Evaluating the Need to Habituate: Modern Approaches to Field Primatology during the COVID-19 Pandemic and Beyond

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Abstract: Although historically habituation has largely been the default method in field primatology, the COVID-19 pandemic has forced us to re-examine the possible detrimental effects of habituation, particularly disease transmission. Fortunately, habituation is no longer our only choice. Remote monitoring techniques have greatly improved over the last decade and can, in many circumstances, help us collect all the data we need and more. Furthermore, recent research shows potential disparities between individuals and species in habituation levels, which compounds what we already know about the not-so-neutral effect habituation can have on primate behavior. Instead, remote technologies may generate standardized and objective results in a more ethically-sensitive way. Here, we discuss the risks and benefits of habituation and possible alternative methods, asking the question: in the COVID-19 era and beyond, should habituation be our default first step?

Key Words: Ethics, non-invasive sampling, remote monitoring, methods, fieldwork, habituation

Introduction

We are entering a 'New Normal' for primatological research, as Lappan *et al.* (2020) argue in their recent paper. A global pandemic has forced us to rethink our approach to fieldwork to address the human-nonhuman primate (hereafter primate) interface and the risk of zoonotic disease transfer. Currently, most field projects begin with a habituation process where primates are desensitized to the presence of researchers (Souza-Alves and Ferrari 2010; Vicente-Alonso *et al.* 2021).

While some of the earliest scientific expeditions to observe primates in the wild resulted in very few detailed observations (e.g., Bingham 1932), subsequent waves of field studies began to recognize the importance of sustained *in situ* observations akin to anthropological fieldwork (e.g., Carpenter 1934) and of achieving "a high degree of rapport" with their study subjects (Emlen 1960, p.322). Clarence Ray Carpenter, an early pioneer in field primatology, advocated for a method that would enable researchers to conduct more detailed studies of primates in their native habitats: through "neutral conditioning of the animal to the observer" (Carpenter 1934 [1964], p.19) or what we now call "habituation." In the current era, habituation is widely understood as the process by which wild animals learn to accept human observers as neutral elements in their environment (Tutin and Fernandez 1991). Habituation is generally considered a critical first step in most types of primate field research because it enables researchers to systematically document complex behavior that would be difficult to accomplish via observations of non-habituated primates (Cheney and Seyfarth 1990). In recent years, however, a growing set of concerns about the process of habituation has emerged. These concerns are largely situated along three axes: critique surrounding the purported goal of primatologists becoming neutral elements of a primate's environment (McDougall 2012; Alcayna-Stevens 2016; Hanson & Riley 2018; Allan *et al.* 2020); the effects of observers on primate behavior and ecology (Jack *et al.* 2008; Crofoot *et al.* 2010; Strier 2013); and the ethical dimensions of habituation (Fedigan 2010; Gruen *et al.* 2013; Riley and Bezanzon 2018), including potential disease risks associated with close proximity of people to primates (Goldsmith 2005; Williamson and Feistner 2003), which is a particularly relevant concern during the COVID-19 era (Lappan *et al.* 2020).

In a recent attempt to evaluate researchers' concerns regarding the ethics of habituating wild primates and their perceived duties vis-à-vis this process and its impacts, Green and Gabriel (2020) carried out a survey that revealed that while researchers had a high concern for indirect harms that result from habituation (e.g., increased risk of being hunted), harms potentially caused during habituation (e.g., impacts on primate behavior and health) were of lower ethical concern. Moreover, the survey results indicated that researchers' perceived ethical concerns (e.g., concern regarding disease transmission) did not always match with their mitigation practices (e.g., adhering to suggested practices to reduce risk of disease transmission). The majority of survey respondents did, however, agree that primatologists should strive to use methods that do not require primates to be fully habituated, although it is unclear how "fully habituated" is defined. Finally, only a few respondents seemed concerned about abandoning field sites after habituating primate groups.

The process of habituation and its role in field primatology is the focus of this commentary, as well as promoting the use of alternative non-invasive methods whenever possible. Our objective is to further explore the ethical issues associated with the habituation of primates for research by addressing the following questions: When is habituation appropriate? And, in the COVID-19 era and beyond, should habituation automatically be a first step? We begin by highlighting recent insights on habituation as a process and briefly review the risks and benefits of habituation. We then showcase a number of methods, some well-established and others emerging, that could serve as alternatives to habituation, including remote monitoring technologies and non-invasive sampling techniques. Based on these sections, we offer some recommendations and present a simple decision tree that can aid researchers in making the decision on whether or not to habituate.

Expanded Understanding of Habituation

Recent research has demonstrated how habituation is better understood as a bidirectional process of mutual attunement between human observers and their animal study subjects (Alcayna-Stevens 2016; Candea 2013; Hanson and Riley 2018). For example, Ampumuza and Driessen (2020) argued that mountain gorillas (*Gorilla gorilla beringei*) play a role in the multi-sided and complex habituation process, thereby demonstrating their agency in the process. The authors explain how gorillas habituate and de-habituate themselves and remind us that primate groups have often been habituated to local human populations through periodic exposure over many years prior to the arrival of researchers. In Manzano, Democratic Republic of Congo, local trackers searched for bonobos (*Pan paniscus*) twice a week as a local community conservation measure before any researchers arrived, which possibly reduced the time needed for habituation for research (Narat *et al.*, 2015). Narat *et al.* (2015) also speculate that a local taboo against the consumption of bonobo meat along with low human density and minimal crop cultivation on the forest edge might also have favored a fast habituation process.

Recent scholarship on habituation has also highlighted the importance of recognizing the complexity of the process, that is, as a spectrum of tolerance rather than a state to be achieved (Hanson and Riley 2018). Gazagne *et al.* (2020), for example, described habituation as comprising five stages: "early" – short interrupted tracking using auditory cues; "minimal" – short interrupted tracking with visual contact; "partial" – long tracking, identification of sleeping sites and possibility of scan sampling; "advanced" – long tracking and full days; and "full" – full consecutive days with the possibility of collecting complex behavioral observations (including individual identification; Hanson and Riley 2018). Similarly, Doran-Sheehy *et al.* (2007) described "complete habituation" as being when observers can move freely within the primate group and conduct focal animal sampling. A sixth stage of habituation has also been identified: "overhabituation," which is defined as when primates have not only lost their natural fear of humans but will also include humans in their social interactions, solicit close contact with them, and possibly even redirect aggression towards them (Williamson and Feistner 2003; Webb and McCoy 2004; Strier 2010). Although "full habituation" has been conflated with "good habituation" (Bertolani and Boesch 2008), what counts as "successful habituation" is more nuanced, and largely subjective (Hanson and Riley 2018). These insights have important implications for the discourse surrounding habituation and the methodology we employ in our research. Namely, by recognizing that habituation comprises an array of stages, such as those described by Gazagne *et al.* (2020), researchers can work towards a habituation stage that aligns with their research goals, which could happen, for example, at "minimal" habituation. In other words, might we accept primates being habituated just enough to answer our research questions?

Researchers have also examined an aspect of the process of habituation that many field primatologists have likely experienced: individual variation in habituation success (Ampumuza and Driessen 2020). For example, in their study monitoring habituated chacma baboons' (*Papio ursinus*) responses to observers, Allan *et al.* (2020) found that individual personality traits in the baboons determined the level of habituation, whereby individuals' Flight Initiation Distances (FIDs) differed greatly within the same group. They further demonstrated that human observers are not perceived as neutral entities in the environment, as the baboons continued to react to observers through passive displacement in 99% of all human approaches. Variation in habituation according to age or sex is also known (Williamson and Feistner 2003). In particular, males often habituate to researchers faster than females (Bertolani and Boesch 2008; Gazagne *et al.* 2020). These documented insights emphasize the importance of understanding habituation as something experienced not just at the group level, but at the individual level as well.

