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RESEARCH ARTICLE

West Side Story: Regional Inter-Troop Variation in Baboon Bark-Stripping at Gorongosa National Park, Mozambique

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ABSTRACT

Objectives: Baboons possess sophisticated physical and social cognitive abilities; hence, the lack of evidence to date of large-scale behavioral variation in these primates is puzzling. Here we studied a candidate for such variation—the stripping of bark from *Acacia robusta* trees for consumption of the sap and soft tissue underneath—in Gorongosa National Park, Mozambique.

Materials and Methods: We surveyed an area inhabited by ~60 troops of chacma baboons, recording the availability and characteristics of the target trees, as well as the presence or absence of bark-stripping at 45 habitat plots distributed across a grid covering an area of ~300 km^2.

Results: Camera traps confirmed the presence of baboons at all habitat plots, and we identified regional clumping in the distribution of the behavior, a pattern consistent across two consecutive years. Proportion and mean height/width of *A. robusta* did not predict whether bark-stripping behavior was present at a given site, nor did broader ecological variables such as habitat type and distance to the nearest water source. However, stripping sites had significantly higher numbers of *A. robusta* than non-stripping sites, and within a given bark-stripping site, baboons preferred to strip taller and wider trees among those available.

Discussion: The prominent geographical clustering we uncovered may have been driven by opportunity (i.e., the prevalence of *A. robusta* at a given site), but is also consistent with a possible (non-mutually exclusive) cultural interpretation. We propose avenues for future research on Gorongosa's baboons to better quantify the relative contributions of ecology, genetics, and social

learning to the prevalence of bark stripping. We also briefly consider the potential relevance of baboon bark stripping to elucidating early hominin foraging strategies.

1 | Introduction

Long-term studies of wild baboons have informed our understanding of many aspects of evolution, ecology, and behavior (e.g., Altmann 2001; Cheney and Seyfarth 2008; Fischer et al. 2017; Jolly 2020; Strum 2001). Six species of the genus *Papio* (*sensu* Jolly 2001) currently range through Africa and the Arabian Peninsula (*Papio hamadryas*, *Papio papio*, *Papio anubis*, *Papio cynocephalus*, *Papio ursinus* and *Papio kindae*) and overlap in several contact zones including around the Awash River, Ethiopia; Amboseli, Kenya; and the Kafue River Valley, Zambia (Chiou et al. 2021; Jolly et al. 2011; Martinez et al. 2019; Phillips-Conroy and Jolly 1986; Rogers et al. 2019; Samuels and Altmann 1986; Zinner et al. 2009). Significant behavioral variation exists both within and between baboon species, including but not limited to foraging behavior (Whiten et al. 1991), social structure (Fischer et al. 2017; Henzi and Barrett 2005; Schreier and Swedell 2009; Smith 1992), social behavior (e.g., greeting and grooming) (Dal Pesco and Fischer 2020; Smuts and Watanabe 1990; Weyher et al. 2014), and levels of male–male cooperation and competition (Kalbitzer et al. 2015; Petersdorf et al. 2019). Inter-troop variation at the same field site has been noted in levels of affiliative and agonistic behavior (Sapolsky and Share 2004; Sapolsky 2006), foraging methods (Bigalke and van Hensbergen 1990; Hall 1962; Strum 1975), and crop raiding (Strum 2010). However, this type of inter-troop variation has remained relatively unexplored, and, as such, many open questions remain surrounding the mechanisms through which they are maintained.

Within-species regional variation in behavior is typically explained as the outcome of some combination of genetic, ecological, and cultural effects, with the relative contributions of these factors being of principal interest to researchers, but most authors acknowledge that there is a complex interplay among these sources of variation and disentangling them can be difficult (e.g., Koops et al. 2013; Laland and Janik 2006). The term "cultural variation" is used here to refer to differences in the behavioral profiles of different groups of the same species, where the behaviors in question are to some extent socially learnt and are not *solely* due to ecological or genetic differences (note the emphasis on "solely"). Among baboons there is, to date, little evidence of cultural variation among populations, despite them possessing sophisticated social and physical cognition (e.g., Strum 2012) and being proficient social learners (e.g., Carter et al. 2014; Carter et al. 2016; Claidière et al. 2014) that can establish traditions (i.e., behaviors acquired through social learning that are shared by members of a troop; Sapolsky and Share 2004; Sapolsky 2006; Strum 1975). But large-scale, persistent, geographically clustered inter-troop differences in baboon behavior—hallmarks of culture—remain to be documented. This is in stark contrast with the extensive, putatively culturally driven regional variation characterized in several other primates (e.g., Robbins et al. 2016; van Schaik et al. 2003; Whiten et al. 1999) as well as non-primates (e.g., Whitehead and Rendell 2015). Cultural variation can occur over a range of spatial scales: from that between neighboring groups to populations separated by continental-scale distances. Importantly, some of the strongest observational evidence for animal culture comes from comparisons of the former type: behavioral differences between neighboring groups that face similar ecological conditions and share migrants, reducing the likelihood that ecological or genetic factors underpin any observed differentiation (e.g., Luncz et al. 2012). Here, we aim to contribute with novel observations of regional variation in primate behavior from a newly established, large-scale field project in central Mozambique. Given that our baboon field studies are in their relative infancy as part of this project, the interpretation of the variation we uncover must remain speculative; nonetheless, our aim will be to highlight promising avenues for future work.

The Paleo-Primate Project at Gorongosa National Park (GNP), Mozambique, was launched in 2016 with the aim of reconstructing the evolutionary history of the previously unexplored southern tip of the East African Rift System in Mozambique, a region that is hypothesized to hold great significance in the biogeography of early hominin origins (Bobe et al. 2020; see also other articles in the present issue). The project combines palaeontological work (e.g., Bobe et al. 2023) with studies of extant primate adaptation to environments analogous to those of early hominin species in eastern Africa (Habermann et al. 2019). The principal primate species studied by the project is the chacma baboon (*P. ursinus*), whose population at GNP exhibits potential hybridisation with yellow baboons (Martinez et al. 2019; da Silva et al. 2024). Aerial surveys estimate the number of troops in the park to have ranged between 185 and 207 from 2014 to 2024 (Stalmans and Peel 2016, 2024; Stalmans et al. 2018), with troops present throughout the surveyed area (see Figure S1a).

