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Short communication

Higher adaptive tolerance with higher risk for sparrows living in airport environments

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ABSTRACT

Adjustments in flight initiation distance (FID) indicate how birds adapt to external environmental changes, including semi-natural ecosystems such as airports with regular disturbances. This study focused on sparrows (*Passer montanus*) as the research subject, because it is a dominant species with a high risk of bird strike events at airports. We investigated the FID and its influencing factors both inside and outside an airport compound to determine sparrows' vigilance and their adaptive adjustments to the airport environment. The FID of sparrows showed no significant variation between inside and outside the airport compound. However, a significant reduction of FID was exhibited during the breeding season. Group size showed a significant positive impact on the FID, somewhat supporting the many-eyes hypothesis, in which larger groups with more individuals may detect predators earlier. Additionally, the stimulus type and location influenced the effect of group size on FID, with most birds showing greater tolerance to vehicles than to humans, and being slightly bolder inside the airport than outside it. Overall, sparrows showed a higher tolerance to disturbance inside the airport compound and less vigilance to vehicles than to humans. Nevertheless, these adaptations may inadvertently form an ecological trap for bird populations around airports, exposing them to the dual threats of higher levels of raptor predation and the hazards of bird strikes. Thus multifaceted bird-scaring strategies and measures should be formulated to ensure flight safety and enhance avian survival during airport management.

1. Introduction

Urbanization leads to drastic environmental changes within short periods, causing permanent changes in habitats and numerous negative effects such as noise pollution, light pollution, and anthropogenic disturbances (Grimm et al., 2008). All these pose significant challenges and conflicts to the wildlife inhabiting these environments (Grimm et al., 2008; Møller, 2008; Marín-Gómez and MacGregor-Fors, 2021). Numerous species are unable to adapt to new environments, leading to local extinction or migration, culminating in a loss of biodiversity within urban landscapes (Lowry et al., 2013). In contrast, some species manage to survive and establish themselves in new environments, even benefiting from urbanization through the abundance of food and reduced predation pressure (Møller, 2009; Møller et al., 2012). In addition, behavioural plasticity allows these urban-adapted species to optimize their

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behaviours to increase their fitness and chances of survival in an environment that is markedly different to natural areas (Lowry et al., 2013; Sol et al., 2013). For example, studies of birds showed that successful urban-colonising species and individuals exhibit modifications to their foraging (e.g., Fuirst et al., 2018), breeding (e.g., James-Reynolds et al., 2019), acoustic communication (e.g., Marín-Gómez and MacGregor-Fors, 2021), and anti-predation behaviour (e.g., Díaz et al., 2013) as part of long-term adaptations to urbanisation.

Escape is a common anti-predation tactic used by animals when facing danger and disturbance, which the optimal response time should be a trade-off between predation risk and cost of escaping (Cooper and Blumstein, 2015). Premature escape diverts time and energy away from foraging and reproductive activities, while delayed flight may elevate the risk of predation (Cooper and Frederick, 2007; LaManna and Martin, 2016). Flight initiation distance (FID), defined as the distance at which the focal bird escapes to avoid the persistent approach of the disturbance, is a widely used metric for evaluating the anti-predation response (Morelli et al., 2022). FID reflects the bird's trade-off between survival benefits and predation risks, and serves as an indicator of the bird's tolerance and adaptability to external disturbances (Cooper and Blumstein, 2015). Non-lethal human activities are a significant source of disturbance in urban environments and usually contributes to potential predation risks (Frid and Dill, 2002). Therefore, the FID of a focal bird could be measured by an approaching human, reflecting the birds' tolerance to its environment (Frid and Dill, 2002; Samia et al., 2015).

Airports are a unique feature of urbanization and a distinctive semi-natural ecosystem, in which part of the native habitat is replaced by buildings and other urban structures, while remnant patches are usually composed of indigenous vegetation and invasive grasses (Hauptfleisch and Dalton, 2015; Alquezar et al., 2020). These remnant patches are very attractive to birds by providing them with both direct and indirect nesting habitats and food sources, thereby inevitably exacerbating the conflict between avian populations and human disturbances in the airport (Sodhi, 2002; Hauptfleisch and Dalton, 2015). In addition, the take-off and landing of airplanes extend this conflict into the low altitude airspace, which results in bird strikes (Dolbeer, 2006). Bird strikes, resulting from these conflicts, lead to significant economic losses, human safety concerns and avian mortality (DeVault et al., 2018; Jeffery and Buschke, 2019). As aviation progresses, bird strikes have emerged as an increasingly prominent issue affecting flight safety and bird conservation (Coghlan et al., 2013). Furthermore, birds at airports have also adapted their behaviours to cope with the high intensity and diversity of anthropogenic disturbances, including human activities, noise pollution and vehicle operation (e.g. Gil et al., 2015; Dominoni et al., 2016; Klett-Mingo et al., 2016).

