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Noninvasive Technologies for Primate Conservation in the 21st Century

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Abstract

Observing and quantifying primate behavior in the wild is challenging. Human presence affects primate behavior and habituation of new, especially terrestrial, individuals is a time-intensive process that carries with it ethical and health concerns, especially during the recent pandemic when primates are at even greater risk than usual. As a result, wildlife researchers, including primatologists, have increasingly turned to new technologies to answer questions and provide important data related to primate conservation. Tools and methods should be chosen carefully to maximize and improve the data that will be used to answer the research questions. We review here the role of four indirect methods—camera traps, acoustic monitoring, drones, and portable field labs—and improvements in machine learning that offer rapid, reliable means of combing through large datasets that these methods generate. We describe key applications and limitations of each tool in primate conservation, and where we anticipate primate conservation technology moving forward in the coming years.

Keywords Endangered · Methods · Monitoring · Remote Sensing · Tools

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Introduction

Observing and quantifying primate behavior in the wild is challenging (Williamson and Feistner 2003). Primates live across a vegetation gradient, from dense tropical and montane forests to savanna mosaics (Lehman and Fleagle 2006). Some are entirely arboreal and others nearly entirely terrestrial; when not habituated to humans, it is common for individuals to flee on contact (Williamson and Feistner 2003). As a result, visual study can be restricted to a few groups already under study or habituated for tourism.

Human presence affects primate behavior (Crofoot *et al.* 2010; Nowak *et al.* 2014) and habituation of new, especially terrestrial, groups is a time-intensive process that carries with it ethical and health concerns (Allan *et al.* 2020; Doran-Sheehy *et al.* 2007; Gazagne *et al.* 2020; Jack *et al.* 2008; Williamson and Feistner 2003), especially during the recent pandemic when primates are at even greater risk than usual (Gillespie and Leendertz 2020; Melin *et al.* 2020). As a result, wildlife researchers, including primatologists, have increasingly turned to new technologies as indirect methods to answer questions and provide important data related to primate conservation.

In this article we attempt to summarize some of the key advances driving data collection and analyses in primate conservation. This is by no means a comprehensive summary of the tools available to primate conservationists. Not only is that beyond the scope of this article, but there is a steady stream of new tools available to eager technologists (e.g., broad reviews on applicable technologies for wildlife conservation: Berger-Tal and Lahoz-Monfort 2018; Marvin *et al.* 2016; Pimm *et al.* 2015). Some of these tools are hardware, some are software, and some integrate them both, and in so doing are transformational. These and other systems generate new questions of inquiry, new methods of data collection, and with them, encourage the development of new analytical tools to investigate them.

These innovative tools take multiple forms and can be implemented at the data collection and analysis stage. In the review that follows, we discuss examples of both: camera traps (CT), passive acoustic monitoring (PAM), drones, and portable genomics labs as means of collecting indirect (and often, remotely sensed) data for primate conservation, and developments in machine learning for analyses of especially big data. At the data collection stage, remotely sensed data often complement direct behavioral observations by human observers in the field, or replace them entirely where ground-truthing has been previously established (Leyequien *et al.* 2007). The diversity of information that we can now extract from indirect evidence has transformed what we can understand about individuals, groups, and populations, all without ever directly observing an animal (Lynn *et al.* 2016). At the data analysis stage, in parallel with improvements in data collection, recent improvements in how we move data means that some of the limitations that have historically plagued research are steadily being overcome.

We begin by reviewing what we consider to be four increasingly common and informative technological developments and describe the ethical consideration necessary in their deployment, and then their application to monitoring primates and threats. We then highlight recent improvements in machine learning and (big) data analysis, before concluding with a discussion on the limitations of these methods, and where we see the future of technology in primate conservation.

Which Technologies?

Camera Traps

Camera trapping is the use of motion-sensitive cameras to record videos or pictures of humans or animals (Kucera and Barrett 2011). The technique dates back nearly a century and has become almost ubiquitous in studies of wildlife research and conservation (Wearn and Glover-Kapfer 2019). CTs have long targeted large, charismatic mammals (Ahumada *et al.* 2011; Cove *et al.* 2013; Gerber *et al.* 2010; Kauffman *et al.* 2007), but have more recently expanded into assessing entire wildlife communities, including small and large species (Cusack *et al.* 2015a; Kays *et al.* 2009).

CTs share critical advantages with other remote sensing technologies. They collect data automatically, can be deployed in remote areas for extended periods (many months), record on a 24-h cycle, and are noninvasive and minimally disruptive to wildlife (Meek *et al.* 2014, 2016). The application of CT has seen remarkable growth and diversification to broad ecological questions and especially in its application to primate research and conservation, including documenting species presence or distribution (Fang *et al.* 2020; Rovero and Zimmerman 2016).

Passive Acoustic Monitoring

Many primate species are characterized by long calls that travel a few hundred meters or even multiple kilometers (Delgado 2006; Mitani and Stuht 1998; Wich and Nunn 2002). These characteristics make call detection an effective way of identifying species presence.

Passive acoustic monitoring describes a system composed of microphones (hereafter acoustic sensors) and in-house storage capacity, which is often synchronized to detect and monitor wildlife sounds in both marine and terrestrial environments. PAM is applicable to any taxa that produces acoustic signals, including insects, fish, herpetofauna, birds, and mammals (Sugai *et al.* 2019). While the first system that listened to wildlife sounds was deployed underwater during World War 1 (reviewed in Sousa-Lima *et al.* 2013), recent advances in bioacoustics have expanded the applications of acoustic sensors for terrestrial species (Blumstein *et al.* 2011; Sugai *et al.* 2019), including primates (Kalan *et al.* 2015; Piel 2018; Spillmann *et al.* 2015). PAM is noninvasive and especially applicable when visual detection is limited, for instance in dense tropical forests, at night, or when weather conditions are poor. It can be deployed for long periods in the field (months or years) and simultaneously at multiple locations and thus offers the possibility to monitor animal calls at large spatiotemporal scales. The increasing interdisciplinary collaboration between engineers and field ecologists is driving new, affordable, and effective PAM-related tools with reduced size and weight.

Drones

The use of drones in primatology started *ca.* 10 yr ago to facilitate data collection on three main aspects that are relevant to primate conservation (Koh and Wich 2012): 1) land-cover classification and monitoring changes, 2) obtaining data on primate presence/absence and density, and 3) detecting

Table 1 Key differences between drone types

	Multirotor	Fixed wing	Hybrid VTOL
Launch requirements	Smallest take-off and landing area required; can launch in a wide range of environmental conditions.	Requires large, open area for launch and landing.	Smaller take-off and landing area required than fixed wing but larger than multirotor; can be launched in a wide range of environmental conditions.
Payload	Can support heavier payload (e.g., several kilograms).	Can support lighter payload (e.g., less than a kilogram, although gasoline powered fixed wings may carry heavy payloads).	Can only support lighter payload (e.g., less than a kilogram).
Flight duration	Shortest flight duration (e.g., less than an hour).	Longest flight duration (e.g., more than an hour).	Intermediate flight duration (e.g., 30–60 min).
Pilot experience	Can be flown with minimal, or no training and experience.	Substantial experience and training required to effectively pilot, especially for take-off and landing.	Intermediate pilot experience required.