Initial behavioral observations in July–August 2017 reported a behavior that appeared to be common within woodland habitats: the stripping, by teeth and hands, of the bark (periderm) of *Acacia robusta*[1] trees (Figure 1a–d). We noted that once the bark is stripped, baboons consume the soft inner tissue (the phelloderm) on the torn strips, and also scrape their teeth along the exposed trunk (the phloem). The latter, food-conducting tissue, is a source of sugars and nutrients (sap), while the former, containing living parenchyma cells, stores starch and other sugars. Both the scraping and the biting to release the bark in the first place leave prominent regularly spaced toothmarks on the branches (Figure 1c), a useful diagnostic for characterizing baboon bark-stripping. (Note that elephants, *Loxodonta africana*, in the region also strip bark, but their activity leaves very different and distinctive marks; see Figure 1f,g, Sections 2 and 3). Within the troop's home range, we often encountered trees showing extensive damage from stripping—indeed, some had died due to a large proportion of their surface having been stripped. We also observed the behavior directly (Figure 1d; Video S1), noting that individuals spent extended periods on the activity (up to about 30 min), several individuals within a troop often performed the behavior simultaneously in the same or nearby trees, and bark-stripping individuals produced wadges (balls of fibrous bark tissue collected in the mouth, sucked, or chewed then spat out; Figure 1e).

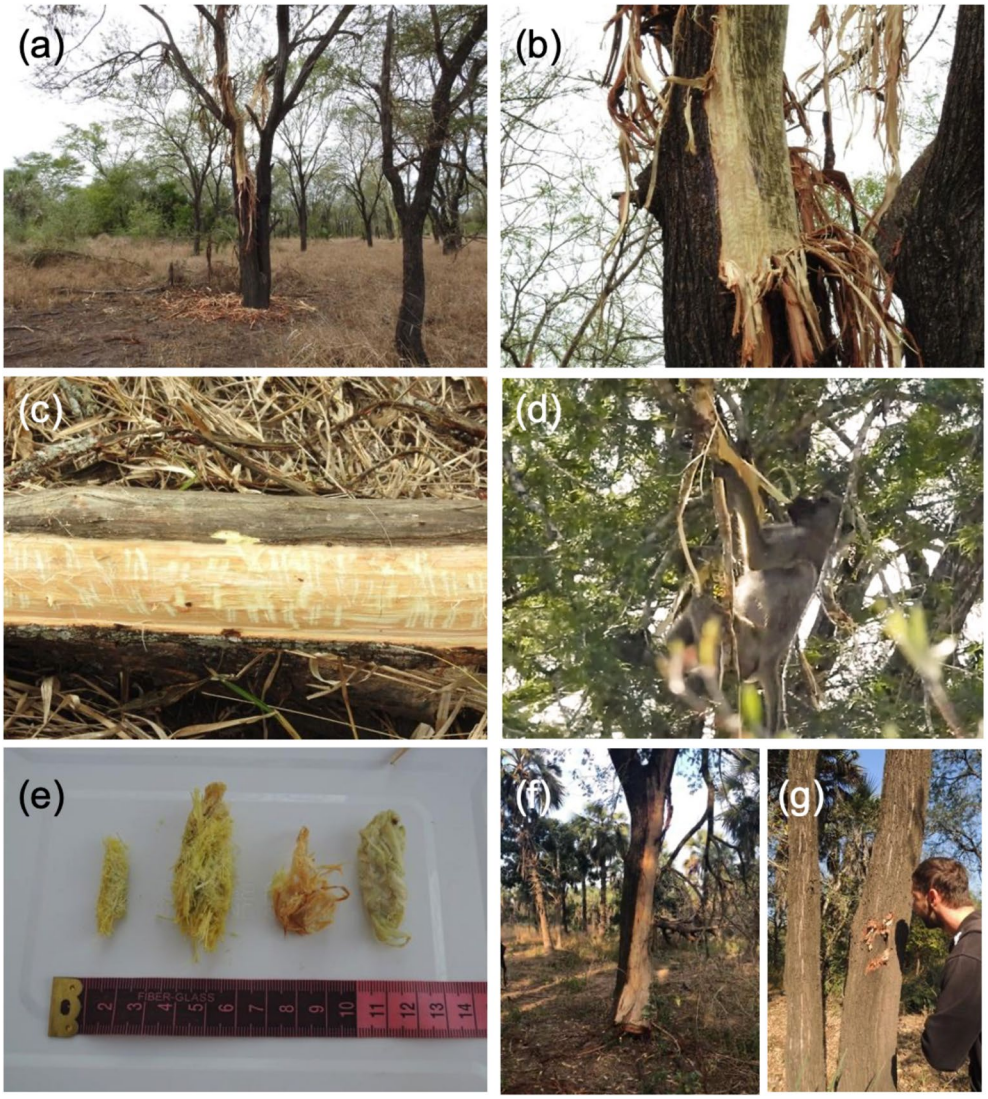

FIGURE 1 | Examples of evidence of bark-stripping. (a) *Acacia robusta* tree showing extensive damage from bark-stripping. Note the accumulation of strips at the base of the tree. (b) Fresh (left) and old (right) stripping damage on the same branch. Note the contrast in shading of the exposed tissue. (c) Branch (on the ground, detached from tree, with approx. 60 cm length shown) with characteristic pattern of baboon toothmarks. (d) Baboon in the process of stripping the bark of *A. robusta*. The individual has already removed several strips of bark (seen hanging off the branch) and is currently pulling on another with its teeth, thus peeling it back. (Screenshot from video taken by PH; see also Video S1). (e) Fresh wadges recovered near stripped *A. robusta* trees. (f) Elephant damage on *A. robusta*. Note large section of bark missing on lower part of trunk, from the ground up to ~2 m. (g) Elephant tusk marks on trunk of *A. robusta*. In this case the bark was not stripped.

