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Correlates of flight response in some common birds of a rapidly expanding African city

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Summary

Human disturbance in urban landscapes is well known to influence wildlife species worldwide, but information on some animal taxa such as birds, particularly in sprawling African cities, is scarce. We investigated factors influencing alert distance (AD) and flight initiation distance (FID) for four urban bird species in the expanding Morogoro municipality in northeastern Tanzania. Data were collected along 30 transects, ten in each of urban core, peri-urban and rural zones, and analysed using mixed models. We found starting distance (the initial distance from observer to bird), species type and urbanization levels the strongest predictors of alert distance. The same factors, along with perch height, also best predicted FID. Alert distance was positively related to starting distance, and FID increased with alert distance and perching height. Little Bee-eater *Merops pusillus* showed the longest alert and flight distances, and House Crow *Corvus splendens* and Southern Cordon-bleu *Uraeginthus angolensis* the shortest, with Common Bulbul *Pycnonotus barbatus* intermediate. Encounter rates for House Crow and Southern Cordon-bleu were highest in the urban core, with Little Bee-eater and Common Bulbul preferring more peri-urban and rural settings. The overall responses are consistent with patterns reported in temperate cities, and demonstrate how African bird species variably adjust their behaviours to live in growing African cities. The results may contribute to planning strategies for continued co-existence of birds and humans in expanding urban landscapes.

Keywords: African city, bird-human interaction, disturbance; alert and flight distances; urbanization gradient

Introduction

Rapid development in many areas globally poses potential threats to urban wildlife. Frequent encounters between wildlife and humans in cities require some adaptation to enhance coexistence (König *et al.* 2020). However, the adaptive strategies of urban wild animals vary by taxon group, species, body size and behaviour (Ditchkoff *et al.* 2006). For example, birds are generally more adaptable to such development impacts than most wild large mammals (Isaksson 2018). Even amongst birds, adaptation to environmental disturbance varies between species, based on their habitats and feeding specialization. For example, forest specialist bird species would quickly disappear following forest clearance for development activities, while forest generalists might persist, and non-forest species might become established (Partecke *et al.* 2006). Generalist birds are particularly adaptable to urban areas because they can capitalize on the anthropogenic changes to their environment: some, such as House Crow *Corvus splendens* can become highly invasive. Understanding how various bird species in the city adapt to disturbances may therefore be useful for designing appropriate conservation plans to improve the provision of ecosystem services by birds (Hedblom *et al.* 2017).

Research on how urban wildlife tolerates human disturbances has mostly focused on measuring responses of animals towards various cues and the influence of environmental variables. For example, studies have investigated flight initiation distances (FID), i.e., the distance at which an individual bird initiates flight when approached by a potential predator such as a human being (Tätte *et al.* 2017). Flight decision is a result of comparison between the costs of fleeing relative to the benefit of staying (Møller *et al.* 2015), consistent with an optimal escape theory that underlies decision making when a predator is encountered (Ydenberg & Dill 1986). Understanding the factors that determine flight distance of birds can help to regulate human-caused disturbances on birds. For example, FID studies have been carried out to establish baseline data for management purposes such as creation of buffer zones (Blumstein *et al.* 2002), walking trails in recreation sites (John 2015) or as indicators of how birds have adapted to coexist with humans in cities (Lin *et al.* 2011). The effect of different environmental factors also reveals varying patterns in the birds' response to predator presence. For instance, Braimoh *et al.* (2017) observed shorter FID of birds inhabiting areas with high human disturbances in Nigeria. In a study in Southern California, perceived predation risk (measured as a function of vigilance and distance to flock size) in the House Finch *Carpodacus mexicanus* was positively correlated with FID in highly urbanized settings but negatively associated with FID in less urbanized areas (Valcarcel & Fernandez-Juricic 2009). Furthermore, habitat characteristics are also known to influence bird FID. For example, Arroyo & Fors (2020) reported positive correlation between bird FID and vegetation cover but negatively correlated with building height in Mexico. Similarly, Rodriguez *et al.* (2001) found vegetation type and distance to vegetation cover significantly affected FID in central Sweden, though in contrast Blumstein *et al.* (2004) who found no correlation between FID and perch height.

