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Non-invasive genetic censusing and monitoring of primate populations

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Knowing the density or abundance of primate populations is essential for their conservation management and contextualizing socio-demographic and behavioral observations. When direct counts of animals are not possible, genetic analysis of non-invasive samples collected from wildlife populations allows estimates of population size with higher accuracy and precision than is possible using indirect signs. Furthermore, in contrast to traditional indirect survey methods, prolonged or periodic genetic sampling across months or years enables inference of group membership, movement, dynamics, and some kin relationships. Data may also be used to estimate sex ratios, sex differences in dispersal distances, and detect gene flow among locations. Recent advances in capture-recapture models have further improved the precision of population estimates derived from non-invasive samples. Simulations using these methods have shown that the confidence interval of point estimates includes the true population size when assumptions of the models are met, and therefore this range of population size minima and maxima should be emphasized in population monitoring studies. Innovations such as the use of sniffer dogs or anti-poaching patrols for sample collection are important to ensure adequate sampling, and the expected development of efficient and cost-effective genotyping by sequencing methods for DNAs derived from non-invasive samples will automate and speed analyses.

KEYWORDS
capture-recapture, conservation genetics, feces, mark-recapture, population estimation, wildlife monitoring

1 | INTRODUCTION

Primate populations in the wild are increasingly threatened by habitat loss and fragmentation (Bergl, Bradley, Nsubuga, & Vigilant, 2008; Campbell, Kuehl, N'Goran Kouamé, & Boesch, 2008; Junker et al., 2012; Roos et al., 2014; Schwitzer et al., 2014; Vijay, Pimm, Jenkins, & Smith, 2016; Wich et al., 2008), illegal activities (Plumptre et al., 2016; Ripple et al., 2016; Svensson et al., 2016), and disease (Leendertz et al., 2006; Rudicell et al., 2011; Walsh et al., 2003). The majority of primate species are thought to be declining in number and threatened with extinction (Estrada et al., 2017). Knowledge of population numbers and their distribution over time is essential for designing and assessing effective conservation measures as well as evaluating the level of threat for a given taxon. Particularly helpful is additional information on membership of individuals in groups and how dispersal by individuals, and consequent gene flow, occurs or is impeded across disrupted or fragmented landscapes. Furthermore, many demographic processes such as ranging, feeding and association patterns are dependent on population density, making these estimates critical to studying primate sociobiology.

Traditional approaches for estimating the abundance of primate populations typically rely upon the systematic assessment of the number and distribution of direct, and often indirect, signs such as nests, vocalizations, or feeding remains (Kühl, Maisels, Ancrenaz, & Williamson, 2008; Plumptre, Sterling, & Buckland, 2013). Obtaining direct counts of primates for population estimates is often challenging due to the low density and elusive behavior of individuals as well as low visibility in forested habitats. When direct counts are possible, distance sampling methods are often employed and estimation of detection probabilities based on visibility and proximity to the observer are required to extrapolate observations into population size estimates (Plumptre et al., 2013), which may vary from observer to observer (Mitani, Struhsaker, & Lwanga, 2000). Furthermore, when indirect signs such as nest counts are utilized, transforming these data into abundance estimates requires knowledge of local accumulation and decay rates, which may vary temporally and among locations and can be time-consuming to estimate (Kouakou, Boesch, & Kuehl, 2009; Todd, Kuehl, Cipolletta, & Walsh, 2008). These methodological issues have likely contributed to the high variability of reported primate densities across sites and habitat types (Buckland, Plumptre, Thomas, & Rexstad, 2010; Devos et al., 2008). Furthermore, as estimates based on the aforementioned assumptions and extrapolations tend to suffer from low precision, comparisons over time to monitor population size changes are highly problematic (e.g., Roy et al., 2014).

In recent years, genetic approaches for estimating population sizes have been used as a complement or alternative to nest count surveys in great apes. "Genetic censusing" may refer to any approach whereby DNA analysis serves to reliably attribute samples to different individuals to achieve an estimate of population abundance or density. To avoid the expense, danger, and behavioral impact of trapping or darting animals, genetic censusing studies largely rely upon non-invasively collected samples such as scats or hair samples. Although the use of non-invasive samples as a means toward population assessments was already demonstrated some 20 years ago (Kohn & Wayne, 1997; Taberlet et al., 1997), it is only in recent years that the approach has been adopted more widely, especially in great apes. To date few studies have utilized this method in other primates, although its potential for primate surveys is substantial (Chang, Liu, Yang, Li, & Vigilant, 2012; Orkin, Yang, Yang, Yu, & Jiang, 2016). Here we provide an overview of how non-invasive genetic censusing methods have been used in the primatology field thus far, highlighting advances in analysis techniques, the wealth of extra information that can be extracted from genetic census datasets, and study design considerations for researchers embarking on their own genetic censusing project.

2 | POPULATION SIZE ESTIMATION FROM GENETIC DATA

2.1 | Minimum count estimates

A genetic census will always produce a count of distinct genotypes, which can serve as a minimum estimate of the number of individuals in a given area. Such minimum count estimates may be the by-product of research aimed at other questions. For example, in a survey of simian immunodeficiency virus (SIV) prevalence in a low density, savanna-dwelling eastern chimpanzee population, genotyping of nearly 400 samples resulted in the identification (and therefore minimum count estimate) of 72 individuals in the area (Rudicell et al., 2011). However, genotype data do not necessarily allow further inference of the number of undetected individuals and, therefore, the estimation of population size. For example, the first attempt to incorporate genetic analysis into a mountain gorilla population survey included microsatellite genotyping of 384 samples of the Bwindi mountain gorilla population, which yielded 354 genotyped samples that were attributed to 257 individuals (Guschanski et al., 2009). The genetic data further documented that individual gorillas may make more than one night nest, and sets of nearby nests may be misattributed to groups, emphasizing the limitations of indirect signs alone as a means of censusing gorillas. Despite the large number of samples analyzed, the collection of all samples in just one field session excluded the possibility of independent resampling, which is necessary to evaluate the capture frequency of individuals and estimate the number of undetected individuals.