Monitoring bark-stripping presents an ideal opportunity for more in-depth study of inter-troop behavioral variation within a field site. Variation in this behavior within and between sites has already been reported in a limited fashion (Bigalke and van Hensbergen 1990), although the behavior's function and distribution are still relatively poorly understood (Di Bitetti 2019). Furthermore, it leaves identifiable physical traces, which reduce the need for direct observation of many troops. This, along with the robust nature of the wooden debris and other material by-products of bark-stripping (strips of bark, gum, and toothmarks on the wooden substrate) makes it, to our knowledge, one of the few studied non-tool-use foraging behaviors that could fossilize and be identifiable in archeological records.

Bark-stripping has been reported widely in primate species, including baboons (Germishuizen et al. 2017; Gwenzi et al. 2007; Henzi et al. 2011; Katsvanga, Jimu, Zinner, et al. 2009; Katsvanga, Jimu, Mupangwa, et al. 2009), gorillas (Rogers et al. 1994; Seiler and Robbins 2016), orangutans (Campbell-Smith et al. 2011), chimpanzees (Lapuente et al. 2020; McCarthy et al. 2017; Russak 2013), barbary macaques (Ciani et al. 2001), howler monkeys (Agostini et al. 2010), capuchins (Hanson 2007; Mikich and Liebsch 2014), and others (for reviews see Di Bitetti 2019 and Nishida 1976), in both native vegetation as well as in commercial tree plantations. Proposed explanations for bark-stripping include nutrient or mineral deficiency (e.g., Rothman et al. 2006), use as a fall-back food (e.g., Mikich and Liebsch 2014), water content (e.g., Ménard and Qarro 1999), sugar content (e.g., Saint-Andrieux et al. 2009), use for self-medication (e.g., McCarthy et al. 2017), and use as a seasonally profitable resource (e.g., Kenward and Parish 1986), with the relevance of each hypothesis

being dependent on both the tree and species in question (Di Bitetti 2019). The development of local bark-stripping traditions has been suggested as an explanation for troop-level spatial variation in bark-stripping damage when other hypotheses were tested unsuccessfully, but has rarely, if ever, been the primary focus of previous studies. In a review of plantation studies, Di Bitetti (2019) notes that in 17 of the 18 studies for which relevant data were available, group-level differences in the presence of bark-stripping existed, suggesting local traditions may be at play (including in chacma baboons: Bigalke and van Hensbergen 1990).

Thus, while the behavior itself has been reported in multiple species, with several non-mutually exclusive functions proposed, open questions remain regarding ecological and social drivers influencing its expression. Importantly, following our initial observations, park rangers reported that they had not observed the characteristic traces throughout GNP, despite the widespread availability of both baboons and *A. robusta* across the park (see Figure S1a and Table S1 for the former, and Results concerning *A. robusta* availability at sites surveyed in the present study for the latter), suggesting that not all GNP baboons strip *A. robusta* in this way.

To confirm whether such inter-troop variation does indeed exist (i.e., some troops perform the behavior while others do not), we systematically recorded the presence or absence of the behavior at 45 sites located in a previously established camera trap grid covering a ~300 km^2 area in the south of GNP, along with local ecological data on the availability of *A. robusta*. We repeated our survey 12 months later to assess the stability of and/or shifts in the distribution of the behavior that may occur on such a timescale. We used these data to investigate putative behavioral variation among GNP baboons and to explore whether any observed differences in *A. robusta* exploitation are likely to be due to differences in ecology or, particularly in the absence of such differences, potentially to patterns of local invention followed by diffusion of the behavior.

2 | Methods

2.1 | Study Site

Gorongosa National Park (–18.96°, 34.36°), in central Mozambique, consists of 3688 km^2 mosaic ecosystem of savanna, dry forest, and grassland environments (Stalmans and Beilfuss 2008; Wilson 2014). From Lake Urema, in the center of the Park, seasonal distributaries branch out onto an alluvial floodplain, and the Park undergoes seasonal flooding with approximately 40% of its area inundated during the wet season (November–April; Tinley 1977). Devastation brought by the Mozambican civil war (1977–1992) led to declines of over 90% in large herbivorous mammals and an almost complete loss of large carnivores; however, natural recovery in the absence of predation together with a dedicated restoration project has aided the significant growth of these populations over the past two decades (Atkins et al. 2019; Bouley et al. 2018; Correia et al. 2017; Daskin et al. 2016; Stalmans and Peel 2024; Stalmans et al. 2019).

Currently, Gorongosa is home to one of the largest populations of baboons in a single national park in Africa (Bobe et al. 2020). Female philopatric baboons (chacma, *P. ursinus*; yellow, *P. cynocephalus*; olive, *P. anubis*; and kinda, *P. kindae*) are wide-ranging and flexible generalists that live in multi-male, multi-female societies where males disperse from their natal troops as adolescents (Altmann and Altmann 1970; Cheney and Seyfarth 2008). Troops' home ranges often overlap, leading to temporal rather than spatial partitioning of space among them (Slater et al. 2018; Hamilton 1985; Markham et al. 2013). A 2018 aerial survey at Gorongosa yielded observations of 193 different troops (Stalmans et al. 2018; Figure S1a). None of these troops are currently habituated, although two troops have been undergoing habituation, with behavioral data collected via daily follows and GPS collaring since 2017 and 2019, respectively (Hammond et al. 2022; Lewis-Bevan 2024). These two troops contain approx. 30 and 90 individuals, and their home ranges have been estimated using the minimum convex polygon of 95% of available GPS collar data as 23.1 and 8.5 km^2, respectively, overlapping partially (Lewis-Bevan 2024; Figure S1b). No data exist on the distribution of other troops' sizes across Gorongosa, but opportunistic on-the-ground observations have revealed a range between approx. 30 and 150 individuals. We also know very little about the movements of troops inhabiting regions that are inundated during Gorongosa's annual floods, except for one of our semi-habituated troops that inhabits the floodplain (the more northerly troop in Figure S1b). GPS collar data from this troop show a northward home range shift from the floodplain during the wet season (November–April), then a return to the floodplain once the waters recede (Lewis-Bevan 2024), hence the relatively large overall home range size.

