

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

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Abstract

Indirect wildlife population surveying largely depends upon counts of artifacts of behavior (e.g., nests or dung). Likelihood to encounter these artifacts is derived from both artifact production and decay, and variability in production behavior is considered to contribute minimally to inaccuracy in wildlife estimation. Here, we demonstrate how ignoring behavioral variability leads to significant population mis-estimation, using an example of an endangered ape, the bonobo (*Pan paniscus*). Until now, a single estimate of nest construction rate has been used to extrapolate bonobo densities, assumed to be broadly representative of bonobo sign production behavior. We estimated nest construction rates across seasons and social groups at the Kokolopori Bonobo Reserve, Democratic Republic of the Congo, and find nest construction rates in bonobos to be highly variable across populations as well as seasonal within populations. Failure to account for this variability led to degradation in the accuracy of bonobo population density estimates, 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 intrapopulation behavioral variation compromises the ability to estimate both relative and absolute wildlife abundances. We argue that variation in sign production is but one of the 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 have upon wildlife population estimation. Our results underline the importance of observational research to wildlife monitoring schemes as a critical component of conservation management. We discuss the avenues through which behavioral variability is likely to impact wildlife monitoring accuracy and precision and propose potential approaches for accounting for behavioral variability in wildlife monitoring.

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 the 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 the surveying of subsets of the areas of interest. Sampling by direct observation has traditionally meant the 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., Howe *et al.*, 2017; Campos-Candela *et al.*, 2018; Moeller, Lukacs & Horne, 2018; Nakashima, Fukasawa & Samejima, 2018; Cappelle *et al.*, 2019; Cruncheon *et al.*, 2020).

For especially elusive species or for surveying in dense vegetation, however, conservationists typically rely on the surveying of indirect signs of animal presence (Plumptre, 2000; Buckland *et al.*, 2001), such as dung (e.g., Rogers, 1987; Mayle *et al.*, 1996; Massei & Genov, 1998;

Plumptre, 2000; Barnes, 2001; Marques *et al.*, 2001; Nchanji & Plumptre, 2001), or remnants of behavior (e.g., nests; Köhl, 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 the rates of sign production and decay (Buckland *et al.*, 2015). While the use of indirect surveying facilitates the possibility of surveying elusive wildlife populations, the additional consideration of sign production and decay represent a significant potential source of error, leading to inherent flaws in what still remains a fundamentally important methodology (Bailey & Putman, 1981, Hayward & Marlow, 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 & Putman, 1981; Strindberg *et al.*, 2018).

For example, the conditions of the local environment are a commonly acknowledged influence on the probability of sign encounter, and heterogeneity is common in metrics of sign decay rates across contexts (e.g., Walsh & White, 2005; Köhl *et al.*, 2007; Bessone *et al.*, 2021). Sign decay has been linked to a number of variables such as climatic seasonality, construction material or dung matrix, storm frequency, and sun exposure (e.g., Plumptre, 2000; Nchanji & Plumptre, 2001; Laing *et al.*, 2003; Kouakou, Boesch & Köhl, 2009; Morgan *et al.*, 2016; Kamgang *et al.*, 2020; Bessone *et al.*, 2021). 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 the validity of inter-site comparisons (e.g., Laing *et al.*, 2003; Köhl, 2008; Mohneke & Fruth, 2008; Bessone *et al.*, 2021).

However, an often overlooked component of wildlife monitoring relates to the variation in the production of indirect signs, which is a derivative of behavior of 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; Morgan *et al.*, 2006; Todd *et al.*, 2008; Kouakou *et al.*, 2009), 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 observable and therefore known already to the surveyor). As indirect surveying rarely occurs when the behavior of the population is directly observable, sign production behavior must typically be measured separately from the surveyed populations.

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 not only be influenced by the environment (e.g., Mitchell *et al.*, 1985; Andersen, Hjeljord & Saether, 1992; Kalan *et al.*, 2020) but can also vary without clear environmental drivers (e.g., Samuni, Wegdell & Surbeck, 2020), and is most frequently tied to seasonality (e.g., Mitchell *et al.*, 1985; Mayle *et al.*, 1996; Rogers, 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 on species population estimates. Consequently, what are the impacts of ignoring behavioral variability on the accuracy of estimates of absolute and relative comparisons of wildlife populations?

