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The relationship between flight initiation distance and cognition of urban-living yellow mongooses, *Cynictis penicillata*

Mijke Müller * **and Neville Pillay**

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa
*Corresponding author's e-mail address: mullermijke@gmail.com
ORCID iDs: Müller: 0000-0002-2519-1726; Pillay: 0000-0002-0778-726X

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Abstract
Reduced flight initiation distance (FID) enables urban-living animals to forage closer to humans, while improved cognitive abilities may be beneficial in assessing the level of danger. We assessed whether yellow mongooses, *Cynictis penicillata*, which are more tolerant to human disturbances, are also better problem-solvers. Mongooses in two locations ($N = 5$), differing in levels of human contact, were presented with a puzzle-box containing a food incentive. FID was longer in the location with more human contact, but reduced at sites closer to humans. With greater human contact, mongooses fled further from the puzzle box and took longer to recover. Despite differences in tolerance to human disturbance and the subsequent recovery, location did not affect problem-solving efficiency. However, the fear response and recovery time decreased in mongooses with lower tolerance of humans, whereas problem-solving decreased in mongooses that were more tolerant to humans, possibly a result of habituation to the humans.

Keywords
anthropogenic disturbance, cognition, FID, problem solving, yellow mongoose.

1. Introduction

Urbanisation is driving behavioural changes in non-human animals (Sol et al., 2013). Urban expansion and the associated increase in human population density reduce the proximity between humans and wildlife, affecting animal population density, distribution and behaviour (Palmer, 2003; Sol et al.,

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2013). Some of the behavioural adaptations of urban-living animals include a reduced fear response, a reduced stress response in the presence of humans and domestic animals, lower levels of aggression and an increased tolerance to high population densities (Møller, 2009; Trut et al., 2009; Wirén et al., 2009). Furthermore, several traits associated with urban-living animals benefit survival in these habitats, such as being innovative and bold (Møller, 2009). As a result, some animals are capable of living alongside the ever-increasing human population.

The distance at which an animal initiates flight from a potential threat, known as flight initiation distance (FID), is an indication of the perceived risk of predation by an individual, weighed against the cost of fleeing (Mikula, 2014). Not only does FID vary among different species (Blumstein et al., 2003), but also among individuals of the same species (e.g., McGowan et al., 2014). FID is thus a flexible behaviour (Mikula, 2014) and is modulated based on various factors such as the distance from the nearest refuge, the speed of the approaching threat, the physiological state of an individual and previous experience (Engelhardt & Weladji, 2011). It further varies based on the level of human exposure in an animal's environment (Engelhardt & Weladji, 2011; McGowan et al., 2014; Mikula, 2014). The literature contains several examples of the effects of increased human activity on animals' FIDs, specifically in areas with greater human activity where animals have shorter FIDs (e.g., birds: northern New Zealand dotterel, *Charadrius obscurus aquilonius*, Lord et al., 2001; Western gulls, *Larus occidentalis*, Webb & Blumstein, 2005; black-billed magpies, *Pica pica*, Kenney & Knight, 1992; reptiles: blue-tailed skinks, *Emoia impar*, McGowan et al., 2014; mammals: Cape ground squirrel, *Xerus inauris*, Chapman et al., 2012). This observation demonstrates the plastic nature of FIDs, indicating that learning plays a role in FIDs (Eason et al., 2006; Mikula, 2014). Furthermore, there is evidence that variability in FID differs with habitat types, with individuals in an urban habitat reducing their FIDs, whereas the FIDs of those in non-urban areas remain constant (Møller et al., 2013), which indicates increased flexibility in FIDs in urban areas.

Flight initiation distance tends to increase with an individual's perceived predation risk as flight becomes more important than foraging or engaging in other activities that increase risk of predation (Bonenfant & Kramer, 1996; Cooper Jr., 1997). Ideally, animals should adjust their response based on the prevailing situation to minimise disturbance and maximise survival

(Ydenberg & Dill, 1986; Bonenfant & Kramer, 1996) by assessing approaching danger and making a decision based on the perceived danger (Møller & Erritzøe, 2014). This method of cognitive monitoring reduces the relative cost of flight by selecting the least costly flight, rather than the fastest flight, in the presence of approaching danger (Møller & Erritzøe, 2014). It may further allow animals to distinguish between potentially threatening and nonthreatening approaches (Mikula, 2014), as well as distinguish between, and respond appropriately to, unfavourable (e.g., humans who appear hostile), neutral (e.g., humans who pay no attention to animals), and rewarding (e.g., humans who feed animals) stimuli, which may be crucial for survival (Belguermi et al., 2011; Goumas et al., 2020). Although longer FIDs may be beneficial in escaping danger early enough (Møller, 2014), they may not always outweigh the costs of fleeing, which include the loss of foraging opportunities and increased energy expenditure (Ydenberg & Dill, 1986). However, the ability to monitor the approaching danger, process the information, conduct a risk assessment, and act on this evaluation may be cognitively demanding (larger brain sizes are associated with shorter FIDs; Møller & Erritzøe, 2014). As a result, differences in cognitive abilities, personality, and prior encounters with humans may influence success in urban areas (Goumas et al., 2020).

