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Seasonal Fear in Urban Dark-eyed Juncos

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Author
Zhou, Xiaodong Suu

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Seasonal Fear in Urban Dark-eyed Juncos

A thesis submitted in partial satisfaction of the requirements for the degree Master of Science in Biology

by

Xiaodong Suu Zhou

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ABSTRACT OF THE THESIS

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by

Xiaodong Suu Zhou

Master of Science in Biology

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Professor Pamela J. Yeh, Chair

Fear response in birds is affected by environmental factors, many of which are related to seasonality, such as temperature or resource availability. The novel conditions of the urban environment may alter avian seasonal behaviours. We ask whether fear response behaviour in urban birds is associated with the differing constraints of the breeding and non-breeding seasons. To examine this, we measured the escape behaviour of a resident breeding population of Dark-eyed Juncos (*Junco hyemalis*) in an urban area. We quantified escape behaviour from 2023-2025 by measuring the flight initiation distance (FID) of individually banded juncos and compared junco FID throughout the calendar year. We found that junco FID was significantly reduced during the breeding season, which highlights the impact of season for behaviour. Other

significant predictors of FID in our model were observer starting distance and group size. Our results suggest that while seasonality plays a major role in determining urban species' behavioural responses, other factors make this relationship more complex. During the breeding season, the perceived threat of predation may be diminished for juncos focusing on parental care, resulting in lower FID. Meanwhile, differing social dynamics during the non-breeding season such as group size may be causing complex effects on urban junco fear response. Our study provides evidence that urban wildlife exhibit a flexible fear response that is seasonally dependent and related to breeding behaviour. These results help us understand the priorities of animals in the urban environment, as well as how they continue to persist under changing conditions.

The thesis of Xiaodong Suu Zhou is approved.

Daniel T. Blumstein

Elsa Ordway

Pamela J. Yeh, Committee Chair

University of California, Los Angeles

2025

This thesis is dedicated to my mother.

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INTRODUCTION

The cyclical nature of seasonal patterns result in differing goals and constraints for wildlife throughout the year (Cooper et al., 2015; Dufour et al., 2020; Helm et al., 2006; Sharma et al., 2022). These seasonal cycles are driven by changing environmental variables such as temperature, precipitation, sunlight, and resource availability (Golabek et al., 2012; Parker et al., 2014; Somveille et al., 2018; E. R. White & Hastings, 2020; T. C. R. White, 2008). However, the environmental factors associated with increasing urbanisation, such as milder temperatures, artificial light at night, and consistent year-round food sources may disrupt the seasonal responses of wildlife (Fleming et al., 2014; Lowry et al., 2013; Marzluff, 2001; Møller et al., 2015; Renthlei et al., 2017; Seress & Liker, 2015). Understanding how seasonality impacts urban animals is therefore important for predicting wildlife fitness and persistence in the city (Johnson & Munshi-South, 2017; Lowry et al., 2013; Shochat et al., 2006).

Wildlife depend on the seasons for cues to exhibit seasonal behaviour, which is impacted by the unique conditions of urban environments (Atwell et al., 2014; Partecke et al., 2005; Schoech & Bowman, 2001; Wingfield et al., 1992). The length, timing, and frequency of animal breeding seasons are affected by factors such as increased resource availability and different temperature gradients (Crick et al., 1997; Forchhammer et al., 1998; Fudickar et al., 2017; Møller et al., 2015; Partecke et al., 2005; Perrins, 1970). Urban wildlife have also shifted their seasonally dependent behaviours such as migration or territorial aggression (Atwell et al., 2014; Bonnet-Lebrun et al., 2020; Hardman & Dalesman, 2018; Łopucki et al., 2021; Tryjanowski et al., 2013; Walters et al., 2023). For example, many formerly migratory birds are beginning to establish resident populations in novel city landscapes (Bonnet-Lebrun et al., 2020; Rutz, 2008; Yeh & Price, 2004). Collectively, these changes in seasonal behaviour represent the ways in which wildlife are impacted by urbanisation.