To investigate the impact of behavioral variation upon issues of accuracy and precision in species monitoring, behaviorally flexible clades like great apes serve as ideal models. Apes are among the most extensively documented taxa to exhibit behavioral variation and likely also among the most flexible (e.g., Kalan *et al.*, 2020). As ape surveying has historically been conducted predominately via indirect surveying with little current methodological alternative (although emerging camera trap methodologies increasingly permit monitoring, albeit on smaller scales; e.g., Howe *et al.*, 2017; Campos-Candela *et al.*, 2018; Moeller *et al.*, 2018; Nakashima *et al.*, 2018; Cappelle *et al.*, 2019; Crunchant *et al.*, 2020; Bessone *et al.*, 2021), evaluating sign production variability in an ape species like the bonobo (*Pan paniscus*) represents a straightforward approach to understanding the impacts of behavioral variability upon accurate population estimation. 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 patterns of 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 (Köhl, 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 a few sites (Supporting Information Figure S1, Supporting Information Table S1), nest construction rates have to date only been measured in a single location (LuiKotale; Mohnke & Fruth, 2008). Furthermore, a portion of bonobo densities have also been estimated under the assumption of a single nest constructed per day (e.g., Van Krunkelsven, 2001; Hashimoto & Furuchi, 2002; Reinartz *et al.*, 2006; Inogwabini *et al.*, 2008). Meanwhile in chimpanzees (*Pan troglodytes*), the sister species of bonobos, nest construction rates vary by *ca.* 5% across populations (Kouakou *et al.*, 2009; Supporting Information Table S1). Generally, bonobos are argued to be comparatively less variable in their behavior than chimpanzees (Hohmann & Fruth, 2003) and occupy a 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. In this study, we first aimed to evaluate variation in nest construction rates, and secondly, to evaluate the impact of behavioral variation of this trait on our ability to accurately estimate bonobo populations from nest counts. Specifically, we consider cross-site as well as intra-site (e.g., season, sex, and social group) variation in nest construction behaviors, and re-evaluate published estimates of bonobo densities to account for the likelihood that both patterns of nest construction and decay can be variable.

Materials and 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, Coxe & Lokasola, 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 follow at least 6 h 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 that meet these criteria, therefore, reduced the dataset from 410 to 386 follow days.

Some 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., Morgan *et al.*, 2006; Mohnke & Fruth, 2008; Kouakou *et al.*, 2009). 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, we argue that 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. Future studies should measure if day nest durability differs from that of night nests, however we include day nest construction in nest construction rates here.

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 tested a potential seasonal effect in nest construction behavior using the sine and cosine of the radian of Julian date of the focal follow (Stolwijk, Straatman & Zielhuis, 1999), as well as for sex differences in nest construction behavior by including the sex of the focal individual as a predictor. We accounted for potential group differences in nest construction behavior by including social group as a predictor (fixed effect) and included focal individual and date of the focal follow as random effects. To account for varying observational effort, we included the log of the duration of a focal observation as an offset term. We found no issues with model overdispersion (dispersion parameter = 0.42), collinearity among predictors, or model stability. We used the intercept of the model to derive an average nest construction rate for the population while correcting for all significant categorical predictors, if relevant. We compared the fit of the model to a null model lacking the predictors of sex and season (but otherwise identical) using a likelihood ratio test (Dobson, 2002). We evaluated predictor significance similarly, by excluding each predictor and comparing each reduced model to the full model using a likelihood ratio 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 dataset. Lastly, we derived confidence intervals by means of parametric bootstraps (function `bootMer` of the package ‘lme4’, version 1.1.27.1; Bates *et al.*, 2015).

Nest construction rates in bonobos have been previously described at only one site (LuiKotale; Mohnke & Fruth, 2008), however, these authors used a different calculation than that used here. Therefore, to contextualize our results in the context of other published nest construction rates, we also sought to verify that potential inter-site differences in nest construction rates could be attributed only to differences in behavior and not to methodological differences in rate calculation. Therefore, we also calculated average nest construction rate using Mohnke & Fruth’s (2008) calculation, which presumes sex differences in construction behavior and estimates an average construction rate based on average party sex ratios, using the party composition from group follows for the same period. For this calculation we used 293 days of data collection and 10,635 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 a survey conducted 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 each survey. Consequently, the nest decay period chosen as well as the date a survey was conducted may impact inter-survey comparability if nest construction behavior is temporally variable. Therefore, to better understand the seasonal variability in average nest construction behavior ultimately relevant for bonobo population monitoring, we used each of the four unique nest decay rates previously published for bonobos (Supporting Information Table S1) as a sampling window prior to each potential survey day during the year ($n = 365$). Because we do not have multiple years of data, we treated date cyclically when sampling, for example, using a 183-day decay rate, the nest construction rate estimated on January 1 calculates a nest construction rate using data collected during 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 (Supporting Information Table S1) for their impact on 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 sampling of either the single published value from LuiKotale (Mohneke & Fruth, 2008) or any of the possible seasonally variable construction rate values from our Kokolopori dataset, based on the decay rate of 76 days (Mohneke & Fruth, 2008). In other words, we allowed for a total of 730 possible nest construction values to be permuted within the model, the 1.37 nest/day from LuiKotale ($n = 365$) and the seasonally varying nest construction rates from Kokolopori ($n = 365$). Thus, with this analysis, we are evaluating the relative change in published density estimates when using different values of nest construction and decay.