Variations in anti-predation responses closely relate to the bird's survival benefits among these adaptive behaviours. Bird individuals generally exhibit a reduction of FID and a stronger adaptation and tolerance under high levels of anthropogenic disturbances in urban environments (Møller, 2008; Díaz et al., 2013). However, in airport environments, a delayed response of anti-predation could be detrimental to the survival of birds because of high frequency of vehicle traffic. Previous studies have focused on the escape strategies of birds, such as the likelihood of initiating escape and FID within airport compounds facing airplane disturbances and other factors (Pan et al., 2018; Blackwell et al., 2019, 2020). Nonetheless, there is a lack of comparative research on the FID of birds inside and outside airport compounds, which could help elucidate how birds respond and adapt to airport disturbances. Understanding the impact of airport environments on bird FID is crucial for prevention of bird strike events and assessing the relationship between airport construction and management, and bird conservation.

The sparrow (*Passer montanus*) is a dominant synanthropic species recorded in the Ningyuan Airport area of China and the surrounding 13 km buffer zone where bird strikes mainly occur (Coccon et al., 2015), and is also a high-risk species in airport bird strike risk assessments (e.g., Zhao et al., 2016; Hu et al., 2020). Therefore, this study focused on sparrows to investigate the changes in FID of birds inside and outside airport compounds when exposed to different disturbance factors. The aim is to understand how birds adapt to airport disturbances and provide theoretical support for bird protection and flight safety as part of airport management.

2. Materials and methods

2.1. Study area

The study area was located at and around Zhangjiakou Ningyuan Airport in the northern part of Hebei Province, China (40°37' – 40°51'N, 114°46' – 115°05'E), situated on the southeastern edge of the Inner Mongolia Plateau, at an average elevation of 856 m. It has a temperate continental monsoon climate with distinct seasons and an average annual precipitation of about 400 mm. Inside the airport perimeter, the main habitats include grasslands, artificial surfaces (runways, taxiways), and human-made structures. Grassland habitats, which constitute the largest proportion, have diverse vegetation types, including green foxtail (*Setaria viridis*), feather fingergrass (*Chloris virgata*), yellow foxtail (*Setaria glauca*), oak-leaved goosefoot (*Chenopodium glaucum*), tall fescue (*Festuca elata*) and dandelion (*Taraxacum mongolicum*). These areas are important aggregating and activity spots for birds. Outside the airport, the main habitats include shrublands, forests, farmlands, mountains, wetlands, rivers, and residential areas.

2.2. Experimental method

From March 2021 to January 2022, surveys were done on clear days without wind and fog. The FID of sparrows inside and outside the airport compound within a 13 km radius were measured using a rangefinder telescope (EDKORS-AS1000, EDKORS Instrument Co., LTD., Changzhou, China). Considering that the airport is a restricted and relatively enclosed environment, and to avoid the impact of repeated surveys, each survey was conducted at an interval of one month. Factors such as the period of the survey, group size, and stimulus type, which affected birds' FID in previous studies (e.g. Legagneux and Ducatez, 2013; McLeod et al., 2013; Shuai et al., 2024), were also considered in this study. The survey periods were divided into the breeding (April to July 2021) and non-breeding seasons (August 2021 to January 2022), respectively.