The Dark-eyed Junco (*Junco hyemalis*, hereafter “junco”) is a small passerine songbird found across North America that serves as a model for studying behavioural changes in urban animals (Atwell et al., 2014; Fudickar et al., 2017; Nolan Jr. et al., 2020; Yeh & Price, 2004). While normally migratory, juncos have established year-round resident populations in multiple urban areas around coastal California cities (Atwell et al., 2014; Becker et al., 2019; Bressler et al., 2020; Newman et al., 2006; Price et al., 2008; Walters et al., 2023; Yeh & Price, 2004). These populations of juncos have adapted to urban challenges in a variety of ways, including a longer breeding season, altered flocking behaviour, reduced fear response, and decreased territorial aggression (Balph, 1979; Bressler et al., 2020; Diamant et al., 2023; Fretwell, 1969; Morelli et al., 2022; Walters et al., 2023; Yeh & Price, 2004). Juncos are well-studied in the urban environment, particularly through their behaviours such as fear response and risk assessment, which we examined in this study.

We used escape behaviour to understand how prey utilise flexible antipredator behaviour to gain fitness benefits. Prey must appropriately assess predation risk in relation to resource acquisition and necessity to maximise survival, which is needed in the context of the urban environment (Bateman & Fleming, 2014; Brown et al., 2013; Ghalambor et al., 2007; Gil & Brumm, 2013; Lowry et al., 2013; Samia et al., 2015). Urban animals have a decreased fear response than their non-urban counterparts in part due to low predation risk and increased resource availability (De

Resende et al., 2024; Diamant et al., 2023; Mccleery, 2009; Morelli et al., 2022; Nepali et al., 2024; Van Donselaar et al., 2018). Different environmental constraints and predator characteristics alter prey priorities and require behavioural plasticity and flexibility in escape timing (Brown et al., 2013; Burger et al., 1991; Cooper & Stankowich, 2010; De Resende et al., 2024; Møller, 2015; Ydenberg & Dill, 1986). Fear response is well known to lessen in the urban environment, but there are few studies on seasonal trends in escape behaviour.

In this study, we compared urban juncos fear response behaviour during the breeding (March – July) and non-breeding seasons (August – February). We conducted behavioural assays for flight initiation distance (FID), which is the distance an animal flees from an approaching human (Blumstein et al., 2015; Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). FID represents both the tradeoff between predation risk, resource availability, and the needs of the individual as well as the relationship between the animal and human during an experimental approach (Blumstein, 2003; Cooper & Blumstein, 2014). Based on previous studies on fear response in urban birds, we predicted that urban juncos would increase their fear response in the breeding season to improve their reproductive fitness (Mikula et al., 2023; Novčić & Parača, 2021; Piratelli et al., 2015). As fear response is a plastic behaviour vital for organisms to survive, studying seasonal patterns in urban bird FID helps us understand how species like juncos may be modifying their behaviour to adapt to an increasingly urbanised world (Chen et al., 2023; Fox & Madsen, 1997; Møller et al., 2015; Morelli et al., 2018; Stankowich & Blumstein, 2005).

METHODS

Study site

We conducted our study within the urban campus of the University of California, Los Angeles (UCLA). Located within the heavily built-up city of Los Angeles, California, the campus is characterised by its buildings, courtyards, paved roads, and strong human presence. Additionally, the campus has gardens, open grassy areas, and densely vegetated areas that are regularly watered and maintained throughout the year. Together, the conditions represent a complex urban habitat that may mitigate the seasonal changes of southern California (Avolio et al., 2020; Fleming et al., 2014; Huntsinger et al., 2017; Markovchick-Nicholls et al., 2008).

Starting in the 2000s, juncos established a resident breeding population at UCLA. This is part of a known trend with this species and other urban populations established across Southern California (Atwell et al., 2014; Bressler et al., 2020; Newman et al., 2006; Price et al., 2008; Walters et al., 2023; Yeh & Price, 2004). As part of a larger collective study on this population, we have banded most of the resident population, as well as collected long-term breeding and behavioural data. Juncos on campus are individually distinguishable due to our long-term banding efforts, where we catch, band, and measure them according to previously established bird banding guidelines. Each bird has a unique combination of four bands, which allows us to identify them in the field for surveying and behavioural assays. Additionally, we monitored junco nest and offspring status across campus, and found 373 nests within the 2024 and 2025 breeding seasons. This allowed us to obtain comprehensive data on the breeding status of almost every bird we monitored.