Results

In our evaluation of Kokolopori nest construction rates and the factors that influence them, seasonality, group, and sex significantly contributed to explaining variation in nest construction rate (full-null model comparison: $\chi^2 = 26.28$, $df = 3$, $P < 0.001$). Specifically, nest construction behavior at Kokolopori varied seasonally ($\chi^2 = 24.31$, $df = 2$, $P < 0.001$), with the highest rates of nest construction observed during October (the wettest month of the year: Samuni *et al.*, 2020) and the lowest number of nests produced during April (Fig. 1). We did not find significant group or sex differences in nest construction rates (Table 1). As rainfall is a common predictor of variability in nest decay (Bessone *et al.*, 2021), we also fitted an *ad hoc* model identical to our Poisson model, but replaced the generic seasonal rainfall (sine and cosine of Julian date) with cumulative rainfall in the 4 weeks prior to each focal follow day. We found that rainfall significantly predicted variation in nest construction rate (full-null model comparison: $\chi^2 = 5.179$, $d.f. = 1$, $P = 0.023$; Supporting Information Table S2), with

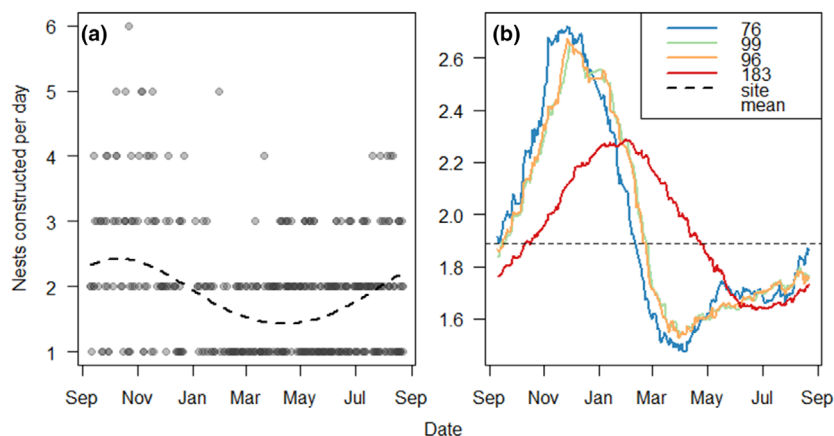


Figure 1 (a) Seasonal variation (represented by sine and cosine of radian of Julian date) of nest construction behavior in two bonobo communities at the Kokolopori Bonobo Reserve in the Democratic Republic of the Congo (12 months; 2020–2021). Circles represent the number of nests constructed by a single individual from dawn to dusk (focal follow), and the dashed line represents the model prediction derived from a GLMM model with Poisson error distribution. (b) Average Kokolopori nest construction rates estimated across four sampling windows (color-coded according to common nest decay rates [in days]).

Table 1 Effect of season (represented by sine and cosine of the radian of Julian date), sex, and group on nest construction behavior of two social groups of bonobos at the Kokolopori Bonobo Reserve in the Democratic Republic of the Congo ($n = 268$; 12 months, 2020–2021), using a GLMM model with Poisson error distribution

Predictor	Estimate \pm SE	CI ^a _(95%)	χ^2 ^b	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) ^c	0.13 ± 0.11	$-0.081, 0.328$	1.494	0.473
Group (Kokoalongo) ^c	0.04 ± 0.08	$-0.115, 0.199$	–	–
Sex (Male) ^d	-0.11 ± 0.08	$-0.276, 0.053$	1.670	0.196

^a 95% confidence interval.

