Failure to account for behavioral variability significantly compromises accuracy in indirect population monitoring

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Indirect wildlife population surveying largely depends upon counts of artefacts of behavior (e.g., nests or dung). Likelihood to encounter these artefacts is derived from both artefact production and decay, and variability in artefact production behavior is considered to contribute minimally to inaccuracy in wildlife estimation. Here we demonstrate how ignoring behavioral variability contributes to significant population misestimation, using an example of an endangered ape, the bonobo (*Pan paniscus*). Until now, a single estimate of (i.e., nest construction) has been used to extrapolate bonobo densities, assumed to be broadly representative of bonobo sign production behavior. We estimated nest construction rate across seasons and social groups at the Kokolopori Bonobo Reserve, DRC and find that nest construction rates in bonobos to be highly variable across populations as well as seasonal. Failure to account for this variability led to potentially severe degradation in accuracy of bonobo population estimates of abundance, accounting for a likely overestimation of bonobo numbers by 34%, and at worst as high as 80%. With this example, we demonstrate that failure to account for inter- and intra-population behavioral variation compromises the ability to estimate both relative and absolute wildlife abundances. We argue that variation in sign production is but one of several potential ways that behavioral variability can affect conservation monitoring, should be measured across contexts whenever possible, and must be considered in population estimation confidence intervals. With increasing attention to behavioral variability as a potential tool for conservation, conservationists must also account for the impact that behavioral variability can play upon wildlife population estimation. Our results underline the importance of observational research to wildlife monitoring schemes as a critical but overlooked component of conservation management. We extensively discuss the various avenues through which behavioral variability is likely to impact wildlife monitoring accuracy and precision and propose potential avenues for accounting for behavioral variability in wildlife monitoring.

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INTRODUCTION

Wildlife monitoring and assessments of population size are crucial components of biodiversity conservation. To effectively monitor species, the information gathered must be an accurate reflection of true status of a population while free of bias and precise enough to allow for differences in status to be informative (Kremen et al., 1994). Wildlife monitoring involves the quantification of direct or indirect observations of animals, which, in lieu of cost-prohibitive censusing, are commonly performed as surveying of subsets of the areas of interest. Sampling by direct observation has traditionally meant quantification of observations of animals by a surveyor (Buckland et al., 2001; Kühl, 2008), although technological and analytical improvements increasingly permit the use of remote methods to estimate animal abundances based on observations during camera trap or acoustic surveying (e.g., Campos-Candela et al., 2018; Cappelle et al., 2019; Crunchant et al., 2020; Howe et al., 2017; Moeller et al., 2018; Nakashima et al., 2018).

For especially elusive species or for surveying in dense vegetation, however, conservationists typically rely on surveying of indirect signs of animal presence (Buckland et al., 2001; Plumptre, 2000), such as dung (e.g., Barnes, 2001; Marques et al., 2001; Massei & Genov 1998; Mayle et al., 1996; Nchanji & Plumptre, 2001; Plumptre, 2000; Rogers 1987), or remnants of behavior (e.g., nests; Kühl, 2008; footprints: Bonesi & Macdonald 2004). As in direct surveying, a great amount of attention centers around designing surveys to ensure sampling effort is sufficient and that animal counts are robust (Buckland et al., 2001). However, unlike direct surveying, the use of indirect surveying also necessitates accounting for auxiliary variables that account for potential sign abundance, such as rates of sign production and decay (Buckland et al., 2015). While the use of indirect surveying facilitates the possibility for surveying elusive wildlife populations, the additional consideration of sign detectability represents a significant potential source of error, leading to inherent flaws in what still remains a fundamentally important methodology (Bailey & Putnam 1981, Hayward & Marlowe 2014). Some authors argue that this component of population estimation requires greater amounts of attention, as this is where potential biases are most easily introduced (Bailey & Putnam 1981, Strindberg et al., 2018).

For example, conditions of the local environment are a commonly acknowledged influence on probability of sign encounter, and heterogeneity is common in metrics of sign decay rates across locations (e.g., Bessone et al., 2021; Kühl et al., 2007; Walsh & White, 2005). Sign decay has been linked to a number of variables such as climatic seasonality, con-

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struction material or dung matrix, storm frequency, and sun exposure (e.g., Bessone et al., 2021; Kamgang et al., 2020; Kouakou et al., 2009; Laing et al., 2003; Morgan et al., 2016; Nchanji & Plumptre, 2001; Plumptre, 2000). Therefore, it is commonly recommended that decay rates are measured locally during surveying, as failure to do so may result in imprecise measurement and hinder validity of inter-site comparisons (e.g., Bessone et al., 2021; Kühl, 2008; Laing et al., 2003; Mohneke & Fruth, 2008).

However, an often-overlooked component of wildlife monitoring relates to the variation in production of indirect signs, which is a derivative of behavior by the species surveyed Rates of production behavior for many indirect signs are typically treated as static entities – derived from a single group (e.g., Hedges et al., 2005; Kouakou et al., 2009; Morgan et al., 2006; Todd et al., 2008), or even one or two individuals (Mitchell et al., 1985; Viquerat et al., 2012) - and considered representative for the species across multiple localities. Single measures are commonly considered sufficient because measurement of production behavior must be directly observed to be quantifiable, which is both frequently unfeasible during surveying while also negates the need for indirect surveying in the first place (as population size is known).