The process of habituation is also variable at the species level. Primate taxa vary in their physical and social cognition which may influence the ways in which they react to humans and thus habituation (Narat *et al.* 2015). For example, McKinney (2014) showed that different primate species have different reactions to tourists, meaning they may also have different reactions to researchers. Indeed, human researchers vary in physical characteristics (e.g., scent, height, voice, posture) that may affect how primates respond to them (Salmi *et al.* 2021). Moreover, smaller primates, which experience greater predation, might benefit from a modified habituation approach relative to larger primates, which experience relatively minimal predation. That said, even amongst the great apes we observe variation in fear responses to novelty (Kalan *et al.* 2019). Perhaps even more pertinent for habituation, species experiencing higher rates of illegal hunting may need to be considered separately from those with relatively minimal rates (Williamson and Feistner 2003; Kasereka *et al.* 2006; Strier 2013). Unfortunately, these aspects have not been examined in detail due to the time-intensive nature of investigating such questions. At the very least, data on predation and illegal hunting could be used to tailor habituation strategies for the target species.

Risks Associated with Habituation

If observers are not neutral, the quality and reliability of data collected may vary, and researchers may want to consider the risks and benefits of habituation. Gazagne *et al.* (2020) argued that habituation benefits the conservation of vulnerable species and species less well known to western science and is a necessary step in the management of these species and for the collection of eco-ethological data. For many studies, some level of habituation may be essential (Green and Gabriel 2020). It does, however, also pose many risks (Table 1).

Table 1. The risks and benefits of habituation (adapted from Green and Gabriel 2020).

Threats	Benefits	Risks
Illegal hunting[1,2]	Protection from illegal hunters through researchers' presence.	Could habituate primates to a point where they will not flee from illegal hunters or may even approach them.
Disease transmission[3, 4, 5]	Researchers have increased capacity for health monitoring.	Increased likelihood of disease transmission.
Negative human-primate interactions[6]	-	Habituated primates may seek food from humans and direct aggression towards observers.
Stress[2]	Researchers can monitor stress levels both through behavioral observations and collection of fecal and urine samples.	Human presence may cause stress. Stress may change the behavior of primates and even force them to abandon home ranges or, individuals may choose to disperse inappropriately. Stress may also increase susceptibility to infections.
Waste management[7]	Researchers can ensure waste is properly managed.	Researchers create more waste.
Separation from group	Researchers can physically reunite group members that have been separated due to natural circumstances or researcher actions.[8]	Researchers may inadvertently distance group members from each other by their presence.
Injuries[1]	Researchers can treat injuries if interventions are deemed appropriate.	That injuries will happen. Primates are very resilient and may not need intervention. Researchers may intervene inappropriately.
Predator/prey dynamics[9]	Protection from predators.	Interrupts natural dynamics, reducing primate vigilance and changing predator behavior and ranging patterns.

[1]**Gruen** *et al.* (2013), [2]Jack *et al.* (2008), [3]Goldsmith (2005), [4]Williamson and Feistner (2011), [5]Lappan *et al.* (2020), [6]Matheson *et al.* (2006), [7]Bezanson *et al.* (2013), [8]Pruetz and Kante (2010), [9]LaBarge *et al.* (2020).

When habituating primates, primatologists are at risk of contact aggression from primates, especially during the early stages (Willamson and Feistner 2003). We are also at risk of disease transmission from primates, but the consequences of us transferring diseases to them are much worse and can be detrimental to entire populations (Wallis and Lee 1999). To mitigate these issues, it is crucial to create Standard Operating Procedures (SOPs) for habituation as well as for actual research post-habituation. These SOPs should include minimum distance to primates, management of waste products, avoiding physical contact, and carefully monitoring the health of researchers, including a protocol for staying home if unwell (Williamson and Feistner 2003).

The close contact between primatologists and primates can alter the latter's behaviors, such as predator avoidance, ranging patterns, and activity budgets, and, besides, its stress levels (Asquith 1989; Rasmussen 1991; Jack *et al.* 2008; Crofoot *et al.* 2010; Shutt *et al.* 2014). Early on in the habituation process, for example, primates may actively avoid researchers, thereby increasing the time spent traveling, imposing potential energetic costs, and inducing stress (Williamson and Feistner 2003). While primates may benefit from the presence of humans via the "human shield" effect (i.e., primates are shielded from the risk of predation; Berger 2007), over time, this might lead to reduced vigilance toward natural predators, which in turn affects our ability to investigate predator-prey interactions (Nowak *et al.* 2014). Accordingly, LaBarge *et al.* (2020) argue that direct observation of primates is not appropriate when researching behaviors that are risk-sensitive.

As discussed above, the process of habituation is complex and nuanced and the decision to habituate should not be taken lightly. Fortunately, remote methodologies that could serve as alternatives to habituation are numerous and improving. We review these alternative methods below.

Alternative Methods to Habituation

Over the last decade, there has been an explosion of research on and development of wildlife monitoring and conservation technologies, including camera trapping (O'Connell *et al.* 2010), passive acoustic monitoring (Deichmann *et al.* 2018), and unmanned aerial vehicles (UAVs) or drones (Koh and Wich 2012) (see also a review of these technologies by Piel *et al.* 2021). To date, drones are primarily used for large-scale remote mapping of habitats and aerial surveys of primates rather than nuanced data at the individual or group-level (e.g., Wich *et al.* 2015), therefore we will not discuss them further here (but see Koh and Wich 2012 and Piel *et al.* 2021 for reviews). Of course, remote technologies may also elicit neophobic or neophilic responses from primates (Kalan *et al.* 2019), which is also the case of habituation itself (see, for example, Gazagne *et al.* 2020), but these effects can be largely corrected by using a carefully designed study and analyses, for example accounting for variation in detection probabilities (Caravaggi *et al.* 2020). Additionally, recent advancements in stable isotope analysis (Crowley 2012) and genotyping methods, including meta-genomic sequencing (Arandjelovic and Vigilant 2018), have extended our ability to extract information about wild, non-habituated primates from non-invasively collected samples. This is significant considering that surveys of wild primates via long-standing methods, such as point transects, line transects, listening posts, etc., normally involve the deployment of a team with limited time available to rapidly assess the abundance and/or presence of individuals or groups (Campbell *et al.* 2016). These survey methods do not require habituating or even interacting with primates, but whilst in the field, these teams can also collect invaluable samples of feces, hair, feeding remains and other artefacts (e.g., tools) that primates discard, and permit monitoring of multiple groups simultaneously. New technologies and methodological advancements for non-invasive sampling provide novel avenues for primatologists to collect data on an array of research topics (Table 2). Considering the risks of habituation then, these modern methods reduce the need and justification for habituating more wild primates for a number of scientific questions. For those research questions that cannot be answered using remote monitoring technologies, whenever possible, scientists should prioritize studying already habituated primates and support sharing knowledge and data within the primatology community, rather than habituating new groups. Researchers should also always be cautious, however, about generalizing results from a few groups to the whole species—and this is true of both habituated and remote methods in primatology. Importantly, these new technologies come with a growing set of ethical concerns for practical applications in the field. Ethical concerns include, but are not limited to, these technologies and their data (a) when revealing detailed spatio-temporal information on the presence of species targeted by illegal hunters, (b) when recording data from humans (voice, images, videos, etc.), (c) when detecting, storing and managing these sensitive records, and (d) when working with local communities to obtain informed consent (Piel *et al.* 2021). Basic codes of conduct should be developed for these new technologies, as has been proposed for camera trap data (Sharma *et al.* 2020), and awareness of these ethical concerns should motivate standards to emerge with respect to each of these technologies and their application in conservation and wildlife research.