The survey methods included human and vehicle surveys. During human surveys, two experimenters, dressed in black clothing and hats, approached the test individual or group at a normal walking speed in a straight line. The FID was measured with the rangefinder telescope as soon as the birds started to fly away. During vehicle surveys, the experimenters conducted the survey at a speed of 15 km/h in an airport patrol car, driven by an airport staff member. A beanbag, which would not roll easily, was prepared and positioned in an experimenter's hand that was extended out the car window. Upon observing that the test birds started to fly away, the beanbag was dropped from the hand. Simultaneously, the vehicle was immediately stopped, and the FID was measured with the rangefinder telescope. During the vehicle surveys, the personnel inside the car remained seated, ensuring minimal disturbance until the focal bird took flight. We corrected the data for the car survey to eliminate FID errors caused by the speed and inertia of the car. We used the same method, with similar height and speed, to drop the sandbag and measured the offset distance of the sandbag (0.93 ± 0.02 m, N = 10), then we used this data to correct the FID data from vehicle survey.

Additionally, the test birds had to meet the following criteria: (1) Free from the influence of predators and other pedestrians; (2) Located on the ground and in open spaces, avoiding situations where birds were too close to hiding spots, which could result in artificially short FIDs; (3) The height at which the test birds were located did not exceed that of the experimenters or the vehicle; (4) In cases where birds were foraging or in a state of alert, the observers would have to retreat and ignore that individual or group for one minute. If the bird(s) flew away during that period, the experiment was abandoned. If the bird(s) was no longer in an alert state, then the test proceeded; (5) Birds in mixed species flocks were not tested; (6) The distance between neighbouring test birds needed to be at least 50 m to reduce the possibility of pseudo-replication. This was an appropriate distance interval to prevent the repeated measurements of the same individual, because the escape distance of sparrows was far less than 50 m according to previous research (e.g. Zhang et al., 2019).

2.3. Data analyses

We used a model selection approach to determine best model based on Akaike's information criterion (AIC, Burnham and Anderson, 2002) in R version 4.1.3, selecting the most important variables influencing FID. A best model with the minimum AIC score was selected using the "dredge" function in the package *MuMIn* (Bartoń 2020). We used the dredge process for the global model, including four influential factors (location, period, group size and stimulus type) and all first-order interactions between two factors (location × period, location × group size, location × stimulus type, period × group size, period × stimulus type and group size × stimulus type). The best model selected from the global model included all the four influential factors and three interaction terms, i.e., location × group size, location × stimulus type and group size × stimulus type.

We then used a Generalized Linear Mixed Model (GLMM), generated using the *glmmTMB* package in R version 4.1.3, to analyse the effects of location (inside or outside the airport compound), period (breeding or nonbreeding season), group size and stimulus type (using a human or vehicle as a surrogate for predators) on the FID of sparrows. In this model, the FID of the sparrows was the dependent variable. The location, period, group size, stimulus type, and the interacting effects of location × group size, location and stimulus type, and group size and stimulus type were considered as fixed effects. The position ID of bird FID was treated as a random effect. All tests were two-tailed, and significance levels were all set at $p < 0.05$.

3. Results

In this study, a total of 348 valid measurements of FID were recorded, including 61 inside and 287 outside the airport compound. The GLMM revealed that the period ($z = 3.473$, $p < 0.001$), group size ($z = 2.371$, $p = 0.018$) and the interaction between group size and stimulus type ($z = -2.473$, $p = 0.013$) significantly influenced the birds' FID. Additionally, the interaction between location and group size almost had a significant effect on the FID of sparrows ($z = 1.803$, $p = 0.071$) (Table 1). Specifically, the FID of sparrows during the breeding season was significantly smaller than during the non-breeding season. The FID of sparrows increased noticeably with group size, and they showed significantly stronger responses to humans than vehicles (Fig. 1), and slightly significantly higher reactions outside than inside the airport (Fig. 2).

Table 1
Generalized linear mixed models of sparrows by different influence factors.

variable	Estimate	SE	*z*	*p*
(Intercept)	3.158	0.773	4.088	<0.001**
Location (outside)	0.677	0.780	0.867	0.386
Period (nonbreeding)	1.191	0.343	3.473	<0.001**
Group size	0.051	0.021	2.371	0.018*
Stimulus type (vehicle)	0.310	0.800	0.388	0.698
Location (outside) × Group size	0.040	0.022	1.803	0.071
Location (outside) × Stimulus type (vehicle)	-1.216	0.830	-1.465	0.143
Group size × Stimulus type (vehicle)	-0.041	0.016	-2.473	0.013*

Note: * $p<0.05$, ** $p<0.01$.

