Risk perception of vervet monkeys *Chlorocebus pygerythrus* to humans in urban and rural environments

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ABSTRACT

Like other animals, primates respond to predation using behavioural adaptations. Hence, they should optimise their escape strategy under the risk of predation, and flee at a distance, referred to as flight initiation distance (FID), when the fitness-related benefits of staying are balanced against the costs of escape. However, there is an absence of FID studies in primates. In this study, we used vervet monkeys *Chlorocebus pygerythrus*, a medium-sized African cercopithecoid, as a model species to investigate the influence of environment type (urban and rural), group size (defined as the number of visible neighbours), sex and age on FID when approached by a human. We found significantly shorter FID among urban than rural monkeys; urban individuals delayed their escape compared to rural individuals. We found no relationship between FID and sex and age class, but FID was positively correlated with group size in both settings; urban monkeys live in smaller groups than monkeys in rural areas. As FID and group size are important predictors of predation risk perception in primates, results suggest that, despite probable effects of habituation, vervet monkeys in Uganda adjust their antipredator behaviour when coping with novel environments within human settlements. Our findings are consistent with some previous studies of risk perception in animals, and indicate that FID could be used as an alternative measure for predation risk in primates.

1. Introduction

Like other animals, primates have to cope with predation (Cheney and Wrangham, 1987; Stanford, 1995; Karpanty, 2006; Bianchi and Mendes, 2007; Gursky and Nekaris, 2007; Strier, 2016). Predation represents a substantial selective force that shapes the evolution of anti-predator strategies in prey, including primates (Isbell, 1994; Cowlishaw, 1997; Hill and Dunbar, 1998; Fichtel and Kappeler, 2002; Stanford, 2002; Hart and Sussman, 2005; Gursky and Nekaris, 2007). Key antipredator strategies, such as vigilance, alarm calls, active defence, escape, and inter-specific associations are all affected by predator type, predator distance, and the location of the predator (Isbell, 1994; Fichtel and Kappeler, 2002; Shultz and Noë, 2002; Stanford, 2002; Oliveira and Dietz, 2011; Murphy et al., 2013; Strier, 2016).

However, direct measurement of the impact of predation is difficult because observations of predation events are rare (Terborgh and Janson, 1986; Isbell, 1994; Gleason and Norconk, 2002; Enstam, 2007). Instead, predation pressure may be estimated indirectly via predation

risk, defined as "the frequency with which groups (or individuals) are subjected to predator attacks" and/or "animals' own perception of the likelihood of being subject to an attack by a predator" (Hill and Dunbar, 1998). Perceived risk of predation is also defined as 'fear' (Blumstein, 2014) and the constant threat of attack by a predator may have more profound consequences on animal behaviour than predation events (Lima and Dill, 1990; Gleason and Norconk, 2002; Blumstein, 2014). Indeed, observations from field studies indicate that primate populations of various species adjust their behaviour according to the perceived risk of being preyed upon (Cowlishaw, 1997; Hill and Lee, 1998; Lycett et al., 1998; Shultz and Noë, 2002; Croes et al., 2007; Enstam, 2007; Bettridge et al., 2010; Oliveira and Dietz, 2011).

Animals presumably have an ability to judge the actual risk of predation and make decisions that influence their risk of becoming prey (Lima and Dill, 1990; Frid and Dill, 2002). According to optimal escape theory, prey animals should have been selected to optimise their escape strategy, making a trade-off between the fitness-related benefits of staying and the costs of escaping (Ydenberg and Dill, 1986; Stankowich