Flight initiation distance assays

All FID assays were conducted between 07:00 and 12:00 h. Upon encountering a foraging junco on the ground, we placed a marker on the ground when we first saw the bird and proceeded towards the bird at 0.5 m/s. Once the bird fled from us, we placed two more markers down: one at the location of the bird when it fled, and the other where we were at that moment. We measured the distance between the junco's final position and the other two markers, rounding to the closest 0.1 m. If the bird was flushed for a reason other than our approach, was agitated, or darted around, we abandoned the experimental approach. When a junco was banded or underwent a behavioural trial (including an FID assay), we considered it recently disturbed and did not conduct an FID assay until two weeks after the last disturbance. Our methodology follows previously established guidelines for urban junco FID, which were modified from previous studies (Blumstein, 2006; Cooper & Blumstein, 2014; Diamant et al., 2023).

For each assay, the observer collected data on a variety of variables that we aimed to include in our model. The list is as follows: FID, starting distance, minutes since sunrise, distance from path, wind, temperature, month, people present, group size, season, breeding status, sex, age, observer, and year.

We had two observers, XSZ and JDL, conduct all FID assays. FID and starting distance were determined from our previously mentioned experimental assay protocol. The minutes since sunrise were subtracted from the time of FID assay using data from the US Naval Observatory

(US Naval Observatory, 2025). The distance from path (m) was determined at the time of FID assay, as well as the junco group size and people present. Wind and temperature were collected from the National Oceanic and Atmospheric Administration (US Department of Commerce, 2025). Breeding status, sex, and age were determined from our banding and nesting data for each bird.

Statistical Analysis

Due to the left-tailed nature of both FID and starting distance, we log-transformed both variables for all analyses. To perform our analyses, we used the statistical software R (ver. 4.4.3) and RStudio (ver. 2024.12.0+467) (Posit Team, 2024; R Core Team, 2024). We used a regression tree analysis to identify variables of interest before analysing the data with a linear mixed model to determine the directional effect of these variables on junco FID. This nested approach allowed us to find the most parsimonious model without risk of overfitting.

Regression tree analysis

To assess the impact of seasonality on fear response, we initially performed a regression tree analysis to determine which variables significantly correlated with FID (Prasad et al., 2006). This method can be used to compare multiple variables, including those that may be strongly correlated, to determine which are the most significant. First, we split the dataset using the "rsample" package 70-30 into two training and testing datasets, respectively (Wickham, 2025). The optimal parameters for a regression tree with the least error were: minimum possible splits = 47, maximum tree depth = 9, and complexity parameter = 0.01000. Using these parameters, we used the training dataset to build the optimal tree with the "rpart" and "rpart.plot" packages (Millborrow, 2025; Therneau et al., 2025). We then performed a 100-fold cross validation using the "caret" package to confirm which variables were biologically relevant to FID (Figure 1) (Kuhn, 2024). The most relevant variables were used for our linear mixed model.

Linear mixed model

Using the "lme4" package, we constructed a linear mixed model to further analyse the data (Bates et al., 2015). Our LMM used log(FID) as the response variable while bird identity was held as a random effect to mitigate any effect of repeated FID assays on the same individual within one season. All other variables were included as fixed effects in the following formula for the linear mixed model:

log(FID) ~ log(Starting distance) + Distance from path + People present + Wind + Temperature + Minutes since sunrise + Month + Season + Group size + Breeding status + (1|Bird ID)

We confirmed the normality of the residuals of this final model using a residuals plot and a qq plot. We then compared the two seasons using the Tukey method (Figure 2) with the "multcomp" package (Hothorn et al., 2008).

RESULTS

Between October 2023 and July 2025, we conducted 328 FID assays (Figure 2) between two observers, XSZ (n = 257) and JDL (n = 70). We conducted 60 FIDs in the 2023 non-breeding season, 117 in the 2024 breeding season, 97 in the 2024 non-breeding season, and 54 in the 2025 breeding season. Urban junco flight initiation distances ranged from 0.3 to 10.7 m (mean ± SD = 2.6 ± 1.6 m, n = 328). FID length during both breeding seasons ranged from 0.3 to 8.0 m (2.26 ± 1.4 m, n = 171), and FID length during both non-breeding seasons ranged from 0.4 to 10.7 m (2.90 ± 1.80 m, median = 2.4, n = 157). Urban junco group sizes ranged from 1 to 14 other birds within 5 m of the target bird (mean ± SD = 1.1 ± 1.5 individuals, median = 1 individual).

