

Navigating Anthropogenic Landscapes: Behavioural Adaptations by Great Apes in
Disturbed Habitats

By

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Abstract

Industrial expansion has brought humans and wildlife into closer contact, and increased conflict. The great apes (chimpanzee, orangutan, gorilla, bonobo), the closest extant relatives to humans, have experienced substantial population declines as a result of anthropogenic activities. However, the effects of human activity on ape behavioural ecology have been minimally considered. Using the literature review method, I address the question: how is human activity influencing great ape behaviour in anthropogenic landscapes? I found that the strongest drivers of documented behaviour change were croplands, signs of human activity, and logging. The most frequently documented adaptations to these activities were crop raiding, changing nesting practices, and biased and fragmented range use. Analysis of human-primate relationships showed that some adaptations like crop raiding are worsening relationships between people and primates, resulting in the trapping and harassment of wild apes. Interestingly, regions where apes and humans had previously maintained a positive or neutral relationship were found to be experiencing shifts towards negative relationships. This invites investigation into tolerance thresholds for behaviour change in sympatric species, and timely mitigation strategies. This research provides a big picture of how human activities and ape behavioural ecology interact and demonstrates that the inclusion of human perspectives is critical to developing locally supported, holistic conservation strategies.

Key Words:

Primates, primatology, anthropocene, behavioural ecology, anthropology

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Introduction

Threats to Primates

The footprint humans have made on the Earth since the rise of industrialization is so vast, that it has been proposed we are in a new geological epoch: the Anthropocene (Crutzen & Stoermer, 2000). Continued expansion of mining, agriculture, urbanisation, logging, and damming threaten remaining biodiversity hotspots, while bushmeat and the pet trade directly deplete non-human primate (NHP or primate hereafter) populations (Estrada et al., 2017). Estimates place the annual loss of animal species at approximately 11,000 – 58,000 species per year, and approximately 60% of extant primate species are at risk of extinction due to unsustainable human activity (Dirzo et al., 2014; Estrada et al., 2017). Threats to primate species vary in severity regionally, but the International Union for Conservation of Nature (IUCN) designates agriculture as being the leading threat to all primate species globally, followed by logging and the livestock industry (IUCN, 2015, as cited in Estrada et al., 2017).

However, part of the success of NHPs stems from their flexibility, and ability to adapt to changes in their environment (Hockings et al., 2015). Species with the most dietary and behavioural plasticity have been shown to have the best chance of survival in degraded or altered habitats, and correlations have been found between environmental variability and behavioural diversity (Estrada et al., 2002; Hockings et al., 2015; Kalan et al, 2020). The great apes (chimpanzees, bonobos, gorillas, and orangutans), a particularly flexible group of species, have shown immense ability to respond behaviourally to anthropogenic environmental change, and many of these behaviours have been interpreted as positive signs that populations will be able to overcome new challenges, reducing concerns for their survival (Gruber et al., 2015; Hockings et

al., 2015). However, the origins, contexts, and outcomes of many of these displays of flexibility are poorly understood. While immediate survival in disturbed landscapes may be enabled by apes adjusting their behaviour, negative outcomes from changes like consuming human food, are resulting in increased human-wildlife conflict, and could lead to degraded physiological health as observed in other species (Hockings et al., 2010; Kirby et al., 2019; Krief et al., 2017; Mazur & Seher, 2008; McLennan et al., 2012; McLennan & Hockings, 2015). These poorly understood outcomes may be increasing the risk of population and species extinctions. Furthermore, the abandonment of behaviours characteristic of certain populations of apes for novel, potentially maladaptive responses to disturbance, suggests that the culture and behaviour of great apes should be protected as an issue of conservation concern (Kühl et al, 2019).

Behavioural Flexibility and Overcoming Challenges

Drastic environmental change and increased threats have incited rapid behavioural adaptation by animals in anthropogenic landscapes (Candolin et al., 2023). In the case of primates, study of direct population loss is relatively thorough, while the research on changes to primate behavioural ecology is more sparse. However, the study of animal behavioural flexibility in the wake of sudden and extensive environmental change is critical for several reasons: it is necessary for the generation of effective conservation strategies, understanding whether certain species will be able to persist in a changing world, and understanding compounding ecological effects of animals changing or vacating their niche (Candolin et al., 2023). In the wake of rapid, and unprecedented global change in the recent past, wildlife has shown diverse attempts at solutions to the novel problems posed by humans, to widely varied levels of success (Sih, 2013). Some species or populations generate novel solutions that may be neutral or beneficial, while others develop coping behaviours which may be deemed maladaptive (Sih, 2013).

The great apes have been observed adapting their behaviour to anthropogenic activity through consuming human foods (crop raiding), adjusting group size and composition to deal with risk, altering nest site selection, displaying biased and fragmented range use strategies, among a plethora of other changes (Hockings et al., 2012; Morgan et al., 2018). Resulting from these changes are rippling effects which can threaten the survival or fitness of individuals, such as crop raiding resulting in humans setting deterrent traps which injure or kill raiding primates, or exposure to pesticides which has been correlated with congenital deformities in chimpanzees and baboons (Krief et al., 2017). Other behavioural changes appear to be neutral or beneficial for the time being, showing the ability of the apes to find space to exist in disturbed landscapes (Hockings et al., 2015; Morgan et al., 2018). Beyond survival of individuals and populations, the potential for cascading ecological effects (should changing animal behaviour result in the abandonment of a primate's niche) is an infrequently discussed outcome (Peres et al., 2016; Sales et al., 2020; Trolliet et al., 2016).

Vast disturbance has also been shown to alter the mechanisms through which behaviours are socially transmitted, which in turn can degrade the cultural diversity of great ape populations (Kühl et al., 2019). This process is distilled in van Schaik's 2002 Disturbance Hypothesis, which posits that disruptions to social learning processes will lead to the loss of local traditions via local extinctions, loss of prime habitat where tolerance among individuals is highest, and through lower populations and habitat fragmentation reducing interactions between individuals and thus opportunities for social learning (van Schaik, 2002). Not only is the potential loss of behaviours and primate cultures concerning in the study of human evolution (assuming anthropologists may never be able to study behaviours before they are gone), but the intrinsic value of primate cultures cannot be lost on researchers, and must be a consideration in conservation (Kühl et al.,

2019; van Schaik, 2002). Even so, my research indicates that understanding the ways in which great apes respond to human activity under varying contexts is critical to planning conservation actions that may prevent future change, in the case of detrimental or potentially detrimental behaviours.

The Human-Primate Interface

Humans and primates have interacted for millennia, and relations between species originate before the advent of the genus *Homo*. However, the rapid time scale of industrialization has altered the nature of these relationships in many regions (Fuentes, 2012). Not only is there a great period of change occurring in the relationship between humans and primates, but the inextricable trajectories of humans and wildlife mean the interests of human groups in conservation and environmental impact mitigation need to be considered for successful, holistic strategies (Fuentes, 2012; Sorice & Donlan, 2015). The notion of a one-way relationship where humans consistently act upon primate populations is falling out of fashion, and primates are increasingly being understood as active participants in the relationships between humans and wildlife (Fuentes, 2012). Ethnoprimateology is the, “theoretically and methodologically interdisciplinary study of the multifarious interactions and interfaces between humans and other primates” (Fuentes, 2012, p. 102), and provides the framework to comprehend the “complexities” of human-primate relations in the Anthropocene.

