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ABSTRACT

Territorial threat is costly and variable across context, behavioural flexibility is favoured to maximise any cost/benefit ratio. This is well illustrated in how animals react to familiar or unfamiliar out-group members. In some situations, neighbours are better tolerated than strangers, resulting in a 'Dear-enemy effect'; in other situations, the pattern is reversed, resulting in a 'Nasty-neighbour effect'. Typically, the effects are species-specific traits, although both can also occur within the same species. Here, we investigated wild Diana monkeys of Taï Forest (Ivory Coast) in their reactions to out-group individuals using playbacks of both, familiar and unfamiliar male alarm calls to eagles. We found that groups living in primary forest (high group density, high food availability and low predation pressure) followed a 'nasty neighbour' strategy whereas groups living in secondary forest (low group density, low resources and high predation risk) followed a 'dear enemy' strategy, suggesting that group density, predation pressure and food availability can impact on how hostile behaviour is displayed in non-human primates. Our results confirm a high behavioural flexibility in primate relationships between conspecifics of different identities depending on ecological traits of the habitat.

Key words: *Cercopithecus diana*; dear enemy; habitat quality; nasty neighbour; primary forest; secondary forest.

INTRODUCTION

Territorial behaviour and hostility towards outgroup individuals is widespread throughout the animal kingdom with evidence from insects and crustaceans (Fogo et al., 2019; Langen et al., 2000), birds (Greenwood et al., 1979; Yoon et al., 2012), fishes (Sogawa & Kohda, 2018), reptiles (Bee & Gerhardt, 2001; Husak & Fox, 2003) and mammals (Monclús et al., 2014; Ostfeld, 1990). Responses and strategies differ in species-specific ways that can be further modified by environmental, social or life history factors (Christensen & Radford, 2018).

For species that live in stable territories, two basic strategies have been observed by which individuals interact with their neighbours. First, individuals distinguish between neighbours and strangers and are relatively more aggressive to strangers than neighbours, the 'Dear-enemy effect' (Temeles, 1994). This may be because stranger individuals pose a greater territorial threat than familiar neighbours if they are actively looking for a territory or trying to get access to sexual partners, which is usually not the case for neighbouring individuals (Temeles, 1994). In the extreme case, neighbouring groups may be able to establish friendly social relations with each other, allowing them to reduce energy, time budget and injury costs (Fisher, 1954; Fogo et al., 2019). Second, the alternative strategy is to be more aggressive to familiar neighbours than unfamiliar strangers, the 'Nasty-neighbour effect' (Müller & Manser, 2007). This is expected when resources are limited and intergroup competition is correspondingly high, suggesting that the costs of intergroup hostility can be outweighed by ecological gains (Sanada-Morimura et al., 2003; Wheeler & Fischer, 2012). Here, unfamiliar strangers are less of a threat because they do not constantly compete for local resources, as neighbours do (Briefer et al., 2008).

High conspecific densities can increase conflict in territorial species, not only by limiting access to resources, e.g. space, food and access to partners, but also by increasing resources active defense (Stamps, 1994; Yoon et al., 2002). For example, sand fiddler crab (*Uca pugilator*) males become more aggressive towards their neighbours following a reduction in the space between burrows, produced by an increase in the number of conspecifics (Praat &

McLain, 2006). Aggression between neighbouring groups can also be necessary to obtain resources, for example, dominant and more aggressive black-and-white colobus (*Colobus guereza*) groups have access to more and better quality food in their territory core areas than subordinate groups (Harris, 2006). Another factor that can influence territorial behaviour is predation pressure. LaManna & Eason (2007) experimentally showed that a higher perception of predation risk reduced the length and intensity level of fights for territorial defense in African blockheads (*Steatocranus casuarius*).

In primates, there are considerable inter-species differences in how individuals interact with neighbouring groups and strangers (Crofoot & Wrangham, 2009; Pisor & Surbeck, 2019; Wich & Sterck, 2007). Most primates live in stable social groups and occupy geographically fixed home ranges, typically surrounded by neighbouring groups with which they have frequent encounters (Buzzard & Eckardt, 2009). These intergroup interactions can range from benign to hostile. With overlapping territories, groups may choose to ignore and avoid each other, or they may engage in agonistic behaviour in order to defend it. In some group species such as baboons (*Papio* spp.), neighbouring groups usually avoid each other (Rowell, 1988) while in some more territorial species such as Campbell's monkeys (*Cercopithecus campbelli*), interactions may be more violent. Encounters with unfamiliar migrants also occur regularly, which can have considerable fitness implications for some group members if migrants are motivated to join an existing group or mate with opposite-sex group members (Wilson et al., 2014). Thus, the ability to discriminate between familiar and unfamiliar individuals is likely to be of considerable relevance, something that can only be acquired during intergroup encounters (Müller & Manser, 2007; Van Dyk & Evans, 2007; Wilkinson et al., 2010). Playback experiments have shown that vervet monkeys (*Chlorocebus pygerythrus*) recognize the calls of their neighbours even though they interacted with them only during intergroup encounters (Cheney & Seyfarth, 1982). Similarly, chimpanzees (*Pan troglodytes*) appear to recognise the calls of neighbouring individuals as they respond differently to those compared to the calls of familiar group members or unfamiliar strangers (Herbinger et al., 2009).

