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Opposing effects of vigilance and foraging on escape behaviour in hooded crows

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Abstract

Escape represents an important component of animals' antipredator behaviour entailing both benefits and costs dependent on a moment an animal flees upon predator's approach. In this study, I examined how the level of vigilance and foraging activity affected escape decision in the urban hooded crow *Corvus cornix*, predicting that alert distance (AD) and flight initiation distance (FID) should be positively affected by the level of vigilance and negatively affected by foraging activity, whereas buffer distance (BD) should be negatively affected by the level of vigilance and positively affected by foraging activity. Using LMMs it was shown that percent of time crows allocated to vigilance was positively correlated with AD and FID, whereas foraging activity of crows had negative impact on AD and FID. In addition, both AD and FID were positively related to starting distance (SD), while AD was also positively influenced by tree coverage. BD was positively affected by foraging activity and AD. This study demonstrated that more vigilant birds detected predators earlier, which is in accordance with the major function of vigilance. Also, it was shown that foraging crows delayed their escape, once the predator has been detected, as benefits of delayed flight, such as feeding on a profitable food item or within a profitable patch, may outweigh costs, which is consistent with the optimal escape theory.

Keywords

alert distance, buffer distance, *Corvus cornix*, escape decision, flight initiation distance.

1. Introduction

Escape represents an important component of animals' antipredator behaviour and thus has received much attention in the last couple of decades (Burger & Gochfeld, 1981; Ydenberg & Dill, 1986; Cooper, 1999; Stan-

kowich, 2008; Møller et al., 2019). One measure of escape behaviour is flight initiation distance (FID) — the distance between an approaching predator and prey when the prey starts fleeing — which is conveniently measured as the distance between an approaching human and escaping animal (Cooper et al., 2003; Cooper & Blumstein, 2015). When quantified this way, escape behaviour can be evaluated in the context of benefits and costs it brings in a given moment, with a number of factors affecting the economy of escape. For example, foraging individuals may delay their escape, i.e., flee at shorter distance when food obtaining outweighs costs of delayed escape (Cooper et al., 2003), whereas individuals guarding their young may flee at longer distances to secure survival of offspring (Ciuti et al., 2008). In addition, animals escape at shorter distances when they are located closer to a refuge (Dill & Houtman, 1989; Cooper & Wilson, 2007), when the vegetation cover is denser (Cooper, 2003; Cooper & Whiting, 2007), or when they are approached in urban compared to rural habitats (Møller, 2008; Uchida et al., 2016).

Escape decisions also greatly depend on the distance at which prey become alerted due to an approaching predator — alert distance (AD) — with prey typically escaping at greater distances if alerted earlier (Blumstein et al., 2005; Stankowich & Coss, 2007; Lagos et al., 2009). Such a relationship may be a consequence of costs incurred by time and energy expenditure needed for monitoring an approaching predator, as proposed by the ‘flush early and avoid the rush hypothesis’ (Blumstein, 2010; Samia et al., 2013), but also of an increasing attack probability as the predator continues approaching (Cooper & Blumstein, 2014). Alert distance increases with the distance at which a predator starts approaching — starting distance (SD) — which, due to above mentioned reasons, positively influences FID as well (Blumstein, 2003; Cooper et al., 2009; Tätté et al., 2018).

Various aspects of the economy of escape have been studied, e.g., the effect of life history traits (Blumstein, 2006; Møller, 2014), human disturbance (Fernández-Juricic et al., 2005; Burger et al., 2010; Li et al., 2011), habitat type (Stankowich & Coss, 2007; Davey et al., 2019; Uchida et al., 2020), distance to refuge (Cooper & Samia, 2018; Morelli et al., 2022), or group size (Braumoh et al., 2018; Morelli et al., 2019). However, not many studies assessed how behaviours of individuals prior to and during approach affect escape decisions. For example, Møller et al. (2008) found that singing male passerines fled at longer distances compared to nonsinging individuals, and that the difference was greater for birds with more exposed

posts, implying that such a risky display behaviour was compensated by earlier flight. Similarly, vigilance, referring to monitoring the environment to obtain information on predators, competitors, and food sources, can affect escape (Beauchamp, 2015a). Animals frequently interrupt their everyday activities, such as foraging, preening or sleeping, to scan their surroundings (Rattenborg et al., 1999; Fernández-Juricic et al., 2004; Randler, 2005). While scanning, individuals may detect predator and, thus, those investing more time to vigilance may become alerted earlier and consequently initiate flight earlier (Cresswell et al., 2003; Fernández-Juricic & Schroeder, 2003; Beauchamp, 2015b). However, such a relationship between vigilance and FID is not always straightforward as more vigilant individuals may opt for delayed flight (Reimers et al., 2011; Tätte et al., 2019). In addition, escape can be influenced by foraging activity as foraging individuals may have motivation to take more risk when feeding in a rich patch or need to satiate hunger (Damsgård & Dill, 1998; Cooper et al., 2003; Killen et al., 2011), although more successful foragers may be better at detecting predators and respond earlier to an approaching threat (Cresswell et al., 2003). Hence, different behaviours may have similar or opposing impact on escape decision in a given moment.

