APES IN THE ANTHROPOCENE: FLEXIBILITY & SURVIVAL

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Abstract

We are in a new epoch, the Anthropocene, and research into our closest living relatives, the great apes, must keep pace with the rate that our species is driving change. While a goal of many studies is to understand how great apes behave in natural contexts, the impact of human activities must increasingly be taken into account. This is both a challenge and an opportunity, which can importantly inform research in three diverse fields: cognition, human evolution, and conservation. No long-term great ape research site is wholly unaffected by human influence, but research at those that are especially affected by human activity is particularly important for ensuring that our great ape kin survive the Anthropocene.

Main text

A primary goal of many field studies of animal behaviour is to obtain data on behaviour in the ecological contexts in which that behaviour is presumed to have evolved. Hence, for many research questions scientists rightly seek to study populations in places remote from dense human settlements and minimally disturbed by human activities. While many researchers have thereby focused little attention on human impacts, the scale of impacts at many sites is now substantial enough that they should be explicitly taken into account. Because great apes (here also referred to as apes) reproduce slowly and require natural forest for food and shelter, impacts such as hunting and deforestation can be devastating, causing local extinctions. Where apes are not directly persecuted, however, and some natural forest remains, apes can prove highly flexible. Here we provide examples of how such behavioural flexibility (see Glossary) can inform research in cognition, human evolution, and conservation. We also explore the reasons why our current knowledge of ape flexibility in response to anthropogenic change is limited. We argue that ape populations most affected by such change provide important opportunities to help ensure the long-term survival of remaining wild ape populations.

Most contemporary ecosystems are affected by anthropogenic land use and activities, albeit to different degrees [1]. Many so-called 'wild' organisms are exposed to a variety of modern human activities such as agriculture, hunting, mining and other extractive industries, and by are affected by roads and settlements [2]. By 2030, it is predicted that less than 10% of currently existing African great ape habitat and only 1% of Asian great ape habitat will remain relatively undisturbed by human infrastructural development [3]. Anthropogenic exposure varies: At one extreme, in near-pristine areas, human–ape interactions are rare; at the other extreme, apes inhabit environments dominated by anthropogenic activities and their behaviour is greatly influenced by humans [4]. In these circumstances, wildlife adjusts its behaviour quickly in response, migrates, or perishes [5]. Here, we focus mostly on situations where great apes and sedentary human communities overlap spatially, such as in forest–farm mosaic landscapes, or at the edges of protected areas, but where apes are not usually hunted for food (i.e. directly persecuted). Where apes are hunted, they fear and avoid people, making detailed studies of their behavioural responses near impossible [but see 6].

How animals respond to human presence and activities are prominent research themes in the behavioural ecology of other charismatic mammals, such as large carnivores and elephants [7-9]. For these taxa there is productive overlap between applied and theoretical research into behavioural flexibility and cognition. In the growing field of ethnoprimatology, research on nonhuman primate behaviour and ecology is combined with anthropological approaches to ensure that humans are considered part of natural ecosystems [10-11]. Such approaches until recently have received relatively little attention from great ape researchers. We suggest there are several reasons for the current limited knowledge.

First, for some species, the link between animal behaviour and human well-being is inescapable. For example, scientists must acknowledge local people's interactions with large-bodied and wide-ranging carnivores when such animals are feared and people want them exterminated because of risks to livestock or human safety [12,13]. In many environments people do not commonly perceive wild apes as presenting severe threats to human safety. Hence, apes do not generally provoke the same level of fear and hostility commonly directed towards large carnivores [14]. As a result, scientists working with apes may be less aware of human-wildlife interactions.

Second, scientists have only recently appreciated the degree to which great apes can survive in disturbed and degraded ecosystems [15-17], which reflects their natural range of behavioural flexibility [18]. This creates new research opportunities that researchers are increasingly exploiting. There are pragmatic reasons for this shift in emphasis: in West African countries, *c.*45–81% of chimpanzees exist outside designated protected areas [19], often in areas markedly modified by humans [20]. In Southeast Asia, >80% of orangutans now survive in multiple-use forests (protected or not) and in transformed ecosystems exploited by people [21]. Human populations in Africa and Asia are expected to increase rapidly in the coming century, and correspondingly, ape populations will be affected by human activities, whether in islands of protected areas or mosaics of relict forest patches and farms.