^b Each chi-squared value was obtained using a likelihood ratio test comparing the full model against a series of models lacking each respective predictor.

^c Reference category: Ekakalala.

^d Reference category: Female.

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: 7–221 mm cumulative rainfall).

When considering average observation duration (9.85 h), we estimated that 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 per day; Mohneke & Fruth, 2008), as well as from the commonly assumed rate of 1 nest per day (Van Krunkelsven, 2001; Hashimoto & Furuichi, 2002; Reinartz *et al.*, 2006; Inogwabini *et al.*, 2008). When calculated following Mohneke & Fruth's (2008) method, nest construction rate (1.92 nests per day) did not differ from the rate derived from the GLMM, indicating that differences in nest construction rate between published construction rate estimates from different research sites (i.e., Kokolopori vs. LuiKotale) are not a methodological byproduct.

In our evaluation of the impacts of date and decay rate used in estimations of nest construction rates, we found that both impacted the range of nest construction rates. 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 construction rate), although average construction rate between estimates using each of the four unique nest decay rates 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; Fig. 2).

To translate the impacts of behavioral variability to species-level monitoring, we evaluated the impact of different nest construction and decay rates on published bonobo

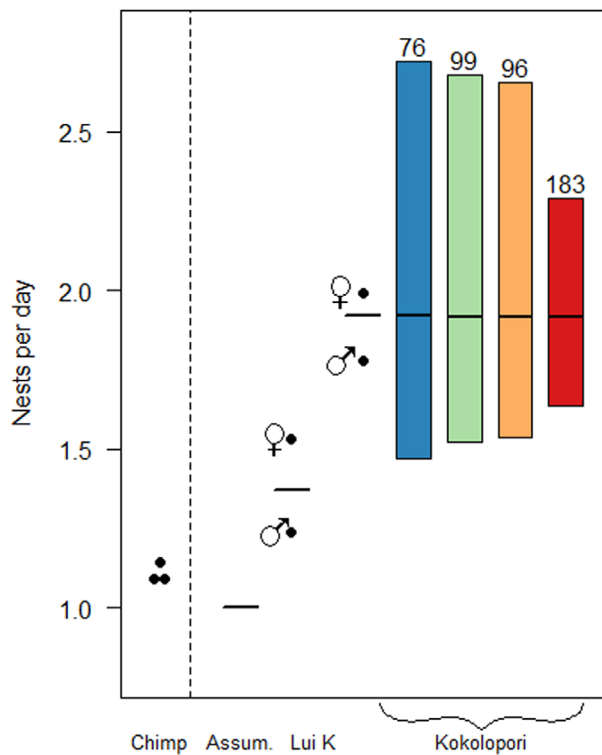


Figure 2 Nest construction rates from chimpanzees ('Chimp', left dots; Kouakou *et al.*, 2009, Morgan *et al.*, 2006, Plumptre & Reynolds, 1997, various locations) and bonobos (right of vertical dotted line, various locations in Democratic Republic of the Congo). Bonobo construction rates include the 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 bonobos at the Kokolopori Bonobo Reserve using Mohneke & Fruth's (2008) calculation (dots and bar), as well as Kokolopori bonobo nest construction rates based on seasonal sampling using four nest decay windows (colored boxes, labeled by days to decay; 12 months study duration, 2020–2021).

densities across their range. In our analyses, we consider there to be potential bias (e.g., over- or underestimation) in bonobo densities when we have identified disparities between published and permuted bonobo densities. Permuted bonobo densities across all potential bonobo nest construction rates were unanimously lower than originally published estimates, suggesting potential overestimation of densities in original values (Table 2). Potential overestimation of bonobo densities averaged $33 \pm 5\%$ (SD) (i.e., positive density bias) when permuted across all site-averaged construction rates, in the most severe case reaching up to an 80% positive bias. Additionally accounting for intra-annual variation in nest construction rates in our permutations reduced potential positive biases of rates minimally (~1%), but increased the potential severity of positive bias in density estimates by up to 15%, as potential permuted nest construction values became increasingly variable and more seasonally extreme. When permuting densities across construction rates only, the five

Table 2 Average positive (underestimate) and negative (overestimate) changes in density estimates from originally reported values (Supporting Information Table S3) based on permutations of all potential nest decay and/or nest construction rates (Supporting Information Table S1), calculated either using site-wide averages or allowing for seasonal variation. Over- and underestimate changes were estimated separately. Note, a negative change in an estimated density would indicate that the original value was overestimated; values represent a change in permuted density relative to original density

