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Ecological Solutions and Evidence

RESEARCH ARTICLE

Are crop fields pharmacies for megaherbivores? From ecophysiological studies of elephant (*Loxodonta cyclotis*) crop raiders in Gabon

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Abstract

1. Damage to crops is a major cause of human–elephant conflict (HEC) in elephant range states. Elephant crop raiding drives farmers' resentment against elephants and reduces local community support for wildlife conservation. While elephant crop raiding ecology is well studied, further investigations on HEC mitigation strategies are still needed. Thus, there is a need to focus on less investigated areas, such as the physiological drivers of elephant crop-raiding behaviour, using multidisciplinary sciences.
2. Two physiological proxies, gastrointestinal parasite infestations (GPI) and faecal glucocorticoid metabolite (fGCM) concentrations, common in animal ecophysiology, were used to help understand differences or motivations in the preferences of crops by elephant raiders.
3. The results show, for the first time, that forest elephants may increase the frequency of crop raiding according to GPI, indicating a self-medication behaviour. Increases in parasitism prevalence (PP) and parasitism intensity (PI) in sampled boluses led to 28% and 0.16% more intakes of all crops, respectively. Parasitism prevalence (PP) increases in elephant boluses also led to 16% and 25% more bananas and papaya intakes, respectively, while PI increases in boluses led to 0.1% more intakes of both bananas and papaya plants. No such predictions

were found for other crops (cassava and palm plant), nor for natural food species intakes. Furthermore, fGCM concentrations were not related to elephant crop raiding. Results highlight a trade-off between the benefit of elephants raiding crops and the danger of encountering farmers by adopting nocturnal crop-raiding behaviours.

4. *Practical implication*. We propose that elephants may choose specific plant parts while raiding crops as a self-medication behaviour. We further discuss the importance of forest elephant conservation as they are not only forest engineers but also appear to be self-medication specialists, which could possibly help humans cope with present and future health issues. Further understanding of that self-medication behaviour can help communities cohabiting with forest elephants to focus on the broader health benefits rather than solely on the immediate issue of crop damage.

KEYWORDS
animal ecophysiology, crop-raiding, forest elephants, parasitism, self-medication, stress

1 | INTRODUCTION

Elephants are the largest living terrestrial animals and mega generalist herbivores (Blake et al., 2009; De La Torre et al., 2022). They spend most of their time exploring extensive areas in search of food and browsing on numerous plant species, including farm crops (Blake et al., 2009; De La Torre et al., 2022; Fairet, 2012). This results in increased levels of competition for both space and resources with humans, and contributes to human–elephant conflict (HEC) (Fairet, 2012; Ngama et al., 2019; Walker, 2012). As a consequence, HEC amplifies food and economic insecurity while reducing the support for wildlife conservation among communities and mostly farmers cohabiting with elephants (Hoare, 2012; Shaffer et al., 2019). As a response, angry farmers implement retaliatory elephant killings that undermine elephant conservation efforts (Fairet, 2012; Hoare, 2012; Shaffer et al., 2019). Recently, farmer and public tolerance towards elephants has drastically decreased in many African countries, and especially in Gabon, due to recurrent crop damage (Ngama et al., 2019; Terada et al., 2021). This is somewhat surprising given that Gabon is highly forested and agriculturally less developed than other countries.

Gabon is among the most forested countries and encompasses the largest forest elephant population (Laguardia et al., 2021). Recent data indicate that Gabon is the remaining stronghold of forest elephants (*Loxodonta cyclotis*), with approximately 95,000 individual elephants representing 75% of forest elephant numbers worldwide. Gabon's forested areas (85%) serve as a primary home range for forest elephants (Gobush et al., 2021; Laguardia et al., 2021). They mainly consist of abundant flora serving as food resources for elephants and patchy agricultural areas representing less than 5% of the landscape (Ngama et al., 2019; Walker, 2012). Unexpectedly, elephants constantly move to human settlements and raid the few available crops (Ngama et al., 2019; Terada et al., 2021; Walker, 2012).

Elephants may move from forests to human settlements and patchy crop areas due to the presence of fruiting trees in farm areas, decreasing availability of staple fruits in the forests because of climate change and increasing extractive activities such as logging (Beirne et al., 2020; Bush et al., 2020; Ngama et al., 2019). Fruiting trees have been recorded as one of the main drivers of elephant crop raiding in Mont De Cristal (Northern Gabon), with all crop areas having fruiting trees also being the most damaged by elephants (Ngama et al., 2019). In Lopé National Parc (Central Gabon), decreases in available staple fruits have been recorded with a direct negative impact on forest elephant health due to climate change's effect on forest trees' fruiting patterns (Bush et al., 2020). In that same way, recent records indicate that most of the Gabonese forests are under extractive concession agreements where there are fewer wildlife vocalizations and presence than in areas free from extractive activities such as national parks and farm areas (Breuer & Ngama, 2021; Yoh et al., 2024). Farm areas attract elephants due to their nutritious crops, surrounding fallows with numerous herbaceous and woody plant species and many fruiting trees (Blake et al., 2009; Hoare, 2012; Ngama et al., 2019; Osborn, 2004). In farm areas, instead of taking all crops, elephants only raid some fields and mostly graze on a few crops, underlying the small contribution of crops found in the overall diet of the elephants (Fairet, 2012; Ngama et al., 2019; Walker, 2012). The daily elephant diet requirement is estimated at about 215 kg of fresh matter for a 3500 kg adult elephant, which would represent more than all crops present in a typical 2000 m^2 traditional Gabonese crop field (Ngama et al., 2019; Pretorius et al., 2012). The elephant diet remains poorly understood, with foraging decisions suspected to be beyond ecology and involve body and physiological conditions (Beirne et al., 2020; Fishlock & Breuer, 2015; Jachowski et al., 2013).