Existing literature on FID reports on the variation in response to predators between and within species. Urban birds often become habituated in densely populated human settlements, resulting in shorter FID (Juricic 2002). For example, Møller *et al.* (2015) and Piratelli *et al.* (2015), studying resident temperate-zone birds, found that urban birds generally have shorter FID than their conspecifics in rural habitats. In contrast, both Carrete & Tella (2010) (in Argentina) and Sunde *et al.* (2009) (in Denmark) reported most bird species showed little or no change in FID in relation to proximity to human settlements and human presence. All the studies above were based in temperate regions, but show contrasting patterns suggesting local variability in disturbance levels and mediating factors such as local human culture and human behaviour directed to the birds (Clucas & Marzluff 2012). While variation in study designs may also be a factor (Lowry *et al.* 2013), this suggests that patterns in one region cannot be generalized to all others.

Cities in tropical developing countries are often fast growing and sprawling (Chamberlain *et al.* 2019). The effects on biodiversity are pronounced, including a decline in bird and insect diversity (Chamberlain *et al.* 2016) and native plant diversity (Rija *et al*. 2014a). While many studies document the impacts of urbanization on overall wildlife populations, relatively little attention has been given on responses of birds towards various disturbance cues in the cities of Africa. Such data, if available, would be useful for improving the conservation outcomes of urban birds and the ecosystem services they offer. The aims of this study, conducted in Morogoro, Tanzania, were (i) to understand the behavioural response to disturbance of different bird species inhabiting the urban ecosystem, and (ii) to investigate the effects of various environmental factors on bird alert and flight initiation distances along an urban-rural-gradient.

Materials and methods

Study area

This study was conducted in Morogoro municipality (6°49′ S, 37°39′ E) located in Eastern Tanzania (Fig. 1). Morogoro is one of the fastest growing cities in eastern Tanzania with a human population nearing 800 000 residents (P. Kihanga pers. comm., December 2021), an increase of nearly 50 % in the last seven years (Rija *et al.* 2014a). Its rapid growth is partly attributable to its location along major roads connecting the cities of Dodoma, Dar es Salaam and the main highway leading to Mbeya in southern Tanzania. Annual rainfall in the municipality ranges from 750 mm to 1050 mm and is bimodal, with short rains from October to December and a longer rainy season from March to May (Msanya *et al.* 2003). The mean monthly temperature varies from 21° C to 27° C through the year.