In previous research, Stephan & Zuberbühler (2016a) reported that Diana monkeys discriminate familiar from unfamiliar conspecifics by their vocalisations. Moreover, when comparing two populations, they found that groups in Taï Forest (Ivory Coast) generally followed a Nasty-neighbour strategy (males responded significantly faster to familiar alarm calls) whereas groups on Tiwai Island (Sierra Leone) showed a Dear-enemy effect (males emitted significantly more call sequences towards unfamiliar male's alarm calls). These results indicate that groups respond more frequently and aggressively to familiar groups during intergroup encounters in Taï Forest, suggesting that intergroup competition was higher than in Tiwai Island. Although the two field sites are about 500km apart they used to be part of a continuous forest habitat, the Upper Guinean forest belt, until at least the 1900s (CILSS, 2016; Parren & Graaf, 1995). Correspondingly, the remaining Diana monkey populations show no differences in social organization (one reproductive male and several adult females with their offspring; (Buzzard & Eckardt, 2009; Oates et al., 1990; Todd et al., 2008), home range size: 0.5-1.0 km^2; (Coye et al., 2015; Höner et al., 1997; Whitesides et al., 1988; Zuberbühler, 2000)) and other socio-ecological parameters (female philopatry and bondedness; (Buzzard & Eckardt, 2009)). Both study sites were subject to heavy logging activities in the 20th century, but Tiwai Island has been more affected resulting in an exclusively secondary forest habitat characterized as a mosaic of degenerated ecosystems (Whitesides et al., 1988) whereas Taï Forest is characterised by a mix of primary and secondary forest (Guillaumet & Adjanohoun, 1971).

In Taï forest, Diana monkeys are confronted with various predators (crowned eagles: *Stephanoaetus coronatus*, leopards: *Panthera pardus*, chimpanzees: *Pan troglodytes* and humans: *Homo sapiens*), and have developed adaptative responses to predation pressure like vigilance, mobbing and temporary cryptic behaviour. Among these predators, crowned eagles are the only one that is abundant in both primary and secondary forest in the Taï forest (Shultz & Thomsett, 2007; Shultz, 2008). They are ambush predators and their hunting success is considerably reduced once they are detected in the surroundings (Shultz & Thomsett, 2007). Group living animals can reduce their risk of predation by either live in a high group density or having heterospecific associations (Höner et al., 1997). Thus, Diana monkey groups living in high densities and forming more heterospecific associations are more likely to detect a predator and less likely to be targeted during an attack.

Here, we followed up on the previously documented behavioural flexibility of Diana monkeys towards their neighbours, with a playback experiment to test whether differences in interacting with neighbours is also present at a local scale in Taï Forest. Although the preferred habitat of highly frugivorous Diana monkeys is the primary forest (Booth, 1956; Groves, 1985) they have been observed in secondary forests (Bourlière et al., 1974), logged forests, farm bush (Davies, 1987) and newly cleared farmland (Jeffrey, 1974). On Tiwai Island group densities are significantly lower in secondary than primary forests (0.7 groups/km^2 vs. 2.5 groups/km^2; (Fimbel, 1994)), most likely because of the lack of large trees, which has a pronounced negative impact on Diana monkey densities (Bourlière, 1985). Therefore, we expect that, within the same population, Diana monkeys living in different types of forests use different strategies to interact with their neighbours. In particular, as primary forest areas contain high group densities of Diana monkeys and lower predation risk by crowned eagles, we generally predicted behaviour consistent with a Nasty-neighbour strategy, whereas we predicted the opposite, i.e. a Dear-enemy effect, for secondary forest areas where intergroup competition is lower and crowned eagle predation pressure is higher.

MATERIALS AND METHODS

Study site

The study was carried out in the Taï National Park, located in Western Ivory Coast (6º20'N to 5º10'N and 4º20'W to 6º50'W) from January to March 2020. Different categories of forests can be found in Taï National Park. The main type is the primary forest, a moist evergreen ombrophilous forest, which is characterized by a large number of tree species. On the other hand, secondary forest is denser with a large number of lianas and smaller trees (e.g., *Anthocleista nobilis* and *Musanga cecropioides*) and a general lack of tall emergent trees of 40-60m (e.g. *Diospyros spp*. and *Tarrietia utilis*). Transitions between primary and secondary forests are graded, due to several stages of regeneration towards mature primary forest. The two types of forest differ in their structure but also in their vegetation composition and quality (Guillaumet & Adjanohoun, 1971). Therefore, food resources (fruits, leaves, and insects) vary from one forest patch to the next, as well as other factors of the habitat such as the stratification, the density, the size, and the nature of the vegetation (Bourlière, 1985). Hence, the differences between these surroundings may have a direct impact on primate distribution and behaviour.

Subjects

The studied groups consisted mostly of non-habituated Diana monkeys (26 of 29 groups in primary forest and all 7 groups in secondary forest were not habituated to human presence), however, the experimenters were careful not to be detected by the monkeys during each trial. Each group was recognized and identified by its estimated size, territory location and polyspecific association composition. Sometimes it was possible to additionally confirm the identity of the group by the identification of the adult male using individually distinct physical features (e.g. scars, ear notches, or broken fingers or tail). Finally, a minimum of 6 GPS points (7.35 ± 1.92) were collected for each group over several days, every time it was seen and identified, as a proxy of the area used by the group one month prior to the study period. When it was not possible to unambiguously identify a group (e.g. encounters of a group in an overlapping area between neighbouring groups), we postponed the playback experiment to another day and did not include its location in the estimation of the groups used area.

Diana monkeys loud alarm calls

One of the most distinctive characteristics of Diana monkeys is their vocal behaviour. Males spend most of their time in the periphery of the group and regularly produce acoustically distinct loud alarm calls to predators, such as crowned eagles (*Stephanoaetus coronatus*) (Fig.1) or leopards (*Panthera pardus*), but also to non-predatory disturbances (e.g. fall of a tree) (Zuberbühler et al., 1997); a strategy that may also have a social function in surveying potential rivals (Gautier & Gautier-Hion, 1983). They propagate over long distances of nearly

1 kilometre within dense forest, much beyond the immediate group, suggesting calls function not only to communicate to local group members but also to distant conspecifics as part of a resource defence strategy; calling is often contagious, with males responding to each other's calls (Zuberbühler et al., 1997; Zuberbühler, 2002). A more recent study (Stephan & Zuberbühler, 2016a) shows that discrimination of alarm calls based on familiarity with the caller is a general cognitive ability of Diana monkeys. Thus, these loud alarm calls not only encode information about the type of event, but also the familiarity with the emitter, suggesting that two types of information can be transmitted by the same signal. As eagles are ambush predators, their hunting success relies on surprise. Once their presence is detected, they usually abandon predation to find less alert individuals (Zuberbühler et al., 1999). Consequently, the predator information encoded in these alarm calls does not imply an immediate threat since at the moment the alarm call is given, the predator is already gone. Therefore, the salient information that remains is the identity of the caller (Stephan & Zuberbühler, 2016a).