Nevertheless, given that behavior is frequently variable within a species it may be problematic to rely on a single measure to represent species-level patterns. Variation in animal behavior may be influenced by the environment (e.g., Andersen et al., 1992; Mitchell et al., 1985; Kalan et al., 2020) but can also vary without clear environmental drivers (e.g., Samuni et al., 2020), and is most frequently tied to seasonality (e.g., Mitchell et al., 1985; Mayle et al., 1996; Rogers et al., 1987; Todd et al., 2008). The scale of variability in sign production behavior is argued to be small and therefore evaluation of sign production variability is scant relative to drivers of sign decay variability (Marques et al., 2001; although see Todd et al., 2008). In few cases when variation in sign production is described, the impact of sign production variability remains relatively unevaluated in the context of its impacts to species population estimates. Consequently, what are the impacts of ignoring behavioral variability on accuracy of absolute and relative wildlife population monitoring estimates?

To investigate the impact of behavioral variation upon issues of accuracy and precision in species monitoring, highly behaviorally flexible clades like great apes serve as ideal models. Apes are among the most extensively documented clades to exhibit behavioral variation and likely also among the most flexible (e.g., Kalan et al., 2020). As ape surveying is conducted predominately via indirect surveying with little current methodological alternative, evaluating sign production variability in a species like the bonobo (Pan paniscus) represents a straightforward approach to understanding the impacts of extensive expressions of behavioral variability upon monitoring accuracy. Indeed, in the case of ape nests, sign construction is known to vary according to weather patterns (Stewart et al., 2018), therefore it is already likely that we have ignored potential behavioral variation which affect ape density estimations. Bonobos are endemic only to the Democratic Republic of the Congo (DRC), and as one of the ape species under greatest threat, accurate population monitoring is critical at both the absolute and relative scales (Fruth et al., 2016). There are only an estimated minimum of 15-20,000 remaining individuals in the wild (IUCN & ICCN, 2012), although surveying is infrequent due to high logistical obstacles and therefore we know comparatively little about their current distribution. Consequently, large-scale models of bonobo abundance rely heavily upon few estimates of local densities. Under-surveying of bonobo populations has also led to an inability to reclassify the species as critically endangered (Fruth et al., 2016), meaning that accurate population monitoring is both of pressing need and a current conservation hurdle because data are scarce.

Bonobos, like all apes, construct nests to sleep in at night (Fruth & Hohmann, 1993), which is the predominant target of observation in bonobo surveys (Kühl, 2008). Bonobos regularly also construct nests for lounging during the day (Fruth & Hohmann, 1993), thereby providing ample opportunity for construction behavior to vary. While nest decay rates for bonobos have been measured at few sites (Figure S1, Table S1), nest construction rate has to date only been measured in a single location (LuiKotale: Mohneke & Fruth, 2008). Furthermore, a portion of bonobo densities have also been estimated under the assumption of a single nest constructed per day (e.g., Hashimoto & Furuichi, 2002; Inogwabini et al., 2008; Reinartz et al., 2006; Van Krunkelsven, 2001). Meanwhile in chimpanzees, the sister species of bonobos, nest construction rate vary by ca. 5% (Kouakou et al., 2009; Table S1). Generally, bonobos are argued to be comparatively less variable in their behavior than chimpanzees (Hohmann & Fruth, 2003) and occupy considerably smaller and less environmentally variable biogeographic range (Fruth et al., 2016). Therefore, it may be expected that behavioral variation in nest construction is comparatively lower in bonobos than in chimpanzees. However, as a member of a behaviorally flexible clade, do bonobos demonstrate cross-site variation in nest construction rates, and what impact might this behavioral variation have on our ability to accurately monitor bonobo populations?

METHODS

To evaluate potential variability in nest construction behavior in bonobos, we collected data on the nesting behavior of three distinct social groups at the Kokolopori Bonobo Reserve in the DRC (Surbeck et al., 2017). We collected data during 410 full-day focal follows over the course of one calendar year (September 2020 – August 2021) on a total of 33 adult individuals (10 male, 23 female; mean days/individual:12.4 days, range: 3-25) from the three neighboring communities (Ekalakala, Kokoalongo, and Fekako) with a mean of 137 observation days per group (range: 77 – 172). During focal follows, observers marked each instance of nest construction and the species used to construct the nest. As observation was occasionally interrupted or focal animals were lost over the course of the day, we restricted all subsequent analyses

to follows at least six hours in length that spanned the entirety of daylight hours (from morning nest to night nest) to reduce the likelihood that observations of nest construction were missed. The restriction of data which meet these criteria therefore reduced the dataset from 410 to 386 follow days.

Few researchers have previously argued that day nests are of flimsier construction than night nests and therefore should not be considered in calculations of nest construction rates (e.g., Fruth & Hohmann, 1993; Van Krunkelsven, 2001), however most studies have nonetheless included day nests in the calculation of nest construction rate (e.g., Kouakou et al., 2009; Mohneke & Fruth, 2008; Morgan et al., 2006). Regardless of structural robustness at construction, because day nests still require the bending of branches in a manner that is indistinguishable from a night nest during surveying, they must be included in nest construction rate, as robustness of nest construction only relates to the durability (i.e., rate of decay) of the nest but not its identifiability. In this sense, future studies should measure if day nest durability differs from that of night nests.

