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Seasonal differences in escape behaviour in the urban hooded crow, *Corvus cornix*

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Abstract. This study examined escape behaviour of hooded crows, *Corvus cornix*, in an urban environment, in Belgrade, Serbia, with the goal of assessing the effect of breeding season on components of escape behaviour; flight initiation distance (FID), distance fled (DF), and escape method (flying *vs.* running/walking). Using GLMMs, it was shown that FID was longer during the breeding season, and increased with alert distance. DF was significantly influenced by escape method, with birds escaping for distances greater than 10 m more often when flying, whereas escape method itself was significantly influenced by FID, with birds escaping more often by flying at greater distances from an approaching predator. The majority of individuals (78%) fled for distances < 10 m after initiating escape, and escaped by walking or running (67%). Our results show that hooded crows, although adapted to living in highly urbanized environments, may be more risk-averse during the breeding season, which may allow them to more successfully take care of their young.

Key words: flight initiation distance, distance fled, escape method, breeding season, crows

Introduction

When approached by a predator, an individual must make a decision on whether to flee or not, depending on the fitness benefits and costs of escape in a given moment (Ydenberg & Dill 1986, Lima & Dill 1990). An obvious benefit of fleeing is avoidance of death or injuries inflicted by a predator. However, if an animal escapes too early, e.g. when a predator is at a safe distance and does not represent an immediate threat, it loses an opportunity to engage in fitness enhancing activities, such as foraging, mating or brood protection (Cooper 1999, 2000, de Jong et al. 2013). The distance between an approaching predator and prey at which prey initiate escape, termed flight initiation distance (FID), is a common measure of trade-off between antipredator behaviour and other activities (Cooper 2015). Because animals

respond to human-caused disturbance as they would to predators (Frid & Dill 2002), FID is typically assessed as the distance at which animals flee from approaching humans (e.g. Burger et al. 1989, Blumstein 2003, Møller 2014).

Many factors affect escape decision in animals (Stankowich & Blumstein 2005). In general, animals escape at longer distances when approached directly, at faster speed, and/or by a greater number of predators (Burger & Gochfeld 1981, Geist et al. 2005, Bateman & Fleming 2011). Also, prey may exhibit longer FID when farther away from a refuge (Engelhardt & Weladji 2011, Guay et al. 2013), in open habitats with reduced cover of vegetation (Cooper 2003), and in rural compared to urban environments (Møller 2008, Møller et al. 2015). By contrast, some activities, such as mate guarding and feeding, as well as morphological

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traits, such as cryptic colouration typically delay escape of prey, leading to shorter FID (Cooper 1999, Cooper et al. 2003, Møller et al. 2019). Some variables, however, may lead to an increase or decrease in FID depending on environmental or social conditions. For example, prey might escape earlier when in larger groups due to collective detection of predators (Tätte et al. 2018, Morelli et al. 2019), or escape may be delayed due to dilution of predation risk or collective defence (Stankowich & Blumstein 2005, Mikula et al. 2018).

As well as the biological attributes of the prey, and the environmental circumstances at a given moment, the distance at which a predator starts approaching prey, the starting distance, strongly affects the escape decision in a wide range of taxa (Blumstein 2003, Cooper et al. 2009, Engelhardt & Weladji 2011). Typically, prey escape earlier when starting distance is greater (Blumstein 2003). Therefore, some properties of escape behaviour are a consequence of the research procedure, specifically the initial distance between an approaching human and focal animal. Moreover, starting distance strongly influences the alert distance (AD), the distance at which an animal becomes alert due to an approaching threat, which itself exerts a strong positive influence on FID (Blumstein et al. 2005, Stankowich & Coss 2007, Samia et al. 2013). For this reason, these variables need consideration when investigating decision-making during predator-prey encounters (Blumstein et al. 2015a).

In addition to FID, distance fled (DF), the distance a prey individual flees before stopping if not pursued by a predator (Cooper & Blumstein 2015), as well as escape method, also represent important determinants of escape behaviour. Greater distance fled increases the chances of successful escape, but entails greater costs in terms of the expenditure of energy and time (Fernández-Juricic et al. 2002, Tätte et al. 2018). Different escape methods vary in relation to the benefits and costs experienced by escaping animals. For example, ground foraging birds may opt to escape by running or flying; running requires less energy but put birds under greater predation risk, whereas flying is energetically more demanding, but reduces predation risk (Rodríguez-Prieto et al. 2008). Therefore, depending on the risk assessment in a given moment, animals are expected to adjust not only the distance from a predator at which they commence their escape, but also the escape method and the distance traversed while escaping.