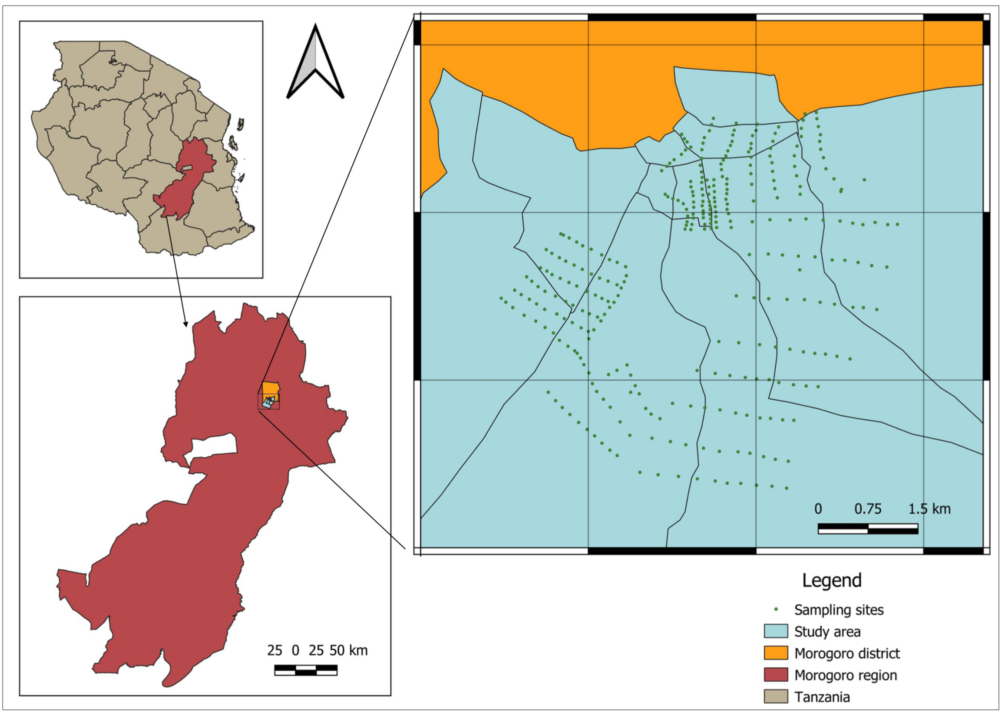


Figure 1. Map of study area in Morogoro Municipality showing the approximate location of the 30 transects where data were collected. Descriptions of the urbanization zones within the study area are provided in the text.

Miombo woodland originally covered much of Morogoro municipality, but this habitat is now heavily modified. For this research, we studied three distinct habitats or urbanization zones following Rija *et al.* (2014a):

1) The urban core, which is now densely built-up (with relatively old buildings), and with most roads and walkways paved and thinly planted trees,

2) The suburbs or peri-urban zone, which is also increasingly built-up but with some open spaces including large backyards with some remnant forest patches (Rija *et al*. 2014a), fruit and ornamental trees to augment any indigenous vegetation, and,

3) A rural-like zone, which is peripheral to the peri-urban zone and characterized by having scattered buildings and large open spaces used for farming and livestock keeping.

Bird species

We selected four focal bird species as models for assessing responses to human disturbances (i.e., approach by a researcher). The selected study species were the Common Bulbul (CB), Southern Cordon-bleu (SCb), Little Bee-eater (LB) and House Crow (HC), all occurring commonly in Morogoro municipality (Rija *et al*. 2014b). None of these species is thought to be subject to substantial human persecution in the study area (Dismas *et al*. 2021), although House Crow is sometimes considered a nuisance and therefore potentially subject to occasional chasing.

Field data collection

Flight Initiation Distances (FID) of the selected bird species were recorded during field observations along transects between 06:30 and 09:30 local time when birds are most active. Ten transects, each 1 km long and 100 m wide, were established in each study zone (urban core, peri-urban and rural) with inter-transect distance of 500 m to avoid double counting. The fieldwork was conducted between 27 December 2019 and 28 March 2020 during the rainy season and each transect was surveyed once over a 2-h period. To collect data, the observer walked slowly along transects, and upon sighting an individual of one of the study species, dropped a marker before moving directly towards the target bird at an average speed of $0.5\,ms^{-1}$ (Samia & Blumstein 2015), while maintaining a direct focus on the target bird(s) (Eason *et al.* 2006). When birds were in a group, only the individual closest to the observer was selected as a target (Piratelli *et al.* 2015). The points at which the target bird detected the observer and begun to show alert behaviour (such as alarm calls, raising up head or tail flicks), was marked by dropping a marker on the ground before continuing the until the target bird took flight (Eason *et al.* 2006). We then took three measures:

- Starting distance, between the first marked point and the position of the target individual when first located.
- Alert distance (AD), between the second marked point and the target individual when alert behaviour was first shown.
- Flight initiation distance (FID), between the position of the observer and the position of the bird when it initiated flight (Blumstein 2003).

All distance measurements over 10 m were taken in metres using a laser rangefinder, while shorter distances were measured directly with a 50-m field tape measure. Details recorded for each observation included: bird species, bird group size, bird activity (preening, resting, foraging or calling), distance to nearest vegetation cover, perch height, perch substrate (rock, grass, shrub or tree), urbanization zone (urban core, peri-urban or rural) and time of day. Group size was determined by counting the number of individuals within a 10-m radius (Braimoh *et al.* 2017). Distance to the nearest vegetation cover was measured using field tapes or a rangefinder. Only birds that were not showing alert behaviour but engaging in other activities such as foraging or resting on perches were approached (Bjørvick *et al.* 2014).