To calculate average nest construction rate at Kokolopori, we fitted a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with Poisson error structure, with the number of nests constructed during the course of a follow as the response. We included the sine and cosine of the radian of Julian date of the focal follow to test for a potential seasonal effect (Stolwijk et al., 1999) in nest construction behavior, as well as the test predictor of sex. We accounted for potential influence of group as a control predictor and included individual and date as random effects. To account for the effect of observational effort we included an offset term of the log of duration of focal observation. Model checks are described in the Supplementary Material. We used the intercept of the model to derive an average nest construction rate for the population, while correcting for all significant predictors, if relevant. For comparability, we also calculated average nest construction rate using Mohneke & Fruth's (2008) calculation, using party composition from group follows for the same period, using 293 days and 10635 30-min party composition scans.

If nesting behavior varies seasonally, surveying conducted during one period of an annual cycle may identify a greater number of nests than during another period of the year, despite no change in the number of nest constructors. Further, the time it takes for a sign to decay represents also the time window within which sign production behavior is relevant to that survey. In order to get a better understanding of the seasonal variability in average nest construction behavior ultimately relevant for bonobo population monitoring, we used each of the four nest decay rates previously published for bonobos (Table S1) as a sampling window prior to each potential survey day during the year. Because we do not have multiple years of data, we treated date cyclically when sampling, e.g., using a 183-day decay rate the nest construction rate estimated on January 1 includes focal follows on the last 183 days of the same calendar year). Then, we calculated the average nest construction rate for each combination of decay rate and date in the year.

Lastly, to contextualize the impact of variable nest construction rates on estimates of bonobo densities across their range, we considered the variability of published nest decay rates and nest construction rates for bonobos (Table S1) for their impact to published bonobo density estimations. Commonly, ape density estimates are derived using the following generalized equation: $D=N / (A \times p \times r \times t)$, where N is the count of nests discovered, A is the area surveyed, p is the proportion of nest builders within the population, r is the nest production rate, and t is the nest decay rate (Buckland et al., 2001; Kühl, 2008). We replaced original nest production and decay rates with all combinations of these values (including rates from Kokolopori derived here) and permuted all possible outcomes of density for each published non-zero density estimate. We additionally considered the effect of seasonal variation on nest construction rate in these permutations by allowing for density estimations to derive from a balanced dataset of either published values from LuiKotale (Mohneke & Fruth, 2008) or any of the possible construction rate values (i.e., seasonally varying construction rates) from our Kokolopori dataset, based on the decay rate of 76 days (Mohneke & Fruth, 2008).

RESULTS

Our test predictors (seasonality, group, and sex) significantly contributed to explaining variation in nest construction rate (full-null model comparison: $\chi2 = 26.28$, df = 3, $p < 0.001$). Specifically, nest construction behavior at Kokolopori varies seasonally, with highest rates of nest construction during October (the wettest month of the year: Samuni et al., 2020) and lowest number of nests produced during April ($\chi2 = 24.31$, df = 2, $p < 0.001$). We did not find group or sex differences in nest construction rates (Table 1). As rainfall is a common predictor of variability in nest decay and nest construction type (Stewart et al., 2018), we also fitted an ad hoc model identical to our Poisson model, but replaced the generic seasonal term with cumulative rainfall in the 4-weeks prior to each focal. We found that rainfall significantly predicted variation in nest construction rate (full-null model comparison: $\chi2 = 5.179$, df = 1, p=0.023; Table S2), with bonobos constructing more nests during periods of high rainfall. This pattern corresponded to a difference of 0.65 nests/day (range: 1.54 – 2.19 nests/day) over the range of monthly rainfall patterns at the site (range: 7-221mm cumulative rainfall).

When considering average observation duration (9.85 hours), average nest construction at Kokolopori was 1.92 ± 0.06 nests per day (SE; model intercept, back-transformed), considerably higher than the previously published estimate from LuiKotale (1.37 nests/day: Mohneke & Fruth, 2008), as well as from the commonly assumed rate of 1 nest/day (Hashimoto & Furuichi, 2002; Inogwabini et al., 2008; Reinartz et al., 2006; Van Krunkelsven, 2001). When calculated following Mohneke & Fruth's (2008) method which presumes sex differences in construction behavior and estimates an average construction rate based on average party sex ratios, nest construction rate (1.92 nests per day) did not