An ethnoprimateological lens helps in the comprehension of the complexity of human-wildlife interaction, appreciating not only that the dynamic between humans and their conspecifics has recently changed on an unprecedentedly rapid time scale, but also that the nature of changes is rooted in local contexts and social norms (Fuentes, 2012). Interspecific

relationships between humans and primates in our current era are neither intrinsically beneficial or detrimental (Hockings et al., 2015). There are areas where apes are exhibiting changes which seem to thus far have neutral effects, or may even be beneficial. For example, in some cases the consumption of human foods has little known impact upon the apes themselves, or the contributing human populations. Duvall (2008) investigated the relationship between Maninka peoples, a group which practises a shifting settlement system of seasonal rotations, and chimpanzees in Mali. In areas previously inhabited by Maninka communities, chimpanzees were found to consume crops which remain in abandoned settlements when wild food quantities are seasonally lower. Importantly this research found that while short term threats to chimpanzees may be evident during active settlement, such as hunting, the overall effects of the apes consuming human cultivars are relatively neutral, as there is low conflict between species over resources. In the case of great apes, across Africa and Southeast Asia, the outlook for their survival is “extremely bleak”, as the majority of the contexts where humans and primates are coming into closer contact are producing negative results for ape populations (Fuentes, 2012).

In Lopé, Gabon, the *Pan*, *Gorilla*, and *Homo* genera have coexisted for an estimated 60,000 years or more (Ancrenaz et al., 2014). However, while historic primates may have been competing for the same resources, the level of disturbance previously posed to one species by another is incomparable to the level of disturbance present on the planet today. Threats from agriculture, mining, logging, and commercial hunting are threats incomparable to past interspecific competition for subsistence resources (Fuentes, 2012). In spite of how relationships between our species are changing, the trajectories of humans and primates are intertwined, and are unable to be teased apart (Fuentes, 2012). Rather, focusing on identifying types of human-disturbed landscapes and the effects they have on local NHPs, will be crucial in

identifying strategies to protect our shared future (Hockings et al., 2015). Approaches to conservation considering local variables will be important, as the local variations of the human-primate interface are unique and must be treated as such.

My Research

Through the method of systematic literature review, my research aims to synthesise how human activities have caused changes in great ape behaviour. I aim to investigate whether there are patterns to behavioural changes and their outcomes which correlate with specific human activities and social contexts, and discuss whether changes to great ape behaviour are heightening threats to ape populations, for example, by increasing the occurrence of negative interactions with humans. These objectives are guided by the central question: *how is anthropogenic disturbance influencing great ape behaviour in the Anthropocene?*

Methods

Included Species

In this study I included all of the great ape species who are documented making behavioural changes in response to human activity. These are two species of orangutans (*Pongo pygmaeus* and *Pongo abelii*), western gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*). The geographic extent of all great ape species are shown in Figure 1.

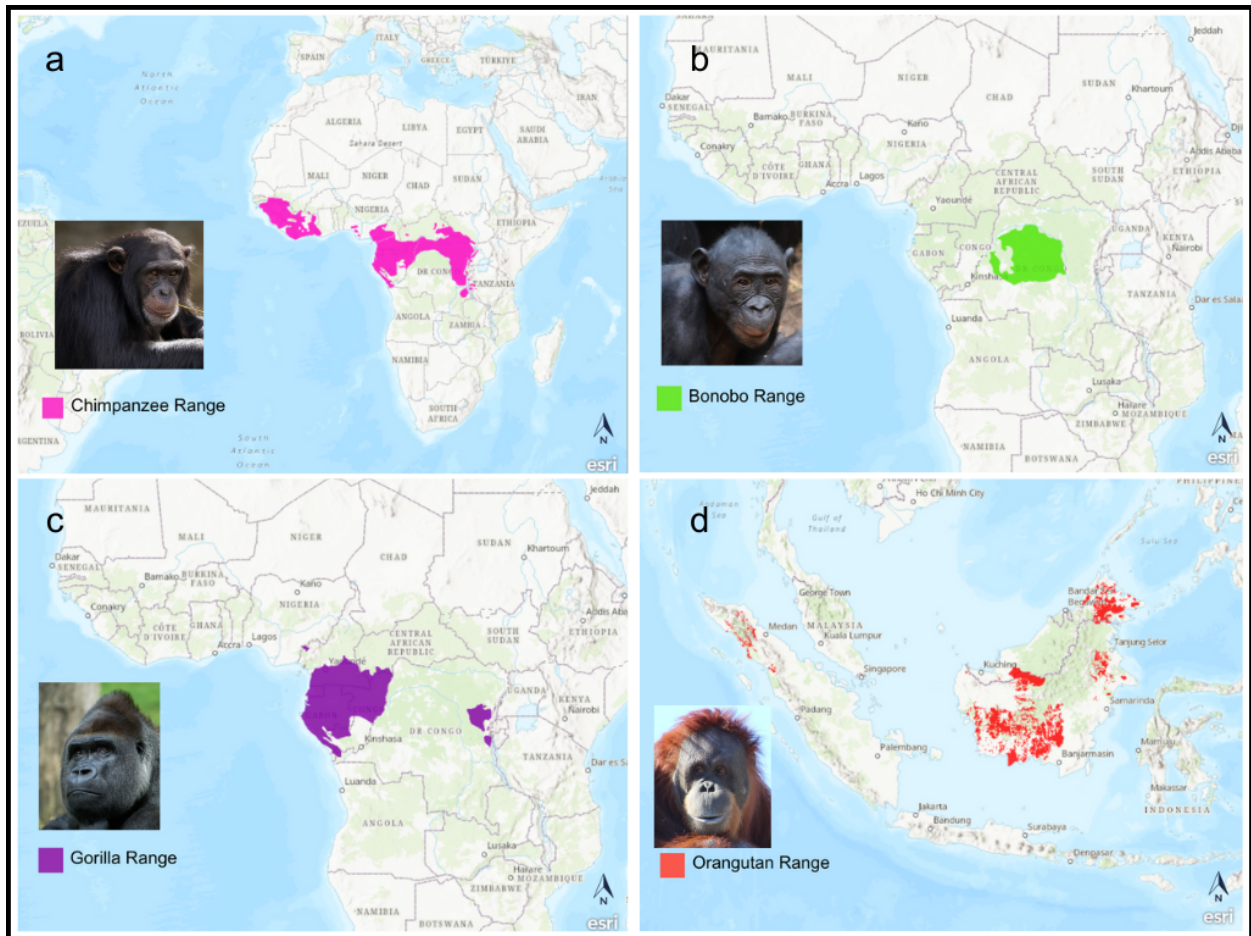


Figure 1. Ranges of the included species. A) Chimpanzee (*Pan troglodytes troglodytes*, includes all four subspecies) B) Bonobo (*Pan paniscus*) C) Gorilla (includes the range of the eastern and western Gorilla: *Gorilla beringei* and *Gorilla gorilla* respectively) D) Orangutan (includes Bornean (*Pongo pygmaeus*), Sumatran (*Pongo abelii*), and Tapanuli Orangutans (*Pongo tapanuliensis*), although only the Bornean and Sumatran are included in my study). Data is sourced from the IUCN’s database (2022), and maps were generated in ArcGIS Online and formatted with images in Canva by Miranda Gilbert.