Shorter FIDs are especially important in urban habitats where animals coexist with humans (Møller et al., 2013). Having short FIDs is less likely to disrupt activities like foraging during frequent, non-threatening disturbances, reducing energy expenditure by fleeing less frequently, and reducing an animal's stress response (Møller et al., 2013). However, urbanisation may change an animal's risk assessment. In urban areas, where human presence is inevitable, animals are expected to display decreased sensitivity to humans, possibly as a result of habituation (Kenney & Knight, 1992; Webb & Blumstein, 2005). However, some animals may become habituated, whereas others may fail to habituate or even become sensitised to humans (Blumstein et al., 2003; Goumas et al., 2020), even if the human-animal interaction is not negative (McGowan et al., 2014). For example, Magellanic penguins, *Spheniscus magellanicus*, appear to habituate to humans through a reduced stress response when exposed to humans (Walker et al., 2006), whereas yellow-eyed penguins, *Megadyptes antipodes*, become sensitised and have an increased stress response when exposed to humans (Ellenberg et al., 2007), compared with their unexposed conspecifics. A better understanding

of the adaptations of animals in urban environments is, therefore, crucial in reducing the impacts of urbanisation on wildlife.

Many behavioural characteristics of animals adapted to the presence of humans are also predictors of innovation, cognition, and problem-solving success. It is for this reason that urban-living animals often display enhanced problem-solving abilities (e.g., Mazza & Guenther, 2021). Some of these characteristics include reduced neophobia (e.g., Bergman & Kitchen, 2009; Biondi et al., 2010; Daniels et al., 2019), the ability to learn (e.g., Thornton & Samson, 2012), and larger brain size (Reader & Laland, 2002), all of which have been suggested to influence animals' fear responses to humans (Eason et al., 2006; Møller & Erritzøe, 2014; Goumas et al., 2020). But are animals with such a reduced fear response to humans better at problem-solving following a human disturbance than those that are more sensitive to humans? If so, these two factors, tolerance to humans and improved problem-solving, may function together to support an animal's ability to thrive in urban habitats. Yet, research is presently lacking about the impact of direct human disturbance on the behaviour and cognitive abilities of urban-living animals, as well as the cognitive mechanisms underlying these behavioural responses (Goumas et al., 2020). Our study aimed to address this question by investigating whether human disturbance affected urban-living yellow mongooses, *Cynictis penicillata*, cognitively.

The yellow mongoose is a small (length 300 mm, weight 500–1000 g; Kingdon et al., 2013) carnivore distributed throughout southern Africa (Do Linh San et al., 2015). It is diurnal and most active in the mornings between 0600 and 1200 h (Cronk & Pillay, 2019a, 2020). This species has a history of persecution by humans since it is considered a pest on farms (Lynch, 1980) and a carrier of rabies (Bishop, 2010). Even so, it has managed to become well-established in urban areas where it lives alongside humans and exploits anthropogenic food (Cronk & Pillay, 2018, 2019a,b). Therefore, the appropriate behavioural responses that involve exploiting the available resources, yet avoiding humans in this human-altered landscape, may be essential for its survival (Goumas et al., 2020).

In a previous experiment (Müller & Pillay, 2023), we showed that the level of disturbance in the environment of urban yellow mongooses might affect their problem-solving ability (problem-solving differed among three urban locations, possibly due to varying levels of human disturbance). A more

direct approach to assess the effects of human disturbance on problem-solving ability may be to relate the response of individual yellow mongooses to human disturbance (and their subsequent stress response and recovery) to their problem-solving efficiency. In this study, we measured the FID and problem-solving efficiency in yellow mongooses at sites with varying levels of human activity to assess the direct effect of human disturbance on problem-solving ability.

The aim of this study was to assess how the direct disturbance by human presence affects yellow mongooses' cognition in an urban habitat. We assessed the level of tolerance mongooses have to human disturbance during a puzzle box problem-solving task. We predicted that mongooses in areas with more human contact would be more tolerant of human disturbances by (i) having a shorter FID, and (ii) fleeing a shorter distance from the puzzle box when approached by a person compared with mongooses in areas with less human contact. We also assessed the recovery rate following a human disturbance and predicted that mongooses in areas with more human contact would recover quicker following a disturbance than those in areas with less human contact. We further assessed the relationship between the tolerance to human disturbance, and subsequent recovery, as well as the problem-solving ability of yellow mongooses, and predicted that mongooses that are able to recover quickly from a human disturbance would be better at solving a puzzle box problem following a human disturbance. Finally, we established whether habituation to the human disturbance would influence the tolerance, recovery, and problem-solving ability of mongooses, and predicted that the (i) FID, (ii) distance fled, (iii) recovery rate, and (iv) latency to consume would decrease over successive trials in the experiments conducted as mongooses become habituated to humans.