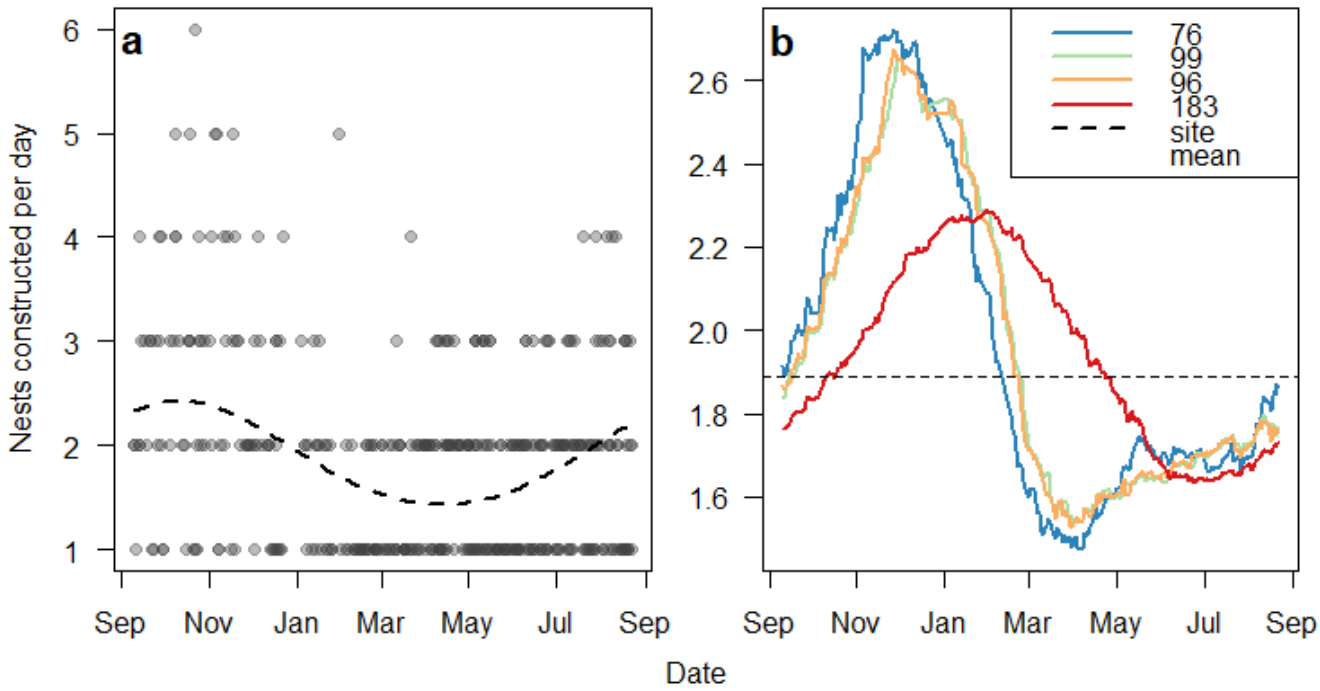

Figure 1. (a) Seasonal variation of nest construction behavior in two communities at Kokolopori Bonobo reserve, circles represent the number of nests constructed per focal follow and the dashed line represents the model line. (b) Average Kokolopori nest construction rates across four sampling windows (color coded according to common nest decay rates [in days]).

differ from the rate derived from the GLMM, indicating that differences in nest construction rate between sites are not a methodological byproduct.

Across the four nest decay sampling windows used, intra-annual variation in construction rate at Kokolopori averaged 1.04 nests/day over the year (range: 0.66 – 1.24 nest/day intra-annual range in decay rate), although average construction rate over the year varied minimally across different nest decay rates used (0.003 maximum difference between averages). All estimated construction rates at Kokolopori averaged higher than the previously published construction rate from LuiKotale (Mohneke & Fruth, 2008; Figure 2).

Permuted bonobo densities across construction rates always predicted overestimation in original values (Table 2). Overestimation of bonobo densities averaged 33 ± 5% (SD) when permuted across all construction rates, reaching up to 80% overestimation. Accounting for intra-annual variation in nest construction rates in our permutations reduced overestimation rates minimally (1%) but increased potential severity of density overestimation by up to 15%. When permuting densities across construction rates only, the five highest bonobo densities (Figure 3) suffered the highest rates of overestimation (mean ± SD: 36.5 ± 11%, range: 27 – 63%). Original densities were only predicted to be underestimated (% change) in cases where nest decay rates were permuted at shorter decay rate than was used in the original study, specifically the density estimates from Serckx et al. (2014) which used the maximum decay rate of 183 days (Figure 3). Misestimation became more severe when variation in both nest construction and decay were permitted, regardless of direction.

Table 1. Effect of season (represented by sine and cosine of Julian date) and sex on nest construction behavior at Kokolopori Bonobo Reserve (n = 268).

Predictor	Estimate ± SE	$CI_{(95\%)}$	χ^2	p-value
Intercept	-1.63 ± 0.06	-1.761, -1.525	-	-
Sine	-0.26 ± 0.05	-0.368, -0.147	-4.869	<0.001
Cosine	0.05 ± 0.05	-0.063, 0.154		
Group (Fekako)[a]	0.13 ± 0.11	-0.081, 0.328	1.494	0.473
Group (Kokoalongo)[a]	0.04 ± 0.08	-0.115, 0.199		
Sex (Male)[b]	-0.11 ± 0.08	-0.276, 0.053	1.670	0.196

[a]Reference category: Ekalakala; [b]Reference category: Female

Table 2. Average changes in density estimations from original reported values based on permutations of all potential nest decay and/or nest construction rates, calculated either using site-wide averages or allowing for seasonal variation.

Permutation type	[Overestimate] Mean ± SE (%)	[Underestimate] Mean ± SE (%)	SD (%)	Range min, max (%)
Decay and construction (site average)	-38.2 ± 1.5	55.8 ± 9.4	38.3	-71.7, 140.8
Decay and construction (with seasonality)	-37.1 ± 0.1	60.0 ± 0.6	39.3	-80.1, 140.8
Construction only (site average)	-29.1 ± 2.8	-	16.4	-47.6, 0.0
Construction only (with seasonality)	-28.2 ± 0.2	-	17.4	-63.3, 0.0
Decay only	-33.5 ± 3.1	35.0 ± 4.4	40.6	-58.5, 140.8