To ensure consistency in data collection only one observer conducted all the observations across the study zones. Furthermore, to minimize variation of bird response resulting from colour of clothes (Eason *et al*. 2006), the observer wore the same type of clothes throughout the survey period. Observations were only made when there was no other potential factor that could be considered a threat and might influence the escape response of the target bird, such as another person nearby (Eason *et al.* 2006). Approaches were initiated only at positions where there was a clear line of sight between the observer and target bird (Braimoh *et al.* 2017).

Data analysis

A preliminary analysis was conducted by plotting histograms of continuous variables (e.g., FID, alert distance, distance to vegetation cover, perch height) to assess the normality of distribution, and conducting correlation tests to detect potential multicollinearity. Most of the response variables we recorded showed a highly skewed distribution but were not correlated. Because of over-dispersion of our data, we used a mixed model (Generalized linear mixed model—GLMM (vs. a generalized linear model)) with the glmer function in the lme4 package (Bolker *et al.* 2009) using a Poisson distribution and log link function. Two models (with seven and nine fixed factors) were built to check the relevance of including all the variables measured in the field in this analysis. Transect was included in the model as a random factor to account for grouping variables in the model results. Model results were evaluated using the Akaike information criterion (AIC). The best fit was for a nine-variable model with one random factor, which was used for all subsequent analyses. Because bird response to predator approach has been related to FID and alert distance (Blumstein 2003), we further explored models involving these response variables specifically. The predictors included in the models were body mass of study species collated from literature (Dunning 2007), starting distance, perch height, distance to vegetation cover, alert distance (for FID model only), species, bird group size, bird activities and habitat (i.e., urbanization zone).

To determine the predictive variables that most strongly influence AD and FID, backward elimination of non-significant terms was used. To assess the significance of the model upon variable removal, drop1 function and Chi-square tests were used following Braimoh *et al.* (2017). This procedure was repeated until a final model that best fitted the data was reached. A conditional r^2 was calculated to assess how well variance was explained by fixed effects in the final model.

To assess the predictive effect of the explanatory variables on the two dependent variables we built a prediction model for each significant fixed effect to visualize its effect on the bird alert and flight initiation distances using "ggplot2" and "gridExtra" packages available in the R program. Finally, we tested for differences in alert and FID distances between species, habitats and bird activities using a Kruskal Wallis test. Where statistically significant differences were found, a multiple comparison test was performed using a Dunn test, which is appropriate for groups with an unequal number of observations (Zar 2010). All analyses were performed in R ver. 4.1.2. (R Core Team 2021).

Results

Bird observations and behavioural responses of birds

A total of 315 focal bird observations and approaches were conducted in this study, 141 in urban, 85 in peri-urban and 89 in rural habitat. These comprised 103 of Common Bulbul, 92 of Southern Cordon-bleu, 65 of Little Bee-eater and 55 of House Crow (Fig.2a). Combined, target bird approaches were initiated at an average distance of 14.05 m (range: 1–39 m), and birds became alert at an average distance of 9.84 m (range: 3–27 m). The average FID was 7.58 m (range: 1–25 m). Additionally, the average perch height displayed by all species combined was 2.59 m (range: 0–10 m).

