Predictors of Population Estimates of the Critically Endangered White-Thighed Black-and-White Colobus *Colobus vellerosus*

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Abstract: Population monitoring is crucial for determining the status and trends of a population, but it is important to assess what factors may influence the reliability of the population estimates. In this study, we conducted a complete count of the Critically Endangered *Colobus vellerosus* in the forests associated with the communities of Boabeng and Fiema in central Ghana. We obtained 178 repeated counts of the same groups. We used both good and unreliable counts to assess what factors predicted the number of individuals counted in each group. The numbers increased with proxies for observation conditions, observer experience, and habituation. We recommend investing in observer training and careful planning to improve the observation conditions. Using good counts only, we calculated a maximum population size of 393 individuals in 25 groups. We found no significant differences in group sizes or immature-to-adult female ratios between groups in the closed forest and those in other habitat types. A relatively high immature to adult female ratio suggests that the population size may still be increasing, albeit at a slower rate compared to previous years. Based on our findings, we recommend prioritizing conservation efforts in specific areas to promote population growth and expansion.

Key words: population monitoring, census, complete population counts

Introduction

Many primate populations are rapidly declining, largely due to habitat loss and change (Estrada *et al.* 2017). Researchers often use population monitoring to understand how well these populations are coping with their changing environments and how interventions to reduce threats may affect their population trajectories (Nichols and Williams 2006). Population monitoring programs can use a variety of techniques to assess population size and trajectories (Ross and Reeve 2003; Plumptre *et al.* 2013; Campbell *et al.* 2016), and it is important to reflect on the accuracy and precision of the chosen method.

One way to assess accuracy is to compare the numbers generated from a population count with that of study groups with known numbers of individuals (Kouakou *et al.* 2009). By comparing the actual number of individuals in eight study groups with counts by field assistants not familiar with the study groups during a census of *Colobus vellerosus* (white-thighed or ursine black-and-white colobus) at Boabeng-Fiema Monkey Sanctuary in Ghana, Holmes

(2011) concluded that the number of individuals counted during the census was approximately 18% lower than the actual number. Also using this methodology, researchers in Taï National Park in Côte d'Ivoire concluded that nest surveys were accurate because the number of chimpanzees (*Pan troglodytes verus*) estimated from nest data overlapped with the true number (Kouakou *et al.* 2009). Another type of critical analysis focused on evaluating how the number of groups encountered and observed individuals of five primate species may be affected by disturbance when cutting trails to set up the line transects for surveying in Salonga National Park, Democratic Republic of the Congo (Bessone *et al.* 2023). When walking the survey route repeatedly on different days, the observers encountered more groups and counted more individuals over time, indicating the primates surveyed were sensitive to this kind of disturbance, and this disturbance had a more prolonged effect on some primate species than others (Bessone *et al.* 2023). For the more disturbance-sensitive species, data from the earlier versus later survey days yielded a three-fold difference in estimated density (Bessone *et al.* 2023). These examples illustrate that

it is important when designing and interpreting the results of population surveys to be aware of factors that can influence the likelihood of encountering primate groups and the number of individuals observed.

African colobines are primates with adaptations for an arboreal lifestyle and a diet consisting mostly of leaves and seeds. The majority are threatened by extinction (Wikberg *et al.* 2022). This study focuses on *C. vellerosus* (Fig. 1), which is closely related to *Colobus guereza* (guerezas) and *Colobus polykomos* (western black-and-white colobus) (Oates and Trocco 1983; Ting 2008). *Colobus vellerosus* is endemic to the Upper Guinean Forest of West Africa, and major threats include habitat change and hunting (McGraw 2005). This led to an elevation of its threat status in 2019 to Critically Endangered, which is the highest threat category on IUCN's Red List of Threatened Species (IUCN 2022). There has been an estimated decline of 80–87% of the *C. vellerosus* populations in Benin, Côte d'Ivoire, Ghana and Togo with only *c.* 975 mature individuals remaining in the wild (Matsuda Goodwin *et al.* 2020). It is possibly extinct in Burkina Faso, and its continued presence in Nigeria is uncertain.

One of the last remaining large populations of *C. vellerosus* occupies the forests by the villages of Boabeng and Fiema in central Ghana (Wikberg *et al.* 2022). Its population trend there contrasts starkly with the trends of most *C. vellerosus* populations elsewhere in its range. Repeated complete counts over 30 years have documented an increase in population size from 127 to 451 (Fargey 1992; Saj *et al.* 2005; Wong and Sicotte 2006; Holmes 2011; Kankam and Sicotte 2013; Kankam *et al.* 2023). The continued presence and size of this population are largely due to conservation initiatives by people in Boabeng and Fiema, who have protected *C. vellerosus* from hunting because of traditional religious taboos (Fargey 1992; Saj *et al.* 2005; Kankam *et al.* 2010). When the taboos eroded over time and only a few dozen monkeys remained in the 1970s, elders from this community approached the Ghana Wildlife Division for their governmental protection (Fargey 1992; Saj *et al.* 2005; Kankam *et al.* 2010). In 1990, people from the community initiated the Boabeng-Fiema Monkey Sanctuary (BFMS) ecotourism project for tourists to come and view the monkeys (Fargey 1992; Saj *et al.* 2005; Kankam *et al.* 2010). This population of *C. vellerosus* may also have been increasing rapidly because of the local extirpation of predators.