Remote Monitoring Tcchnologies

Camera trapping has become the most widely adopted remote monitoring technology in wildlife research and conservation (O'Connell *et al.* 2010; Steenweg *et al.* 2017). The success of camera trapping can be attributed to the relative cost-efficiency for data collection, the durability of the small devices for use in a variety of field conditions, and the low maintenance that is demanded of the researchers (Burton *et al.* 2015; Caravaggi *et al.* 2020). Commercial-camera traps are usually set to record photos or short videos, the latter requiring considerably more power and storage space but having the benefit of being able to record live action clips complete with audio. To date, camera traps have been successfully used to study the occurrence (Bowler *et al.* 2017), behavior (Luncz *et al.* 2017; Estienne *et al.* 2019), sociality (McCarthy *et al.* 2019), and ranging patterns (Head *et al.* 2012) of wild primates. The method is particularly helpful for behaviors that occur in predictable locations, such as specific topographical places (e.g., cave-use; Boyer Ontl and Pruetz 2020), for monitoring extractive foraging of rare resources (Boesch *et al.* 2017; Luncz *et al.* 2017; Estienne *et al.* 2019), and for observing behaviors that would be difficult or ethically problematic to observe directly (e.g., crop foraging behavior; Loría *et al.* 2021; Zak and Riley 2017). Camera traps can also provide valuable data on primate interactions with other species, including predators (Klailova *et al.* 2012). Moreover, as many primates can be individually identified using unique visual markings, facial and/or body coloration, camera traps allow primatologists to track individuals over time and space. These kinds of data can then be used to construct the group structure, association indices, or social network of wild, non-habituated populations (Galvis *et al.* 2014; McCarthy *et al.* 2019; Table 2).

Passive acoustic monitoring (PAM), like camera trapping, has also recently expanded in its use and application for animal behavior and conservation research (Deichmann *et al.* 2018; Sugai *et al.* 2019). Because this remote technology is newer than camera trapping, there are fewer options when it comes to autonomous recording units (ARUs) for collecting audio data in the field. That said, within the last decade technical advancements have meant that there are now a number of commercially available ARUs (Browning *et al.* 2017). The application of PAM to study wild primates is relatively new, but thus far it has provided information on the occurrence of species (Kalan *et al.* 2015), localizing individuals (Spillmann *et al.* 2015), changes in communicative behaviors (Duarte *et al.* 2018), territoriality and ranging patterns (Kalan *et al.* 2016) as well as detecting threats to wild populations (Astaras *et al.* 2017; Table 2). Similar to camera traps, PAM is a cost-effective method of collecting data on wild primates at large spatial and temporal scales, it requires minimal maintenance after the initial installation of devices and is an effective means by which primatologists can garner information on wild populations without having to habituate individuals to human observers. However, it is worth mentioning that validation studies demonstrating the reliability and accuracy of these remote methods have only

Table 2. Summary of remote methods and non-invasive sampling that can be used to research various topics of interest on wild primates without habituation.

Research Topic	**Remote Method(s)**	**Samples Needed**
Diet	Stable isotope analysis DNA metabarcoding Fecal macroanalyses Camera trapping	Hair, Feces, Videos Rare: Teeth, Bones
Behavior	Camera trapping Passive acoustic monitoring	Videos, Audio recordings
Communication	Camera trapping Passive acoustic monitoring	Videos, Audio recordings
Ranging & territoriality	Camera trapping Passive acoustic monitoring Genetic monitoring	Video/photos, Audio recordings, Feces
Predator-prey interactions	Camera trapping Passive acoustic monitoring Microbiome sequencing Fecal macroanalyses	Video/photos, Audio recordings, Faces
Social structure & demography	Camera trapping Genetic monitoring	Video/photos, Faces
Population dynamics*	Camera trapping Passive acoustic monitoring Genetic monitoring	Video/photos, Audio recordings, Feces
Health status	Microbiome sequencing Pathogen and viral sequencing Fecal microanalyses	Feces, hair

*Samples collected over a long time-period are needed to draw inferences.

been possible to test because of habituated primate groups (e.g., PAM: Kalan *et al.* 2016; camera traps: McCarthy *et al.* 2019).

Despite the relative success of camera trapping and passive acoustic monitoring in recent years, many difficulties remain in processing the large volumes of data produced by these remote monitoring methods. These data require substantial storage space, although cloud computing has made this more feasible. The data of interest must also be filtered out from all the data collected because remote monitoring devices will indiscriminately record all wildlife (and even non-wildlife, such as tree branches swaying in front of a camera trap lens). Automated, or more aptly named, semi-automated approaches to detecting species of interest have been developed for PAM, usually by commercial companies (e.g., Arbimon Acoustics <www.sieve-analytics.com/>; Kaleidoscope Pro Software <www.wildlifeacoustics.com/products/kaleidoscope-pro>). Some researchers have also teamed up with computer scientists to develop customized algorithms for detecting and classifying primate sounds (Heinicke *et al.* 2015; Clink *et al.* 2018). Customized approaches are often limited, however, in their application to data collected elsewhere, using different hardware with different recording parameters. There are also other, less technically demanding, methods that can help speed up PAM data processing, such as Long Term Spectral Average visualization (Wiggins *et al.* 2010). With respect to camera trap data, some progress has been made in developing automated methods for detecting species of interest from photo captures (Yu *et al.* 2013; Norouzzadeh *et al.* 2018), but few such methods exist for video data. Instead, camera trapping has overwhelmingly benefited from enlisting the help of citizen or community science projects, where the public are asked to help watch or look at the data to find the species and information of interest. Some of these projects have been running for years and enjoy worldwide participation thanks to online citizen science platforms such as Zooniverse (e.g., Chimp&See: <www.chimpandsee.org>). For camera trap video data of wild primates, semi-automated methods for processing data have enabled researchers to glean more detailed information, in particular facial recognition of individuals (Loos and Ernst 2013; Crunchant *et al.* 2017; Schofield *et al.* 2019). Data sets from habituated primate groups where individuals were known *a priori* were, however, used to develop and test these algorithms; therefore, their ability to aid researchers working solely with non-habituated primates remains difficult to ascertain. Despite these challenges, advancements in machine learning techniques are continuously improving automated approaches to data processing and there is no doubt that further progress will be made in the coming years. An important caveat though is that if researchers are using the above technology in areas used by people, then the technology should be used in a socially responsible way (e.g., acquiring permission, explaining the purpose of the research and use of technology, disclosing the locations where technologies will be used; safeguarding peoples' privacy; and encouraging community participation (Sharma *et al.* 2020; Sandbrook *et al.* 2021).

Critics of remote monitoring may argue that if we let remote monitoring devices do all the work, the importance of local people and role of field assistants with respect to carrying out research activities may be diminished. However, the careful installation and maintenance of these devices, both ARUs and camera traps, require human attention and expertise. Local collaborators are essential for identifying optimal recording locations, periodically collecting the data, and ensuring devices are powered and functioning optimally. Researcher expertise is still, therefore, critical for data collection even when primates are not habituated. This is important considering that the existence of long-term research sites, which is dependent upon human presence, can help protect wild primate populations (Campbell *et al.* 2011; Piel *et al.* 2015). Moreover, whilst installing and maintaining devices, researchers can collect non-invasive samples left behind by the primates which in turn provide an abundance of information.