Third, many great ape researchers are interested in understanding the adaptive significance of behavioural tendencies, which are assumed to have evolved in habitats undisturbed by human activity. Behaviour evinced by great apes in human-influenced habitats can therefore be perceived as being less interesting (for the 'tainted-nature delusion' see [22]). In reality, few long-term great ape research sites are unaffected by human influences (Figure 1). The environment and behaviour recorded at most sites is always influenced to varying extents by current or former human presence and activities (for chimpanzee crop-feeding see [17], for orangutan terrestriality see [23]; for changes in gorilla demography see [24]; but see [25] for chimpanzee conspecific killing).

We offer three examples of how research on apes in the Anthropocene can advance both pure and applied science, specifically in the fields of great ape behaviour, human evolution, and conservation.

How apes see their changing world: cognition

Great apes are known for their behavioural flexibility, frequent innovation, and high degree of cultural variation [26-28]. Therefore, we expect them to modify their behaviour in response to anthropogenic change. As flexible learning ultimately underlies much of the behaviour of these species, a cognitive analysis [29] offers new ways to improve the efficacy of behaviourally focused conservation efforts [30]. Whenever great apes are exposed to novel and potentially dangerous stimuli (e.g., vehicles, farmers, snares, crop protection techniques, domestic dogs [31,32]), or new food sources (e.g., crops; [15,17,33]), we have opportunities to examine their behavioural flexibility and the role it might play in their survival (Figure 2). We do not suggest that great apes are unique in their abilities to exhibit flexible responses to perceived and/or actual anthropogenic risk; rather that understanding the extent of this flexibility should form part of our tool-kit for unravelling the limits of their adaptability.

Behavioural flexibility in response to varied anthropogenic risk patterns

Chimpanzees evaluate and respond flexibly to challenges posed by humans and their activities, for example by taking account of the risks of including agricultural crops in their foraging decision-making. At Bossou, feeding parties are more cohesive during crop feeding than wild foraging, but this does not apply to orchards abandoned by farmers, suggesting increased perception of risk is important (Figure 3a). At Bossou, party sizes are larger on days when crops are consumed than not [34] (Figure 3b); and at Kibale, Uganda, chimpanzee parties foraging in croplands contained more males yet produced fewer pant-hoot vocalisations than parties at the core of the range, likely due to elevated perceived risks of detection by humans [35]. Elsewhere at Kibale, chimpanzees feed on crops at night when maize fields are left unguarded [36], while at Bulindi, Uganda, where farmers frequently harass the apes, chimpanzees show increased willingness to risk costly encounters with people to feed on crops when wild fruit availability is low [37].

Chimpanzees at Bossou cross roads daily to access parts of their home range. While no evidence indicates that Bossou chimpanzees have been killed or injured during road-crossings, the positioning of dominant and bolder individuals varies according to the apparent degree of risk posed by human and vehicle traffic [31]; adult males also exhibit guarding behaviour in response to a visible threat: local people (Figure 2a).

Snare detection and behavioural adaptations to snare injury

Chimpanzees at Bossou understand the potential danger of wire snares, and some individuals deactivate snares safely [38]. Elsewhere, chimpanzees remove snares from the limbs of conspecifics (Budongo, Uganda [39]; Taï, Cote d'Ivoire [40]), while bonobos at Wamba, Democratic Republic of Congo, attempted with mixed success to do so [41] (Figure 2c). Mountain gorillas at Karisoke, Rwanda, show “snare awareness”, with reactions to snares varying from avoidance, to displaying near the snare, or threatening and/or biting individuals who approach it [42]. Despite this, many individuals still suffer limb injuries from snares (16% of mountain gorillas at Karisoke and 21% of chimpanzees at Budongo [43]). Individuals of both species adapt their feeding techniques to their disabilities, thus enabling them to survive under natural conditions. They retain the same processing techniques (i.e. overall plan, organization) as the able-bodied, but work around each of the constituent actions in compensatory ways. For example, gorilla nettle feeding is a complex six-stage process that normally requires both hands. Injured gorillas show behavioural adaptations that solve the problems posed by the disability such as using the support of tree branches, or foot or mouth instead of hand, modified grips, or the stump of the other hand instead of the thumb of the primary hand [44].