The 100-fold regression tree model confirmed that starting distance, minutes since sunrise, distance from path, temperature, month, wind, people present, and group size were as or more important than season status (Figure 1). A variable with increased importance was more likely to appear in a regression tree and cause a split in the data. We determined that a variable was biologically significant if it explained greater variation in the data than whether it was the breeding or non-breeding season. The less important a variable was, the less likely it was to influence the FID of a bird under the simulated conditions; junco sex, age, group status, and the observer identity were not significant predictors of FID.

In our linear mixed model, we found that the season, starting distance, and group size were significant predictors of FID (Table 1). The other fixed effects of distance from path, people present, wind, temperature, month, year, and breeding status were not significant predictors of FID. Furthermore, our pairwise contrast using the single-step Tukey method found that junco

FID in the breeding season was significantly lower in comparison to the non-breeding season (p-value = 1.13e-07, estimate = 0.329, standard error = 0.062, z-value = 5.304).

DISCUSSION

Our results show that seasonality impacts urban junco behaviour and leads to a reduction in FID during the breeding season in comparison to the non-breeding season. This contrasts with both previous research and our prediction for increased FID during the breeding season (Mikula et al., 2023; Novčić & Parača, 2021; Piratelli et al., 2015). We posit that the breeding juncos are more tolerant to risk and are prioritising the fitness benefits of offspring survival (Chen et al., 2023; Dowling & Bonier, 2018; Ghalambor, 2002; Minias, 2016; Montgomerie & Weatherhead, 1988). On the other hand, the increased FID during the non-breeding season may be due to larger group size or the lack of pressure to maintain territories and provide for offspring (Davies & Sewall, 2016; Morelli et al., 2019; Shuai et al., 2024). Our population of dark-eyed juncos still exhibit seasonal changes in behaviour that are not mitigated by novel urban conditions. These findings advance understanding of animal behavioural responses to the challenges of urban environments.

Increased group size is a known antipredator behaviour that we found resulted in lower junco FID (Goldman, 1980; Lima, 1995; Morelli et al., 2019; Shuai et al., 2024). In general, the association between group size, a known antipredator behaviour, and FID can vary greatly, with previous studies citing positive, negative, and even no correlation between FID and increasing group size (Ardila-Villamizar et al., 2022; García-Arroyo & MacGregor-Fors, 2020; Møller, 2015; Morelli et al., 2019; Shuai et al., 2024; Zhao et al., 2024). The effect of group size on FID may be species specific: house sparrows (*Passer domesticus*) have greater FID within a flock, while orange breasted bunting (*Passerina leclancherii*) FID is not significantly correlated to group size (García-Arroyo & MacGregor-Fors, 2020). Similarly, wading birds were found to have a stronger positive correlation between FID and group size than many other groups, including passerines (Møller, 2015; Shuai et al., 2024). In the context of our study, junco fear response decreases in a group setting, which may be due to a reduced likelihood of predation for each individual bird (Hammer et al., 2023; Lima & Bednekoff, 1999).

Factors that did not significantly affect FID were wind, temperature, and the number of people present within 20 m. We expected higher wind speed and extreme temperatures to be detrimental to birds' vigilance and escape capabilities, which would increase FID (Boysen et al., 2001; Carr & Lima, 2010, 2012; Studd et al., 2022). We predicted increasing pedestrian presence would impact FID, but our results show that nearby people may not be a factor in urban juncos' risk assessment (Beale & Monaghan, 2004; Cavalli et al., 2018; Rodriguez-Prieto et al., 2009; Samia et al., 2015; Vincze et al., 2016). However, we were more likely to successfully conduct FIDs during comfortable weather conditions without many people nearby, which led to limited variability in wind, temperature, and pedestrian presence in our study.

Further studies should be conducted with variables that differ more broadly in order to holistically determine the impact of seasonal elements of FID. Our study found that observer starting distance was one of the most significant predictors of FID, which aligns with the established knowledge that FID increases with increasing starting distance (Cooper & Blumstein, 2015; Møller, 2015; Stankowich & Blumstein, 2005). Thus, including more variation in observer approach tactics beyond starting distance such as multiple approaching researchers may lead to more nuanced understanding of risk assessment behaviour (De Resende et al., 2024; Geist et al., 2007). The impact of time of day on avian escape decisions is also worth pursuing further (Ferguson et al., 2019; Valcarcel & Fernández-Juricic, 2009). Integrating different variables under different conditions will help shed more light on the dynamics of fear response in an urban environment and contribute to determining the most crucial variables that affect FID.

