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The fear response of the white wagtail (*Motacilla alba*) in two Finnish cities

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Tiivistelmä — Referat — Abstract

Behavior is one of the fastest ways wildlife can cope with environmental change, such as urbanization. In human-wildlife interactions, animals tend to assimilate humans with predators and respond accordingly. This fear response is species- and situation-specific but can be quantified by using behavioral indicators such as alert distance (AD), flight initiation distance (FID), and escape distance (ED). Fear can shape species’ distribution, abundance, and their ability to inhabit urban areas.

In this thesis, I collected ADs, FIDs, and EDs of the white wagtail (*Motacilla alba*) in two cities in Finland, Helsinki and Lahti. I aimed to find whether bird age, sex, flock size, pedestrian activity, distance to refuge, land use, built cover or escape method relate with any of the indicators and whether these relations differ by city. For analysis, I used linear models (LM) and classification and regression trees (CART).

Flock size related positively with AD and distance to refuge positively with both AD and FID. Juveniles were shyer with higher FIDs and EDs. Escapes by running were shorter. Additionally, in Helsinki, higher pedestrian presence was positively related with AD and ED, flock size with FID, and in commercial land use, birds escaped shorter distances. In Lahti, there was less correlations, so that distance to refuge had a positive correlation with AD, juveniles had higher FIDs, and runners had shorter EDs. Built cover had a non-linear relationship with all indicators.

Understanding fear is crucial when assessing how species respond to environmental change. At the same time, it offers tools for manipulating animal behavior, be it for conservation or non-lethal deterring. However, in the light of this study, it is important to consider holistically all parts of fear response and conduct species-specific and situational studies before moving to practical applications.

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Västäräkin (*Motacilla alba*) pelkovaste kahdessa suomalaisessa kaupungissa

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Tiivistelmä — Referat — Abstract

Käyttäytyminen on yksi nopeimmista tavoista, joilla villieläimet voivat sopeutua ympäristömuutokseen, kuten kaupungistumiseen. Ihmisten ja villieläinten kohtaamisissa eläimet pitävät ihmisiä petoina ja reagoivat vastaavasti. Tämä pelkovaste on laji- ja tilannekohtainen, mutta mitattavissa käyttämällä käyttäytymisindikaattoreita, kuten valpastumisetäisyyttä (AD), pakoetäisyyttä (FID) ja paettua etäisyyttä (ED). Pelko voi ohjata lajien levinneisyyttä, runsautta ja kykyä asuttaa kaupunkialueita.

Tässä tutkielmassa keräsin västäräkin (*Motacilla alba*) AD:ita, FID:itä, ja ED:itä kahdessa suomalaiskaupungissa, Helsingissä ja Lahdessa. Tarkoituksenani oli selvittää, liittyykö linnun ikä tai sukupuoli, parvikoko, jalankulkijoiden määrä, turvapaikan etäisyys, maankäyttömuoto, rakennetun pinta-alan määrä tai pakotapa mihinkään indikaattoreista, ja ovatko nämä yhteydet erilaiset kaupunkien välillä. Käytin analyysissa lineaarisia malleja (LM) ja luokittelu- ja regressiopuita (CART).

Parvikoko oli positiivisesti yhteydessä AD:hen, ja etäisyys turvapaikkaan positiivisesti yhteydessä sekä AD:n että FID:n kanssa. Poikaset olivat pelokkaampia, sillä ne pakenivat aiemmin ja kauemmas. Juosten paetut etäisyydet olivat lyhyempiä. Helsingissä jalankulkijoiden määrä korreloi positiivisesti AD:n ja ED:n kanssa, parvikoko FID:n kanssa, ja maankäytöltään kaupallisilla alueilla linnut pakenivat lyhyempiä etäisyyksiä. Lahdessa korrelaatioita oli vähemmän, vain turvapaikan etäisyys korreloi positiivisesti AD:n kanssa, nuoret linnut pakenivat nopeammin ja pako juosten oli lyhyempi. Rakennettu pinta-ala korreloi ei-lineaarisesti kaikkien indikaattoreiden kanssa.

Pelon ymmärtäminen on elintärkeää, kun arvioidaan kuinka lajit reagoivat ympäristömuutokseen. Samalla se tarjoaa työkaluja eläinten käytöksen ohjaamiseen, olipa kyse suojelusta tai ei-tappavasta karkottamisesta. Kuitenkin tämän tutkimuksen perusteella on tärkeää huomioida kaikki pelkovasteen osat ja tehdä laji- ja tilannekohtaista tutkimusta ennen käytännön sovelluksiin siirtymistä.