and Blumstein, 2005; Blumstein, 2006; Cooper, 2009; Díaz et al., 2013; Uchida et al., 2016). The distance at which an animal starts to flee from an approaching predator is referred to as flight initiation distance (hereafter FID). FID is commonly used as a metric to reliably quantify risk taking in animals because it reflects these trade-offs (Ydenberg and Dill, 1986; Stankowich and Blumstein, 2005; Díaz et al., 2013) and also has high individual consistency in similar contexts (Carrete and Tella, 2010). Indeed, escape distance has been shown to be influenced by multiple factors, including predator type (including their size and speed), the prey's past experience with the predator, distance to refuge, degree of crypsis, reproductive state, body and group size, as well as sex and age (Stankowich and Blumstein, 2005). Among vertebrates, FID has been studied in numerous animal groups, but has been mainly utilised to study predation risk in lizards (Capizzi et al., 2007; Cooper, 2009; Cooper et al., 2009; Grolle et al., 2014) and birds (Blumstein, 2006; Møller and Ibáñez-Álamo, 2012; Díaz et al., 2013). In mammals, the majority of studies have been performed in rodents (Dill and Houtman, 1989; Engelhardt and Weladji, 2011; Uchida et al., 2016), ungulates (reviewed by Stankowich 2008) and, to a lesser extent, carnivores (Karlsson et al., 2007).

FID studies are still absent in many mammal groups, including primates. Primates are good candidates for studying FID because of their abilities to distinguish between different fear levels within an array of antipredator strategies (Seyfarth et al., 1980; Cowlishaw, 1997; Fichtel and Kappeler, 2002; Murphy et al., 2013). However, primates have also developed cognitive capabilities (Reader and Laland, 2002) and their ability to quickly adapt to new challenges and environments means that they can readily habituate to humans when they come into contact with them (Else, 1991; Sillero-Zubiri and Switzer, 2001; Hill, 2005; Jack et al., 2008). Similarly, other larger-brained animals, such as birds, incorporate their past experience with humans in their assessment of them as potential predators (Tarjuelo et al., 2015), as well as a myriad of other factors (e.g., directness of approach, approach speed, head orientation and presence of eye contact) (Bateman and Fleming, 2011; Møller and Tryjanowski, 2014). Even so, we expect large-brained primates to be even more sensitive in assessing predator threats, hence, FID studies in primates could provide additional insights into behavioural adaptations and evolutionary mechanisms that underpin optimal escape theory.

In recent decades, the permanent and on-going expansion of human settlements responsible for the conversion of natural habitats to urban areas (Grimm et al., 2008) has led to an increasing number of studies focused on the effects of urbanization on risk taking in wild animals (Engelhardt and Weladji, 2011; Møller and Ibáñez-Álamo, 2012; Díaz et al., 2013; Grolle et al., 2014). Species successfully inhabiting urban areas have to cope with changed ecosystem patterns and processes, including altered predation risk and human presence, by adjusting their antipredator strategies to local settings. Indeed, one of the most consistent patterns in risk taking is that urban animals have much shorter FID (i.e., the individual delays fleeing from the risk) than those from areas with decreased human exposure. This effect has been widely attributed to animals' habituation to humans (typically associated with non-lethal interactions) and a relaxed predation risk around human settlements (e.g., as observed in reptiles, mammals and birds) (Grolle et al., 2014; Díaz et al., 2013; Engelhardt and Weladji, 2011; Chapman et al., 2012).

Several non-human primate species, including rhesus macaques *Macaca mulatta* (Singh, 1968), Hanuman langurs *Semnopithecus entellus* (Waite et al., 2007), chacma baboons *Papio ursinus* (Hoffman and O'Riain, 2012), crab-eating macaques *M. fascicularis*, and Barbary macaques *M. sylvanus* (Klegarth et al., 2017), have successfully invaded urbanized areas. Many of these so-called 'weed species' thrive on their association with humans, e.g. exploiting human resources (Lee and Priston, 2005). In fact, interactions with humans can buffer non-human primates against the negative impact of environmental factors (Richard et al., 1989; Waite et al., 2007). For example, primates that associate

with humans generally live at higher densities (Brennan et al., 1985), exhibit greater levels of intra-specific aggressivity (Singh, 1968; Brennan et al., 1985), spend less time feeding and more time grooming (Jaman and Huffman, 2013), and have decreased levels of stress hormones over time, when encountered by observers (Jack et al., 2008). This evidence suggests that primates alter their behaviour when they share sites with humans.