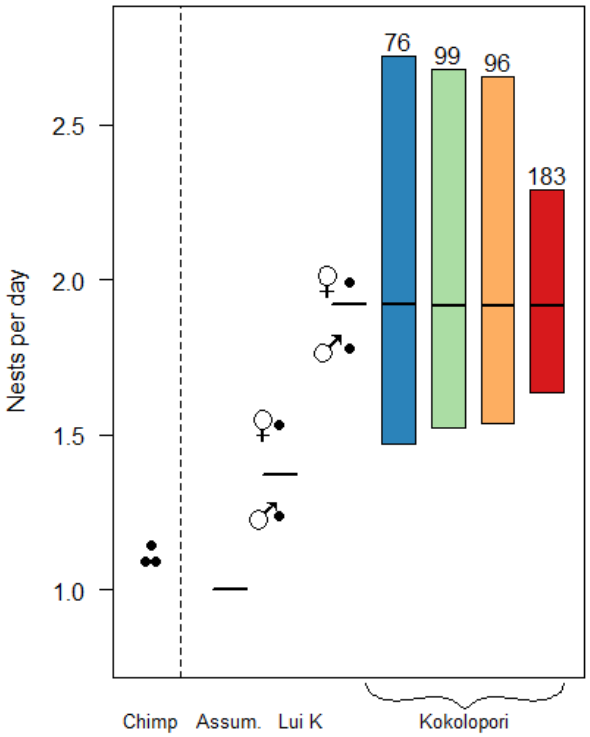

Figure 2. Nest construction rates from chimpanzees ('Chimp', left dots; Kouakou et al. 2009, Morgan et al. 2007, Plumptre & Reynolds 1997) and bonobos. Bonobo construction rates include the common assumption of 1 night nest/day ('Assum.', left bar), calculated rates from LuiKotale males, females, and average ('Lui K', dots and bar; Mohneke & Fruth 2008), construction rate from Kokolopori using Mohneke & Fruth's (2008) calculation (dots and bar), as well as Kokolopori nest construction rates based on seasonal sampling using four nest decay windows (colored boxes, labeled by days to decay).

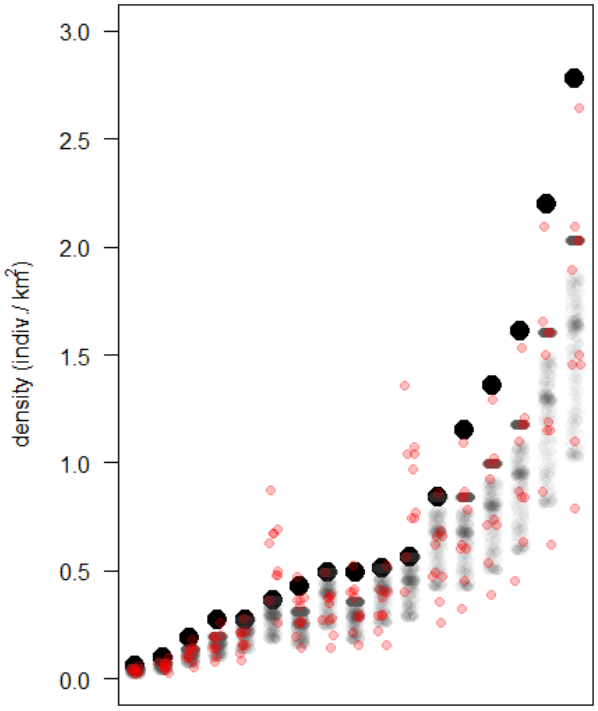

Figure 3. Bonobo density estimations (larger black dots, ordered low to high) and density values permuted from all observed bonobo nest construction rates (grey dots; including seasonal variation at Kokolopori) or observed nest construction rates and nest decay rates (red dots; site-based average values only).

DISCUSSION

When counts of animal populations depend on artefacts of behavior, wildlife monitoring methods must consider variability in animal behavior to estimate populations accurately. Our analysis demonstrates that in addition to environmental influence on sign persistence, behaviors relevant to monitoring wildlife populations can be considerably variable and significantly impact population assessment. We provide a particularly severe example, as we demonstrate that bonobos not only differ between populations in the number of nests that they construct per day, but also that within a single population this behavior is highly variable. Consequently, this variability leads to potential overestimation in the number of bonobos remaining in the wild by an average of 34%, with worst case scenarios predicting an overestimation by up to 80%.

The case of the bonobo. Overestimation of this species predominantly derives from historical reliance upon a single measure of production behavior being used for bonobo population density estimates. Here, we presented a second measure of nest construction rate and evaluated its seasonal variability. As the construction rate at Kokolopori was considerably higher than the single previously published estimate and that Kokolopori does not represent any overt environmental or behavioral outlier, it is likely that we have historically overestimated bonobo abundance. While methodological comparison with camera trap studies suggests that nest counts may commonly underestimate ape densities (7.5%: Cappelle et al., 2019) the severity of potential overestimation described here still outpaces potential methodological underestimation from using nests as indirect signs during surveying.

The likelihood for overestimation of bonobo populations becomes clearest when we consider the following scenarios. First, as all directly observed calculations of bonobo nest construction rates are greater than an assumed value of one nest/day, then estimates of populations using this assumed value are certainly overestimated. We found that published bonobo densities which relied on the assumption of one nest constructed per day were not only among the highest estimates, they also were the most likely to be severely overestimated. Second, given the Kokolopori nest construction rate is higher than the only other published rate (Mohneke & Fruth, 2008), it is parsimonious to assume that bonobo nest construction rates at other, non-measured sites likely fall closer to one of the two measured estimates than to the assumed single nest constructed per day.