2. Materials and methods

2.1. Study area

This study was conducted in the Meyersdal area situated in the south of Johannesburg, South Africa. Two areas were selected for study, the Meyersdal Nature Estate (26°18′08.2″S 28°04′55.9″E; 300 ha) and the Meyersdal Eco Estate (26°17′03.6″S 28°04′50.8″E; 480 ha). These locations were adjacent to one another but separated by a double-laned tar road which the mongooses in this area rarely crossed (Cronk & Pillay, 2021). The Nature

Estate (location with less mongoose–human contact) had a nature area that was fenced off from the residential area, with low levels of interaction between human residents and wildlife, although it was occasionally accessed by human hikers, runners and cyclists. The Eco Estate (location with more mongoose–human contact) had no separate nature area, and instead, the residences were dispersed throughout a nature area resulting in increased interaction between the residents and wildlife. A total of five sites (individuals) were selected for this study based on the occurrence of yellow mongooses, and a distance of at least 200 m from any other site. Three of these sites were in the Nature Estate (more human contact), and two were in the Eco Estate (less human contact). Only five sites were viable for conducting this experiment due to mongooses' generally cryptic behaviour and reluctance to emerge from their burrows in the presence of humans. The sites used in this study were the only sites where mongooses were frequently present during the experimental set-up and engaged with a puzzle box in the experimenter's presence.

2.2. Experimental design and protocol

The yellow mongoose is diurnal, and accordingly, this experiment was conducted between 0600 and 1200 h daily when the mongooses were the most active (Cronk & Pillay, 2019a, 2020). For this experiment, mongooses were exposed to puzzle boxes constructed of clear Perspex with a lid that could open and close with hinges. Meat offcuts (1 teaspoon) were placed inside the box as an incentive to solve the puzzle box problem. This study took place between May and July 2021. The mongooses were trained to open the puzzle boxes at all sites. This included two stages: stage 1, where the mongooses were exposed to a puzzle box with an open lid allowing for habituation, and stage 2, where mongooses were exposed to a puzzle box with a mostly closed lid propped up with a stick, leaving a 1 cm opening. The mongooses had to obtain the food incentive from the puzzle box successfully for a total of five trials at stage 1 before proceeding to stage 2. After the mongooses successfully obtained the food incentive from the puzzle box at stage 2 for a total of five trials, the lids of the puzzle boxes were closed completely, and the experiment commenced. This puzzle box design tested whether mongooses could learn to open a feeding device using a novel behaviour that they do not use during foraging in their natural environment (lifting of an object with their snouts in an upwards motion) to obtain a food incentive.

The puzzle box with the closed lid containing the food incentive was either placed near the den entrance or in a location near the dens that mongooses were observed visiting frequently. A human observer (the same person constant during all trials and at all sites) remained at approximately 10–20 m from the puzzle box (at two sites, the mongooses were tolerant of human observers at a distance of 10 m from the box, whereas at the remaining three sites, mongooses only emerged from their dens when human observers were 20 m away). Once a mongoose contacted the box, the human observer approached the box at a slow pace and in a non-threatening manner. The location of the human observer at the exact moment the mongoose fled from the box was marked by placing a placeholder on the ground. Once the mongoose stopped fleeing, the location of the mongoose was marked visually using landmarks (e.g., rocks, bushes, burrows) by a second observer (same person during all trials and at all sites) who remained at the starting position. After the mongoose stopped fleeing, the first observer slowly retreated to the starting position. The recovery time was recorded as the time (in seconds) that elapsed from when the mongoose fled from the box to when it contacted the box again. Whenever the mongoose did not return to the puzzle box for over 10 min, the trial was terminated, and the recovery time was recorded as 600 s (i.e., the maximum time). The latency to consume the food incentive, which indicated problem-solving efficiency, was recorded as the time elapsed from when the mongoose contacted the box until it solved the problem and consumed the food after returning to the puzzle box. After the mongoose had consumed the food incentive and abandoned the puzzle box, the distance between the first marker and the puzzle box, as well as the puzzle box and the second marker, were measured (in metres) using a measuring tape. The first measurement indicated flight initiation distance (FID), and the second indicated the distance fled. The experiment was repeated at each site for a total of five trials per site. Sampling for FID experiments were opportunistic since the presence of the same focal mongoose at the puzzle box in the presence of the observer occurred infrequently. Five was therefore the maximum number of trials possible without mongooses being absent during the experimental set-up for several consecutive days, possibly impacting the results (the intertrial time ranged from zero days when two trials were done on the same day to a maximum of ten days between trials). The straight-line distance between the site and the nearest human residents was measured using Google Earth™ and used as a measure of the effect of human resident

proximity on the yellow mongooses' FID, distance fled, recovery rate, and latency to consume.