Apart from elephant body condition, which has been related to fruit abundance, knowledge on correlations between physiological

traits and elephant diet, foraging, crop raiding and other behaviours is limited (Beirne et al., 2020; Bush et al., 2020). To bridge this knowledge gap, the use of methods from multidisciplinary animal ecophysiology science is suitable (Blaustein et al., 2012; Bradshaw, 2003; Bryan, 2013; Chiyo et al., 2011; Finch, 2013; Jachowski et al., 2013; Pokharel & Brown, 2023). Animal ecophysiology methods are mainly noninvasive and enable insight into how environmental constraints and internal needs affect animal behaviours (Bradshaw, 2003). Animal ecophysiology methods use common proxies such as gastrointestinal parasite infestation (GPI) and faecal glucocorticoid metabolites (fGCM) in many species, including elephants (Blaustein et al., 2012; Bradshaw, 2003, 2010; Bryan, 2013; Chiyo et al., 2011; Pokharel & Brown, 2023).

Studies on savanna elephants (*Loxodonta africana africana*) have reported that risky crop-raiding behaviour may have fitness benefits in the form of lower helminth levels (Chiyo et al., 2011; Finch, 2013; Jachowski et al., 2013). Self-medication by the use of some plants for antiparasitic and antimicrobial purposes has been reported in situ for many species, including African savanna and Asian elephants (Greene et al., 2020; Pattanayak, 2024). In forest elephant crop raiding, preference for crops having anthelmintic properties, such as bananas (*Musa* spp), has been recorded without any correlation with body condition proxies (Fairet, 2012; Gregory et al., 2015; Marie-Magdeleine et al., 2010; Ngama et al., 2019; Santos et al., 2012). Therefore, we first predicted that forest elephants seek specific crop species, such as bananas, when faced with GPI. Furthermore, raiding on crops could results in elevations in fGCM due to encounters with farmers and the fear of potential retaliatory killings, while low fGCM are observed in areas with reduced threats (Ahlering et al., 2011; Kely et al., 2021; Kolowski et al., 2010; Munshi-South et al., 2008). We secondly hypothesized that in farming areas, elephants would have to trade-off the fear of encountering farmers with the need to nocturnally crop-raid to address parasite load, thereby needing to balance high fGCM with the benefits of low GPI.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in Monts De Cristal National Park (MDCNP; 1200 km^2; Figure 1). MDCNP is divided into two blocks (Mbè and Séni), with a bush road passing between them, and hosts more than 3000 species of plants (Kenfack, 2013; Ngama et al., 2019). It comprises approximately 246 species of birds, 25 species of reptiles, 27 species of amphibians, unnumbered insect species and 35 mammal species, including approximately 3500 forest elephants (Kenfack, 2013; Laguardia et al., 2021). The forest landscape is divided into logging concessions (65%), MDCNP area (18%) and local people usages (17%) with approximately 3% devoted to traditional farming in villages' vicinities (Kenfack, 2013; Ngama et al., 2019). Industrial agriculture is absent, human density is low (2 people per km^2) and the landscape experiences two wet seasons interrupted by two dry seasons, with an annual rainfall averaging 2800 mm (Kenfack, 2013; Ngama et al., 2019).

2.2 | Data collection

Data were collected from February 2016 to July 2017 during five consecutive seasons: S1 (long dry season in 2016), S2 (short wet season in 2016), S3 (short dry season, end of 2016 and early 2017), S4 (long wet season in 2017) and S5 (long dry season in 2017). We monitored productive crop areas (new fields), abandoned farms (old fields) and forests in between along 70 km of bush roads connecting focal villages using an off-road car twice per month (Figure 1). We used noninvasive data collection techniques of animal ecophysiology, suitable when studied animals are difficult to observe and to avoid stressing them (Blaustein et al., 2012; Bradshaw, 2003; Bryan, 2013; Freeman et al., 2010; Munshi-South et al., 2008). A threshold trail distance of 500 m was defined based on the longest daily distance of forest elephants' displacement and the daily mean defecation rate, resulting in two bolus deposits per elephant per kilometre (Nchanji et al., 2008; Theuerkauf & Gula, 2010). Therefore, fresh trails (less than 48 h old, with mucosa present on elephant boluses) were opportunistically found along the bush road and followed on foot at a distance of 500 m for sample collection. Collected samples included elephant defecation events and surrounding plant materials (leaves, bark, roots, trunks, fruits and flowers) that had evidence of elephant feedings.

2.3 | Faecal sample collecting and processing

Faecal sampling protocols were adapted from Osborn (2004), Munshi-South et al. (2008), Kolowski et al. (2010), Chiyo et al. (2012), Finch (2013) and Huffman (2022). The sampling protocol focused on fresh trails with boluses deposited by individual elephants. This approach was informed by studies documenting self-medication behaviours in mammals, including Asian and savanna African elephants (Greene et al., 2020; Huffman, 2022; Hutchings et al., 2003; Pattanayak, 2024). Fresh trails, boluses and plant intakes were crucial to capture the potential self-medication behaviour of individual forest elephants, as food takes approximately 40 h to pass through the elephant's gut, making it difficult to determine if an elephant had only fed on crops (Meyer et al., 2022). Sample collections were thus opportunistic, depending on the fresh elephant trails we found. In fresh trails, only boluses from adult elephants (>20 cm in diameter) were collected to avoid sampling young elephants that learn to raid on crops from elders. During the first season (S1), 60 defaecation events were registered, but only 18 were identified as coming from individual elephants using the methods described in Figure 2. To avoid over-sampling a particular seasonal group, this number was balanced over the five seasons to total 90 samples (18×5). Each bolus from the same elephants was mixed while avoiding contamination with the soil. Thereafter, two 50 g samples were collected, one for fGCM and one for GPI. All sampled boluses were stored at −18°C in a field facility freezer until analysis.