2. Contemporary models for paleoanthropological reconstructions: human evolution

Understanding how flexible great apes are when challenged (e.g. through habitat degradation and other forces, human-induced or not) can potentially provide insight into hominin evolution. Documenting what major habitat perturbation does to extant ape populations allows researchers to generate hypotheses about the origin of behaviours that are responses to those conditions. For example, Bossou chimpanzees, which spend much of their time in small forest fragments amid agricultural land [45], exploit underground storage organs of cultivated cassava as fallback foods [46]. They also transport stone tools and crops bipedally – both items that are unpredictable in availability [47]. And they share large-sized crops (e.g. papaya fruit) among unrelated individuals more frequently than wild foods, especially under ‘riskier’ conditions such as when crops are further from the forest and humans are present [48,49]. Bossou chimpanzees thus engage in several behaviour patterns thought to be important for human evolution, but less commonly seen in other chimpanzee populations.

Understanding how well, and for how long, a species can withstand a deteriorating environment provides insights into how ancestral and fossil populations might have coped with similarly deteriorating conditions in the past. Although conservation efforts ideally seek to halt and reverse population declines, tracking the extinction of local ape populations can potentially identify the point at which the equilibrium between ecological change and behavioural flexibility breaks down [18]. Moreover, by understanding how populations of extant apes change their behaviours to human-driven environmental pressures, we can develop models for how, in the course of evolution, synchronic and variably sympatric hominins could have responded to changing local conditions [50].

Coexistence of different hominins

Apes have coexisted with humans, human ancestors, and other early relatives of humans for millions of years. The fossil evidence makes clear that several hominin species occupied the same region simultaneously (Figure 4). In the Omo-Turkana Basin of southern Ethiopia and northern Kenya, early *Homo* and *Paranthropus* species co-occurred not just regionally but also at some of the same paleontological sites for at least one million years [51]. Similarly, there was coexistence for perhaps a few thousand years between *Homo neanderthalensis* and *Homo sapiens*, with attendant competition over space and resources, including plant and meat foods [52]. The first and last appearances of fossil hominin species likely underestimate the true extent of their temporal overlap. Therefore, understanding how sympatric apes interact (e.g., sympatric gorillas and chimpanzees [53,54]), as well as the ways apes interact with sympatric humans, can help to elucidate the ways in which different hominin species might have coexisted. For example, in Lopé, Gabon, three hominoid genera (*Pan*, *Gorilla*, and *Homo*) have coexisted for at least 60,000 years [55], but likely much longer. There probably has always been dietary overlap among these genera, with competition over certain foods such as fruits and honey.

3. Ape survival alongside local people: conservation

All great ape species and subspecies are listed as Endangered or Critically Endangered by the International Union for Conservation of Nature, and all but one subspecies (mountain gorillas, with approximately 880 individuals remaining), are declining in numbers [56]. Successful conservation of great apes requires both legally protected areas and means of ensuring the survival of populations outside of formally protected areas. Hence, the need to understand short- and long-term responses to human pressures by great apes is urgent [57]. Although apes (with species and subspecies differences) show behavioural flexibility to immediate anthropogenic pressures, this does not justify further modification of their habitats. Their ability to cope with human impacts is limited by requirements for intact forests for food and shelter. It is unlikely that extensively farmed landscapes can sustain viable populations of great apes in the long term [58]. With increasing habitat destruction and conversion of forest to other land uses, great apes will be compressed into ever-smaller pockets (potentially at unusually high population densities), hanging-on for a while, but with little chance of surviving long term, especially if climate change affects the distribution of forest such that relict areas are no longer forested [57]. Changes in the demography of ape populations, with their slow life histories, can occur over long periods, with a lag effect between human pressures and demographic change. Some behavioural responses (e.g., crop feeding, livestock depredation, and aggression towards humans) ultimately might be maladaptive if they provoke human retaliation [59], or increase risk of exposure to deleterious human and livestock pathogens [60], leading to increased extinction risk. Where apes are viewed as problematic by their human neighbours, retaliatory killings and lethal crop protection methods take their toll [32,61]. The close phylogenetic relationship between humans and great apes facilitates the risk of disease exchange in closely-shared landscapes [62]. To date, no quantitative assessment of the long-term viability of apes (i.e., analysis of birth, death and migration rates) across sites of varying anthropogenic disturbance has been attempted, but an important factor precipitating rapid population collapse, and thus local extinction, is small population size [57].