Figure 1. *Colobus vellerosus* is a diurnal, medium-sized arboreal African colobine which lives in cohesive social groups and has a folivorous diet. Photograph by Eva C. Wikberg.

However, threats to this population remain. The closed forest cover in this area has decreased dramatically (Amankwah *et al.* 2021), and smaller forest fragments and lower tree species richness are associated with lower colobus population densities based on a comparison between 11 forest fragments by Boabeng, Fiema, and other surrounding communities (Kankam and Sicotte 2013). Forest loss in combination with an increasing population size may lead to increased competition for access to limited resources (Arseneau-Robar *et al.* 2023; Glotfelty *et al.* in prep.). The increase in home range overlap (Glotfelty 2021), between-group interactions (Arseneau-Robar *et al.* 2023), and within-group interactions (Teichroeb *et al.* 2003; Wikberg *et al.* 2013; Wikberg *et al.* 2014) over time may also lead to an increased risk of disease transmission (Nunn and Dokey 2006; MacIntosh *et al.* 2012; Silk *et al.* 2019). Thus, it is important to continue to monitor this population closely to detect changes in size and, besides, to assess the accuracy and precision of the monitoring methods.

Holmes (2011) reported that census counts of this population were approximately 18% lower than the actual numbers, but there has been little analysis of what factors lead to more accurate counts. Our first objective, therefore, was to analyze what factors predicted the observed number of individuals in each encountered group. We believed that increased habituation level, ideal observation conditions (e.g., high visibility), and observer experience would be associated with higher counts (Ross and Reeve 2003). Our second objective was to obtain a current estimate of the population size and age-sex class composition. We anticipated: a) a continued positive population trend, resulting in a larger estimated population size compared to previous studies; and b) a positive immature-to-female ratio within the range previously reported from this population, indicating a growing population (Fargey 1992; Saj *et al.* 2005; Wong and Sicotte 2006; Holmes 2011; Kankam and Sicotte 2013; Kankam *et al.* 2023). Our third objective was to evaluate whether group characteristics differed between habitat types, which could suggest that the colobus monkeys thrive in certain types of habitats. We predicted that we would find larger groups with higher immature-to-female ratios in the closed forest based on previous findings of variation in habitat quality and population density across forest fragments (Kankam and Sicotte 2013). Based on our findings, we suggest ways to improve the accuracy of future population counts and to further support population growth and expansion.

Methods

This study was conducted in a dry semideciduous forest habitat in central Ghana (7°43'N and 1°42'W) (Hall and Swaine 1981). The 1.92 km² of land that is set aside for the Boabeng-Fiema Monkey Sanctuary is a mix of old-growth forest, derived savannah that is regenerating farmland, planted trees, and areas that border roads, villages, and farmland (Fargey 1992; Kankam and Sicotte 2013) (Fig.

2). The forest fragment is surrounded by farmland but connected to other, smaller forest fragments via narrow riparian forest corridors (Fargey 1992; Kankam and Sicotte 2013).

Colobus vellerosus is a diurnal, medium-sized arboreal African colobine (Saj and Sicotte, 2013; Wikberg *et al.*, 2022). They live in cohesive groups with up to 36 individuals (Wong and Sicotte 2006). The groups typically consist of one or several adult males, one or several adult females, and immatures. As expected for a folivorous primate (Saj and Sicotte 2007; Teichroeb and Sicotte 2009), they spend a high proportion of their time resting (Teichroeb *et al.* 2003). All groups in our study area range in proximity to villages, roads, or trails in the forest that are used by community members, tourists, and researchers. All groups are, therefore, at least partly habituated to the presence of humans. Because population counts have been conducted since the 1990s and field assistants are working in the forest year-round, we have good knowledge of the location of the groups. For groups that are not long-term study groups, group identities are matched up between different census years mostly based on location. Group identities are also determined from individuals with unique features (e.g., bent tail, scars, pink nipples, hairless tail) or group-specific behaviors such as one group's particular agonistic scratch display (i.e., rapidly moving fingers against tree trunks) that has not been observed in any other groups. These characteristics of the species and study population conditions make obtaining complete counts of the population more feasible (Campbell *et al.* 2016; Plumptre *et al.* 2013; Ross and Reeve 2003). This is the method we used to count the number of individuals in all groups in the Boabeng and Fiema forests. The composition of the four long-term study groups was recorded three times per week year-round.