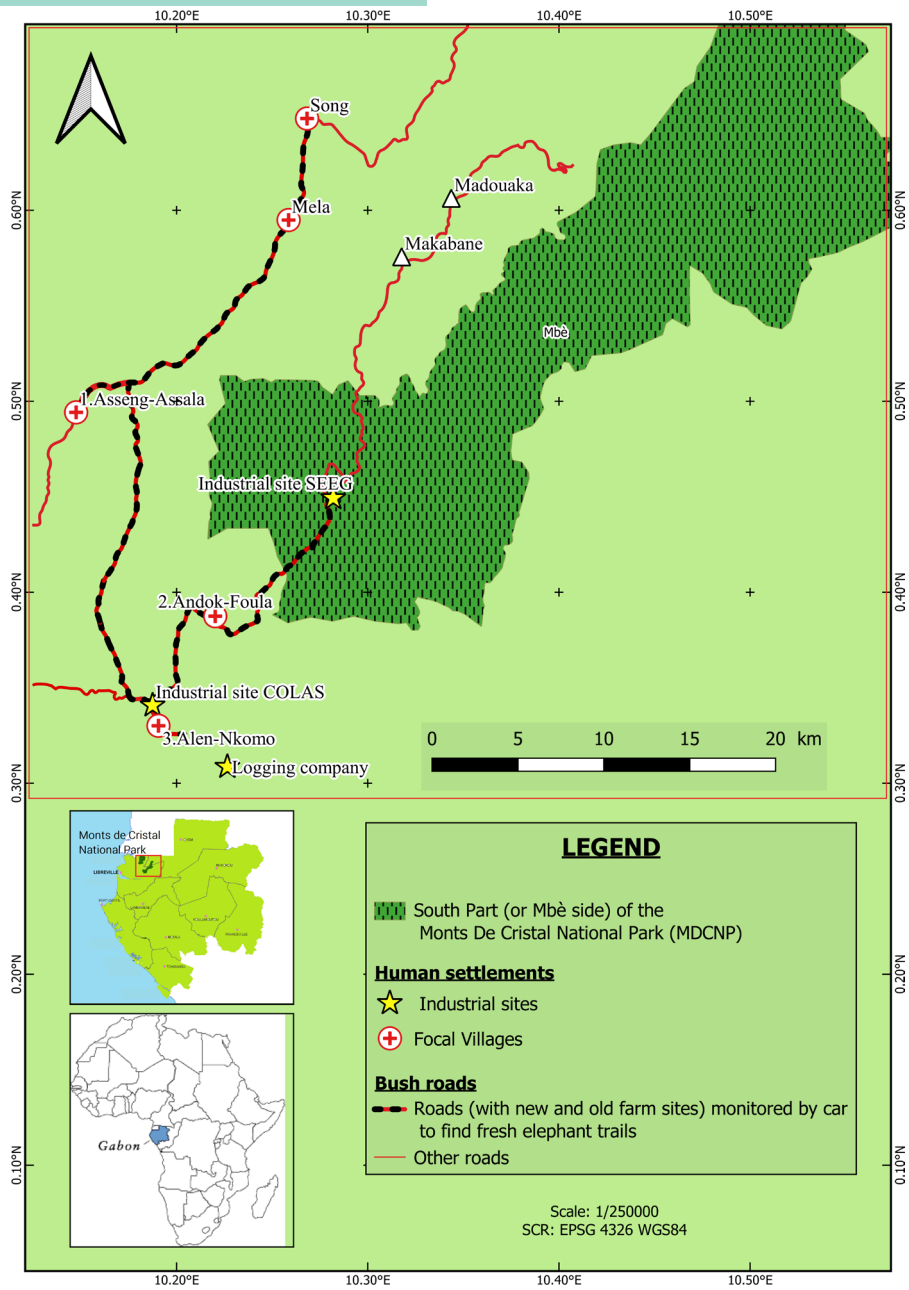

FIGURE 1 The study site consisted of MDCNP and a few human settlements. Elephant boluses were collected in new and old farm areas (and surrounding forests) along the 70-km bush roads connecting focal villages.

Food items were collected following methods adapted from Osborn (2004), Pretorius et al. (2012) and Fishlock and Breuer (2015). Plants with evidence of elephant feeding were visually recognized and collected within 5 m around the sampled boluses to ensure that boluses and intakes were from the same elephants. Plants were identified at the Gabonese National Herbarium. Due to the large number of plants fed on by elephants and based on our field observations, few plants were repeatedly fed on by elephants. Thus, to comply with our first hypothesis related to elephants targeting specific crops, only plant species with more than five records of being eaten by elephants were included in the final analyses. Eight plant species were recorded: four natural food species—*Bambusa* sp., *Costus* sp., Ferns (*Pteridium* sp., *Nephrolepis* sp.) and *Ficus* sp.; and four crop species—banana (*Musa sp*), cassava (*Manihot esculenta*), papaya (*Carica papaya*) and palm trees (*Elais guinenseis*). Other species (with less than five feeding records) were noted as 'Others'.

2.4 | Gastrointestinal parasite infestation (GPI) and fGCM analyses

Parasitological analyses were performed based on Nakandé et al. (2007). For that, the McMaster technique designed specifically for gastrointestinal parasitology and a digital field

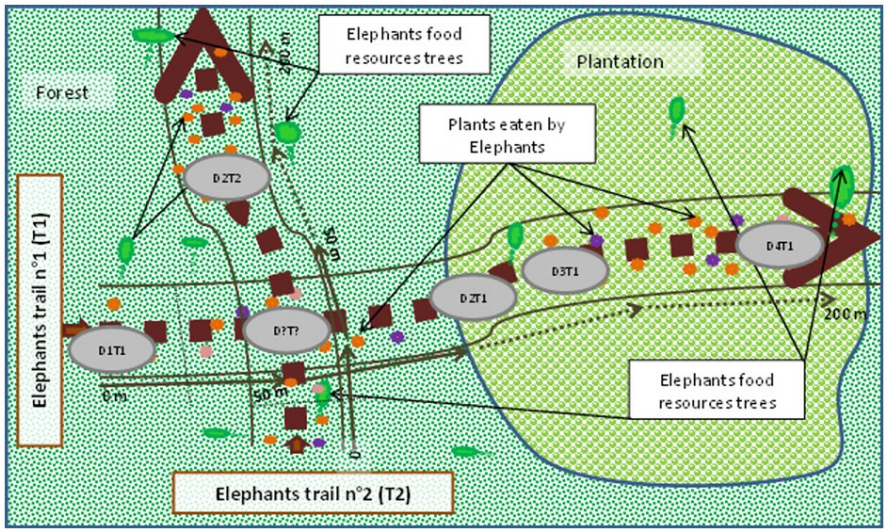

FIGURE 2 Schematic elephant boluses collection processes within the 500 m trails. Boluses were collected randomly as most elephant individuals suffering parasitism would be most willing to adjust their food selection and feed on plant species having antiparasitic properties. Trails (T) are mostly created and/or followed by many elephants, with some only passing through crop areas without any crop consumption. As elephants mostly defecate in places where they rest and feed (personal observations), only boluses with evidence of surrounding eaten plants and being >50 m apart were collected (that is D1T1, D2T1, D2T2 and D4T1). Thus, T1 is a trail with and without elephants raiding on crops. T2 is a trail without elephants raiding on crops. The first boluses seen in T1 are noted as D1T1. D2T1 and D3T1 are too close (<50 m apart), so only one (D2T1) was sampled. D1T1 and D2T2 were considered as from different non-crop raiding elephants, while D2T1 and D4T1 were considered as from different crop raiding elephants.