2.2 | Surveys

Surveys were conducted during the dry season, in August 2018 and August 2019, over a period of 8 and 11 days, respectively. The two surveys covered the same 300 km^2 area, which encompassed the home ranges of about 60 baboon troops based on a 2018 wildlife aerial survey (Stalmans et al. 2018). Surveys consisted of habitat plots around locations that were defined by a camera trap grid (set up in 2016 by Kaitlyn Gaynor of UC Berkeley; see e.g., Gaynor et al. 2021), with each camera ~3 km from its nearest neighbors. Figure 2 shows the locations of the 48 individual cameras around which the habitat plots were centered (three of these were ultimately not surveyed—see Section 3). For each habitat plot, we recorded, within a 30 m radius of the location of the camera, (i) the number of *A. robusta* present, (ii) the number of these trees that showed any stripping damage on their branches (noting whether damage appeared fresh or old, based on the colouration of the hanging strips and of the exposed tissue underneath; see Figure 1b for examples of both) or on their trunks (Figure 1f), and (iii) the total number of trees of any species. During the 2019 survey, we also recorded (iv) the height and (v) diameter at breast height (DBH) of each *A. robusta* and noted (vi) the presence of any wadges at each site by inspecting the ground within the 30 m survey perimeter. Distances and tree heights were measured using a Nikon Forestry Pro Laser Rangefinder. Bark damage that included tusk marks (Figure 1g) was attributed

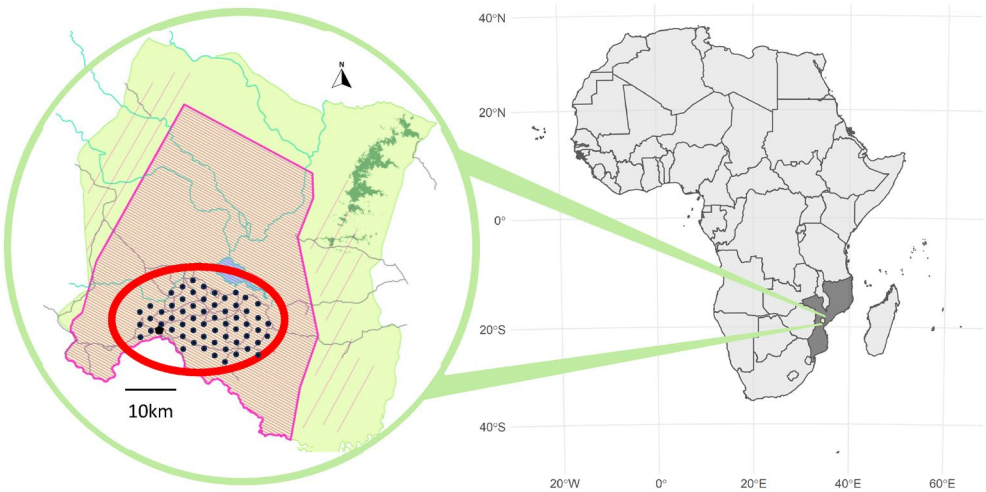

FIGURE 2 | Location of Gorongosa National Park (GNP) within central Mozambique (right), and of the surveyed area within GNP (left). Light green area corresponds to GNP; pink striped area shows area surveyed for wildlife in 2018 by Stalmans et al. 2018; red oval bounds the location of the camera trap grid; black dots correspond to the locations of individual cameras (i.e., the centres of habitat plots; note that the figure shows all 60 locations, of which a subset of 45 were accessible and sampled for the present study). Black pentagon shows the location of the research base, Chitengo camp.

to elephants; this was typically located on the trunk, which required extra force to strip due to the extreme thickness of the bark (see also Section 3). Damage higher up, on branches, was categorized as baboon-inflicted due to their height and the presence of characteristic toothmarks (Figure 1b,c) but not of tusk marks. Where stripping by elephants was suspected, we further examined the stripped surface for the presence of baboon toothmarks.

Based on these data, sites were assigned to the following categories: NA—*A. robusta* absent; NS—*A. robusta* present but not stripped; BS—*A. robusta* present and stripped. Furthermore, camera trap footage from each of the 45 sites surveyed was examined to confirm the presence of baboons at each of the sites.

Finally, for each site, habitat type, and the distance to the nearest major water source (river or lake) was determined at the time the camera trap grid was established (Gaynor 2019, 106). Habitat type was classified on an ordinal scale from 1 to 4, corresponding to the percentage of tree cover (1: < 1%, grassland; 2: 1%–10%, open woodland; 3: 10%–75%, sparse woodland; 4: 75%–100% closed woodland/forest). This broad scale allowed us to examine the effect of variation in *A. robusta* numbers at each site on the likelihood of bark-stripping, both within and between different vegetation types.

2.3 | Statistical Analysis

To characterize regional variation in the stripping of *A. robusta* across the area surveyed, we plotted the distribution of NA, NS, and BS sites. In order to explore potential ecological correlates for the behavior, we tested three main questions: (i) whether *A. robusta* number, proportion, mean height, and mean DBH, as well as habitat type and distance to the nearest major water source, predicted whether a given site was categorized as NS or BS; (ii) whether the distribution of the height and DBH of all *A. robusta* measured differed between NS and BS sites; and (iii) whether height and/or DBH predicted whether specific *A. robusta* were stripped at BS sites. Across these questions, we hypothesized that if ecological factors primarily determine whether baboons exploit *A. robusta* bark at a given site, then variables such as distance to water (acknowledging the hypothesis that bark may be stripped for water content; Ménard and Qarro 1999), habitat type (as a proxy for the availability of alternative resources), and the characteristics of available *A. robusta* trees will have a significant impact on the likelihood of bark-stripping being observed.