We followed the methodology used in some previous population counts at this site (Saj *et al.* 2005; Wong and Sicotte 2006; Holmes 2011). Two to three weeks before the census started, trails were cut in the inaccessible areas of the Boabeng and Fiema forests to find groups that ranged far from the existing trails. A team of six observers conducted the census from 6–30 July 2022. Team members were already adept at determining age-sex classes based on their observations of long-term study groups. During this period, we alternated between conducting group counts (for a total of 10 days) and monitoring colobus sleeping trees (for a total of 10 days). On days dedicated to monitoring sleeping trees, all observers walked together from 16:00 until a group was located. The groups were identified by the most experienced observers, and one less experienced observer stayed with that group until 18:00 when the group would be in their sleep tree. The other observers continued searching for additional groups and followed the same process until each observer was assigned to one group. On group-count days, at 6:00, each observer either went to a tree where a group had spent the night (see description of sleep trees below) or walked trails to find a group. Once a group was found, the observer stayed with that group until the group

Figure 2. The forested study area, surrounding farmland, and built-up areas by Boabeng and Fiema in central Ghana with letter codes indicating identities of the groups encountered in the Boabeng forest (grey text = current year-round study group, white text = census group).

count period ended at 10:00. Once a group was detected, the observer recorded the group's identity, the location where it was first found (i.e., a trail, a specific tree, or a location in the village), the number of individuals in each age-sex category visible every half hour, whether the count was good or unreliable (based on the observer's certainty that the recorded number matched the actual number), and any comments on visibility, behaviors, and potential errors in age-sex classifications. Individuals were classified as adult male (i.e., large size with continuous white thigh patches), adult female (i.e., smaller than adult males, visible nipples, and white patches on the thighs separated by a thin strip of black fur), juvenile (i.e., moving independently from mother and smaller than adults but larger than infants), infant (i.e., smaller than juveniles and often ventral on adult females), or unknown age-sex class. The observers focused on walking trails to locate groups that had not been contacted or from which they had not yet obtained two good counts. They rotated between the groups, ensuring that each observer was with a group only once. Each group was censused two to three times during the study. During each census day, the observer completed one to eight counts of the group members.

We used the repeated counts obtained during the population census days to create a linear mixed model for assessing whether the observed number of individuals in each encountered group could be predicted by variables associated with observation conditions, habituation level, and observer experience. The observer's assessment of whether it was a good count served as a proxy for observation conditions, as unreliable counts often occurred during periods of low visibility. Additionally, we considered the time of day as another proxy for observation conditions, as colobus groups tend to be more cohesive when still in their sleeping tree—they spread out more when they begin to move and forage. The time of day was entered as the minutes since the census start time. In the absence of specific indicators for habituation level, we used population identity (Boabeng or Fiema) as a proxy. The colobus groups in Boabeng encounter researchers and tourists more often, and we considered the Boabeng groups to have a higher level of habituation than those in Fiema. We included census day as a proxy for habituation level and observer experience. Groups that do not regularly see observers may become more habituated with each census day, and the observers become more skilled in observing and assigning age-sex categories. The observer-specific experience was classified as 1 for first-time field experience with this study species, 2 for some previous field experience but no prior population census work, 3 for previous population census work and past field assistant experience, 4 for previous population census work and current full-time field assistant, 5 for multiple population censuses and approximately 10 years as a full-time field assistant, and 6 for multiple

population surveys and the longest tenure as a field assistant for the Boabeng-Fiema colobus research project. We performed this analysis using R version 4.1.0 with the packages lme4 (Bates *et al.* 2015) and multcomp (Hothorn *et al.* 2014). We used the R packages DHARMa (Hartig 2021) and performance (Lüdecke *et al.* 2021) to evaluate model fit and compute Variance Inflation Factors (VIF). We found no evidence of collinearity, as indicated by low VIF values (range: 1.04–1.10).

We used data from our four long-term study groups and the census groups for the following calculations. First, we calculated population density by dividing the total number of individuals by the size of the area (1.92 km²). Second, we calculated the total biomass (kg/km²) using published weight estimates for males (8.5 kg), adult females (6.9 kg), and juveniles (3.85 kg) (Oates 1994). For individuals for which age-class could not be determined, we calculated their biomass using the mean weight of individuals of known age-sex classes. We excluded infants from the biomass calculations to facilitate comparisons with previous estimates (Holmes 2011). Lastly, we calculated the immature-to-adult female ratio by dividing the number of infants and juveniles by the number of adult females.