Modified from Koh and Wich (2018).

poachers. Other drone usages such as monitoring of food availability, remotely studying social behavior, or identifying individuals have not yet been conducted. Despite the decade since their introduction to the field, there have been relatively few published studies on the use of drones in primatology (Bonnin *et al.* 2018; Spaan *et al.* 2019; Zhang *et al.* 2020). For a more in-depth overview of the usage of drones in conservation we refer the reader to several review articles (Chabot and Bird 2015; Jiménez López and Mulero-Pázmány 2019; Nowak *et al.* 2019) and a recent book (Wich and Koh 2018). Here, we summarize the advantages and disadvantages of the three primary drone models (Table 1).

Portable Genomics Labs

Primate feces have long been used in endocrinological, diet, and genetic studies. Endocrinologically, hormonal data reveal mechanisms that inform on primate behavior, health, causes and consequences of stress, and even life history (Beehner and Bergman 2017; Higham 2016). Feces also provide researchers with a catalog of consumed plant species and parts, enabling us to map important food sources and assess the role of primates as seed dispersers for forest regeneration (Kalbitzer *et al.* 2019). More recently, we can now apply metagenomics to primate feces to more comprehensively reveal primate diet, parasites, and population genetics (Srivathsan *et al.* 2016). The genetic material in primate feces allows us to identify individuals and use those data for censusing (Arandjelovic and Vigilant 2018; Vigilant and Guschanski 2009), to understand genetic structure, and to identify population boundaries (Eriksson *et al.* 2004). Feces have long revealed key data on the health of wild primates (Nunn and Gillespie 2016), especially in light of increasing anthropogenic activity (Chapman *et al.* 2005).

Genomics is an increasingly valuable tool in wildlife conservation (Frankham *et al.* 2010). It is important for species identification and the dynamics of endangered populations (McMahon *et al.* 2014) and contributes to identifying inbreeding depression, population structure, and the effect of population fragmentation (Hoban *et al.* 2013). Moreover, molecular epidemiology from genomic data is an increasingly common tool in primate health monitoring (Gilardi *et al.* 1999). Several studies have now shown the potential of combining noninvasive samples with portable genomics for, e.g., parasitology (Knot *et al.* 2020), sexing (Guevara *et al.* 2018), and species identification (Seah *et al.* 2020). Portable genomics has been demonstrated across habitats, from rainforests (Menegon *et al.* 2017; Pomerantz *et al.* 2018), to dry forests (Guevara *et al.* 2018), mountainous terrains (Parker *et al.* 2017), and even polar regions (Goordial *et al.* 2017; Johnson *et al.* 2017) and offers a way to address some of the critical limitations to traditional lab work that relies on field samples.

Despite the benefits of molecular research for primate conservation, traditional molecular labs are located far away from field sites and consist of bulky and expensive machines. This means researchers often invest many weeks and much funding toward storing, processing, and transporting samples for later analyses. At the same time this often creates dependency of local researchers on foreign collaborators, and numerous range countries are now encouraging if not requiring researchers to conduct analyses in

Table II Summary of recent miniature tools for molecular processing of field samples

Type of equipment	Product name	Company	Price (US\$) ^a	Website
All-in-one DNA laboratory	Bento Lab	Bento Lab	1600–2000	https://www.bento.bio
Gel electrophoresis and visualization system	blueGel/GELATO	Ampliyus	350–890	https://www.minipcr.com/product-category/gel-electrophoresis/
PCR	mini8/mini16	Ampliyus	650–840	https://www.minipcr.com/products/minipcr/
qPCR	Liberty16	Ubiquitome	6000	http://www.ubiquitomebio.com
qPCR	Mini RT-PCR	Mygo	9200	http://www.mygopcr.com
qPCR	Open qPCR	Chai	4500–6500	https://www.chaibio.com/openqpcr
qPCR	Franklin one9 / two9/-three9	Biomeme	5950–9950	https://info.biomeme.com/mobile-qpcr-thermocyclers
qPCR	MIC qPCR	BMS	9600–12,000	https://biomolecularsystems.com/en-gb/mic-qpcr/
Sequencer	MinION/Mk1C	Oxford Nanopore Technologies	1000–4900	https://nanoporetech.com/products
Sequencing flow cells	Flongle/flow cell	Oxford Nanopore Technologies	90–900	https://store.nanoporetech.com/us/flowcells.html
Lab workspace	Mercury Lab	MRIGlobal	>50,000	https://www.mriglobal.org/mercury/

^a Price is an indication only. True prices will be subject to exchange rates, shipment costs, etc. The most up-to-date information and technologies can be found at portablegenomics.org.

country. Thanks to a revolution in miniaturizing molecular equipment (Table II), this presents new opportunities for a decentralization of conservation research efforts. One example is from Oxford Nanopore Technologies, which launched the MinION in 2014, a portable and compact USB-powered sequencer (Jain *et al.* 2016). This miniaturization is now pervasive, from portable real-time polymerase chain reaction (qPCR) and gel electrophoresis systems to thermocyclers and even all-in-ones that offer extraction and sequencing preparation (Marx 2015). Incorporating fecal samples into field research protocols will be a valuable approach to obtain more information on a wide variety of primates, and these current technological advances present an exciting opportunity to analyze this information on site.

Ethical Considerations of Remote Monitoring

Before we discuss the application of these technologies to primate conservation specifically, we must first address the ethical and logistical considerations of access and exposure. As has been described elsewhere in detail (Sandbrook *et al.* 2018), new technologies are not a panacea for all primate conservation challenges. Although those described here offer clear benefits to data collection and analyses, their deployment must be thoroughly considered before use. The ability of remote sensing tools to incidentally (or deliberately, in the case of poachers) reveal the location, movement, and behavior of individuals raises concerns about informed consent, privacy, civil liberties, and fear of arrest. To our knowledge, there is no standard for determining when images or sounds captured from remote sensing can be shared or used (Pebsworth and LaFleur 2014), despite the growing need for universal agreements on these and related contexts that require formal guidance.

A recent discussion of the ethical issues related to camera trapping, for example, laid out recommendations for a basic code of conduct (Sharma *et al.* 2020). These include discussion of steps to obtain appropriate permission to use and deploy cameras to the consultations and meeting necessary to agree on terms that govern disclosure decisions. These issues are permeated by questions and differences in culture, value, power, and even law (Brittain *et al.* 2020). Historically, even well-intended conservation efforts have had negative consequences for some groups of people. For example, protecting wildlife can displace indigenous communities, even when local stakeholders are engaged in conservation policy (Adams and Hutton 2007). Aware of these negative repercussions, as practitioners our obligation is to identify the beneficiaries but also those who are likely to suffer from these decisions. In this sense, we echo recent calls for a more holistic approach to these complex issues of the ethics of conservation research, beyond what institutions require and inclusive of what local stakeholders deserve (Brittain *et al.* 2020).

It is also important to critically examine who controls how information flows and is processed, and how can these processes be democratized (Arts *et al.*, 2015). For example, researchers in the Canadian territories of Manitoba and Nunavut are involving indigenous communities in the camera trapping process and tapping into their traditional ecological knowledge of the region (Clark *et al.* 2018). We support these

improved attempts at inclusivity when planning and especially implementing the deployment of remote sensing technology for data collection.