Non-invasive Sampling

As wild primates move throughout their home range or territory, they leave behind a variety of signs in the environment indicating their presence (Ross and Reeve 2003). These signs include feces, feeding remains, and artefacts, such as discarded tools, or old sleeping sites and many more (Arandjelovic and Vigilant 2018; Ross and Reeve 2003; Stewart *et al.* 2018). These samples can be collected non-invasively, i.e., without making contact or even being in the presence of a primate. Researchers have applied state-of-the-art analytical methods on such samples to extract detailed data on the lives of wild primates (e.g., Archie and Tung 2015; de Mesquita *et al.* 2021; Fahy *et al.* 2013; Hagemann *et al.* 2018).

One of the most successful applications of genotyping outside of human-related research is that for wildlife monitoring and conservation (Frankham *et al.* 2020). As sequencing technology has become exponentially more cost-efficient over the years, it has permitted genotyping studies of non-invasive animal samples to become a standard monitoring and survey methodology, including for wild primates (Arandjelovic and Vigilant 2018). Intestinal cells are shed in the fecal matter of wild primates where the DNA present in these cells can be extracted, amplified and sequenced to identify the individual and its sex (Arandjelovic and Vigilant 2018). The fresher the sample, the more likely the DNA in the feces will be of good quality and quantity for the analysis. These individually identified fecal samples can then be used to reconstruct association indices, group structure and ranging patterns (Arandjelovic *et al.* 2010; McCarthy *et al.* 2015), and even population dynamics over the long term, including immigration, emigration, group formation and dissolution (Hagemann *et al.* 2018). Although feces are the most common material used, food remains, hair, urine and artefacts can also be used as good sources of DNA (Arandjelovic and Vigilant 2018; Stewart *et al.* 2018).

Fecal samples can also provide important information regarding the health status of primate populations. Microscopic analyses can be used to identify gastrointestinal pathogens present in samples (Gillespie 2006) or with the aid of targeted DNA sequencing (e.g., malaria parasites; De Nys *et al.* 2017). Primatologists can further combine genotyping of fecal samples to permit identifying and monitoring individuals over time. Microbiome sequencing of fecal samples can also provide data on pathogens in wild primates (Stumpf *et al.* 2016), which is a relatively novel technique for wildlife research due to recent advancements in high throughput or next generation sequencing for genomic research (Cullen *et al.* 2020).

More commonly, microbiome sequencing and DNA metabarcoding of fecal samples are used to assess the diversity and composition of the gut microbiota (Stumpf *et al.* 2016; Dunn *et al.* 2020). Recent studies have illustrated the potential for microbiome sequencing to reveal new data on the evolution and ecology of microbiota and their implications for primate nutrition, diet, health, and sociality (Archie and Tung 2015; Stumpf *et al.* 2016; Clayton *et al.* 2018; Dunn *et al.* 2020). For example, a recent study on chimpanzee microbiomes across Equatorial Africa demonstrate that the microbiota of some populations may be influenced by gaining access to particular food resources aided by tool use (de Mesquita *et al.* 2021). Microbiome research in field primatology has only scratched the surface of its possible uses (Dunn *et al.* 2020).

Another methodological advancement used to study the diets of wild primate populations using non-invasive sampling is stable isotope analysis (Sandberg *et al.* 2012). This analysis relies on the fact that organic samples, such as the tissues of organisms, have particular isotopic signatures based on the amount of stable isotopes accumulated, which can then be used to draw inferences regarding the diet, lifestyle and geoprovenance of samples (Sponheimer *et al.* 2009; Crowley 2012). In order to draw such inferences, however, samples can only be evaluated by comparing ratios of stable isotopes against a backdrop of environmental and geographic baselines in isotope values (Crowley *et al.* 2011; Oelze *et al.* 2016). In primatology, non-invasively collected hair samples are most often used to study the diet of primates in recent time. Here, collagen in the hair accumulates stable isotopes of carbon and nitrogen which can be used to make inferences regarding the diet, such as what kinds of food items constitute the diet of a wild population (Crowley *et al.* 2011; Fahy *et al.* 2013; van Casteren *et al.* 2018), or if primates are experiencing nutritional stress (Wessling *et al.* 2019). With hair samples collected from non-habituated primates, one does have to consider how to avoid potential pseudoreplication, i.e., multiple hairs from the same individual (Mundry and Oelze 2016). This can be minimized by sampling at locations far apart from one another, sampling from individually-specific locations (e.g., sleeping nests), or combining isotope analyses with genotyping of individuals (Mundry and Oelze 2016). Bones and teeth are also a rich source for investigating additional stable isotope signatures over longer timescales (Sponheimer *et al.* 2009; Crowley 2012); however, such samples are expected to be rare when researching non-habituated primates.

Recommendations

With all the methodological advances and the risks of habituation mentioned above, it is time for researchers to reconsider when habituation is necessary. This may be a difficult decision, however, and we understand that many primatologists may argue that habituation is still necessary for some research questions, such as some forms of communication and subtle behaviors or social interactions (Williamson and Feistner 2013). To help researchers determine whether or not to habituate, we have created a simple decision tree (Fig. 1). In 2013, Gruen *et al.* raised concerns regarding habituation of great apes and created a decision tree to help researchers determine when to habituate. Building on their work, we have expanded upon the decision tree concept by including alternative methods and the need for an exit strategy, as well as ensuring it is applicable to all primate species.

First and foremost, it is of the utmost importance to ensure that habituation is of benefit to the primates in question, and preferably the whole ecosystem, through research that results in greater protection and increased awareness. While there tends to be a great division between fundamental research and applied research in academia (Caro 2007), such a divide should not exist for conservation work. If, therefore, researchers wish to carry out studies that require habituation, they should also include an applied component, which ultimately contributes to the conservation and protection of the species (Nekaris and Nijman 2013; Riley and Bezanson 2018).

Second, when primatologists decide that habituation is warranted, they should also be keenly aware of the difficulties in finding a balance between full habituation and over-habituation and pay careful attention to the reactions of habituated primates towards humans. Ultimately, researchers should recognize that full habituation may not be necessary for some research questions, and, hence, we recommend prioritizing the use of observational techniques that necessitate only minimal or partial habituation stages whenever possible (Gazagne *et al.* 2020).