microscope were used. Parasite loads were counted in boluses using a PARACOUNT-EPG fecal analysis kit (Chalex Corp., Issaquah, Washington, USA) and according to the manufacturer's instructions. Counts of parasite loads were expressed as the number of eggs per gram of boluses (epgd). Based on a threshold median of 555 epgd calculated using all sampled boluses, counts of parasite loads were used to determine the GPI according to two variables: parasite prevalence (PP) with two modalities High (>555 epgd) or low (<555 epgd); and parasitism intensity (PI) expressed as total counts of epgd in samples.

Extraction of fGCM was based on field methods from Freeman et al. (2010). Briefly, 1.0 g of faeces was weighed and placed in capped plastic tubes, followed by the addition of 5 mL of 90% ethanol:water. Plastic tubes were vigorously agitated for 30 s and left to sit overnight at room temperature. The next day, plastic tubes were mixed again and allowed to settle for 5–10 min. Then, 0.5 mL of sample supernatants were transferred to clean plastic tubes and left to dry under a fan. The dry extracted samples were frozen (< −18°C) until fGCM measurements.

Faecal glucocorticoid metabolites (fGCM) were measured in dry extracts at Gembloux Agro Bio Tech Zootechnical laboratory (University of Liège, Belgium) using a DetectX® corticosterone kit (Arbor Assays, K014-H1) as described by Oduor et al. (2020). The sensitivity of the assay was 0.03 ng/mL, and the results were expressed in ng/g. The interassay coefficient of variation (CV) was 15.1% for the high-concentration control and 9.4% for the low-concentration control. The intra-assay CV was 9.71% for the high-concentration control and 8.93% for the low-concentration control.

2.5 | Data analyses

Data were analysed from 2020 to 2024 according to well-established statistical protocols (Bates et al., 2015; Bolker et al., 2009; Ngama et al., 2019; Winter, 2014). According to our first hypothesis, which states that elephants seek out specific crop species when facing GPI, we considered PP, PI and fGCM as our explanatory variables. Our observational experimental blocks were seasons with five modalities (S1, S2, S3, S4 and S5, as described above). Each food item species was a response variable with two modalities noted as '1' (for consumed) and '0' (for not consumed). We compared every targeted species' intakes with all others noted as 'Others'. 'Others' indicate all consumed plants (both crops and natural vegetation) with less than five intake records and different from the species of interest written in bold in result tables.

We performed descriptive and inferential statistical calculations using Excel software and R version 4.0.4. We performed descriptive statistics, including percentage calculations, charts' design and principal component analyses (PCA) showing correlations between variables. In inferential statistics, the *Shapiro* test was used to assess the normality of response variables, while the χ^2 dependency test was used to assess whether variables were dependent. As most of our data were counts, we used nonparametric ANOVA tests (Kruskal and Wilcoxon) to calculate PP, PI and fGCM differences according to plant intakes. We also used the *lme4* package to perform generalized linear mixed models (GLMMs) analyses to predict the effects of PP, PI and fGCM on elephant plant species intakes over time. In GLMMs, the seasons were treated as random effects to account for

TABLE 1 Overview of plant species consumed by elephants, number of feeding intakes and means (±SEM) of faecal glucocorticoid metabolite concentrations (fGCM), as well as parasite prevalence (PP) and parasite intensity (PI) in nearby sampled boluses and expressed in median numbers.

Combinations of food species consumed by forest elephants	Feeding intakes	Infested boluses samples	Sampled boluses with high PP (>555 epgd)	fGCM	Median numbers of PI in sampled boluses
Palm	10	2	0	99.21 ± 16.7	75
Bamboo	30	6	0	84.41 ± 19.6	156
Costus	20	4	1	105.37 ± 19.5	375
Palm+Bamboo+Ficus	45	3	0	76.33 ± 15.5	375
Palm+Costus+Bamboo	75	3	1	107.02 ± 8.0	388
Others	1032	43	6	90.65 ± 19.0	415
Bamboo+Ficus	10	1	0	93.55 ± 10.0	500
Banana+Cassava+Papaya+Costus	120	6	2	91.71 ± 17.4	617
Costus+Bamboo+Fern+Ficus	40	2	1	66.73 ± 11.5	750
Ferns	40	8	3	93.88 ± 11.3	806
Papaya+Ficus	70	7	6	88.51 ± 19.9	1071
Banana+Bamboo	20	2	2	76.82 ± 12.4	1500
Banana+Costus	20	2	2	90.81 ± 8.3	1925
Papaya	6	1	1	111.53 ± 10.0	2250
Totals and General means	1538	90	25	90.77 ± 18.9	555

Note: The plants are sorted according to the PI. Here 'Others' indicate less consumed crops (sugar cane, yams, sweet potatoes, etc.) and natural vegetation (plentiful herbs and tree species).

changes over time. The Akaike Information Criterion (AIC) was used to compete models.

3 | RESULTS

During the 15 months of data collection, a total of 2100 km were monitored by car and 46 fresh elephant trails (23 km) were investigated on foot. We encountered 420 elephant boluses, of which 90 were selected with their 1538 paired records of evidence of elephant plant intakes. The feeding of elephants on crops mainly occurred at night (90%). In the sampled boluses, two families and three species of gastrointestinal parasites were found, including helminths with two species (*Strongles* sp. and *Strongyloide* sp.) and Coccids with one species, *Eimeria* sp. The most frequent combinations of plants fed on by elephants in crop areas included banana+cassava+papaya+*Costus* sp. ($n = 120$), followed by palm+*Costus* sp.+bamboo ($n = 75$) and papaya+*Ficus* sp. ($n = 70$) (Table 1). The highest PI (1071 to 2250 epgd) was found in boluses deposited near the intakes of the trunks and leaves of banana and/or papaya crop species (Table 1).