Traits such as group size, sex, and the age of an individual have also been shown to affect perception of risk in primates (Alexander, 1974; van Schaik et al., 1983; Dunbar, 1988, 1996; Hill and Dunbar, 1998; Hill and Lee, 1998; Lycett et al., 1998; Stanford, 2002; Bettridge et al., 2010; Murphy et al., 2013). The effect of group size on fearfulness has often been tested in different animal groups, but empirical studies have yielded mixed results (Stankowich and Blumstein, 2005). Studies on the relationship between predation and primate grouping behaviour have similarly revealed some interspecific discrepancies (Alexander, 1974; van Schaik et al., 1983; Cheney and Wrangham, 1987; Isbell, 1994). For instance, a positive relationship between predation risk and group size has been found in some cercopithecoid primates (van Schaik et al., 1983; van Schaik and van Noordwijk, 1985; Hill and Lee, 1998), but there was no such effect of group size in arboreal Thomas' leaf monkeys *Presbytis thomasi* or lar gibbons *Hylobates lar* (van Schaik et al., 1983). This suggests that, beside a species-specific component of antipredator behaviour, primates also possess an intraspecific flexibility in adjusting their group size with respect to local environmental settings (Dunbar, 1988, 1996; van Schaik et al., 1983; Singh and Vinathe, 1990; Stanford, 1995; Bettridge et al., 2010; Pasternak et al., 2013).

In their meta-analysis, Stankowich and Blumstein (2005) revealed no consistent cross-taxon effect of sex and age on FID among vertebrates, and at the species level, relationships varied widely. In some primates, sex differences in vigilance and antipredator responses have been observed, with males being typically more vigilant and able to detect potential predators sooner than females (Cheney and Wrangham, 1987; van Schaik and van Noordwijk, 1989; van Schaik and Hörstermann, 1994). Resident adult male blue monkeys *Cercopithecus mitis,* for example, have been shown to scan the area for the presence of predators and defend group members by emitting alarm calls (Murphy et al., 2013). The effect of sex on flight distance may also be expected in sexually dimorphic species in which longer FIDs are predicted in the more conspicuous sex, such as those with larger body size or more prominent colouration pattern, because such individuals are more likely to attract the attention of predators (Capizzi et al., 2007). Alternatively, the larger sex (usually males) is more likely to be more dangerous to a predator and therefore potentially more able to defend itself and the group, possibly resulting in decreased FID (Leutenegger and Kelly, 1977; van Schaik and van Noordwijk, 1989). Sex-dependent risk perception in primates may also be associated with an individual's reproductive state, for instance in humans, risk taking is lower in females with children, compared to males (Wang et al., 2009). Similarly, in other mammals, such as Thomson's gazelle *Eudorcas thomsonii*, females caring for their young have longer FID than males (Walther, 1969).

As the results of previous predator avoidance studies in primates are mixed, it might be informative to use FID to explore the effect of risk perception in primates living in different environments and how this might correlate with individual traits. Here, we used vervet monkeys *Chlorocebus pygerythrus*, as a model species to investigate the relationship between FID when approached by a human and environment type (urban and rural), group size, and sex and age. This primate is a medium-sized, sexual dimorphic African cercopithecoid (Turner et al., 1997) that lives in groups of variable size (reviewed by Pasternak et al., 2013) and has successfully invaded urban areas. This is the first study to investigate differences in FID in primates.

2. Material and methods

2.1. Study site

Data was collected throughout February 2016 in eight sites in Uganda. The country is located on the East African Plateau, lying mostly between latitudes 4°N and 2°S, and longitudes 29° and 35°E. Observations were carried out in urban parks of big cities: Kampala (N0°18′47″, E32°27′33″), Entebbe (N0°3′10″, E32°25′28″), Masaka (S0°20′17″, E31°43′4″) and Hoima (N1°25′56″, E31°20′2″) (hereafter called urban sites) and in peripheries of the national parks and agricultural areas around (hereafter called rural sites): Murchison Falls National Park (N2°12′44″, E31°40′42″), Kibale National Park (N0°29′10″, E30°23′15″), Queen Elizabeth National Park (S0°9′51″, E30°1′5″), and Bwindi Impenetrable National Park (N0°20′45″, E25°47′06″). In urban parks, humans (i.e., tourists) mainly interact with monkeys by attracting them with food; during data collection, negative interactions between human and monkeys were not observed. Interactions between humans and monkeys in rural sites range from observation at a distance by tourists and rangers in national parks (i.e., minimal human interaction; food provisioning by tourists was prohibited in the national parks visited in this study), to hostile encounters from farmers protecting crops. In fact, in rural sites, the majority of intentional interactions between humans and monkeys observed in this study had a negative impact on the monkeys. It is noteworthy that, although human density is typically higher in urban areas, > 70% of Uganda's population live in rural residences (Uganda Bureau of Statistics and ICF, 2017). Rural populations of monkeys therefore frequently encounter people because human population density is so high (estimated at > 200 inhabitants/km^2) (http://worldpopulationreview.com/countries/uganda-population/). Hence, the main difference in human–monkey interactions seems to be the way in which people from urban and rural sites treat monkeys. We consider that, even if differences in levels of habituation exist between urban and rural populations of monkeys, negative interactions with humans may be considered analogous to predation risk by the natural predators of monkeys. Furthermore, although human–monkey interactions differ from site to site, all observations at rural sites (even within borders of national parks) were carried out in farmlands, which are potentially dangerous to monkeys in terms of human–monkey interactions.