Avenues for Investigation

Detection, Presence–Absence, Prioritization

An important first step in wildlife conservation is detecting a species presence and thereafter, identifying priority areas (Groves *et al.* 2002). In most cases, this involves weighing important metrics such as forest loss and forest loss rate, size of the area in need of protection, relative species (or overall phylogenetic) diversity, and measures of irreplaceability or vulnerability (Carvalho *et al.* 2020; Isaac *et al.* 2007; Ondei *et al.* 2019). Just as important is assessing a species presence, especially for cryptic, elusive, or rare species where distribution and ranging patterns are unknown. Although challenging, establishing species presence is an early and fundamental step in conservation, necessary for studying population trends.

One common analytical tool for doing this is to model occupancy (Cove *et al.* 2013; Crunchant *et al.* 2020). Occupancy is the proportion of an area used by a species (MacKenzie *et al.* 2017; MacKenzie and Royle 2005). Occupancy models use detection/nondetection data from multiple visits of a given area to infer the probability of species presence and provide a useful tool to assess the population status (i.e., declining, stable, or increasing). They also allow researchers to determine the predictors, such as vegetation, season, etc., that most influence animal presence (e.g., Crunchant *et al.* 2020). Although a common technique across wildlife studies, occupancy modeling is far less common in primatology. CTs, PAM, and drones can provide data on animal habitat use, especially important across vast areas that researchers cannot regularly monitor.

CT is widely used to reveal primate habitat use. For instance, in a case study from western Tanzania, occupancy models built from CT data revealed chimpanzee (*Pan troglodytes*) use of an extremely large home range to be highly variable across space and season (Crunchant *et al.* 2020). Seasonal changes in habitat use and in diet have been observed using CT in wild mandrills (*Mandrillus sphinx*: Hongo *et al.* 2018), blonde capuchin monkeys (*Sapajus flavius*: Medeiros *et al.* 2019) and wild Japanese macaques (*Macaca fuscata*: Hanya *et al.* 2018).

Besides documenting animal presence, CT footage has the advantage over other techniques (e.g., PAM) in revealing the sex and age of those that pass by cameras (e.g., Head *et al.* 2013). From a conservation perspective, monitoring life history landmarks, such as births, deaths, and immigrations/dispersal events reveal demographic patterns that inform and are informed by conservation strategies (Galvis *et al.* 2014; Strier 1991). While confirming a species presence is a critical first step toward conserving it, establishing group demography can offer insight into population health, especially given that some threats disproportionately affect individuals of certain age–sex classes (i.e., with younger individuals more susceptible; Lilly *et al.* 2002).

For decades researchers have deployed CTs terrestrially, tacitly acknowledging that cameras could not access higher-canopy-level dwelling species. The last few years, however, have seen the emergence of arboreally deployed cameras. Early studies

targeted areas such as canopy crossing points, thought to be used by numerous taxa, including primates (Gregory *et al.* 2014), where high canopy-species inventories were conducted (Whitworth *et al.* 2016). In some cases, arboreal deployments have targeted particular primate species (e.g., *Prolemur simus*) and shown that, in some areas, arboreally deployed cameras have higher detection rates than subcanopy cameras (Olson *et al.* 2012). More recent studies have focused on extracting CT data for building occupancy models and revealing species richness (Chen *et al.* 2021; Johnson *et al.* 2020; Moore *et al.* 2020).

The use of PAM is well established in wildlife behavior and conservation (Balantic and Donovan 2019; Brauer *et al.* 2016; Campos-Cerqueira and Aide 2016; Comer *et al.* 2014), but it is seldom used to confirm primate presence and habitat use. Two reasons may explain this. First, the historic success of long-term projects that rely on direct observations of habituated groups may have favored a methodological inertia that suppressed innovation and creativity. Second, all the great apes (Fruth *et al.* 2018) and some strepsirrhines (Kappeler 1998) build nests for sleeping, which remain on the landscape for months, and from which researchers can derive habitat use, saving them the financial and logistical burden of deploying a new technology. Thus, although the application of PAM remains atypical in primate research, there is a growing niche for this method to reveal primate presence, abundance, and behavior.

Two of the earliest studies applied PAM to wild great apes. In one of these, researchers deployed 20 acoustic sensors in the Taï National Park, Côte d'Ivoire, to assess the potential of a customized algorithm for the automated detection of chimpanzee buttress drumming and the loud calls of Diana (*Cercopithecus diana*) and king colobus (*Procolobus badius*) monkeys over 35–45 km² (Kalan *et al.* 2015). The use of PAM and a semiautomated call detector provided similar results to data collection via walked transects. The authors argued that sensor deployment is far less time consuming than walking transects. That same year, the second study was published, where researchers deployed 20 sensors successfully detected wild male orangutans (*Pongo pygmaeus*) from ≤900 m, including localizing callers to <60 m (Spillmann *et al.* 2015). Detection algorithms correctly identified species from almost half a mile (700 m), demonstrating the geographic reach of such a system, especially when individual callers can be identified (Spillmann *et al.* 2017).

Two other studies compared the efficiency of CT and PAM in primate detection. In one, camera traps and acoustic sensors were deployed to study sika deer (*Cervus nippon*) and Japanese macaques (*Macaca fuscata*) in Japan (Enari *et al.* 2019) used. The authors showed that acoustic sensors were superior, largely due to the increased (spatial) detection coverage—100–7000 times larger—than CTs, as well as far more reliable when using automated detectors for auditory compared to visual signals. In comparing automated detectors for acoustic vs. camera trap footage of the monkeys, they noted that whereas images of animals rarely change, call parameters respond to the intrinsic (age–sex class) and extrinsic physical (rainfall, wind) and social (activity) context. Alas, although PAM offers more effective detection, automated detection may be more complicated, with many species exhibiting high intracaller acoustic variability (Bouchet *et al.* 2012; Zimmermann and Lerch 1993).

The second study compared the efficiency of PAM and CT in detecting chimpanzees in the Issa Valley, Tanzania (Crunchant *et al.* 2020). Detectability with both methods varied across seasons, likely due to social and ecological factors that influence

chimpanzee party size and vocalization rate. Nonetheless, PAM was more efficient than CT, confirming chimpanzee absence in fewer than 10 days of recordings, 5 times faster than CT data (Crunchant *et al.* 2020). Additional work comparing methods is necessary to more comprehensively understand the advantages of each method and which questions they can best address.

The use of drones to detect animals is a growing application across taxa and habitats. Although for some species the animal–background color contrast is sufficient to facilitate detection, for many species that is insufficient (Chabot *et al.* 2019; Linchant *et al.* 2015). As a result, conservation scientists sometimes use other evidence of wildlife to assess their presence and distribution, such as nests (chimpanzees: Bonnin *et al.* 2018; alligators: Elsey and Trosclair 2016). In one of the first demonstrations of this application, researchers used a camera on a fixed wing drone and flew line transects over chimpanzee habitat in Gabon (van Andel *et al.* 2015). The fraction of ground nests detected in the aerial images was far higher (49%) in open, coastal forests than closed, inland forests (8%), suggesting an important nest–forest color contrast in aiding detection. A follow-up study in a mosaic landscape in western Tanzania compared nest detections from ground surveys and aerial images (Bonnin *et al.* 2018). Only a fraction (9.6%) of the ground nests were detected from the aerial images, but there was a significant, but weak relationship between the ground and aerial nest numbers. The fraction of nests observed in aerial images compared to the ground (39.9%) was lower in this study than in Gabon, likely due to methodological differences (van Andel *et al.* 2015). In Tanzania, detection probability of nests was mainly influenced by image resolution (Bonnin *et al.* 2018).