2.2 | Genetic capture-recapture population size estimation

More informative than a single sampling session are repeated visits to an area for sample collection over a prolonged period, allowing for the use of genetic capture-recapture (CR) population size estimators (Miller, Joyce, & Waits, 2005; Pennell, Stansbury, Waits, & Miller, 2013; Petit & Valière, 2006; Schwartz, Luikart, & Waples, 2007; Waits & Paetkau, 2005). Instead of tagging actual individuals, genetic CR studies build on the long history of use of capture-mark-recapture (CMR) in wildlife studies (Seber, 1982) by relying upon repeated "tagging" of an individual's DNA, such as through use of genetic characterization of feathers, fur, or scat. During ongoing collection of such non-invasive samples the individuals are sampled "with replacement" and can be "recaptured" multiple times. In contrast to traditional CR studies, which are characterized by distinct sampling sessions with samples from different sessions considered independent, ongoing sample collection for genetic CR requires explicit criteria for defining independent sampling events. For example, different samples from the same individual may be considered independent if they are separated geographically (by a specified minimum distance such as an average day travel distance) and/or temporally (as estimated by sample decay) (e.g., Arandjelovic et al., 2010; McCarthy et al., 2015).

In genetic CR studies, the probabilities of capturing individuals a single time, twice, three times, and so forth are computed from the number of times independent samples from the same individual are identified in the data set. From this, the probability of not sampling some individuals is calculated and the total population estimate along with its statistical uncertainty is thereby derived (for a detailed review see Lukacs & Burnham, 2005). Such estimation is often conducted using models implemented in the program CAPWIRE, which was developed to accommodate data from non-invasive genetic sampling

studies by allowing for multiple captures per individual in a session (Miller et al., 2005; Pennell et al., 2013). One model assumes that all individuals have the same probability of being captured, the Equal Capture Model (ECM). However, as certain individuals are more likely to be sampled and genotyped than others, in the Two Innate Rates Model (TIRM) individuals are assigned to have either a high or low capture probability in a way that optimizes the two capture probability distributions. An extension of TIRM, TIRMpart, allows for testing whether the exclusion of any individuals sampled anomalously frequently improves the fit of the rest of the data to two detection probabilities. After using the models to infer the maximum likelihood estimates of population size with confidence intervals derived from parametric bootstraps, researchers can select the model best fitting the data using likelihood ratio tests (Pennell et al., 2013). However, because differences in individual detection probability are a plausible outcome of behavioral differences linked to sex, age, or reproductive status (Petit & Valière, 2006), neglecting to account for capture heterogeneity can downwardly bias population size estimates. Small data sets may lack the power to statistically support TIRM over ECM, and thus it is prudent to employ the TIRM unless biological evidence suggests even capture probabilities (Puechmaille & Petit, 2007). Importantly, simulations testing the robustness of these estimators have shown that the confidence interval of point estimates includes the true population size when assumption of the models are met (Puechmaille & Petit, 2007), and therefore the range of population size minima and maxima should be emphasized in population monitoring studies rather than the point estimate.

Ideally, genetic censuses will not occur once or intermittently but be integrated into a long-term management scheme incorporating opportunistic collection and repeated systematic surveys (Brand et al., 2016; Gray et al., 2013). However, extension of sampling over several years risks violating the assumption of demographic closure, a requirement that there are no births, deaths or migrations in the study population. To investigate this issue using empirical data, researchers compared population size estimates inferred from 3 months versus 3 years of genetic sampling of a well-habituated eastern chimpanzee population (Granjon, Rowney, Vigilant, & Langergraber, 2017). Although the number of detections per sampled individual increased only modestly from 1.7 to 2.0, the estimate from the 3-year-period was markedly more precise (Confidence interval [CI] width: 46% of the estimate for 3 years, 60% for 3 months) and both estimates were similar to the known number of individuals present. Although this community increased from 173 to 195 individuals over the 3-year study period, nearly all of this growth was due to the birth of infants, who are very rarely sampled in opportunistic studies. Similarly, it was found that sampling of a western gorilla population over 3 years rather than shorter 1-year long sampling sessions provided more precise estimates of the total population size (Confidence interval [CI] width: 21% of the estimate for 3 years, 33% for 1 year) and did not effectively violate the assumptions of closure in capture–recapture estimators (Arandjelovic et al., 2010). This suggests that in primates with slow life histories, such as apes (Cheney, Crockford, Engh, Wittig, & Seyfarth, 2015), the improvement in precision obtained from lengthened sampling periods exceeds any biases arising out of slight violation of demographic closure assumptions such as may commonly arise from births of offspring.

Assessment of the effectiveness of conservation measures may require determining whether a population is decreasing, maintaining, or increasing in abundance. Ongoing genetic censusing can be used to infer population size changes between surveys if abundance estimates are sufficiently precise, which may be particularly challenging in species with slow life histories and hence low potential rates of growth. Forward simulations, using realistic parameter settings obtained from empirical studies, can aid in study design. For example, mountain gorillas have been the subject of several genetic censuses, which do not involve continuous sampling but rather intense effort during sessions lasting a few weeks or months. Roy et al. (2014) used empirical data on capture frequencies to estimate that as many as four or five independent capture sessions, repeated at five year intervals, would be necessary to confidently detect a low but realistic population growth rate of 2% per year in unhabituated Bwindi mountain gorillas.

3 | GENETIC ESTIMATES OF POPULATION SIZE AS COMPARED TO TRADITIONAL ESTIMATORS

Both indirect surveys and genetic studies require substantial effort in the field, so it is important to know if the additional time and expense of genetic laboratory analyses is justified by higher accuracy or precision. Because samples are unambiguously assigned to individuals, genetic censusing of wildlife can provide estimates that are more informative than those that can be inferred from indirect signs, such as feeding remains, nests, or paw prints. For example, results of one of the first studies employing a genetic census suggested twice as many giant pandas in a key reserve as had been previously estimated using bite sizes in feeding remains (Zhan et al., 2006). Similarly, a study of otters in a complex environment found twice as many individuals via genotyping of feces than snow tracking (Hájková, Zemanová, Roche, & Hájek, 2009). In a direct comparison accounting for the duration of the field effort expended either counting nests or collecting fecal samples for a genetic census of western lowland gorillas, researchers showed that population estimates obtained were of similar precision for both approaches for up to 3 months of field work, but with further fieldwork the genetic census was more precise than the nest estimate (Arandjelovic et al., 2010).