Observers also collected ranging data throughout the year from the Boabeng groups, which are either study groups or groups that frequently encounter our study groups. Observers recorded the group location using a map on which all trails and large trees (>40cm DBH) were marked, once an hour for study groups when they were with them and opportunistically from other Boabeng groups when they encountered them. We categorized their home ranges as either consisting mostly of closed forest or consisting mostly of other habitat types. The closed forest typically has multiple canopy layers and over 40% tree cover (e.g., SK in the area with dark green tree cover in Fig. 2). Many of the groups outside the areas with closed growth forest range in areas where the forest is heavily disturbed and in areas with regenerating farmland. These areas typically have a single canopy layer, more shrubs, and herbaceous vegetation (e.g., DA in areas with browner colors in Fig. 2). Although the colobus groups range in a variety of habitat types, we lacked the fine-grained data required to further classify home ranges based on the different habitat types (i.e., closed forest, open forest, riparian forest, savanna-woodland, savanna, built-up areas) described in previous publications (Kankam *et al.* 2010; Kankam and Sicotte 2013). We conducted an analysis to determine if Boabeng groups in the closed forest versus other habitat types differ in group size or immature-to-adult female ratio using Mann-Whitney U-tests. We did not characterize the habitat type of the Fiema groups because we lacked long-term data on their ranging patterns, and encounter locations during the census may be biased to open areas and proximity to the community, roads, and trails.

Results

Count reliability

Of the 178 group counts, 49% were considered good counts, 41% were considered unreliable, and 10% were not classified as good or unreliable. Each group had one to seven good counts. The observer described the observation condition for good and unreliable counts. Low visibility due to dense vegetation and/or undergrowth was the most common reason cited for unreliable counts (20 comments). Unreliable counts also occurred during intergroup encounters and/or chases (four comments), when the group was spread out (three comments), or during bad weather (two comments). Good counts were often not accompanied by a comment, but described conditions for good counts included the group resting in trees (three comments) or following a similar path of movement from one large tree to another with high visibility (one comment). More surprisingly was that some good counts occurred during intergroup encounters and when chases were occurring (three comments), when there was some movement (two comments), and when the group was spread out (two comments).

In a few cases, the observers noted potential recording errors. In one case, an error in the recorded age-sex class occurred when a jump-displaying individual was initially assumed to be a male but was later confirmed to be a female. Males jump display more frequently than females, and it is also challenging to determine the sex of individuals when they are moving quickly in the canopy. In one case, the observer heard an infant squealing but was unable to locate it, leading to an underestimation of group size. The observers also identified potential errors in their recordings that may have resulted in an overestimation of group size. Two of these cases occurred during intergroup encounters. In the third case, the observer acknowledged the possibility of double-counting one individual.

Predictors of observed group size

In the analysis of observed group size, we included the 158 group counts from 21 groups when at least some individuals were visible and the observers had recorded whether their count was reliable. The observed number of individuals was lower when the count was classified as unreliable by the observer (estimate: -3.43, 95% CI: -4.27 to -2.58), increased with observer experience level (estimate: 1.15, 95% CI: 0.59 to 1.69), and increased with the number of days since the census started on July 7 (estimate: 0.78, 95% CI: 0.22 to 1.35) (Fig. 3). The observed number of individuals was not predicted by time since the start of the census at 6:00 in the morning (estimate: -0.3, 95% CI: -0.71 to 0.11) or by population ID (estimate: -0.56, 95% CI: -4.04 to 2.92) (Fig. 3). The model explained 23% of the observed variation without random effects and 73% of the observed variation with random effects.
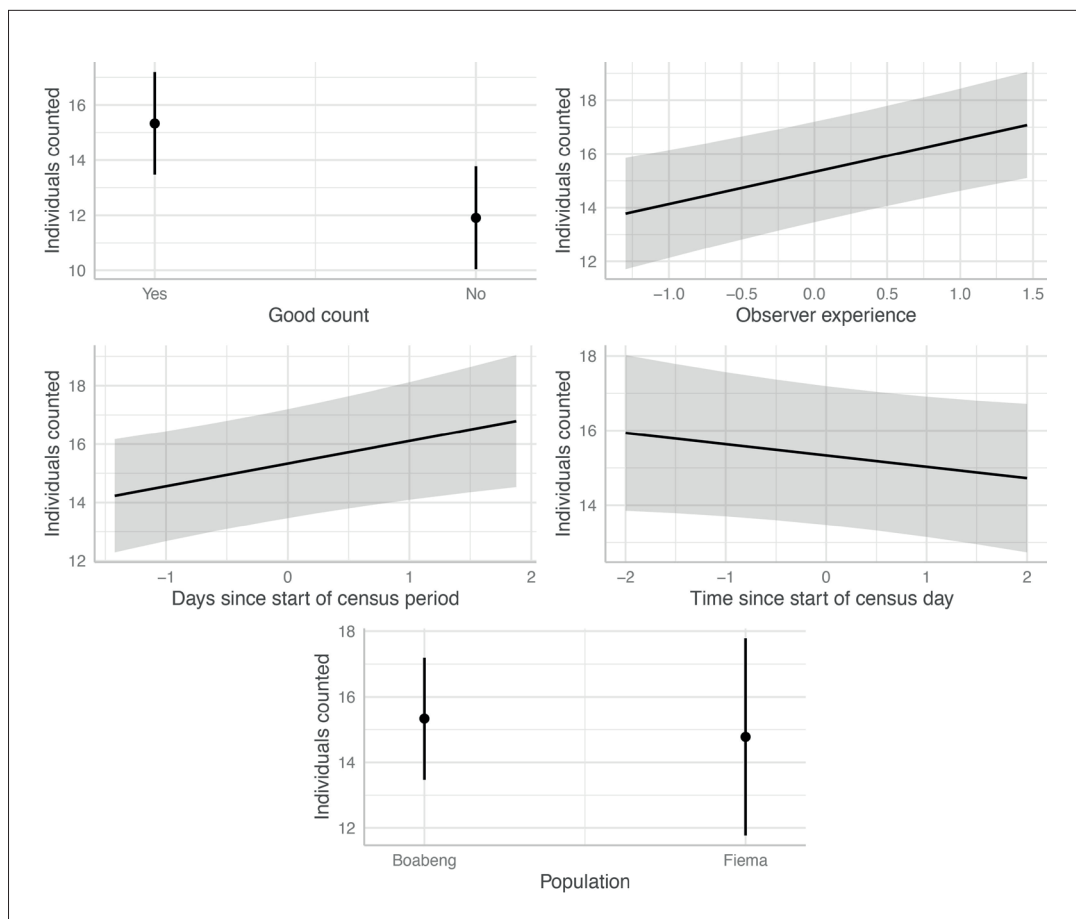
Figure 3. The predicted relationship between the number of individuals counted in each social group and whether the observer classified it as a reliable count, observer experience, days since the first census day, hours since start of the census that day, and whether the group ranged by Boabeng or Fiema. Shaded areas represent the 95% confidence interval, and the y-axis with numerical values has been square root transformed.