To address each of these questions, we first assessed correlations among our response variables (Table S2). Two pairs of variables were found to be strongly correlated (*A. robusta*) number and proportion at a given site, and the height and DBH of individual trees); hence, these pairs of variables were never included in the same models. For (i), we then ran a generalized linear model (GLM) with binomial error and the structure SiteCategory[stripping (yes/no)] ~ ArNumber[or ArProportion] + MeanHeight[or MeanDBH] + HabitatType + WaterDistance to test whether these variables predicted site category (NS or BS); $n = 34$ sites categorized as either NS or BS. For (iii), to test which variables predicted whether an individual tree at a BS site was stripped, we ran a generalized linear mixed-effects model (GLMM) with site ID as a random effect and the variables listed under (iii) as fixed effects (TreeCategory[stripping yes/no] ~ Height + (1|Site) and TreeCategory[stripping yes/no] ~ DBH + (1|Site); $n = 150$ trees across 17 BS sites. For (ii), separate GLMMs assessed whether height or DBH varied with site category (BS or NS, fixed effect), with site ID as a random effect (Height ~ SiteCategory + (1|Site) and DBH ~ SiteCategory + (1|Site)); $n = 206$ trees across 34 sites categorized as either NS or BS (see also Table S3 for all model structures). Throughout, significance was assessed through maximum-likelihood comparisons to models without the relevant fixed effect (i.e., full-null model comparisons). Variance inflation factor (VIF) values were calculated for all models in (i) to test for multicollinearity. All statistical analyses were conducted in R (version 4.4.2).

3 | Results

Of the original 48 cameras, two had been removed and nine were inaccessible in 2018 and one was inaccessible in 2019. At all the remaining sites (37 for 2018 and 45 for 2019), camera traps positioned at the center of the habitat plots confirmed the presence of baboons in the area (mean ± SD number of camera trap sightings of baboons between June 2016 and June 2017 = 115.1 ± 86.1 per camera; note that 2016–2017 was used as that was the closest year in which the camera trap grid was operational year-round, with processed data available).

Table 1 presents the distribution of sites across the NA, NS, and BS categories for the 2018 and 2019 surveys. In 2018, at nine sites, *A. robusta* was absent; at 11 sites, *A. robusta* was present with at least one tree showing stripping damage on its branches (at nine sites this was fresh, at two sites only old stripping damage was found; see Figure 1b for the contrast between fresh and old damage), and at 17 sites, *A. robusta* was present, but no stripping damage was found. By 2019, five sites had changed classification compared to 2018, all of which became BS (four were previously NS, one was NA; the latter was a case of a bark-stripped *A. robusta* being encountered just outside of the survey radius in 2019, but that same tree not being seen in 2018). Among the eight sites not surveyed in 2018 but surveyed in 2019, three were NA, four were NS, and one was BS. All sites classified as BS in 2019 showed evidence of recent bark-stripping (fresh stripping damage on branches and/or fresh wadges on the ground). The locations and classifications of NA, NS, and BS sites are summarized in Figure 3. These show clear regional clumping, with most BS sites falling in the western half of the grid.

Table 1 also shows that BS sites had a greater number and proportion of *A. robusta* than NS sites, while NS sites had, on average, taller *A. robusta* with greater DBH than did BS sites. NS sites also tended to be further from a major water source than BS sites (mean ± SD distance to nearest lake or river: NS: 4.56 ± 1.83 km, BS: 3.70 ± 2.36 km) and scored higher in terms of overall tree cover (mean ± SD habitat-type score: NS: 2.41 ± 0.69, BS: 2.09 ± 0.67). However, of these variables, only *A. robusta* number emerged as a weakly significant predictor of site category (NS or BS) in our models (Table S4; GLM with binomial error, maximum-likelihood comparison to model without the fixed effect, *A.r.* number: $\chi^2 = -3.88$, $p = 0.049$, *A.r.* proportion: $\chi^2 = -1.42$, $p = 0.234$, mean *A.r.* height: $\chi^2 = -1.51$, $p = 0.219$, mean *A.r.* DBH: $\chi^2 = -0.002$, $p = 0.963$, habitat type: $\chi^2 = -0.60$, $p = 0.438$, distance to water: $\chi^2 = -3.65$, $p = 0.056$; VIF values varied from 1.044 to 1.581 across all models, suggesting negligible correlations among the predictors included in the same models, in line with Table S2).

Given these results, and the stark contrast in the prevalence of bark-stripping in different regions of our study area, we performed post hoc correlations between our predictors and longitude and latitude. Longitude was significantly correlated with mean DBH and habitat type, while latitude correlated with mean height and habitat type (Table S2). Longitude (but not latitude) also significantly predicted site category, that is, whether a given site was classified as NS or BS (binomial GLM, longitude: $p < 0.001$, latitude: $p = 0.167$). This suggests that the regional clumping of bark-stripping is primarily exhibited along the

TABLE 1 | Results from habitat plot surveys. Shown are the number of sites where *A. robusta* is absent (NA), present but not stripped (NS), and present and stripped (BS), as well as the median and IQR for the number and percentage of *A. robusta* recorded among all trees at each site and their percentage stripped, and the mean ± SD for the height and diameter at breast height (DBH) of stripped and unstripped trees. All except the second column are based on 2019 data. Note that at three sites ($n = 12$ trees), height data are unavailable.