In this study, I examined how the level of vigilance and foraging activity influenced escape behaviour in urban hooded crows (*Corvus cornix*). Simultaneous assessment of such conflicting activities prior to predator's approach may help better understanding of escape decisions in prey species. For example, feeding activity can modify the effect of vigilance, due to energy individuals gain from ingested food, leading to delayed escape even though a predator had been detected in earlier stages of approach. Being a successful urban colonizer, the hooded crow (hereafter crow) is a convenient model for a cost-effective study on escape behaviour as it is highly visible in the city environment, habituated and tolerant to humans (Vuorisalo et al., 2003), but it still reacts to approach by escaping (Tätte et al., 2020). The objectives of this study were to examine whether the level of vigilance prior to predator approach, as well as foraging activity during approach, affected AD, FID and buffer distance (BD), while controlling for other confounding variables. Buffer distance, also known as assessment interval, is the distance between FID and AD, i.e., that is an interval during which prey evaluate risk and make a decision on escape (Fernández-Juricic et al., 2002; Cooper & Blumstein, 2015). Longer BD implies that an individual delayed flight as more

time passed between a moment it became alerted and a moment it escaped. Therefore, I predicted that (1) AD should be positively affected by the level of vigilance prior to approach and negatively affected by foraging activity during approach; (2) FID should be also positively affected by the level of vigilance and negatively affected by foraging activity; and (3) BD should be negatively affected by the level of vigilance and positively affected by foraging activity.

2. Material and methods

2.1. Fieldwork

The study took place in Belgrade (Serbia), from 19 September to 10 November 2022. Data were collected on 10 locations within the city representing public parks or green maintained areas; all study sites are used for recreational and leisure activities, as well as dog walking (Figure 1; characteristics of the study sites are provided in Table 1 and in Table A1 in the Appendix). Each location was visited two to four times, with interval between subsequent visitation ranging from 10–26 days. Data were collected during daylight, in the period 0800–1600 h, in the absence of wind and rain. The study was conducted during two months of the fall in order to avoid previously demonstrated seasonal effect on escape behaviour of crows (Novčić & Parača, 2021).

Upon arrival to a study location, I searched for crows being active on the ground (for example, walking, foraging, preening) and chose a focal bird that was far enough not to be disturbed by my presence (approx. 20–40 m). I aimed to reduce the possibility of observing the same individual more than once in two ways: (1) walking along transects (pedestrian trails) in one direction, recording birds I encountered, or (2) observing the entire area from a couple of vantage points, which was possible in the case of small parks, and approaching birds in different sections within the study location. With the goal of obtaining information on the level of vigilance prior to approach, the focal bird was continuously observed for 60 s, when the sequence of behaviour was dictated on a voice recorder. I distinguished the following categories of behaviour: (1) vigilant, (2) feeding, (3) stationary, (4) walking, (5) running, (6) flying, (7) social interaction, (8) self-maintenance and (9) vocalization. The crow was considered to be vigilant while in posture with the upright head scanning its surroundings, watching ahead of or above itself

Table 1.

Description of the study locations, including the approximate area of the study locations, and sample size (N) at each location.