In conclusion, seasonality does influence urban junco escape behaviour, with the breeding season having a negative impact on urban junco FID. Our results suggest that during the breeding season, the perceived risk of predation would be overshadowed by the greater demands of engaging in parental care and feeding offspring. Meanwhile, differing social dynamics during the non-breeding season such as group size cause complex effects on urban junco fear response. Urban juncos have flexible fear response behaviours that vary seasonally and are related to breeding cycles.

FIGURES AND TABLES

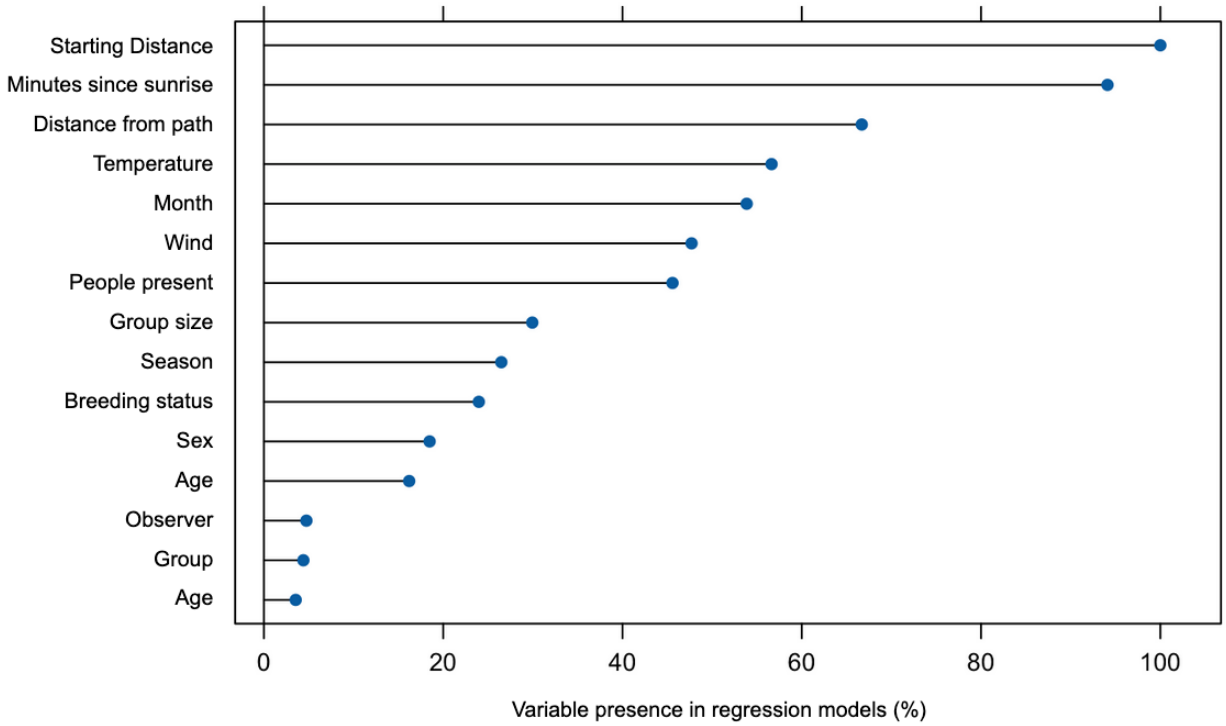

Figure 1: Chart showing the relative importance of each variable from the regression tree cross validation. A variable being higher up in the chart with a longer bar means it is a greater predictor of variation in FID. Starting distance caused splitting in the data in 100% of the modeled regression trees. Nine variables were as or more biologically important than season status.