In some cases, drones provide imagery from which animals themselves—and not nests—can be detected. A comparison of ground observations of spider monkeys (*Ateles geoffroyi*) in Mexico with detections by human analysts on thermal infrared images showed that there was good concordance between the ground and aerial counts for small parties, but the aerial counts were higher for larger parties, indicating that ground observers do not see as many individuals as aerial cameras do (Spaan *et al.* 2019). Owing to the difficulties of detecting primates directly in the tree canopy with visual spectrum cameras, scientists have resorted to thermal infrared cameras that can detect the heat radiated from primates (Burke *et al.* 2019; Kays *et al.* 2019; Spaan *et al.* 2019). These studies have used multicopter drones with a variety of thermal infrared cameras to detect several primate species and have the best detection probabilities at dawn and dusk when the vegetation is relatively cool. A study that focused on Bornean orangutans (*Pongo pygmaeus morio*) in Sabah established that orangutans, and the smaller proboscis monkeys (*Nasalis larvatus*), can be detected and distinguished from each other in the thermal signal on the basis of their size (Burke *et al.* 2019). As early demonstrations of the efficacy of drones and especially thermal imagery to detect wild primates, these studies have been enormously constructive. Limitations remain, however, in detections.

Specifically, although thermal cameras are effective in detecting species in the upper canopy, individuals even just under the top level of the canopy are generally not detected (Kays *et al.* 2019). In fact, in general, we know little about false negatives, which remains an issue during analyses. Figuring out ways to correct for that is important. Further, once daytime temperatures rise and the canopy warms, higher individuals will not be as detectable given the low temperature differential (Kays

et al. 2019). Even though detection was high at night, distinguishing between species was difficult, which the authors argued could potentially be remedied by combining thermal imagery with flash photography or infrared illumination so that visual spectrum cameras can be used to facilitate species classification (Kays *et al.* 2019).

Lastly, innovations in portable labs have also enhanced our ability to remotely detect primates. Several studies have demonstrated the possibility of using portable sequencers for species identification in the field through DNA barcoding, which is limited to one gene region per sample (Blanco *et al.* 2020; Menegon *et al.* 2017; Pomerantz *et al.* 2018). Further, metabarcoding offers the potential to sequence mixed DNA barcode amplicons from bulk community or pooled samples (Krehenwinkel *et al.*, 2019b). Metabarcoding using Illumina sequencing has been applied to a variety of primatological research questions, for example to assess parasite diversity (Gogarten *et al.* 2020; Pafčo *et al.* 2018). Metabarcoding is also possible using MinION sequencing, but few studies have taken advantage of this (Krehenwinkel *et al.*, 2019b). This is largely due to the fact that the individual reads have error rates between 5% and 15%, meaning the more closely related the individuals, the more unreliable the readout. For spatially restricted species, this is likely less of a concern. There are signs of improvement in reducing these errors, however (Krehenwinkel *et al.* 2019a), with recent reported sequencing accuracy up to 97% (Baldi and La Porta 2020) and the R10.3 chemistry having a >99.87% accuracy compared to Illumina sequencing (Chang *et al.* 2020). Furthermore, bioinformatics pipelines still focus mostly on Illumina or PacBio data. Development of new pipelines designed to handle MinION data is expected to improve the applicability of metabarcoding for species identification from community or pooled samples and thus offer another way to indirectly confirm species presence.

Abundance and Density

Once species presence is confirmed, a natural next parameter to establish is abundance (or density), especially important in species monitoring, evaluating extinction risk, and assessing the efficacy of conservation policy and practice. Estimations of population size have long on extractions from observations made on line transects (Buckland *et al.* 2010; Kolowski and Alonso 2012; Teelen 2007) or from feces (Goossens *et al.* 2006; Guschanski *et al.* 2009; Lynn *et al.* 2016), nest counts (Kouakou *et al.* 2009; Morgan *et al.* 2006), and vocalizations (Kidney *et al.* 2016).

Different statistical approaches can be used to estimate animal density from camera footage, whether animals are individually recognizable or not. When individuals are individually recognizable through a combination of facial and bodily characteristics (e.g., ear colors and forms, presence of scars), spatial capture–recapture (SCR) models can be applied (e.g., Borchers and Efford 2008; Efford 2004), for example to estimate chimpanzee density (Després-Einspenner *et al.* 2017; Head *et al.* 2013). The accuracy of SCR with CTs has been empirically evaluated based on known individual chimpanzees at Tai Forest, Ivory Coast (Després-Einspenner *et al.* 2017). Results indicated that nearly all weaned individuals were detected on only 5 cameras deployed for 38 weeks and camera trap derived densities were highly accurate and precise. SCR models can also be used when individuals are unmarked/unidentified but this requires intensive sampling and generates low-precision estimates (Chandler and Andrew Royle 2013).

When animals are not recognizable via identifiable markings, as can occur for example in, nocturnal species, the random encounter model (REM) can estimate density using average animal group size and day range, and the distance and angle within which it detects animals. It requires camera sensitivity and animal speed movement to be measured (Rowcliffe *et al.* 2008, 2011, 2016). The REM model was later expanded (and relabeled as REST: random encounter and staying time) to assess densities even when individuals were not recognizable (Nakashima *et al.* 2018). The accuracy of the REM model remains to be demonstrated with more tests needed under field conditions (e.g., Cusack *et al.* 2015a; Rovero *et al.* 2013).

Another approach when individuals are not recognizable is camera trap distance sampling (CTDS). This applies distance sampling methods (e.g., Buckland *et al.* 2015) with extended point-transect methods (Howe *et al.* 2017). CTDS has been evaluated with chimpanzees in Tai Forest, Ivory Coast. The results showed that the CT-derived density estimate was accurate (0.66 ind./km² vs. a true density of 0.67 ind./km²) and less biased than that calculated from line transects with nest counts (0.78–0.84 ind./km² vs. a true density of 0.89 ind./km²; Kouakou *et al.* 2009), further demonstrating the efficacy of CTs in assessing primate density. CTDS is not dependent on previous knowledge of known individuals and thus can be applied in areas where little other information is available, as shown recently in a broad-based wildlife survey in Salonga National Park, DRC (Bessone *et al.* 2020).

Like CTs, acoustic sensors can also both detect animal presence and reveal animal density. This was initially demonstrated for marine species (e.g., Minke whales [*Balaenoptera acutorostrata*]: Martin *et al.*, 2012); reviewed in Marques *et al.* 2013; McDonald and Fox 1999) before being expanded to terrestrial species (e.g., Cape peninsula moss frog [*Arthroleptella lightfooti*]: Borchers *et al.* 2015; Measey *et al.* 2017; Stevenson *et al.* 2015; ovenbirds [*Seiurus aurocapilla*]: Dawson and Efford 2009; Efford *et al.* 2009). Like with CT data, the main approaches to estimate abundance have been adapted from observational encounters and include capture–recapture (CR), distance sampling (DS), and acoustic spatial capture–recapture (aSCR), reviewed in more detail in Marques *et al.* (2013). No study has yet used PAM to estimate primate density. However, spatially explicit CR methods with humans acting as acoustic detectors was used to estimate yellow-cheeked gibbon (*Nomascus annamensis*) density in northeastern Cambodia, using bearing estimates to detected groups to improve density estimates, and results were promising (Kidney *et al.* 2016). aSCR methods require *a priori* knowledge of call rate (the number of calls produced per unit of time), to convert the density of calls (the number of calls per unit time per unit space) derived statistically from the acoustic survey into caller density (the number of animals per unit space). Call rate data can be obtained by following animals and recording call events.