Population size and group composition

Observers counted 19 groups in the Boabeng forest and six groups in the Fiema forest (Table 1). One Boabeng group and two Fiema groups that had been present during previous population counts could not be located. Only including the counts classified as good counts by the observer, the number of counted individuals ranged from a minimum of 349 to a maximum of 381. The calculated density ranged from 181.77 to 198.44 individuals/km² if using minimum versus maximum counts. If using the maximum number of individuals counted, the calculated biomass was 663.00 kg for adult males, 938.40 kg for adult females, 350.35 kg for juveniles, and 127.98 kg for individuals of unknown age-sex class. If including individuals with known and unknown age-sex classes, the total biomass is 2,079.73 kg.

Each group contained 1 to 7 adult males, 1 to 10 adult females, and 0 to 15 immatures based on the maximum numbers observed in each group (Table 1). The median group size was 16 in both the closed forest (range: 4 to 22) and the other habitat types (range: 13 to 19), and there was no significant difference in size between groups in these two habitat types (Mann-Whitney U-test, W = 39, p = 1.10, N = 19).

We counted a total of 136 adult females and 178 immatures (using maximum values for number of individuals counted), which yields an overall immature-to-adult female ratio of 1.31. Although the median immature-to-adult female ratio was slightly higher in groups occupying the closed forest (1.20, range: 0 to 4) than that in groups in the other habitat types (1.08, range: 0.80 to 1.83), there was no significant difference in immature-to-adult female ratio between groups in these two habitat types (Mann-Whitney U-test, W = 49.5, p = 0.38, N = 19).

Discussion

We conducted a complete count of the Boabeng-Fiema population of the Critically Endangered *Colobus vellerosus*. Our analysis indicates that the number of counted individuals was influenced by observation conditions, observer experience, and habituation. Based on these results, we make recommendations to improve census methodology in future studies. Using reliable counts only, the calculated maximum population size was 393 individuals in 25 groups, and below we discuss potential explanations for why this estimate was

Table 1. Composition of the groups inhabiting the forests by Boabeng and Fiema.