Because yellow mongooses are predominantly solitary foragers (le Roux et al., 2008; Manser et al., 2014), the same focal individual consistently visited the puzzle box (confirmed using facial recognition technology; School of Computational and Applied Mathematics, University of the Witwatersrand, Johannesburg, South Africa). Only adult mongooses participated in this study, and juveniles never attempted to solve the puzzle box problem. Males and females could not be distinguished due to yellow mongooses' lack of sexual dimorphism, and therefore sex was not considered in this study. Furthermore, the Meyersdal management did not approve the collaring or marking of individuals in this study.

2.3. Data analyses

All statistical analyses were conducted using R Statistical Software (R version 3.4.3; R Core Team, 2013; http://www.R-project.org/). Shapiro–Wilk tests were used to test for normality. Non-normal variables were transformed using a Box-Cox transformation (R package: MASS). Flight initiation distance (FID) was adjusted as a ratio of the starting distance by dividing the FID by the starting distance, to account for the variation in starting distance among sites. A linear mixed effect model (LMER; R packages: lme4, lmerTest) was used to analyse differences in (i) the flight initiation distance (FID), (ii) distance fled, (iii) recovery time, and (iv) latency to consume. Location was a fixed effect, site and trial were random factors, and proximity to the nearest human residents was a covariate. When proximity to the nearest human residents was significant, a Pearson's product-moment correlation was used to assess the relationship between the relevant response variable (FID, distance fled, recovery time, latency to consume) and the proximity to the nearest human residents. Effect sizes were evaluated using Cohen's D (R package: EMAtools). Linear models (regressions) were used to assess whether (i) FID, (ii) distance fled, and (iii) recovery rate influenced the latency to consume the food incentive.

2.4. Ethical approval

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2021/06/03/B).

3. Results

For the FID experiments, five active sites (one focal individual per site) were identified and used (three sites in the location with less human contact and two sites in the location with more human contact). At three sites, two in the location with more human contact and one in the location with less human contact, mongooses were reluctant to emerge from their refuge and approach the puzzle box with the human observer 10 m away from the puzzle box. At these sites, the starting distance of the human observer was increased to 20 m whilst keeping the starting distance constant at 10 m at the remaining two sites. The mongooses in this experiment rarely fled to the nearest refuge (28% of all trials) and mostly stopped fleeing while still in sight of the observer. Further, except for one trial, mongooses always recovered from the human disturbance before returning to the puzzle box to obtain the food incentive. During the one trial where the mongoose did not return to the puzzle box within the 10-min limit, the recovery rate was recorded as 600 s. Despite the small sample size in this study ($N = 5$), the difference between means was sufficiently large, as indicated by the large effect size (Cohen's D) for significant results.

3.1. Flight initiation distance (FID)

Location ($\chi^2 = 25.83$, df $= 1$, $p < 0.001$; LMER; Cohen's $D = -6.08$; Figure 1a) and the proximity to the nearest human residents ($\chi^2 = 31.66$, df $= 1$, $p < 0.001$; Cohen's $D = 6.74$; Figure 1b) were significant predictors of the FID. The flight initiation distance (m), when adjusted for the starting point of the human observer (10 m vs 20 m), was significantly longer in the location with more human contact compared with the location with less human contact (Figure 1a). There was a positive, significant relationship between the flight initiation distance (m) and the distance to human residents ($r_p = 0.42$, $p = 0.035$; Pearson's product-moment correlation; Figure 1b). Flight initiation distance increased with increased distance of the nearest human residents.

A change in FID over trials would have indicated that mongooses changed their FID as they became habituated to the human disturbance. However, the FID did not change in any particular direction over the five trials (Figure 2).

3.2. Distance fled

Location ($\chi^2 = 13.53$, df $= 1$, $p < 0.001$; LMER; Cohen's $D = -3.30$; Figure 3) was a significant predictor of the distance fled, but the proximity