During the survey, target birds were initially seen engaged in one of four activities: preening, foraging, calling, and resting (Fig. 2b). We found a significant difference in the frequency of different activity types performed by the four species combined ($\chi^2=19.83$, df = 3, $p<0.05$). Birds were observed engaging in significantly more foraging than preening (Dunn test, $z=-2.53$, $p<0.05$) or resting (Dunn test, $z=-4.12$, $p<0.05$). We detected no difference in these behaviours based on urbanization zone. Furthermore, we found variation in alert responses among species particularly when performing foraging and resting activities: Little Bee-eater showed significantly longer AD when foraging ($\chi^2=42.76$, df = 3, $p<0.05$), and resting ($\chi^2=50.169$, df = 3, $p<0.05$) than the other three bird species (Fig. 3a). Similarly, Little Bee-eater showed significantly longer FID than other bird species during foraging ($\chi^2=57.86$, df = 3, $p<0.05$) and resting activities ($\chi^2=56.386$, df = 3, $p<0.05$; Fig. 3b).

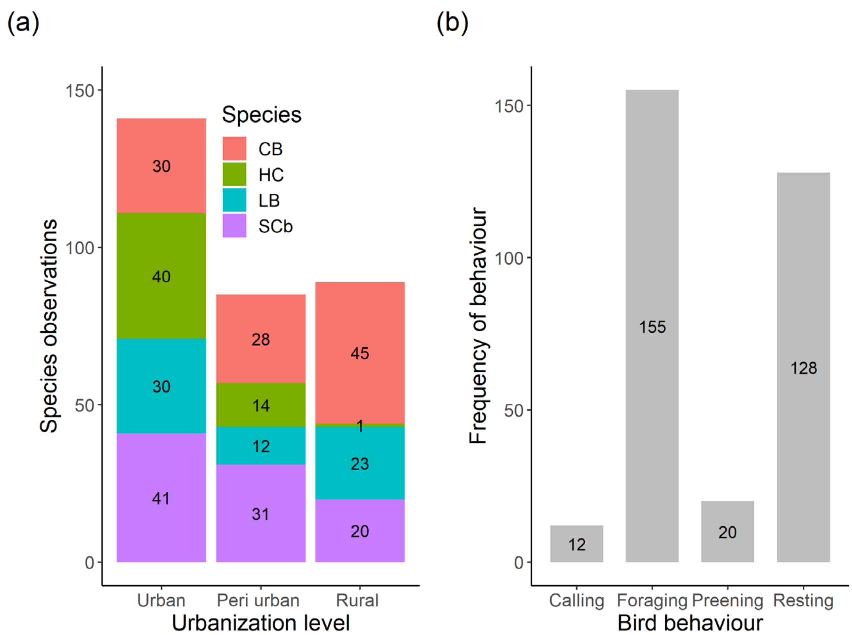


Figure 2. Graphs showing (a) the combined number of focal species encounters by urbanization zone, and (b) the behaviours in which focal birds were initially engaged.

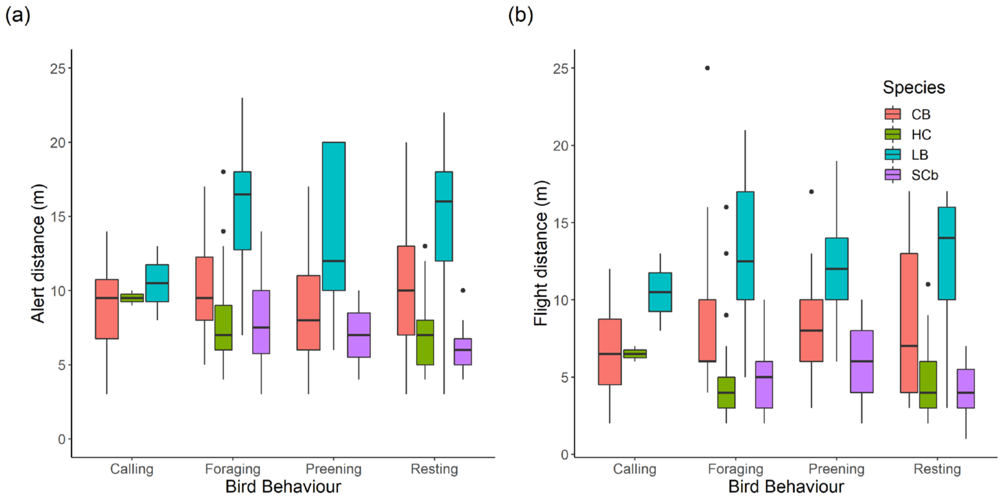
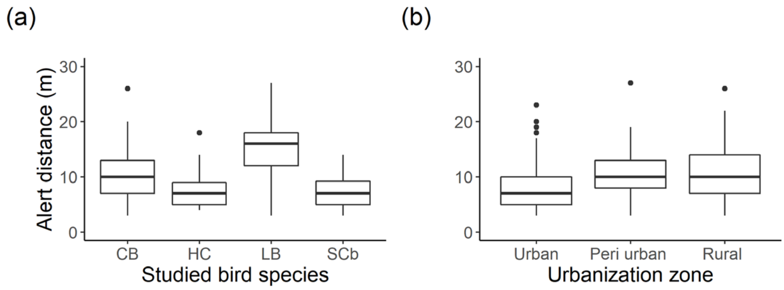