Research Approach

Research syntheses aim to collect and analyse many different studies and their statistical results, to integrate their findings (Koricheva et al., 2013). These can be useful in revealing gaps in knowledge, and areas for future research. Specifically for my purposes I will be following a

systematic review method, which is becoming more and more popular in environmental management (Koricheva et al., 2013). Systematic reviews are characterised by following strict protocols for search strategies (such as search terminologies, publication timelines, and databases), and inclusion criteria (Koricheva et al., 2013). The most important component for this approach is to adhere to predetermined review protocol, to ensure the process is repeatable and rigorous. The role of systematic reviews when conducted correctly, can inform resource management with a “weight of evidence” approach, and reveal patterns across many studies and subdisciplines (Bezanson & McNamara, 2019; Koricheva et al., 2013). In recent years, systematic reviews have been used to identify research biases in the field of primatology (Bezanson & McNamara, 2019), to describe the prevalence of the use of colonial names in species naming (Chen-Kraus et al., 2021), to find cross-species patterns in primate behaviours regarding death and dying (Gonçalves & Carvalho, 2019), and to amalgamate definitions of innovation in chimpanzees, to make research terminology more cohesive (Bandini & Harrison, 2020).

Given the fact that the great ape behaviours included in this study are responses to human activity, I have incorporated an ethnoprimate lens into my study by including local human perspectives where data is available. For data analysis the included human activities such as croplands and logging are reduced to single variable terms, however during data interpretation and discussion, more nuanced contexts such as local attitudes regarding great ape behaviour are considered. Under an ethnoprimate methodology, humans and primates are each understood as ecological actors in shared landscapes. As described previously, methodologies incorporating this approach understand that humans and primates have maintained dynamic relationships on both deep and recent timescales, which may or may not be undergoing rapid

changes amidst the emergence of unprecedented landscape change driven by global industrial capitalism (Fuentes, 2012).

Search Methodology & Inclusion Criteria

Given the relatively recent focus on human disturbance and primate behaviour, I did not set a beginning date to my literature search. For ease of handling and analysing data, I set February 8, 2023 as my end date for publications to review, and this is when analysis of collected data began. I used Scopus and Web of Science for my literature searches, given how many publications are accessible through these resources, and their advanced search functions. Searches included species names and human stimuli shaping primate adaptations (for example “croplands”), and were constructed using Boolean operators. As defined as best practice by Koricheva et al., 2013, I incorporated wildcard symbols ([?] and [*]) to allow search engines to return publications using multiple tenses, spellings, and hyphenated terms. Furthermore, searches using words where there is an American and British spelling were done with both spellings to prevent eliminating publications using either. Search strings and the number of returns for each are shown in the spreadsheet in Appendix 1.

Example Search String:

```
[chimpanzee* AND (“human activity” OR "human impact" OR "disturbance" OR "anthropogenic" OR “anthropocene” OR "cropland*" OR "logging" OR “plantation” OR “poaching” OR “human footprint” OR "mining" OR "forestry" OR "concession*" OR "deforest*" OR "cultivat*")]
```

I then scanned titles and abstracts to see if a publication pertained to great ape behaviour changes in response to human activities (Bandini & Harrison, 2020; Bezanson & McNamara, 2019). Papers which did pertain to this topic and satisfied the other inclusion criteria were

retained for further review. To be included in the analysis dataset, papers must be studying a non-human great ape species, directly analysing a specific behavioural dataset(s) to investigate correlations between human activity and great ape behaviour, or must be analysing the outcomes of a specific behaviour change. For example, looking at occurrence of great ape roadkills following the introduction of road crossing behaviour. They cannot be review publications secondarily discussing data from other studies. I did not think it necessary to eliminate papers using the same behavioural dataset (as per Bezaonson & McNamara, 2019), as the same dataset may yield information about more than one behavioural response to anthropogenic stimuli.

Data Organisation

A potential shortcoming of systematic review and/or meta-analysis, is discrepancies in reporting across publications; not all publications are equally forthcoming or descriptive of methods and results. This can make comparison more challenging and potentially skew outcomes (Koricheva et al., 2013). As per Bezaonson and McNamara (2020), to compensate for these issues, missing information like study site location or habitat type was inputted by following up on sources in a study's reference list that took place at the same study site. Google Earth and Google Maps also proved useful in finding study site coordinates that were left out of some studies.

The issue of standardising reporting is addressed through the creation of set variable categories. In my study, a set list of human activities, habitat types, consequences, and behavioural changes have been defined to group highly specific variables under more general categories. This makes it possible to analyse studies once data collection is complete, preventing highly specific variables from skewing data as outliers. For example, in Morgan et al. 's 2018 study, a long list of logging related activities ranging from machete cut marks on trees to log

parks were listed as stimuli influencing local gorilla and chimpanzee communities. In order to allow this study to be considered alongside others which may have used different terms to describe the same stimuli, logging related activities were all organised under the “logging” variable. The same was done for other categories, such as the primate behavioural responses to human activities. My dataframe and variable categories were created in Google Sheets, during an initial review of the literature on the topic of great ape behaviour and human disturbance, which was conducted in October, 2022. This initial review allowed me to see what kinds of information are included in these types of studies, what can be extracted, and how I could group highly specific data into comparable categories. The dataframe and list of variable input definitions are included in Appendix 1 via the Google Sheets file.

Behavioural responses were split into set dataframe inputs which fall under behavioural shift, and addition categories. Shifting behaviours means the apes are altering the ways they express naturally occurring behaviours. Addition behaviours are those that were never documented before apes were exposed to some human disturbance. For example, reduced frequency of vocalisation behaviours would place a study under the “behavioural shifts” category, as would alteration of nesting behaviours like nest tree selection or preferential nesting sites. Novel behaviours like crop raiding or road crossing fall under the “additions” designation. One study (Kühl et al., 2019) documented behavioural diversity loss, and thus the loss category was also included in initial data organisation. However, since loss of behaviours is hard to quantify (as of yet), it is largely absent from the literature. It was thus not included in the majority of analysis, aside from being included in reporting of the total number of studies documenting behavioural change by the great apes.

My method of standardisation allows data from a diverse array of studies to be arranged and analysed together (Bandini & Harrison, 2020). Furthermore, this organisation of specific behaviours under broader categories allows the analysis of broader trends in ape behavioural change: the high degree of flexibility required for the innovation of novel behaviours as opposed to the shifting of how naturally occurring behaviours are expressed is expected to be reflected in higher frequencies of behaviour shifts compared to additions.

Analysis

The majority of data analysis included visualising the data graphically to find trends and differences within and between species, in regards to the stimuli they are responding to, and with what types and variations of behaviour. Data visualisation was completed using the ggplot2 (version 3.4.1) package in RStudio (version 2023.03.0+386) and Canva. Visualisations provide graphical, easily comprehensible representations of patterns present in the data (Bezanson & McNamara, 2019). Summary statistics, for example counts of studies per species, are communicated through tables created in Microsoft Excel. Data analysis was broken into four broad groups: big picture data (inter-specific comparisons of behavioural response and to what stimuli they are responding to), chimpanzee subspecies data (finding trends within the four chimpanzee subspecies, which make up a large portion of the literature), analysis of how human perspectives are or are not included in the literature, and consequences (how many studies documented negative outcomes from behaviour change, and what these outcomes are).