In this study we examined escape behaviour of hooded crows *Corvus cornix* Linnaeus, 1758 (hereafter crows) in an urban environment. We aimed to assess the effect of breeding season on components of escape behaviour – FID, DF, and escape method, while controlling for other confounding variables. Although escape behaviour has been examined in various vertebrates, there is little information on how breeding season influences escape decisions in birds. During the breeding season, birds may take more risk due to increased costs of parental care (Clutton-Brock & Godfray 1991), or they may be more cautious in order to successfully complete breeding (Lima 2009). Populations of the hooded crow have been increasing in European cities over the last several decades (Vuorisalo et al. 2003, Kövér et al. 2015), leading to frequent conflicts with humans due to noisy vocalization, pollution from faeces, and scattering garbage (Pokorný et al. 2014). Therefore, information on the escape strategies of hooded crows during the breeding period may aid future efforts in the management of this species in urban environments.

Material and Methods

Study area

The study was conducted in four parks in the centre of Belgrade, Serbia (44.81 N, 20.47 E): Vukov Spomenik (~ 1.3 ha), Tašmajdan (~ 9.9 ha), Pionirski Park (~ 1.88 ha), and Manjež (~ 2.2 ha). The parks are separated by multi-storey buildings and busy streets; the distance between parks ranges between 250–1,300 m. All parks have similar habitat structure, with high tree cover of conifers and deciduous trees, extensive areas of maintained grasslands with decorative flowers, intersected by walking trails. In addition, all parks with the exception of Vukov Spomenik have playgrounds for children, whereas Tašmajdan and Pionirski Park have water fountains. The parks are frequented by visitors throughout year and are used for recreational and leisure activities.

Behavioural and environmental variables

The data were collected in November and December 2020, and in April and May 2021. As part of another project, we actively monitored crow nests in several locations in the city, so we were confident that observations conducted in April and May included the period of reproduction. Each park was visited once per day, two–three times each week, with at least an interval of one day between successive

visits to the same park; all visits were conducted between 10–12 h, to avoid potential effects of time of day on escape behaviour (Rodríguez-Prieto et al. 2008, Burger et al. 2010). Upon arrival at a study location, we searched for crows actively foraging or feeding on the ground. When we encountered a group of birds, we chose one that could be easily approached, e.g. a bird that was not moving fast, where there were no physical obstructions between the bird and us, or there were no dogs or humans near the bird. In addition, we did not approach birds that were alert prior to our approach, or birds fed by visitors. Several focal individuals that were engaged in aggressive interactions with their neighbours were not included in analyses.

We measured behavioural parameters following the protocol of Blumstein (2003). Once the focal bird had been chosen, we measured starting distance using a laser range finder; we did not approach the bird if the starting distance was less than 10 m or greater than 35 m. One of us (always Vanja Parača, wearing dark clothes) directly approached the bird at a steady speed, approximately one step/s (one step \sim 0.5 m), and stopped when the bird fled (on all occasions the birds reacted by fleeing from the approaching researcher). Counting the number of steps from the moment the bird started monitoring our approach we approximated AD, as well as FID at the moment the bird departed. We also scored four categories of DF (0–10 m, 11–20 m, 20–30 m, > 30 m), escape method (flying *vs.* walking/running), and the chosen end-point of escape (ground, tree, or other).

We also measured environmental variables that could affect escape behaviour, including air temperature (Fernández-Juricic et al. 2002), wind speed (McGowan et al. 2002), and flock size (Morelli et al. 2019). Temperature and wind speed were measured with a digital thermometer/anemometer, whereas flock size was determined by counting all crows within a 10 m radius of the focal bird; for each focal individual, these measurements were taken prior to our approach. In addition to these variables, distance to the nearest refuge can exert a significant influence on escape behaviour in a range of taxa (Stankowich & Blumstein 2005). In terrestrial birds, the nearest object (e.g. tree or bush) is typically considered as the closest refuge (e.g. Fernández-Juricic et al. 2001, Tätté et al. 2018). Nevertheless, during preliminary observations, crows never used the closest objects as refuges and, thus, we did not consider this variable for analysis.

Statistical analysis

We used (generalized) linear mixed models to examine the effect of breeding season, including confounding variables, on FID, DF, and escape method. We used the “dredge” function from the package “MuMIn” (Bartoń 2020) to generate all possible models, with different combinations of predictors used in global models, which were ranked based on corrected AIC (AICc) values. To obtain parameter estimates we conducted averaging of models in cases where Δ AICc < 4 (Grueber et al. 2011). Estimates of predictors in which 95% confidence intervals did not overlap zero were considered to have a significant effect on dependent variables (Nakagawa & Cuthill 2007).