Figure 3. Box plots showing median AD (a) and FID (b) of focal species sampled in relation to behaviour.

Effect of local habitat characteristics and urbanization on alert distance

Alert distance differed significantly by species (Kruskal Wallis test $\chi^2=101.18$, df=3, $p<0.05$; Fig 4a) with Little Bee-eater most alert and Southern Cordon-bleu and House Crow least alert ($z=-0.005$, $p>0.05$). Alert distance also differed significantly across urbanization levels (Kruskal Wallis test $\chi^2=25.17$, df=2, n=315, $p<0.05$, Fig. 4b), being higher in peri-urban and rural than in urban zones. Paired comparisons confirmed differences between the peri-urban and urban zones ($z=4.45$, $p<0.05$) and between rural and urban zones ($z=3.84$, $p<0.05$) but not between the peri-urban and rural zones ($z=0.59$, $p>0.05$). Alert distance was also strongly positively correlated with starting distance ($r=0.819$, $p<0.05$; Fig. 4c).



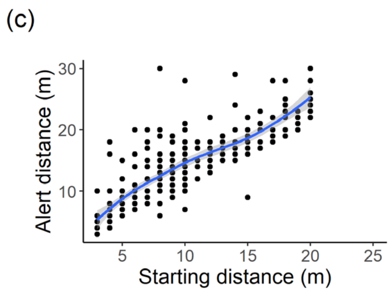


Figure 4. Box plots showing median alert distance by species (a) and urbanization zone (b), and graph showing the relationship between bird alert distance and starting distance (c) in Morogoro municipality. CB=Common Bulbul, HC=House Crow, LB=Little Bee-eater, SCb=Southern Cordon-bleu.

In a combined mixed model, AD was most strongly predicted by starting distance, species and urbanization zone (model AIC = 1470.3, n = 315, $p < 0.05$; Table 1). Across the study area, starting distance increased significantly with AD but this varied by species. Alert distance was mostly likely to be shorter for both Southern Cordon-bleu and House Crow while Little Bee-eater showed significantly longer AD. Conversely, most birds showed generally longer AD in rural and peri-urban zones.

Table 1. Results from best fitting model showing the effect of starting distance, species identity and urbanization levels on alert distance in birds of an urban ecosystem. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, HC = House Crow, LB = Little Bee-eater, SCb = Southern Cordon-bleu.

Model item	Estimate	Std error	z-value	AIC	nparameter	p(z)
Intercept	1.58	± 0.059	26.731	430.7		0.0001 ***
Start distance	0.045	±0.003	15.236	1653.3	1	0.0001 ***
Species				**1515.8**	**3**	**0.0001 *** **
-HC	-0.221	±0.061	-3.607			0.0001 ***
-LB	0.143	±0.049	2.926			0.003 **
-SCb	-0.207	±0.05	-4.105			0.0001 ***
Habitat				**1473.8**	**2**	**0.023 ***
-Peri-urban	0.124	±0.045	2.763			0.005 **
-Rural	0.078	±0.045	1.713			0.086
Pseudo R^2	0.570					
Conditional R^2	0.706					