Permutation type	[Overestimate]	[Underestimate]	SD (%)	Range _{min, max} (%)
	Mean ± SE (%)	Mean ± SE (%)		
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

highest bonobo densities (Fig. 3) suffered the highest positive bias (mean ± SD: 36.5% ± 11%, range: 27%–63%). Original densities were only potentially underestimated (% change) in cases where nest decay rates were permuted at a shorter decay rate than was used in the original study, specifically the density estimates from Serckx *et al.* (2014) which used the longest decay rate in our dataset of 183 days (Fig. 3). Disparity between permuted and published density

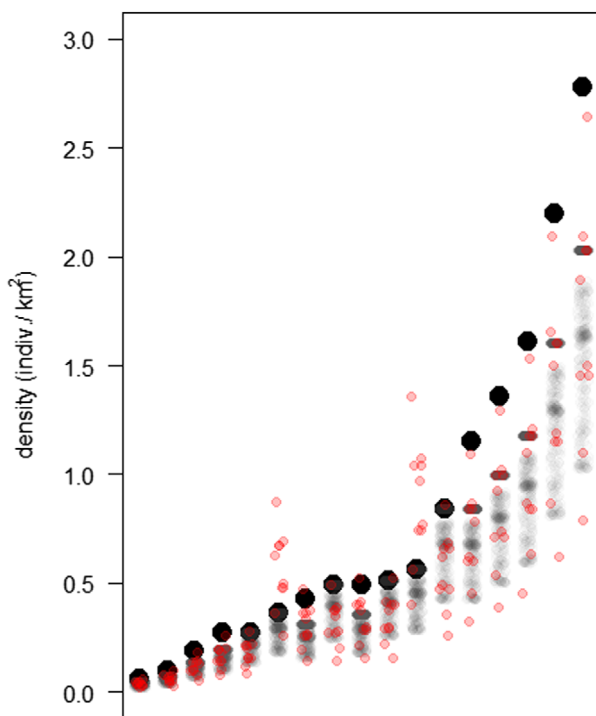


Figure 3 Bonobo density estimates (larger black dots, ordered low to high; data derived from density estimates provided in Supporting Information Table S3) and density values permuted from all observed bonobo nest construction rates (gray dots; including seasonal variation at Kokolopori; data available in Supporting Information Table S1 and from this study) or observed nest construction rates and nest decay rates (red dots; site-based average values only).

estimates became more severe when we permitted variation in both nest construction and decay, regardless of the direction of the misestimation.

Discussion

When counts of animal populations depend on artifacts 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 indirect monitoring of 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, failure to measure and account for behavioral variability leads to potential overestimation in the number of bonobos remaining in the wild by an average of 34%, with worst-case scenarios suggesting an overestimation up to 80%.

The case of the bonobo

Population overestimation of this species has predominantly derived from historical reliance upon a single measure of nest 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 as 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 the severity of potential overestimation described here still outpaces potential methodological underestimation from using nests as indirect signs during surveying (7.5% negative bias: Cappelle *et al.*, 2019).

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 that relied on the assumption of one nest constructed per day were not only among the highest estimates, but they also were the most likely to be severely overestimated. Second, given that the Kokolopori nest construction rate is higher than the only other published rate (Mohneke & Fruth, 2008), it is likely that bonobo nest construction rates at other, non-measured sites fall closer to one of the two measured estimates than to the assumed single nest constructed per day.

Consequences of ignoring behavioral variation in population monitoring

The example of the considerable inter- and intrapopulation variability in nest construction behavior has consequences for the ways in which we use population estimates derived from behavior or behavioral artifacts. Cross-population differences in indirect sign production rates considerably hamper our ability to reliably compare inter-site differences in densities. In the case of nest surveying, several authors have argued for the necessity of measuring nest decay rates locally for each survey due to environmental influence on decay (e.g., Plumptre & Cox, 2006; Mohneke & Fruth, 2008; Bessone *et al.*, 2021), 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 additional, more nuanced potential sources of biases for comparison of population estimates, that may vary from taxon to taxon. For example, we did not detect sex differences in bonobo 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 night nests (Supporting Information Video S1; E. 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 criteria for each indirect sign surveyed, and these decisions should reach consensus across surveys within a taxon or methodology. Further investigation into decay rate differences between day and night nests

would further illuminate the impacts of decisions surrounding inclusion criteria on population monitoring.