Third, all research projects involving habituated primates should have exit strategies in place. Defined as "plans to end involvement in an endeavor once certain criteria are met or conditions reached," exit strategies are often neglected in research and conservation (Ruiz *et al.* 2020, p.203) but they should be high priority in a project involving the habituation of wild primates. A plan to safeguard the wellbeing of habituated primates or groups of primates

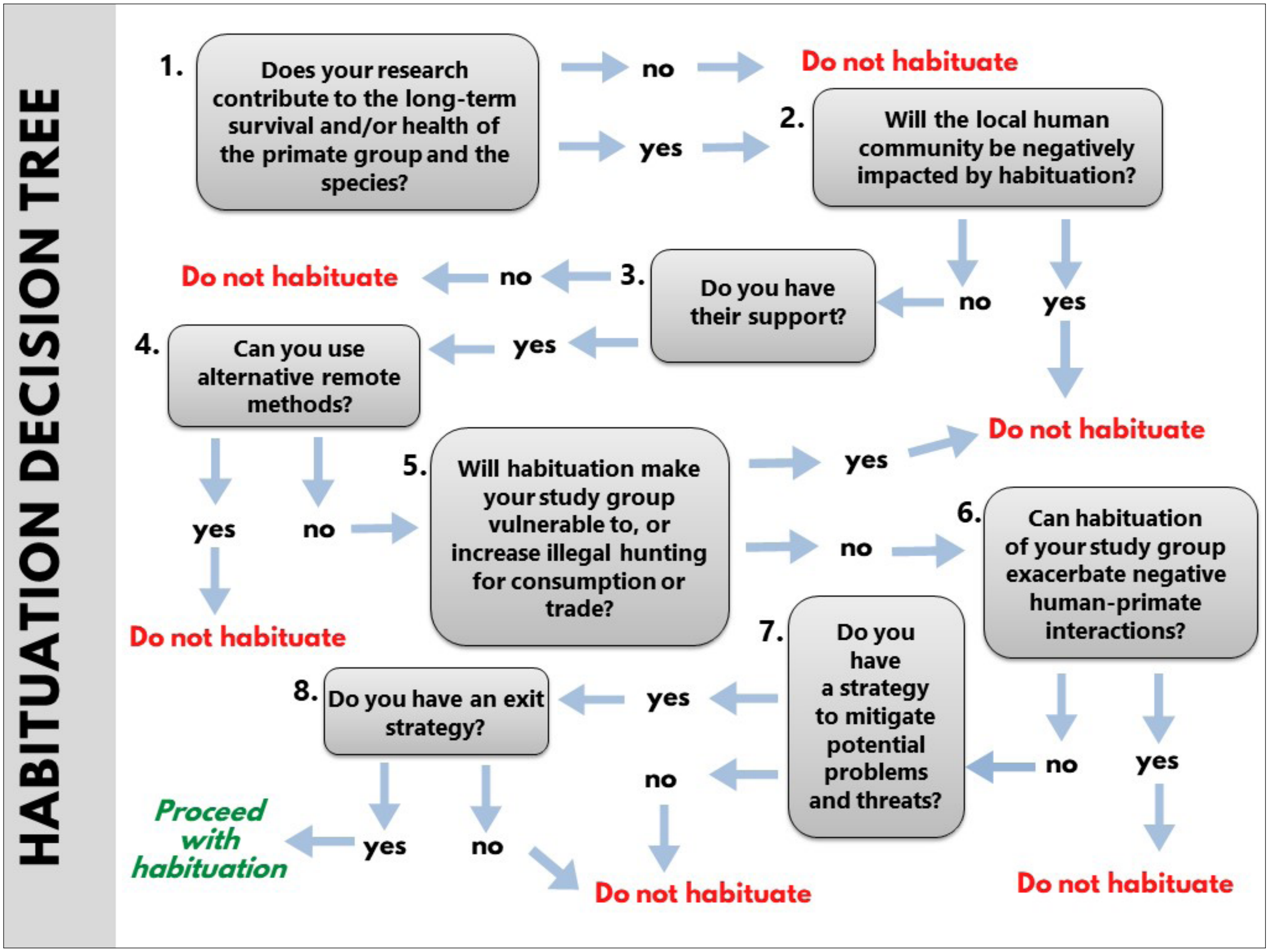

Figure 1. A decision tree to assist primatologists in assessing their need to habituate wild primates (with inspiration from Gruen *et al.* 2013).

when a research project terminates should be included in a project's exit strategy. Although this may be a requirement to receive ethics approval, not all countries require animal ethics approval prior to research, and we therefore urge researchers and practitioners to also consider it themselves. If there are no plans for researchers to return to the study site, they should decrease the number of people following the groups as well as decreasing the frequency of follows to encourage the primates to become less accustomed to daily encounters with researchers. Further safeguards may be an agreement with local communities, NGOs and/or local law enforcement agencies to maintain a presence in the field to monitor the habituated primates. Importantly, such a strategy needs to be considered in advance of habituation and not postponed until the termination of that project's funding and a research team's imminent departure. Failure to exit from a project responsibly will also impact local people who may have been employed by the project on a long-term basis. Abrupt unemployment may lead to resentment among those affected, which they may direct at the habituated primate groups. For further information on how to plan for a sustainable exit, see <http://awsassets.panda.org/downloads/Sustainability_and_Exit_Strategies_March_2017.pdf>.

All research and conservation projects should have a contingency plan for unexpected departures of project staff, something the COVID-19 pandemic has reinforced. Unexpected departures can occur for a variety of reasons such as security concerns, a change in political circumstances, rescinding of research permits, and major disease outbreaks (e.g., Ebola) and global pandemics (e.g., COVID-19). If a project is being terminated, then local staff should be assisted in finding further employment where possible. If the habituated species is a target of illegal hunting for its parts or for the pet trade, then there should be safeguards in place to ensure that the habituated group(s) is not decimated by hunting. Providing funding for local agencies to patrol and monitor the habituated groups after research ceases is an example.

We also recommend that the inclusion of exit strategies for both planned terminations and abrupt departures of research teams from sites where primates are habituated for study should be mandatory in all ethics protocols and be requested by donors in any funding applications. It would also be prudent to secure a minimum number of years of funding before initiating habituation although we understand this can be quite difficult in practice, hence why donors should also consider longer term investments for projects involving habituated research groups.

Conclusions

In the past two decades, primatologists have increasingly begun to consider the effects habituation has on their study subjects and the reliability of the data they collect. One outcome of these efforts is the broader recognition that habituation is a dynamic process in wild primates that progresses in stages. We advocate that researchers continue to monitor the effects of habituation even after "full" habituation has been achieved, in particular to be wary of the risks associated with over-habituation, disease transmission and the disruption of natural behaviors. More importantly, however, we ask that primatologists reconsider using habituation as the default first step in field research, and instead (a) carefully decide whether habituation should be attempted in the first place, and, if yes, (b) assess whether minimal stages of habituation are sufficient for the questions being asked, c) have a detailed plan of action where individuals are monitored for potential stress and behavior disruptions as a result of habituation, and d) have an exit strategy in place for the termination of the project, whether planned or not. When deciding whether to habituate, we have provided researchers with concrete questions they should ask themselves while weighing potential benefits and risks. Importantly, we recommend using alternative remote methods for collecting data whenever possible before resorting to habituation. These methods have improved substantially in the last decade and can often provide unprecedented datasets on the behavior, ecology and health status of wild primates. In the midst of the continuing COVID-19 pandemic, the risks of zoonotic disease transmission are increasingly evident; we, therefore, have a responsibility to the wild primates and the human populations living next to them to mitigate any and all risks associated with habituating primate groups for research. For this, and the many reasons we have described above, we hope that primatologists will reconsider habituation as the default method in field research.

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Literature Cited

Alcayna-Stevens, L. 2016. Habituating field scientists. *Soc. Stud. Sci.* 46: 833–853.

Allan, A. T. L., A. L. Bailey and R. A. Hill. 2020. Habituation is not neutral or equal: individual differences in tolerance suggest an overlooked personality trait. *Sci. Adv.* 6: eaaz0870.

Ampumuza, C. and C. Driessen. 2020. Gorilla habituation and the role of animal agency in conservation and tourism development at Bwindi National Park, southwestern Uganda. *Environ. Plan. A: Nature and Space*. doi.org/10.1177%2F2514848620966502

Arandjelovic, M., J. Head, H. S. Kühl, C. Boesch, M. M. Robbins, F. Maisels and L. Vigilant. 2010. Effective non-invasive genetic monitoring of multiple wild western gorilla groups. *Biol. Conserv.* 143: 1780–1791.