2.2. Data collection

All FID data were collected by one of the authors (PT) with experience studying FID, removing potential bias caused by a multiple collector effect. FID data were collected using a standard procedure (e.g. Blumstein, 2006; Møller and Ibáñez-Álamo, 2012; Díaz et al., 2013). Briefly, a focal monkey individual was approached directly at normal walking speed; eye contact was maintained during this phase. FID was estimated as the number of approximately one-meter long steps, from the point where the collector was located, to the point where the monkey started to flee. As such, a longer FID is associated with an individual fleeing earlier when approached by human.

We examined only individuals positioned on the ground and in open space (< 20 m from cover such as tree or building) to avoid the potential effect of vegetation structure or presence of cover on their risk perception (van Schaik et al., 1983). We also ensured focal monkeys showed no signs of distress behaviour; thus mainly resting individuals or individuals engaged in foraging and grooming were sampled. Since the response of individuals in a group may depend on the responses of the most risk-sensitive individual, when approaching a group of monkeys, FID from only one randomly chosen, focal individual was measured (i.e. there were no replicates for the same group). Moreover, when a focal monkey was selected (at a long distance using binoculars), the researcher waited 10 s before approaching the focal individual. All focal monkeys were approached wearing the same (i.e., standardized)

outdoor clothing with no bright colours. Altogether, we collected FIDs for 83 vervet monkey individuals with 50 measurements from urban and 33 from rural sites.

Several previous studies have shown that FID is correlated with starting distance, resulting in problems with collinearity (e.g. Blumstein, 2006, Díaz et al., 2013). We tried to eliminate this problem by performing the measurements by approaching urban monkeys from > 75 m away. In rural areas, the approach distance could be up to approximately 200 m due to the monkeys' greater vigilance.

Group size was defined as the number of visible neighbours and was calculated as the number of individuals present in the group at a maximum distance of 10 m between neighbours. To minimize the effect of variation in visibility, we collected data only for monkeys located in open habitats such as the grassy areas of open parks in urban locations and semi-open savannah, edge of villages, arable fields and roads in rural locations. For longer distances (usually > 75 m), the number of individuals in each group was recorded using binoculars prior to FID measurements to avoid bias, in the case that some (non-focal) individuals in the groups escape earlier than others. Sex and age (adult/juvenile) of the focal individual was identified using a field guide (Petter and Desbordes, 2013).

2.3. Statistical analysis

Effect of site type, group size, and sex–age on FID was explored using generalized linear models (GLM) in which FID was the dependent variable, while site type, group size, and sex–age were used as the predictors. All FIDs were ln-transformed before analyses to achieve distributions that did not differ from normality. We used an individual-based approach here with each individual representing a single point in analysis. All interactions between site type, group size, and sex–age were non-significant, we therefore removed interactions from the final model. Adjusted deviance explained by the final model was calculated using "Dsquared" function in *modEvA* package (Barbosa et al., 2014). Normality of model residuals was checked by Shapiro–Wilk test; we revealed no violation of the assumptions of normality (W = 0.991, p = 0.823).

