Opinion

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Apes in the Anthropocene: flexibility and survival

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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.

Understanding the human–ape interface

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. Given that 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. However, where apes are not directly persecuted 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 that are 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,

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 humans 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].

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mining, and other extractive industries, and 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 humans, 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, humans do not commonly perceive wild apes as presenting severe threats to their 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 humans [21]. Human populations in Africa and Asia are expected to increase rapidly over 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. Therefore, behaviour evinced by great apes in human-influenced habitats can 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 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. Given that 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, or 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 have 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 during wild foraging, but this does not apply to orchards abandoned by farmers, suggesting that an 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 compared with 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 humans 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