Like with PAM, drone data show good promise in providing data on primate density, but few empirical studies have been conducted to date. Although drones have been used to obtain data on the distribution of a wide variety of taxa (Barasona *et al.* 2014; Chabot and Bird 2015; Mulero-Pázmány *et al.* 2015; Wich and Koh 2018), few studies have applied this technique to primates. This could be due to the fact that primates often occur in vegetation types that pose challenges for data collection (Ancrenaz *et al.* 2005). Studies with manned aircrafts have indicated that orangutan nests can be detected by observers on a small, low-flying helicopter and converted into

orangutan density (Ancrenaz *et al.* 2005). A natural extension of this was to evaluate whether an off-the-shelf visual spectrum camera fitted to a drone could be used to detect nests and compare these observations to ground surveys. Results of two studies, one on orangutans (Wich *et al.* 2015) and another on chimpanzees (Bonnin *et al.* 2018), showed that a low, but consistent, proportion of nests that were observed from the ground are detectable from the air. A third study using a drone with a thermal infrared camera to determine the presence and count the number of spider monkeys in Mexico showed similarly encouraging results, with high reliability between aerial and ground counts of individual monkeys (Spaan *et al.* 2019). These studies indicate that aerial counts from camera-fitted drones offer an exciting new tool to monitor population trends in wild primate populations.

Because great ape nest numbers have to be converted into great ape densities through a conversion that involves other variables such as nest decay and nest building rate, the confidence intervals from survey data are usually large, which make them less suitable for detecting small population changes (Kouakou *et al.* 2009; Piel *et al.* 2015). From the aforementioned studies it thus seems that counting primates from the air also requires correction factors in most cases to yield accurate estimates. It remains to be determined whether such correction factors can be established and how they differ between vegetation types for the same species and between species living in the same vegetation types. It is likely that aerial counts using thermal infrared will work best for primate species that sleep in relatively open canopies of emergent, relatively large trees. For those species, correction factors may not even be necessary. For species that are smaller and/or sleep below the canopy or in tree holes the usage of thermal infrared will be less suitable and correction factors far more important (and larger).

Main Threats

Poaching

The technologies that we review here can detect more than animals themselves; these tools are potentially capable of revealing threats to primates and their habitat as effective as the primate themselves. All over the world wild primates are extracted from their natural habitat for either consumption, use in traditional medicine, the exotic pet trade, or used as trophy and status symbols, causing major threats to their distribution and abundance worldwide (Ni *et al.* 2018; Nijman *et al.* 2017). Poaching occurs predominantly for food and for some species also during human-primate conflict situations, and is one of the major causes leading to species declines (Meijaard *et al.* 2010, 2011; Wich and Marshall 2016).

Poaching is widespread and occurs across protected areas, plantations, logging concessions, and forest reserves. As a result there is considerable interest in reducing poaching pressure on primate species and evaluating whether technology can facilitate such a reduction (Mulero-Pázmány *et al.* 2014; Wich and Koh 2018). When poaching occurs in large landscapes that are covered in dense vegetation, poacher detection is challenging. This means that technological solutions need to cover large swaths of an area rapidly and with high poacher-detection probability. Due to poachers often operating outside of daylight hours, one direction that conservation managers

and researchers have turned to is the employment of thermal infrared cameras to detect poachers. Further, predictive modelling can be used in areas where poaching has the highest likelihood of occurring to automate such missions (Olivares-Mendez *et al.* 2015).

Although the application of drones to detecting poachers is promising, areas for improvement remain. First, habitat type will impact the proportion of detected (and thus missed) poachers. One study found that drones using thermal infrared cameras in relatively open miombo woodland failed to detect ~60% of human subjects even during optimal flight times that maximized the thermal contrast of subjects to the surrounding vegetation (Hambrecht *et al.* 2019; see also Mulero-Pázmány *et al.* 2014). Canopy cover, distance from the flight path, and flight altitude all negatively influenced detection probability. Because thermal infrared signals do not carry through thick layers of vegetation it is unlikely that poachers in dense forest will be detected with this method, although potentially this offers opportunities for indirect detection from camp fires (Burke *et al.* 2018). Machine learning is important to remove variability that arises from human analysts and is poised to dramatically improve detection success rates (Bondi *et al.* 2019; Longmore *et al.* 2017). Second, predictive modelling for optimizing drone flights would benefit from more studies and easy-to-use software applications for users. Third, long-flight drones are essential due to the large areas that need to be covered. This could be achieved through fixed-winged drones with power systems such as gas engines, batteries in combination with photovoltaic cells on wings (for areas and/or seasons with high solar radiation), or hydrogen. Such systems will likely be larger than the relatively small fixed-wing systems that are predominantly used in conservation and hence will likely need to land on wheels instead of the belly and need some sort of runway. An alternative to cover large areas is to have several take-off and landing areas throughout an area and use swarms of smaller drones to cover larger areas.

Acoustic information can also be used to inform wildlife crime units of the presence of poachers. When combined, PAM and acoustic localization systems (ALSs) can reveal key threats to wild primates when used to identify the source of e.g. gunshots, axe, or chainsaw sounds. For example, CARACAL, a low-cost hardware and software platform, can identify gunshot origins from over 1 km with an accuracy of less than 35 m (Wijers *et al.* 2019). AudioMoth, another low-cost platform, can detect gunshots from up to 500 m (Hill *et al.* 2018).

Finally, genetic wildlife forensics aids bushmeat identification and illegally trafficked animals (McDowall 2008). Species identification benefits from molecular techniques, especially in cases where animal parts cannot be morphologically identified. For example, DNA barcoding can be used in forensic species identification (Comstock *et al.* 2003), whereas microsatellite data reveal the origins of seized illegal wildlife products and aid efforts to enhance law enforcement (Mondol *et al.* 2015). The latter technique is well-established when elephant or rhinoceros parts are confiscated by authorities (Wasser *et al.* 2004), but has not been used yet with primates, despite a growing demand (Oklander *et al.* 2020).

Traditionally, genetic wildlife forensics took place in a central lab. However, using portable genomics labs to investigate wildlife trade and crime from the field decentralizes otherwise bureaucratic processes, improves turnaround times for analyses, and reduces costs. In a recent study that used a qPCR to detect the illegal trade of the critically endangered European eel (*Anguilla anguilla*) at Hong Kong International

Airport (Cardenaosa *et al.* 2019). The process of extracting and sequencing DNA was rapid (~2 hr), mobile, and cost-effective (<US\$1.00 per sample). Additionally, DNA amplification using PCR and subsequent detection by electrophoresis have been performed on site for microsatellite genotyping of two primate species (*Propithecus verreauxi* and *P. coquereli*) in Madagascar (Guevara *et al.* 2018) (Guevara *et al.* 2018), and a fully portable field lab including the MinION facilitated the molecular species assignment of a Malagasy lemur species within a week, from animal capture to tissue collection, to phylogenetic analysis (Blanco *et al.* 2020). Finally, a recent study using three-gene PCR and high resolution melting analysis showed encouraging accuracy for East African wildlife species identification (Ouso *et al.* 2020). This method is rapid, low-cost, and reliable, using melting profiles of ribosomal RNA gene PCR products, as opposed to mass barcode sequencing, as has been traditionally used for bushmeat (forensic) surveillance (Kimwele *et al.* 2012). These and other diverse applications of portable laboratories highlight the potential of field-based genomics to address data gaps in traded primate species and to improve data access for species conservation and management.