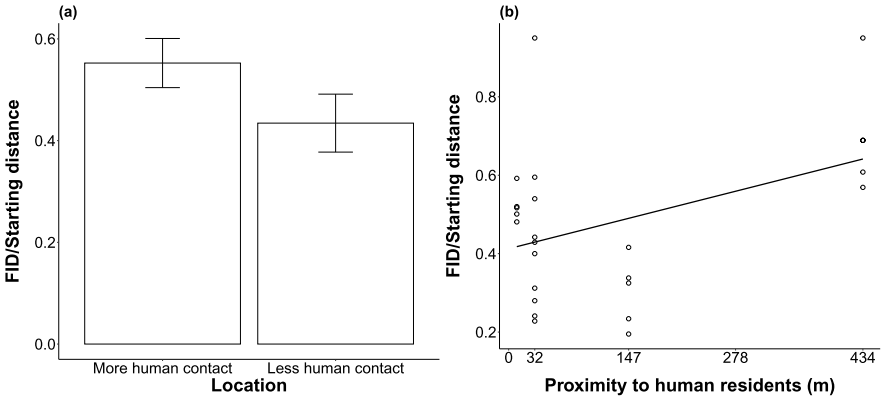

Figure 1. (a) The mean flight initiation distance (FID) adjusted for starting distance of yellow mongooses ($N = 5$) during puzzle box experiments in the location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate). Error bars indicate standard error. (b) The relationship between the adjusted flight initiation distance and distance to human residents (m). The trend line is significant ($p = 0.035$; Pearson's product-moment correlation).

to human residents was not ($\chi^2 = 0.01$, df $= 1$, $p = 0.910$; Cohen's $D = -0.10$). The distance fled from the puzzle box was significantly longer in the location with more human contact compared with the location with less human contact (Figure 3a). A decrease in the distance fled over trials would

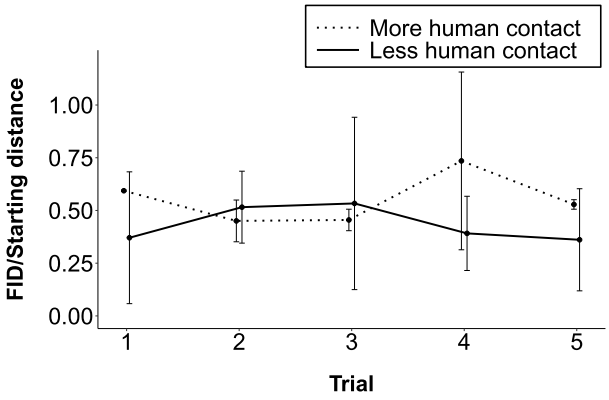

Figure 2. The change in mean flight initiation distance (FID) of yellow mongooses ($N = 5$) over five trials in the location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate) in response to an approaching human observer during FID experiments. The FIDs are adjusted for starting distance. Error bars indicate confidence intervals.

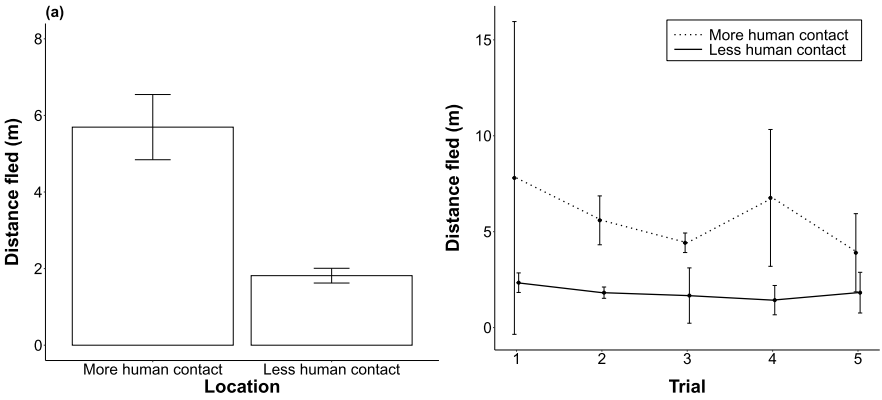

Figure 3. (a) The mean distance (m) yellow mongooses ($N = 5$) fled from the puzzle at the location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate). Error bars indicate standard error. (b) The change in mean distance fled (m) of yellow mongooses over five trials in the location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate) in response to an approaching human observer during flight initiation distance (FID) experiments. Error bars indicate confidence intervals.

have indicated that mongooses adjusted their response as they became used to the human disturbance. The distance fled from the box decreased over trials in both locations, especially after the first trial, with the spike at trial 4 in the location with more human contact probably anomalous (Figure 3b).

3.3. Recovery rate

The recovery rate was measured as the time elapsed since a mongoose terminated fleeing until it returned to the puzzle box. This was a measure of the rate at which a mongoose was able to recover from human disturbance and return to the place of the initial disturbance. Location was a significant predictor of the recovery rate ($\chi^2 = 13.48$, df $= 1$, $p < 0.001$; Cohen's $D = -5.19$; Figure 4a), whereas proximity to the nearest human residents was not a significant predictor of the recovery rate ($\chi^2 = 1.85$, df $= 1$, $p = 0.174$; Cohen's $D = 1.92$). The recovery rate was significantly longer in the location with more human contact compared with the location with less human contact. A decrease in the recovery rate over trials would have indicated that mongooses were able to recover faster following a human disturbance as they became used to the disturbance. The recovery rate decreased over the five trials in the location with more human contact, especially after the first trial,