Category	# sites 2018	# sites 2019	# *A.r.*	% *A.r.*	% *A.r.* stripped	Height stripped (m)	Height unstripped (m)	DBH stripped (cm)	DBH unstripped (cm)
NA	9	11	0	—	—	—	—	—	—
NS	17	17	3.5 [2.0–7.0] ($n = 56$)	16.01 [4.74–44.23]	0	—	12.05 ± 1.83 ($n = 54$)	—	36.59 ± 8.75 ($n = 56$)
BS	11	17	7.5 [4.2–13.5] ($n = 150$)	29.52 [13.67–47.28]	66.6 [44.6–73.1]	9.60 ± 2.27 ($n = 94$)	8.42 ± 3.32 ($n = 46$)	32.16 ± 10.65 ($n = 100$)	25.28 ± 10.29 ($n = 50$)
Total	37	45	206			94	100	100	106

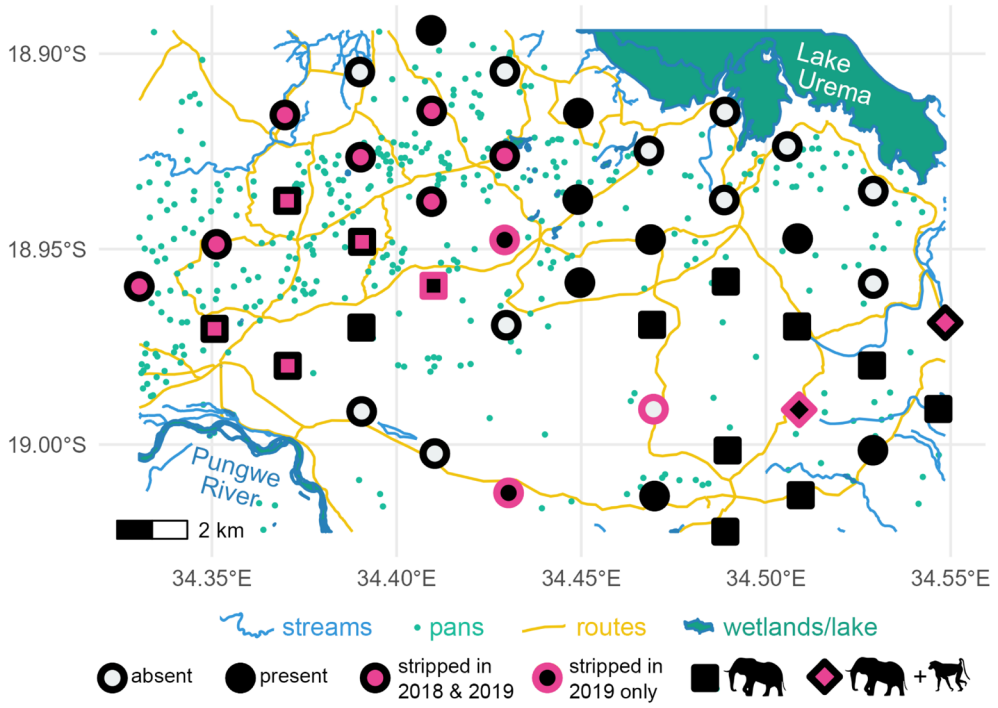

FIGURE 3 | Summary of habitat plot survey results. Symbols (circles, squares, and diamonds) correspond to camera trap locations; shapes and colors distinguish between sites where *A. robusta* is absent (NA; white circles), present but not stripped by baboons (NS; filled black circles) or present and stripped by baboons (BS; pink circles). Sites where stripping was not found in 2018 but found in 2019 are shown as pink-rimmed black symbols. Black squares denote sites where stripping on the trunks was observed but no baboon toothmarks were visible (i.e., likely elephant damage, with no evidence of subsequent utilization by baboons); pink diamonds show where baboon toothmarks were also visible on the trunks of such trees (i.e., elephant damage, with subsequent utilization by baboons). Also shown are roads and the locations of water sources (streams, wetland/lake, as well as pans, i.e., shallow depressions in the ground where rainwater accumulates).

east–west axis, with sites containing *A. robusta* more towards the west having a significantly higher likelihood of being bark-stripping sites.

When considering all *A. robusta* trees measured across all sites (rather than their means per site), height and DBH did differ significantly between NS and BS sites (GLMM, maximum-likelihood comparison to model without the fixed effect, height: $\chi^2 = 314.95$, $p < 0.001$; DBH: $\chi^2 = -1844.7$, $p < 0.001$), with taller and greater DBH at NS sites. At BS sites, height and DBH were both significant predictors of the stripping state of individual trees (binomial GLMM, height: $\chi^2 = -43.34$, $p = 0.013$, DBH: $\chi^2 = -1575.9$, $p < 0.001$): stripped trees were taller and had greater DBH than unstripped trees.

Finally, at 16 sites, we also noted a different kind of damage on *A. robusta*: the stripping of bark at the base of the tree rather than higher up in the branches, without the characteristic baboon toothmarks (though see below) and involving the removal of very long strips (often from ground level to several meters up; Figure 1f). We never observed baboons perform any bark-stripping on tree trunks: this type of trunk damage requires far greater strength due to the thickness of the bark and is due to elephant activity, as confirmed by published reports (Midgley et al. 2005; Tweheyo et al. 2013) as well as GNP park rangers, and as apparent by the frequent presence of tusk marks on the trunks (Figure 1g). Squares and diamonds in Figure 3 summarize the distribution of locations where this type of damage was recorded. Interestingly, at two sites where elephant damage was noted (diamonds in Figure 3), a small number of baboon toothmarks were also visible on the stripped part of the trunk.

4 | Discussion

We surveyed an area of ~300 km^2 in Gorongosa National Park (GNP), central Mozambique, for variation in bark-stripping behavior across a range that aerial surveys have estimated to contain ~60 different troops of wild chacma baboons. While the target species for the behavior, *A. robusta*, appears absent in certain areas (specifically in the northeast, north-northwest and south-southwest of the range surveyed), in the areas where it *is* present it is not always stripped. Hence, there is evidence of variation in the exploitation of this resource across GNP, even though baboons are present ubiquitously, as confirmed through camera-trapping at every one of the habitat plots. Furthermore, bark-stripping sites appear geographically clustered along a rough east–west divide of our range, with the presence of the behavior significantly correlated with longitude: bark-stripping is prevalent in the western part of the range but much rarer in the east. Although in the absence of a one-to-one correspondence between troops and survey locations we cannot ascertain precisely which troops do or do not perform the behavior, we are nonetheless able to infer that (i) any location with evidence of bark stripping has at least one troop within range that performs the behavior, and (ii) any location without bark stripping (but *A. robusta* present) is likely to have no bark-stripping troops within range.