Although it is challenging to definitively compare methods when the absolute number of animals is not precisely known, some studies that have compared known or approximately known wildlife population sizes to those estimated using genetic approaches suggest genetic estimates are accurate and reasonably precise. In one such study researchers compared the number of brown bears estimated using a helicopter survey aided by radio telemetry with estimates made using genetic methods. Results showed that the genetic estimate was more precise and probably more accurate, as well as markedly less expensive and less stressful to the subjects (Solberg, Bellemain, Drageset,

Taberlet, & Swenson, 2006). Genetic and field population size and survival estimates were similar for a study comparing 10 years of data from the approximately 30 members of the Isle Royale wolf population, which was subject to yearly counts using a light aircraft during a 2-month field season (Marucco, Vucetich, Peterson, Adams, & Vucetich, 2012). For another small population, an area thought to number between 24 and 34 European badgers was genetically surveyed and estimated to contain some 29 (range: 20–43) individuals (Frantz et al., 2003). There may be individual differences in the tendency for members of some species to leave feces as scent marks directed at conspecifics, but one study found a similar sex ratio in a sampling of feces as in a set of otter carcasses collected over time in the same area, suggesting no large sex difference in fecal deposition rates (Dallas et al., 2003).

With regard to primates, several studies of great apes have compared results from genetic CR studies with expectations based upon direct monitoring and found good agreement between estimates. For example, a diminished forest reserve of only 9 km^2 was estimated, via opportunistic observation, to contain 19 eastern chimpanzees. Complementary genetic analysis of 70 samples and CR estimation suggested a population size of 22 individuals with a CI of 19–29 (Chancellor, Langergraber, Ramirez, Rundus, & Vigilant, 2012). Similarly, a genetic CR estimation of eastern chimpanzee population sizes in a fragmented forest region in Uganda produced estimates for two fragments of 19 (95%CI 17–21) and 38 (95%CI 31–56), which are consistent with estimates of 19 and 34, respectively, from conservation monitors (McCarthy et al., 2015). However, the genetic estimate for a third fragment appeared low (8, 95%CI 8–9) as compared to a monitoring estimate of 15, possibly due to lower temporal and spatial sampling intensity. In a study of a larger eastern chimpanzee population, Granjon et al. (2017) employed opportunistic sampling of fecal samples for genetic analysis across the 35 km^2 territory of a habituated eastern chimpanzee group of known size (~190 individuals). The study effectively accounted for observed differences in sampling probabilities between individuals, resulting in accurate population size estimates with confidence intervals encompassing the known number of individuals (Granjon et al., 2017). Taken together these studies suggest that with proper planning, genetic censusing can provide equally, and in some cases more, accurate population size estimates when compared to traditional survey methods.

4 | RECENT INNOVATIONS IN CAPTURE RECAPTURE ANALYSIS

4.1 | Spatially explicit mark recapture (SECR) population density estimation

Programs to estimate population size such as CAPWIRE assume that individuals are mixing (i.e., the "urn" model) and grid simulations have shown that CAPWIRE is fairly robust to spatial structure as it is encompassed in the capture heterogeneity (Miller et al., 2005). However, researchers may be interested in incorporating information about spatial distribution of individuals directly in an estimation of population density. Spatial models account for differences in capture probability among individuals arising out of differential use of the landscape, as might occur when individual home ranges vary in their proximity to fixed "traps": sample or photo/video collection points. Spatially explicit models also accommodate variable temporal sampling effort at different trap locations. The two key parameters estimated in SECR models are the probability of detecting an individual at at trap placed at its activity center (g_0) and a measure of how quickly detection probability decreases with increasing distance between the trap and the activity center (σ) (Borchers, 2012). An extension of distance sampling methods, these models are an area of active research (Borchers & Marques, 2017) and have already met widespread usage in studies of solitary carnivores occurring at low density and utilizing large ranges, such as in a study employing genetic sampling of bears using hair (Howe, Obbard, & Kyle, 2013). Given the fixed location of "sampling points," spatially explicit models are particularly applicable to photo trap data and have been applied to studies of bobcats (Thornton & Pekins, 2015), tigers (Karanth, Nichols, Kumar, & Hines, 2006), as well as apes (Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Head et al., 2013). Because the quantity estimated is the density of individuals rather than the number, spatially explicit models are particularly applicable to situations where the spatial limits of the population to be estimated are not apparent, such as in a survey of a portion of a large forest (Borchers & Efford, 2008).

When compared to non-spatial models, spatial models produce similar estimates (e.g., Granjon et al., 2017; McCarthy et al., 2015; Whittington & Sawaya, 2015) and some researchers have considered the statistical performance of spatial approaches better than non-spatial methods (Blanc, Marboutin, Gatti, & Gimenez, 2013). One recent study compared the performance of two different spatial CR model estimates applied to a grid-trapping sampling of a population of small mammals whose density was independently estimated using extensive trapping (Gerber & Parmenter, 2015). Results showed that both Bayesian and likelihood approaches provided biased density estimates of low precision and suggested that assumptions of independent activity of individuals and similar patterns of space use by each individual are unlikely to be met in real animal populations. High heterogeneity arising out of individual variation may be substantial in primate populations due to territoriality, social behavior, sex differences, and other factors, making it challenging to incorporate these factors into models. While extensive sampling can aid in detecting and modeling such detection heterogeneity (Howe et al., 2013; Spehar, Loken, Rayadin, & Royle, 2015) the effort involved means that non-spatial approaches based upon simply redetecting a large proportion of the population may be more effective (e.g., Gerber & Parmenter, 2015).