Landscape Integrity and Human–Wildlife Conflict Because habitat loss, fragmentation, and degradation are negatively influencing primate populations, it is important to determine the vegetation classes in which primates occur and monitor habitat change (Estrada *et al.* 2017). One of the most effective and efficient ways of doing that is with drones, and especially those using multispectral cameras. Although the number of sensors (and thus bands) in multispectral cameras can differ, these are often green, red, red-edge, and near-infrared (NIR) (Assmann *et al.* 2019). These sensors are often used for vegetation monitoring given that they allow for the calculation of band ratios such as the normalized difference vegetation index (NDVI), which is useful for land-cover classification and plant health (Pettorelli 2013). Although these sensors are common tools in various remote sensing studies, for example to monitor protected areas (Coulter and Stow 2009) and rapidly assess ecological integrity (Diaz-Delgado *et al.* 2018), multispectral cameras have not yet been used in primate studies. Their potential use is diverse, however, capable of providing information on phenological patterns and for tree species detection, for instance. Traditionally, satellite images have been used for this process and these are still the method of choice for large-scale analyses (Voigt *et al.* 2018). However, new sensors offer comparable data for phenology (Brede *et al.* 2018). At a smaller scale, drones can offer advantages over satellite images, such as flexible data collection, capturing imagery below cloud cover and providing much higher resolution imagery than commercially available satellites (Rodríguez *et al.* 2012; Wich and Koh 2018). Such data allow the detection of very low impact logging activities, for instance, that would not be picked up by satellite images (Koh and Wich 2012).

Broadly, very few studies have used drones to map primate habitats. One study mapped Sumatran orangutan habitat with a fixed-wing drone that was equipped with a standard RGB camera to examine whether various vegetation classes in a reforested area could be distinguished from each other on drone images (Wich *et al.* 2018). This study indicated that some classes such as oil palm plantations were classified with a high accuracy, as were some of the reforestation classes, but that others such as logged forest had low accuracy and were classified as reforested. The use of multispectral data should improve such classifications. Another use of drone data can be as training data

for classification algorithms for satellite image classifications (Szantoi *et al.* 2017). Owing to the very high resolution of drone images, they can potentially be used as an alternative to ground truthing, depending on location size, area accessibility, and the classes in need of classification. In two areas where Sumatran orangutan presence was mapped with a fixed-wing drone, researchers obtained very high resolution orthomosaics of the area in which seven land-cover classes could be distinguished (Szantoi *et al.* 2017). Drone-truthing data from these flights were subsequently used to train a supervised classification model on Landsat 8 images from the same data collection period. The accuracy of the classification was assessed with high-resolution satellite data and indicated that accuracy was high for mature oil palm (89%), logged (76%), and reforested areas (76%), but that riverine forest had a much lower accuracy (23%) (Szantoi *et al.* 2017). These results indicate that the use of drones to acquire training data for algorithms that use satellite images to scale to larger surface areas is promising.

Drone images can also be used to obtain more detailed data on primate habitats. An early study examined the potential to determine tree species in chimpanzee habitat in Gabon on visual spectrum images taken from a camera on board a fixed wing drone (van Andel *et al.* 2015). Results indicated that 14 important chimpanzee food tree species could be identified in the images. This is a small number of species in a very diverse habitat, but the results reflect the potential of such an approach. The use of multispectral (and hyperspectral—which has hundreds of bands) cameras will allow the identification of much larger numbers of species and thus relatively large-scale tree species inventories of primate habitats and facilitate studies of primate behavioral ecology. In addition, such methods could be applicable in assessing whether areas are suitable for primate reintroduction.

An additional application of drones is assessing plant phenology (D’Odorico *et al.* 2020; Klosterman and Richardson 2017). In primatology, phenology monitoring is often conducted in a number of plots or along transects that are distributed throughout study sites (Marshall and Wich 2013), which gives a very useful but still limited dataset that does not cover a whole site and, in cases of primate species with large home ranges, might not be distributed throughout their whole range. If visual spectrum, multispectral, or hyperspectral drone images can be leveraged to provide such data through the calculation of various indices (e.g., enhanced vegetation index [EVI], normalized difference vegetation index [NDVI], and the entitled green-red normalized difference (GRND)) associated with leaf phenology (see Klosterman and Richardson 2017 for a nonprimate example), this would expand the spatial coverage of phenological patterns and allow studies to associate primate ranging (Peres 1994) and feeding behavior over large scales and in high detail. Studies in which drone-derived phenology indices are compared to phenology data from ground plots are needed to test this in areas where primates occur and should ideally address flower and fruit phenology as well as leaf phenology. Such studies have not been conducted yet. In a further step, actual leaf, flower, and fruit availability might be assessed from visual, multispectral, or hyperspectral data. This is as yet unexplored in primatology but methods are being developed and tested for fruits in the agricultural sector (Apolo-Apolo *et al.* 2020; Sarron *et al.* 2018; Senthilnath *et al.* 2016).

CTs are also useful in areas that researchers have trouble accessing, such as agricultural areas and human settlements. Human–wildlife conflict pervades these areas, and cameras can reveal primates’ use of them. In Guinea, for example, CT footage showed that chimpanzees temporally offset their use of key resources by visiting certain food trees when people are absent (Garriga *et al.* 2019). Similarly a study in Kibale National Park, Uganda, showed that chimpanzees crop-foraged during the night (Krief *et al.* 2014). Chimpanzees are not the only great ape that competes for land with humans. Orangutans range across forest of varying protected status, from national parks to commercial forest plantations, and abundance estimates require an understanding of their abundance over this mosaic landscape. A deployment of CTs across orangutan distribution revealed that individuals use two different types of commercial forest (*Acacia* and *Eucalyptus*), and secondary forest patches; the proximity to natural forest was the best predictor of their abundance (Spehar and Rayadin 2017). A similar study sought to assess Moor macaque (*Macaca maura*) use of farmland in Sulawesi, Indonesia. CTs provided data on the crop that monkeys foraged on most and the times of year monkeys were most active in people’s fields (Zak and Riley 2017). Although these data were informative, the authors acknowledged that for they would need observational for monkey identity, group size, and amount of crop eaten. In this case, however, camera data contributed toward resolving human–wildlife conflict, providing data on what crops primates ate and when crop foraging occurred for farmers and conservationists alike.

Disease

Along with habitat loss, disease (and especially zoonoses) is a key threat to wild primates and to great apes specifically (Gilardi *et al.* 1999). Of the technologies described so far, portable genomics offers the most promising means of transforming how field workers study and respond to outbreaks. *In situ* genomics decreases turnaround times, due to the lack of logistical barriers to transport samples to a different location. Short turnaround times make the diagnostics especially important for research on disease outbreaks, as demonstrated by successful use of the MinION sequencer in human healthcare for real-time detection of Ebola virus in West Africa (Quick *et al.* 2016), Zika virus in Brazil (Quick *et al.* 2017), and the current global SARS-CoV-2 pandemic (Fauver *et al.* 2020). In the current SARS-CoV-2 pandemic, viral whole genome sequences of (human) patient samples have been produced at unprecedented rates, in such a way that they are actively informing government response to the outbreak (Oude Munnink *et al.* 2020). During such global crises, reliably diagnosing infected patients, or especially molecularly characterizing viral or bacterial strains, can have dramatic effects on mediation at the local and also international level.