Results

The Big Picture

A total of 56 studies were included in my final sample of reviewable papers. Some studied only one species, whereas others included sympatric species. For example, 7 studies examined behavioural responses by sympatric western chimpanzees (*Pan troglodytes verus*) and western lowland gorillas (*Gorilla gorilla gorilla*) to the same disturbances. Overall, 46 studies included chimpanzees, 11 included gorillas, 4 included orangutans, and 1 studied bonobos. Figure 2 represents these results, with the size of each animal reflecting the portion of the sample the species makes up. Chimpanzees most likely make up the bulk of the sample for several reasons: they are particularly flexible, their range is the largest, extending across a large portion of central Africa (Figure 1a) thus providing more opportunity for their populations to be exposed to disturbance, and there is a prolific amount of study sites dedicated to studying the chimpanzee species.

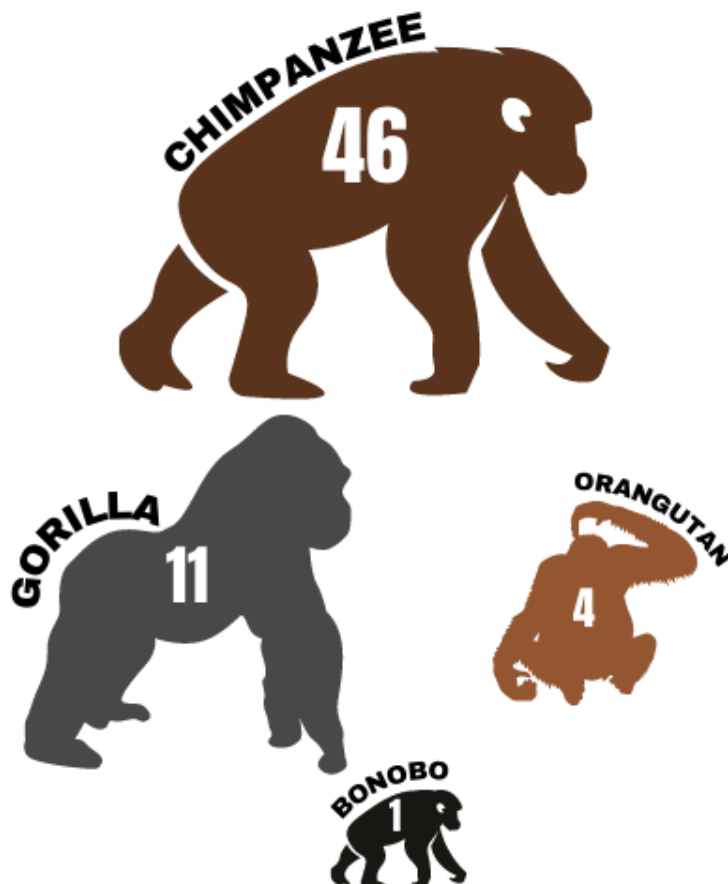


Figure 2. The number of studies tracking behavioural change by species. The size of each figure represents the portion of the sample made up by each species (total papers n = 56). Some studies include more than one species. Miranda Gilbert, 2023.

Human Stimuli

The top three most documented drivers of behavioural responses in apes were croplands (29 studies), indirect observations of human activity (this category includes machine, human and vehicle noise, faeces, paths, garbage, roads) (20 studies), and logging (17 studies). A full description of how many studies documented responses to human stimuli by great ape species is shown in Figure 3.

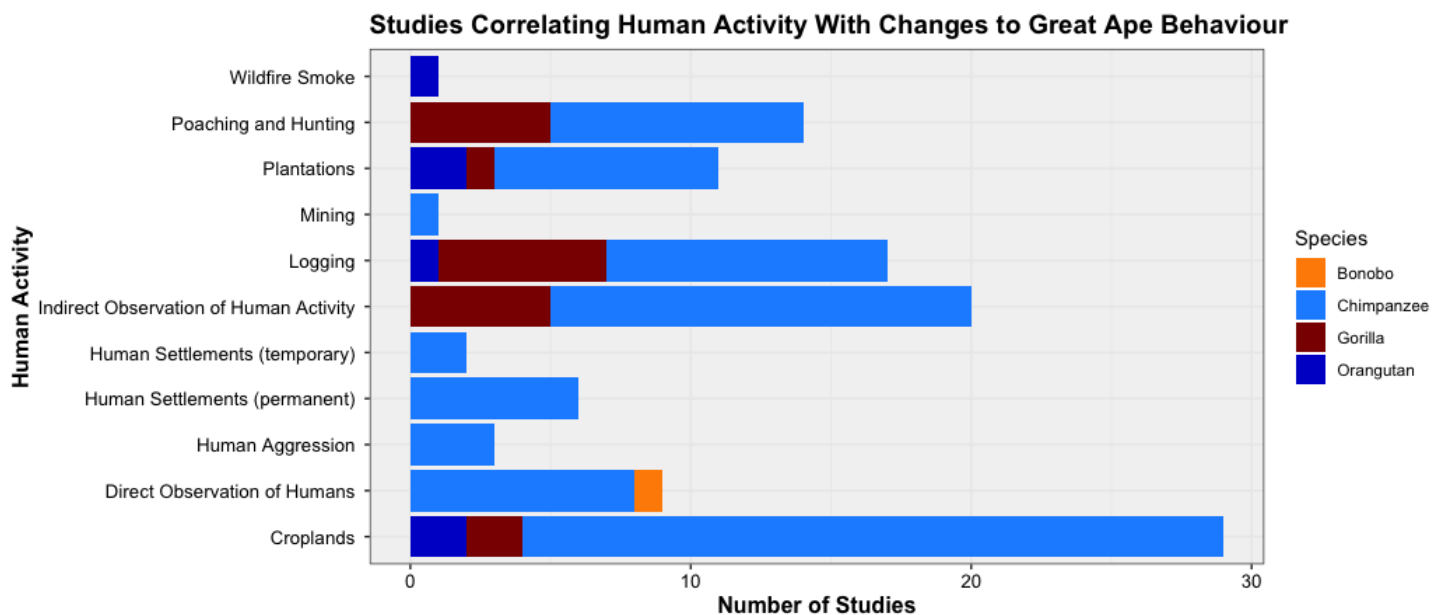


Figure 3. Count of studies documenting human activity resulting in behaviour change, and portions of each made up by each species.

Behavioural Responses

Behavioural shifts were more common than behavioural additions overall, but not by a large margin. Orangutans and bonobos for example displayed equal amounts of shifting existing behaviours and innovating new ones. However, literature on both orangutans and bonobos was

such a small sample that this should not be taken into much consideration. Among gorillas and chimpanzees, there is more evidence of animals shifting their behaviour, however in chimpanzees the two are closer with 20 studies documenting shifts, and 15 documenting additions, whereas 9 studies documented shifts in gorillas, and 2 documented additions. These results are depicted in Figure 4.