Despite the fact that intergroup encounters in Diana monkeys are rare, it is not uncommon to see intense agonistic interactions between groups when competing for territory occupancy (Buzzard & Eckardt, 2009). During these agonistic encounters, males produce loud alarm calls, approach and chase the intruder and adopt a vigilant behaviour. A similar response to that elicit by crowned eagles.

Experimental design

Male alarm calls were obtained by playing back two different recordings of eagle shrieks to wild groups of Diana monkeys. We only used eagle-related stimuli because eagle alarm calls are generally more common than leopard alarms and because leopards supposedly rarely venture into the secondary forests near the park border (Jenny, 1996). As a consequence, subjects either heard a familiar neighbour's or an unfamiliar stranger's eagle alarm calls. Unfamiliar males' calls were recorded from non-neighbouring males, at least 2km from the target male's current location, which corresponds to twice a home range diameter (Zuberbühler et al., 1997). Playback stimuli were edited such that each consisted of three alarm call sequences separated by 5s of silence. Each stimulus served in two different conditions, either as eagle alarms from a familiar and an unfamiliar male. From the available master recordings, we selected exemplars for further editing if they were free from overlap with other individuals' calls (conspecific or other primate species). For background bird and insect sounds, we applied bandpass filters provided this did not affect the acoustic structure of the male alarm calls. All recordings used as playback stimuli were of good recording quality, i.e., high signal-to-noise ratio and recorded at close distances from 10 to 20 metres. All records were edited, normalised and analysed with Audacity 2.0.6.0 and Raven 1.4 software.

Data collection

We carried out playback trials on N=29 males in primary forest areas and N=7 males in secondary forest areas. We used a total of N=45 loud alarm calls as playback stimuli, N=37 calls were used only in one trial, N=6 calls were used in two trials and N=2 stimuli used more than twice (the first one was used in 4 trials and the second one in 5 trials). We ensured that the same stimulus was not played more than once within a radius of 500m during the same week to prevent habituation effects. Male subjects were tested twice, once in the neighbour and once in the stranger condition (primary forest: N=15 males; secondary forest: N=7 males); another N=14 primary forest males only heard neighbouring alarm calls (N=3) or only stranger alarm calls (N=11).

Two experimenters carried out each playback trial. First, the group was located by auditory cues. Then, experimenter 1 silently approached the group to a distance of 10-15m, while experimenter 2 positioned the playback equipment around 20-50m away from the group, out of sight of individuals. As Diana monkeys are arboreal primates, to better emulate natural conditions and to decrease attenuation by vegetation, the speaker was positioned on elevated places, such as trunks of fallen trees or small hills (Fischer et al., 2013; Zuberbühler et al., 1997). Before each trial, the group was observed for 15 min prior to starting the playback to ensure there were no external stimuli modifying their behaviour. We proceeded to broadcast the playback stimulus if no alarm calls were produced during this time period, neither by the focal male or any other conspecific or hetero-specific. Once the stimulus was played, the male's vocal response was recorded until he stopped alarm calling for at least 2min but no more than 10min. We excluded all trials from analysis if other monkey species started alarm calling before the focal Diana monkey group.

We coded the following vocal and locomotor variables on the focal male (Spehar & Di Fiore, 2013): latency from playback start to first call response, number of calls, number of call sequences, average call duration, total duration of calls emitted, mean interval between call sequences, total interval between call sequences, approach behaviour and response within the first ten seconds (Table A1). Approach behaviour was the only response registered in real time during the trials; all the other variables were extracted from audio recordings in the laboratory. Moreover, whenever possible we noted whether focal male approached or moved away from the location of the speaker, by keeping track of him either visually or by substrate noise created by his movements. Finally, we estimated the group size when it was possible, identified all other monkey species present, and registered their vocal responses.

All stimuli were broadcasted using an Apple iPod touch digital player connected to an AER alpha speaker amplifier. We used Audacity 2.0.6.0 to edit the playback stimuli, and a Dostmann MS85 (Dostmann) amplitude level meter to adjust the sound level. Absolute amplitude levels of the different stimuli variated between 102–107 dB(C), measured at 50 cm from the speaker, to match natural males' loud calls characteristics. Vocal responses were recorded with a Sennheiser ME67 directional microphone and a Marantz PMD 661 solid-state recorder (44.1 kHz sampling rate, 16 bits amplitude resolution, and stored in wav format). All acoustic parameters were manually extracted using Raven 1.4 software.

Analyses

To investigate whether the familiarity of a simulated intruder had an impact on Diana monkey males response in different habitats, we used a series of Generalized Linear Mixed Models (GLMM) (Bolker et al., 2009) fit by maximum likelihood and Laplace approximation using the 'glmer' function (in R lme4 package) based on 9 response variables (Table A1). To reduce manifold testing, redundancy and correlations between variables, we carried out a Factor Analysis utilizing the 'factanal' function (in R psych package) and chose the variable with the most grounded stacking from every one of the four coming about factors (Factor 1: Number of call sequences; Factor 2: Latency; Factor 3: Average call duration; Factor 4: Mean interval between call sequences) (Table A2). We tested these four variables as response variables in four separated models. We included the familiarity (i.e. familiar, unfamiliar) and the type of forest (i.e. primary, secondary) as fixed factors. The used stimulus was taken as random factor to account for repeated measurements. After checking for over-dispersion. We used different laws in the GLMM depending on how our data were distributed. We applied a GLMpoisson model for continuous variables (factor 1), while a GLMgamma model was used for temporal data (factor 2) and a GLMgaussian model for transformed data normally distributed (factor 3), finally a GLMbinomial-negative model was constructed for continuous decimal variables (factor 4). Spatial autocorrelation was tested for each model and when an effect was detected it was corrected in the model. Finally, for each model created, we verified that the difference in sample size had no impact on the results obtained using the 'PermTest' function (in R pgirmess package) and the 'Anova' function (in R car package) performing a type II ANOVA Wald Chi-Square Tests.