To assess the effect of predictors on FID we used linear mixed models (the package “nlme”, Pinheiro et al. 2021). The global model included season, AD and flock size as fixed factors, whereas the date of observation nested within location was treated as a random factor. Because air temperature was significantly higher, and wind speed significantly lower, during the breeding season (Wilcoxon test: $P < 0.001$), without unexpected extreme values in both study periods, these variables were not included in the analysis. Moreover, as the majority of crows were solitary while foraging, whereas the maximum number of individuals within a group was seven, the variable “flock size” was represented with two levels; “single” and “in flock”.

Seasonal differences in DF were examined using Fisher’s exact test, for each park separately. To account for effects of other variables, we used generalized linear mixed models with a binomial distribution. Although we recognized four categories of DF, we used a binomial distribution since nearly 80% of birds fled for a distance of less than 10 m, and only a few birds fled for distances over 20 m. Therefore, for this analysis, we combined levels of DF > 10 m, with DF coded zero if \leq 10 m, or one if > 10 m. Thus, the global model included season, FID, flock size, and escape method as fixed factors, and the date of observation nested within location as a random factor; AD was not included in this analysis as it was highly correlated with FID (Pearson correlation: $r = 0.77$, $P < 0.001$), which was shown to exert significant influence on DF in other studies (Tätté et al. 2018). We used Bayesian inference (the package “blme”, Dorie et al. 2021), to overcome problems of a singular model fit (Bolker 2015).

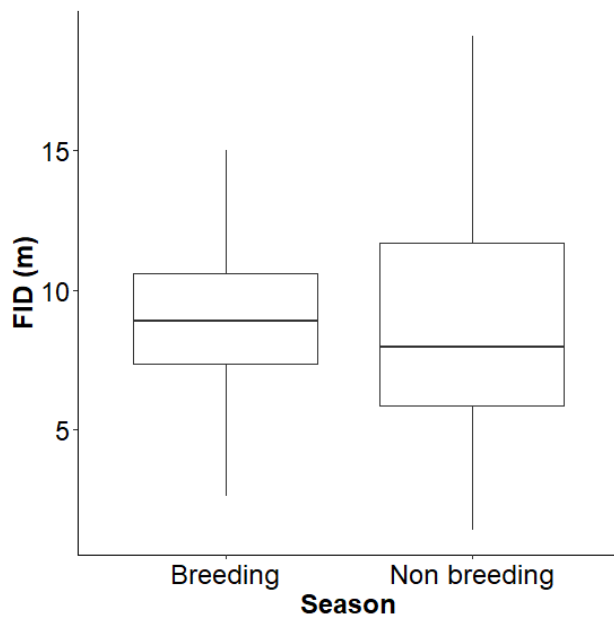


Fig. 1. Seasonal difference in flight initiation distance (FID).

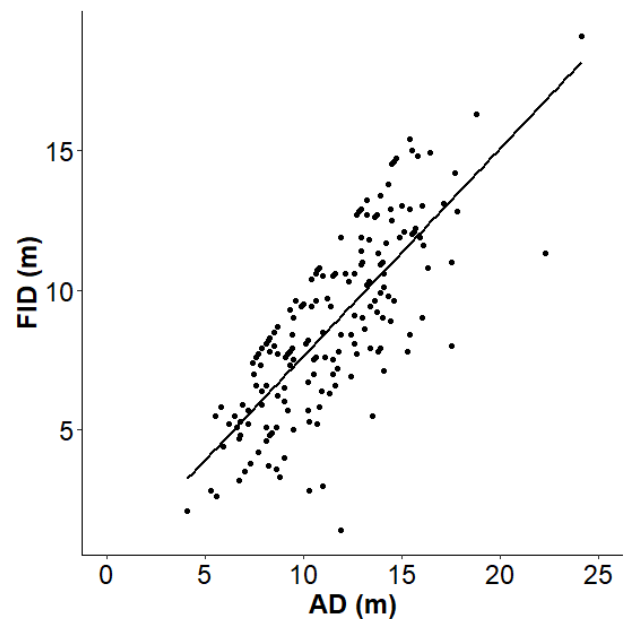


Fig. 2. Flight initiation distance (FID) in relation to alert distance (AD).

Table 1. Descriptive statistics of variables measured during the breeding and non-breeding season; median values and range are presented.

