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RESEARCH ARTICLE

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Sooty mangabeys scavenge on nuts cracked by chimpanzees and red river hogs—An investigation of inter-specific interactions around tropical nut trees

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Carrion scavenging is a well-studied phenomenon, but virtually nothing is known about scavenging on plant material, especially on remnants of cracked nuts. Just like meat, the insides of hard-shelled nuts are high in energetic value, and both foods are difficult to acquire. In the Taï forest, chimpanzees (*Pan troglodytes*) and red river hogs (*Potamochoerus porcus*) crack nuts by using tools or strong jaws, respectively. In this study, previously collected non-invasive camera trap data were used to investigate scavenging by sooty mangabeys (*Cercocebus atys*), two species of Guinea fowl (*Agelestres meleagrides; Guttera verreauxi*), and squirrels (*Scrunidae* spp.) on the nut remnants cracked by chimpanzees and red river hogs. We investigated how scavengers located nut remnants, by analyzing their visiting behavior in relation to known nut-cracking events. Furthermore, since mangabeys are infrequently preyed upon by chimpanzees, we investigated whether they perceive an increase in predation risk when approaching nut remnants. In total, 190 nut-cracking events were observed in four different areas of Taï National Park, Ivory Coast. We could confirm that mangabeys scavenged on the nuts cracked by chimpanzees and hogs and that this enabled them to access food source that would not be accessible otherwise. We furthermore found that mangabeys, but not the other species, were more likely to visit nut-cracking sites after nut-cracking activities than before, and discuss the potential strategies that the monkeys could have used to locate nut remnants. In addition, mangabeys showed elevated levels of vigilance at the chimpanzee nut-cracking sites compared with other foraging sites, suggesting that they perceived elevated danger at these sites. Scavenging on remnants of cracked nuts is a hitherto understudied type of foraging behavior that could be widespread in nature and increases the complexity of community ecology in tropical rainforests.

KEYWORDS
auditory cues, community ecology, interspecific interactions, nut-cracking, scavenging, tropics

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1 | INTRODUCTION

In the African tropics, 10 kg carcasses can be consumed within 3 days by invertebrate scavengers (Houston, 1985), or rendered inaccessible for animals by toxins produced by microbial decomposers (DeVault, Rhodes Jr, & Shivik, 2003). For fast and efficient carrion localization, scavengers use sensory cues (DeVault et al., 2003) or information from a social network (Dermody, Tanner, & Jackson, 2011). To feed on animal remnants, scavengers often approach areas at which predators may be present. Thus, approaching animal remnants involves a risk of being chased away, attacked, or even predated on (Wikenros, Ståhlberg, & Sand, 2014). Scavenging therefore determines a trade-off between taking a risk and obtaining a food reward that can be of high energetic value (Atwood & Gese, 2008). Meat, for example is one of the most energy-rich scavenged foods (raw rat meat: 166.2 kCal/100 g; raw beef: 157.4 kCal/100 g; Boback et al., 2007).

Although scavenging is mostly studied in the context of carrion scavenging, there are other energy-rich food sources that can be scavenged, such as tropical nuts. Similar to meat, nuts are a high-energy food source, rich in fatty acids and often difficult to acquire due to the high resistance of the shell protecting the kernel (145 kCal/100 g, on average, in West African tropical nut species; Boesch & Boesch, 1982; Kalan, Mundry, & Boesch, 2015). To access nut kernels, animals need either strong jaws (such as those of red river hogs [*Potamochoerus porcus*], the main nut predator in Gabon; Moupela et al., 2014), or sophisticated cognitive abilities, manual dexterity, and strength in order to crack them open with the use of tools. West African chimpanzees (*Pan troglodytes verus*), brown tufted capuchins (*Sapajus* spp.), and long-tailed macaques (*Macaca fascicularis aurea*), are known to crack a variety of hard-shelled nut species using tools (Boesch & Boesch, 1982; Canale, Guidorizzi, Kierulff, & Gatto, 2009; Gumert, Kluck, & Malaivijitnond, 2009; Luncz et al., 2017; Visalberghi et al., 2015).

Anecdotal observations indicate that, in the Taï Forest (Côte d'Ivoire), sooty mangabeys (*Cercocebus atys*, Mittermeier, Rylands, Hoyo, & Anandam, 2013), white-breasted Guinea fowl (*Agelestres meleagrides*), crested Guinea fowl (*Guttera verreauxi*, del Hoyo, Collar, Christie, Elliott, & Fishpool, 2014), and several species of rodents, including squirrels (*Scrunidea* spp.), scavenge on the remains of coula nuts (*Coula edulis*) and panda nuts (*Panda oleosa*) that are left behind by nut-cracking species (pers. obs. K. Janmaat, G. Sirianni & P. Gratton).

Mangabeys, Guinea fowl, and squirrels have different levels of morphological adaptation to access hard-shelled nuts by their own means. Sooty mangabeys have strong premolar teeth indicating durophagy (McGraw, Vick, & Daegling, 2011; Rowe & Myers, 2016) and feed on several nut species. For example, mangabeys can crack open *Sacoglottis gabonensis* nuts with their teeth (McGraw et al., 2011). Coula nuts, however, are spherical and non-lobed and are therefore more difficult to crack, and mangabeys mainly crack them when the nuts are old and the shell has softened (pers. obs. K. Janmaat; pers. comm. A. Mielke; Bergmüller, 1998; McGraw et al., 2011). There are observations of adult male mangabeys peeling and cracking fresh nuts, but with this action taking a considerable time (up to 2 min per nut; K. Janmaat unpublished data). To date, there are no reports of mangabeys eating panda nuts, the hardest nut found in the Taï forest (Boesch & Boesch, 1982). Little is known about the diet of crested Guinea fowl and white-breasted Guinea fowl in the Taï National Park, but the morphology of their beaks makes it unlikely that they are capable of opening any nuts, and previous studies suggested that their diet mainly consists of invertebrates and unprotected seeds (del Hoyo et al., 2014; Francis, Penford, Gartshore, & Jaramillo, 1992). Current knowledge about the diet of African rodents is extremely limited, but many species of rodents were reported to be able to open and eat fresh and old coula nuts in Gabon (Moupela et al., 2014). In Taï National Park, signs of rodents eating coula nuts are common (personal observation B. van Pinxteren & K. Janmaat).