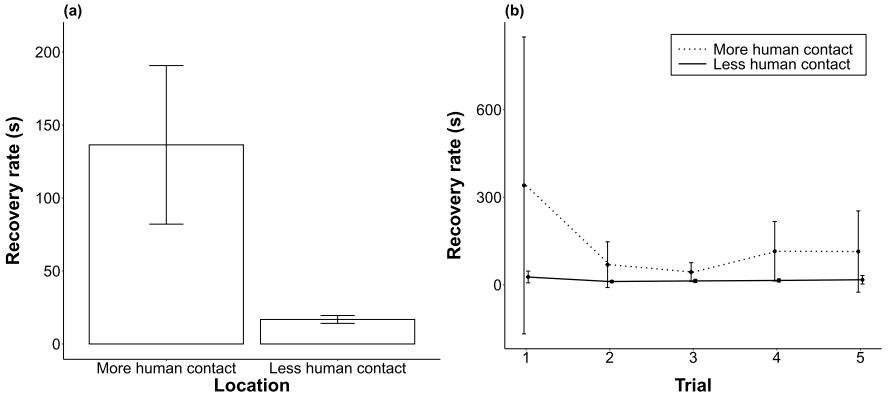

Figure 4. (a) The mean recovery rate (s) after yellow mongooses ($N = 5$) fled from the puzzle box at location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate). Error bars indicate standard error. (b) The change in mean recovery rate (s) of yellow mongooses over five trials in the location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate) in response to an approaching human observer during flight initiation distance (FID) experiments. Error bars indicate confidence intervals.

with an increase at trials 4 and 5, and no considerable change in recovery rate over the five trials in the location with less human contact (Figure 4b).

3.4. Latency to consume

The latency to consume the food incentive was a measure of mongooses' problem-solving efficiency after being exposed to, and having recovered from, a human disturbance. Location ($\chi^2 = 0.60$, df $= 1$, $p = 0.440$; Cohen's $D = 0.34$) and the proximity to the nearest human residents ($\chi^2 = 0.01$, df $= 1$, $p = 0.917$; Cohen's $D = -0.05$) did not significantly predict the latency to consume the food incentive. Furthermore, linear models revealed that the latency to consume was not influenced by the FID ($t = -0.33$, $p = 0.747$), the distance fled ($t = -1.53$, $p = 0.141$), or the recovery rate ($t = -1.34$, $p = 0.193$).

A decrease in the latency to consume the food incentive over trials would have indicated that the mongooses had improved efficiency at solving the puzzle box problem as they became used to the human disturbance. The latency to consume the food increased after the first trial in the location with more human contact and decreased after the first trial in the location with less human contact (Figure 5).

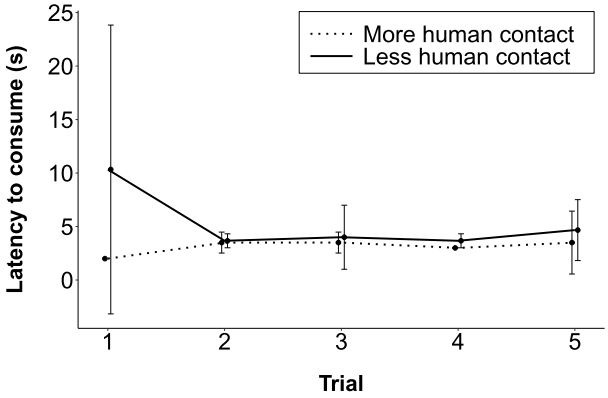

Figure 5. The change in mean latency to consume (s) a food incentive by yellow mongooses ($N = 5$) over five trials in the location with more human contact (Meyersdal Eco Estate) and the location with less human contact (Meyersdal Nature Estate) in response to an approaching human observer during flight initiation distance (FID) experiments. Error bars indicate confidence intervals.

4. Discussion

We conducted flight initiation distance (FID) experiments to assess the impact of direct human disturbance on the problem-solving abilities of an urban population of yellow mongooses. The mongooses in our study showed significant differences in their tolerance to human disturbance based on their location. Mongooses in areas with greater human disturbance had longer flight initiation distances than those in a more natural habitat with reduced human presence. Conversely, mongooses occurring further away from human residents had longer flight initiation distances than those in close proximity to human residents. In addition, the mongooses in areas with greater human disturbance fled further away from the puzzle box, and took longer to recover following a human disturbance, than those in a more natural area. Although mongooses had different levels of tolerance to direct human disturbance based on their locality, the mongooses showed no difference in problem-solving efficiency following the disturbance. Moreover, mongooses' problem-solving efficiency was not predicted by their FID, distance fled, or recovery rate, but still changed over the various trials.