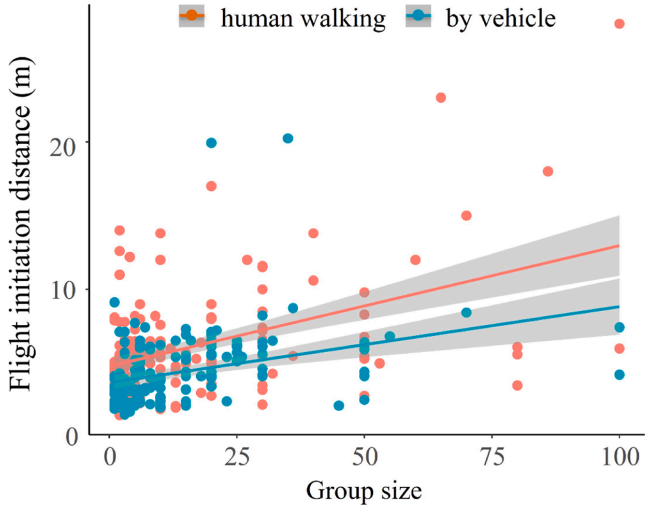

Fig. 1. FID of sparrows across different group size and stimulus types.

4. Discussion

This study found that the FID of sparrows varies seasonally and was significantly affected by group size. Additionally, the stimulus type and location influenced the effect of group size on FID, indicating that sparrows showed a slightly higher tolerance inside than outside the airport compound, and less vigilance to vehicles than humans.

Previous research has shown that birds in environments with high-intensity disturbances tend to have shorter FID (Samia et al., 2015; Bötsch et al., 2018). This could be because only those birds with higher tolerances can survive in environments with intense human disturbances, while less tolerant individuals and species are displaced, leading to a shorter overall FID in the bird population (Møller, 2008). Additionally, birds may exhibit strong behavioural plasticity. Intense but non-lethal disturbances can lead to behavioural changes in birds, reducing their fear and allowing them to allocate more energy to other activities such as foraging (Fossett and Hyman, 2021; Caspi et al., 2022). For example, changes in FID in birds before and after the COVID-19 pandemic were observed to vary with changes in human activity and disturbance levels, but the trends differed between birds in urban and rural areas with varying levels of indigenous disturbance (Díaz and Møller, 2023). Further studies found that due to the prolonged wearing of masks during the pandemic, birds that frequently encountered humans wearing masks exhibited shorter FIDs (Jiang et al., 2020; Fabrero et al., 2023).

In this study, we found that there was no significant change in the FID of birds inside and outside airports, but the FID of birds outside airports increased more significantly with group size. This may be because the airport is located on the outskirts of the city, which also suffers from high interference. In addition, ambient noise slows down anti-predator reactions in prey species (Petrelli et al., 2017; Abou-Zeid et al., 2024). The exceptional noise interference caused by the take-off or landing of aircraft will be at the worst inside

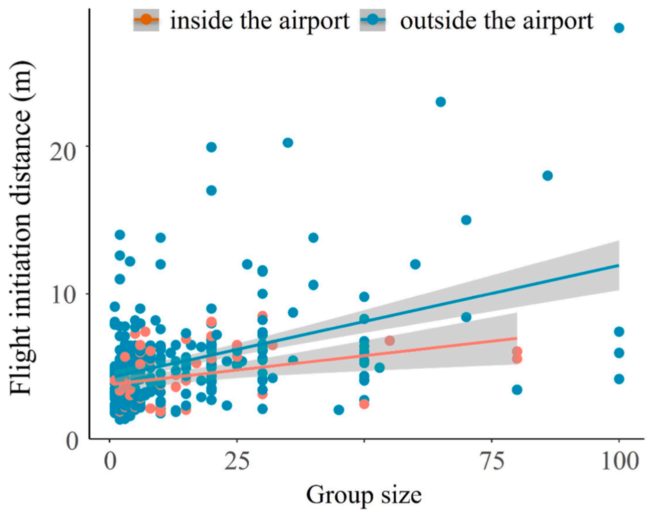

Fig. 2. FID of sparrows across different group size and observation areas.

the airport compound and reduce radiatively, which may result in weaker perception of external danger and anti-predation behaviour for individuals within the airport compound. This adaptation increases their tolerance to the environment, enabling them to survive in these dynamic conditions. While the airport environments, which differ from urban areas, would also attract and congregate a variety of raptor predators (e.g. Blackwell et al., 2019, 2020; Wang et al., 2024), the noise caused by aircraft taking off or landing may be more tolerated by raptors (Wang et al., 2024). Consequently, a reduction in FID, indicating a delayed response of anti-predation, could lead to higher predation risks.