Effect of environmental variables on flight initiation distance (FID)

Flight initiation distance of birds increased significantly from urban to peri-urban to rural zones (Kruskal-Wallis $\chi^2 = 41.603$, df = 2, $p < 0.05$; Fig. 5a). Paired comparisons also showed significantly longer FID in rural than urban ($z = 6.209$, $p < 0.05$), and in peri-urban than urban ($z = 3.98$, $p < 0.05$), but FID between peri-urban and rural was not significant ($z = -1.939$, $p < 0.05$). Additionally, FID also varied across species (Kruskal-Wallis $\chi^2 = 136.2$, df = 3, $p < 0.05$). The LB showed longer FID than HC ($z = 0.5323$, $p < 0.05$), CB ($z = -5.389$, $p < 0.05$) and SCb ($z = 5.623$, $p < 0.05$). Meanwhile, CB showed significantly longer FID than SCb ($z = 10.247$, $p < 0.05$). The FID was positively correlated with AD ($r = 0.937$, $p < 0.05$).

In a mixed model, urban zone and alert distance strongly influenced FID, with a smaller residual effect of species and perch height (model AIC = 1291.4, n = 315, $p < 0.05$; Table 2). Both, longer AD and higher perch height were strongly positively associated with FID for the studied birds. FID was mostly likely to be shorter for HC and SCb while it was positively associated with the LB. Furthermore, birds were mostly likely to show higher FID in rural and peri-urban zones than in urban. The relationship between FID and perch height was positive but weak overall ($r = 0.291$, $p < 0.05$; Fig 5b).

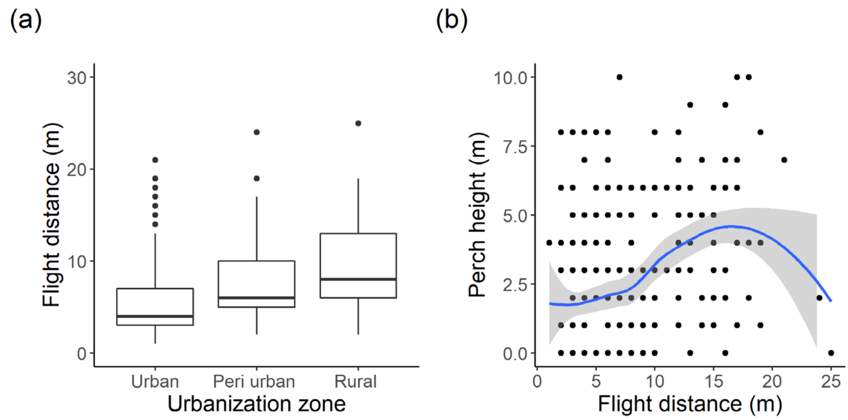


Figure 5. Box plot showing (a) FID based on urbanization zone, and graph showing (b) the relationship between perch height and flight distance.

Table 2. Results from final best fitting GLMM model showing the effect of alert distance, perch height, species identity and urbanization levels on the flight initiation distance by birds in an urban ecosystem. *p < 0.05; **p < 0.01; ***p < 0.001.

Model item	Estimate	Std error	z-value	AIC	n-parameter	p(z)
Intercept	0.920	±0.086	10.593	1291.4		0.0001***
Alert distance	0.089	±0.004	18.27	1593.0	1	0.0001***
Perch height	0.021	±0.009	2.213	1294.3	1	0.026
Species				1292.1	3	0.084
-HC	-0.148	±0.079	-1.856			0.063
-LB	0.044	±0.056	0.799			0.424
-SCb	-0.142	±0.071	-1.980			0.047
Habitat				1300.8	2	0.001**
-Peri-urban	0.111	±0.053	2.071			0.038
-Rural	0.193	±0.052	3.661			0.0001***
Pseudo R2	0.868					
Conditional R2	0.658					

Discussion

This study aimed to describe the pattern of behaviours of birds when approached by a potential predator and to investigate the factors that influence both alert and flight initiation distances in an urban ecosystem. We found bird alertness and flight initiation distance to be consistently variable between species and urbanization types.