Consequences of ignoring behavioral variation. The example of the considerable inter- and intra-population variability in nest construction behavior has consequences for the ways in which we use population estimates. Specifically, cross-population differences in construction rates considerably hampers our ability to reliably compare inter-site differences in densities, or any subsequent inference upon differences in density therewithin. Several authors have argued for the necessity of measuring nest decay rates locally for each survey due to environmental influence on decay (e.g., Bessone et al., 2021; Mohneke & Fruth, 2008; Plumptre & Cox, 2006), however our results indicate that variability in nest construction behavior must likewise be considered. Without accounting for behavioral variation, our ability to discern drivers of variation in densities across populations remains obscured, which may consequently misinform conservation action.

Our results highlight further, more nuanced potential sources of biases for comparison of population estimates, which may vary from taxon to taxon. In bonobos, we did not detect sex differences in nest construction rates, whereas this was a clear (albeit statistically untested) pattern elsewhere (Mohneke & Fruth, 2008). Inconsistencies in the influence of sex on behaviors which are also variable across populations further complicate our ability to account for these biases in population estimation, especially across populations with varying sex ratios (Plumptre & Cox, 2006).

Behavioral variability may be especially important if sign production itself can be variable across populations. For bonobos, some surveyors choose to ignore day nests during surveying because they are considered to be smaller or less robust in construction (e.g., Fruth & Hohmann, 1993; Hashimoto & Furuichi, 2002), whereas day nests at Kokolopori can appear largely indistinguishable from day to night (Supplementary Video 1; Wessling unpubl. data). Consequently, it is likely difficult to reliably differentiate day from night nests during surveying in a manner that is objective across populations. Therefore, clear (objective) decisions must be made about inclusion criterion for each indirect sign surveyed.

Further, seasonality in artefact production behavior has potential impacts on comparisons of population estimates across both time and space. First, monitoring of population change relies on repeated surveying of the same population, which rests upon the assumption that variation in the observation of behavioral artifacts solely reflects variation in animal densities. However, this assumption is violated if artefact production rates vary within a site. Consequently, it is necessary to understand the effect of within-population variability in relevant behaviors (e.g., nesting seasonality) on the robustness of trends derived from population resampling. A second consequence of behavioral seasonality is also that if it is commonplace across populations, that cross-site comparisons of bonobo densities may be simple artefacts of differences in surveying timing. That we find seasonality in artefact production behavior (ape nests: this study, defecation: Rogers 1987, Todd et al., 2008) as well as decay rates (e.g., nests: (Barnes, 2001; Bessone et al., 2021; Kühl et al., 2007; Nchanji & Plumptre, 2001) implies that conservationists must not only account for cross-site environmental differences, but also consider potential intra-annual environmental variation during indirect survey planning and analysis.

Collectively, by failing to account for variation in sign production behavior we observe both clear overall biases (i.e., overestimation) in population assessment of an understudied species, as well as uncertainty in estimation and comparison of individual estimates. These effects have devastat-

ing consequences for bonobo conservation – a species for which severely data deficiencies hamper adequate conservation evaluation and prioritization (IUCN & ICCN, 2012). The demanding logistics of surveying in extremely remote region of the Congo Basin necessitate accurate and comparative surveying because the resulting datapoints serve as the basis for understanding environmental correlates of density, which then are extrapolated to predict species densities across their range (e.g., Hickey et al., 2013; Nackoney & Williams, 2013). If behavioral variation in nesting imparts unaccounted for variation in these densities, we may not only be inaccurately estimating the size of remaining populations, but also inaccurately evaluating predictors of population persistence or decline.

Our results further underline that taxa surveyed need not necessarily be behaviorally flexible for behavioral variability to be relevant for monitoring accuracy. Bonobos demonstrate muted behavioral diversity relative to chimpanzees (Hohmann & Fruth, 2003), a species well documented to exhibit a great amount of behavioral variation across its range (Kalan et al., 2020). Despite comparatively minimal ecological variation across the bonobo range (Furuichi, 2009), it is notable that bonobo nest construction rates varied considerably more than chimpanzee construction rates, and bonobo nest decay rates extend across the majority of observed variation in chimpanzee nest decay rates (Figure S1). That bonobos still demonstrate substantial behavioral variability with clear impacts to monitoring, and that remnants of behavior can be just as variable (e.g., decay rates) or more variable (e.g., construction rates) than in a species like the chimpanzee known for its behavioral flexibility (Kalan et al., 2020), our results therefore underline that variability in behaviors relevant to monitoring may not necessarily follow general patterns of behavioral variability across taxa.

How to address behavioral variability in population monitoring. While the consequences of behavioral variation on population estimation may be extreme in this example, these results should caution conservation practitioners whose methods to quantify wildlife populations may be impacted directly by wildlife behavior (e.g., temporal patterns of camera trap triggering, trappability) or relics of behavior (e.g., dung counts). For example, circadian patterns (e.g., diurnal, cathemeral) vary by local conditions and animals can be variably cryptic depending on environmental context (e.g., Oberosler et al., 2017; Rowcliffe et al., 2014). Collectively, these patterns point to the necessity of accounting for behavioral variation in conservation monitoring, and negate the argument that the importance of behavioral variability has relatively minor impact among potential sources of error in indirect surveying (Marques et al., 2001; Mitchell et al., 1985). par But how can this reasonably be accomplished? It may be tempting to argue for direct sampling of behavior at each survey locality. However, the ability to directly observe wildlife behavior in a manner in which rates could be calculated negates the necessity of abundance sampling. Unlike artefact decay rates which can be observed without needing to directly observe individual animals, collecting information on artefact production behavior does necessitate direct observation, which may only be possible in few locations. Therefore, we could consider including variance introduced by inter- and intra-site variation within the confidence intervals of computed values. However, this may not be a realistic solution, as allowing for variance of potential nest construction rates introduced 60% variance in density estimates across our sample. Expanding the confidence intervals to include this variation would render cross-sample comparison functionally meaningless, an issue that no increase in the amount of survey effort could allow researchers to evade (Buckland et al., 2001).par Instead, a promising way forward may be to understand predictors of behavioral variation, such as environmental drivers like rainfall, which could be used as a proxy of artefact production behavior where behavioral sampling is not possible. To accomplish this, researchers who depend on metrics of behavior in surveying should aim to increase sampling efforts of that behavior across populations where behavior can be observed, and within those populations across time periods and seasons, to characterize behavioral variation for that species. Only then, once behavioral variability can be reliably tied to predictors for a species and then modeled across time and space, could this variability be included in subsequent interpretation of inter-survey variance. Because indirect monitoring of a given species therefore must depend on estimates acquired through direct behavioral observation, long term animal research sites must continue to be viewed as crucial components of species conservation (Campbell et al., 2011).