Variables	Breeding season	Non-breeding season
Starting distance (m)	20.8 (11.8-30.6)	20.9 (10.9-33.6)
Alert distance (m)	10.6 (5.3-17.5)	12.5 (4.1-24.1)
Flight initiation distance (m)	8.9 (2.6-15.0)	7.8 (1.4-19.1)
Flock size (number of individuals)	1 (1-4)	1 (1-7)
Air temperature (°C)	21.0 (14.0-26.0)	5.5 (1.0-5.0)
Wind speed (ms ⁻¹)	0 (0-1.3)	0 (0-4)

Table 2. Model-averaged estimates of coefficients with standard error (SE), for regression models including flight initiation distance (FID) as a dependent variable, distance fled (DF), and escape method; estimates of predictors where 95% confidence intervals (CI) did not overlap zero were considered to have a significant effect on FID. AD refers to alert distance; flock size (FS) is represented by two levels – single and in a group; season is also represented with two levels – breeding and non-breeding; escape refers to escape method and is a binary variable, with flying coded 1 and running/walking coded 0.

Predictor	Coefficient	SE (Coef)	95% CI
Estimates for FID			
AD	0.792	0.043	0.706-0.878
Season (non-breeding)	-1.391	0.346	-2.091-(-0.691)
Flock size (single)	-0.213	0.307	-1.055-0.125
Estimates for DF			
FID	0.013	0.053	-0.134-0.228
Season (non-breeding)	-0.094	0.359	-1.614-0.885
Flock size (single)	0.179	0.437	-0.712-1.695
Escape	5.560	0.941	3.742-7.456
Estimates for escape method			
FID	0.177	0.057	0.064-0.289
Season (non-breeding)	-0.128	0.292	-1.152-0.411
Flock size (single)	0.020	0.193	-0.650-0.798

To model the effects of predictors on escape method we also used Bayesian generalized linear mixed models. The escape method was a binary response variable, coded one, if the focal bird escaped by flying, or zero, if it escaped by running/walking. The global model included season, FID, and flock size as fixed factors, and the date of observation nested within the location as a random factor. All statistical analyses were carried out using R v4.1.0. (R Core Team 2021).

Results

We measured escape behaviour in 183 individuals, 92 in winter, 91 in spring (Vukov Spomenik: 13, Tašmajdan: 93, Pionirski Park: 52 and Manjež: 25). Descriptive statistics on measured variables are presented in Table 1. The majority of individuals fled distances ≤ 10 m, 78% ($n = 143$), with 10 % (19) of individuals fleeing 11–20 m, 3% (6) 21–30 m, and 8% (15) of individuals fled distances > 30 m. Significant differences in DF between seasons were detected for only one location (Pionirski Park, Fisher's exact test: $P = 0.005$). The end point of escape in 83% of individuals was the ground, 14% fled into a tree, and 3% used other objects. Escape method was running/walking in 67% of individuals, whereas 33% escaped by flying.

Season and AD had significant effects on FID, with birds escaping at longer distances during the breeding season, and when they were alerted at greater distances (Table 2, Figs. 1 and 2). DF was significantly influenced by escape method, with birds escaping for distances greater than 10 m more often if they escaped by flying (Table 2). Finally, escape method was significantly influenced by FID, with birds escaping more often by flying at greater distances from an approaching predator (Table 2).

Discussion

During the breeding season, animals experience increased energetic costs due to mate acquisition and/or guarding (Byers et al. 2010, Lane et al. 2010), nest building (Mainwaring & Hartley 2013) and parental care (Clutton-Brock & Godfray 1991). In addition, many animals experience limited opportunities to find mates during the period of breeding (Székely et al. 1999, Segoli et al. 2006, Reading & Backwell 2007, Stenzel et al. 2011). Under such circumstances, antipredator responses might be relaxed as a trade-off between reproduction and

antipredator behaviour (Cooper 1999, Martín et al. 2003). Conversely, as animals are often exposed to higher predation risk while breeding (Lima & Dill 1990, Magnhagen 1991), their antipredator response could be enhanced to successfully protect their offspring and themselves (Ciuti et al. 2008). Previous studies examining the effects of breeding on escape behaviour in animals has generated contrasting results. For example, Glover et al. (2011) did not find a difference in FID between breeding and non-breeding masked lapwings *Vanellus miles*, whereas seasonal differences in FID were registered in only one out of 11 bird species studied in the Neotropics (Piratelli et al. 2015). By contrast, some studies have demonstrated a decrease in risk-taking behaviour, i.e. longer FID, during the breeding season. Hence, females of ungulates with offspring escaped at greater distances compared to males, or females without offspring, most likely to minimize predation risk on their young (Ciuti et al. 2008, Stankowich 2008). Similarly, shorebirds fled at longer distances on breeding sites than on migratory stopovers, thus reducing predation risk at this stage of the annual cycle (Mikula et al. 2018).