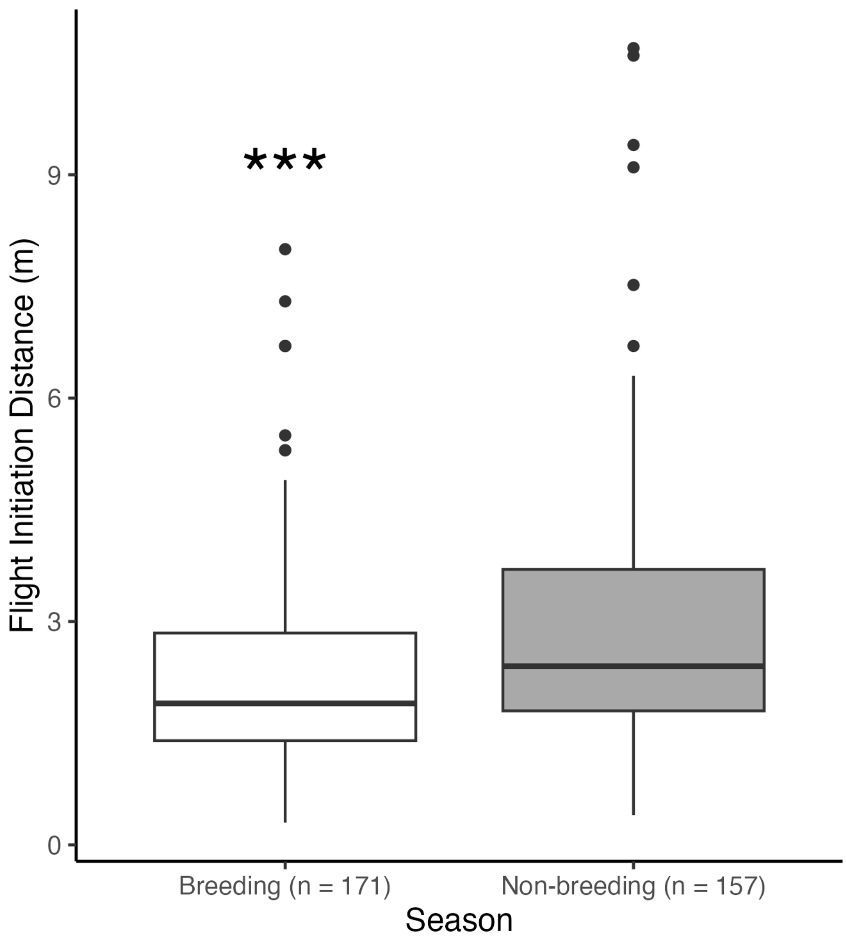

Figure 2: Box and whisker plot of flight initiation distance (FID) between the breeding and non-breeding season. Data was analysed with ANOVA and Tukey HSD. Both boxplots represent urban junco FID during the 2024 and 2025 breeding seasons compared to the 2023 and 2024 non-breeding seasons. The black bar within the boxplot represents the median, the limits of the boxes represent the IQR, and the lines extending from the boxes represent the extremities of the data. Black dots are outliers in the data. "***" represents the significant difference to the $p < 0.0001$ level between the seasons. (Estimate = 0.32942, standard error = 0.06211, z-value = 5.304, p-value = 1.13e-07)

log(FID)

Predictors	*Estimates*	*CI*	*Chisq*	*Df*	*p-value*
(Intercept)	-0.22	-0.75 - 0.32			0.424
Distance from path	-0.00	-0.02 - 0.01	0.0940	1	0.759
People present	-0.00	-0.02 - 0.01	0.1676	1	0.683
Wind (kph)	-0.01	-0.03 - 0.02	0.2844	1	0.594
Temperature (°C)	0.01	-0.02 - 0.03	0.2941	1	0.588
Starting distance [log]	0.43	-0.27 - 0.59	27.0119	1	**<0.001**
Month	0.00	-0.02 - 0.03	0.0273	1	0.869
Minutes since sunrise	-0.00	-0.00 - 0.00	0.9074	1	0.342
Season [non-breeding]	0.25	0.05 - 0.45	5.8456	1	**0.016**
Group size	-0.06	-0.11 - -0.02	7.4854	1	**0.007**
Breeding status [active]	-0.10	-0.27 - 0.07	1.3743	1	0.242

Random Effects	*Variance*	*SD*
Bird identity	0.05	0.22
Year	0.24	0.4939

Table 1: Summary statistics for linear mixed model. The results of the linear model, which predicted log(FID) based on the fixed effect variables (distance from path, people present, wind, temperature, log(starting distance), month, minutes since sunrise, season, group size, breeding status, and year). The random effects were the bird identity and year, to mitigate the effects of repeat birds within one season and of different yearly conditions.

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