Several studies recently explored the use of both non-spatial and spatial population size estimation as applied to chimpanzee populations. Results from spatial and non-spatial estimators were of similar precision, but these studies highlight the difficulty of extrapolating from spatially-explicit density estimates to abundance estimates in social animals with unknown territory boundaries while illustrating the potential to compare density estimates among habitat types

(McCarthy et al., 2015; Moore & Vigilant, 2014). It has proven difficult to employ a standardized grid cell design for collection of fecal samples from great apes, as the rate of sample encounter is very low without the use of additional information such as trail signs, vocalizations, or other information. This suggests that, as in other taxa (e.g., cougars, Davidson, Clark, Johnson, Waits, & Adams, 2014), although researchers will explore use of multiple non-spatial and spatial estimators, non-spatial methods may remain more practicable for primate genetic CR studies (Granjon et al., 2017; Moore & Vigilant, 2014, L. Hagemann personal communication).

4.2 | Kinship- and pedigree-based population size estimation

Innovations in capture-recapture models may improve the precision and accuracy of estimates in the future by better capturing the particular characteristics of individual and population dynamics. Motivated by a need to extend the CR framework to include large populations where resampling of individuals is unrealistic or impossible (as in a commercial fishery), researchers have generated population size estimates based on the sampling of close kin (Bravington, Skaug, & Anderson, 2016). However, this approach requires sparse sampling of large populations to avoid violating an assumption of approximate independence of pairwise comparisons, and so may not be applicable to small, intensively sampled primate populations. Approaches based on pedigree inference are subject to the difficulties of accurate pedigree reconstruction from wild populations (Städele & Vigilant, 2016) and it remains to be seen if these approaches are superior to CR population estimation (Creel & Rosenblatt, 2013; Spitzer, Norman, Schneider, & Spong, 2016).

5 | SAMPLE COLLECTION CONSIDERATIONS

5.1 | Number of samples to collect

Capture-recapture population size estimates increase in accuracy and precision as the frequency of recaptures increases. A rule-of-thumb suggests that 3–4 times as many samples as individuals expected to occupy the area should be collected, although relatively fewer samples may suffice for populations numbering more than a hundred individuals (Miller et al., 2005; Mumma, Zieminski, Fuller, Mahoney, & Waits, 2015; Petit & Valière, 2006). For example, after analyzing more than 865 chimpanzee samples, McCarthy et al. (2015) achieved an average of 3.5 captures per genotyped individual and using the TIRM model as implemented in CAPWIRE obtained a population size estimate of 256 (95%CI: 246–321), supporting an argument that the previous estimate of 70 chimpanzees based on indirect signs was a severe underestimate. Even small samples can aid in pilot and survey research, such as at a new bonobo research site where the collection of 53 samples over 8 days lead to the inference that at least 19, and possibly as many as 66 individuals used the surveyed area (Brand et al., 2016).

Genotyping success should also be considered when planning sampling design. Not all fecal samples yield analyzable DNA, and the success rate may be influenced by myriad factors such as diet, ambient temperature and rainfall, time since defecation, individual health status, sample storage methods, training of the collector, and DNA extraction methods. Studies of habituated or semi-habituated primates may have genotyping success rates approaching 90% or higher (chimpanzees: 97%, Chancellor et al., 2012; gorillas: 90%, Roy et al., 2014), probably due to prompt collection of fecal samples upon production by identifiable individuals (Nsubuga et al., 2004; Reddy et al., 2012). In contrast, in a survey context in which animals are not closely followed, samples tend to be highly variable in quality with some studies reporting high genotyping success rates DNA (gorillas: 82–95%, Arandjelovic et al., 2010, 2015; chimpanzees: 77–83%, McCarthy et al., 2015; Moore & Vigilant, 2014; coyotes: 76–86%, Mumma et al., 2015; brown bears, 70–80%, Solberg et al., 2006) and others demonstrating more moderate success such that in some cases, less than half of collected fecal samples may yield analyzable DNA (chimpanzees: 39–59%, Arandjelovic et al., 2011; Basabose et al., 2015; Granjon et al., 2017; Sichuan snub-nosed monkeys: 58%, Chang et al., 2012; black bears, 29–33%, Mumma et al., 2015). Pilot studies, particularly for species or areas not previously genetically analyzed, can aid in estimating the success rate of analysis from fecal samples and inform sampling and fieldwork design (Figure 1).

5.2 | Field collection design

It may be hypothesized that systematic acquisition of samples might be aided by defining grid cells across the survey area, thereby allowing broad, repeated, and evenly distributed visits throughout a study area. Such grid cells are typically of dimensions that can be easily searched by a survey team in a single day, such as 1×1 km or 2×2 km (accounting also for time needed to travel back and forth to the grid cells). However, due to the typically uneven temporal use of home ranges or territories in many primate species, a strict grid-based study design with a fixed schedule and completely consistent effort may not be feasible and incorporation of knowledge concerning subject whereabouts in real time can improve chances of sample detection (Arandjelovic et al., 2015; Olson, Cameron, Reed, Ondzie, & Joly, 2012). For example, knowing where a species may be feeding and ranging at a certain time of year thanks to camera traps or knowledge of fruiting trees and phenology can allow researchers to visit certain grid cells when individuals are more likely to be in those areas. However, daily searches of targeted grid cells should be as independent as possible, with researchers searching cells with as little bias from the previous day's search success as possible (Arandjelovic et al., 2015). All cells of the grid should be searched before any cells are revisited to promote evenness of search effort across the study zone (Figure 1). A simulation of sampling design based on chimpanzee densities and fecal deposition rates found that combining transects with reconnaissance sampling was optimal for estimating ape density over a 4,225 km^2 landscape (Olson et al., 2012).