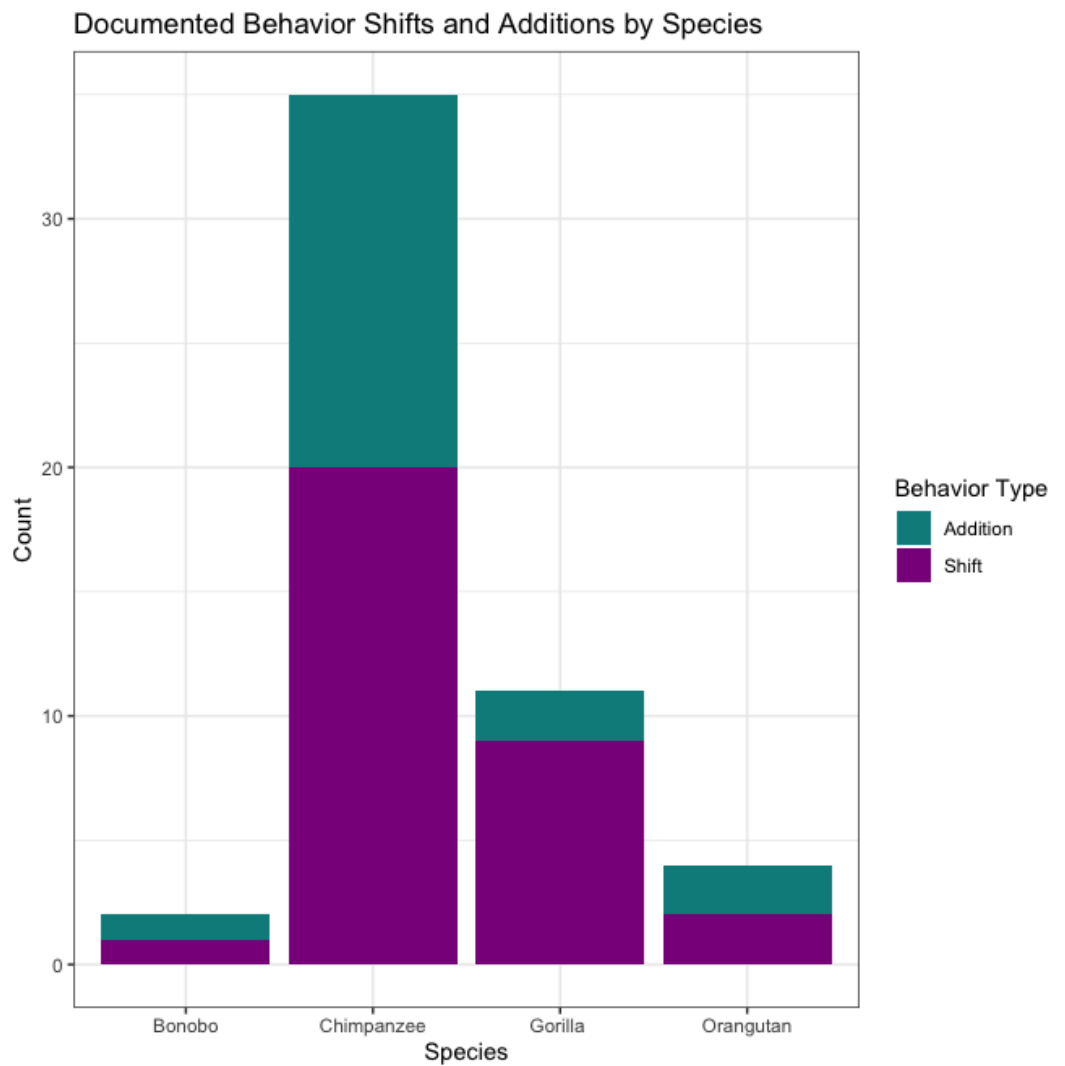


Figure 4. The number of studies documenting behaviour shifts versus additions, grouped by species.

More specifically, the six most frequently observed behavioural responses among all included species were crop raiding (26 studies), altered nest site selection or characteristics (25

studies), fragmented or biassed range use (7), increased or decreased group cohesion (5 studies), road crossing (5 studies), and increased or decreased travel distance (5 studies) (Table 1).

Behaviour Response		Species		
		Chimpanzee	Gorilla	Orangutan
Behaviour Addition	Crop Raiding	23	1	2
	Road Crossing	5	1	na
Behaviour Shift	Nesting	16	9	na
	Range Use	6	1	na
	Cohesion	5	na	na
	Travel Distance	2	na	3

Table 1. Most commonly documented behavioural responses to human activity across chimpanzees, gorillas, and orangutans. Bonobos are not included here due to their small sample size.

Chimpanzee Subspecies

Within the chimpanzee subspecies, *P.t. schweinfurthii* followed by *P.t.verus* were shown to be exhibiting the most documented behavioural changes in response to human activity. Overall shifts of existing behaviours are the more commonly occurring method of response, but the difference between documented occurrences of behaviour shifts versus additions is only 5 studies. Percentages of behaviour changes grouped by shift versus addition are recorded for each subspecies and shown in Appendix 2. The most common behavioural responses by the chimpanzee subspecies are crop raiding (24 studies), altered nest site selection or nest characteristics (16 studies), increased or decreased cohesion (5 studies), food transport (transport of food to a secondary consumption site) (5 studies), road crossing (5 studies) and altered group

composition (5 studies). The number of studies referencing each of these changes is shown by subspecies in Table 2.

Behaviour Response		Subspecies			
		Eastern Chimpanzee	Western Chimpanzee	Central Chimpanzee	Nigeria-Cameroon Chimpanzee
Behaviour Addition	Crop Raiding	14	9	na	na
	Food Transport	1	4	na	na
	Road Crossing	3	1	1	na
Behaviour Shift	Altered Nest Site Selection or Characteristics	6	1	7	2
	Group Composition	3	2	na	na
	Cohesion	1	4	na	na
	Fragmented or Biased Range	2	3	na	na

Table 2. Most commonly documented behavioural responses to human activity amongst the chimpanzee subspecies.

Human Perspectives

Of the total 56 studies included, 31 (approximately 55%) made mention of the local human contexts, human perspective on the studied behaviour change, or both. Mention of the human perspective varied from a brief statement about frequent bushmeat hunting (Carvalho et al., 2013) or absence of hunting (Hashimoto, 1995), to in depth descriptions of social contexts (Bersacola et al., 2021) or inclusion of human perspectives in study design and analysis (Rundus et al., 2022).

Of the crop raiding studies, 16/26 (approximately 61.5%) made some reference to human perspectives on the same aforementioned scale. Of the papers that did record local perspectives on crop raiding behaviour, there was a 50/50 split between reports of negative relationships between humans and the animals, and positive/neutral relationships. Eight studies documented

an emerging shift from positive/neutral relationships between the apes and humans towards negative.

Consequences

Consequences were most commonly documented in studies looking at behavioural changes in chimpanzees. This is likely because they make up such a large portion of the sample size, and also perform the majority of the more risky behaviours (such as crop raiding). Injury and death were the most commonly observed consequences of behavioural change, followed by increased stress and deformities. The most documented consequences are listed in Table 3. All recorded instances of injury and death were in studies documenting road crossing behaviour or crop raiding behaviour. 2/4 of the studies documenting increased stress in great apes occurred in areas where there is high conflict between humans and people as a result of crop raiding (Hockings 2009; Krief et al., 2014).

Consequence	Species				Total
	Chimpanzee	Gorilla	Orangutan	Bonobo	
Death	7	na	na	1	8
Injury	7	na	na	1	8
Increased Stress	4	na	na	na	4
Deformities	2	na	na	na	2

Table 3. The most frequently cited consequences of behavioural change by all included great ape species in the sample papers.