These *in situ* tools may be most applicable to African great apes owing to their higher terrestriality and sociality, but also because of their close genetic relationship with humans, compared to orangutans which means that cross-species infection is a threat to both great apes and humans alike. Emerging infectious diseases are thus considered to be one of the three main threats for great apes, alongside poaching and deforestation (Nunn and Gillespie 2016). Respiratory diseases are responsible for outbreaks in chimpanzees (Negrey *et al.* 2019; Patrono *et al.* 2020) and gorillas (Grützmacher *et al.* 2016) and can cause significant mortality

(Emery Thompson *et al.* 2018). Some of these outbreaks originate from human transmissions, confirmed through molecular analyses, and more of these early tests are being conducted on site. For example, at Dzanga Sangha Protected Areas in the Central African Republic, DNA amplification using PCR and subsequent detection by electrophoresis were performed on site to screen for human respiratory syncytial virus in western lowland gorillas (*Gorilla gorilla gorilla*). Tests revealed identical sequences of the virus in humans and gorillas (Grützmacher *et al.* 2016). Besides offering diagnoses, field labs that have qPCR facilities can provide quantitative information about viral loads in infected individuals. Evidence of rapid improvements to these field-facilities continues, with recently validated portable qPCR tests for canine distemper virus (Tomaszewicz Brown *et al.* 2020); the platform can be readily adapted to test for pathogens that pose high risks for primates.

These tools are particularly pertinent given the SARS-CoV-2 outbreak and its potential to inflict wild primates (Gillespie and Leendertz 2020). Several early studies suggest that African and Asian monkeys and apes, as well as some lemurs, are all likely to be highly susceptible to SARS-CoV-2. In comparison, platyrrhines and some strepsirrhines and tarsiers are less at risk of infection (Damas *et al.* 2020; Liu *et al.* 2020; Melin *et al.* 2020). Macaques (*Macaca mulatta* and *M. fascicularis*) have already been shown to be susceptible to this virus, whereas early results show no susceptibility for the virus in the common marmoset (*Callithrix jacchus*) (Lu *et al.* 2020).

Simultaneous molecular and observational *in situ* health monitoring of nonhuman primate species over the next few years offers the potential to reveal to what extent SARS-CoV-2 has infiltrated wild primates and simultaneously shine light on other infections currently going unnoticed.

Data Processing

One advantage of some of the techniques described in the preceding text is that they generate a large amount of data in a relatively short amount of time. Although data are typically beneficial to the conservation effort, the timely analysis of such data is a challenge (Norouzzadeh *et al.* 2018). For example, wildlife poaching is a global issue that impacts many primate species (Estrada *et al.* 2018) and although technologies produce useful raw data at short notice and real time, the significant delays in data processing limit its usefulness for poaching prevention and mitigation (O'Donoghue and Rutz 2016).

Until recently, data processing was often a manual process requiring hundreds of human-hours to deduce meaningful information that would inform conservation strategy. Areas such as computer vision and deep learning (DL) are helping to transform traditional data analysis processes undertaken by conservationists (Chen *et al.* 2019; Rowcliffe *et al.* 2016). Machine learning and advanced analytics that are already used in other domains such health and industry have seen limited use in conservation but have significant power in processing data and deriving new insights. By using these approaches data obtained from conservation studies can be directly used to identify trends and useful insights regarding animal and environmental health and behavior (Joseph *et al.* 2017). Machine learning can be used to automatically identify patterns and information of interest while discarding useless data (Kwok 2019).

Analytical platforms can automatically analyze data and provide useful visualizations to provide a clear understanding of primate populations across wide geographical

boundaries. For example, object detection allows us to automatically detect and report specific individuals in large image and video catalogs and even live streams (Brust *et al.* 2017; Buehler *et al.* 2019), and count populations over to model biodiversity and population health. This significantly decreases (manual) analysis time therefore potentially reducing costs and streamlining conservation studies. In its application to PAM data, where manual data processing is extremely labour intensive and time consuming, automated signal processing; for example, deep learning for efficient data extraction is increasingly required (Bianco *et al.* 2019). These techniques have proven highly efficacious, for example for chimpanzee drumming, Diana and king colobus monkey loud calls (Heinicke *et al.* 2015; Kalan *et al.* 2015), male orangutan loud calls (Spillmann *et al.* 2015), and female gibbon calls (Clink *et al.* 2019), with potential to expand these analytical techniques to other taxa.

Traditional analytic approaches in conservation are reactive in nature, with data collected over long durations and analyzed retroactively. In many instances intervention strategies to address threats such as poaching require data long before they have traditionally been available. For example, when researchers rely on feedback from global positioning system (GPS) tracking devices that have been attached to animals, signal loss often suggests the death of the animal, often by poaching, which can trigger a response by a nearby team to confirm the death (Massawe *et al.* 2017). This is a reactive approach that does not prevent the poaching event (Tan *et al.* 2016). Preventive efforts are in place to detect poachers, for example using drones (Bondi *et al.* 2018a,b). However, these approaches either require in-field human participation or off-line processing of video footage, and both contribute to output delays.

This is an area where it makes sense to use computer vision and DL to automate the process. Although drones (more recently equipped with DL capabilities) have shown great utility in surveying geographical locations, this power can be extended through the distribution of global system for mobile communications (GSM)-enabled camera traps. GSM cameras can detect the onset of incidents such as poaching and react as the event occurs to allow an early intervention (Chalmers *et al.* 2019; Wang *et al.* 2019). Distributing technology in this way has proven useful in illegal logging where networks of sensors connecting trees allow rangers to detect when a break in communications is detected because trees are cut down (Mporas *et al.* 2020). These systems are still reactive; however, the latency between incident and detection is reduced dramatically compared to traditional methods. Visualizing the network on an analytics platform it is possible to see black holes appear where trees are being removed. This allows rangers to detect and intervene when trees are being cut down, potentially resulting in a significant reduction in illegal logging.

Similar applications concern the identification of rare or cryptic species of high conservation value from automating species or even individual detection. DL and other facial recognition algorithms have been used to automatically or semiautomatically identify species or individuals in ring-tailed lemurs (*Lemur catta*: Crouse *et al.* 2017), chimpanzees (Crunchant *et al.* 2017; Loos and Ernst 2013; Schofield *et al.* 2019), and gorillas (Brust *et al.* 2017), with clear implications for many other species (Norouzzadeh *et al.* 2018).

Limitations

Costs

We hope to have made a compelling argument for the diverse applications of conservation technology to protect primate biodiversity. Cameras, acoustic sensors, drones, and portable labs have all been demonstrated to be reliable means of providing important data for practitioners and analysts alike. Technology comes at varying types and amounts of cost, though, which we summarize here.