Population	Group name (code)	Group size	Adult male	Adult female	Immature	Immature: adult female ratio	Habitat type
Boabeng	Akonkodie (AK)	20	4	7	9	1.29	Closed forest
Boabeng	Akonkodie extension (AE)	13	2	6	6	1.00	Other
Boabeng	Stream (ST)	22	3	6	10	1.67	Closed forest
Boabeng	Bentensua (BS)	18	3	4	9	2.25	Closed forest
Boabeng	Bomosua (BO)	16	2	6	8	1.33	Closed forest
Boabeng	Dadie (DA)	19	3	6	11	1.83	Other
Boabeng	Falls (FA)	19	7	8	9	1.13	Closed forest
Boabeng	Falls extension (FE)	15	4	5	6	1.20	Closed forest
Boabeng	Nippy (NP)	16	3	6	7	1.17	Closed forest
Boabeng	Odum (OD)	16	5	7	6	0.86	Other
Boabeng	Penelope (PN)	16	4	6	7	1.17	Other
Boabeng	Red tail (RT)	19	3	4	12	3.00	Closed forest
Boabeng	Saviour kazio (SA)	13	3	5	8	1.60	Other
Boabeng	Scratchy (SC)	17	5	6	6	1.00	Other
Boabeng	Skittish (SK)	16	2	6	11	1.83	Closed forest
Boabeng	Splinter (SP)	6	1	1	4	4.00	Closed forest
Boabeng	Village 1 (VI)	15	6	5	4	0.80	Other
Boabeng	Wawa (WW)	4	1	3	0	0.00	Closed forest
Boabeng	Winter (WT)	8	2	4	2	0.50	Closed forest
Fiema	Group 3	29	6	10	15	1.50	-
Fiema	Group 4	16	3	7	7	1.00	-
Fiema	Group 5	17	7	6	7	1.17	-
Fiema	Group 6	12	1	5	7	1.40	-
Fiema	Saviour	10	3	4	3	0.75	-
Fiema	Yaw Skeya	15	2	6	7	1.17	-

slightly lower than the previously published estimate and what can be done to promote population persistence over time.

Predictors of observed group size

We used repeated counts of the same groups to analyze what factors predicted the number of counted individuals in each group. The observed number of individuals was predicted by whether the count was classified as reliable by the observer. Unreliable counts often occurred during low visibility as expected (Ross and Reeve 2003). However, observers were still able to obtain good counts during some challenging observation conditions such as during intergroup encounters. Likely due to their prior knowledge of colobus behaviors, they could in some cases single out extra-group individuals even when they were attached to the group being counted.

Observer expertise is likely very important for the accuracy and precision of complete counts (Ross and Reeve 2003). As expected, the observed number of individuals increased with observer experience level. The observed number of individuals also increased with the number of days since the census started, which could be another proxy for observer experience with the underlying reasoning that observers get more experienced in observing and assigning age-sex categories during the study. It can also be a proxy, however, for increased habituation level of the groups over time, making it easier to count individuals from groups that do not typically see observers on a regular basis. In contrast, Bessone and colleagues (2023) argued that an increased number of individuals counted over time was due to decreased disturbance with increasing time since trails were cut. We believe it is unlikely that trail cutting would have affected the monkeys' behaviors in our study

as the trails were cut two to three weeks before the start of the census and all individuals are at least partly habituated to humans. In contrast to our predictions, there was no significant difference in the observed number of individuals in Boabeng and Fiema. We had expected it to be more difficult to count individuals in the Fiema forest as these groups encounter tourists and researchers less frequently than the groups in the Boabeng forest do. Although our results could indicate that population ID is a poor proxy for habituation and/or that the habituation levels of groups in Boabeng and Fiema are similar, the Fiema groups directed more displays to and fled from the only foreign researcher on the census team. Similar behaviors were reported by Holmes (2011), who also described how some colobus groups would flee at the sight of foreign objects such as binoculars. However, she was still able to obtain reliable counts when the group members leaped between trees or fled into taller trees with high visibility (Holmes, 2011).

The study species' activity patterns may affect the likelihood of obtaining complete counts (Ross and Reeve 2003). We predicted that the observed number of individuals would decrease with the number of hours since the start of the census day because the groups typically spend the night in tall trees (Teichroeb *et al.* 2012) and are more cohesive and visible early in the morning before they start to travel and forage in the dense undergrowth closer to the ground. In contrast to our prediction, the time of day did not predict the number of observed individuals, and we conclude that variables linked to observation conditions, observer experience, and habituation are more important.

Based on these findings, we provide the following recommendations to improve the accuracy of future population estimates. Observer experience was an important predictor of the number of individuals counted, and ideally, people on the census team should be well-trained before the census starts. For future census work, it may also be worthwhile to have a team of observers locating all non-study groups before the census starts to become more familiar with their ranging patterns and increase habituation levels. Our descriptive data suggest that the less habituated monkeys responded differently to the foreign researcher on our census team, which should be considered when deciding who will focus on which forest fragment. Because the observers' perceived quality of the count was an important predictor of the number of individuals observed, we recommend that they keep detailed notes on the perceived quality of their count, conditions that may affect the observed number, and any uncertainties about double-counting, mis-sexing individuals, or including extra-group individuals in their count.

We conducted our population census during the rainy season, similar to several but not all previous counts of this population (Wong and Sicotte 2006; Holmes 2011). Due to time constraints, we were not able to repeat the census in different seasons to analyze the effect of seasonality. However, there are several months (often from November to March) with no or little rainfall and less foliage (Saj and Sicotte 2007), and it is ideal to perform the complete counts during seasons when it is easier to count all individuals (Ross and Reeve 2003). Thus, there may be several ways to refine population monitoring methods, which may make it possible to detect smaller changes in population trajectories.