Arandjelovic, M. and L. Vigilant. 2018. Non-invasive genetic censusing and monitoring of primate populations. *Am. J. Primatol*. 80: e22743.

Archie, E. A. and J. Tung. 2015. Social behavior and the microbiome. *Curr. Opin. Behav. Sci.* 6: 28–34.

Asquith, P. J. 1989. Provisioning and the study of free-ranging primates: history, effects and prospects. *Am. J. Phys. Anthropol.* 32: 129–158.

Astaras, C., J. M. Linder, P. Wrege, R. D. Orume and D. W. Macdonald. 2017. Passive acoustic monitoring as a law enforcement tool for Afrotropical rainforests. *Front. Ecol. Environ*. 15: 233–234.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* 3: 620–623.

Bertolani, P. and C. Boesch, C. 2008. Habituation of wild chimpanzees (*Pan troglodytes*) of the south group at Tai Forest, Cote d'Ivoire: empirical measure of progress. *Folia Primatol.* 79: 162–171.

Bezanson, M., R. Stowe and S. M. Watts. 2013. Reducing the ecological impact of field research. *Am. J. Primatol.* 75: 1–9.

Bingham, H. C. 1932. *Gorillas in a Native Habitat*. Carnegie Institution, Washington, DC.

Boesch, C., A. K. Kalan, A. Agbor, M. Arandjelovic, P. Dieguez, V. Lapeyre and H. S. Kühl. 2017. Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *Am. J. Primatol.* 79: e22613.

Bowler, M. T., M. W. Tobler, B. A. Endress, M. P. Gilmore and M. T. Anderson. 2017. Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps. *Remote. Sens. Ecol. Conserv.* 3: 146–157.

Boyer Ontl, K. and J. D. Pruetz. 2020. Mothers frequent caves: lactation affects chimpanzee (*Pan troglodytes* *verus*) cave use in southeastern Senegal. *Int. J. Primatol.* 41: 916–935.

Browning, E., R. Gibb, P. Glover-Kapfer and K. E. Jones. 2017. Passive Acoustic Monitoring in Ecology and Conservation. *WWF Conservation Technology Series* 1(2): 74pp. WWF-UK, Woking, UK.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenwig, J. T. Fisher, E. Bayne and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* 52: 675–685.

Campbell, G., J. Head, J. Junker and K. A. I. Nekaris. 2016. Primate abundance and distribution: background concepts and methods. In: *An Introduction to Primate Conservation*, S. A. Wich and A. J. Marshall (eds.), pp.79–110. Oxford University Press, Oxford, UK.

Campbell, G., H. Kühl, A. Diarrassouba and C. Boesch. 2011. Long-term research sites as refugia for threatened and over-harvested species. *Biol. Lett.* 7: 723–726.

Candea, M. 2013. Habituating meerkats and redescribing animal behaviour science. *Theory. Cult. Soc.* 30: 105–128.

Caravaggi, A., A. C. Burton, D. Clark, T. Fisher, A. A. Grass, S. E. Green, C. Hobaiter, T. Hofmeester, A. K. Kalan, D. Rabaiotti and D. Rivet. 2020. A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conserv. Sci. Pract*. 2: e239.

Caro, T. 2007. Behavior and conservation: a bridge too far? *Trends. Ecol. Evol.* 22: 394–400.

Carpenter, C. R. 1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psychol. Monogr.* 10: 1–168.

Cheney, D. L. and R. M. Seyfarth. 1990. *How Monkeys See the World*. University of Chicago Press, Chicago, IL.

Clayton, J. B. *et al.* 2018. The gut microbiome of nonhuman primates: lessons in ecology and evolution. *Am. J. Primatol.* 80: e22867.

Clink, D. J., M. C. Crofoot and A. J. Marshall, A. J. 2018. Application of a semi-automated vocal fingerprinting approach to monitor Bornean gibbon females in an experimentally fragmented landscape in Sabah, Malaysia. *Bioacoustics* 28(3): 193–209.

Crofoot, M. C., T. D. Lambert, R. Kays and M. C. Wikelski, M. C. 2010. Does watching a monkey change its behavior? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Anim. Behav.* 80: 475–480

Crowley, B. E. 2012. Stable isotope techniques and applications for primatologists. *Int. J. Primatol.* 3: 673–701.

Crowley, B. E. *et al.* 2011. Explaining geographical variation in the isotope composition of mouse lemurs (*Microcebus*). *J. Biogeogr.* 38: 2106–2121.

Crunchant, A.-S., M. Egerer, A. Loos, T. Burghardt, K. Zuberbühler, K. Corogenes, V. Leinert, L. Kulik and H. S. Kühl. 2017. Automated face detection for occurrence and occupancy estimation in chimpanzees. *Am. J. Primatol.* 79: e22627.

Cullen, C. M. *et al.* 2020. Emerging priorities for microbiome research. *Front. Microbiol.* 11: 136.

De Mesquita, C. P. B., L. M. Nichols, M. J. Gebert and C. Vanderburgh. 2021. Structure of chimpanzee gut microbiomes across tropical Africa. *mSystems* 6(3): e01269–20.

De Nys, H. M., T. Löhrich, D. Wu, S. Calvignac-Spencer and F. H. Leendertz. 2017. Wild African great apes as natural hosts of malaria parasites: current knowledge and research perspectives. *Prim. Biol.* 4: 47–59.

Deichmann, J. L. *et al.* 2018. It's time to listen: there is much to be learned from the sounds of tropical ecosystems. *Biotropica* 50(5): 713–718.

Doran-Sheehy, D. M., A. M. Derby, D. Greer and P. Mongo. 2007. Habituation of western gorillas: the process and factors that influence it. *Am. J. Primatol.* 69(12): 1354–1369.

Duarte, M. H. L., M. C. Kaizer, R. J. Young, M. Rodrigues and R. S. Sousa-Lima. 2018. Mining noise affects loud call structures and emission patterns of wild black-fronted titi monkeys. *Primates* 59: 89–97.

Dunn, R. R., K. R. Amato, E. A. Archie, M. Arandjelovic, A. N. Crittenden and L. M. Nichols. 2020. The internal, external and extended microbiomes of hominins. *Front. Ecol. Evol.* 8: 1–12. doi.org/10.3389/fevo.2020.00025

Emlen, J. T. Jr. 1960. Current field studies of gorillas. *Curr. Anthropol.* 1: 332pp.

Estienne, V., B. Robira, B., R. Mundry, T. Deschner and C. Boesch. 2019. Acquisition of a complex extractive technique by the immature chimpanzees of Loango National Park, Gabon. *Anim. Behav.* 147: 61–76.

Fahy, G. E., M. Richards, J. Riedel, J.-J. Hublin and C. Boesch. 2013. Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. *Proc. Natl. Acad. Sci. USA* 110(15): 5829–5833.

Fedigan, L. M. 2010. Ethical issues faced by field primatologists: asking the relevant questions. *Am. J. Primatol.* 72: 754–771.

Frankham, R., J. D. Ballou and D. A. Briscoe. 2002. *Introduction to Conservation Genetics.* Cambridge University Press, Cambridge, UK.

Galvis, N., A. Link and A. Di Fiore. 2014. A novel use of camera traps to study demography and life history in wild animals: A case study of spider monkeys (*Ateles belzebuth*). *Int. J. Primatol.* 35: 908–918.