In our study, crows escaped at greater distances during the breeding season implying that the birds were more risk-averse throughout the period of reproduction. By reducing predation risk, the birds were more likely to successfully complete care of their young. In addition, a shorter FID detected during the winter period may be partly a consequence of unfavourable environmental conditions (lower temperatures/stronger winds) in that part of the year. Under harsher environmental conditions, animals may expose themselves to a higher predation risk in response to an elevated risk of starvation (McGowan et al. 2002, Yasué et al. 2003). As ambient temperature affects metabolic rates (Bakken et al. 1991), birds feed more in colder weather (Pravosudov & Grubb 1998), and thus, to avoid interruption of foraging, the crows may have tolerated the closer approach of a predator.

Flight initiation distance was strongly influenced by alert distance – the increase of AD was followed by a significant increase in FID. The positive relationship between AD and FID has been consistently observed in diverse taxa (Samia et al. 2013). This relationship could be partly a consequence of a mathematical artefact arising from the fact that FID is always lower or equal to AD (Dumont et al. 2012), but it could be also arise from costs associated with predator

monitoring once a predator has been detected (Blumstein 2010). The costs of not fleeing entail physiological costs of monitoring an approaching predator, which increase with the duration of monitoring, as well as the greater probability that the predator will attack as the approach toward prey is prolonged (Cooper & Blumstein 2014). Preliminary analyses showed that AD in observed crows, while simultaneously controlling for starting distance, was significantly lower in the breeding period (Parača 2021). Therefore, a longer FID during reproduction indicates that the crows did not escape at longer distances because they were more alert, but because they escaped soon after detecting the approaching predator. During the breeding season, 21% of focal individuals escaped at the moment they detected an approach (i.e. AD was equal to FID), corroborating our belief that the birds were less inclined to risk-taking during the reproductive period.

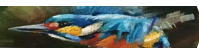
We detected a significant seasonal difference in distance fled at only one study location. In the regression model, which took into account other confounding variables, a seasonal effect was absent. In general, the majority of birds we observed displaced themselves less than 10 m away after simulated attacks. One of the reasons for such short DF may be the fact that we observed crows in an urbanized environment where they were continuously exposed to high encounter rates with humans throughout the year. This situation may lead to habituation in response to non-lethal stimuli from humans resulting in a decreased antipredator response (Stankowich & Blumstein 2005, Rodriguez-Prieto et al. 2009). Comparison of escape tactics in urban and rural environments show that animals in urban habitats typically exhibit shorter FID, as well as DF (Møller 2008, Tätté et al. 2018, 2020, Hall et al. 2020). Risk assessment is a dynamic process, occurring before but also after escape initiation (Cooper 2008). For example, corvids are able to discriminate among different types of predator approach and adjust their escape strategy, with escape duration being shortest when the predator's approach terminates in the moment of flight initiation (Tätté et al. 2020). As our study protocol did not include pursuit of crows once they initiated escape, the birds were able to evaluate our approach as non-threatening and cease their escape shortly after it started.

Distance fled was strongly influenced by escape method (flying *vs.* running), with the crows more likely to flee longer distances while flying, which

is similar to other studies (Rodriguez-Prieto et al. 2008, Tätté et al. 2018). Flying is a faster means of locomotion than running, but energetically more demanding (Butler 2016), thus birds may opt to use it under a higher level of risk. In our study, 67% of birds escaped by running, which is consistent with a decreased antipredator response associated with urban environments (Uchida et al. 2016, Tätté et al. 2018). The only variable that significantly influenced escape method in crows was FID, with increased probability of flying after longer FID. This result contrasts with the study of Rodriguez-Prieto et al. (2008), who found that the probability of aerial escape in the blackbird, *Turdus merula*, decreased as FID increased; in this way blackbirds most likely reduced predation risk once a predator had approached closely. We did not detect such risk compensation in crows, but the relationship between FID and escape method may reflect differences in boldness of individuals (Blumstein et al. 2015b), with bolder birds allowing a closer approach and choosing energetically less costly escape tactics.

Social status of focal birds did not influence escape decision in crows. Previous studies have yielded varied results on the relationship between escape strategies and group size. In larger groups, due to collective detection, approaching predators can be detected earlier, leading to an increase in FID with group size (Tätté et al. 2018, Morelli et al. 2019). In contrast, risk dilution and collective defence may lead to a decrease in FID/DF with group size (Stankowich & Blumstein 2005, Mikula et al. 2018, Kalb et al. 2019). However, many studies, ours included, have failed to detect a significant relationship between group size and components of escape behaviour (e.g. Glover et al. 2011, Tätté et al. 2018, 2020, Kalb et al. 2019). The reason for the lack of such a relationship may be a failure to properly define a group; we defined a flock as the number of crows in a 10 m radius from the focal individual, but the birds may have reacted to the presence of more distant neighbours. In addition, opposing effects of the above mentioned mechanisms may obscure the overall impact of group size on escape decisions.