Name	Description	Area (ha)	N
1. Zvezdara	Urban forest outside the city centre intersected by walking trails, with open grassland areas and children playgrounds.	5.5	10
2. 'Hala Pionir' area	Green area close to the sport complex 'Hala Pionir'. It consists of extensive grassland with scattered trees, a small wooded area, as well as a dog run.	2.3	12
3. Šumice	Remains of an urban forest close to the city centre intersected by walking trails, with children playgrounds and a dog run.	11.1	30
4. Tašmajdan	Park in the city centre with high tree cover of conifers and deciduous trees, extensive areas of maintained grasslands with decorative flowers, intersected by walking trails. Contains children playgrounds, a dog run and water fountain. As a spatial cultural-historical unit, it is under the state protection.	9.5	29
5. Manjež	Park in the city centre with extensive pavement, grasslands with decorative flowers, shrubs and high tree cover of conifers and deciduous trees. It also contains a children playground.	2.2	15
6. Karađorđev Park	Park in the city centre with grasslands, high tree cover of conifers and deciduous trees, shrubs, a children playground and dog run.	2.3	10
7. Hajd Park	Park at the edge of the city centre, it consists of woodland area with trails for walking and running, as well as children playground.	18.3	13
8. Topčider	Forested park outside the city centre. It consist of wooded areas with high tree cover of conifers and deciduous trees, shrubs, grasslands, several ponds, children playgrounds, as well as the Topčiderska River running through the park. As a spatial cultural-historical unit, it is under the state protection.	8.3	11
9. Kalemegdan	Park in the city centre with open grasslands, grasslands with decorative shrub and flowers, areas with high tree cover of conifers and deciduous trees, children playgrounds, walking trails, the old town fortress, galleries and restaurants. It is under the state protection.	28.5	23
10. Ušće	Extensive green area close to the city centre, at the confluence of the rivers Sava and Danube. It consists of wooded areas, open grasslands with scattered deciduous and coniferous trees, children playgrounds, walking and bicycle trails.	31.2	41

The park numbers correspond to those in Figure 1.

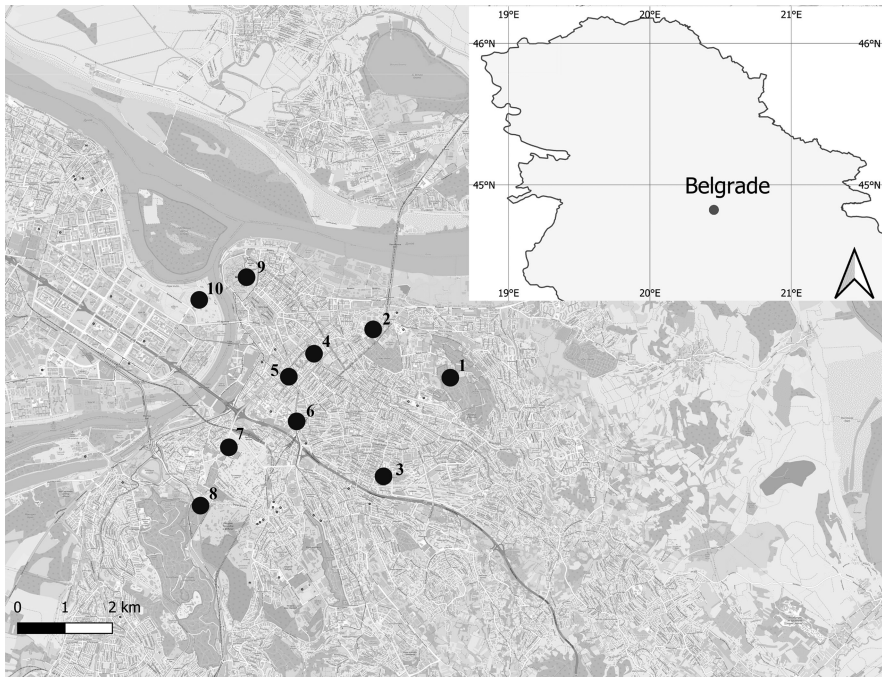


Figure 1. Map of Belgrade (Serbia) showing the study locations.

and/or moving head from side to side. After recording behavioural data I began approaching the focal bird following the protocol of Blumstein (2003), which was slightly modified: I directly approached the bird at a steady speed, approximately one step/s (one step approx. 0.5 m), wearing dark clothes, dictating the number of steps on the voice recorder. I stopped when the bird began fleeing and measured FID using a laser range finder; counting the number of steps I approximated AD (in the moment the bird started monitoring my approach), as well as SD. I also notified whether the focal bird was engaged in food obtaining during the approach (e.g., pecking, digging) and/or food manipulation (e.g., swallowing, carrying food in the beak). If the focal bird started moving fast, or became alerted or fled due to reasons other than my approach, such as activity of nearby pedestrians or dogs, I stopped recording. In addition, I stopped recording if during approach the focal crows engaged in activities other than feeding, such as social interactions, preening, bathing, that could additionally divert their attention from my approach.