Unlike ripe fruit and rotting meat, long-range olfactory detection of nuts is unlikely, since nuts do not emit an obvious smell (Janmaat, Ban, & Boesch, 2013a). Nut remnants are also very small and partly covered by foliage when on the ground, making the ability to use visual cues over long distances limited, especially in forest environments with short visual detection distances (Janmaat, Ban, & Boesch, 2013b). Hence, employing olfactory or visual cues to detect nut remnants at distance are unlikely to be an efficient search strategy. One anecdotal observation (described below) suggests that mangabeys use the sounds of the nut-cracking chimpanzees to anticipate the availability of nut remnants. These sounds can be heard up to 400 m or more (unpublished data K. Janmaat). In the following observation of K. Janmaat, recorded on 25/1/2002 in the Taï National Park, Côte d'Ivoire, the action of the mangabeys is noted in detail.

> *Three adult chimpanzees and three juvenile chimpanzees were observed cracking Coula edulis nuts. Within the same visual field (about 5–10 m apart) we saw the sooty mangabeys, resting. Some were facing the direction of the chimpanzees and gazed at the nut-cracking chimpanzees for a period of at least 5 min. At 14:08, 1 min after the last chimpanzee had left the cracking site, an adult mangabey male (Falco) approached the cracking site and ate from the leftovers. At 14:11, Falco walked in the direction of other nut cracking sounds. At 14:16, he arrived at another nut-cracking site and ate again from the leftovers after the chimpanzees had left. A second adult mangabey male (Marlone), a subadult male (Pieter), an adult female (Tina), and a juvenile male (Piscu) joined Falco and ate from the leftovers at the same cracking site. At 14:17, Falco left in the direction in which the chimpanzees had left. At 14:23, we observed that part of the group arrived at a third cracking site. They again approached the chimpanzees between five and 10 m. The mangabeys stopped moving when approaching the site, some were resting others were feeding on Anthonota fragans fruits. At 14:29 the chimpanzees stopped cracking and left. At 14:30 four*

mangabeys (adult female (Kora), two subadult males (Emiel and Pieter) and an unknown individual) approached the cracking place and ate.

A variety of studies have shown that primates approach food calls of conspecifics (reviewed in Zuberbühler & Janmaat, 2010). Whether foragers also use auditory cues of other sympatric species to locate food is not well studied to date (Zuberbühler & Janmaat, 2010).

Similar to the dangers faced by a scavenger, which forages on carrion, chimpanzee nut-cracking sites can be dangerous for nut-cracking scavengers, particularly for mangabeys, since chimpanzees in the Taï National Park are known to hunt primates and infrequently prey on mangabeys (Boesch & Boesch, 1989). Chimpanzee hunts on Guinea fowl or squirrels have not yet been observed in the Taï forest (Boesch & Boesch-Achermann, 2000), but chimpanzees have been observed to eat Guinea fowl in Kibale National Park, Uganda (Watts & Mitani, 2002). The perceived predation risk can influence the antipredator behavior in animals, for example, by increasing cohesion or increasing vigilance (Campos & Fedigan, 2014; Dupuch, Morris, & Halliday, 2014; Favreau, Goldizen, & Pays, 2010; Laundré, Hernández, & Ripple, 2010; Lima, Valone, & Caraco, 1985; Périquet et al., 2012). Other behaviors can also be changed due to perceived risk, as illustrated by the following anecdote concerning mangabeys:

On 6/2/2002 at 10:28 K. Janmaat observed mangabeys suddenly changing travel direction and running just before she heard chimpanzee vocalizations. The females with young ran, but the adult males walked slowly behind.

In this study, we used camera-trap video recordings to describe previously unknown foraging interactions among mangabeys, Guinea fowl, squirrels, and sympatric rainforest nut-cracking species (chimpanzees and red river hogs), in the form of an understudied foraging strategy: scavenging for energetically valuable nut remnants. First, we aimed to confirm feeding by mangabeys, Guinea fowl, and squirrels on the nut remnants produced by red river hogs and chimpanzees. Furthermore, we investigated whether these scavengers used sensory cues associated with nut-cracking behavior to locate fresh nut remnants. We hypothesized that, especially Guinea fowl and mangabeys, which cannot rely on their own abilities to open fresh nuts efficiently, will be particularly motivated to approach the nut-cracking sites when abundant fresh nut remnants are available. Hence, we hypothesized that especially Guinea fowl and mangabeys would benefit from using sensory cues to locate sites where a recent nut-cracking event occurred. To test these hypotheses, we predicted that especially Guinea fowl and mangabeys, but not rodents, would be observed at nut-cracking sites more often recently after a nut-cracking by chimpanzees or red river hogs occurred than before such events. Lastly, we investigated whether the mangabeys, which are infrequently preyed upon by the chimpanzees, perceived an increased predation risk at chimpanzee nut-cracking sites. We predicted that, if the mangabeys perceived an elevated risk at the chimpanzee nut-cracking sites, they will display more vigilance behaviors at nut-cracking sites as compared with non-nut-cracking sites in the forest.

2 | METHODS

2.1 | Study site and animals

Our study was conducted in the rainforest of the Taï National Park, Ivory Coast (Figure 1). Taï National Park is the largest protected area of primary lowland rainforest in West Africa, covering 3,300 km^2 and located in southwest Ivory Coast at 5° 26′ longitude, 7° 11′ latitude (N'Goran et al., 2013).