The hooded crow is a successful urban colonizer, showing population increase in European cities since the 1960s (Kövéř et al. 2015). Such population growth is a consequence of increased anthropogenic food sources, availability of nesting sites, as well as a lack of the crows' predators within cities (Kövéř



et al. 2015, 2019). Limited persecution in urban habitats has also led to habituation and tolerance in crows of the presence of humans (Vuorisalo et al. 2003). Nevertheless, seasonal differences in flight initiation distances we observed indicate that even animals adapted to living in highly urbanized environments, such as crows, may be less prone to risk-taking during the breeding season, which may allow them to more successfully care for their young. This finding could be taken into account when planning urban green areas, along with limiting human food sources and available breeding habitats, which have proven to be the

most important factors for management of crows within cities (Takenaka 2003, Kövér et al. 2019, Preininger et al. 2019).

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Literature

- Bakken G.S., Murphy M.T. & Erskine D.J. 1991: The effect of wind and air temperature on metabolism and evaporative water loss rates of dark-eyed juncos, *Junco hyemalis*: a standard operative temperature scale. *Physiol. Zool.* 64: 1023–1049.
- Bartoń K. 2020: MuMIn: multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bateman P.W. & Fleming P.A. 2011: Who are you looking at? Haded ibises use direction of gaze, head orientation and approach speed in their risk assessment of a potential predator. *J. Zool.* 285: 316–323.
- Blumstein D.T. 2003: Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manag.* 67: 852–857.
- Blumstein D.T. 2010: Flush early and avoid the rush: a general rule of antipredator behavior? *Behav. Ecol.* 21: 440–442.
- Blumstein D.T., Fernández-Juricic E., Zollner P.A. & Garity S.C. 2005: Inter-specific variation in avian responses to human disturbance. *J. Appl. Ecol.* 42: 943–953.
- Blumstein D.T., Flores G. & Munoz N.E. 2015b: Does locomotor ability influence flight initiation distance in yellow-bellied marmots? *Ethology* 121: 434–441.
- Blumstein D.T., Samia D.S., Stankowich T. & Cooper W.E., Jr. 2015a: Best practice for the study of escape behavior. In: Cooper W.E., Jr. & Blumstein D.T. (eds.), *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge, UK: 407–419.
- Bolker B.M. 2015: Linear and generalized linear mixed models. In: Fox G.A., Negrete-Yankelevich S. & Sosa V.J. (eds.), *Ecological statistics: contemporary theory and application*. Oxford University Press, Oxford, UK: 309–334.
- Burger J. & Gochfeld M. 1981: Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. *J. Comp. Physiol. Psychol.* 95: 676–684.
- Burger J., Gochfeld M., Jenkins C.D. & Lesser F. 2010: Effect of approaching boats on nesting black skimmers: using response distances to establish protective buffer zones. *J. Wildl. Manag.* 74: 102–108.
- Burger J., Gochfeld M., Saliva J.E. et al. 1989: Antipredator behaviour in nesting zenaida doves (*Zenaida aurita*): parental investment or offspring vulnerability. *Behaviour* 111: 129–143.
- Butler P.J. 2016: The physiological basis of bird flight. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371: 20150384.
- Byers J., Hebets E. & Podos J. 2010: Female mate choice based upon male motor performance. *Anim. Behav.* 79: 771–778.
- Ciuti S., Pipia A., Ghiandai F. et al. 2008: The key role of lamb presence in affecting flight response in Sardinian mouflon (*Ovis orientalis musimon*). *Behav. Process.* 77: 408–412.
- Clutton-Brock T. & Godfray C. 1991. Parental investment. In: Krebs J.R. & Davies N.B. (eds.), *Behavioural ecology: an evolutionary approach*, 3rd ed. Blackwell Scientific Publications, Oxford, UK: 234–262.
- Cooper W.E., Jr. 1999: Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. *Behav. Ecol. Sociobiol.* 47: 54–59.
- Cooper W.E., Jr. 2000: Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (*Eumeces laticeps*). *Behaviour* 137: 1175–1189.
- Cooper W.E., Jr. 2003: Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Can. J. Zool.* 81: 979–984.
- Cooper W.E., Jr. 2008: Visual monitoring of predators: occurrence, cost and benefit for escape. *Anim. Behav.* 76: 1365–1372.
- Cooper W.E., Jr. 2015: Theory: models of escape behavior and refuge use. In: Cooper W.E., Jr. & Blumstein D.T. (eds.), *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge, UK: 17–60.
- Cooper W.E., Jr. & Blumstein D.T. 2014: Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. *Behav. Ecol.* 25: 44–52.
- Cooper W.E., Jr. & Blumstein D.T. 2015: Escape behavior: importance, scope, and variables. In: Cooper W.E., Jr. & Blumstein D.T. (eds.), *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge, UK: 3–14.
- Cooper W.E., Jr., Hawlena D. & Pérez-Mellado V. 2009: Interactive effect of starting distance and approach speed on escape behavior challenges theory. *Behav. Ecol.* 20: 542–546.