Discussion

What Behaviour Changes Mean for the Apes

The literature reveals that wide-scale land-use changes such as forest clearing for croplands, or forestry activities, are the strongest documented drivers of behavioural response by the great apes compared to smaller-scale disturbances like encounters with humans. Furthermore, my review reveals that while some behaviours may prove beneficial in allowing individuals to survive in the immediate future, there may be long term detrimental effects on the health and even survival of individuals and populations. The same disturbance can differentially affect the behaviour of different populations of a species across locales, and different species within the same area.

Differential Responses to Disturbance

The shifting of nest site preference and nest characteristics, the second most documented behavioural change, at this time has no documented detrimental side effects. In all, existing studies show this to perhaps be a demonstration of rapid flexibility by the apes in response to logging disturbances. Gorillas in particular have been documented nesting in recently logged areas, to exploit early succession vegetation that results from open canopy (a naturally occurring phenomenon, but brought on rapidly at larger scales by logging activities) (Haurez et al., 2014; Haurez et al., 2016; Morgan et al., 2018). However, two studies documented a decreased occurrence of western lowland gorilla nests in recently logged areas (Arnhem et al., 2008; Hicks et al., 2009). The literature documenting responses by apes to logging has been an example of how differences in species' behavioural ecology produces contrasting outcomes in ape behaviour following disturbance. In particular, chimpanzees have been documented as explicitly avoiding logged areas, where gorillas are engaging with the disturbed landscape (Arnhem et al., 2008; Morgan et al., 2018). Chimpanzees may avoid these areas by relocating nest sites away from harvesting zones, and instead nesting on steep slopes to avoid contact with people and logging

operations (Fotang et al., 2021). The potential for differential responses by conspecifics to the same disturbance should thus be considered during the planning of mitigation measures, since the literature shows there is not a one-size-fits-all solution for different species of great ape. While gorillas may be reaping some level of benefit from having increased access to early succession vegetation, the instances where either or both chimpanzees and gorillas are actively avoiding logged areas and exhibiting cryptic behaviours, currently have uncertain outcomes. However, the potential for these changes to result in loss of overall behavioural diversity is discussed in a later section.

Crop Raiding

The most commonly documented behavioural change, crop raiding, has been shown to result in detrimental effects for great apes. However, under some circumstances, this response may not be resulting in immediately negative outcomes. The differences in outcomes documented in the literature indicate that consideration of local contexts is central to understanding whether this behaviour may become maladaptive in a population. One study from Kibale National Park in Uganda noted deformities and high conflict between humans and apes, due to crop raiding behaviours (Krief et al., 2014). At the time of this study, 40% of this community, the Sebitoli chimpanzees, were mutilated from snares laid by farmers protecting crops, and farmers had taken to staying in huts in their fields at night to deter raiding animals. Under this circumstance, following the initial behavioural response to cropland disturbance by crop raiding, the negative responses by humans in turn drove behavioural changes, such as increased displays of guarding postures, feeding in larger group sizes to mitigate perceived risk, and most uniquely, displaying nocturnal behaviours. The Sebitoli chimpanzees have adopted nocturnal crop raiding to reduce detection by humans, a behaviour highly uncommon in the great

apes (Krief et al., 2014). The Sebitoli chimpanzees at Kibale have also exhibited deformities correlated with exposure to pesticides used on the crops they consume (Krief et al., 2017; Lacroux et al., 2022).

Elsewhere, populations of chimpanzees have been differentially grappling with the outcomes of crop raiding, under varying human social contexts. Bossou Village, in the Republic of Guinea, has historically protected the local population of western chimpanzees as a totemic species, spiritually significant to the Manon family (Bryson-Morrison, 2017; Hockings, 2009; Hockings et al., 2012). Recently, given the increased tension between apes and humans following adoption of crop raiding behaviours, this traditionally positive relationship has shifted towards a negative one. Members of the community have begun throwing stones at chimpanzees, chasing them, and overall there has been an increase in fear of the animals by local people, as chimpanzees show increased aggression during times of wild food scarcity (Bryson-Morrison, 2017; Hockings et al., 2009; Hockings et al., 2010; Hockings et al., 2012). In contrast, Duvall (2008) found that intermittent crop-raiding by chimpanzees in Maninka settlement areas in Mali did not seriously impact the relationship between humans and wildlife. The chimpanzees exploited cultivated crops during times of wild food scarcity, and the Maninka's rotational settlement pattern meant the apes mostly exploited abandoned crops. As a result, conflict has emerged infrequently between the two groups (Duvall, 2008). However, there have been some informal reports of retaliatory killings of raiding chimpanzees (Duvall, 2008). The Nalu peoples of Guinea-Bissau protect areas of habitat that have symbolic and spiritual meanings, and have traditional taboos against hunting chimpanzees (Hockings & Sousa, 2012). These cultural norms, alongside chimpanzees raiding a relatively commercially unimportant crop (cashew fruit) affords

the apes a high degree of protection, although some community members find the chimpanzees' consumption of the fruit irritating since it can be used to make liquor (Hockings & Sousa, 2012).



Figure 5. A female western chimpanzee carrying cacao raided from cultivated fields. Copyright PanAf/MPI-EVA, 2015

Besides aggressive retaliation by humans resulting in negative effects for crop raiding apes, potential physiological outcomes documented in other species suggest that this response to cropland disturbance might prove detrimental (Kirby et al., 2019; Leith et al., 2020). Black bears (*Ursus americanus*), who increasingly adopt the behaviour of consuming human garbage in developed areas, have shown disruptions to hibernation patterns and increased ageing rates (Kirby et al., 2019). Cubs that learn the behaviour of foraging human food from their mothers, show increased chance of mortality before maturity, due to these activities bringing them into closer contact with humans along roadways, and euthanasia due to the public safety risk these habituated bears pose. Increased aggression towards humans by crop raiding chimpanzees has already resulted in increased fear and harassment, and most likely retaliatory killing by local people (Hockings et al., 2010; McLennan & Hockings, 2015). Baboons in South Africa have

shown correlations between frequent consumption of human food, and worsened dental health, obesity, and low occurrence of the IRS-1 molecule, which is a sign of potentially developing diabetes (Leith et al., 2020). A similar fate could lay ahead for other crop raiding species. This suggests that, even if there are no signs of increasing conflict between humans and primates, adaptations like foraging human food can not be immediately interpreted as promising signs of flexible adaptation to novel problems, but rather signs of a worsening conservation crisis (Hockings et al., 2015). My review of the literature reveals that while exploitation of human cultivars may assist apes with surviving land-clearing disturbance in the immediate sense, the knock-on negative effects may outweigh the benefits in many contexts. Some mechanisms through which crop raiding can become detrimental are visualised in Figure 6.