Forest elephants mostly fed on mixtures of several plant species along the trails, and records of plant fragments with evidence of intake included all parts of plants (i.e. leaves, stems, roots, barks and fruits; Table 2). The highest percentages of PP and PI were found in boluses sampled near the intakes of banana (60% and 1055 epgd) and papaya (64% and 961 epgd) (Table 2). The least PP and the lowest PI were found in boluses sampled near the intakes of palm trunks and leaves (8% and 279 epgd) and bamboo leaves (18% and 430 epgd) (Table 2).

All papaya and banana intakes involved only leaves and trunks and matched PI higher than 555 epgd in surrounded boluses (Table 2; Figure 3). Elephant consumptions varied throughout the seasons, with all dropping to zero during at least two seasons (Figure 4). There were no records of palm and cassava intakes during three and four seasons, respectively, while papaya and banana intakes decreased during seasons S2, S4 and S5, respectively; and PI was under 555 epgd in nearby boluses (Figures 3 and 4). At season S4, there was no record of any crop plant intakes around collected boluses, and mean PI was found under 555 epgd.

Principal component analyses (PCA) results showed strong and positive correlations between PP, PI in elephant boluses, banana and papaya intake frequencies (Figure 5). There were no correlations found between fGCM and crop consumptions (Figure 5). Results from χ^2 independency tests revealed that only the intakes of *banana* and *papaya* plants were dependent on PP ($\chi^2 = 8.96$, df = 1, $p < 0.05$; $\chi^2 = 4.15$, df = 1, $p < 0.05$) and PI ($\chi^2 = 35.38$, df = 18, $p < 0.05$; $\chi^2 = 147.71$, df = 18, $p < 0.05$) respectively. PI was dependent on seasons ($\chi^2 = 96.12$, df = 72, $p < 0.05$) but not PP.

Kruskal–Wallis and Wilcoxon nonparametric ANOVA tests showed that 56% of boluses with high PP ($n2 = 14$ over $N2 = 25$) were collected near evidence of crop intakes (Kruskal–Wallis-$\chi^2 = 5.63$, df = 1, $p < 0.05$). There were seasonal effects on parasitism with boluses collected in S3 having higher PP (Kruskal–Wallis-$\chi^2 = 5.824$,

TABLE 2 Statistical results of mean comparisons related to PP, PI, and fGCM (in 90 selected bolus samples) as well as species and parts of plants consumed by elephants. In every line, 'Others' indicates all consumed plants (both crops and natural vegetation) apart from the species written in bold.

	Number of sampled boluses			Mean of fGCM		Parasite loads (median numbers)				
	(N1 = 90)	(%)				PP (>555 epgd) (N2 = 25)			PI	
Plant consumed	(n1)	(n1 × 100/N1)	Most taken parts	(ng/g)	Stats	(n2)	(%) (n2 × 100/n1)	Stats	(epgd)	Stats
Crops	***30***	***33***	*L, T, R*	91.6 ± 18.92	a	***14***	***47***	**b**	***788***	**b**
Others	60	67	–	90.4 ± 19.16	a	11	18	a	438	a
Palm	***12***	***13***	*T, L*	94.2 ± 19.93	a	1	***8***	**b**	279	a
Others	78	87	–	90.2 ± 18.91	a	24	31	a	597	a
Cassava	***6***	***7***	*L, R*	91.7 ± 19.09	a	2	**33**	**b**	617	a
Others	84	93	–	90.7 ± 19.1	a	23	27	a	551	a
Papaya	***14***	***16***	*T, L*	91.5 ± 19.71	a	***9***	**64**	**b**	***961***	**b**
Others	76	84	–	90.6 ± 18.98	a	16	21	a	480	a
Banana	***10***	***11***	*T, L*	88.6 ± 17.03	a	***6***	**60**	**b**	***1055***	**b**
Others	80	89	–	91.0 ± 19.29	a	19	24	a	493	a
Costus	***18***	***20***	*T, L, Fl*	95.3 ± 19.85	a	7	39	a	672	a
Others	72	80	–	89.6 ± 18.73	a	18	25	a	526	a
Bamboo	***22***	***24***	*T, L*	85.2 ± 19.96	a	4	18	a	430	a
Others	68	76	–	92.6 ± 18.44	a	21	31	a	596	a
Fern	***10***	***11***	*L*	88.4 ± 16.56	a	4	40	a	795	a
Others	80	89	–	91.1 ± 19.34	a	21	26	a	525	a
Ficus	***14***	***16***	*L, Fr*	***82.3 ± 19.63***	***b***	***7***	**50**	**b**	***786***	**b**
Others	76	84	–	92.3 ± 18.57	*a*	18	24	a	513	a

Note: (*L* = leaves; *T* = trunks; *Fr* = fruits; *Fl* = flowers; *R* = roots; *all* = leaves, trunks, fruits, flowers and bark) The letters (a, b) from the same lines show the results of the Kruskal–Wallis and Wilcoxon tests; and different letters indicate significant differences between figures in the lines (a for $p > 0.05$ and b for $p < 0.05$).

df = 1 $p < 0.05$) and PI (Wilcoxon = 88.5, $p < 0.05$). The boluses sampled nearby banana and papaya intakes had the highest PP (Wilcoxon = 570, $p < 0.05$; Wilcoxon = 743, $p < 0.05$) and PI (Wilcoxon = 617, $p < 0.05$; Wilcoxon = 816.5, $p < 0.05$) respectively (Table 2). Among the natural plant species, only the boluses collected near the intakes of *Ficus* had high PP (Wilcoxon = 743, $p < 0.05$) and PI (Wilcoxon = 743.5, $p < 0.05$; Table 2). Parasitism intensity (PI) was found to be high in seasons S3 (Wilcoxon = 388.5, $p < 0.05$) and S4 (Wilcoxon = 962, $p < 0.05$), respectively. fGCM measures were high in seasons S4 (Kruskal–Wallis-$\chi^2 = 4.11$, df = 1, $p < 0.05$) and S5 (Kruskal–Wallis-$\chi^2 = 6.61$, df = 1, $p < 0.05$; Figure 3) and low in S2 (Kruskal–Wallis-$\chi^2 = 7.52$, df = 1, $p < 0.05$) and S3 (Kruskal–Wallis-$\chi^2 = 4.44$, df = 1, $p < 0.05$).