To test the significance of the fixed factors and their relations, we used the 'Anova' function in each model, performing a type III ANOVA Wald Chi-Square Tests. Originally, all explanatory variables and interactions involving the 'Familiarity' and 'Forest' factors were integrated into the full models. Then, insignificant interactions were removed to simplify the model (Engqvist, 2005). Finally, as post hoc analyses, we used Tukey's test with "TukeyHSD" function (in R multcompView package). All statistical analyses were performed using R Studio v. 3.6.1. The significance threshold α was set at 0.05.

Estimating densities

During each group encounter, we registered the GPS *points*. We then estimated a minimal sampled area using a 100% minimum convex polygon (MCP) (Mohr, 1947; Hayne, 1949) method for all the groups, which allowed us to compare group densities between forests. We calculated a minimal sampled area via ArcGIS Online. To estimate the number of groups per km^2 we used the following formula:

$$\text{Number of groups/km}^2 = \text{Number of groups} \div \text{Surface area (km}^2\text{)}$$

(formula 1)

RESULTS

Group densities and used area

We sampled a minimal area of 3.78 km^2 in the primary forest and 1.6 km^2 in the secondary forest (using MCP). Within these areas, we tested 29 and 7 Diana monkey groups, respectively (Fig. A1), suggesting group densities of 7.7 and 4.4 groups per km^2 in primary and secondary forest, respectively, an approximate ratio of 1.75 : 1. Moreover, the average areas used one month prior to the study period by groups in the primary and secondary forest were 0.38 ± 0.14 km^2 and 0.41 ± 0.18 km^2, respectively.

Vocal responses

When analysing the number of call sequences in response to playback stimuli, we found a significant interaction between forest and familiarity (χ^2_1 = 8.11, P = 0.004) (Table A3). Moreover, we found that males from secondary forest emitted significantly more call sequences towards unfamiliar than to familiar callers (χ^2_1 = 6.53, P = 0.0105; secondary forest males' number of call sequences given to familiar vs. unfamiliar males: 22.67 ± 6.41 vs. 37 ± 5) (Fig. 2). Furthermore, there was a difference between males of both forest types, with secondary forest males giving more sequences of calls than primary forest males in both familiar (χ^2_1 = 11.17, P < 0.008; number of call sequences given to unfamiliar males by secondary forest males vs. familiar males by primary forest males: 37 ± 5 vs. 10.24 ± 6.45. χ^2_1 = 9.78, P < 0.002; number of call sequences given to familiar males by secondary vs.

primary forest males: 22.67 ± 6.41 vs. 10.24 ± 6.45) and unfamiliar conditions (χ^2_1 = 10.12, P < 0.001; number of call sequences given to unfamiliar males by secondary vs. primary forest males: 37 ± 5 vs. 10.83 ± 2.25. χ^2_1= 10.36, P < 0.001; number of call sequences given to familiar males by secondary forest males vs. to unfamiliar males by primary forest males: 22.67 ± 6.41 vs. 10.83 ± 2.25) (Fig. 2).

After analysing the response latency, we found a significant interaction between forest and familiarity (χ^2_1 = 6.05, P = 0.014) (Table A3). Post hoc test showed that primary forest males responded to familiar males' alarm calls faster than to unfamiliar ones (χ^2_1 = 4.14, P = 0.042; primary forest males' response latency to familiar vs. unfamiliar callers: 16.97 ± 10.91sec vs. 28.96 ± 16.30sec) (Fig. 3). On the contrary, secondary forest males responded to unfamiliar males' alarm calls faster than primary forest males did (χ^2_1 = 3.99, P = 0.046; response latency to unfamiliar males by secondary vs. primary forest males: 8.37 ± 2.8sec vs. 28.96 ± 16.3sec) (Fig. 3).

When analysing the average call duration in response to playback stimuli, we did not find a significant interaction between both factors, type of forest and familiarity (χ^2_1 = 1.77, P = 0.184) (Table A3). However, the average call duration varied from one forest to another (χ^2_1 = 4.76, P = 0.029): primary forest males produced longer calls than secondary forest males (2.06 ± 0.74sec vs. 1.67 ± 0.57sec) (Fig. 4a). Moreover, the familiarity of the simulated intruder had an effect on the call duration emitted by the focal male (χ^2_1 = 6.69, P = 0.01): the playback of familiar males elicited longer calls than the unfamiliar males ones (2.14 ± 0.74sec vs. 1.72 ± 0.62sec) (Fig. 4b).

Finally, the mean interval between call sequences did not differ across different playback conditions (χ^2_1 = 0.64, P = 0.423) (Table A3).

Lack of response:

In the primary forest, ten of the tested males (40%, n = 25) did not respond to the stimulus of calls from unfamiliar males, compared to only one (5.9%, n = 18) ignored stimuli when calls from familiar males were played back (Table 1). In the secondary forest, all males responded to each playback experiment. The results of the exact Fisher's tests with a Yates' correlation indicate that the probability of observing these behaviours in primary forest is significantly lower than to the expected by chance ($\chi^2_1 = 6.52$, $P = 0.011$). Thus, the non-response of Diana monkeys in primary forest when they hear an unfamiliar individual is not random.

Association with other monkey species:

During the playback trials, primary (n=44) and secondary (n=14) forest Diana monkeys were found mostly when associated with other monkey species (95% and 93% of the trials, respectively). Primary forest Diana monkeys associated the most with red colobus (*Procolobus badius*), 88% of mixed groups, while Campbell's monkeys (*Cercopithecus campbelli*) were always present in Diana monkeys' mixed associations in secondary forest. Moreover, secondary forest Diana monkeys formed mixed groups with three or more monkey species 77% of the time, while primary forest Diana monkeys did only in 27% (Table A4).