The mongooses in the location with more human contact spent less time engaging with the puzzle box problem before fleeing from an approaching human, and therefore had longer FIDs compared with those in the location with less human contact, which remained at the box until the human observer

was much closer. This is contrary to our prediction and the literature, which suggests that animals in areas of greater human density have shorter FIDs (e.g., Lord et al., 2001; Webb & Blumstein, 2005; Chapman et al., 2012; Møller et al., 2013; McGowan et al., 2014). Interestingly, the FIDs of mongooses decreased with increased proximity to human residents, which, in fact, supports both our prediction and the literature. The differences in FID between the two locations must, therefore, be unrelated to human presence and more likely the result of other differences between the two locations. There are many potential reasons for this observed difference in FID, including naivety in areas with reduced human contact, familiarity with the human observer, previous experience, response to novelty, the presence of domestic animals, the effects of indirect disturbances, and food availability. Although it is not possible to determine which one of these factors, or possibly a combination of factors, caused this disparity in FID between the two locations, each one will be discussed briefly below.

The first possible explanation for the differences in FID between the two locations in this study is the naivety of animals occurring in areas with low levels of human encounters. Naivety of animals towards predators is a common phenomenon (e.g., on islands) when native animals are isolated from alien predators, resulting in inappropriate antipredator responses in the presence of introduced predators (naive prey hypothesis; Sih et al., 2010). Similarly, when human encounters are rare or non-existent, animals may not exhibit the usual fear responses in the presence of humans (e.g., Galapagos Islands' marine iguanas, *Amblyrhynchus cristatus*, Vitousek et al., 2010). Mongooses in the location with more human contact, where residents lived in areas utilised by mongooses, likely encountered humans daily, resulting in a greater fear response compared with those in the location with less human contact, which rarely encountered humans and, accordingly, do not show such a fear response. This seems to be the least likely explanation for the observed difference in FID since mongooses in the location with less human contact encountered humans occasionally and are likely to be moderately familiar with humans. If, however, animals have encountered humans before, habituation can occur over time, leading to a reduced fear response. For animals to habituate to humans, they must be able to categorise all humans as one group (Goumas et al., 2020). In this case, an encounter with one human may influence an animal's reaction to another human as a result of experience (Belguermi et al., 2011; Goumas et al., 2020). Additionally, for animals

to habituate only to certain humans who are rewarding, and sensitise to other humans who are dangerous, they must have the ability to distinguish between different humans (Goumas et al., 2020), which many species of animals are capable of (e.g., wild jackdaws, *Corvus monedula*, Davidson et al., 2015; feral pigeons, *Columba livia*, Belguermi et al., 2011; house sparrows, *Passer domesticus*, Vincze et al., 2015; honeybees, *Apis mellifera*, Dyer et al., 2005; sheep, *Ovis aries*, Knolle et al., 2017). This ability to discriminate between dangerous, neutral, and rewarding humans may be advantageous when living in close proximity to humans (Belguermi et al., 2011; Goumas et al., 2020), especially since fleeing during a non-threatening approach is costly (Ydenberg & Dill, 1986). The mongooses in the location with less human contact were often already present or emerged from their dens during the set-up of various experiments by the same human observer and may have learned to recognise the observer as non-threatening, thereby reducing their fear response. This is in direct contrast to the mongooses in the location with more human contact who were rarely present during experimental set-up and never had the opportunity to associate the observer with any reward or recognise them as non-threatening. Additionally, the mongooses in the location with more human contact may have had negative encounters with humans previously or lacked the ability to discriminate between threatening and non-threatening humans, and consequently responded to the observer's approach based on prior experience (some urban animals fail to adapt their behavioural responses to threatening and non-threatening humans in areas with high human population densities; Vincze et al., 2015). Similarly, the mongooses in the location with less human contact may have had positive experiences with humans previously and subsequently were attracted to the human observer (e.g., Sabbatini et al., 2006) due to prior associations between humans and food rewards.

Differences in response to novelty (neophobia/neophilia) may impact animals' general processing of cues in their environment and, as a result, may influence their response to humans (Greggor et al., 2019; Goumas et al., 2020). In a previous experiment conducted on the same population of mongooses, those occurring in the location with more human contact were initially more neophobic when presented with a novel object (Müller & Pillay, 2023). Their increased neophobia, generally, may have resulted in an increased sensitivity and fear response towards humans. Further, animals' fear responses to humans may be influenced by the predation risk in

their environment (Goumas et al., 2020), promoting antipredator responses towards humans. For example, double-banded plovers, *Charadrius bicinctus*, have longer FIDs in areas with more domestic animals (St Clair et al., 2010). Domestic animals were prohibited from entering the fenced-off area in which mongoose sites were located in the location with less human contact, with the complete prohibition of domestic cats in the estate, whereas both dogs on-leash and free-roaming cats occurred in the location with more human contact. This increased exposure to domestic animals in the location with more human contact may have increased mongooses' sensitivity to predation overall, raising antipredator responses to humans in general.