The GLMM models showed that PP and PI were associated with crop intakes in general and especially for banana and papaya. Increases in PP and PI in elephant boluses led to 28% and 0.16% more intakes of all crops, respectively (Table 3). PP increases in elephant boluses also led to 16% and 25% more bananas and papaya intakes, respectively; while PI increases in boluses led to 0.1% more intakes of both bananas and papaya plants (Table 3). No such predictions were found for other crops (cassava and palm plant), nor for natural food species (Table 3).

4 | DISCUSSION

Forest elephants appear to rely on self-medication to survive and overcome parasites and diseases by feeding on numerous plant species, including crops (Blake et al., 2009; Hoare, 2012). Banana and papaya crop intakes were correlated with and predicted by PP and PI in boluses. Thus, this study shows for the first time that forest elephants may adapt their crop selection behaviours according to the GPI levels. The results suggest the existence of a trade-off between the health of elephant crop-raiding and the threats associated with encountering farmers. We consequently suggest that crop-raiding may be a self-medication behaviour and that crop fields might serve as forest elephant pharmacies, further complicating HEC issues.

Previous studies emphasize that elephants raid farms due to the high nutrient value of crops, with energy being a key driver (Hoare, 2012; Osborn, 2004). However, in this study, forest elephants were observed to mostly feed on banana and papaya leaves and trunks rather than fruits. Banana leaves and trunks have less energy (<15 Kcal) than fruits (>80 Kcal) and have been reported to reduce GPI in lambs through the actions of terpenoid and flavonoid compounds (Chota et al., 2010; Gregory et al., 2015;

FIGURE 3 Correlations between plant species fed on by elephants and parasite load (expressed in EPGD) as measured from paired bolus samples. Read abbreviations as follows: fGCMc = faecal glucocorticoid metabolite concentrations; EPGD = egg per gram of boluses.

Krishna et al., 2008; Marie-Magdeleine et al., 2010; Santos et al., 2012; Sudhakar et al., 2014). Similarly, papaya leaves and trunks have lower energy content (<20 Kcal) than fruits (>42 Kcal) and have been reported to control GPI in chickens due to the presence of benzyl isothiocyanate and papain (Chota et al., 2010). This aligns with our findings, which indicate that PP and PI significantly predicted 16%, 25% and 0.1% more bananas and papaya intakes, respectively. Although only 33% of elephants occasionally raided crops, as reported in Monts De Cristal National Park farm areas (Ngama et al., 2019). These behaviours may indicate self-medication practices when experiencing parasitic discomfort. This self-medication behaviour is consistent with reports in other mammalian species, including savanna and Asian elephants (Greene et al., 2020; Hart & Hart, 2018; Huffman, 2022; Hutchings et al., 2003; Pattanayak, 2024; Villalba et al., 2014). This hypothesis is further supported by the fact that 56% of boluses with high PP were found near where crops were ingested, which would include banana and papaya crops. PP and PI predicted 16%, 25%, 0.1% and 0.1% more bananas and papaya intakes, respectively, suggesting that elephants consumed these crops in response to parasitic infestations. These trends were different from those of fGCM.

In this study, fGCM in boluses of crop raiders was low and not different from non-raiding elephants. Similar data have been reported in other human-dominated landscapes (Munshi-South et al., 2008; Pokharel & Brown, 2023). The low fGCM, irrespective of whether boluses were collected from crop-raiding elephants or not, is indicative of the risk avoidance tactics of forest elephants. Crop-raiding elephants have learned to come near human habitations at night when the risk of encounters with farmers will be minimal. This behaviour suggests the elephants in this study made a trade-off between the potential medicinal benefits involved in crop-raiding particular plants and the risks associated with encountering farmers. High fGCM that is linked to certain seasons requires further investigation into the stressors involved in crop-raiding behaviour (Ganswindt et al., 2010; Kely et al., 2021). Beyond fGCM and stressors, further investigations are needed to understand the attraction of elephants to specific wild plants such as *Costus*, which are reported to have medicinal properties (Baba & Onanuga, 2011; Deepa et al., 2018).

This study focused on gastrointestinal parasites. Other diseases were not investigated due to limited DNA analyses that restricted measuring with greater accuracy the effect of *Costus*, *Ficus*, cassava and other plants known for their medicinal properties and individual