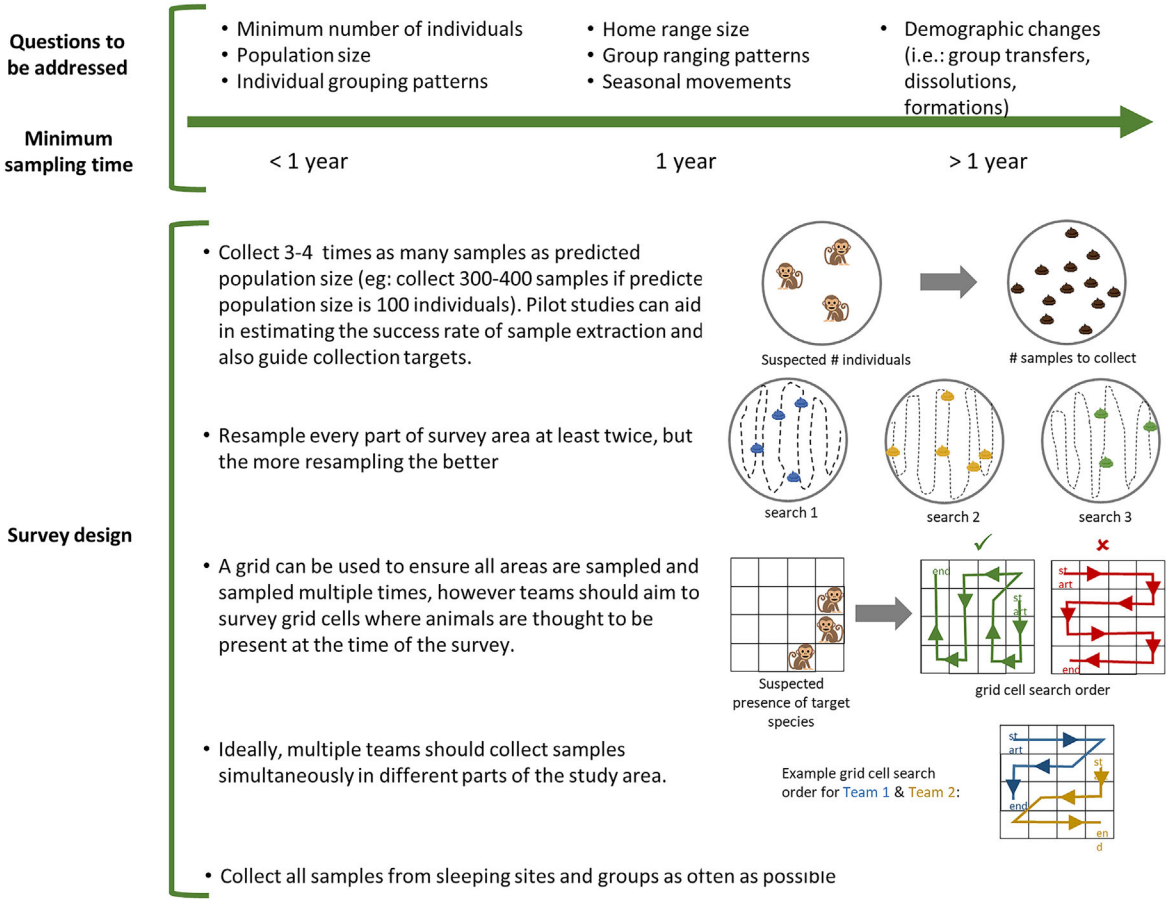

FIGURE 1 Aspects to consider when designing a genetic capture-recapture study

Uneven use of home ranges in primate species may also make hair trapping, another non-invasive genetic sampling method, challenging for many primate species. Hair trapping involves placing wire or sticky tape at locations that the animals are known to frequent (or are lured to using scent baits) and in such a position that the animal will rub against it (Taberlet, Waits, & Luikart, 1999). For example, hair traps have been effectively used to collect samples for genetic censusing of Australian wombats, which are fossorial and nocturnal, by suspending double sided sticky-tape across their burrow entrances over-night (Banks, Hoyle, Horsup, Sunnucks, & Taylor, 2003; Sloane, Sunnucks, Alpers, Beheregaray, & Taylor, 2000). Hair traps have also been frequently used to survey grizzly bear populations by using scent baits to lure individuals to the location where low hanging wire, which catches hair, has been suspended (Kendall et al., 2008; Mowat & Storbeck, 2000; Proctor, McLellan, Strobeck, & Barclay, 2004). While hair trapping can decrease field effort by removing the need to search for samples, its use for genetic censusing in primate species has yet to be demonstrated, although in principle could be possible for some species (Oka & Takenaka, 2001).

To increase the time- and cost-efficiency of fieldwork, collection of fecal samples for genetic monitoring may be combined with other activities, such as surveys of illegal activities. For example, field assistants associated with the Ngogo Chimpanzee Project in Kibale National Park, Uganda routinely search for illegal snares in areas of the park occupied by other, unhabituated chimpanzee groups. The opportunistic collection and subsequent genotyping of chimpanzee samples acquired on such "snare patrols" provides information on the number and distribution of chimpanzees through the park (K. Langergraber & C. Rowney, personal communication).

Another strategy for improved sample collection efficiency relies on scat-detecting dogs and their superior ability, after appropriate training, to find feces from target species (Mackay, Smith, Long, & Parker, 2008; Wasser et al., 2004). In a pilot study of Cross River gorillas, scat-detecting dog teams were better than humans at detecting solitary fecal piles and were less biased toward collecting certain individuals, thereby resulting in improved population estimates (Arandjelovic et al., 2015). A major limitation of using scat-detecting dogs in primate range countries has been the expense and challenge of importing and acclimating dogs trained in North America. However, by engaging in supplemental training of dogs already used in local law enforcement, researchers recently demonstrated a more cost-effective approach by concurrently collecting fecal samples from three sympatric Asian primate species in China (Orkin et al., 2016). Furthermore, as dogs can be trained on multiple targets, partnering with in-country organizations already using detection dogs for anti-poaching or wildlife product detection would be another option for reducing the costs associated with scat-detection initiatives.

6 | GENETIC ANALYSIS CONSIDERATIONS

6.1 | Microsatellite genotyping

Analysis of multiple microsatellite loci is typically used to genotype fecal DNA extracts. These loci represent repeats of short DNA motifs, varying in the number of repeats and, therefore, length. Microsatellites are highly variable, and so analysis of as few as 8–12 loci is typically sufficient to distinguish even related individuals with statistical confidence (PID_{sibs}: Waits, Luikart, & Taberlet, 2001). Microsatellite data can also be used to reveal species of origin if it is difficult to distinguish among scats from closely related species (Arandjelovic et al., 2010; Kohn et al., 1999; Orkin et al., 2016). Similarly, sex-linked markers can be used to determine the sex of individuals (e.g., Bradley, Chambers, & Vigilant, 2001; Di Fiore, 2005).