There are various ways in which altered habitats affect animals. Indirect effects, for example, vehicular traffic, noise pollution and domestic animals (McGowan et al., 2014), should be considered in combination with the direct effects of human presence. This is because these indirect effects alter the way in which animals behave and perceive risk, and it may limit their ability to acquire resources (Gill, 2007). Observed changes in FID may thus be the result of indirect disturbances altering the perceived risk of predation, and not necessarily the direct impact of human presence exclusively (Li et al., 2011). Since the location with more human contact is mostly residential and developed (e.g., presence of tar roads, vehicles, domestic animals, and noise from residents), mongooses here likely encountered indirect disturbances much more frequently than the mongooses in the location with less human contact did, possibly increasing their sensitivity to human presence.

The FIDs did not decrease over the five trials as expected. Instead, it remained constant, with the first and last trials having similar FIDs in both locations. This indicates that mongooses did not adjust their FIDs even when they became habituated to the human disturbance (as indicated by the reduced fear response via distance fled and recovery rate over the five trials) in both locations. After conducting an FID experiment on birds across Europe, Møller et al. (2013) disputed that differences in FID between different environments result from phenotypic plasticity, especially since individual animals tend to have consistent FIDs across different habitats (Møller & Garamszegi, 2012). The results from our study also did not support habituation as a driver of variations in FID between the two locations since, if that were the case, those in areas with greater human density would have exhibited shorter FIDs (Møller et al., 2013). Phenotypic sorting, the distribution

of individuals among environments that best suit their specific FIDs (Carrete & Tella, 2010), was also considered an unlikely explanation due to the high genetic variation in urban populations as well as their reduced dispersal ranges (Björklund et al., 2009; Møller et al., 2013; O'Donnell & delBarco-Trillo, 2020). Thus, the most likely explanation was that urban individuals with long FIDs have higher mortality rates due to the costs associated with frequent flights (e.g., reduced foraging time and high energy expenditure; Ydenberg & Dill, 1986), resulting in microevolutionary changes (Hendry et al., 2008; Møller et al., 2013). In this way, each location may have selected for the optimal FID based on the environmental pressures. An interesting future study would be a non-urban, urban comparison to establish whether the FIDs of the mongooses in the location with more human contact are significantly shorter, indicating variation in the reduction of FIDs based on environmental pressures in various urban areas.

When taken together, the FID, distance fled, and recovery rate results suggest that the mongooses in the location with more human contact were less tolerant of human disturbances than those in the location with less human contact. Based on these findings, we predicted that mongooses in the location with more human contact would be slower at solving the puzzle box problem than those in the location with less human contact due to their reduced tolerance to human disturbance. However, the mongooses were equally efficient in solving the puzzle box problem in both locations, irrespective of their FID, distance fled, and recovery rate. This suggests that direct human disturbance did not affect the problem-solving ability of urban-dwelling yellow mongooses in our study. The mongooses' problem-solving ability changed over the five trials, with those in the location with more human contact becoming less efficient, and those in the location with less human contact becoming more efficient, after the first trial. Thus, although a human disturbance did not affect the mongooses' problem-solving, the eventual habituation to the disturbance did improve problem-solving efficiency in mongooses with greater tolerance to human disturbance, whereas the problem-solving efficiency worsened in mongooses with a lower level of tolerance during frequent disturbances by humans. It is possible that the behaviour of the two mongooses investigated in the location with more human contact was anomalous and differed from the rest of the population, which would have impacted the results observed. Increasing the sample size by including additional sites

in future studies would be beneficial to ensure that the observations made are representative of all individuals within a specific location.

The mongooses in our study had distinct fear responses to humans based on their location, with those in areas of increased human disturbance fleeing earlier during a human disturbance, fleeing further away from the site of the disturbance, and taking longer to recover from the disturbance than those in a more natural habitat with less human disturbance. Even so, the mongooses showed adaptation to the level of disturbance, as demonstrated by their shorter FIDs in closer proximity to human residents. Furthermore, their FIDs were consistent over time even though the distance fled from the disturbance and the time to recover decreased, indicating that mongooses became used to the human disturbance but did not alter their initial fear response accordingly. Notably, their problem-solving abilities were not associated with direct human disturbances, but the ability to adapt to these disturbances may have affected their problem-solving efficiency. Problem-solving efficiency may be more closely linked to tolerance to human disturbance than previously thought, with reduced problem-solving efficiency in mongooses with lower levels of tolerance to humans, even after improved recovery from direct disturbances. Together, adaptation to human disturbances may benefit survival in urban settings by promoting foraging opportunities through shorter FID and improved problem-solving when obtaining a food incentive.

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