Behavioral variation broadly impacts population monitoring. The necessity of accounting for behavioral heterogeneity across individuals has received increasing attention in the conservation literature (Kelleher et al., 2018; Merrick & Koprowski, 2017). Behavioral variability can considerably impact conservation effectiveness in a number of ways, from understanding its impact upon individual fitness to how it affects the suitability of conservation action across contexts and populations. However, the relevance of behavioral variability has rarely been discussed in the context of conservation monitoring, with two notable exceptions. First, behavioral variation in the form of movement as a behavioral trait creates considerable opportunity for biases in detectability (e.g., Hammond et al. 2021), but can also increase the variance and/or accuracy of population estimates, or the fidelity of connecting animal abundances to their potential drivers (e.g., Osipova et al., 2019; Rosenblatt et al., 2013). For wildlife monitoring, these issues can occur, e.g., if individuals or groups show spatiotemporal variation in territory use, variable tolerance to territory overlap, or even inter- or intra- population variation in distribution of where behavioral artefacts are deposited. These patterns therefore contribute to variable stochasticity, clustering, or spatiotemporal distribution of behavioral artefacts which consequently impacts monitoring accuracy and inter-estimate stability (Buckland et al., 2001). For example, if an ape population sleeps next to their food resources, and resources vary within the year between clumped and evenly-spaced distributions, so too would their nests. However, variation in the distribution of nests over time would also be ex-

pected to affect patterns of detectability and appropriate surveying design.

Further, individual variability in boldness, neophobia, or other behavioral patterns (e.g., sex biases in nesting or marking behavior) can bias detection probability and consequently population monitoring. Whereas the impacts of individual behavioral variability upon monitoring is well documented (Biro, 2013; Carter et al., 2012; Marescot et al., 2011), the impacts of inter-population behavioral variation creates entirely unique implications for monitoring and remains largely ignored. In addition to variability in behavioral artefact construction, as remote monitoring methods become increasingly popular, variability in components such as camera trap shyness (e.g., Kalan et al., 2019) also impacts our ability to accurately estimate wildlife populations and to reliably compare estimates across species and populations. The relevance of group-level behavioral variation to conservation has recently gained a significant amount of attention, as it has been argued to be a necessary and valuable tool to guide conservation action if applied effectively (Brakes et al., 2019; Carvalho et al., 2022). However, our results demonstrate how group-level behavioral variation has important impacts upon conservation monitoring beyond inter-individual level variation. We further illustrate the impact of temporal variation in behavior on the accuracy of population estimation. In addition to using behavioral variability as a tool for conservation, we must also understand the impacts of this variation to our ability to evaluate conservation action and apply it effectively. To do so, further research characterizing behavioral variation of relevant monitoring behaviors across individuals, time periods, populations, and environments must be performed simultaneously with measuring and mitigating its impacts upon population estimation more broadly.

CONCLUSIONS

In sum, in addition to using animal behavioral diversity as a tool for conservation, here we present evidence that behavioral diversity also can considerably obscure population monitoring reliability. Growing evidence indicates that presumably stable metrics used in population assessment must be given greater attention than previously afforded, and that ways to account for animal behavioral flexibility must be considered in a variety of conservation contexts. Given current widespread loss of wildlife, identifying how to best incorporate behavioral variation into population monitoring and conservation intervention is becoming not only pertinent but absolutely necessary.

SUPPORTING INFORMATION

Additional information is available online in the Supporting Information section at the end of this online version. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Author contributions

EW conceptualized, designed, and conducted the study; MS provided access to the data and assisted with conceptualization, and interpretation. Both authors contributed to the writing of the manuscript and have approved of the final submitted version.

Statement on animal subjects

This study complies with the ethical standards for animal research by the standards of the American Society of Primatology and the MSRT.

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Failure to account for behavioral variability significantly compromises accuracy in indirect population monitoring

SUPPLEMENTARY MATERIAL

Model checks

We found no issues with model overdispersion (dispersion parameter = 0.42) collinearity among predictors, or model stability. To evaluate model significance, we compared the fit of the model to a null model lacking the test predictors of sex and seasonal terms (but otherwise identical) using a likelihood ratio test (Dobson & Barnett, 2018). We evaluated predictor significance similarly, by excluding each predictor and comparing each reduced model to the full model using a likelihood ration test (*ibid.*). We assessed model stability by excluding each level of the random effects one at a time and comparing the estimates with those derived for the full data set. Lastly, we derived confidence intervals by means of parametric bootstraps (function *bootMer* of the package 'lme4'; Bates et al., 2015).