Human-ape interactions and conflict mitigation

Human-wildlife ‘conflict mitigation’ strategies to reduce crop damage or aggressive interactions (but see Glossary for discussion of the term ‘human-wildlife conflict’) should take into account the complex adaptive responses of large-brained species, because solutions often are not straightforward [2,4]. For great apes, information about which crops are eaten and which are ignored, and their potential to generate conflict, can help stakeholders to develop effective management schemes in anthropogenic habitats [17]. For example, chimpanzees predictably target fruit crops, but their selection diversifies over time to incorporate more non-fruits including underground storage organs and staple human crops [63]. Effective crop-foraging deterrents must address these dynamic feeding changes, as well as attempt to increase an ape’s perceived risk of exploiting croplands. At Budongo, guarding of fields, involving regular patrolling of field perimeters by a male guard armed with a stick, was highly effective (albeit time-consuming) for deterring chimpanzees [64]. At Batan

Serangan, Sumatra, the experimental introduction of hand-held firecracker cannons as noise deterrents and tree barrier nets to close off arboreal travel pathways reduced crop feeding by orangutans at randomly selected farms compared to control farms where crop feeding increased [65].

Humans kill great apes for various reasons, including for food and medicine, to obtain infants to sell, and in retaliation for crop losses or ape attacks on people. Although the risk of aggressive encounters between humans and wild apes is low, the causes of ape aggression towards humans are complex and varied [4]. Most documented ape attacks on people involve chimpanzees and occur on village paths or in fields bordering forest. As with chimpanzee aggression more generally [25,66], most attackers are males. Most victims are children (of both sexes), and attacks sometimes, but not always, appear driven by predatory tendencies [59,67,68]. Triggers for non-predatory attacks might include provocation by people, sudden unexpected encounters at close range, over-habituation to humans, and adult male chimpanzees asserting their dominance. At Bossou, local people employ simple measures to reduce the likelihood of surprise encounters with chimpanzees, such as cutting down crop trees along forest edges, or regular small-scale cutting back of vegetation in areas frequented by humans and chimpanzees such as fields, paths and trails [67]. Simple, transparent and cost-effective methods for protecting people and reducing crop damage need to be identified and developed to gain the support of local communities and industries alike for great ape conservation. However, problematic great ape behaviour is only one aspect of conflict, with social drivers (such as cultural norms and expectations, social tensions, fear and lack of knowledge) often increasing the intensity of conflict generated. Conservation conflicts are fundamentally driven by humans [69], who have different goals, agendas, and levels of empowerment [70].

Conclusions

We are in a new epoch, the Anthropocene, and research must keep pace with the speed at which our species is driving global change. To predict the threshold beyond which ape populations are unable to accommodate human presence and activities, and local people can no longer tolerate apes and other wildlife, research is needed on populations at different stages of the anthropogenic continuum. To do this, we should abandon a simplistic 'anthropogenic-or-not' approach and instead identify variables, including human activities and customs, which accurately characterize the different types of anthropogenic landscapes, and determine their influence on ape and other wildlife behaviours.

Research on apes across the anthropogenic continuum offers new opportunities to develop understanding of great ape flexibility in the face of unprecedentedly rapid environmental changes; doing so will potentially open a window into the evolution of modern human and ape adaptability. Social as well as natural science approaches are crucial and must be tied to conservation and behavioural research [10,70]. Care should be taken when conducting research in human-impacted habitats to ensure ethical practice and support by local people [71,72]. For example, researchers following apes into crop fields might be perceived negatively by local farmers as disregarding their needs, and might also contribute to ape habituation to human presence in croplands, reducing apes' fear of these areas. Scientists will have to approach the proposed research agenda with open minds, and conventional beliefs might well be challenged [73]. Conservation should "focus on the inevitably novel future rather than the irretrievably lost past" [74, p.38], as the time for delegating pristine 'natural' environments to be the sole solution for preserving great apes in the 'wild' is, unfortunately, long gone. While parks and other protected areas must remain a key conservation strategy, the survival of large, diverse populations requires finding ways for humans and apes to coexist outside protected areas as well.