Further, seasonality in artifact 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 artifact production rates vary within a site unless surveying only occurs during certain periods of the year, both within-sites (e.g., trend analysis) and between-sites. 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. In cases where behavioral variability in sign production is observed, monitoring design must, in turn, accommodate and reduce the impacts of biases introduced by this variability (e.g., by sampling during identical times of the year if nest production is seasonally variable). The second consequence of behavioral seasonality, is that cross-site comparison of bonobo densities may be simple artifacts of differences in surveying timing. That we find seasonality in multiple artifact production behaviors (ape nests: *this study*, defecation: Rogers, 1987, Todd *et al.*, 2008) as well as artifact decay rates (e.g., nests: Barnes, 2001; Nchanji & Plumptre, 2001; Kühl *et al.*, 2007; Bessone *et al.*, 2021) implies that conservationists must not only account for cross-site environmental differences but also consider potential intra-annual environmental variation during indirect survey planning, analysis, and synthesis.

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 substantial consequences for bonobo conservation—a species for which severe data deficiencies hamper adequate conservation evaluation and prioritization (IUCN & ICCN, 2012). The demanding logistics of surveying in extremely remote regions of the Congo Basin necessitate accurate surveying because the resulting datapoints serve as the basis for extrapolation of species density 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 comparative minimal ecological variation across the bonobo range (Furuichi, 2009), it is notable that bonobo nest construction rates varied considerably more between sites than the few chimpanzee

construction rates recorded until now, and that bonobo nest decay rates extend across the majority of the observed variation in chimpanzee nest decay rates (Supporting Information Figure S1). Considering that bonobos demonstrate substantial behavioral variability with clear impacts on monitoring, and that remnants of behavior can be just as variable (e.g., decay rates) or more variable (e.g., construction rates) than behaviors in a species like the chimpanzee known for its behavioral flexibility, our results 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 which rely upon relics of behavior (e.g., dung counts). For example, circadian patterns (e.g., diurnal, cathemeral) can vary by local conditions and animals can be variably cryptic depending on environmental context (e.g., Rowcliffe *et al.*, 2014; Oberosler *et al.*, 2017). 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 a relatively minor impact among potential sources of error in indirect surveying (Mitchell *et al.*, 1985; Marques *et al.*, 2001).

But how can this reasonably be accomplished? It may be tempting to argue for direct sampling of relevant behaviors at each survey locality. However, the ability to directly observe wildlife behavior in a manner in which sign production rates could be calculated negates the necessity of using sign-based sampling because members of that population would be directly observable, and populations would therefore be more suitably measured using other methodologies. Unlike artifact decay rates which can be observed without needing to directly observe individual animals, collecting information on artifact 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 (range in density bias for ‘construction only [with seasonality]’ in Table 2) 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 solve (Buckland *et al.*, 2001). Some of the uncertainty introduced by behavioral variability could be reduced via the application of multiple methodological approaches (e.g., genetic sampling, camera trapping, and sign counts), to yield estimate

averaging across methods, and therefore allow for cross-method validity, the avoidance of methodology-specific biases, and subsequent narrowing of possible estimate ranges (Nuñez *et al.*, 2019). However, such an approach would require parallel surveying efforts, and thus, (potentially prohibitively) high monitoring costs.

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 artifact production behavior where behavioral sampling is not possible. The approach of replacing locally measured metrics of sign discoverability with environmental proxies has been previously suggested as a useful method for accommodating variability in sign decay (Bessone *et al.*, 2021; Meier *et al.*, 2021), and therefore may be suitably extended to proxies of behavioral variability. 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 interpretations 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 indirect monitoring

The impacts of behavioral variability upon population monitoring have wide reaching consequences across a variety of taxa, as all sign-based monitoring is largely dependent in some form on behavior of the individuals who leave behind these traces. A wide range of taxa are surveyed using indirect methods like tracks (e.g., ungulates: Reyna-Hurtado & Tanner, 2007; Licona *et al.*, 2011), feces/scat (e.g., elephants: Meier *et al.*, 2021, small carnivores: Espirito-Santo, Rosalino & Santos-Reis, 2007; García & Mateos, 2009, deer: Bailey & Putman, 1981; Massei & Genov, 1998; Marques *et al.*, 2001), and nest or drey counts (e.g., apes: Kouakou *et al.*, 2009, this study, squirrels: Gurnell *et al.*, 2004) that are clearly linked to behaviors that can vary. Furthermore, methodologies like hair traps (e.g., mustelids: García & Mateos, 2009), scent stations (e.g., bees: Almeida *et al.*, 2019), and exuviae (Raebel *et al.*, 2010) can also be argued to be dependent in some manner on behaviors that vary across scales (e.g., time, individual, social unit, population, and species). In Table 3, we provide a few examples of the avenues through which behavioral variation can impact sign-based monitoring, with far-reaching impacts on a range of species and methodologies.