Previously developed and tested microsatellites are available for many primate species. It is also possible, if microsatellites have not been developed for a particular species, to use loci developed for a related species, although pilot data should be obtained to test the efficiency of genotyping (Primmer, MøLler, & Ellegren, 1996). The need for taxon-specific markers stems from the fact that PCR primers require a high degree of homology to the target region in order to function. If microsatellite loci have not been developed for the study species or any close relatives, new markers will need to be developed. Traditionally this was a cumbersome process involving cloning and sanger-sequencing (e.g., Muniz & Vigilant, 2008). However, the recent advent of high-throughput sequencing now allows microsatellite markers to be identified relatively quickly and cost-efficiently, without *a priori* selection of repeat type or sequence (De Barba et al., 2017; Gardner, Fitch, Bertozzi, & Lowe, 2011).

6.2 | Error minimization

Errors in microsatellite genotyping may arise due to the typically low concentration and quality of DNA extracts obtained from non-invasive samples (Constable, Packer, Collins, & Pusey, 1995; Vigilant, 2002). As has been extensively addressed elsewhere, errors can be minimized by extensive replication of results, monitoring of DNA concentrations to identify particularly problematic extracts (Arandjelovic et al., 2009; Morin, Chambers, Boesch, & Vigilant, 2001; Pompanon, Bonin, Bellemain, & Taberlet, 2005; Taberlet et al., 1996), and checking of results for patterns suggestive of non-amplification of alleles (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998), with any remaining low levels of residual error not expected to notably bias population size estimates (Petit & Valière, 2006). Genotyping errors can also be introduced if microsatellite loci used for genetic analysis are not sufficiently variable. To determine whether chosen loci are informative enough to accurately distinguish individuals, probability of identity (PID) analysis should be performed. PID analysis uses allele frequencies to estimate the probability of two random individuals (Paetkau & Strobeck, 1994) or, more conservatively, two full siblings (PID_{sibs}, Waits et al., 2001) being erroneously identified as the same individual. A PID_{sibs} value of 0.01–0.0001 is usually considered sufficiently low for genetic censusing studies (Waits et al., 2001).

6.3 | Beyond microsatellites

Microsatellite analysis involves the assessment of allele length relative to a standard, not elucidation of a nucleotide sequence, and so it is difficult to automate or standardize between laboratories. High-throughput analysis of hundreds or thousands of samples will become feasible when researchers turn to automated analysis of sequence variation at multiple single nucleotide polymorphisms (SNPs) across the genome. However, despite several publications demonstrating that genomic scale DNA sequence or SNP information can in principle be extracted from fecal DNAs (de Manuel et al., 2016; Hernandez-Rodriguez et al., 2017; Perry, Marioni, Melsted, & Gilad, 2010; Seeb et al., 2011; Slate et al., 2009; Snyder-Mackler et al., 2016), successful extension to the larger sample sizes needed for population assessments has not yet appeared and may await further increases in efficiency and decreases in costs.

7 | ADDITIONAL INSIGHTS FROM GENETIC CENSUS DATA

7.1 | Community membership, range size estimation

Members of primate social groups typically spend time in the proximity of one another within the confines of the home range of the group. This means that the spatial and temporal association of non-invasive samples can provide clues regarding the membership of even wholly unobserved groups as well as the areas occupied by those groups. Group associations are inferred using the principle that two individuals who are sampled in close proximity, such as from the same group of nests, are members of the same social group. If one of those individuals is subsequently found near a third individual, all three individuals are assumed to be members of the same group (Figure 2). Group dynamics of red howler monkeys were investigated in a series of pioneering studies incorporating genetic analysis using allozymes, a now obsolete means of gauging relationships via similarities in protein electrophoretic profiles (Pope, 1992, 1998). Similarly, Arandjelovic et al. (2010) used genotypes from nearly 3 years of sampling at a 101 km^2 area of Loango National Park to infer the presence of at least seven and potentially as many as 11 groups using that area. Along with minimum home ranges for that period, it was also possible to identify a group dissolution event and multiple instances of individuals changing group affiliation. By extending the sampling period by 2 years, the researchers elucidated further group dissolutions and formations and individual dispersal events (Arandjelovic, Head, Boesch, Robbins, & Vigilant, 2014). Similarly, researchers effectively used genetic analysis of samples from a habituated as well as unhabituated western gorillas to elucidate the changes in group membership following death of the silverback gorilla (Jeffery, Abernethy, Tutin, Anthony, & Bruford, 2007). Going beyond assessment of group membership, in two

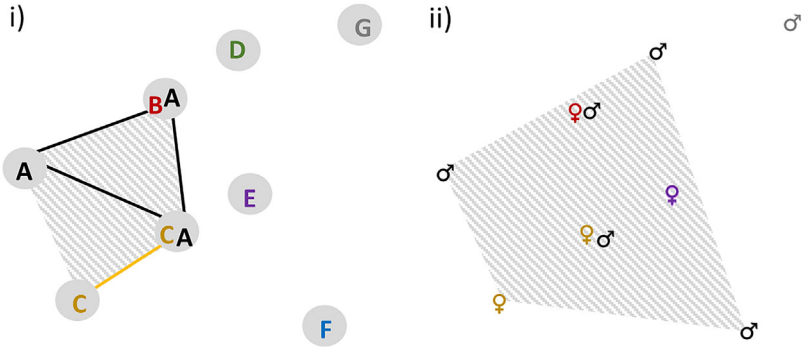

FIGURE 2 Determination of group compositions and minimum home range/territory size. (i) Each coloured letter represents a unique individual and its relative sampling location. Light coloured circles represent sampling locations, samples found at the same sampling location are assumed to be members of the same social group. When samples from the same individual are found multiple times over the course of the study we are able to delineate the minimum home range/territory of the social group (hatched areas) by linking the samples together (solid lines). (ii) Additionally, in the case of patrilocal primates with territories (e.g, chimpanzees), males (♂) that carry the same Y-chromosome haplotype (here, designated by the same colour ♂ symbol) are assumed to belong to the same community and the minimum territory designation can be extended to include these males (males A, D, and F). Females (♀) found within these territories can also be assumed to belong to the males' community (e.g female E)

different studies of multiple unhabituated western gorillas, parentage and kinship analyses were used to infer that female gorillas are found with female kin more often than chance and therefore may have the potential to benefit from kin-biased behavior (Arandjelovic et al., 2014; Bradley, Doran-Sheehy, & Vigilant, 2007).