2.1.1 | Scavengers

Sooty mangabeys are West African cercopithecid monkeys that live in the rainforests to the west of the Sassandra River (Mittermeier et al., 2013). They live in groups numbering from 30 to 120 individuals that occupy home ranges estimated at 5 km^2 (Janmaat, 2006; Shultz & Noë, 2002). White breasted Guinea fowl are indigenous to West Africa. They live in flocks up to 15 individuals in a home range of ca. 1 km^2, which is fiercely defended against intruders (Francis et al., 1992). White-breasted Guinea fowl can form polyspecific groups with crested Guinea fowl. Crested Guinea fowl have also been seen to forage alongside monkeys, as well as forage on fruits dropped from trees, and are thought to have a similar range size as white-breasted Guinea fowl (Hoyo, Elliott, & Bierregaard, 1994; Taylor, 2015). Knowledge about the behavior of tropical squirrels is extremely limited (Moupela et al., 2014). In the Taï National Park, four different species of squirrel have previously been observed (*Funisciurus pyrrhopys; Finusciurus lemniscatus; Protoxerus stranger; Epixerus ebii*; Boesch & Boesch-Achermann, 2000).

2.1.2 | Nut-crackers

West African chimpanzees use stone or wooden hammers to crack open nuts (Boesch & Boesch, 1990, Sirianni, Mundry, & Boesch, 2015). During an average nut-cracking event, lasting for 2 hr, a chimpanzee can crack up to 270 coula nuts (reviewed in Visalberghi et al., 2015, Figure 2). The sound of nut cracking can be heard from up to 400 m (pers. obs. K. Janmaat). Chimpanzees live in fission-fusion groups, of which the mean party size for Taï is 5.2 individuals (Wittiger & Boesch, 2013). Taï chimpanzees are ripe fruit specialists (Goné Bi, 2007), but occasionally eat meat which can come from several different species, including monkeys (Boesch & Boesch, 1989). The home ranges of chimpanzees of Taï National Park vary from 10 to 26 km^2 (Herbinger et al., 2001; Kouakou, Boesch, & Kuehl, 2011).

Red river hogs have an average group size of 10 individuals (Oduro, 1989), but have been shown to increase group size in favorable habitats such as secondary forests, near roads, and in selectively logged forests (Laurance et al., 2006; Vanthomme, Kolowski, Korte, & Alonso, 2013; White, 1994). The population density of red river hogs in Taï National Park is 1.51 individuals/km^2 (Hoppe-Dominik, Kühl, Radl, & Fischer, 2011), however the ranging behavior of red river

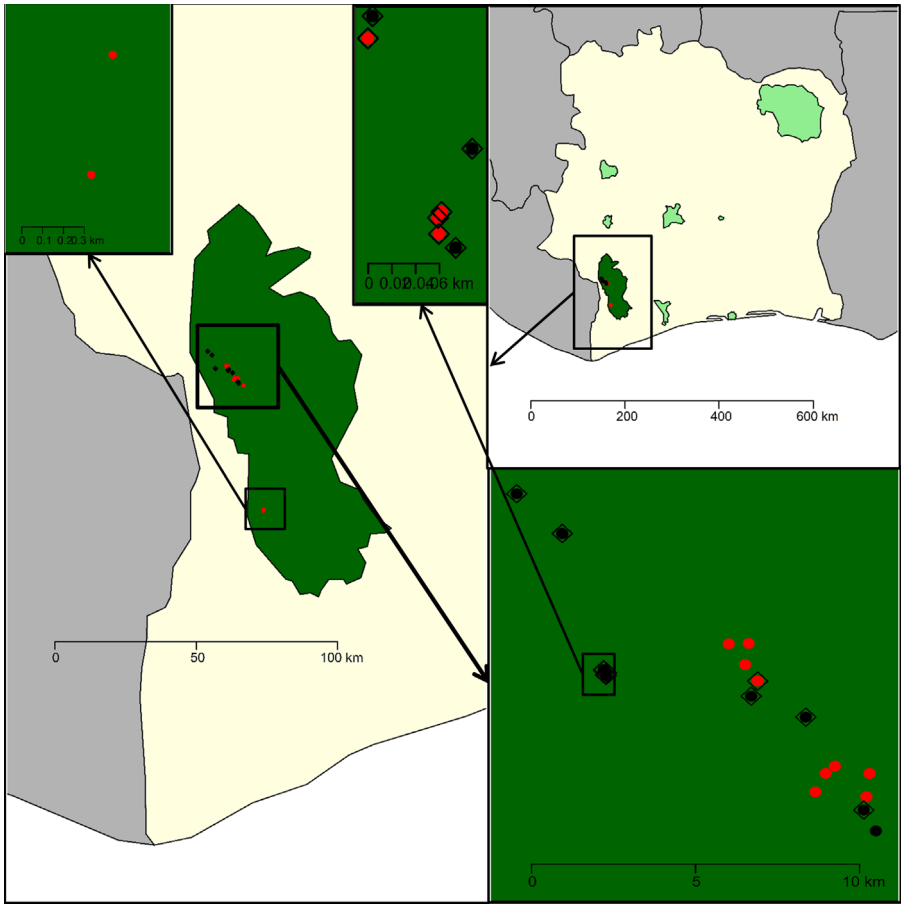

FIGURE 1 A map of Ivory coast with in light green all National Parks and in dark green Taï National Park including all the cameras selected for analyses depicted. Red dots indicate camera sites that have been used for the probability of approach analysis. Black dots are cameras where nut cracking also has been observed. A diamond surrounding the site indicates that scavenging has been observed at these sites. The latter two could not be used for the probability of approach analysis because there were no visitations 24 before or after a nut-cracking event. The bottom site is the Guiroutou site (n = 2) and the rest of the sites are in Taï (n = 23)

hogs is unknown (Leslie & Huffman, 2015). Red river hogs preferably eat drupes, including the coula nut (Moupela et al., 2014; Malbrant & Maclatchy, 1949 cited by Leslie & Huffman, 2015; Leus & Vercammen, 2013). The sounds produced by red river hogs while nut cracking with their teeth can be heard from several hundred meters away (Abernethy and White, 1999). Hogs show some diurnal activity but are mostly nocturnal or crepuscular (Gessner, Buchwald, & Wittemyer, 2014).