DISCUSSION

Our results show that free-living male Diana monkeys respond differently to loud conspecific alarms calls (familiar or unfamiliar) depending on the type of forest they inhabit. Within the same population of Tai Forest, Ivory Coast, males responded to playbacks of familiar conspecifics from neighbouring groups in habitat-specific ways. Males living in primary forest responded faster and gave longer call sequences to familiar individuals, whereas secondary forest males gave more calls sequences in response to unfamiliar individuals' calls, suggesting that the habitat, and the intergroup competition that results from it (Stephan & Zuberbühler, 2016a), determines how individuals interact with outgroup conspecifics. A similar pattern has been found in a previous study that compared Diana monkeys from two different study sites, showing that responses to neighbours can vary depending on local circumstances (Stephan & Zuberbühler, 2016a).

In primary forest areas, we found that males responded faster to familiar neighbours than to unfamiliar strangers (Fig. 3) and often (40%) even ignored the calls of strangers (Table 1). We interpreted these two findings as a Nasty-neighbour effect, suggesting that primary forest individuals are highly intolerant to their neighbours and less concerned about unfamiliar strangers. This strategy is relevant in social species where the number of resident groups, and therefore neighbouring individuals, surpass the amount of potential intruders in a given area. In our case, the group density in the primary forest area was higher than in the secondary forest (7.7 vs. 4.4 groups/km^2, respectively), leading to more frequent encounters with neighbouring groups. This is in line with previous research showing that group densities in primary is higher than in secondary forest for Diana monkeys (Fimbel, 1994; Höner et al., 1997). Considering the high group density in primary forest, it is reasonable to assume this habitat is closer to saturation, increasing the pressure to defend territories against encroachment from neighbouring groups. Hence, a vigorously defence of an established territory from surrounding groups seems to be favoured. This strong competition leads to aggressive behaviours towards familiar groups that pose a threat to access to resources. In addition, effective defence can reduce the chances of the intruder returning to the same territory at another time (Christensen & Radford, 2018).

At the same time, the average area used by Diana monkey groups one month before the study (primary forest: 0.38 km^2; secondary forest: 0.41 km^2) and the home range sizes reported on other studies are similar in primary and secondary forests (Coye et al., 2015; Höner et al., 1997; Whitesides et al., 1988; Zuberbühler, 2000), suggesting that primary forest groups have higher rates of intergroup encounters than secondary forest groups. Primary forest groups also have high rates of territory overlap with neighbouring groups, suggesting that high rates of intergroup encounters (0.36 per day) (Buzzard & Eckardt, 2009) are caused by high group densities. Hence, higher accessibility of resources preferred by Diana monkeys (e.g. fruits) in primary than secondary forests (Brearley et al., 2004; Nadkarni et al., 2004; Parry et al., 2007; Schwitzer et al., 2007) will lead to higher group densities which in turn will generate higher rates of intergroup competition and neighbours a constant threat. Unfamiliar stranger males, on the other hand, are possibly considered as less threatening floaters, which are just passing through and hence pose no threat to resource availability. Non-resident males disperse and spend time on their own or in polyspecific groups. These individuals are unlikely to successfully compete for territory usurpation because: (1) Diana monkey males leave their natal group when they reach adulthood. Hence, non-resident males are likely to be inexperienced adults (Cords, 1987), and (2) floater males could have a lower feeding efficiency, be in a lower energetic and physical condition and be more likely outcompete by resident males (Buzzard & Eckardt, 2009). For example, floater ovenbird males (*Seiurus aurocapilla*) have lower body condition indexes compared with resident males due to a reduced access to high-quality food resources (Brown & Sherry, 2008; Winker, 1998). Primary forest Diana monkeys, in sum, perceive neighbouring groups as more threatening in territorial conflict, and show behaviour consistent with a Nasty-neighbour effect.

Conversely, secondary forest Diana monkey males produced significantly more call sequences in response to unfamiliar strangers than familiar neighbours (Fig. 2), which indicated a Dear-enemy effect. This behaviour may be linked to low group density and a subsequent low competition between neighbouring groups (Stephan & Zuberbühler, 2016a). In territorial species, population and group densities have a direct impact on territoriality pressure and active territory defense (Isbell, 1994). Moreover, low group densities decrease the frequency of intergroup encounters, relaxing competition with neighbouring groups. Furthermore, although in general terms primary forest habitats have higher productivity and better quality of resources than those in secondary forest (Bourlière, 1985), Diana monkeys are able to consume a wide variety of fruits and can adapt to changes in food availability (Oates et al., 1990). This diet flexibility allows Diana monkey groups to establish permanent territories in secondary forest without increasing intergroup competition. As a result, secondary forest males are less likely to come into contact with neighbouring groups, experience less territoriality pressure and are less often engaged in aggressive interactions with their neighbours.

Although differences in food availability (and group density) are a plausible explanation for the observed patterns, it is possible that differences in predation pressure were the main cause. Diana monkeys often form mixed groups with other monkey species to reduce the risk of predation (Bshary & Noë, 1997; Höner et al., 1997). Diana monkeys prefer associate with red colobus (*Procolobus badius*), as both species live in large groups and actively form and maintain these associations (Holenweg et al., 1996). Mixed groups benefit from higher number of individuals and sentinels (Bshary & Noë, 1997), which leads to dilution and safety-in-number effects. According to our observations, Diana monkeys and red colobus associated more in primary forest than in secondary forest. Whether this has to do with the availability of red colobus groups or differences in predation pressure by crowned eagles (*Stephanoaetus coronatus*) or chimpanzees would have to be tested. Crowned eagles are certainly a main predator of Diana monkeys (Shultz & Thomsett, 2007) and densities in primary and secondary forests are more or less equal (one pair every 6.5 km^2: Shultz & Thomsett, 2007; Shultz, 2008). With fewer red colobus groups available, secondary forest Diana group may be forced to rely more on neighbouring groups than primary forest groups. In sum, secondary forest males are likely to experience higher predation risk and lower intergroup competition than primary forest males, suggesting that their attitude towards neighbours may be more tolerant than those of primary forest groups.