During the field work, I also measured environmental variables that could affect escape — time of recording, air temperature, flock size and vegetation

cover (Fernández-Juricic et al., 2001, 2002; Burger et al., 2010; Morelli et al., 2019). Temperature was measured with a digital thermometer, the flock size was determined by counting all crows within a 10 m radius from the focal bird, whereas the vegetation cover was estimated following the protocol of Prodon & Lebreton (1981), when the percentage of area covered with grass, shrub or horizontal projection of foliage of the tree canopy was approximated; vegetation variables were estimated in a 30 m radius from the point of escape.

From the recorded material, for each focal individual I estimated three common measures of vigilance: scan frequency (the number of scans per minute), average scan duration (mean duration of all scans, measured in seconds, throughout an observation session), and percent of time allocated to scanning during an observation session (Beauchamp, 2015a). In addition, I also estimated the percent of time each focal individual allocated to above mentioned behavioural categories.

2.2. Statistical analyses

To examine the effect of vigilance and foraging on AD, FID, and BD, I used linear mixed models (LMMs). Prior to analysis, data were checked for collinearity using Pearson coefficient of correlation; as the average scan duration and percent of time being vigilant were highly correlated ($r_p = 0.820$, $p < 0.001$), only the percent of time allocated to scanning was included in analyses (Zuur et al., 2009). Multicollinearity was additionally checked using the variance inflation factor (VIF) — for all variables of interest, in all models, VIF was below 1.5, indicating low collinearity among predictors (Zuur et al., 2010). In addition, as temperature range was relatively low, without extremely high or low temperature (12–24°C), the temperature was not included in analyses. Also, the variable on flock size was represented as a binary variable — ‘single’ or ‘in group’ — as 60% of focal birds was single during approach. The models examining AD and FID as predictors included: SD, the scanning frequency, the percent of time being vigilant, foraging activity during approach (a binary variable coded one if the bird had been foraging, and zero if had not), time of recording (expressed as a continuous variable representing the number of hours from sunrise), the group status, and vegetation cover; to account for specific variation on each study location at time of recording, the date of observation nested within the location was treated as a random factor. The model on FID included SD instead

of AD due to high positive correlation between FID and AD ($r_p = 0.922$, $p < 0.001$) (Tätte et al., 2018). The model examining BD was similar to the previous two models, with the exception of SD being substituted with AD. To improve the model fit, FID and (BD + 1) were Box-Cox transformed (Mangiafico, 2016). In addition, to solve the problem with singular model fit, all models were fitted using a weakly informative prior for the covariance matrix (Chung et al., 2013; Bolker, 2015). The underlying assumptions of the models were met, which was confirmed using diagnostic plots (Q-Q plots and residuals plotted versus fitted values) (Zuur et al., 2009).

In this study, the level of vigilance in focal birds was assessed in the period prior to approach, whereas the foraging activity was recorded during it. Such a protocol was applied as crows rapidly switched among behavioural states; for example, some birds would intensely peck at the beginning of an observation session, but then completely ceased during my approach. In fact, such a mismatch in feeding activities before and during approach occurred in 36% of focal individuals. To check whether feeding activity of crows prior to approach affected their escape behaviour, I also ran LMMs where feeding activity of birds during approach was replaced with their feeding activity before approach, expressed either as a binary variable or percent of time spent feeding; the models included all other predictors as explained above.

All statistical analyses were carried out using R v4.2.1. (R Core Team, 2022), using the packages: lme4 (Bates et al., 2015), blme (Chung et al., 2013), car (Fox & Weisberg, 2019), predictmeans (Luo et al., 2021), MASS (Venables & Ripley, 2002) and ggplot2 (Wickham, 2016).

3. Results

Escape behaviour of 194 individuals was measured. On average, prior to approach, focal individuals spent 33% of time feeding, 27% walking, 22% being stationary and 17% of time being vigilant; crows devoted less than 1% of time to other behavioural categories. The mean value of AD (\pm SD; range) was 12.96 m (6.04 m; 3–32.5 m), of FID was 10.00 m (6.30 m; 1–32 m), and BD 2.96 m (2.44 m; 0–13.5). Descriptive statistics on predictors is presented in Tables 2 and A1. Percent of time crows allocated to vigilance prior to approach was positively correlated with AD ($\beta = 3.647$, $SE = 1.764$, $p = 0.039$), whereas foraging activity of birds during approach was negatively correlated with AD ($\beta = -4.147$, $SE = 0.585$, $p < 0.001$). In addition,

Table 2.

Descriptive statistics on predictors included in analyses of alert distance, flight initiation distance and buffer distance.