FIGURE 2 A close up of a chimpanzee nut-cracking site for coula nuts. The white pieces surrounded by a yellow square in the picture are remnants of the coula nut that can be eaten by the scavengers (picture made by G. Sirianni)

2.1.3 | Camera placement

From 2012 to 2015, a total of 170 camera traps (Bushnell Trophy Cam™; model #119576C and model #119476) were placed in Taï and Guiroutou (Ivory Coast) during a biomonitoring study (Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Pan African Project), and a behavioral study on chimpanzees (Sirianni, Wittig, Gratton, Schüler, & Boesch, 2018). For all the studies, cameras were placed in either a systematic manner, using a grid of cells of 1 km^2, or a targeted manner, at locations frequently visited by chimpanzees, or both, according to the specific study (see details in Després-Einspenner et al., 2017; Sirianni et al., 2018). For this study, we selected 73 cameras (Taï: n = 66, and Guiroutou: n = 7, Figure 1). Forty-one camera-traps were placed at sites containing evidence of chimpanzees cracking *Panda oleosa* (n = 3) or *Coula edulis* (n = 38) nuts, in the form of cracked nuts or previous direct observation of nut-cracking chimpanzees (PanAf field

guide; Pan African Program: The Cultured Chimpanzee, unpublished data; Boesch & Boesch, 1989). Determination of nut species was conducted by trained assistants of the Taï Chimpanzee Project (http://www.eva.mpg.de/primat/research-groups/chimpanzees/field-sites/tai-chimpanzee-project.html), or by using a botanical reference. At 32 camera-trap sites, no evidence of nut cracking was observed. Each camera was set at a height of 0.3–1.6 m to optimize the detection rate of medium-sized mammals, and operated for different amounts of time for a maximum of up to 1 year, according to the design of the study for which the camera trap data were initially collected. The recordings were sometimes interrupted due to various reasons (e.g. camera failures via empty batteries, damages by leopards or elephants, accumulation of humidity within the camera, etc.).

2.2 | Behavioral data collection

2.2.1 | Visitations

We checked camera-trap videos for the presence of the scavenging taxa (mangabeys, Guinea fowl, and squirrels) by playing them in VLC player [http://www.videolan.org/vlc/]). If at least one individual of a scavenging taxon was observed in the video, we scored one visitation for the respective taxon. Animals were identified using zoological reference (Petter & Desbordes, 2013; Rosevear, 1969). We marked which videos occurred before or after nut cracking by chimpanzees or red river hogs were seen or heard at the camera-trap site. The "before" period included all visitations to the nut-cracking sites 24 hr before the chimpanzees or red river hogs began cracking nuts. The "after" period included all visitations that were observed within 24 hr after the last nut-cracking sound. The limit of 24 hr was selected to give the foragers sufficient opportunity to visit the nut-cracking site when the nuts were cracked at dusk. On certain occasions, chimpanzees would leave a nut-cracking site and other chimpanzees would arrive and begin cracking nuts at a later time. We defined a nut-cracking event as including all nut-cracking bouts that were separated by less than 24 hr from any nut-cracking bout that took place at the same site.

2.2.2 | Vigilance

To test if the mangabeys perceived greater risk at the nut-cracking sites of chimpanzees compared to other sites, we compared vigilance behavior at nut-cracking sites to vigilance behavior at randomly selected sites where no nut cracking had been observed (non-nut-cracking sites). Due to time limitations not all nut-cracking sites were analyzed, but a selection of seven out of 29 nut-cracking sites and seven out of 32 selected non-nut-cracking sites where feeding was present was made. Vigilance behavior is known to be influenced by feeding frequencies (Wilkenros et al., 2014). To rule out the chance that potential differences in vigilance behavior were caused by the presence or absence of food, we additionally conducted the same test on sites in which the mangabeys had been observed feeding or emitting food twitters (Range & Fischer, 2004). Vigilant behavior is defined as being stationary or moving less than 2 m and looking into the surroundings further than an arm's length away without performing any other activity (Cowlishaw, 1998; Smith, Kelez, & Buchanan-Smith, 2004; Treves, Drescher, & Ingrisano, 2001). Since vigilance in mangabeys is a behavioral event, we recorded the frequency of occurrence instead of duration (Martin & Bateson, 2007). To obtain comparable measures for the different camera recordings, the frequency with which the focal animal showed vigilant behavior was divided by the total time the focal animal was observed and was clearly visible. The total observed video time was 192 min. Vigilant behavior was assessed at each site for at most three different individuals per video, which were the first visible individuals. Behavioral measurements were conducted using BORIS (version 2.2, Olivier Friard, University of Torino, 2015) and performed by one observer.