Gazagne, E., A. Hambuckers, T. Savini, P. Poncin, M.-C. Huynen and F. Brotcorne. 2020. Toward a better understanding of habituation process to human observer: a statistical approach in *Macaca leonina* (Primates: Cercopithecidae). *Raffles Bull. Zool*. 68: 735–749,

Gillespie, T. R. 2006. Noninvasive assessment of gastrointestinal parasite Infections in free-ranging primates. *Int. J. Primatol.* 27: 1129–1143.

Goldsmith, M. L. 2005. Habituating primates for field study: ethical considerations for African great apes. In: *Biological Anthropology and Ethics: From Repatriation to Genetic Identity*, T. R. Turner (ed.), pp.49–64. State University of New York Press, Albany, NY.

Green, V. M. and K. I. Gabriel. 2020. Researchers' ethical concerns regarding habituating wild-nonhuman primates and perceived ethical duties to their subjects: results of an online survey. *Am. J. Primatol.* 82: e23178.

Gruen, L., A. Fultz and J. D. Pruetz. 2013. Ethical issues in African great ape field studies. *ILAR J.* 54(1): 24–32.

Hagemann, L., C. Boesch, M. M. Robbins, M. Arandjelovic, T. Deschner, M. Lewis, G. Froese and L. Vigilant. 2018. Long-term group membership and dynamics in a wild western lowland gorilla population (*Gorilla gorilla gorilla*) inferred using non-invasive genetics. *Am. J. Primatol.* 80: e22898.

Hanson, K. T. and E. P. Riley. 2018. Beyond neutrality: the human–primate interface during the habituation process. *Int. J. Primatol.* 39: 852–877.

Head, J. S., M. M. Robbins, R. Mundry, L. Makaga, and C. Boesch. 2012. Remote video-camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. *J. Trop. Ecol.* 28: 571–583.

Heinicke, S., A. K. Kalan, O. J. J. Wagner, R. Mundry, H. Lukashevich and H. S. Kühl. 2015. Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods Ecol. Evol.* 6: 753–763.

Jack, K. M., B. B. Lenz, E. Healan, S. Rudman, V. A. M. Schoof and L. M. Fedigan. 2008. The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *Am. J. Primatol.* 70: 490–494.

Kalan, A. K., R. Mundry, O. J. J. Wagner, S. Heinicke, C. Boesch and H. S. Kühl. 2015. Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. *Ecol. Indic.* 54: 217–226.

Kalan, A. K., R. Piel, R. Mundry, R. Wittig C. Boesch and H. S. Kühl. 2016. Passive acoustic monitoring reveals group ranging and territory use: a case study of wild chimpanzees (*Pan troglodytes*). *Front. Zool.* 13: 34.

Kalan, A.K. *et al.* 2019. Novelty response of wild African apes to camera traps. *Curr. Biol.* 29: 1211–1217.

Kasereka, B., J. B. B. Muhigwa, C. Shalukoma and J. M. Kahekwa. 2006. Vulnerability of habituated Grauer's gorilla to poaching in the Kahuzi-Biega National Park, DRC. *Afr. Study Monogr*. 27(1): 15–26.

Klailova, M., C. Casanova, P. Henschel, P. Lee, F. Rovero and A. Todd. 2012. Non-human predator interactions with wild great apes in Africa and the use of camera traps to study their dynamics. *Folia Primatol.* 83: 312–328.

Koh, L. P. and S. A. Wich. 2012. Dawn of drone ecology: low-cost autonomous aerial vehicles for conservation. *Trop. Conserv. Sci.* 5:121–132.

Labarge, L. R., R. A. Hill, C. M. Berman, S. W. Margulis and A. T. L. Allan 2020. Anthropogenic influences on anti-predator behavior and implications for research and conservation. *Am. J. Primatol.* 82: e23087.

Lappan, S., S. Malaivijitnond, S. Radhakrishna, E. P. Riley and N. Ruppert, N. 2020. The human-primate interface in the new normal: challenges and opportunities for primatologists in the COVID-19 era and beyond. *Am. J. Primatol*. 82: e23176.

Loría, L. I., S. Gallina, S., J. C. Serio Silva, and E. P. Riley. 2021. Farmers' perceptions of white-faced capuchins (*Cebus imitator*) and human–primate coexistence in rural communities of Renacimiento District, Chiriquí Province, Panama. *Int. J. Primatol*. doi.org/10.1007/s10764-021-00244-0

Loos, A. and A. Ernst. 2013. An automated chimpanzee identification system using face detection and recognition. *J. Image. Video. Proc.* (49). https://doi.org/10.1186/1687-5281-2013-49

Luncz, L. V., M, S. Svensson, M. Haslam, S. Malaivijitnond, T. Ptoffitt and M. Gumert. 2017. Technological response of wild macaques (*Macaca fascicularis*) to anthropogenic change. *Int. J. Primatol.* 38: 872–880.

Matheson, M. D., L. K. Sheeran, J. H. Li and R. S. Wagner. 2006. Tourist impact on Tibetan macaques. *Anthrozoös* 19(2):158–168.

McCarthy, M. S. *et al.* 2019. Camera traps provide a robust alternative to direct observations for constructing social networks of wild chimpanzees. *Anim. Behav.* 157: 227–238.

McCarthy, M. S., J. D. Lester, E. J. Howe, M. Arandjelovic, C. B. Stanford and L. Vigilant. 2015. Genetic censusing identifies an unexpectedly sizeable population of an endangered large mammal in a fragmented forest landscape. *BMC Ecol.* 15: 21. https://doi.org/10.1186/s12898-015-0052-x

McDougall, P. 2012. Is passive observation of habituated animals truly passive? *J. Ethol.* 30:219–223.

McKinney, T. 2014. Species-specific responses to tourist interactions by white-faced capuchins (*Cebus imitator*) and mantled howlers (*Alouatta palliata*) in a Costa Rican wildlife refuge. *Int. J. Primatol.* 35: 573–589.

Mundry, R. and V. M. Oelze. 2016. Who is who matters—the effects of pseudoreplication in stable isotope analyses. *Am. J. Primatol.* 78: 1017–1030.

Narat, V., F. Pennec, B. Simmen, J. C. B., Ngawolo and S. Krief. 2015. Bonobo habituation in a forest-savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context. *Primates* 56: 339–349.

Nekaris, K. A. I. and V. Nijman. 2013. Complex and heterogeneous ethical structures in field primatology. In: *Ethics in the Field: Contemporary Challenges*, J. McClancy and A. Fuentes (eds), pp.108–123. Berghahn, New York.

Norouzzadeh, M. S., A. Nguyen, M. Kosmala, A. Swanson, M. S. Palmer, C. Packer, and J. Clune. 2018.

Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. *Proc, Natl. Acad. Sci. USA* 115: E5716–E5725.

Nowak, K., A. le Roux, A., S. A. Richards, C. P. J. Scheijen and R. A. Hill. 2014. Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* 25: 1199–1204.

O'Connell, A. F., J. D. Nichols and K. U. Karanth, K. U. (eds.). 2010. *Camera Traps in Animal Ecology: Methods and Analyses.* Springer, New York.

Oelze, V. M. *et al.* 2016. Comparative isotope ecology of African great apes. *J. Hum. Evol.* 101: 1–16.

Piel, A. K., A. Lenoel, C. Johnson and F. A. Stewart. 2015. Deterring poaching in western Tanzania: the presence of wildlife researchers. *Glob. Ecol. Conserv*. 3: 188–199.