To check for collinearity between predictor variables, we examined the variance inflation factors. In general, a variance inflation factor higher than four is considered to be an indication of possible collinearity, and a variance inflation factor higher than ten indicates strong collinearity (Neter et al., 1996). Our analysis revealed very weak collinearity between predictors (in all predictors < 1.28). This procedure was carried out using the "vif" function in *car* package (Fox and Weisberg, 2016).

Differences in group size between urban and rural populations of monkeys were tested with a two-sided *t*-test. Relationships between FID and groups size for urban and rural sites was visualized using the *visreg* package (Breheny and Burchett, 2016). Significance was set at p < 0.05 for all tests. All analyses were conducted in RStudio 0.98.1103 (R Core Development Team, 2014).

3. Results

The GLM model (explaining 79.7% of the variation present in the data, Table 1) found strong significant differences in FID between urban and rural populations of monkeys (raw mean (m) ± SD = 3.62 ± 3.02 for urban and 49.55 ± 39.81 for rural monkeys, respectively) (Fig. 1). Despite monkey group size (i.e., the number of visible neighbours) being significantly smaller in urban than in rural environments (t-test: t-value = −3.032, df = 44.889, p = 0.004; urban: mean ± SD = 3.94 ± 3.66, rural: mean ± SD = 7.79 ± 6.66), FID was significantly positively correlated with group size in both settings (Fig. 2, Table 1). There was no effect of sex and age on FID (Table 1).

Table 1

Generalized linear model (GLM) examining the effect of environment type (urban/rural), group size, and sex–age (female, male, juvenile) on flight initiation distance (FID) of vervet monkeys. Boldface indicates statistical significance.

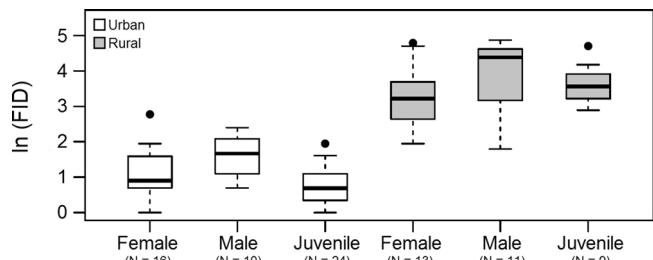| Variable	Estimate ± SE	t-value	p
Intercept	0.113 ± 0.206	0.548	0.585
Environment type (rural)	2.166 ± 0.159	13.641	**< 0.001**
Group size	0.629 ± 0.113	5.546	**< 0.001**
Sex (juvenile)	0.317 ± 0.185	1.716	0.091
Sex (male)	0.290 ± 0.194	1.493	0.131

Fig. 1. Differences in flight initiation distance (FID) among vervet monkey individuals living in different environment types (urban/rural) and of different sex and age classes. Box plots show the median (line in the middle of rectangles), upper and lower quartiles, maximum and minimum values (vertical lines) and outliers (black dots).

4. Discussion

4.1. Urban vs. rural areas

The type of environment occupied by a primate species can have considerable influence on determining predation risk and the subsequent development of antipredator strategies (Dunbar, 1996; Hill and Dunbar, 1998; Hill and Lee, 1998; Boinski et al., 2003; Enstam and Isbell, 2004; Enstam, 2007; Bettridge et al., 2010). Our results support this by showing pronounced differences in FID between urban and rural populations of vervet monkeys, with individuals inhabiting human settlements delaying their escape (i.e., having shorter FID).

Firstly, we suggest that differences in FID between urban and rural areas can, to some extent, be explained by the differences in human-monkey interaction between these sites (i.e., habituation). In Uganda's urban parks, monkeys attract tourists and are often provisioned with food from park managers, as well as the general public (see also Brennan et al., 1985). In contrast, rural monkeys are either observed from a distance by tourists and locals or are negatively perceived, which often leads to mistreatment by local people and farmers because vervets raid vegetable patches and cash crops (e.g. Else, 1991; Hockings and McLennan, 2016). In fact, non-human primates are one of the most frequent crop raiders globally, but particularly in Africa and Asia (Else, 1991; Sillero-Zubiri and Switzer, 2001; Lee and Priston, 2005; Tweheyo et al., 2005). In Uganda, vervet monkeys are frequently reported as pests and, in some cases, vervets are killed by farmers (Hill, 2000, 2005; Saj et al., 2001). Moreover, there is also the effect of the bushmeat trade and pet trade on primate morbidity (Chapman et al., 2016).