Variable	Mean (SD)	Range
Starting distance (m)	22.93 (6.11)	12–37.10
Alert distance (m)	12.96 (6.04)	3–32.50
Scan frequency (s^{-1})	0.07 (0.04)	0–0.22
Percent of time scanning (%)	16.80 (15.79)	0–80.83
Time of recording (h)	5.07 (1.81)	1.78–9.38
Grass cover (%)	76.12 (20.66)	5–100
Shrub cover (%)	4.67 (8.89)	0–40
Tree cover (%)	46.49 (20.01)	0–100

Time of recording is expressed as a continuous variable representing the number of hours from sunrise. Mean values (with standard deviation (SD)) are presented.

AD was associated with SD ($\beta = 0.396$, $SE = 0.059$, $p < 0.001$) and tree coverage ($\beta = 2.997$, $SE = 1.420$, $p = 0.035$); other variables were not statistically significant (Table 3, Figures 2a and 3a). Similarly, percent of time allocated to vigilance was positively correlated with FID ($\beta = 0.909$, $SE = 0.366$, $p = 0.013$), while association between foraging activity and FID was negative ($\beta = -0.871$, $SE = 0.121$, $p < 0.001$); FID was also positively correlated with SD ($\beta = 0.076$, $SE = 0.012$, $p < 0.001$), (Table 3, Figures 2b and 3b). Buffer distance was positively associated with foraging activity ($\beta = 0.394$, $SE = 0.124$, $p = 0.001$) and AD ($\beta = 0.029$, $SE = 0.012$, $p = 0.015$); no other variables reached statistical significance (Table 3, Figure 2c).

When feeding activity measured in the period prior to approach was substituted for the feeding activity during approach, the significant correlation between components of escape behaviour and foraging was lost in statistical models. Estimates and p -values are given for the feeding activity expressed as a binary variable or percent of time spent feeding, respectively. FID: $\beta = 2.377$, $SE = 1.739$, $p = 0.172$, and $\beta = 1.197$, $SE = 1.433$, $p = 0.404$; AD: $\beta = 0.095$, $SE = 0.340$, $p = 0.779$, and $\beta = 0.065$, $SE = 0.280$, $p = 0.818$; BD: $\beta = 0.452$, $SE = 0.296$, $p = 0.127$, and $\beta = 0.094$, $SE = 0.244$, $p = 0.188$.

Table 3.

Estimated parameters for predictors included in the mixed effect models examining alert distance (AD), flight initiation distance (FID) and buffer distance (BD): starting distance (SD), foraging status (1, foraging; 0, non-foraging), percent of time the focal bird allocated to scanning, scanning frequency, time of recording, group status of individual (single or in group), percent of area covered with grass, percent of area covered with shrub, percent of area covered by foliage projection of the tree canopy.

Predictor	Coefficient	SE (Coef)	<i>p</i>
Estimates for AD			
SD	0.396*	0.059*	<0.001*
Foraging	-4.147*	0.585*	<0.001*
Percent scanning	3.647*	1.764*	0.039*
Scanning frequency	-4.080	6.221	0.512
Time of recording	-0.047	0.178	0.790
Group status (single)	0.153	0.550	0.781
Grass cover	1.093	1.551	0.481
Shrub cover	4.473	3.391	0.187
Tree cover	2.997*	1.420*	0.035*
Estimates for FID			
SD	0.076*	0.012*	<0.001*
Foraging	-0.871*	0.121*	<0.001*
Percent scanning	0.909*	0.366*	0.013*
Scanning frequency	-0.503	1.291	0.697
Time of recording	0.014	0.036	0.703
Group status (single)	-0.098	0.114	0.390
Grass cover	0.438	0.320	0.172
Shrub cover	0.833	0.699	0.233
Tree cover	0.561	0.291	0.054
Estimates for BD			
AD	0.029*	0.012*	0.015*
Foraging	0.394*	0.124*	0.001*
Percent scanning	-0.457	0.348	0.188
Scanning frequency	-0.057	1.224	0.963
Time of recording	-0.020	0.034	0.553
Group status (single)	0.124	0.107	0.248
Grass cover	-0.488	0.283	0.085
Shrub cover	-1.194	0.637	0.061
Tree cover	0.011	0.258	0.965

Estimates for the group status are provided for single individuals with respect to those being in a group.

*Significant effect.