Another surprising finding in our study was that secondary forest males not only produced more call sequences than primary forest males (Fig. 2) but also that their calls were shorter (Fig. 4a). To a human listener, the eagle alarm call sequences of secondary forest males possessed a more intense quality compared to the eagle call sequences of primary forest males, which consisted of longer calls but fewer call sequences. The only explanation we have for this phenomenon is that males adapt call production to the sound propagation properties of the local habitat (Brown & Waser, 2017; Ey & Fischer, 2009) . In one relevant study, ambient noise, attenuation and signal degradation were higher in riverine forests (comparable to secondary forests) than primary rain forests (Waser & Brown, 1986); especially for sounds with a fundamental frequency below 1 kHz, such as Diana monkey eagle loud calls (Zuberbühler et al., 1997). Whether Diana monkeys are actively trying to compensate differences in acoustic distortion and dissipation in the environment by varying call intensity and duration will have to be addressed by future research (Brown & Waser, 2017).

One last result is that both primary and secondary forest Diana monkeys responded with longer calls (but not longer call sequences) to familiar neighbours than unfamiliar strangers (Fig. 4b). One possible explanation for this finding is that males could be marking familiarity with acoustic cues, which may be of importance for other group members and conspecifics (i.e. males may make their calls longer in response to neighbours to provide cues to conspecifics about the caller identity and familiarity). Primates are particularly good at discriminating and extract information from differences in their vocalization's temporal parameters, like call duration (Benítez et al., 2016; Maciej et al., 2011). Similar findings have been reported in other primates, where auditory cues are linked to assessments of familiarity of other conspecifics (*Mandrillus sphinx*: Levréro et al., 2015; *Macaca mulatta*: Pfefferle et al., 2016).

Loud alarm calls produced by male Diana monkeys are complex signals because they contain different information as predator type and location, and caller identity and familiarity. However, there are different reasons to be confident that the differences in male's reactions, here founded, were caused by the familiarity with the caller and not by the potential predator in the vicinity. First, as eagles are ambush predators who are high likely to leave once detected (Shultz & Thomsett, 2007), by the time a raptor is spotted and an eagle alarm call is given, the predation risk substantially decrease and the salient information that remains is the identity of the caller (Stephan & Zuberbühler, 2016a). Secondly, in Taï, crowned eagles living in both primary and secondary forest are abundant and have the same hunting behaviour (Shultz & Thomsett, 2007; Shultz, 2008). Finally, we used stimuli in which the predator message, i.e. eagle, was constant, while the only condition that consistently changed was the familiarity with the caller. Thus, the opposite patterns founded in both types of forest in response to conspecifics are explained by social familiarity.

In sum, we here show that Diana monkeys adjust their vocal response to conspecific alarm calls depending on the familiarity with the caller in habitat-dependent ways. We found that males living in primary forest areas show behaviours consistent with a 'nasty neighbour' strategy, whereas males in secondary forest areas show behaviours in line with a 'dear enemy' strategy. Differences in intergroup competition due to habitat structure and predation pressure by crowned eagles are likely factors to explain the differences in calling behaviour. Such context dependence has also been found in other species. For instance, Yoon et al (2012) reported a Nasty-neighbour effect in orange-crowned warblers (*Oreothlypis celata*) when breeding density was high, but a Dear-enemy effect in a sparsely populated area. Comparing Diana monkeys from two different locations, Stephan & Zuberbühler (2016a) showed that the combination of low predation/high group density (as in our primary forest scenario) favoured a Nasty-neighbour effect, whereas high predation/low group density (as in our secondary forest scenario) favoured a Dear-enemy effect. This would explain why primary forest males perceive neighbours as more of a threat, and why in secondary forests, the threat of predators outweighs the threat posed by neighbouring conspecifics and may even select for higher tolerance given that neighbouring groups may reduce predation threats.

This behavioural flexibility allows Diana monkeys to optimise their cost-benefit ratios and thus increases their fitness. Since we studied the same population, the most likely explanation is that the observed behavioural flexibility was in response to specific ecological traits of each habitat. It would be interesting to conduct a comparative study of groups of Diana monkeys alone vs. in association with other monkey groups (e.g. *Procolobus badius* or *Cercopithecus campbelli*) to understand how perceived predation risk impacts on perceived intergroup competition. Moreover, the effect of group size on the perceived threat of intruders and territorial defence should be tested to provide additional information on Diana monkeys' habit-dependant intergroup hostility response. Likewise, how familiarity among conspecifics could have different levels of categorization depending on the type of forest, due to particular environmental constraints, should be addressed in more detail in a complementary study. Finally, how seasonal changes in fruit availability impact Diana monkeys' behaviour and competition pressure should be also explored in future studies.

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TABLES

Table 1. *Number of responses and non-responses in primary and secondary forests depending on familiarity*

	Response	No response
Primary forest		
Familiar	17	1
Unfamiliar	15	10
Secondary forest		
Familiar	7	0
Unfamiliar	7	0

Table A1. *Vocal and locomotor variables and definitions*

Variable	Definition
Latency	Time between beginning of stimulus and first vocalization by focal male.
Number of calls	Total number of calls made by focal male.
Number of call sequences	Total number of call sequences by focal male.
Total duration of calls	Sum of the duration of call.
Average call duration	Average length of a call.
Duration between call sequences	Total duration of the silences between each call sequence.
Mean interval between call sequences	Average of the duration of each silence between each call sequence.
Approach behaviour	Approach of the male towards the speaker.
Response within the first ten seconds	Male first response within ten seconds of stimulus.