- Cooper W.E., Jr., Pérez-Mellado V., Baird T. et al. 2003: Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behav. Ecol.* 14: 288–293.
- De Jong A., Magnhagen C. & Thulin C.G. 2013: Variable flight initiation distance in incubating Eurasian curlew. *Behav. Ecol. Sociobiol.* 67: 1089–1096.
- Dorie V., Bates D., Maechler M. et al. 2021: blme: Bayesian linear mixed-effects models. R package version 1.0-5, 1.15.6 <https://CRAN.R-project.org/package=blme>
- Dumont F., Pasquaretta C., Réale D. et al. 2012: Flight initiation distance and starting distance: biological effect or mathematical artefact? *Ethology* 118: 1051–1062.
- Engelhardt S.C. & Weladji R.B. 2011: Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can. J. Zool.* 89: 823–830.
- Fernández-Juricic E., Jimenez M.D. & Lucas E. 2001: Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environ. Conserv.* 28: 263–269.
- Fernández-Juricic E., Jimenez M.D. & Lucas E. 2002: Factors affecting intra-and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Can. J. Zool.* 80: 1212–1220.
- Frid A. & Dill L.M. 2002: Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6: 11.
- Geist C., Liao J., Libby S. & Blumstein D.T. 2005: Does intruder group size and orientation affect flight initiation distance in birds? *Anim. Biodivers. Conserv.* 28: 69–73.
- Glover H.K., Weston M.A., Maguire G.S. et al. 2011: Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landsc. Urban Plan.* 103: 326–334.
- Grueber C.E., Nakagawa S., Laws R.J. & Jamieson I.G. 2011: Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24: 699–711.
- Guay P.J., Lorenz R.D., Robinson R.W. et al. 2013: Distance from water, sex and approach direction influence flight distances among habituated black swans. *Ethology* 119: 552–558.
- Hall M.J., Burns A.L., Martin J.M. & Hochuli D.F. 2020: Flight initiation distance changes across landscapes and habitats in a successful urban coloniser. *Urban Ecosyst.* 23: 785–791.
- Kalb N., Anger F. & Randler C. 2019: Flight initiation distance and escape behavior in the black redstart (*Phoenicurus ochrurus*). *Ethology* 125: 430–438.
- Kövér L., Gyüre P., Balogh P. et al. 2015: Recent colonization and nest site selection of the hooded crow (*Corvus corone cornix* L.) in an urban environment. *Landsc. Urban Plan.* 133: 78–86.
- Kövér L., Lengyel S., Takenaka M. et al. 2019: Why do zoos attract crows? A comparative study from Europe and Asia. *Ecol. Evol.* 9: 14465–14475.
- Lane J.E., Boutin S., Speakman J.R. & Humphries M.M. 2010: Energetic costs of male reproduction in a scramble competition mating system. *J. Anim. Ecol.* 79: 27–34.
- Lima S.L. 2009: Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biol. Rev. Camb. Philos. Soc.* 84: 485–513.
- Lima S.L. & Dill L.M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619–640.
- Magnhagen C. 1991: Predation risk as a cost of reproduction. *Trends Ecol. Evol.* 6: 183–186.
- Mainwaring M.C. & Hartley I.R. 2013: The energetic costs of nest building in birds. *Avian Biol. Res.* 6: 12–17.
- Martín J., López P. & Cooper W.E. 2003: Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. *Behav. Ecol. Sociobiol.* 54: 505–510.
- McGowan A., Cresswell W. & Ruxton G.D. 2002: The effects of daily weather variation on foraging and responsiveness to disturbance in overwintering red knots *Calidris canutus*. *Ardea* 90: 229–237.
- Míkula P., Díaz M., Albrecht T. et al. 2018: Adjusting risk-taking to the annual cycle of long-distance migratory birds. *Sci. Rep.* 8: 1–9.
- Morelli F., Benedetti Y., Díaz M. et al. 2019: Contagious fear: escape behavior increases with flock size in European gregarious birds. *Ecol. Evol.* 9: 6096–6104.
- Møller A.P. 2008: Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* 63: 63–75.
- Møller A.P. 2014: Life history, predation and flight initiation distance in a migratory bird. *J. Evol. Biol.* 27: 1105–1113.



