive rates will have found it difficult to compete with younger ones for the provisions of males. Obviously, other scenarios can be and have been entertained (Kim et al., 2012), and at present we see no way to distinguish between them. Moreover, when females began to show grandmothering remains unclear.

In conclusion (Fig. 4), life on the open savanna must have required effective defense against large carnivore predators. In non-hominin primates, active defense involves large group size and coordinated counter-attacks by multiple males, occasionally made more effective by the use of weapons. These are therefore characters that can safely be inferred for *H. ergaster*. These very large and male-bonded groups probably later became the communities or macro-bands of foragers. Living in such large groups, especially given opportunities for the frequent sharing of valuable foods and combined with unpredictable ovulation, may readily give rise to intersexual friendships, as well as loss of natal dispersal. If these characters are also inferred for *H. ergaster*, then we can see the contours of the social organization of modern mobile foragers emerge over time, with home bases and grandmothering as the only unknowns in terms of their first appearance.

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Appendix A. Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2017.05.003>.

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