2.2.3 | Statistical analysis

To test if the sympatric rainforest foragers were more likely to visit nut-cracking site after a nut-cracking event than before it, we ran a Generalized Linear Mixed Model (GLMM) with binomial error structure and logit link function. The binomial response was the presence/absence of each of the scavenging species in a camera-trap video and the predictors were: *before or after nut cracking* and *forager taxon* (sooty mangabey, Guinea fowl, or squirrel). We structured our data so that each observation consisted of a combination of one nut-cracking event, one of the two possible outcomes of the response (presence or absence), and one of the three forager taxa (6 data points per nut-cracking event). To test our hypothesis that foragers that are unable or have physical difficulties to open fresh nuts (Guinea fowl and mangabeys, respectively), were more likely to approach nut-cracking events using sensory cues, we initially included an interaction effect between *forager taxon* and *before or after a nut-cracking event*. Overdispersion was not an issue (dispersion parameter = 0.57). Since we analyzed multiple observations at the same camera and nut-cracking event (e.g., one detection of mangabeys and one of guinea fowl after a chimpanzee cracked nuts), we controlled for pseudoreplication by including *camera* and *nut-cracking event* as random effects. To keep type I error rate at the nominal level of 5% (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009), we included all possible random slope components (*before or after nut-cracking event* and *forager taxon* within *camera* as well as *before or after nut-cracking* and *forager taxon* within *nut-cracking event*). We assessed model stability by comparing the estimates derived by a model based on all data with those obtained from models with the levels of the random effects excluded one at a time. This indicated that the assumption of normally distributed random effect components was not met, due to the large number of nut-cracking events that were not preceded or followed by a camera detection of any of the three foragers. We therefore decided to exclude all the nut-cracking events where none of the scavengers were detected to visit the nut-cracking site (before or after the cracking event). The resulting model, however, exhibited an unstable behavior (presence of influential cases), suggesting to remove the interactive effect of *forager taxon* and *before or after nut-cracking sound* to reduce its complexity. This

resulted in a stable model that was based on a much smaller dataset and a less complex structure (initial sample size: total number of data points = 1140, nut-cracking events = 190; cameras = 29; final sample size: total number of data points = 150, nut-cracking events = 25; cameras = 16).

To assess the significance of the predictors as a whole, we compared the full model comprising all predictors and the random effects with a null model comprising only the intercept and the random effects (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson & Barnett, 2008).

A Mann-Whitney U (MWU) test was used to compare the averages of vigilance behaviors of mangabeys at camera sites where chimpanzees cracked nuts and other camera sites. To measure vigilance behavior, we analyzed a total of 10.02 hr video material. Total observation time was 98.3, 60.8, and 93.9 min for nut-cracking sites, non-nut-cracking sites, and non-nut-cracking sites at which feeding behavior was observed, respectively. The GLMM was conducted using the R (version 2.12.2, R Core Development Team, 2013) function glmer (R package lme4, Bates, Maechler, & Bolker, 2013), while the R function exactRankTests was applied to test for differences in vigilance levels (R package exactRankTests, Hothorn & Hornik 2011).

3 | RESULTS

Twenty-nine out of the 73 camera locations within Taï and Guiroutou have recorded a nut-cracking event during the study periods with a total of 190 nut-cracking events, of which 154 and 27 consisted of nut cracking by chimpanzees and red river hogs, respectively.

3.1 | Scavenging

Compared to the number of nut-cracking events, the number of recorded visits by scavengers was low ($N = 31$, Table 1). All three scavenger taxa were recorded while feeding at nut-cracking sites. However, for the Guinea fowl and squirrels, the quality of the camera image was not sufficient to confirm with certainty that the food consumed was nut remnants and, thus, not sufficient to confirm scavenging of nut remnants beyond any doubt. The occurrence of scavenging by sooty mangabeys, however, was clearly confirmed in images from 16 different cameras (Figure S1). Sooty mangabeys were observed to scavenge from both chimpanzee and red river hog nut-cracking sites. Usually the mangabeys first rummaged through the ground at the nut-cracking site, after which they brought a certain substance towards their mouth. Due to the distance of the camera to the nut-cracking site, it was often difficult to see what the mangabeys were eating. But in the clear videos, mangabeys could be seen bringing a piece of nutshell towards their mouth and scraping the inside of the shell after which chewing commenced (see videos in supplementary materials). This behavior was observed for both *Coula* nuts (Figure 3) and *Panda* nuts (Figure 4).

TABLE 1 Visitation of the three types of rainforest foragers 24 hr prior to a nut-cracking event and 24 hr after a nut-cracking event.

	Sooty mangabey	Guinea fowl	Squirrel	Total
Before	4	2	5	11
After	13	2	5	20
Total	17	4	10	31

The visitation was counted if at least one individual was observed during this period.

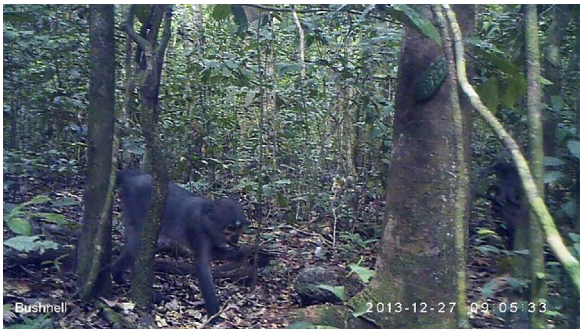

FIGURE 3 Image of a scavenging event by a sooty mangabey at a *Coula edulis* nut-cracking site

3.2 | Visitation timing

Overall, the full model was a significantly better fit to the data than the null model (Chi-square = 10.56; df = 3; $p = 0.014$, Observations = 150, Nut-cracking events = 25, Cameras = 16; Table 2). The foragers visited the nut-cracking sites significantly more often after nut-cracking events took place compared to before (Tables 1 and 2; Figure 5). It is difficult to draw conclusions on which forager caused significance of the effect of nut cracking on approach probability, due to the unstable nature of the model with the interaction effect. However, we did find that the number of visits before and after nut cracking were equal for Guinea fowl and rodents but not for mangabeys (Table 1). Hence, these results strongly suggest that the mangabeys caused the significant effect and that the mangabeys were actively approaching nut-cracking sites after nut-cracking events of both chimpanzees and red river hogs took place (Table 1). In addition, our GLMM revealed a statistical trend indicating that the three forager taxa visited the nut-cracking sites with unequal

FIGURE 4 Image of a scavenging event at a *Panda oleosa* nut-cracking site by a sooty mangabey

TABLE 2 Summary of model results: influence of nutcracking and forager on visiting probability (N = 150).