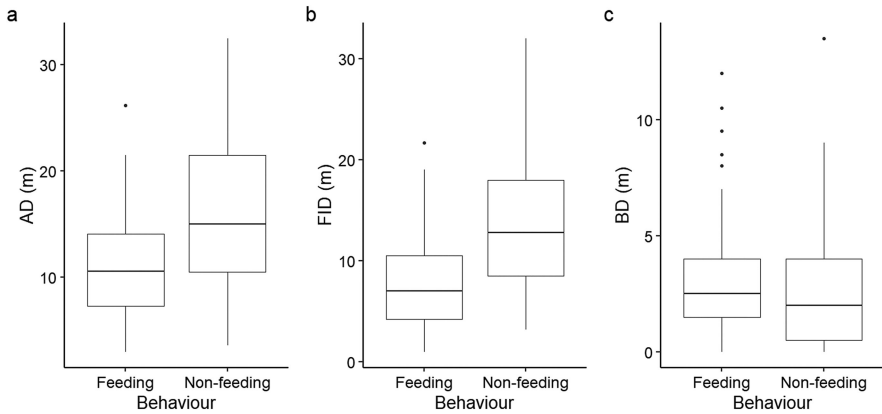


Figure 2. Difference in (a) alert distance (AD), (b) flight initiation distance (FID) and (c) buffer distance (BD) between crows actively feeding during approach and those not feeding.

4. Discussion

This study demonstrates opposing effects of vigilance and foraging on components of escape behaviour in the hooded crow. As vigilance is aimed at detecting threats from the environment, animals investing more time to vigilance may detect an approaching predator earlier (Beauchamp, 2015b). Indeed, AD in crows increased with the proportion of time focal birds being spent vigilant prior to my approach. Although many of the vigilance bouts

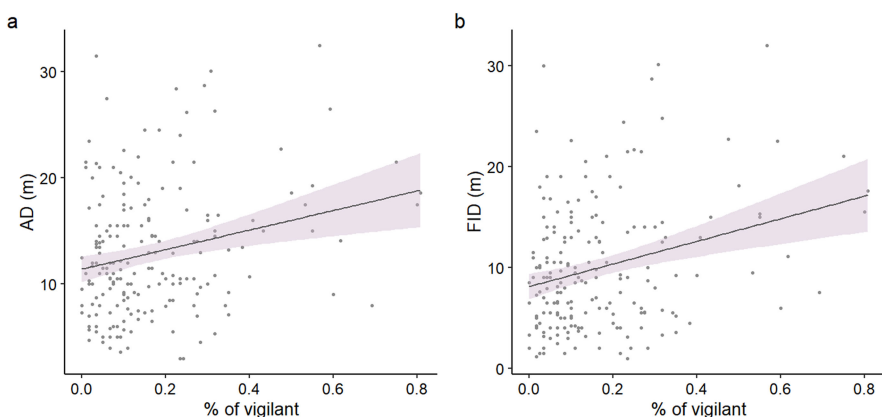


Figure 3. (a) Alert distance (AD) in relation to percent of time crows allocated to vigilance; (b) flight initiation distance (FID) in relation to percent of time crows allocated to vigilance. Shaded area represents 95% confidence interval.

were induced by pedestrians or behaviour of other crows (e.g., flight or calls), it seems that overall vigilance did help earlier predator detection. In addition, more vigilant birds escaped at a longer distance, which could be a consequence of earlier detection. Even though the model examining FID did not include AD, there was a strong positive correlation between these two variables. Animals detecting predators earlier are typically those escaping earlier, as physiological costs of monitoring an approaching predator once it had been detected increase with time, along with the increasing attack probability as the predator approaches the individual (Blumstein, 2010; Samia & Blumstein, 2015; Cooper & Blumstein, 2014). In my study, the level of vigilance did not influence BD of crows, implying that more vigilant birds most likely escaped earlier due to earlier detection of predators.

Other studies, however, provided diverse findings with respect to the role of vigilance in escape decision. Analysing the relationship between vigilance and pre-detection distance for a range of avian species in Europe, Tatte et al. (2019) concluded that vigilance did not play an important role in predator detection, most likely due to high level of anthropogenic disturbance in urban habitats, which prevented birds to react to approaching threat. Moreover, in the same study the proportion of time being vigilant prior to approach positively affected assessment interval (i.e., BD), implying that vigilant individuals also devoted more time to monitor an approaching predator and thus escaped at shorter distances. The authors reasoned that increased level of distraction in urban environments overburdens the cognitive system of birds, which in turn need more time to assess risk. In another study, duration of quadrupedal vigilance of Daurian ground squirrels (*Spermophilus dauricus*) positively affected AD, indicating that this type of vigilance was associated with earlier detection of predators. Nevertheless, more vigilant squirrels delayed escape and fled at shorter distances (Shuai et al., 2022).