There may also be cultural differences in the perception of monkeys between people living in urban and rural areas. For instance, monkeys may be considered potential reservoirs of zoonotic diseases (Wolfe et al., 2005), with rural human populations being more vulnerable because of reduced access to health care; unfortunately, no such data are available for Uganda. Vervet monkeys appear to have the ability to sort predators into different categories (Seyfarth et al., 1980). Thus, it is possible that sharp differences in FID between urban and rural environments may have resulted from habituation differences between positive and largely non-lethal interactions with people in urban areas, and negative, potentially lethal interactions with humans in rural areas leading to heightened predation risk perception to monkey populations (i.e., human can be perceived equivalent to natural predators).

While acknowledging that habituation to the usual type of human–monkey interactions likely affected our results, we suggest that this pattern may also be explained by relaxed predation risk in urban environments associated with lower numbers of natural predators; for instance, large carnivores are known to avoid human settlements in Africa (Singh and Vinathe, 1990; Bateman and Fleming, 2012). In contrast, in rural Uganda, smaller-sized monkeys are preyed upon by eagles (Mitani et al., 2001), chimpanzees *Pan troglodytes* (Watts and Mitani, 2002), and humans (Mittermeier, 1987; Chapman et al., 2016). Moreover, in Uganda, dogs also prey upon vervet monkeys (Chapman et al., 2016) and appear to be more prevalent in rural than urban sites (P. Tryjanowski, pers. obs.).

Furthermore, urbanization may present similar selection pressures to domestication (Møller, 2010), favouring certain behavioural phenotypes. For example, monkeys that have reduced risk perception to predators may thrive amongst people in urban environments because they are able to acquire more food (i.e., through scavenging or tourists). Møller (2010) reported that birds successfully invading cities are characterised by shorter FID, compared to longer and more variable FIDs in ancestral rural populations. Variance in FID was also positively correlated with the time since urbanization of the population, probably because urban populations became adapted to the urban environment (Møller, 2010). In addition, FID has high individual consistency in similar contexts determining how individuals cope with fluctuating environments through behavioural traits (Carrete and Tella, 2010). This may provide an alternative explanation for short FID in urban areas: urban monkeys are descended from rural populations having shorter FID. Further investigation may help us to understand which species, or populations of primates are expected to invade, or have already
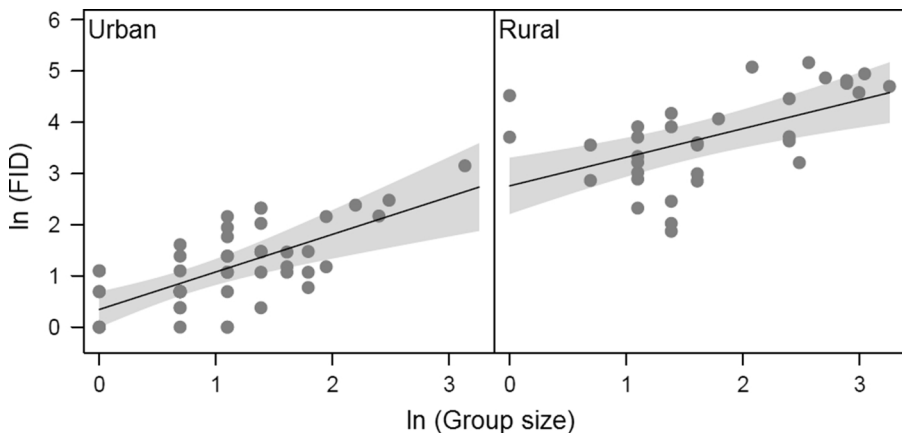

Fig. 2. Generalized linear model (GLM) output for relationship between flight initiation distance (FID) and group size of vervet monkeys with data points (grey dots) visualized separately for urban and rural environments. Each line represents model output within each cross section of the data. Shaded regions correspond to 95% confidence intervals for each section.

invaded, human settlements.