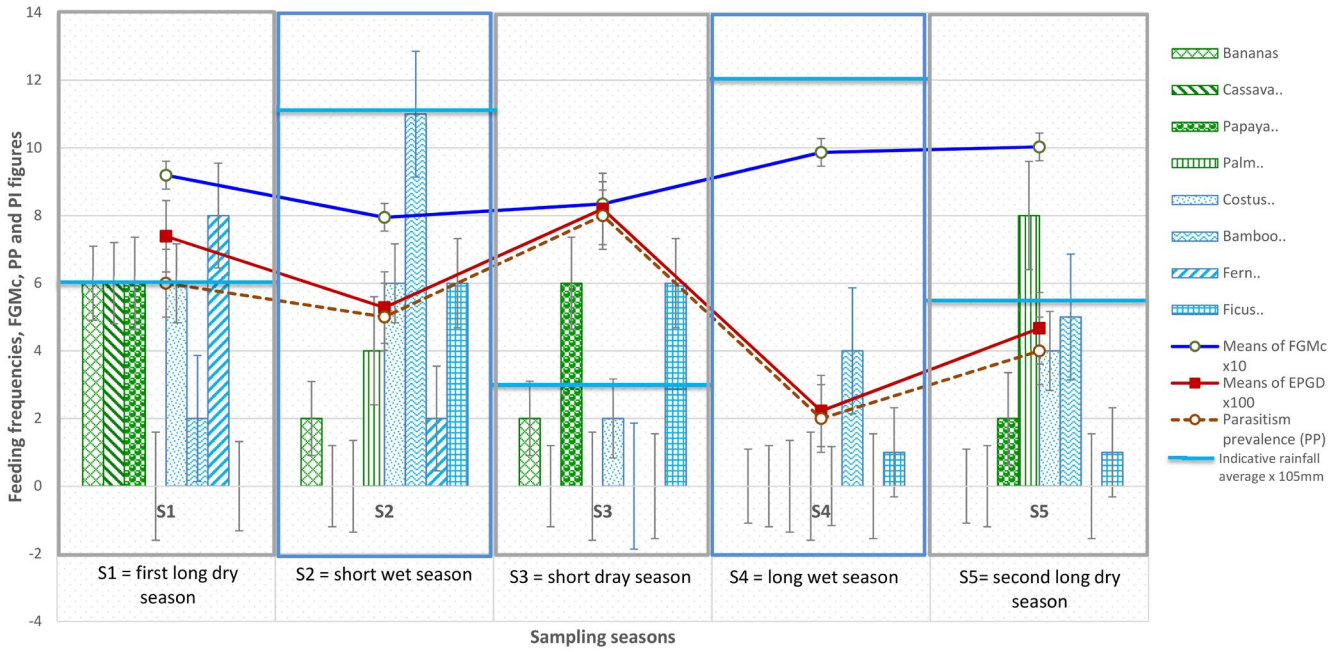

FIGURE 4 Records of elephant plant species feedings, PI, PP and fGCM with regard to sampling seasons. Read abbreviations as follows: PP = parasitism prevalence; EPGD = egg per gram of boluses; fGCMc = faecal glucocorticoid metabolite concentrations; S1 = Long dry season; S2 = short wet season; S3 = short dry season; S4 = long wet season; S5 = second long dry season.

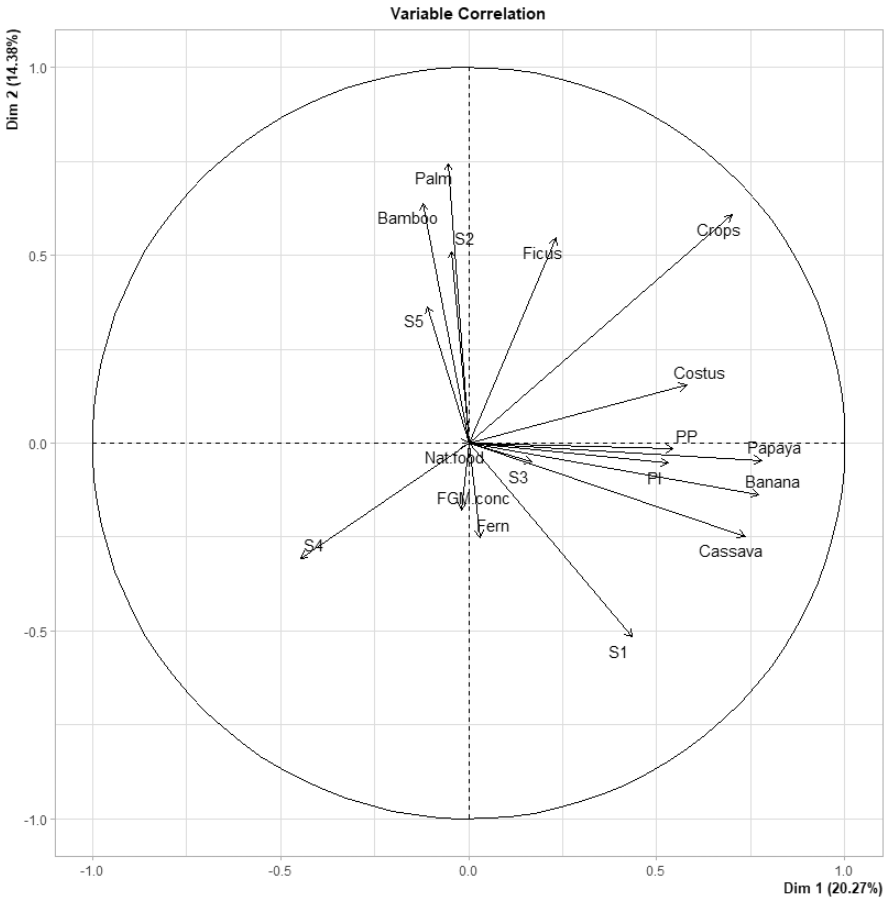

FIGURE 5 Correlation circle from PCA results. Read abbreviations as follows: PP = parasitism prevalence; PI = parasitism intensity; fGM = faecal glucocorticoid metabolite concentrations; S1 = long dry season; S2 = short wet season; S3 = short dry season; S4 = long wet season; S5 = second long dry season.

TABLE 3 Detailed results of the best-fitted generalized linear mixed models (GLMMs) with season as a random effect.

	Response variables									
Explanatory variables	**Est.**	**SE**	**df**	***t***	***p***	**Est.**	**SE**	**df**	***t***	***p***
	All crops intakes					**Papaya intakes**				
Intercept	0.25	0.08	4.91	2.84	0.03	0.087	0.068	4.83	1.27	0.087
PP	**0.28**	0.1	86.5	2.71	**0.008**	**0.25**	0.078	86.48	3.13	**0.025**
PI	**1.6e-04**	7.4e-05	8.7e+01	2.1	**0.03**	**1.1e-04**	5e-05	8e+01	1.98	**1.1e-04**
	Banana intakes					**Palm plant intakes**				
Intercept	0.06	0.05	4.94	1.11	0.31	0.16	0.08	4.41	1.83	0.16
PP	**0.16**	0.07	86.6	2.26	**0.026**	−0.11	0.07	85.28	−1.59	−0.11
PI	**1.1e-04**	4.9e-05	8.79e+01	2.29	**0.024**	−7.7e-5	5.1e-05	8.6e+1	−1.51	−7.7e-5
	Cassava intakes					**Costus intakes**				
Intercept	0.06	0.06	4.38	0.96	0.38	0.17	0.068	5.37	2.51	0.17
PP	0.002	0.05	85.2	0.044	0.96	0.1	0.09	87.32	1.07	0.1
PI	−1.8e-5	3.7e-5	8.6e+1	−0.48	0.63	4.2e-05	6.6e-05	8.7e+1	0.63	4.2e-05
	Bamboo intakes					**Ficus intakes**				
Intercept	0.26	0.105	4.52	2.54	0.056	0.114	0.073	4.83	1.57	0.114
PP	−0.082	0.093	85.6	−0.87	0.382	0.147	0.081	86.38	1.81	0.147
PI	−3.9e-5	6.7e-05	8.6e+01	−0589	0.55	7.1e-05	5.8e-05	8.7e+1	1.249	7.1e-05
	Ferns intakes									
Intercept	0.097	0.087	4.36	1.11	0.322					
PP	0.048	0.065	85.15	0.738	0.462					
PI	3.4e-05	4.6e-05	8.6e+01	0.728	0.468					