Unlike gorilla groups, which are fairly stable in composition over the course of weeks or months but unstable over the longer-term, chimpanzee social groups or communities exhibit short-term instability due to the daily formation of small subgroups or "parties." This fission-fusion dynamic does not, however, prevent the elucidation of group membership using non-invasive samples and repeated sampling as described above. In addition, chimpanzees are characterized by female dispersal and male philopatry, and consequently the paternally-transmitted Y-chromosomes are expected to differ between groups. A comparison of Y-chromosome microsatellite haplotypes among habituated eastern chimpanzee communities demonstrated that distinct Y-haplotypes are typically not shared between groups (Langergraber et al., 2007), although low levels of male-mediated gene flow may be present in western chimpanzees and bonobos (Schubert et al., 2011). Using the assumption that the distributions of differing Y-chromosome haplotypes delineate chimpanzee territories, a study of central chimpanzees identified seven spatially distinct Y-chromosome haplotype clusters. Due to the territorial nature of chimpanzees, it could be further assumed that all female genotypes identified within these clusters belonged to the same community of chimpanzees (Arandjelovic et al., 2011). This method was further utilized in a study of eastern chimpanzees living in a savannah habitat (Moore & Vigilant, 2014) and a study of eastern chimpanzees in a fragmented forest which argued for the presence of at least nine communities based upon the spatial distribution of associated genotypes and the mostly concordant distribution of distinct Y-chromosome haplotypes among putative communities (McCarthy et al., 2015).

These studies illustrate the potential to gain insights by combining genetic assessment of group membership and dyadic relationships with targeted observational information encompassing several groups. However, a study of multiple groups of black and white colobus raises an important cautionary note by illustrating how the sole use of genetic data, without supplementary demographic information, may lead to incorrect inferences regarding dispersal patterns (Harris, Caillaud, Chapman, & Vigilant, 2009).

7.2 | Behavioral inferences

Information from genetic sampling can aid and add context to efforts to habituate selected social groups to human observation. Habituation of great ape social groups can take as many as 10 years or more, and is typically accomplished by persistent attempts to consistently follow a selected group. Genetic analysis of samples can reveal whether a particular group is consistently followed and highlight interactions with neighboring groups when habituation is not complete and groups cannot be followed constantly (Bradley, Doran-Sheehy, & Vigilant, 2008). For example, researchers at a newly started research site heard vocalizations and saw subsequent evidence of a fatal encounter among wild chimpanzees in Loango National Park, Gabon (Boesch et al., 2007). Genetic analysis of DNA derived from fecal samples collected at the attack site and nearby and analyzed as part of a CR study (Boesch et al., 2007) showed that the presumed attacking males all shared a particular Y-chromosome haplotype distinct from that of the dead male, lending support to the inference that this represented an inter- and not intra-community killing.

In a study using genetic capture-recapture for analysis of an Asian primate, researchers assessed the number and distribution of Sichuan snub-nosed monkeys across a portion of a 705 km^2 reserve (Chang et al., 2012). In addition to providing an abundance estimate, repeated genetic detection of individuals from one group at different locations

demonstrated that monkeys are capable of crossing a heavily used road that bisects the park.

7.3 | Monitoring reintroductions and translocations

Release of captive individuals into the wild may be done in order to improve the chances of population survival and/or benefit captive, often orphan, individuals. Genetic monitoring of individuals via sampling prior to release and periodic collection of non-invasive samples is essential not only for tracing the fate of individuals, but to evaluate whether the goals of increasing genetic diversity and reducing inbreeding depression are met (IUCN/SSC, 2013). Genetic analyses following the reintroductions and translocations of golden lion tamarins over the last 30 years demonstrate that while populations may grow, genetic diversity in the form of allelic diversity tends to decrease, particularly when habitat fragmentation limits gene flow (Moraes et al., 2017). As in the golden lion tamarins, mortality was substantial among 37 chimpanzees introduced into the Conkouati-Douli National Park, Republic of Congo (Goossens et al., 2005). However, observers reported that four released females produced five offspring, one of which was genotyped and attributed to a released male (Goossens, Setchell, Vidal, Dilambaka, & Jamart, 2003).

A meta-analysis of "genetic rescue" studies in wild species suggests that the benefits of increasing gene flow to isolated populations exceeds the risks of outbreeding depression (Frankham, 2015) and increasing population fragmentation may motivate greater implementation of such translocations in many species, including primates. Guidelines for such interventions advocate genetic assessment of donor and recipient populations and long-term genetic monitoring (Hedrick & Fredrickson, 2010). Such guidelines post-date reintroductions carried out at a captive orang-utan rehabilition site in the 1970s and 1980s, but recent genetic analysis has traced the origin of some individuals and demonstrated that introgression between subspecies has occurred, possibly to a considerable extent (Banes, Galdikas, & Vigilant, 2016).

7.4 | Complementary information on diet, parasites, and pathogens

In addition to genetic information from the depositor, non-invasively collected fecal material can provide genetic data from the depositors' diet and commensal organisms that could usefully complement a capture-recapture study. For example, there has been an appeal for systematic health monitoring of great ape population including use of non-invasive as well as necropsy samples (Leendertz et al., 2006). The extensive literature on molecular epidemiology studies in primates utilizing feces is beyond the scope of this review, but includes insights such as the African origin of the malaria parasite *Plasmodium vivax* (Liu et al., 2014) and the primate origins of the viruses causing AIDS in humans (Sharp & Hahn, 2011). Additionally, food resources play a key role in structuring the social lives of primates, and macroscopic examination of feces has long been used to infer the components of primate diets but is tedious and limited to the identification of visible remains (Moreno-Black, 1978; Phillips & McGrew, 2014; Tutin & Fernandez, 1993). Recent studies have shown that DNA sequences derived from primate diets (Bradley et al., 2007b; Hamad, Delaporte, Raoult, & Bittar, 2014; Mallott, Malhi, & Garber, 2015; Mallott, Garber, & Malhi, 2017; Quéméré et al., 2013), and gut microbiomes (e.g., Aivelo, Laakkonen, & Jernvall, 2016; Degnan et al., 2012; Tung et al., 2015) can be amplified from primate fecal extracts (Mallott et al., 2017). However, caution is warranted as it is possible to obtain valid but misleading results arising out of contamination of samples (such as from soil or insect eggs) or inadvertent consumption (such as insects present in fruit) of exogenous DNA (Hofreiter, Kreuz, Eriksson, Schubert, & Hohmann, 2010; Mallott et al., 2015; Pompanon et al., 2012).