Drones used by conservation researchers range in price from less than USD 1000 to more than USD 1 million, depending on factors such as sensors, flight duration, and durability. Increasingly, reliable drones can be purchased for hundreds (rather than thousands) of dollars, and thus have become more affordable to primatologists than even just a few years ago. The sensors that are attached to drones and that determine data type and quality drive the cost up. For example, one reason that hyperspectral cameras have not yet been used in primatology is their price tag, *ca.* USD 50,000 for a Rikola camera at the time of writing. This is easily the annual budget for many field-based projects and several times the annual budget for other field projects. Another limitation to drone use is that in most countries drone operations need to follow government guidelines, which almost always hamper operations in large areas because drones are restricted to being operated close (e.g., with 500 m) to the remote pilot on the ground. Whilst such guidelines are important for safety, exemptions for drone usage beyond 500 m from the remote pilot would facilitate primate research.

For PAM, the cost of commercial devices and accessories (microphones, batteries) has likely prevented primatologists from using this monitoring technology to date. The good news is that, although initial systems were expensive, the costs of acoustic sensors have declined as technology has improved (e.g., Solo: *ca.* USD 100; Whytock and Christie 2017) or Audiomoth: *ca.* USD 75; Hill *et al.* 2018) and now align more closely with primatologists' research budgets.

The infrastructure necessary to run any portable genetics machinery (e.g., power) and support for running costs are necessary concerns for any future field genomicist. Both the cost per sample and the necessary equipment are obstacles for any initial project. A maximum per sample cost of USD 25 (which would satisfy 53% of potential users) and a maximum instrumentation cost of USD 6000 per unit (which would work for 60% of users) was recently estimated (Masters *et al.* 2019). Portable genomics instrumentation is approaching these desired price ranges.

Power

Camera traps and acoustic sensors typically run on AA batteries, often the type readily available in any nearby town. Power for drones and genomics labs is far more complicated and expensive. Flying drones to assess habitat or density of wide ranging, low-density primates such as orangutans requires long flights over large areas (e.g., >5 km²), as the camera footprint is small, meaning flight duration must be several hours to capture sufficient ground (Burke *et al.* 2019). This means that multiple batteries need to be available to avoid charging during the day. Most drone batteries cost below USD

250, but some drone systems use multiple batteries (e.g., six for the DJI Matrice 600) simultaneously, which increases costs.

As any field biologist knows, the basic layout of a field lab can vary greatly. Some are basic tent or wooden structures without access to reliable electricity (Gowers *et al.* 2019; Menegon *et al.* 2017), whereas others are proper buildings with semi-reliable access to electricity (through access to the main electrical grid, a generator or solar panels) (Pomerantz *et al.* 2018; Quick *et al.* 2016). However, even the most luxurious field labs regularly have to deal with short or longer disruptions in the power supply. This complicates the scheduling of experiments that require a reliable energy supply for a fixed time, such as a 24-h run on a sequencing machine. Solar panels can offer solutions in some sun-rich areas, and power stations can provide temporary energy solutions, allowing for 1 or 2 days of genetic analyses depending on the type of research being done. The energy requirements will have to be assessed per research project and location, but complete off-grid analyses are possible (Blanco *et al.* 2020; Gowers *et al.* 2019; Guevara *et al.* 2018).

Sample Capacity and Networking

For field genomics, a current limitation is that it is not high-throughput. Because of limited budgets, some researchers pursue the lowest possible costs per sample, sequencing, for example 3500 samples on one MinION flow cell (Srivathsan *et al.* 2019). However, collecting, preserving, and preparing this quantity of samples requires considerable time, which will be challenging to achieve with the limited capacity offered by current portable molecular labs such as Bento Lab and miniPCR. Currently, there is a trade-off between high-throughput/cost-effectiveness and near real-time analyses/flexibility of sample processing (Chang *et al.* 2020; Knot *et al.* 2020).

Another limitation of the MinION is the error rate, which some argue limits the utility for metabarcoding (Loit *et al.* 2019), although there is a growing expectation that this is soon to improve, with rapid developments in flow cell chemistry and bioinformatics pipelines (Baldi and La Porta 2020; Chang *et al.* 2020; Krehenwinkel 2019b). Currently field implementation of metabarcoding requires more testing and validation. Offline bioinformatics is also a limitation, as most remote field sites lack sufficient network capability. Even offline bioinformatic pipelines, including relevant databases, need to be prepared before undertaking any field genomics.

Conclusion and Future Perspectives

The technologies presented in this review are already essential tools for wildlife biologists, providing data on species diversity, abundance, habitat, threats, and animal movement. They are not yet common in the typical primatologist's toolbox, but there are signs of their proliferation. None of these should be seen as a silver-bullet for primate surveys, but rather as tool for use under specific circumstances, sometimes with particular species. For example, acoustic sensors work best with loud calling species and drones with those that can be spotted from above.

For all technologies, access is limited to those with sufficient resources. For institutions and researchers with poor access to facilities or funds, large, upfront costs are prohibitive. Although successful deployment of some of these tools (e.g., drones, MinIONS) is necessarily restricted to those with training and expertise, others offer more potential for in-house research and development. In some cases, the support and training can be acquired remotely. For example, WILDLABS.NET supports an interdisciplinary community where researchers using field labs share ideas, challenges, and needs, and where collaborations are fostered, maintained, and expanded. Additional examples include hardware modifications to suit local needs, for example, tweaking the focal length and sensor sensitivity for the species of interest in camera traps (Welbourne *et al.* 2019), or else taking advantage of low-cost hardware such as the audiomoth (<USD50; Hill *et al.* 2018). In these ways, technologies can be developed in-house, independent of resource availability, so that their cost is not an impediment to their use, and their deployments can be sustained for conservation-related data gathering.

Nearly all of these techniques share scope for interdisciplinary collaboration. Those partnerships can be between scientists (e.g., biologists and engineers), and between academia and industry, where field primatologists can greatly benefit from the research and development of technologies that rely on large budgets to propel them forward. Together these groups can develop custom systems (and detectors) for particular habitats and species, and improve automated data mining, processing, and analysis. For example, Microsoft's AI for Earth platform provides a suite of tools under development, including for species classification and camera trap image processing (Joppa 2017).

Current technologies described here will also benefit in the near future from advances in microelectronics and the expansion of wireless communication networks (mobile networks or internet) that facilitate data transmission in real time, which is particularly important for responding to conservation threats at short notice (e.g., poaching) and to save unnecessary visits to collect them in person (e.g., SD cards for camera traps or acoustic sensors).

Combining technologies can further improve species monitoring. Drones have already been equipped with microphones that capture bat and bird sounds (August and Moore, 2019; Wilson *et al.*, 2017), and there are plans to diversify drone-acoustic applications to monitor terrestrial species, such as gibbons (Borchers, *pers. com.*). Similarly, by integrating camera traps with acoustic sensors, we can capture complementary data on biotic interactions and animal behavior across multiple scales and provide a more thorough picture of animal presence, movement, and communication than by using any single method on its own (Buxton *et al.* 2018). Further integrating physiology and remote sensing adds an even higher resolution of data on animal behavior and conservation (Kays *et al.* 2015). A further step in this approach is the Internet of Things (IoT), where heterogeneous sensors (e.g., camera traps, environmental sensors, biologgers) can communicate with each other without human intervention, opening avenues for gathering data on animal behavior and environmental changes at matching spatiotemporal scales.

Costs are declining for most of these tools, and access is improving; there is rich scope in the application of these new technologies to help conserve and protect primate biodiversity.

Ethical Note

This manuscript is a review of current technologies; there are no empirical data. This review adheres to the American Society of Primatologists principles for the ethical treatment of primates. The authors declare no conflicts of interest.

Data Availability This manuscript is a review of current technologies; there are no empirical data.

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