	Original estimate	St. error	*p*-value	Estimate min.	Estimate max.
(Intercept)	−2.67	0.76		−3.88	−2.36
Target predictors					
Time of approach (before)	−1.30	0.67	0.02853	−2.14	−0.94
Forager Sooty Mangabey	2.23	0.95		1.75	4.20
Forager Squirrel	1.28	1.05		0.70	2.22
Forager			0.05363		

Full model versus control model comparison: $\chi^2 = 10.56$; df = 3, $p = 0.014$, $N_{\text{cracking events}} = 25$, $N_{\text{sites}} = 16$. To describe the model stability, we present the minimum and maximum estimates of all models for which we took out the data belonging to one level of each random effect (e.g., one camera or nutcracking event) one by one.

frequency (Table 2), with mangabeys being the most commonly recorded, followed by squirrels and Guinea fowl (Table 2).

3.3 | Vigilance behavior of sooty mangabeys at chimpanzee nut-cracking sites

We found that the vigilance frequency of sooty mangabeys at the chimpanzee nut-cracking sites ($n = 7$) was significantly higher than that at other randomly selected non-nut-cracking sites ($n = 7$) (Mann-Whitney U test: Nncs = 7, Nnncs = 7, U = 6; $p = 0.017$; mean vigilance per minute NCS = 6.26; mean vigilance per minute NNCS = 3.75). This effect remained a trend when we only considered sites at which the mangabeys were observed feeding or emitting food twitters, (Mann-Whitney U test: Nncs = 7, Nnncs = 7, U = 10; $p = 0.072$; mean vigilance per minute NCS = 6.26; mean vigilance per minute NNCS = 3.97) (Figure 6).

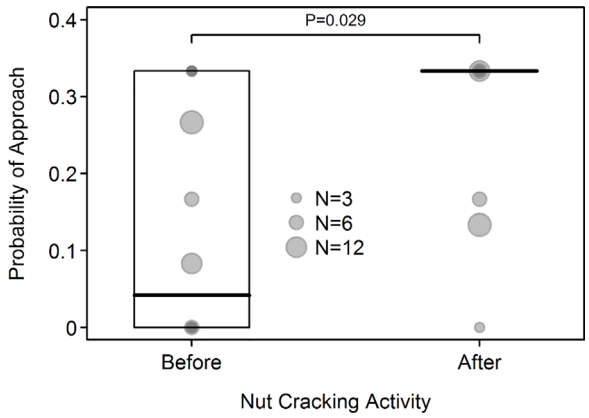

FIGURE 5 Probability of approach before and after a nut-cracking event. The probability of approach is the number of visitation by a forager (sooty mangabey, Guinea fowl, or squirrel) 24 hr before or 24 hr after nut cracking divided by the total amount of nut-cracking events at this camera site. The bars and the upper and lower boundaries of boxes represent the median, and the upper and lower quartiles, respectively. The area of the circles represents the number of visitations before and after all nut-cracking events for each forager per camera

4 | DISCUSSION

Our study confirms anecdotal observations that sooty mangabeys scavenge on the remnants of cracked nuts from chimpanzees and is the first to report that they also scavenge on nuts cracked by red river hogs. The scavenging of the Guinea fowl and squirrels could not be confirmed during this study because the limited quality of the camera images did not allow us to determine what exactly they were foraging on at the nut-cracking sites. However, since in previous studies we have observed guinea fowl and squirrels feeding on the remnants of the nuts (pers. obs. K. Janmaat, G. Sirianni, & P. Gratton), we continued to investigate and compare each forager's visiting behavior towards the nut-cracking sites. We found that foragers were more likely to visit nut-cracking sites after nut-cracking events compared to before such an event took place. A significant interactive effect of forager and time of approach could not be confirmed due to model instability. However, comparisons of approach frequencies suggest that it were the mangabeys and not the other foragers who were actively approaching the nut-cracking events (Table 1).

Our findings contradict our predictions that both Guinea fowl and mangabeys (which have difficulty opening fresh nuts themselves) would approach nut-cracking events using sensory cues. As it seems

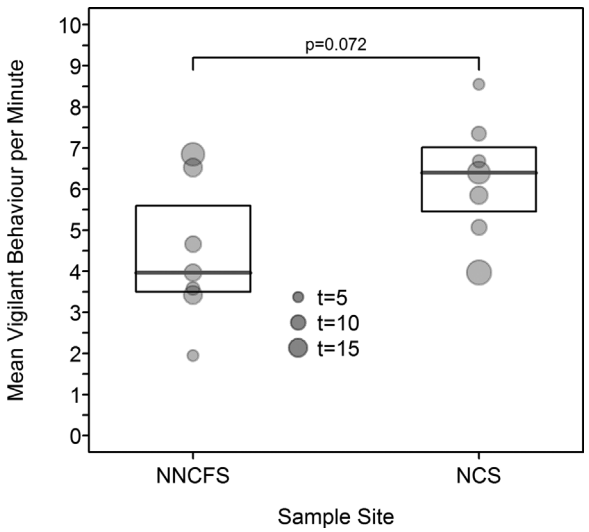

FIGURE 6 Frequency of vigilant behavior at nut-cracking site and other feeding site. The mean vigilant frequency showed a trend when nut-cracking sites (NCS; $n = 7$) were compared to non-nut-cracking feeding sites (NNCFS; $n = 7$). Time (t) is in minutes. The bars and the upper and lower boundaries of boxes represent the median, and the upper and lower quartiles, respectively. The size of the circles represents the number of minutes mangabeys have been observed per home range site

very unlikely that Guinea fowls are not able to use sensory cues and associative learning to locate recent nut-cracking (Shettleworth, 2010), this result suggests that mangabeys were more motivated to approach the nut-cracking events than Guinea fowl. In fact, Guinea fowl, which have relatively small territories, may be sufficiently efficient in finding nuts by systematically traversing their home ranges using visual search strategies. Mangabeys, on the other hand, could more strongly benefit from locating fresh nut remnants from a distance. In addition, the monkey's larger body and brain may be in more need for the highly nutritious nut remnants.