Population size and group composition

During our complete count of *C. vellerosus* in the summer of 2022, observers contacted 25 groups and counted 350–393 individuals in the area by Boabeng and Fiema. The number of mature individuals in this population represents approximately 20% of the estimated 975 mature C. vellerosus living in the wild (Matsuda Goodwin *et al.* 2020), and our study population is the largest known population of *C. vellerosus* (reviewed in Wikberg *et al.* 2022). Based on the maximum observed number of individuals, the population density at Boabeng and Fiema is estimated to be 198.44 individuals/km², which is at the upper range reported from other populations of black-and-white colobus monkeys (reviewed in Wikberg *et al.* 2022). Notably, the *C. vellerosus* population density in the Dinaoudi Sacred Grove in Côte d'Ivoire was a staggering 1000 individuals/km², but it only consisted of 30 individuals in a 3-ha fragment (Gonedelé Bi *et al.* 2010). Several populations of red colobus (*Piliocolobus* spp.), closely related to the black-and-white colobus, also occur at very high population densities (reviewed in Wikberg *et al.* 2022). Although some colobus populations can reach such high densities, several of these cases likely consist of populations being compressed in shrinking forest patches. It is uncertain whether such compressed populations can persist long-term, especially if the population is small.

The maximum number of counted individuals during our 2022 census was 393, which is 58 individuals less than that of the Kankam and colleagues' (2023) 2020 census. Kankam and colleagues (2023) worked in teams of two, however, and it is possible that this increased the number of observed individuals. Also, their census was conducted approximately three months later in the year, and it is possible that less rainfall led to better observation conditions. Our methodology followed that of Holmes (2011), who determined that this method underestimates the size by approximately 18% (Holmes 2011). If this is the case, the actual number of individuals in the population in 2022 would be 463 individuals, which is similar to the 451 individuals counted during the 2020 census (Kankam *et al.* 2023). Both complete count methods used at this site should lead to an accurate number of groups because we have a good understanding of the number and approximate locations of groups. Three known groups were missing during our census, and our total number of groups was two groups fewer than during Kankam and colleagues' (2023) 2020 census. These groups may have dissolved or moved out of the study area. Groups have previously been reported not to reside year-round in Fiema (Kankam *et al.* 2010).

When comparing our population count to those conducted in the past, the population appears to have increased at an average rate of 6.75 individuals per year based on the maximum number during the current census in 2022 (393 individuals) and the maximum number counted in 2010 (312 individuals), which was the last census that used the exact same methodology (Holmes 2011). This is only about half the rate at which the population size increased between the census years 2003, 2007, and 2010 (Wong and Sicotte 2006; Kankam *et al.* 2010; Holmes 2011).

On a positive note, the overall immature-to-adult female ratio during our population count was at the high end of those reported previously (Saj *et al.* 2005; Wong and Sicotte 2006; Holmes 2011; Kankam and Sicotte 2013; Kankam *et al.* 2023), and positive numbers suggest that the population is still increasing. In contrast, having more adult females than infants and juveniles would likely signal a negative population trajectory as was the case in the decreasing *Alouatta palliata* (mantled howler) populations in Panama and Costa Rica (Heltne *et al.* 1976). Also, we did not find any significant differences in group size or immature-to-adult female ratios between groups inhabiting the closed forest versus other habitat types. This preliminary finding needs to be further investigated in future studies with more detailed ranging data and habitat categories. It is possible, however, that this and other species of black-and-white colobus are able to survive and reproduce well even in forests that consist of regenerating farmland and cultivated trees (reviewed in Wikberg *et al.* 2022). Cultivated tree species make up (during some months) 32% of the diet of *Alouatta guariba clamitans* (brown howlers) in the state of Rio Grande do Sul, Brazil (Chaves and Bicca-Marques 2017). The authors conclude that cultivated tree species that both humans and non-human primates utilize can have an important conservation value (Chaves and Bicca-Marques 2017), and this may be especially true in human-dominated landscapes.

Evidence-based conservation

It is important to keep in mind that determining actual population trajectories can be difficult due to between-year variation and sampling effects (Nichols and Williams 2006), and it may take up to 10 years of data to accurately determine population trends (Maxwell and Jennings 2005). This timeframe would be too long to wait before incorporating the results of studies in management plans (Nichols and Williams 2006) because the threats to primate survival are escalating rapidly (Estrada *et al.* 2017). For example, a small population of *C. vellerosus* in Soko sacred grove in Côte d'Ivoire went locally extinct between surveys conducted three years apart (Gonedelé Bi *et al.* 2010). Because the population of *C. vellerosus* in the Boabeng and Fiema forests appears to be increasing less rapidly than two decades ago based on our findings, it is important to evaluate why this may be, what actions should be put in place to promote future population growth and expansion, and then follow

best practices to assess the effectiveness of these actions (Junker *et al.* 2020; Christie *et al.* 2021).