Table A2. *Factor Loadings of vocal and locomotor variables. The factor analysis was justified as shown by the Kaiser-Meyer-Olkin measure of sampling adequacy (0.71) and the Bartlett test of sphericity (χ^2=342.8, df = 36, P < 0.001).*

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Latency	0.029	**0.986**		
Number of calls	0.895	0.384		
Number of call sequences	**0.917**	0.150	-0.402	-0.223
Total duration of calls	0.842	0.342	0.101	-0.163
Average call duration	-0.201		**0.752**	0.269
Space between two call sequences	0.897	0.186	-0.378	0.113
Mean interval between call sequences			0.201	**0.766**
Approach	0.339	-0.185	-0.131	
Response within the first ten seconds		-0.642		

Table A3. *Influence of predictors variables on behavioural response after the playback experiment.*

Predictor variable	Estimates	SE	Z	P
I. Number of call sequences				
Intercept	2.30	0.10	[a]	[a]
Familiarity (Unfamiliar)	0.04	0.13	0.27	0.790
Forest (Secondary)	0.79	0.16	4.94	**<0.001****
*Familiarity*Forest*	0.53	0.19	2.85	**0.004****
II. Latency				
Intercept	0.16	0.02	[a]	[a]
Familiarity (Unfamiliar)	-0.05	0.02	-3.2	**0.002***
Forest (Secondary)	0.02	0.03	0.88	0.381
*Familiarity*Forest*	-0.09	0.04	2.46	**0.014***
III. Average call duration				
Intercept	2.33	0.16	[a]	[a]
Familiarity (Unfamiliar)	-0.56	0.22	-2.59	**0.010****

Forest (Secondary)	-0.65	0.30	-2.18	**0.029***
*Familiarity*Forest*	0.47	0.35	1.33	0.184
IV. Mean interval between call sequences				
Intercept	1.97	0.10	[a]	[a]
Familiarity (Unfamiliar)	-0.17	0.13	-1.38	0.169
Forest (Secondary)	-0.18	0.18	-1.05	0.293
*Familiarity*Forest*	0.18	0.22	0.80	0.423

[a] Omitted given that there is no interpretable result. () denote the variable level that reflects the estimate when tested against the alternative level: Familiar vs. Unfamiliar, Secondary vs. Primary.

* $P < 0.1$ and ** $P < 0.01$ following Bonferroni correction

Table A4. *Number and size of interspecific associations of Diana monkeys for primary and secondary forests during the trials; and number of times each species was observed in a mixed group with the focal group.*

	Primary forest	**Secondary forest**
Alone	-	1
Diana monkeys + 1 spp.	18	1
Diana monkeys + 2 spp.	13	2
Diana monkeys + ≥3 spp.	12	10
Cercocebus atys	7	6
Cercopithecus campbelli	16	13
Cercopithecus nicitans	3	0
Cercopithecus petaurista	11	11
Colobus polykomos	5	0
Procolobus badius	36	3
Procolobus verus	4	6

FIGURE LEGENDS

Figure 1. *Spectrogram of Diana monkey male response to a playback of crowned eagle shrieks in Taï Forest, Ivory Coast.*

Figure 2. *Box-plot of the number of call sequences to playbacks of familiar (blue boxes) and unfamiliar (yellow boxes) males in both primary and secondary forest of Taï (** $P < 0.01$, *** $P < 0.001$). Horizontal lines indicate medians, boxes indicate data within the 25th to 75th percentiles, and whiskers include values that amount to 1.5 times the height of the box, black circles indicate outliers. The letters above the boxes indicate Tukey's test significance.*

Figure 3. *Box-plot of response latency to playbacks of familiar (blue boxes) and unfamiliar (yellow boxes) males in both primary and secondary forest of Taï. Different letters indicate significant difference levels ($P < 0.05$), horizontal lines indicate medians, boxes indicate data within the 25th to 75th percentiles, and whiskers include values that amount to 1.5 times the height of the box, black circles indicate outliers. The letters above the boxes indicate Tukey's test significance*

Figure 4. *Box-plot of average call duration to playbacks of familiar (blue boxes) and unfamiliar (yellow boxes) males depending on forest (a) and familiarity (b), (* $P < 0.05$, ** $P < 0.01$). Horizontal lines indicate medians, boxes indicate data within the 25th to 75th percentiles.*

Figure A1. *Distribution map of Diana monkeys in Taï forest with polygons created using the MCP method and applied to estimate the minimal sample area in primary (blue) and in secondary (red) forest.*

Figure 1.

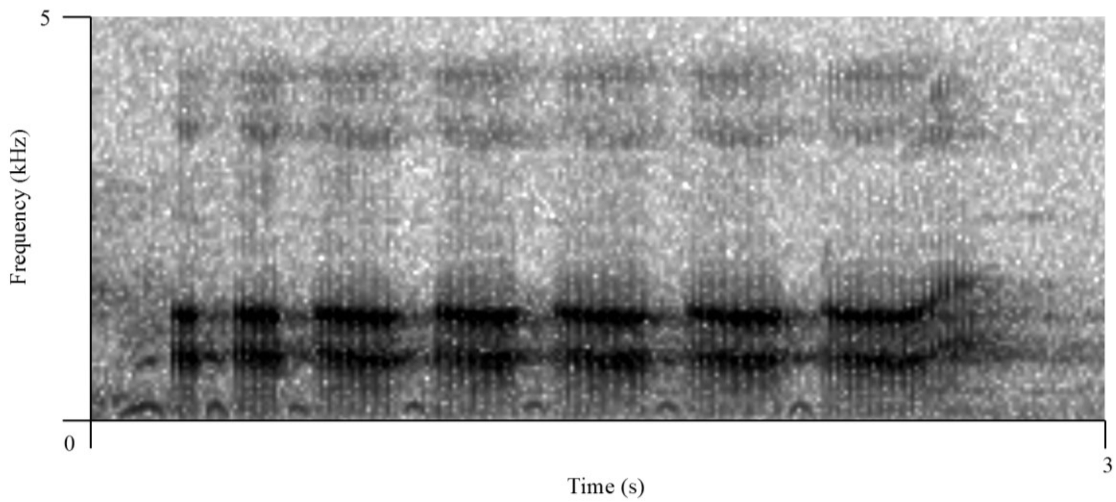

Figure 2.