Our main aim besides documenting variation in the prevalence of bark-stripping was to assess potential predictors of this variation. In line with studies applying the "method of exclusion" (which assesses support for the contributions of genetic, ecological, or cultural drivers to regional behavioral variation through demonstrating the lack of influence of one or more of these factors—a method exemplified in one of the earliest large-scale surveys of wild chimpanzee regional behavioral variation in Whiten et al. 1999), our goal was to evaluate evidence for potential ecological predictors. Thus we aimed to assess whether the behavioral variation could have arisen primarily out of ecological differences between sites (not only in the availability and characteristics of *A. robusta* themselves, but also as proxies for differences in the availability of alternative resources), or if it may have been indicative of differential invention and diffusion of the behavior (i.e., cultural differences) between troops. While in the absence of much more comprehensive information on the former (ecology) the latter (culture) must remain speculative, considering the possibility allows us to pinpoint future research that will allow us to better distinguish between these possibilities.

Analysis of the characteristics of *A. robusta* at sites where the species was present showed that of the variables examined (number or proportion of *A. robusta*, mean height, mean DBH) only the number of *A. robusta* was a significant predictor of a site's classification as stripping versus non-stripping. At the same time, neither habitat type nor distance from major water sources predicted the variation in stripping. Interestingly, while *A. robusta* were taller and had greater DBH at non-stripping sites, at stripping sites it was in fact the taller/greater-DBH trees that baboons chose to strip—that is, those that were closer in size to the range available to them at non-stripping sites. Therefore, based on our initial surveys, most broad-brush ecological factors examined are not sufficient to explain the variation we observed in the expression of the behavior, except for *A. robusta* density (number within 30 m-radius habitat plot). Nonetheless, this latter point is important as it may suggest opportunity-driven exploitation of the resource at sites where the species is abundant.

An alternative explanation may argue that the regional clustering is indicative of social transmission of the behavior first within troops and then from troop to troop. The latter may happen either via dispersal (of, primarily in chacma baboons, sexually mature males) which provides any previously naïve troop with opportunities to directly observe a knowledgeable individual performing the behavior, or via the exposure of troops to the products of another troop's activity, that is, in the form of encountering already stripped trees in overlapping home ranges. If this were the case, any gaps in the distribution of *A. robusta* across the range surveyed would strongly influence the behavior's potential spread through direct/indirect social learning. Ongoing habituation of two troops in GNP (both in the western half of the range surveyed here) has revealed home range sizes of approximately 9–23 km^2 (Lewis-Bevan 2024; Hammond et al. 2022): given that we did find areas lacking in *A. robusta* (primarily in the north-east and south–south-west), it thus appears conceivable that some troops do indeed encounter *A. robusta* very rarely.

Nonetheless, other explanations for the apparent paucity of bark-stripping by baboon troops in the east are possible. We outline four here. The first is simply to do with our sampling procedure: it may be that the present methods missed the behavior in some areas where it is present. Given that *A. robusta* were taller on average at sites we classified as non-stripping than at stripping sites—and hence their upper branches would have been less visible from the ground—we may indeed have misclassified some of the former. Re-sampling our range in two consecutive years, and the broad agreement between the two datasets, gives us some confidence that this was not the case; however, since the two surveys examined the same habitat plots, it is possible that bark-stripping was repeatedly missed if all trees exhibiting the damage fell in between their locations. Second, although baboons were detected at all camera traps within our grid (Table S1) thus confirming baboon presence at all sites, the density of troops did vary in different regions of the surveyed area (Figure S1a). The lower densities in the southern half of the grid, for example, likely affect troops' ranging behavior and feeding ecology in ways that may impact their likelihood to engage in bark-stripping. The third explanation is based on considerations of necessity. Namely, it is possible that the feeding ecologies baboons in the eastern and western regions are different in that the nutrients that baboons in the west are getting from *A. robusta* bark and sap, baboons in the east are obtaining from other sources. If this were the case, there would be less "need" for baboons in the east to engage in the behavior. Bark-stripping is likely an energetically costly behavior given that it appears to require a significant amount of strength—indeed, our opportunistic direct observations suggested that younger individuals tended to "re-use" previously stripped branches rather than strip the bark themselves, though this requires further study. This explanation (along with other need-based hypotheses, such as the use of *A. robusta* as a fallback, seasonal or medicinal resource, or as a source of water/sugar) could be further explored by more detailed studies of the environments baboons inhabit across our range (see also below)—if significant differences are found, this would weaken the case for a cultural argument. Conversely, the fourth explanation, which may strengthen the case for cultural variation, is provided by considering the baboon toothmarks we found on some of the elephant-stripped trees (observed exclusively in the east). An intriguing explanation here would be that baboons in the east *do* want the nutrients from the bark and sap, but either do not know how to strip by themselves (and opportunistically exploit elephant-stripped trees), potentially because of exclusion due to elephants' dominance in accessing the trees in the area, or have less *need* to strip given that elephants strip the trees extensively in the area. Elephant damage is rarer in the west (out of the total of 16 sites where elephant stripping was noted, 6 fall in the western half of the grid and 10 in the eastern half); hence, baboons there may be forced to strip by themselves more than those in the east.