One of the most likely ways mangabeys might detect fresh nut remnants seems to be to follow the sound emitted from nut cracking, which can be heard across several hundred meters (unpublished data K. Janmaat). In fact, the species difference in approach behavior between the three taxa (Table 1) is consistent with the possibility that mangabeys show a higher reliance on auditory cues for food detection, due to their relatively large home range size and the notoriously low visual detection distance in rain forests (Janmaat et al., 2013a). However, we cannot fully rule out the possibility that the monkeys used other sensory cues such as odor of the nutcrackers, visual detection of the nutcrackers, or tracks of the nutcrackers to find the nut remnants. Another alternative explanation of our findings could be that the mangabeys inspected the nut-cracking sites for nut remnants from a distance and then moved away when they failed to see nuts before entering the camera trap detection field, which would then result in a lower visitation rate before a nut-cracking event compared to after a nut-cracking event and would be unrelated to the cues emitted by the nut-cracking itself. We consider this unlikely since the nut remnants are very small and often hidden under leaf foliage and can only be observed from very close to the anvil when the white kernel leftovers become visible (Figure 2). This is supported by observations of the monkeys' foraging behavior, where we see that they often find nut remnants by moving away leaves with their hands. Hence, the monkeys would need to approach within an arm's length of the anvil in order to see that nothing is there, which would trigger the camera traps. In addition, the lack of nut remnants could then also be visually detected by the other foragers, for which we did not detect a difference in approach frequency before and after a nut-cracking event.

Yet another alternative explanation could be that mangabeys did not use the cues emitted by the nut cracking but simply trail chimpanzees through their home range to scavenge on nuts and therefore are more likely to visit nut-cracking sites after the chimpanzees have left. Although we cannot fully exclude this explanation, we think it is unlikely for the following reasons. First, indications for such a polyspecific association have not been observed within the 30 years of research in the Tai region (McGraw, Zuberbühler, & Noë, 2007). Second, a sooty mangabey's estimated home range size that is only one third of a chimpanzees home range size, which makes a consistent trailing strategy inefficient (sooty mangabeys: 7–8 km^2 (Janmaat, 2006; Shultz & Noë, 2002), mean for Taï chimpanzees: 20.36 km^2 (Kouakou et al., 2011)). Third, chimpanzee predatory behavior would furthermore make it highly unlikely that these monkeys would associate with the chimpanzees for long time periods.

Finally, mangabeys might use their own social networks to find nut remnants. Sooty mangabeys are observed to broadcast twitter-like vocalizations at food sites, after which other mangabeys rush the site (Range & Fischer, 2004; K. Janmaat unpublished data). The use of a social network to locate food resources is also suggested to be used by scavenging vultures (Dermody et al., 2011).

Our study further suggests that the vigilant behavior of mangabeys is higher at chimpanzee nut-cracking sites as compared to other feeding sites. Since, there was overlap between nut-cracking sites of chimpanzees and red river hogs it is possible that the increased vigilance was caused by red river hog presence. However, since aggression from, or predation by red river hogs on mangabeys have not been reported so far, we consider this unlikely. Another potential explanation of the observed difference in vigilance levels between the two types of sites could be that at nut-cracking sites food was more clustered than at other feeding sites. This could in turn have resulted in higher rates of competition and thus social vigilance at nut-cracking sites, which is a topic for future studies.

An elevated level of vigilance can indicate a higher perceived landscape of fear (Campos & Fedigan, 2014; Dupuch et al., 2014; Lima et al., 1985; Périquet et al., 2012). The elevated level of vigilance during scavenging is therefore consistent with the possibility that the mangabeys encounter a trade-off between an opportunity to gain a high amount of "free" energy and increased predation risk.

Due to the poor quality of the images produced by the cameras we were unable to identify the mangabeys to an individual level. This created a potential pseudoreplication problem, since several observations might be accounted for by the same social group or individual. This is more likely to have occurred for mangabeys, which have larger home ranges than Guinea fowl and squirrels. One approach we used to mitigate this problem was by only assessing the presence of foragers for each nut-cracking event, rather than considering each individual recorded by camera-traps as a separate observation. Furthermore, mangabeys visits to nut-cracking sites were well distributed across a large area. Assuming a typical home range radius of 1.5 km (Janmaat, 2006; Shultz & Noë, 2002), our data involved no less than five different mangabey social groups (see figure S1). Hence, we can confidently conclude that our results are not driven by the idiosyncratic behavior of a single group or a few individuals.