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GLOSSARY

Anthropocene: current geological epoch of human dominance of geological, biological and chemical processes on earth (term coined by [75]), usually dating from 1945 in ecology and conservation [74].

Behavioural flexibility: behavioural responses to changing local conditions, reflecting solutions to ecological or social problems (sometimes referred to as behavioural ‘adaptability’).

Co-occurring species: species that occur at the same time, but not in the same location (also known as synchronic species)

Co-existing species: species that occur at the same time period *and* in the same place, and thus can potentially interact (also known as sympatric species).

Ethnoprimatology: interdisciplinary study combining primatological and anthropological practice to examine the multifarious interactions and interfaces between humans and other primates living in integrated and shared ecological and social spaces [10,11].

Human-wildlife conflict: negative interactions between people and wildlife. Researchers are increasingly moving away from the term when referring to scenarios in which wildlife impact on people's livelihood, security, or personal safety. Its use obscures the fact that these 'conflicts' often stem from 'differential values, needs, priorities and power relations between the human groups concerned'. For further information see [70,76].

Social learning: learning that takes place in a social context and from the behaviour of others.

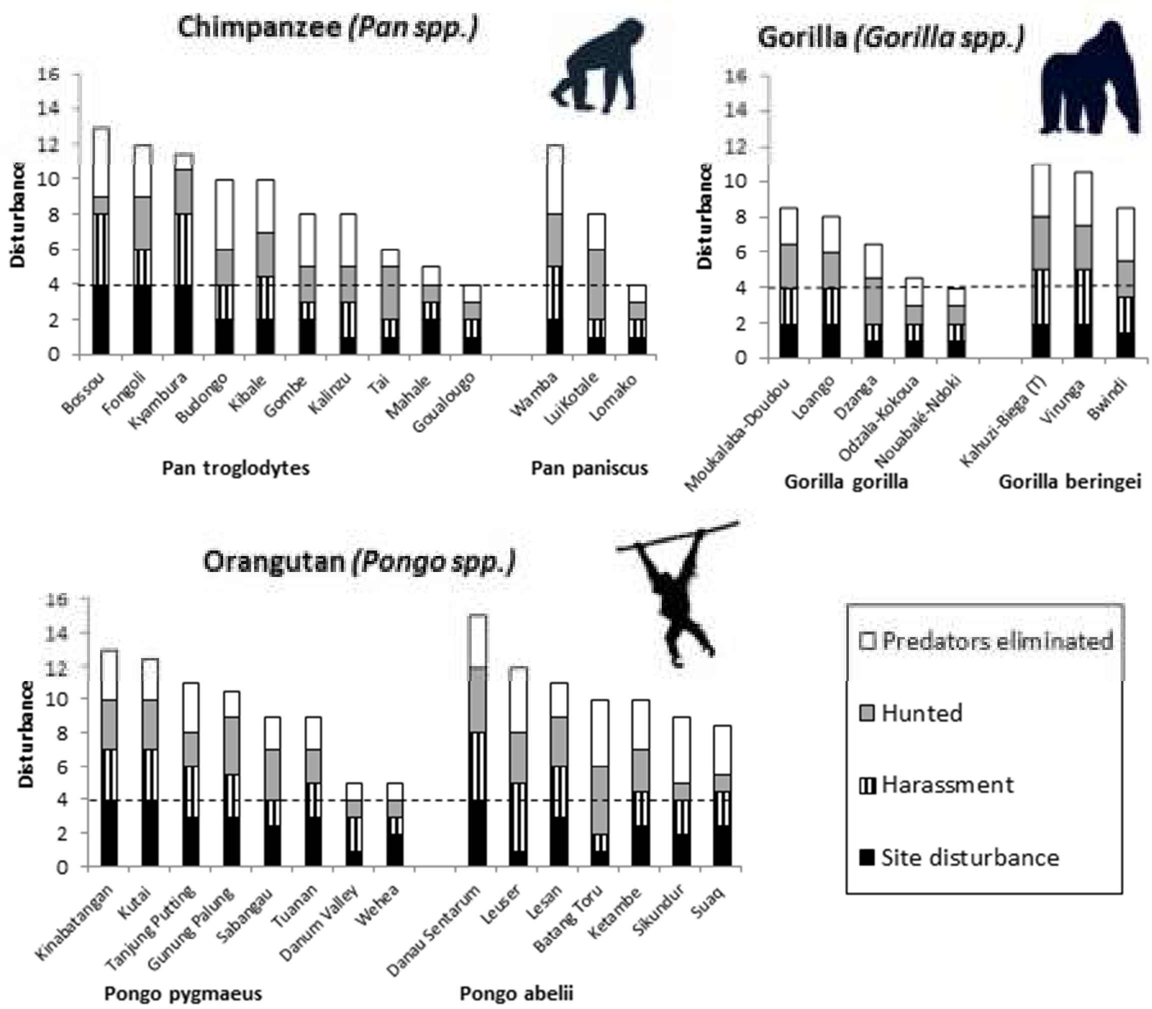

Figure legends

Figure 1. Ratings of human-driven disturbance for great ape populations that are habituated to human observers and have been monitored for at least 10 years demonstrate that few long-term ape research sites are unaffected by human influence. (adapted and extended from [25]). Great ape research and/or tourist sites in the same region are clumped and median ratings for disturbance are presented. For eastern gorillas, Kahuzi-Biega is a group habituated for tourism (T). Human disturbance is the sum of four separate ratings, each scored on a 1 (minimum) to 4 (maximum) point scale, giving a possible range of 4–16 points. We rated whether major predators have been eliminated (Predators), amount of hunting of study

animals (Hunted), harassment of study animals by people (Harassment), and disturbance to habitat (Site Disturbance). Horizontal dashed line indicates the baseline of least disturbance.

Figure 2. Great apes are frequently exposed to humans and their activities: (a) chimpanzees at Bossou, Guinea, crossing a road frequented by vehicles and pedestrians (photo by Kimberley Hockings), (b) an orangutan feeding on oil-palm fruits and pith in a plantation in Borneo (photo by Mohamed Daisah bin Khapar), (c) bonobos at Wamba, DRC, examining a metal snare on the fingers of an adult female (photo by Takeshi Furuichi) (d) mountain gorillas stripping the bark of eucalyptus trees planted at the periphery of Volcanoes National Park, Rwanda (photo by Magdalena Lukasik-Braum/MGVP Inc.).