4.2. Habituation vs. predation risk

Delayed escape, or dampened behavioural responses (e.g. vigilance, alarm calls) to potential threats from a human observer could be attributed to habituation, which has been a fundamental part of studies of wild primates for several decades (Williamson and Feistner, 2003; Bertolani and Boesch, 2008; Jack et al., 2008). Hence, one could argue that inter-site differences in FID of vervet monkeys are indistinguishable from habituation (e.g. to increased human density in urban environments). Although changes in anti-predator behaviour in urban animals can be attributed to habituation, it is not the only mechanism explaining reduced fear response of individuals and/or populations in urbanized environments (Rodriguez-Prieto et al., 2008; Chapman et al., 2012; Møller and Ibáñez-Álamo, 2012; Díaz et al., 2013; Lowry et al., 2013).

FID studies on different animal groups show that it is both habituation and perceived risk of predation that act as two complementary mechanisms determining FID (Webb and Blumstein, 2005; Rodriguez-Prieto et al., 2008). This was empirically demonstrated by Rodriguez-Prieto et al. (2008) in which humans and a radio-controlled vehicle were used to approached urban blackbirds *Turdus merula* in order to simulate an attack of usual and novel potential predator, respectively. They found that blackbird individuals from sites with higher human activity had shorter FID than individuals from sites with low levels of disturbance in response to both human and novel stimulus. Moreover, it has been shown that, even when non-lethal, human-related disturbance indirectly affects the fitness of animals, such stimuli could be considered analogous to predation risk (Frid and Dill, 2002). Similar to predation, human disturbance can affect the behaviour of individuals, including vigilance and escape (Frid and Dill, 2002; Blumstein, 2014). Since vervet monkeys in rural areas of Uganda are exposed to more threats from people (e.g., farmers) and human-associated predators, such as dogs or natural predators, they likely adjust their escape strategies and are expected to increase their FID (Engelhardt and Weladji, 2011; Chapman et al., 2012; Díaz et al., 2013).

Moreover, while habituated animals may show no visible signs of distress, the presence of a human observer should not be considered a neutral state in habituated animals (Williamson and Feistner, 2003; Jack et al., 2008; McDougall, 2012; Nowak et al., 2014). For instance, stumptail macaques *Macaca arctoides* and capuchin monkeys *Cebus capucinus* individuals were shown to still respond to human observers even after 14 years, and more than 20 years of research, respectively (Rasmussen, 1991; Jack et al., 2008). Similarly, it was found that some chimpanzee females in the Taï Forest were not completely habituated to human presence even after 15 years of observations (Boesch-Achermann and Boesch, 1994). These findings suggest that, even after prolonged periods of exposure to humans, primates could exhibit an evolved response to the risk of predation (Frid and Dill, 2002). While both urban and rural monkeys exhibited increased vigilance when approached by our observer (e.g., alarm calls, increased head movements linked to scanning of environment), these behaviours were more marked in rural, than urban individuals. So, although the effect of habituation on the FID of vervets cannot be disregarded, pronounced differences in FID between rural and urban populations of vervet monkeys in Uganda also seem to reflect changes in risk perception, and are therefore consistent with optimal escape theory (Ydenberg and Dill, 1986; Díaz et al., 2013).

4.3. Group size

We have found that vervet monkeys living in larger groups (i.e., large number of visible neighbours) initiate flight at a greater distance (Alexander, 1974; van Schaik et al., 1983). This may suggest that vervet monkeys are better able to detect approaching predators when in larger

groups (van Schaik et al., 1983) and use behaviours of conspecifics as cues about predation risk (Murphy et al., 2013). Our finding that rural vervet monkeys live in larger groups and exhibit longer FID, is consistent with studies on primate grouping behaviour in response to predation risk. Among cercopithecoid primates a significant positive correlation between predation risk and group size has been found (van Schaik and van Noordwijk, 1985; Dunbar, 1988, 1996; Singh and Vinathe, 1990; Hill and Lee, 1998; Bettridge et al., 2010). However, the effects of predation risk on group size are also likely to vary with the type of predator and substrate the group occupies (i.e., terrestrial and/or arboreal). While bonnet monkeys *Macaca radiata* live in larger groups in more risky terrestrial environments occupied by ground-dwelling mammal predators, such as tigers, leopards, and dogs (Singh and Vinathe, 1990), the group size of arboreal red colobus monkeys *Piliocolobus tephrosceles* was positively correlated with the distance from the chimpanzee core hunting area at Gombe (Stanford, 1995). The evidence suggests that composition of local predator communities and the nature of species-specific predation on prey animals, as well as the substrate the animal occupies, should all be considered when studying links between predation risk and group size.