Piel, A. K., A. Crunchant, I. E. Knot, C. Chalmers, P. Fergus, M. Mulero-Pázmány and S. A. Wich 2021. Noninvasive technologies for primate conservation in the 21st century. *Int. J. Primatol.* doi.org/10.1007/s10764-021-00245-z

Pruetz, J. D. and D. Kante. 2010. Successful return of a wild infant chimpanzee (*Pan troglodytes verus*) to its natal group after capture by poachers. *Afr. Primates* 7(1): 35–41.

Rasmussen, D. R. 1991. Observer influence on range use of *Macaca arctoides* after 14 years of observation? *Lab. Prim. Newsl.* 30(3): 6–11.

Riley, E. P. and M. Bezanson. 2018. Ethics of primate fieldwork: toward an ethically engaged primatology. *Ann. Rev. Anthropol.* 47: 493–512.

Ross, C. and N. Reeve. 2003. Survey and census methods: population distribution and density. In: *Field and Laboratory Methods in Primatology*, J. M. Setchell and D. J. Curtis (eds.), pp.33–49. Cambridge University Press, Cambridge, UK.

Ruiz, C. R. R., L. I. Vilchis and R. R. Swaisgood. 2020. Exit strategies for wildlife conservation: why they are rare and why every institution needs one. *Front. Ecol. Environ.* 18: 203–210.

Salmi, R., Jones, C. E. and Carrigan, J. 2021. Who is there? Captive western gorillas distinguish human voices based on familiarity and nature of previous interactions. *Anim. Cogn.* doi.org/10.1007/s10071-021-01543-y

Sandberg, P. A., J. E. Loudon and M. Sponheimer. 2012. Stable isotope analysis in primatology: a critical review. *Am. J. Primatol.* 74: 969–989.

Sandbrook, C., D. Clarke, T. Toivonen, S. Simlai, S. O'Donnell, J. Cobbe and W. Adams. 2021. Principles for the socially responsible use of conservation monitoring technology and data. *Conserv. Sci. Pract.* hdoi.org/10.1111/csp2.374

Schofield, D. P., A. Nagrani, A. Zisserman, M. Hayashi, T. Matsuzawa, D. Biro and S. Carvalho. 2019. Chimpanzee face recognition from videos in the wild using deep learning. *Sci. Adv.* 5: eaaw0736.

Sharma, K., M. Fiechter, T. George, J. Young, J. S. Alexander, A. Bijoor, K. Suryawanshi. and C. Mishra. 2020. Conservation and people: towards an ethical code of conduct for the use of camera traps in wildlife research. *Ecol. Sol. Eviden.* doi.org/10.1002/2688-8319.12033

Shutt, K., M. Heistermann, A. Kasim, A. Todd, B. Kalousova, I. Profosouva, K. Petrzelkova, T. Fuh, J.-F. Dicky, J.-B. Bopalanzognako and J. M. Setchell. 2014. Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. *Biol. Conserv.* 172: 72–79.

Souza-Alves, J. P. and S. F. Ferrari. 2010. Responses of wild titi monkeys, *Callicebus coimbrai* (Primates, Platyrrhini: Pitheciidae), to the habituation process. *Zoologia* 27: 861–866.

Spillmann, B., M. A. van Noordwijk, E. P. Willems, E. P., T. M. Seia, U. Wiplfi and C. P. van Schaik. 2015. Validation of an acoustic location system to monitor Bornean orangutan (*Pongo pygmaeus wurmbii*) long calls. *Am. J. Primatol.* 77: 767–776.

Sponheimer, M., D. Codron, B. H. Passey, D. J. de Ruiter, T. E. Cerling and J. A. Lee-Thorp. 2009. Using carbon isotopes to track dietary change in modern, historical, and ancient primates. *Am. J. Phys. Anthropol.* 140: 661–670.

Steenweg, R. *et al.* 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Front. Ecol. Environ.* 15: 26–34.

Stewart, F. A., A. K. Piel, L. Luncz, J. Osborn, Y. Li, B. H. Hahn, and M. Haslam, 2018. DNA recovery from wild chimpanzee tools. *PLoS One* 13: e0189657.

Strier, K. B. 2010. Long-term field studies: positive impacts and unintended consequences. *Am. J. Primatol.* 72: 772–778.

Strier, K. 2013. Are observational field studies of wild primates really non-invasive? In: *Ethics in the Field: Contemporary Challenges*, J. MacClancy and A. Fuentes (eds.), pp.67–83. Berghahn Books, New York.

Stumpf, R. M., A. Gomez, K. R. Amato, C. J. Yeoman, J. D. Polk, B. A. Wilson, K. E. Nelson, B. A. White and S. R. Leigh. 2016. Microbiomes, metagenomics, and primate conservation: new strategies, tools, and applications. *Biol. Conserv.* 199: 56–66.

Sugai, L. S. M., T. S. F. Silva, J. W. Ribeiro and D. Llusia. 2019. Terrestrial passive acoustic monitoring: review and perspectives. *BioScience* 69: 15–25.

Tutin, C. E. and M. Fernandez. 1991. Responses of wild chimpanzees and gorillas to the arrival of primatologists: behavior observed during habituation. In: *Primate Responses to Environmental Change*, H. O. Box (ed.), pp.187–197. Springer, Dordrecht.

Van Casteren, A. *et al.* 2018. Food mechanical properties and isotopic signatures in forest versus savannah dwelling eastern chimpanzees. *Nature Comm. Biol.* 1: 109. doi.org/10.1038/s42003-018-0115-6

Vicente-Alonso, S., L. Sánchez-Sánchez and S. A. Solas. 2021. On the way to systemize habituation: a protocol to minimize the effects of observer presence on wild groups of *Leontocebus lagonotus*. *Primates* 62: 407–415.

Wallis, J. and R. D. Lee, R. D. 1999. Primate conservation: the prevention of disease transmission. *Int. J. Primatol.* 20: 803–826.
Webb, S. E. and M. B. McCoy. 2014. Ecotourism and primate habituation: behavioral variation in two groups of white-faced capuchins (*Cebus capucinus*) from Costa Rica. *Rev. Biol. Trop.* 62: 909–918.
Wessling, E. G., V. M. Oelze, V. M., Eshuis, H., J. D. Pruetz and H. S. Kühl. 2019. Stable isotope variation in savanna chimpanzees (*Pan troglodytes verus*) indicate avoidance of energetic challenges through dietary compensation at the limits of the range. *Am. J. Phys. Anthropol.* 168: 665–675.
Wich, S., D. Dellatore, Houghton, M., R. Ardi and L. P, Koh. 2015. A preliminary assessment of using conservation drones for Sumatran orang-utan (*Pongo abelii*) distribution and density. *J. Unmanned Veh. Syst.*, 4: 45–52.
Wiggins, S. M., M. A. Roch and J. A. Hildebrand. 2010. TRITON software package: Analyzing large passive acoustic monitoring data sets using MATLAB. *J. Acoust. Soc. Am.* 128(4): 2299.
Williamson, E. A. and A. T. C. Feistner. 2003. Habituating primates: processes, techniques, variables and ethics. In: *Field and Laboratory Methods in Primatology*, J. M. Setchell and D. Curtis. (eds), pp.33–49. Cambridge University Press, Cambridge, UK.
Yu, X., J. Wang, R. Kays, P. A, Jansen, T. Wank and T. Huang. et2013. Automated identification of animal species in camera trap images. *EURASIP J. Image. Video. Process*. 52. https://doi.org/10.1186/1687-5281-2013-52
Zak, A. A. and E. P. Riley. 2017. Comparing the use of camera traps and farmer reports to study crop feeding behavior of moor macaques (*Macaca maura*). *Int. J. Primatol.* 38: 224–242.

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