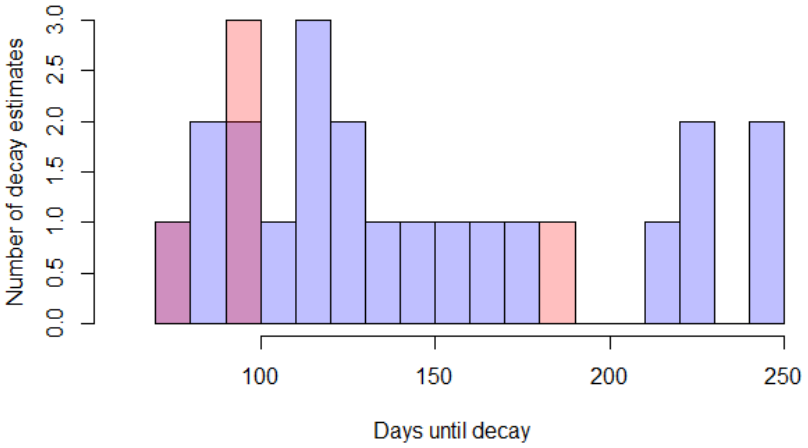

Figure S1. Summary of published nest decay rates of chimpanzees (blue) and bonobos (pink).

Table S1. Published (a) nest decay rates and (b) construction rates for chimpanzees and bonobos.

(a) Nest decay rates			
Species	**Days**	**Location**	**Reference**
Bonobo	76	LuiKotale, DRC	Mohneke & Fruth 2008
Bonobo	96	LuiKotale, DRC	Bessone et al. 2021
Bonobo	99	Lomako, DRC	van Krunkelsven 2001
Bonobo	99	Lomako, DRC	Eriksson 1999
Bonobo	183	Malebo, DRC	Serckx et al. 2014
Chimpanzee	73	Taï, Côte d'Ivoire	Marchesi et al. 1995
Chimpanzee	95	Taï, Côte d'Ivoire	Kouakou et al. 2009
Chimpanzee	161	Taï, Côte d'Ivoire	Wild Chimpanzee Foundation; via Heinicke et al. 2019
Chimpanzee	85	Djoroutou, Côte d'Ivoire	Wild Chimpanzee Foundation; via Heinicke et al. 2019
Chimpanzee	179	Comoé, Côte d'Ivoire	Laupuente et al. 2020
Chimpanzee	106	Lope, Gabon	Hall et al. 1998
Chimpanzee	114	Belinga, Gabon	Tutin & Fernandez 1984
Chimpanzee	146	(Goualougo) Nouabalé–Ndoki National Park, Republic of Congo	Morgan et al. 2016
Chimpanzee	90	(Goualougo) Nouabalé–Ndoki National Park, Republic of Congo	Morgan et al. 2006
Chimpanzee	111	Kibale, Uganda	Ghigleri 1979; Ghigleri 1984
Chimpanzee	243	Dindefelo, Senegal	Heinicke et al. 2019
Chimpanzee	243/432*	Issa, Tanzania	Stewart et al. 2011
Chimpanzee	218	Fouta Djallon, Guinea	Wild Chimpanzee Foundation; via Heinicke et al. 2019
Chimpanzee	221	Fouta Djallon, Guinea	Ham 1998
Chimpanzee	229	Haut Niger, Guinea	Fleury-Brugiere & Brugiere 2010
Chimpanzee	154	Sapo, Liberia	PanAfrican Programme; via Heinicke et al. 2019
Chimpanzee	146	Sapo, Liberia (marshes)	PanAfrican Programme; via Heinicke et al. 2019
Chimpanzee	135	TRIDOM Landscape, Cameroon	Nzooh Dongmo et al. 2016
Chimpanzee	127	Mbam-Djerem, Cameroon	Kamgang et al. 2020
Chimpanzee	97	Dja, Cameroon	Bruce et al. 2018
Chimpanzee	130	Campo Ma'an, Cameroon	Matthews & Matthews 2004
Chimpanzee	133	Campo Ma'an, Cameroon	Nzooh Dongmo et al. 2015
(b) Nest construction rates			
Species	**nests/day**	**Location**	**Reference**
Bonobo	1.92	Kokolopori, DRC	*This study*
Bonobo	1.37	Lomako, DRC	Mohneke & Fruth 2008
Chimpanzee	1.09	Budongo, Uganda	Plumptre & Reynolds 1997
Chimpanzee	1.09	Goualougo, Rep Congo	Morgan et al. 2006
Chimpanzee	1.14	Taï, Côte d'Ivoire	Kouakou et al. 2009

* Differentiated between vegetation coverage types, no site average provided

Table S2. Effect of rainfall, group, and sex on nest construction behavior at Kokolopori Bonobo Reserve (n = 210). Statistically significant results ($p \leq 0.05$) appear in bold italics.

Predictor	Estimate ± SE	χ^2	p-value
Intercept	-1.833 ± 0.118	-	-
Rainfall	0.002 ± 0.001	***5.179***	***0.023***
Group (Fekako)[1]	0.061 ± 0.115	0.341	0.843
Group (Kokoalongo)[1]	0.041 ± 0.094		
Sex (Male)[2]	-0.111 ± 0.094	1.404	0.236

[1]Reference category: Ekalakala; [2]Reference category: Female

Supplementary Video 1. A bonobo constructs a day nest in the Kokolopori Bonobo Reserve, DRC. [*embargoed until publication*]

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