- Møller A.P., Liang W. & Samia D.S. 2019: Flight initiation distance, color and camouflage. *Curr. Zool.* 65: 535–540.
- Møller A.P., Tryjanowski P., Díaz M. et al. 2015: Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behav. Ecol.* 26: 861–865.
- Nakagawa S. & Cuthill I.C. 2007: Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev. Camb. Philos. Soc.* 82: 591–605.
- Parača V. 2021: Escape behavior in the urban hooded crow (*Corvus cornix*). MSc thesis, University of Belgrade, Belgrade, Serbia.
- Pinheiro J., Bates D., DebRoy S. & Sarkar D. 2021: nlme: linear and nonlinear mixed effects models. R package version 3.1-153, <https://CRAN.R-project.org/package=nlme>
- Piratelli A.J., Favoretto G.R. & Maximiano M.F. 2015: Factors affecting escape distance in birds. *Zoologia* 32: 438–444.
- Pokorny B., Flajšman K. & Jelenko I. 2014: The importance and impacts of crows, with emphasis on hooded crow (*Corvus cornix*), in the (sub) urban environment. *Acta Silvae et Ligni* 103: 47–60.
- Pravosudov V.V. & Grubb T.C. 1998: Body mass, ambient temperature, time of day, and vigilance in tufted titmice. *Auk* 115: 221–223.
- Preininger D., Schoas B., Kramer D. & Boeckle M. 2019: Waste disposal sites as all-you-can eat buffets for carrion crow (*Corvus corone*). *Animals* 9: 215.
- R Core Team 2021: R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.
- Reading K.L. & Backwell P.R.Y. 2007: Can beggars be choosers? Male mate choice in a fiddler crab. *Anim. Behav.* 74: 867–872.
- Rodriguez-Prieto I., Fernández-Juricic E. & Martín J. 2008: To run or to fly: low cost versus low risk escape strategies in blackbirds. *Behaviour* 145: 1125–1138.
- Rodriguez-Prieto I., Fernández-Juricic E., Martín J. & Regis Y. 2009: Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* 20: 371–377.
- Samia D.S., Nomura F. & Blumstein D.T. 2013: Do animals generally flush early and avoid the rush? A meta-analysis. *Biol. Lett.* 9: 20130016.
- Segoli M., Harari A.R. & Lubin Y. 2006: Limited mating opportunities and male monogamy: a field study of white widow spiders, *Latrodectus pallidus* (Theridiidae). *Anim. Behav.* 72: 635–642.
- Stankowich T. 2008: Ungulate flight responses to human disturbance: a review and meta-analysis. *Biol. Conserv.* 141: 2159–2173.
- Stankowich T. & Blumstein D.T. 2005: Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc. B: Biol. Sci.* 272: 2627–2634.
- Stankowich T. & Coss R.G. 2007: Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav. Ecol.* 18: 358–367.
- Stenzel L.E., Page G.W., Warriner J.C. et al. 2011: Male-skewed adult sex ratio, survival, mating opportunity and annual productivity in the snowy plover *Charadrius alexandrinus*. *Ibis* 153: 312–322.
- Székely T., Cuthill I.C. & Kis J. 1999: Brood desertion in Kentish plover: sex differences in remating opportunities. *Behav. Ecol.* 10: 185–190.
- Takenaka M. 2003: Crows problems in Sapporo area. *Glob. Environ. Res.* 7: 149–160.
- Tätte K., Møller A.P. & Mänd R. 2018: Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. *Anim. Behav.* 136: 75–86.
- Tätte K., Møller A.P. & Mänd R. 2020: Corvids exhibit dynamic risk assessment during escape. *Behav. Process.* 170: 104017.
- Uchida K., Suzuki K., Shimamoto T. et al. 2016: Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. *J. Zool.* 298: 225–231.
- Vuorisalo T., Andersson H., Hugg T. et al. 2003: Urban development from an avian perspective: causes of hooded crow (*Corvus corone cornix*) urbanisation in two Finnish cities. *Landsc. Urban Plan.* 62: 69–87.
- Yasué M., Quinn J.L. & Cresswell W. 2003: Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. *Funct. Ecol.* 17: 727–736.
- Ydenberg R.C. & Dill L.M. 1986: The economics of fleeing from predators. *Adv. Study Behav.* 16: 229–249.