The necessity of accounting for behavioral heterogeneity across individuals has received increasing attention in the

Table 3 Examples of ways that behavioral variability can potentially impact the accuracy and precision of wildlife population estimates derived from sign-based monitoring, and the comparability of these estimates across contexts, the potential consequences of this variation, and measured examples of either behavioral variation and/or their impacts upon population quantification, comparison, and general estimation

Behavior variants	Affected parameters	Potential scenario	Potential consequences	Example contexts
Activity timing	Production rate	Deer mothers reduce home-range size when in parturition, and therefore, tracks are less likely to be detected during birthing seasons. Bears who hibernate during winter months are less likely to defecate during these months	Difficulty in comparing estimates obtained at different times of the year, biases in signs produced by a subset of a population (i.e., over- or underestimate of abundance)	Deer (Henrich <i>et al.</i> , 2022), duikers (Howe <i>et al.</i> , 2017); other mammals (Rowcliffe <i>et al.</i> , 2014)
Movement speed	Detectability	Individual deer vary in travel speed, creating inter-individual variability in the between-track distance, for example, female deer tend to travel faster in open habitats than males	Signs may be variably detectible, which may create biases according to population, location/space, or individual characteristics (e.g., sex and age)	Deer (Henrich <i>et al.</i> , 2022)
Movement distance	Production rate	Deer travel longer distances during certain seasons (and therefore produce more tracks)	Difficulty in comparing estimates obtained at different times of the year.	Amphibians (Hammond <i>et al.</i> , 2021), elephants (Osipova <i>et al.</i> , 2019), alligators (Rosenblatt <i>et al.</i> , 2013)
Sign production	Production rate	Hoofed herbivores defecate more frequently during periods when their diet contains a higher proportion of fiber Bonobos construct a greater number of nests during rainier seasons Female bonobos construct more nests than males	Difficulty in comparing estimates obtained at different times of the year or from different populations, biases in estimates according to group composition or individual characteristics (e.g., sex and age)	Gorillas (Todd <i>et al.</i> , 2008), and bonobos (this study)
Sign medium	Decay rate, detectability	Chimpanzee groups differ in their preference of tree species to construct their night nests with nests in certain tree species degrading quicker than another Feces of cottontails variably decay according to diet	Difficulty in comparing estimates obtained at different times of the year or from different populations.	Chimpanzees (Badji <i>et al.</i> , 2018), gorillas (Todd <i>et al.</i> , 2008), and cottontails (Cochran & Stains, 1961)

Table 3 Continued.

Behavior variants	Affected parameters	Potential scenario	Potential consequences	Example contexts
Sign conspicuousness	Detectability	Certain carnivores prefer to defecate in more conspicuous areas. Gorilla ground nests decay quicker and are less discoverable than arboreal nests but their construction is variable between individuals. Ground nesting rates can differ between social groups of chimpanzees	Difficulty in comparing inter-specific estimates, or estimates obtained from different populations, differences dependent on individual characteristics (e.g., sex and age)	Chimpanzees (Koops <i>et al.</i> , 2012; Njukang <i>et al.</i> , 2019); small carnivores (Espírito-Santo <i>et al.</i> , 2007)
Sign location	Detectability, observation rate	Ringtails bias latrine use to certain areas within a landscape Badgers bias latrine use towards territorial boundaries Monkeys return regularly to specific locations during a particular fruiting season and therefore signs of their presence are seasonally clumped Tolerance to home-range overlap or preference for particular habitats can create heterogeneous patterns in sign deposition	Inefficient sampling unless surveying design accounts for discrepancies in sign deposition location, decrease in estimate precision.	Deer (Bailey & Putman, 2006), chimpanzees (Normand, Ban & Boesch, 2009), ringtails (Barja & List, 1986), badgers (Roper, Shepherdson & Davies, 1986), genets (Espírito-Santo <i>et al.</i> , 2007)
Sign aggregation	Detectability, observation rate	Hyenas, ringtails, and several terrestrial carnivores concentrate defecating to latrines Dragonfly exuviae counts are variable comparable to adult dragonfly surveying depending on season	Difficulty in comparing across methodologies, difficulty in differentiating unique signs, and difficulty in trend monitoring or in comparison of surveys from different time intervals	Dragonflies (Raebel <i>et al.</i> , 2010), hyenas (Hulsman <i>et al.</i> , 2010), ringtails (Barja & List, 2006)