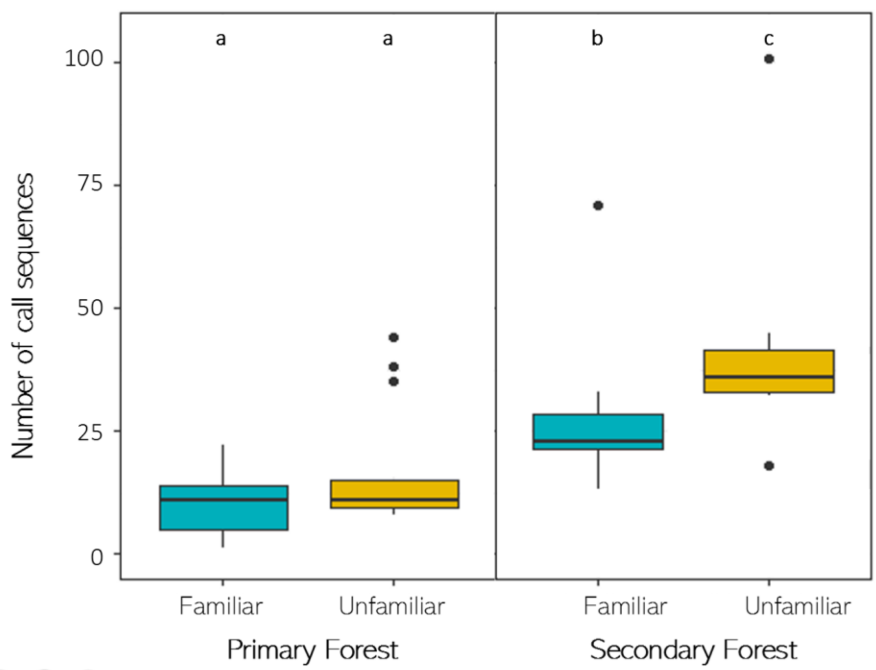

Figure 3.

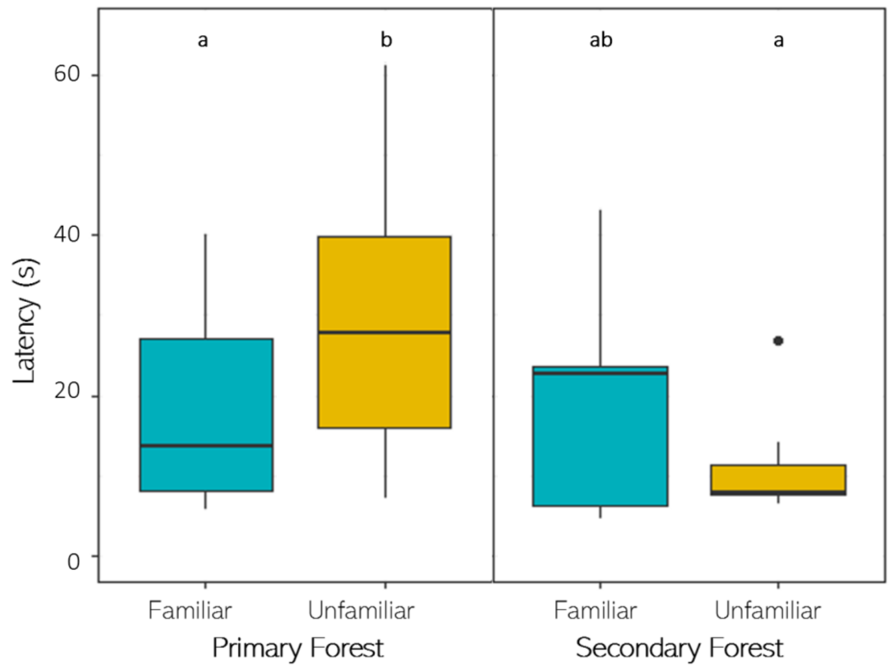

Figure 4.

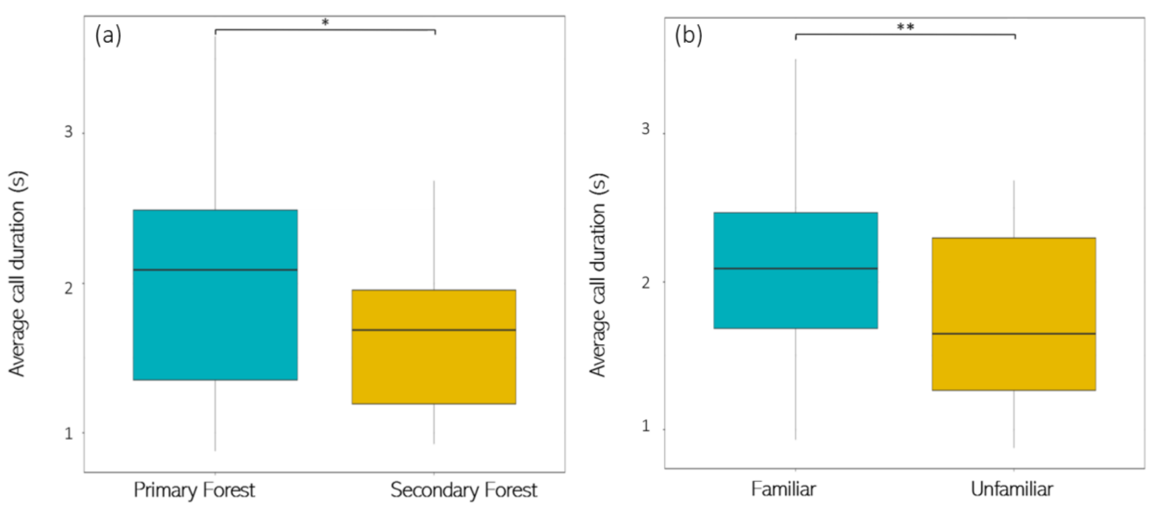

Figure A1.


N
Soubré
Bas-Sassandra
LIBERIA
Legend :
Primary forest monkeys
Secondary forest monkeys
Forest opening