In addition to vigilance, foraging activity of crows during approach affected all three measures of escape — actively foraging birds became alerted and escaped at a shorter distance, whereas a period of risk-assessment increased. Cresswell et al. (2003) showed that in chaffinches (*Fringilla coelebs*) response time to approaching predator — measured as time to freezing or escape — decreased as pecking rates increased, implying that foraging does not necessarily interfere with predator detection and earlier escape. However, active searching or handling of food may have deterred attention

of crows leading to slower detection of predators. Also, behaviours of foragers may be riskier if they are hungry or resources are abundant (Damsgård & Dill, 1998; Lagos et al., 2009), so the benefits of delayed escape may outweigh costs. Thus, Bonaire whiptail lizards (*Cnemidophorus murinus*) escaped at shorter distances in trials in which food was supplied (Cooper et al., 2003). Similarly, wild hyraxes (*Heterohyrax brucei* and *Procavia capensis*) and oystercatchers (*Haematopus ostralegus*) exhibited shorter FID when feeding than resting or being vigilant (Mbise et al., 2019; Azaki & Cresswell, 2021). The fact that feeding crows delayed their escape once the predator has been detected (reflected through greater BD) is consistent with the optimal escape theory (Ydenberg & Dill, 1986). Such delayed flight may be a consequence of willingness of animals to take additional risk in order to continue feeding on a profitable food item or within a profitable patch (Cooper, 2000).

Starting distance was a positive predictor of both AD and FID, whereas AD was a positive predictor of BD. The influence of SD on escape behaviour is well documented in a wide range of taxa (Blumstein, 2003; Cooper, 2005; Engelhardt & Weladji, 2011; Samia et al., 2013). Typically AD and FID increase with SD for the reasons explained by the above mentioned ‘flush early and avoid the rush hypothesis’. Once an approaching predator has been detected, any prolonged monitoring, as the approach continues, incurs additional costs in terms of time and energy (Blumstein, 2003, 2010). Nonetheless, the positive relationship between SD, AD and FID may be partially artefactual due to mathematical constraints arising from the fact that SD is always greater or equal to AD and FID (Dumont et al., 2012), due to approach at short SD that is close to optimal FID, or spontaneous movement of prey individuals occurring during approach (Cooper, 2008). The latter could be responsible for significant, although weak positive effect of AD on BD.

Vegetation also influenced escape behaviour of crows as AD increased with the canopy cover around the focal bird. Vegetation cover may interfere with perception of visual cues from the environment leading to delayed detection of predators (Burger & Gochfeld, 1981). In addition, vegetation can provide concealment and additional refuges reducing perceived risk of predation, which may also delay predator detection and escape (Fernández-Juricic et al., 2001; Cooper, 2003; Camp et al., 2012) Therefore, the positive relationship between AD of crows and the canopy cover is surprising, as it would be expected that in woody areas crows detected approach with a delay,

either due to lower visibility or lower perceived predation risk. One possible explanation is that crows, due to lower visibility, payed more attention to auditory cues, such as sound produced by my approach, which put them in alert state earlier. Also, trees may obstruct detection of other predators making birds less tolerant to threats (Fernández-Juricic et al., 2002).

According to my knowledge, this study is one of few (e.g., Cresswell et al., 2003) examining simultaneous effects of two types of behaviour on escape decision in animals. It shows that vigilance and foraging act jointly, with differing effects on the moment an individual initiates escape, implying that these variables represent important determinants of escape behaviour. In addition, this study indicates that, in some species, a behavioural state of individuals before approach may not be a good predictor of distances at which predators are detected or prey start fleeing. It should be noted, however, that several confounding variables were not controlled during data collection, imposing some limitations to this research. For example, as identity of focal individuals could not be determined, a certain level of pseudoreplication might have occurred, influencing both vigilance and escape behaviour through differences in personality traits of sampled crows (Cooper, 2009; Carrete & Tella, 2010; Edwards et al., 2013). Similarly, the quantity and quality of food in parks, which were unknown, could also affect vigilance and, consequently, detection and escape distances (Beauchamp, 2015b).

Crows are known for their cognitive abilities and ecological flexibility allowing them to successfully colonize urban ecosystems (Emery, 2004, 2006; Kövér et al., 2015). They are capable of dynamic risk assessment and adjustment of behavioural responses depending on the properties of attack and environmental variables (Tätte et al., 2020). This study identified vigilance and foraging as important determinants of crows' escape behaviour, although the effects of anthropogenic disturbance (e.g., noise, pedestrian traffic, pets) or food type (anthropogenic vs. natural) on escape decisions in this urban species remains unknown and should be considered for future research.