In sum, our results have revealed some interesting differences in the prevalence of bark-stripping behavior by chacma baboons across the ~300 km^2 range surveyed. While one limitation of the current study is that we have no information on individual troops and the boundaries of and overlaps between their home ranges (and as such we are unable to match

the survey results to the distribution of the behavior across specific troops), it appears that the behavior is performed by some, but not by other, troops. However, since our work was based primarily on indirect data (material traces), the interpretation of this variation must remain speculative for now, and future work will need to address several additional outstanding questions. First, systematic direct observation will be needed to quantify how common the behavior is *within* given troops—is bark-stripping group-typical in the areas that we surveyed, or is it restricted to a few individuals? The latter is possible but unlikely since it does not seem to be the case in one of the troops under habituation, where we have directly observed multiple individuals stripping, often at the same time. Nonetheless, previous work has demonstrated considerable variation even in the diets of members of the same primate group (Schneider et al. 2023), potentially driven by competition, and the impact of such intra-group effects on observed inter-group variation deserves attention in our study system too. Second, we also need detailed, longitudinal behavioral data: information on how the behavior emerges in young individuals and whether social learning, for example, through young directing observations at older individuals performing the behavior, or young re-using previously stripped sites, contributes to acquisition is essential. Third, importantly, we need more detailed ecological data from throughout the area surveyed. How does food availability and the feeding ecology of baboons vary between east and west, and more specifically at sites with and without evidence of stripping? How does the productivity, nutritional composition, and pharmacological composition of *Acacia* vary along the east–west axis? Fourth, on a related note, laboratory analysis of the inner bark tissue will be needed to identify what nutrients baboons are obtaining through the behavior, and therefore how exploiting this resource may be driven by the constraints of the remainder of their diet or health. The chewing or consumption of bark from a variety of plant species has been reported to be a potential self-medicating behavior in primate species including red colobus monkeys, hooded capuchins, chimpanzees, and chacma baboons (Ghai et al. 2015; McCarthy et al. 2017; Ndagurwa 2007, 2012; Smith and Payne 2017). Given *A. robusta*'s frequent mention in ethnobotanical literature (Belayneh et al. 2012; Kaingu et al. 2014; Kimondo et al. 2015) and its antibacterial and antifungal properties (Hamza et al. 2006; Mlambo 2008), this may be a promising direction for further research. Fifth, we have hypothesized that elephant stripping may impact baboons' likelihood to bark-strip themselves as opposed to utilizing already-stripped trees—more detail on this indirect interaction between baboons and elephants would shed further light on what drives the presence versus absence of the behavior in wild troops. Sixth, since we are dealing with putative hybrids in GNP (Martinez et al. 2019; Santander et al. 2022), with potentially differing levels of hybridization, we will also be aiming to correlate these behavioral differences with any genetic differences. Seventh, we will aim to continue to survey for other non-technological candidate behaviors that may show regional differences across troops to build a fuller picture of putative baboon behavioral variation in GNP.

Finally, as an additional extension, further analysis of the physical traces left by baboon bark-stripping may provide important comparative data and context for the study of early hominin foraging strategies. Ethnographic records from indigenous Scandinavian (Sami) and American Pacific Northwest groups show that bark-stripping (termed bark-peeling) has also been used recently by modern humans. Their bark-peeling tools have been used in the interpretation of antler and wooden tools from the Paleolithic, leading to the suggestion that bark-stripping was a common foraging method in Neanderthals across Europe (Sandgathe and Hayden 2003). Archeological surveys of "culturally modified-trees" in Scandinavia and the Pacific Northwest have demonstrated that bark-peeling scars are identifiable and have the potential to preserve archeologically (Östlund et al. 2005, 2009; Rautio et al. 2014; Sandgathe and Hayden 2003; Zackrisson et al. 2000). However, a link between the archeology of bark-stripping and bark-stripping in extant primates has yet to be made. Studying stripping by primates such as baboons could add valuable data on the traces left by tool-free bark-stripping, diversity in this behavior across a population, and the underlying causes of this foraging behavior in a genus often used as a model for early hominin evolution. Trees regularly fossilize in the right environmental context (Bamford 2017), meaning that a behavior that leaves marks on robust wood has a reasonable chance for fossilization and opens the door to the identification of bark-stripping as far back as the emergence of tool use (Carvalho 2021; Rolian and Carvalho 2018). Further study of bark-stripping in GNP using a primate archeology approach would improve our ability to identify taphonomic processes associated with bark-stripping, aid in identifying the behavior in hominin archeological records, and deepen our knowledge of the adaptive benefit of bark-stripping in an environment comparable to that inhabited by our early ancestors.

Author Contributions

Dora Biro: conceptualization (lead), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), project administration (equal), visualization (equal), writing – original draft (equal). **Jana Muschinski:** conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), project administration (supporting), writing – original draft (equal). **Philippa Hammond:** conceptualization (supporting), investigation (supporting), writing – original draft (supporting). **René Bobe:** conceptualization (supporting), writing – original draft (supporting). **Marion K. Bamford:** conceptualization (supporting), investigation (supporting), methodology (equal), writing – original draft (supporting). **Cristian Capelli:** conceptualization (supporting), writing – original draft (supporting). **João d'Oliveira Coelho:** conceptualization (supporting), visualization (equal), writing – original draft (supporting). **Rassina Farassi:** conceptualization (supporting), investigation (supporting), writing – original draft (supporting). **Tina Lüdecke:** conceptualization (supporting), investigation (supporting), writing – original draft (supporting). **Felipe I. Martinez:** conceptualization (supporting), investigation (supporting), writing – original draft (supporting). **Jacinto Mathe:** conceptualization (supporting), writing – original draft (supporting). **Maria Joana Ferreira Silva:** conceptualization (supporting), investigation (supporting), writing – original draft (supporting). **Susana Carvalho:** conceptualization (equal), investigation (supporting), methodology (equal), project administration (equal), writing – original draft (equal).

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Ethics Statement

All data collection was observational and involved no direct contact with animals. Ethical clearance was obtained from the University of Oxford (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018 and PNG/DSCi/C93/2018).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data collected for this study are available from the corresponding author upon request and will be posted to a public repository upon publication.

Endnotes

[1] Note that this species' name has recently been revised to *Vachellia robusta* (Kyalangalilwa et al. 2013), but this has not been uniformly accepted within the literature; here we follow the taxonomy maintained in Burrows et al. (2019).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.