Alternatively, differences in group size between urban and rural environments may also be a function of food competition between individuals within the same group, and variation in the distribution and density of food resources may constrain group size in both settings in different ways (Terborgh and Janson, 1986; Dunbar, 1988; Chapman et al., 1995; Janson and Goldsmith, 1995; Bettridge et al., 2010). For instance, Singh and Vinathe (1990) suggest that at least in some cases rural sites may support higher food supplies for monkeys feeding on cultivated crops than urban environments, which may suffer from relatively higher food shortage. Nevertheless, differences in feeding opportunities between urban and rural sites, and their potential impact on group size should also be taken into account in further studies.

Under less plentiful conditions, living in larger groups increases within-group food competition and costs associated with feeding, since individuals are forced to travel further and forage over a greater area to meet their nutritional and energy requirements (Chapman et al., 1995; Janson and Goldsmith, 1995; Gillespie and Chapman, 2001; Pride, 2005; Majolo et al., 2008). While predation risk puts a lower limit on minimum group size (Dunbar, 1996), costs from competition over food set its upper limit (Janson and Goldsmith, 1995). Indeed, in environments with dispersed resource patches, populations of chimpanzees and red colobus live in subgroups of a small number of individuals (Chapman et al., 1995). In frugivorous, but also folivorous primates, greater feeding competition again results in smaller foraging groups (Janson and Goldsmith, 1995; Gillespie and Chapman, 2001; Snaith and Chapman, 2007; Borries et al., 2008). Thus, the size of primate groups is probably a consequence of balancing the risks of predation and the nutritional and physiological requirements of individuals in the group (Isbell, 1994; Janson and Goldsmith, 1995; Dunbar, 1996; Cowlishaw, 1997; Majolo et al., 2008; Bettridge et al., 2010).

4.4. Sex and age

Although we did not find any significant effect of sex and age on FID in vervet monkeys, which may be an effect of a relatively low sample size, males had slightly longer FID than females and juveniles in both urban and rural environments. This may be associated with the fact that, as in other cercopithecines, dominant males of vervet monkeys spend more time scanning environments (Isbell and Young, 1993; Murphy et al., 2013), which may allow them to identify potential threats earlier than other individuals. Alternatively, larger body size in males may make them more conspicuous and more easily detectable by predators; male perception of predation risk may therefore be higher resulting in longer FID (Capizzi et al., 2007). The vulnerability of monkeys to predation, according to their sex and age, may be variable and linked to local composition of predator communities. For instance,

Mitani et al. (2001) have shown that male monkeys were over-represented in the diet of crowned hawk-eagles *Stephanoaetus coronatus*. However, we found that males had longer FID irrespective of the site type (and thus potentially differing predator communities), which suggests that other confounding factors might operate in determining males' responses to the risk of predation.

5. Conclusions

Our study demonstrates sharp differences in escape distances among urban and rural populations of vervet monkeys in Uganda. Site type was the strongest predictor of FID, followed by group size. In contrast, only small differences in FID were detected between sex and age groups. Our results are consistent with evidence from risk perception studies in both non-primate taxa and primates by demonstrating that, besides the probable effect of habituation, monkeys adjust their antipredator behaviour to the level of predation risk when coping with novel environments within human settlements. This is consistent with optimal escape theory. We propose that measuring FID can be considered as an alternative and practical tool for measuring predation risk in primates. Results of FID studies can also be used in primate conservation, for instance, to determine buffer zones around animals to reduce human impacts on wildlife (e.g., to provide guidelines for viewing distances for tourists) (Hockin et al., 1992). Finally, FID studies may bring novel insight into the research on the effects of urban ecology on primates and potential evolutionary mechanisms underlying colonization of human settlements.

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