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Table A1. Descriptive statistics on predictors included in analyses of alert distance, flight initiation distance and buffer distance, per study location.

Location	Variable							
	Starting distance (m)	Alert distance (m)	Scan frequency (s^{-1})	Percent of time scanning (%)	Time of recording (h)	Grass cover (%)	Shrub cover (%)	Tree cover (%)
1. Zvezdara								
Mean (SD)	21.83 (5.18)	14.73 (5.46)	0.07 (0.03)	21.92 (14.23)	4.64 (1.58)	49.3 (25.62)	9.2 (8.4)	91 (5.38)
Range	12–31.9	6.5–22.6	0.03–0.12	2.5–50	2.43–7.07	10–80	0–20	80–100
2. “Hala Pionir” area								
Mean (SD)	22.32 (4.81)	11.2 (4.81)	0.06 (0.02)	87.5 (7.66)	12.78 (7.66)	4.34 (2.12)	9 (10.82)	52.5 (22.78)
Range	15.6–29.8	7.3–18	0.03–0.1	4.17–27.5	1.78–8.72	0–30	50–100	10–80
3. Šumice								
Mean (SD)	20.01 (4.04)	11.83 (4.13)	0.06 (0.04)	15.58 (14.14)	3.98 (0.99)	82.67 (13.65)	2.13(4.27)	61.5 (18.31)
Range	12–27.9	5–21.5	0–0.18	0–55	2.22–5.88	30–100	0–20	30–90
4. Tašmajdan								
Mean (SD)	18.67 (3.79)	8.21 (3.28)	0.07 (0.04)	18.22 (18.16)	5.74 (1.34)	73.79 (16.49)	2.27 (5.49)	40 (15.76)
Range	12.5–26	3–16.5	0–0.15	0–67	3.3–7.6	40–100	0–20	10–80
5. Manjež								
Mean (SD)	19.75 (5.01)	7.95 (3.29)	0.06 (0.02)	13.5 (10.36)	5.28 (0.95)	58.67 (17.83)	8.73 (7.78)	38 (18.81)
Range	13.5–31.5	4.5–14.5	0.02–0.1	16.67–35	3.95–7.5	30–90	0–20	10–70

Table A1.
(Continued.)

Location	Variable							
	Starting distance (m)	Alert distance (m)	Scan frequency (s^{-1})	Percent of time scanning (%)	Time of recording (h)	Grass cover (%)	Shrub cover (%)	Tree cover (%)
6. Karadordjev Park								
Mean (SD)	19.82 (3.59)	9.32 (3.08)	0.08 (0.03)	11 (8.97)	4.39 (1.6)	57.5 (25.42)	3.7 (8.89)	33 (17.35)
Range	14.5–25.5	4–16	0.02–0.12	0–30	2.43–6.8	5–90	0–30	10–60
7. Hajd Park								
Mean (SD)	26.41 (4.89)	16.18 (3.94)	0.08 (0.04)	23.85 (22.15)	4.66 (2.05)	80.77 (15.42)	2.31 (7.99)	66.92 (16.35)
Range	17.5–33.5	11–27.5	0.02–0.15	0.83–80	1.88–6.93	50–100	0–30	30–90
8. Topčider								
Mean (SD)	31 (2.67)	22 (6.63)	0.09 (0.03)	32.83 (20.98)	4.37 (0.6)	83.63 (8.81)	21.81 (13.36)	57.27 (13.54)
Range	28–37.1	10–30.1	0.04–0.13	7.5–80.8	3.85–6.23	70–90	0–40	40–80
9. Kalemegdan								
Mean (SD)	20.43 (4.32)	10.9 (3.6)	0.08 (0.05)	14.06 (9.15)	5.81 (2.51)	70.87 (20.19)	5.43 (9.5)	41.3 (15.41)
Range	12.5–29.5	5–17.2	0.03–0.22	1.67–38.3	2.25–9.38	30–90	0–40	10–70
10. Ušće								
Mean (SD)	28.58 (5.18)	17.65 (5.62)	0.06 (0.03)	13.88 (14.82)	5.6 (1.86)	86.58 (17.34)	0.32 (1.55)	27.44 (20.45)
Range	14.9–35	8.1–32.5	0–0.15	0–75	1.9–8.62	20–100	0–10	0–100

Time of recording is expressed as a continuous variable representing the number of hours from sunrise. Mean values (with standard deviation: SD) are presented. The park numbers correspond to those in Figure 1.