conservation literature (Merrick & Koprowski, 2017; Kelleher, Silla & Byrne, 2018; Henrich *et al.*, 2022). Behavioral variability can considerably impact conservation effectiveness in a number of ways, from 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 some exceptions. Behavioral variation in the form of movement, space use, and the relationship between activities that create artifacts for monitoring and landscape characteristics not only create considerable opportunity for biases in sign detectability, but can also increase the variance and/or decrease the accuracy of population estimates, or the fidelity of connecting animal abundances to their potential drivers (e.g., elephants: Osipova *et al.*, 2019; alligators: Rosenblatt *et al.*, 2013). For wildlife monitoring, issues can occur, for example, if individuals or groups show spatiotemporal variation in territory use, variable tolerance to territory overlap, or variation in distribution of where behavioral artifacts are deposited. These patterns therefore contribute to variable stochasticity, clustering, or spatiotemporal distribution of behavioral artifacts which consequently impacts monitoring accuracy and inter-estimate comparability (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 expected to affect patterns of detectability and appropriate surveying design tailored to best monitor these signs.

Many of these examples point to a need for careful planning in surveying, quantification and accounting of potential behavioral variation and biases, and this variability included in estimate precision in population monitoring. Such biases are not insurmountable if adequately acknowledged and subsequently addressed. For example, where seasonal variation in sign production behavior has been observed in a species, estimation of population densities should either be restricted to certain periods of a season or systematically averaged across a seasonal cycle. In some cases, more intensive surveying methods which may not be as susceptible to behavioral variation, such as capture–recapture methods, may offer avenues for evading the impacts of behavioral variability on population monitoring; however, such methods may not always present a feasible methodological alternative in many monitoring contexts. Moving forward, for effective and accurate indirect monitoring, it will be important that behavioral variability is considered and quantified, its impacts understood, and those impacts mitigated whenever possible, and the limitations on subsequent inference accounted for when those impacts cannot be mitigated.

Lastly, these results further underline the importance of group-level behavioral variation relative to individual-level behavior (which has been the predominant focus in the conservation literature). Whereas, the impacts of *individual* behavioral variability upon monitoring are well documented (Marescot *et al.*, 2011; Carter *et al.*, 2012; Biro, 2013), the impacts of *intrapopulation* or *group-level* behavioral variation have

additional consequences for monitoring and remain largely ignored. The relevance of group-level behavioral variation to conservation has recently gained a significant amount of attention as a potentially valuable tool to supplement traditional conservation targets if applied effectively (Brakes *et al.*, 2019; Carvalho *et al.*, 2022). However, our results demonstrate how group-level behavioral variation has important impacts on conservation monitoring beyond inter-individual level variation. We further illustrate the impact of temporal variation in behavior on the accuracy of population estimation. Our results support the argument that behavioral variability is relevant to conservation in other ways than just as a potential tool for advocacy or a conservation target, but has implications on our ability to effectively measure populations of concern and evaluate conservation need. Further research characterizing behavioral variation of behaviors relevant to population monitoring across individuals, time periods, populations, and environments must be performed simultaneously with measuring and mitigating its impacts upon population estimation more broadly. 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 also absolutely necessary.

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Conflict of interest

The authors declare no conflicts of interest.

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 the final submitted version.

Data availability statement

Data will be made available on the Data Dryad Repository by the time of publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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.

Table S2. Model effect from a GLMM (Poisson error) of rainfall, group, and sex on bonobo nest construction behavior in two social groups at the Kokolopori Bonobo Reserve, DRC between 2020–2021 (12 months; $n = 210$). Statistically significant results ($P \leq 0.05$) appear in bold italics.

Video S1. A bonobo constructs a day nest in the Kokolopori Bonobo Reserve, DRC. <https://youtu.be/Os5sEyXQuD8>.

Table S3. All published bonobo density estimates included in the permutations of the effects of variation in nest construction and decay rates, and the nest construction and decay rates use.