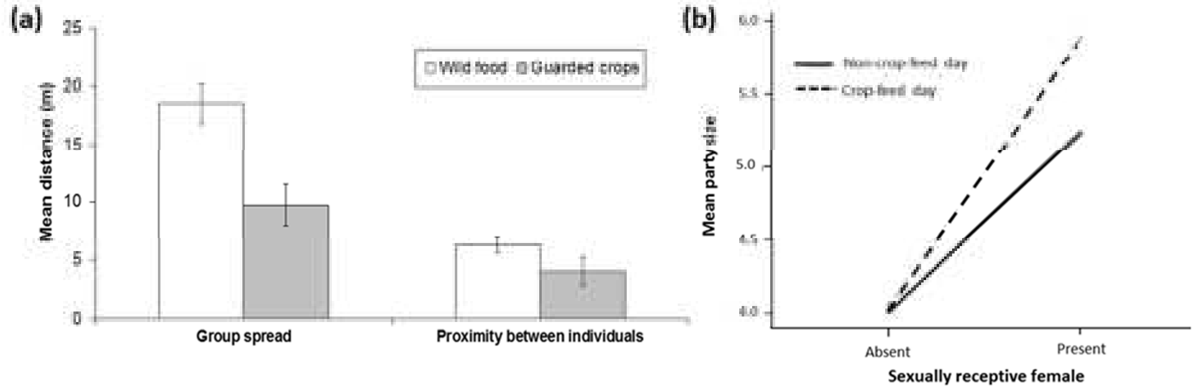

Figure 3. Chimpanzees modify their grouping patterns according to anthropogenic risk: (a) Mean ±SE chimpanzee party spread and proximity of nearest neighbours when feeding arboreally on wild foods versus guarded crops at Bossou (adapted from [34]). In contrast, no significant differences emerged when party spread and proximity were compared during arboreal wild feeds and abandoned crop feeds (which are similar in size and/or density), suggesting degree of perceived risk associated with feeding on crops guarded by people is the most likely explanation. (b) Effect of guarded crop feeding and female sexual receptivity and their interaction on party size. To show the interaction effect data are presented on line graphs. Chimpanzees entered guarded agricultural areas to feed on crops when party size was larger, but only when a maximally swollen female was present. Other social and ecological factors did not influence daily party size. This interaction might reflect male mate guarding (and a desire for males in general to remain in proximity to the female) during periods of female sexual receptivity, with associated perception of increased security by party members. Males might be more willing to engage in risky raids when other males are present in larger party sizes for support, or to ‘show off’ their boldness to females through crop raiding during these periods.

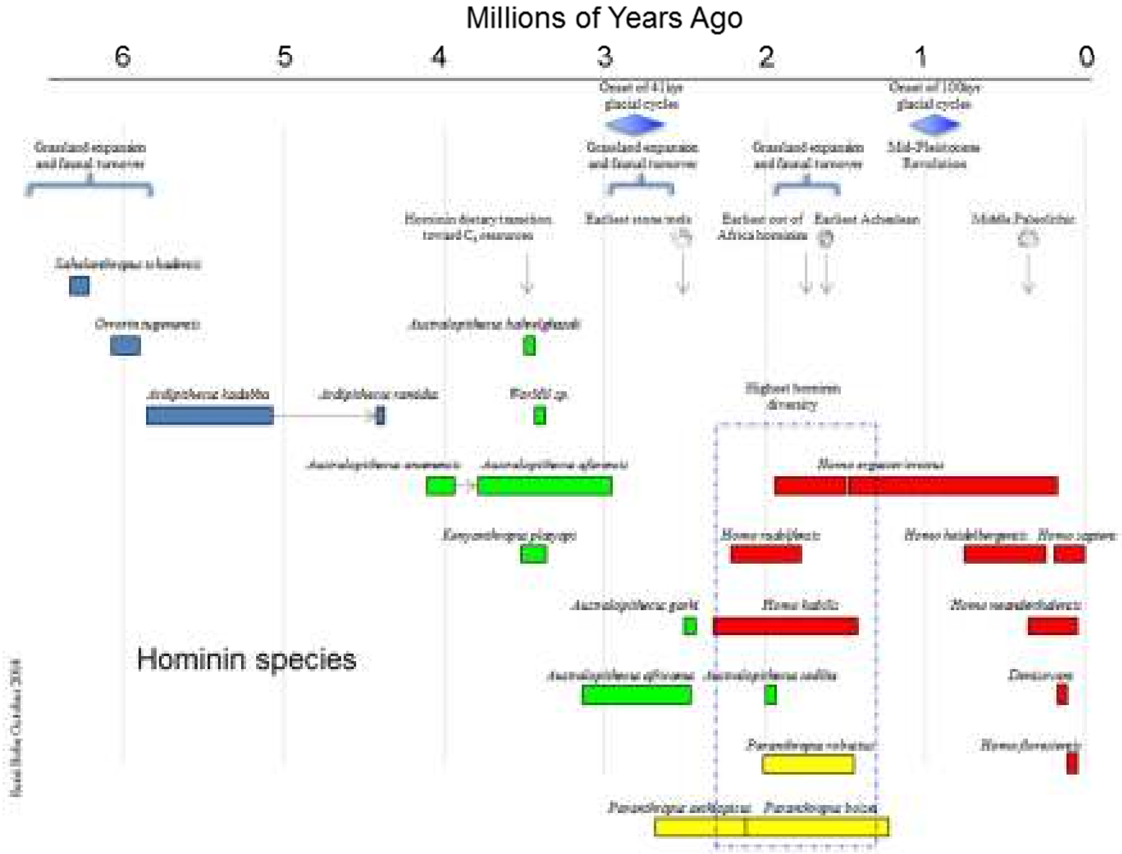

Figure 4. Time range of hominin species, with major climatic, environmental, and cultural developments. At about 3.4 Ma, there were at least four hominin species in Africa, but so far there is no evidence for their sympatry. Between about 2.5 and 1.4 Ma, there is evidence of *Homo* and *Paranthropus* species co-occurring (and possibly co-existing) at several sites in the Omo-Turkana Basin of Ethiopia and Kenya.