Our study species, *C. vellerosus,* and some other African colobines show a greater degree of behavioral flexibility than anticipated for species adapted to a highly specialized diet, and they can persist in human-modified environments (Wikberg *et al.* 2022). The ability to use human-modified landscapes such as human settlements and secondary forests is associated with reduced extinction risk (Galán-Acedo *et al.* 2019). Less strictly arboreal species with increased dietary diversity are more likely to use human-modified environments (Galán-Acedo *et al.* 2019), and dietary diversity also reduces extinction risk (Jernvall and Wright 1998; Machado *et al.* 2023). This behavioral flexibility may increase their chances of population persistence in changing environments (Buskirk 2012; Beever *et al.* 2017). However, there may be a limit to how much the individuals can change their diet and habitat use. Similarly, howler monkeys also use individual behavioral flexibility to cope with habitat loss, but they seem less likely to persist long-term in smaller compared to larger habitat patches (Bicca-Marques *et al.* 2020). Indeed, behavioral changes may not always be adaptive or sufficient to cope with environmental changes, and these changes may indicate a future population collapse (Berger-Tal *et al.* 2011).

Alternatively, it may be that the forest cannot accommodate a higher number of colobus monkeys. In line with this notion, we have observed behavioral changes in our study groups over time that indicate increased competition for food resources (Wikberg *et al.* 2013; Arseneau-Robar *et al.* 2023; Glotfelty *et al*. in prep.). Under this scenario, more individuals may be motivated to disperse either temporarily or permanently to the surrounding forest fragments (Jones 2005). Indeed, seven nearby forest fragments have been recolonized by colobus in the last decades, most likely by dispersing individuals from the Boabeng and Fiema fragments (Wong and Sicotte 2006; Kankam *et al.* 2010).

Although *C. vellerosus* at our study site has recolonized some of the surrounding forest fragments, some fragments remain unoccupied or contain only a very small number of individuals (Wong and Sicotte 2006; Holmes 2011; Kankam and Sicotte 2013; Kankam *et al.* 2023). Planting trees and building landscapes that take the needs of forest-dwelling animals and humans into account could facilitate dispersal between fragments (Arroyo-Rodríguez *et al.* 2020). Local community members and other stakeholders built forest corridors and stepping stones in the Pontal do Paranapanema region of the state of São Paulo, Brazil, to promote the dispersal of *Leontopithecus chrysopygus* (black lion tamarin) (Chazdon *et al.* 2020). It is important to evaluate whether the location of these corridors and stepping stones compete with the socioeconomic and cultural values of that land (Ruiz-López *et al.* 2022). For example, planting a series of stepping stones using habitat not suitable for farmland may not interfere with human livelihoods but could still link surrounding fragments to the Kibale National Park in Uganda and encourage *Piliocolobus tephrosceles* (red colobus)

dispersal (Ruiz-López *et al.* 2022). It is possible that similar approaches to building landscapes that consider the needs of the colobus monkeys and humans could facilitate dispersal between forest fragments at our study site.

Besides facilitating movement between fragments, it is also important to improve chances for population persistence in the fragments once a population is established there. Colobus monkeys are arboreal and leaves from large trees make up the majority of their diet (Saj and Sicotte 2007; Teichroeb and Sicotte 2009). The rapid loss of forest in this area is, therefore, concerning (Kankam *et al.* 2010; Amankwah *et al.* 2021). Some of the forest loss has been accidental due to forest fires. Although our study group started using a burnt area relatively soon after the regrowth of vegetation (CK, pers. obs.), severe fires can have a long-term effect on primates. Siamangs, *Symphalangus syndactylus*, did not use heavily burnt areas, while they did resume ranging in other areas with less severe fire effects within 18 years after a forest fire (Lappan *et al.* 2021). Improved forest protection could be achieved by preventing additional cutting of large trees and allocating more resources to fire management. It may also be possible to promote further increase and/or persistence of the *C. vellerosus* population by planting trees in certain areas with low tree coverage to increase habitat carrying capacity. Unfortunately, this is a slow process that requires long-term care to prevent the trees from being outcompeted by faster-growing plants.

The Boabeng and Fiema communities have also taken action by sharing revenue from the ecotourism projects with the surrounding communities, which is likely an important incentive for them to protect the colobus as they do not have the same traditional beliefs as the Boabeng and Fiema communities do (Kankam *et al.* 2010). Revenue sharing could increase the chances for population expansion and persistence. By finding ways to mitigate threats to non-human primates while also considering human livelihoods and improving human well-being, we may be able to enhance the conservation outlooks for the many threatened non-human primates living in close proximity to humans (Kareiva and Marvier 2012).

Ethics Statement

Acknowledgments

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