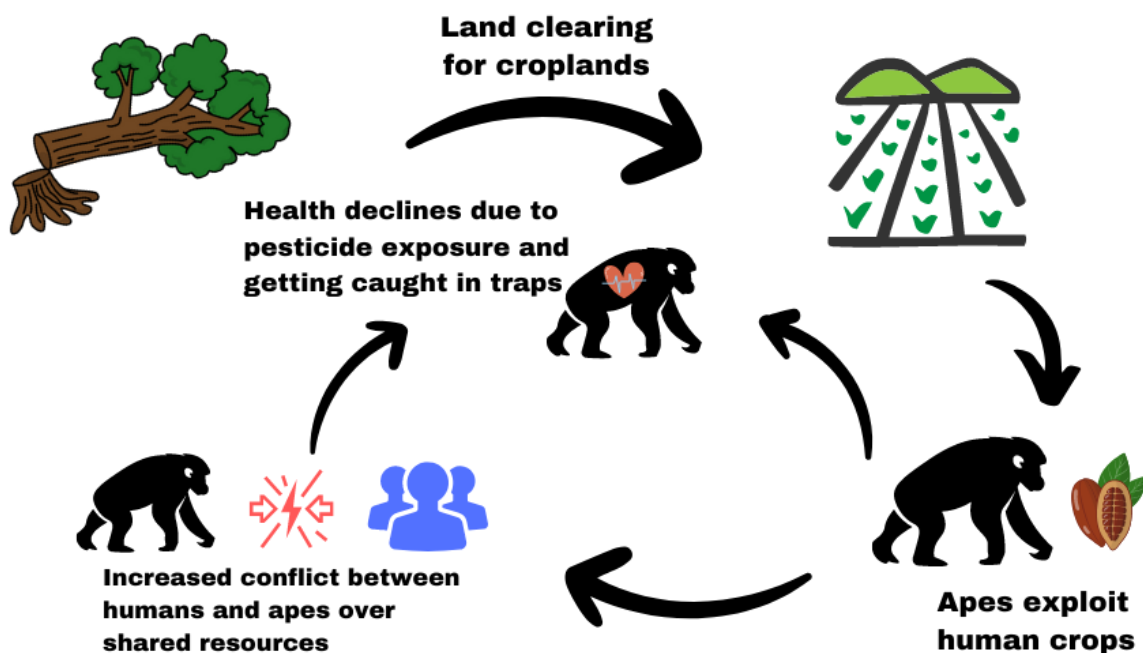


Figure 6. A visualisation of the interconnected factors resulting in negative outcomes for apes adopting crop raiding behaviour. Copyright Miranda Gilbert, 2023.

Implications for Behaviour and Cultural Diversity

A plausible but understudied outcome, is the potential for there to be altered opportunities for social learning and behaviour transmission, in areas where apes are nesting in lower densities, or spending less time together due to anthropogenic disturbance (Arnhem et al., 2009; van Dijk et al., 2021; van Schaik, 2002). This aligns with van Schaik's Disturbance Hypothesis, that great ape cultures will be degraded via human activity interrupting social learning processes, processes which allow culture to be maintained across generations (van Schaik, 2002). Already, research has shown that a high degree of human activity in a landscape correlates with an 88% reduced likelihood of chimpanzees exhibiting a behaviour (Kühl et al., 2019). Five documented cases of altered cohesion, five reports of altered group composition and two reports of altered group size in my sample suggest that responses to disturbance may have the potential to impact social learning processes by the apes, which is a mechanism of impacting, specifically degrading, great ape culture (van Schaik, 2002).

Van Schaik's Disturbance Hypothesis is concerned with disruptions to the ways in which behaviours and thus culture are transmitted (van Schaik, 2002). Given the detrimental effects that behaviours like crop raiding can have on great apes, I argue that these adverse effects on both the individual and population levels may further enforce the Disturbance Hypothesis' prediction of reduced social transmission through population declines and reduced interactions between populations. Behaviours like crop raiding are novel and thus, some have argued, are a display of increasing behavioural diversity and possibly the creation of new cultural traditions (Gruber et al., 2015). However, since these "new traditions" can contribute to detrimental effects to population health through the threats brought on by increased conflict with humans, the value of these new behaviours is debatable (Hockings et al., 2010; Hockings et al., 2012; Krief et al.,

2014). Even cases where there are currently unknown effects of behavioural changes, such as relocating nest-site and nesting practice preferences to avoid logged areas, could potentially result in loss of behavioural diversity, through the apes less-frequently exhibiting behaviours to remain undetected by people, or nesting in smaller group sizes thus altering social learning opportunities (Hockings et al., 2012; Morgan et al., 2018; Rundus et al., 2022; Satsias et al., 2022). During land-use planning processes, these potential outcomes must be considered when decision-makers are determining what impacts might result from industrial activity, and how thresholds for significant adverse effects are defined. Perhaps loss of culture and behavioural diversity should be considered negative outcomes of industrial development, even in places where great ape survival is not currently threatened by the behavioural responses discussed here (Kühl et al., 2019).

Recommendations for Conservation Strategy

Only 55% of total studies and 61.5% of crop raiding studies included mention of human perspectives on the documented behaviour changes, which is disconcerting given the ways behaviours like crop raiding affect humans economically and socially. Integrating qualitative and quantitative approaches to better understand feedback and relationships between humans and primates in shared spaces can better inform ethical and effective conservation strategies within the NHP taxa and beyond (Fuentes, 2012; Sorice & Donlan, 2015). The different studies reviewed here, and their emerging patterns and contrasts, indicate that human contexts are in themselves predictors of whether apes will experience negative outcomes from their behavioural responses to disturbances. Furthermore, they may predict whether further behavioural responses to human retaliation will be generated by the apes, as seen in the adoption of nocturnal behaviour

to reduce detection by humans guarding crop fields (Krief et al., 2014). The indication by my results that human reactions to the great ape behaviour changes can be predictors of whether outcomes will be negative or neutral for the primates, strongly implies that considering human contexts in conservation strategies is central to their success.

Noting the limited consideration for social contexts in the existing body of literature, it is important that conservation biologists take complex human-wildlife relationships into consideration when putting forth solutions, and draw upon qualitative data from the affected parties to supplement where traditional primatological methods may be lacking (Campbell-Smith et al., 2010; Krief et al., 2017; Rundus et al., 2022). This approach will in turn help researchers understand not only what disturbances are driving specific behavioural responses, but how human reactions to these responses influence further change. For example, as seen in Krief et al.'s (2014) study of nocturnally crop raiding chimpanzees, reference to the immense conflict between humans and apes following the initial adoption of crop raiding behaviour, provides context to understand why nocturnal behaviour is being exhibited. This has become a secondary behavioural response by apes to be less conspicuous while raiding. Other cases have similarly shown that aggressive responses by humans to crop raiding have resulted in increased vigilance behaviours, larger feeding parties and higher presence of males to mitigate risk, or reduced conspicuousness through lower frequencies of vocalisations (Hockings 2009; Wilson et al., 2007).

A critical takeaway from my research is the evident shift from a positive or neutral relationship between apes and humans towards a negative one in circumstances where behaviour change is increasing competition between the human and non-human primate species. Under these circumstances, I argue that the potential for pre-existing support from communities for the

conservation of species may be lost, worsening the primate conservation crisis. Ongoing support by local communities for conservation initiatives is critical to the long term survival and success of projects, and co-design and collaboration when generating conservation actions can facilitate this support (Sorice & Donlan, 2015). Understanding the factors of human social and economic life that may be affected by changing great ape behaviour is critical to catching early signs of deteriorating human-wildlife relationships.