8 | DISCUSSION

Genetic evaluations of population size, social grouping, and population dynamics in primates are still underused but highly valuable for studying populations non-invasively. Genetic estimates of primate density and abundance are often more accurate and precise than those obtained using other survey methods. Nonetheless, research and monitoring goals should be considered carefully prior to implementing a genetic census to ensure adequate sample sizes and appropriate sampling design, as well as the collection of valuable ancillary data. Careful study design can also help ensure that assumptions of CR models are not violated during analysis.

When interpreting results from a genetic CR study, it is important to note that the variation encompassed within the confidence intervals around the obtained point estimate is the more informative value for understanding the true population size and subsequent growth or loss over time. Therefore, emphasis should not be placed on reporting the point estimate from estimators but rather the population size minima and maxima. Subsequent analyses on population growth or retraction should also focus solely on whether there is a statistically significant change in the population size given the confidence interval widths (Figure 3).

In addition to the insights provided by employing genetic census methods to estimate primate density and abundance, such data can also be used to make inferences regarding group dynamics, dispersal patterns, ranging behavior, and kinship. Even in the absence of direct observational data, therefore, genetic monitoring methods may help address critical questions related to primate behavioral ecology and conservation.

As mentioned, few genetic CR studies have been undertaken in primate taxa beyond the great apes. Mark-recapture studies using radio collars or body markings which require animals to be trapped have been carried out in some species (e.g., Azari night monkeys: Fernandez-Duque & Rotundo, 2003; brown mouse lemurs: Weidt, Hagenah, Randrianambinina, Radespiel, & Zimmermann, 2004) although there is an increasing move away from such studies whenever possible (Cunningham, Unwin, & Setchell, 2015). The collection of feces from unhabituated wild primate populations is

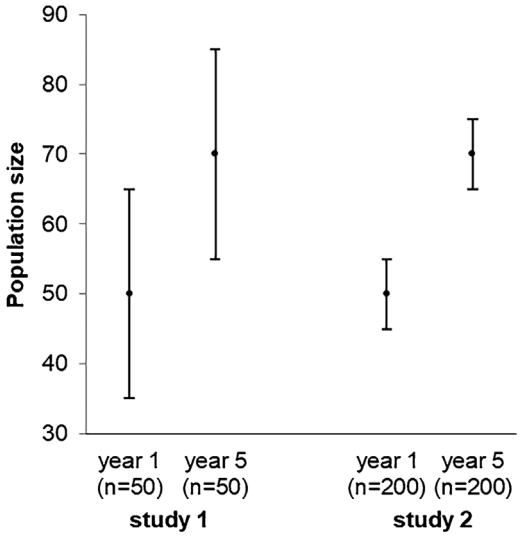

FIGURE 3 Higher precision (narrower confidence intervals) allows for greater statistical power for inferring changes in population size when they occur. In this hypothetical example, surveys were conducted 5 years apart on the same population. In the first study only 50 samples were collected each year, whereas in the second study 200 samples were collected each year. Larger sample sizes increase the chance that individuals will be resampled during a survey. Population estimates for both year 1 and year 5 surveys result in the same point estimates; however, the surveys in study 2 with the larger sample sizes have much higher precision and allow for the detection of a population increase. In study 1 there is no statistical difference between the survey estimates as the confidence intervals overlap to a high degree

possible and has been undertaken in a variety of new and old world primates to examine questions regarding population history and diversity (see reviews: Di Fiore, 2003; Vigilant & Guschanski, 2009). Extending these studies so that sampling areas are revisited over time to ensure multiple samples from individuals temporally and spatially would allow for CR population estimates. Due to the generally faster life histories of most monkey species as compared to great apes, future studies in the field will need to focus on the maximum length of sampling periods that are possible without violating the assumptions of current population estimation models. Many non–ape primate species have significantly smaller home ranges than most great apes which should allow more groups to be monitored simultaneously while also ensuring better sampling overall in a given area. Furthermore, the utility and cost-efficiency of using detection dogs for collecting fecal samples from multiple primate species at a time has already been demonstrated, suggesting that this methodology is very promising for primates in general (Orkin et al., 2016).

Finally, information from genetic CR studies may be usefully integrated with data from other approaches. Recent studies have shown that integrating GPS telemetry, camera trapping, acoustic monitoring and other sources of species detection with genetic surveys can help direct survey effort and improve estimates (Caniglia, Fabbri, Galaverni, Milanesi, & Randi, 2014; Galaverni et al., 2012; Lesmerises, Rebouillat, Dussault, & St-Laurent, 2015; McClintock, 2015). For example, camera trapping or monitoring can reveal innovative behavior such as algae fishing or termite fishing by chimpanzees (Boesch et al., 2017; Sanz, Morgan, & Steven, 2004). If incorporated with non-invasive sampling, as done in some other species (Braczkowski et al., 2016), it would be possible to link behaviors to individuals and potentially reveal sex biases in behavior (Kendal et al., 2015; Yeaman, Bshary, & Lehmann, 2011) and the spread of behaviors among individuals or social units (Lind & Lindenfors, 2010). Given the need to efficiently conduct baseline research and to sustain monitoring efforts of primate populations, many of which are endangered, the use of complementary methods including genetic approaches will likely become increasingly relied upon to provide essential data on remaining populations.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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