Previous studies have shown mixed effects of population size on birds' FID, with some finding that it increases with increasing group size (e.g., Morelli et al., 2019; Ekanayake et al., 2022; Ncube and Tarakini, 2022), while others have shown that FID decreases (e.g., Ye et al., 2017; Ardila-Villamizar et al., 2022) or remains unaffected (e.g., Guay et al., 2013; Reynolds et al., 2020). In addition, the effect of group size on FID may be noticeably influenced by the effects of other confounding factors (Shuai et al., 2024). This study found that the FID of sparrows increased significantly with the size of the group, possibly because larger groups are more likely to detect predators, somewhat supporting the many-eyes hypothesis that there are progressively more individuals scanning the environment for predators and detecting the danger earlier with increasing group size (Lima, 1995).

The stimulus type affects the effect of group size on FID of the sparrows, with most birds showing greater tolerance to vehicles than to humans, which is consistent with previous research (Holmes et al., 1993; McLeod et al., 2013). This may be because vehicles, being relatively recent inventions, are perceived as less threatening to birds than walking humans. However, birds' assessment of motor vehicles and other man-made devices could form an ecological trap, especially in the case of high-speed vehicles. Incorrect assessment by birds may result in insufficient escape time, leading to collisions (Legagneux and Ducatez, 2013; DeVault et al., 2015). Within airport compounds, the juxtaposition of paved runways with patches of grass creates an ideal habitat for birds to gather and be active, thereby amplifying the risk of being struck by vehicles. Additionally, the airplanes that move rapidly when they take off and land, disrupt birds' flight patterns, and such situations may hinder birds' ability to evade oncoming planes effectively, causing bird strikes, further contribution to bird deaths and affecting flight safety (Blackwell et al., 2019, 2020).

The survey period was another factor affecting birds' FID. Previous studies have found that birds tend to have longer FIDs in the autumn and winter seasons (Legagneux and Ducatez, 2013). Similarly, this study found that sparrows had longer FIDs during the non-breeding season. This could be due to the presence of juvenile sparrows during the breeding season, which, as past research on sparrows has shown, tend to have shorter escape distances than adults (Zhang et al., 2019). This might be because juveniles are less capable of assessing external risks, a finding that is consistent with studies on other bird species (Martín et al., 2006; Jablonszky et al., 2017). However, previous studies on the hooded crow (*Corvus cornix*) found that urban birds have longer FIDs during the breeding season to better nurture their offspring (Novčić and Parača, 2021), which were different from the results of this study. This discrepancy could be due to species differences, as crows have less experience in urban environments and human interactions compared to sparrows. Additionally, the noise and habits of crows may conflict more with human activities (Pokorny et al., 2014), prompting them to maintain a higher level of risk aversion in urban settings.

5. Conclusion

This study investigated the effect of airport environment on anti-predation behaviour of birds. They showed a higher tolerance to disturbances inside the airport compound than outside, and less vigilance to vehicles than to humans, likely as an adaptation to the intense and repetitive disturbances present. Nevertheless, this adaptation of reduced anti-predation behaviour may inadvertently form an ecological trap for bird populations around airports, exposing them to the dual threats of higher predation by raptors and the hazards of bird strikes. Therefore, it is imperative to develop multifaceted bird-scaring strategies to ensure flight safety and enhance avian survival as part of airport management. On one hand, airports should mitigate the factors attractive to birds, such as food resources and shelters, to reduce the diversity and number of birds (e.g., Blackwell et al., 2011; Hauptfleisch and Dalton, 2015; Marateo et al., 2015). On the other hand, the means used to drive birds should be subject to regular reassessment and rotational usage, considering the plasticity and adaptability of birds. Through such strategies, it may be possible to achieve the dual goals of enhancing aviation safety and preserving avian biodiversity.

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CRediT authorship contribution statement

Jianhua Hou: Writing – review & editing, Funding acquisition, Conceptualization. **Laikun Ma:** Writing – original draft, Methodology, Data curation. **Jiaojiao Wang:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Qiqi Liu:** Investigation, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02967.

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