House Crow and Southern Cordon-bleu showed the shortest alert and flight distances and Little Bee-eater the longest, with Common Bulbul intermediate. These differences are likely to be related to intrinsic differences in species ecology and behaviour, in the context of an urban landscape. House Crow and Southern Cordon-bleu were most often encountered in the urban core, with Little Bee-eater and Common Bulbul showing preference for less urban zones. Behavioural adaptation towards utilizing resources in areas densely populated by humans may take the form of habituation and reduced wariness of humans approaching (Lord *et al.* 2001, Ikuta & Blumstein 2003). This is despite House Crows being the target for occasional chasing in the study area. Corvids are intelligent birds and may adapt quickly to changing situations (Emery & Clayton 2004, Marzluff & Angell 2005), in this case learning that approaching humans no longer pose a threat (Marzluff *et al*. 2010 for an account of the American Crow *Corvus brachyrhynchos*).

Longer alert and flight distances in peri-urban and rural zones, compared to the urban core, may be related to lower habituation rates as well as a shift in relative encounter rates between species, with Common Bulbul and Little Bee-eater more common outside the urban core and likely to have been attracted to city gardens with trees and related fruit and insect food resources (Rija *et al.* 2014a, Rija *et al.* 2014c). In Berlin, Seattle and Washington, Clucas & Marzluff (2012) found flight initiation distances of most passerines (including corvids) increased from urban core to rural area, and that bird wariness was influenced by human activities to discourage certain 'nuisance' species, such as crows, starlings and woodpeckers in Seattle.

The relationship between alert distance and starting distance is consistent with previous studies in some temperate countries (Cooper 2005, Blumstein 2003), suggesting that birds are vigilant to any unusual behaviour (in this case, purposeful approach) from humans in the urban ecosystem. The positive correlation of FID with alert distance also suggests that foraging birds prefer to escape a potential threat rapidly rather than incur the energy costs of prolonged monitoring (Cooper *et al*. 2015, Samia *et al*. 2017). Other studies elsewhere have reported similar results to ours: strong positive correlations between FID and alert distance (Møller *et al.* 2015, Stankowich & Coss 2005, Eason *et al*. 2006).

There is no documented current human persecution for most of our focal bird species in the study area. However, in cities where human persecution of wildlife is evident, birds are often vigilant and have relatively longer alert distances (average: 15.58 m) than in our study area (average: 9.84 m), perhaps to avoid being caught or killed (Valcarcel & Fernandez-Juricic 2009). Similarly, in the wild where hunting pressure is high, predation risks associated with hunting or poaching disturbance has been reported to increase AD and FID in the Ostrich *Struthio camelus* (Magige *et al.* 2008).

Our study showed a positive, though not pronounced, relationship between FID and perch height whereby most focal birds perching at an intermediate height of 4.8 m were likely to take flight at a distance of 18 m away from an approaching human (Fig. 5b). This result is of interest particularly in promoting conservation of birds and urban bird tourism, especially in areas designated as urban conservation parks. Managers of urban wildlife resources may be able to implement strategies that improve urban bird biodiversity by encouraging planting of urban trees to be used as perches for the birds, facilitating their ability to detect potential danger and forage (Tätte *et al.* 2017). It is not clear how the height distribution (and use) of potential perches may change with urbanization, for example as large trees become less common, and this is a potential topic for future research.

Implications for species conservation in urban landscapes

Understanding the differences in the behaviour of wildlife along urban-rural gradients has important implications for wildlife management in an increasingly urbanized world. Our study of commonly encountered urban species shows apparent differences in habituation and tolerance of human disturbance, reflected in responses to threats and preferences for different urban zones. One conclusion is that maintaining areas of lower human density and trees within the built-up urban matrix, including cultivated gardens and remnant natural habitats, is likely to be important in maintaining populations of urban wildlife, even for seemingly adaptable species of birds.

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