The use of camera traps to systematically study detailed aspects of behavior in wild animals is still restricted to a few studies (e.g., De Moraes, Da Silva Souto, & Schiel, 2014; Estienne, Stephens, & Boesch, 2017; Kühl et al., 2016; Sirianni et al., 2018). Here we took advantage of camera traps to investigate interspecific interactions involving unhabituated foragers. This created an opportunity for us to be the first to confirm that sooty mangabeys scavenge on remnants of nuts cracked by chimpanzees as suggested by unpublished anecdotal observation, but also that mangabeys scavenge on the nuts cracked by red river hogs. Earlier research found that human observers alter the perceived landscape of fear in monkeys (Nowak, le Roux, Richards, Scheijen, & Hill, 2014), as the presence of humans potentially keeps terrestrial predators, such as leopards, at a distance. Our study records vigilance behavior without the presence of human observers, which

potentially results in observations that are more reflective of true animal behavior in comparison with earlier vigilance studies (i.e., Bridges & Noss, 2011). However, the use of camera traps also invoked some problems. Sometimes animals gazed at the cameras, showed a startled behavior towards the camera, or examined the camera up close. This could alter the revisitation of these sites where cameras were placed, as well as their vigilance behavior. Hence, the behavior observed by the camera traps was not entirely unaltered. Future research should therefore set up cameras that do not produce a red light when the animal is being filmed. However, since this behavior would be expected to occur equally at all camera sites we do not think camera characteristics, such as the red light, explain the observed differences in vigilance nor visitation frequencies. In this study, we were most surprised by the low visitation frequency (Table 1) of all three foragers, which complicated the statistical analysis. We argue that the low recorded visitation rate is due to the relative small detection area of the cameras which do not cover the entire area where potential anvils are present (with a mean area of detection of 12.2 m^2 (min = 1.13, max = 34.9; Després-Einspenner, unpublished data). Cameras of higher quality could potentially improve individual recognition and therefore sample size. Other options would be to follow a habituated group of foragers, especially the mangabeys which already showed visitation differences during this study, and to investigate changes in travel directions, in reaction to nut-cracking sounds at distances which the use of alternative sensory cues would be highly unlikely. Alternatively, these observations could be combined with playback experiments of nut-cracking sounds. Such experiments could also reveal if mangabeys use their spatial memory to locate nut-cracking sites, or how they integrate spatial and auditory information (Janmaat, Byrne, & Zuberbühler, 2006; Zuberbühler & Janmaat 2010). This could provide insight into whether mangabeys have a knowledge of the location of nut-cracking sites, if they use this information in combination with auditory cues, and what they would do if auditory information and memory are conflicting. These studies could then fully confirm whether indeed the mangabeys were using the auditory cues to find nut remnants or whether the results were simply a result of them not approaching the site after visual inspection revealed that no remnants were present. Also, one could test if the inspection rate of the nut-cracking sites by the mangabeys is elevated after hearing sounds of nut cracking, or if it is seasonally bound. Such experimental approaches do invoke potential ethical problems concerning the chimpanzees who might interpret the experimental sounds as sounds emitted by strange individuals who entered their territory (pers. obs. K. Janmaat), which should be taken into consideration before applying such an approach.

Nut scavenging is an understudied form of scavenging, as scavenging has been so far primarily studied in carnivorous species (DeVault et al., 2003). With this study, we encourage future research on the extent of scavenging by mangabeys by measuring the amount of nut remnants left by chimpanzees and hogs in order to estimate the potential energy that scavenging can provide in relation to the rest of the mangabeys' daily diet. Coula and panda nuts are extremely nutritious and rich in crude fats (Ban et al., 2016; Boesch & Boesch, 1982). It has been shown that the fluctuations in coula nut availability alter the birth sex ratio of chimpanzees (Kühl, N'Guessan, Riedel, Metzger, & Deschner, 2012). We argue that it is therefore worthwhile to study the effects of these fluctuations on nut scavenging behavior. Nut scavenging not only enabled mangabeys to obtain "free" access to a difficult to open coula nut, but it also enabled them to access fresh panda nut. This nut is too hard to be cracked by mangabeys using their teeth when it is fresh, and chimpanzees need to use heavy stones to open them (Visalberghi et al., 2015). Scavenging therefore provides mangabeys an access to food they otherwise could not eat.

The relation between the mangabey scavengers and the nut-cracking chimpanzees is puzzling. On one hand mangabeys can be infrequently predated on by chimpanzees (Boesch & Boesch, 1989) and we observed clear behavioral fear reactions by (i) anecdotal observation of rapid changes in location in reaction to chimpanzee sounds and (ii) increased vigilance at the chimpanzee nut-cracking sites. On the other hand, we observe the monkeys approaching the chimpanzees up to 5–10 m (pers. obs. K. Janmaat). Similar intriguing prey-predator interactions were reported anecdotally with the gray-cheeked mangabeys (*Lophocebus ugandii*) in the Kibale National Park in Uganda (Janmaat 2006; Zuberbühler & Janmaat 2010). Here, mangabeys were observed to feed together in the same fruiting trees as the chimpanzees, but were also observed to stay at the same spot close to a feeding tree that was occupied by chimpanzees, only to enter after the chimpanzees had left one and half hour later (Zuberbühler & Janmaat 2010; pers. obs. K. Janmaat). In addition, these same mangabeys were observed to chase solitary female chimpanzees out of feeding trees (pers. obs. K. Janmaat; Zuberbühler & Janmaat 2010), but were also predated on by these same chimpanzees (pers. comm. David Watts). Somehow the monkeys' behavior seems to be driven by decisions that are based on contextual knowledge that helps the monkeys to know when they are safe and when they need to be vigilant or move into a safe position, which is an intriguing topic for future studies.

In conclusion, our study shed light on the nature of an understudied foraging behavior—the scavenging of an energy rich rainforest food source—the remnants of cracked nuts, the potential search mechanisms, and trade-offs that are associated with this behavior. Considering the threats that tropical forest and their inhabitants in West Africa face (Craigie et al., 2010; Estrada et al., 2017; Junker et al., 2012) and the endangered and critically endangered status of sooty mangabeys and West African chimpanzees, respectively (Rowe & Myers 2016), we urge future research to further elucidate the exact nature of these fascinating inter-specific interactions before this is no longer possible.

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SUPPORTING INFORMATION

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

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