Understanding human-wildlife relations as dynamic and locally specific will be important in gaining support for conservation initiatives (Fuentes, 2012) and ideally should mobilise the positive relationships between apes and humans before positive predispositions are lost. Future research should assemble early-warning signs of potentially deteriorating relationships between humans and wildlife, before intervention becomes difficult, or impossible. For example, my study's particular focus on crop raiding already indicates that great apes selecting commercially valuable crops for raiding is a stressor between humans and NHPs (Bersacola et al., 2021; Bryson-Morrison et al., 2017; Campbell-Smith et al., 2011; Hockings et al., 2009; Hockings et al., 2012; Krief et al., 2014; Lacroux et al., 2022; McLennan & Hill, 2012; Rundus et al., 2022; Tweheyo & Lye, 2005). Conversely, where great apes select crops that are not commercially valuable, or raid areas where crops are not actively used by humans, there is much less conflict and retaliation by human communities (Duvall, 2008; Hockings & Sousa, 2012; McLennan & Hockings, 2014). Reduced instances of retaliation mean less strain is on the human-primate relationship in a landscape, even if apes are exploiting human food sources. Since increasingly stressful relationships between humans and apes have been shown to lead to secondary behavioural responses like attacks on humans or nocturnal behaviour (Hockings et al., 2010; Krief et al., 2014; Lacroux et al., 2022; McLennan & Hockings, 2015), we can expect to see that

early intervention in areas prone to negative responses by humans would reduce the negative side effects of those initial behaviour changes made by great apes and reduce further behaviour change. There are emerging strategies for dealing with crop raiding mitigation, indicating that hope is not lost. For example, before funding and staffing hindered the continuation of the project, relocating commercial maize, (frequently raided by chimpanzees) to greater than 500 metres from the forest edge and replacing crops close to the forest with subterranean plants, drastically reduced crop raiding in Gishwati forest, Rwanda, and reduced the strain on the local community (Rundus et al., 2022). This study also engaged local research assistants, garnering local investment in and support for the project (Rundus et al., 2022; Sorice & Donlan, 2015).

Conclusions

Primates are documented showing a diverse array of behavioural responses to human disturbances. However, the ability of NHPs to adapt to disturbance as well as the growing understanding that humans and NHPs share ecosystems does not justify further degradation to habitat, nor can adaptations be immediately interpreted as positive signs of their ability to endure rapid change (Gruber et al., 2015; Hockings et al., 2015). Rather, species and populations respond differentially to environmental change, showing different levels of success as a result (Sih, 2013). While gorillas may show a preference for selectively logged areas due to its correlation with early succession vegetation, chimpanzees can become more reclusive (Morgan et al., 2018). Where some chimpanzee populations are able to merely supplement their wild diet with abandoned human crops and maintain a comparatively neutral relationship to human communities (Duvall, 2008), others see increasing conflict between themselves and humans (Hockings et al., 2010; Krief et al., 2014; Lacroux et al., 2022; McLennan & Hockings, 2015).

Both the similarities and differences observed across landscapes and social contexts show that considering the human-primate interface in conservation strategies is critical to addressing the roots of problems facing the great apes, and garnering local support (Fuentes, 2012; Sorice & Donland, 2015). Accounting for the nuance of human-wildlife relationships will more adequately prevent some of the negative outcomes of high-risk behavioural changes like crop raiding, since early interventions into increasingly strenuous relationships may reduce instances of retaliatory trapping or harassment of raiding wildlife. In this same vein, great ape behavioural changes must be appreciated as phenomena with uncertain outcomes; the interpretation of these adaptations to rapid landscape change cannot be taken as positive signs of their ability to survive in disturbed areas, nor as a compensation for the loss or shift away from pre-existing cultural traditions (Gruber et al., 2015; Hockings et al., 2015; Köhl et al., 2019). While some cases are quite plainly revealing changes like crop raiding to be producing negative outcomes for the fitness and survival of great apes (Bersacola et al., 2021; Hockings et al., 2012; Krief et al., 2014; McLennan et al., 2020), other circumstances can be interpreted with much less certainty, such as the potential outcomes of changes to group composition and size, which may have an influence on social learning processes and thus the carrying-on of cultural traditions (van Schaik, 2002). Even those behaviours like crop raiding which are resulting in widespread detriments to great ape populations, present circumstances that are still not black and white, since the human social contexts can in part be the predictor of whether this behaviour is maladaptive. While the potential for metabolic health conditions to worsen may be present as seen in other mammals (Kirby et al., 2019; Leith et al., 2020), the exploitation of non-commercially valuable crops, or taking only limited amounts of cultivars, seems to reduce the desire by humans to retaliate (Duvall, 2008; Hockings & Sousa, 2012; McLennan & Hockings, 2014).

Further research might aim to construct statistical models that can predict the potential for a behaviour to become maladaptive to animals, based on ecological as well as human social factors. While the field of ethnoprimateology has stressed the importance of incorporating human-wildlife relationships in conservation and research for years, my study further punctuates the argument that threats to primates, and primate responses to these threats, do not occur in a vacuum. Rather, how much conservationists and researchers can rely on behavioural flexibility to help great apes survive in the Anthropocene hinges heavily on whether humans will respond positively or negatively to their behavioural change, alongside the potential physiological effects of primates altering their niches which may threaten their survival. Given the rapid temporal and extensive spatial scales on which humans are altering ecosystems, conservation approaches which incorporate the intersections of biology, culture, and behaviour, are necessary in order to respond to the locally-specific needs of both humans, and the wildlife they share landscapes with.

Appendix 1

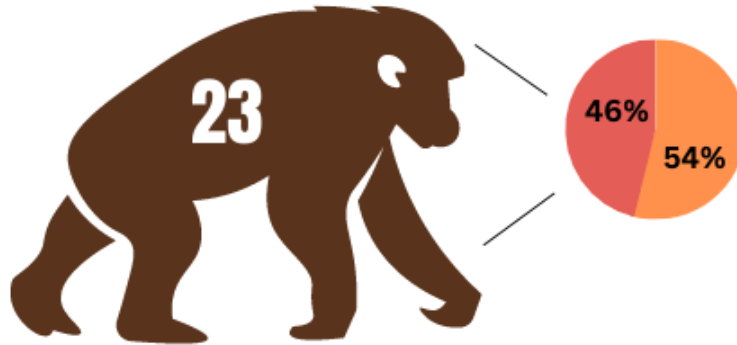
Google Sheets Dataframe:

https://docs.google.com/spreadsheets/d/1bRIUtrPrOXF_Jw2v8Xj9eNpX5IBHUmP0YoUuLvYv6fo/edit?usp=sharing

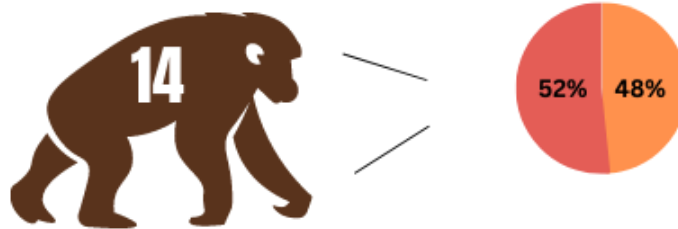
This Google Sheets file includes data extracted from the included studies, variable definitions, and the number of papers returned from each search string.

Appendix 2

EASTERN CHIMPANZEE



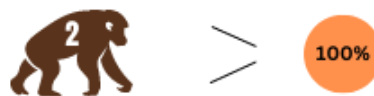
WESTERN CHIMPANZEE



CENTRAL CHIMPANZEE



NIGERIA-CAMEROON CHIMPANZEE



The number of studies documenting behavioural changes in the chimpanzee subspecies, and the percentage of these totals that documents behaviour shifts versus innovation of novel behaviours (additions).

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