Note: The results examine how explanatory variables (i.e. PP, PI, fGCM) explain the response variables (banana and papaya crop intakes) across the entire dataset ($N = 90$). The size of the estimates (Est.) for each independent explanatory variable gives the size of the effect that variable has on response variables. The sign of the estimate gives the direction of the effect. The significant effects ($p < 0.05$) are given in bold. Therefore, parasitism prevalence (PP), for example, significantly predicts banana intakes, with every increase in PP leading to 0.16 or 16% more banana intakes by elephants ($p = 0.026$).

Abbreviations: df, degree of freedom; Est., estimate; *p*, *p* value; SE, standard error; *t*, *t*-test.

elephant preferences properties (Baba & Onanuga, 2011; Deepa et al., 2018). However, these findings are of importance for future HEC management and conservation strategies for endangered forest elephants.

Knowing that elephants can use crop fields as pharmacies to combat parasite infestations offers a new window in management strategies. Future strategies should incorporate examining crop-raided plants with medicinal properties and/or creating artificial mineral supply sites with medicinal properties for forest elephants. Similar strategies involving elephant physiology are already being used to improve HEC management with savanna elephants through birth limitation (Bertschinger & Caldwell, 2016). Additionally, plant chemistry and mineral salts are known to influence the movement of elephants and other wildlife (Biru & Bekele, 2012; DeGabriel et al., 2009; Fishlock & Breuer, 2015). Providing antiparasitic treatments through mineral salts could potentially reduce farm intrusions and HEC events.

In the context of HEC, future mitigation strategies would be more effective if they incorporated the placement of agricultural fields away from fruiting trees, wildlife corridors and other ecological attractants, as recommended by Ngama et al. (2019) and Beirne et al. (2020). Management authorities should also include the development of medicinal leeches in HEC mitigation strategies to assist the elephants in combating the parasites. This study mostly points out the significance of health and physiological processes in elephant crop-raiding behaviour using gastrointestinal parasitism and fGCM as proxies. Future investigations should focus on improving our understanding of elephant crop-raiding behaviour in relation to reproduction and other physiological conditions at individual and group levels, as suggested by Finch (2013), Jachowski et al. (2013) and Pokharel and Brown (2023). To achieve this, employing longitudinal studies combined with noninvasive ecophysiological methods would be beneficial, allowing efficient investigations without causing stress to the animals. Additionally, collaring elephants could facilitate the collection of boluses from individuals over a 48-h period, enabling the identification of consumed plant species and parts through macroscopic examination (using epidermis identification) or DNA barcoding. This approach should be integrated with monitoring gastrointestinal parasite loads and other pathogens while tracking both herds and solitary elephants. Measuring boluses' circumferences and the number of elephants on a path could provide insights into potential sex and age-related differences. DNA analysis could

also help determine sex-related distinctions and develop selectivity indices to assess dietary shifts in plant and crop preferences with regard to its self-medication behaviour.

This study provides evidence, albeit limited, that forest elephants engage in self-medication behaviour by feeding on specific crops. With a life expectancy of about 50 years in the wild, comparable to the African savanna species, forest elephants may rely on this behaviour to stay healthy as its counterparts (Greene et al., 2020; Huffman, 2022; Hutchings et al., 2003; Pattanayak, 2024; Turkalo et al., 2017). Consequently, the forest elephant not only acts as a forest engineer but may also be considered one of the most adept self-medicating animals in rainforest regions, albeit largely unrecognized. In Asia, observations of elephant self-medication have already facilitated the transfer of valuable medical knowledge to humans sharing their habitat, enhancing the health and well-being of both humans and elephants (Dubost et al., 2022; Greene et al., 2020). Further, longer term investigations focusing on the wild plant species consumed by forest elephants will provide wisdom and deeper insights into how these animals maintain their health. Knowledge about forest elephant self-medication may assist humanity in addressing current and future health challenges. A popular Chinese proverb says, 'When the wise man points to the moon, the fool looks at his finger'. Knowledge about forest elephant self-medication can help communities to focus on the broader health benefits (the 'moon') rather than solely on the immediate issue of crop damage (the 'finger').

AUTHOR CONTRIBUTIONS

Our study allowed authors from different backgrounds, scientific disciplines and countries to collaborate and share their experiences. The main authors have collaborated and contributed as follows: Steeve Ngama, Cédric Vermeulen, Jerome Bindelle, John R. Poulsen, Jean-Luc Hornick, Lisa Korte, Annick Linden, Jean-Louis Doucet and Philippe Lejeune designed and validated the research protocol; Steeve Ngama, Monique Bouanga Banfoui epse Ngama and Mireille Bawe Johnson organized field logistics and performed field sampling; Steeve Ngama and Monique Bouanga Banfoui epse Ngama performed field hormone extractions and sample packaging. Steeve Ngama, Janine L. Brown and Stephen Paris carried out hormone analyses; Steeve Ngama and Jean-Luc Hornick carried out parasite analyses and parasite identification; Steeve Ngama and Jerome Bindelle performed statistical analyses and performed data interpretations; Steeve Ngama, Jerome Bindelle, Janine L. Brown, John R. Poulsen, Jean-Luc Hornick, Annick Linden, Lisa Korte, Jean-Louis Doucet, Auguste Ndoutoume Ndong, Jacques François Mavoungou, Monique Bouanga Banfoui epse Ngama, Stephen Paris, Mireille Bawe Johnson, Philippe Lejeune and Cédric Vermeulen wrote and revised the paper.

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CONFLICT OF INTEREST STATEMENT

We do not have any conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data collected and used during this study has been stored in DRYAD. The dataset is publicly accessible at this link: https://doi.org/10.5061/dryad.7wm37pw1p (Ngama et al., 2025).

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