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Abbreviations

AD alert distance

ED escape distance

FID flight initiation distance

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1 Introduction

Human activities, especially urbanization, continue to conquer more area (Seto et al., 2012), forcing natural environments and their inhabitants to adapt. Behavior is one of the fastest ways animals can cope with environmental change (Sol et al., 2018). One cornerstone of behavior is antipredator tactics, the ways animals avoid becoming victims of predation: hiding, camouflage, deterring, and escape (Kalb et al., 2019). Animals tend to assimilate anthropogenic disturbance, such as approaching humans, with predation and respond similarly (Frid & Dill, 2002). A disturbance stimulus creates a trade-off situation, since monitoring the possible threat or fleeing costs time, attention, opportunities, and energy that could have been spent on fitness-enhancing activities, such as foraging or tending young instead (Frid & Dill, 2002). In contrast, staying in place increases the risk of injury or death. The inner calculation of the cost of escape stem from risk assessment or its perception, coined as “fear” (Gaynor et al., 2021). This fear response is tangled to intrinsic and extrinsic factors, being complex enough to have birthed the research field of “ecology of fear” focused on studying these links and their consequences.

Behavioral indicators, such as distances measured by approaching a target individual in a standardized manner, are a common way of studying and quantifying fear response (Blumstein, 2006). One indicator is alert distance, hereafter referred to as AD, which is the distance between the observer and the individual when it shows alert behavior (Fernández-Juricic et al., 2001). A more widely used indicator is flush distance or flight initiation distance (Ydenberg & Dill, 1986), FID for short, meaning the distance between the observer and the individual when it flees (Blumstein, 2003). Risk assessment happens in the buffer distance between AD and FID (Fernández-Juricic et al., 2001). Therefore, AD represents the vigilance of the animal, while FID is the distance where the risk from staying overrides the cost of fleeing (Blumstein, 2003) or where the utmost disturbance tolerance is crossed. Escape distance, ED for short, or distance fled (e.g., in Tätte et al., 2018) is a third independent and informative indicator (Tätte et al., 2018), albeit less commonly used. It can give a more integrative view of the cost of escape (Tätte et al., 2018).

These indicators allow comparing the fear responses of species to assess their disturbance tolerance, behavioral flexibility, and the cost of escaping. FID variation in species and close relatives is consistent or similar (Sol et al., 2018), being tied to species traits such as brain and eye size (Møller & Erritzøe, 2014), body size (Blumstein et al., 2006; Møller and Erritzøe, 2014), sociability (Blumstein et al., 2006), and life history (Sol et al., 2018). Intraspecies FID can vary (e.g., Blumstein 2003), for example, depending on age (e.g., Eason et al., 2006), life stage (Hammer et al., 2025), and personality, which can range from shy to bold (Evans et al., 2010). FID is often consistent in individuals (Evans et al., 2010; Carrete & Tella, 2013; Møller, 2014; Hammer et al., 2022; McDonald et al., 2025), while AD is potentially not (Hammer et al., 2022).

The fearfulness of a species can direct its abundance, distribution, and vulnerability to environmental change, as well as its ability to coexist with human presence (Blumstein 2006). On the other hand, humans visiting habitats can hinder breeding, foraging, and nesting (Chace & Walsh, 2006). Animals may avoid more disturbed areas while foraging (Gill et al., 1996), possibly leading to insufficient foraging and starvation (Blumstein, 2006). Therefore, brief shifts in behavior may eventually lead to long-lasting effects in the form of population loss (e. g. Flemming et al., 1988). For instance, warier bird species in Europe have been declining (Møller, 2008a). Apart from understanding ecological links and responses to environmental change, fear can become handy in practice. Gaynor et al. (2021) introduced an applied framework for the ecology of fear, where fear becomes a tool for achieving conservation goals and mitigating human-wildlife conflicts. For instance, risk cues can deter unwanted animals non-lethally and reduce conflicts, as successfully done with felid growl playbacks and crop-raiding elephants (*Elephas maximus*) in India (Thuppil & Coss, 2016). Vice versa, limiting disturbance can recover populations like seen with snowy plovers (*Charadrius nivosus*) in California (Lafferty et al., 2006).

Tolerance to human presence is necessary in urban areas, where habitats are most altered and where 55 % of humanity, the number ever-growing, is concentrated (United Nations 2018). Urbanization density forms an urban-rural gradient, which can be quantified and characterized in many ways and correlated with biodiversity responses (McDonnell & Hahs, 2008). Species attempting to colonize urban areas have been suggested to face a multi-dimensional filter of extrinsic and intrinsic factors, which determine their success (MacGregor-Fors et al., 2022). Indeed, urban birds are bolder and show lower FIDs compared to rural birds, found both on species-level and between conspecific individuals (e.g., Evans et al., 2010; Clucas & Marzluff, 2012; Samia et al., 2015; Vincze et al., 2016; Sol et al., 2018, Nepali et al., 2024). Many hypotheses for the mechanism exist, including habituation where repeated exposure to disturbance leads to dulled responses (Whittaker & Knight, 1998), habitat selection where only bolder individuals can colonize urban areas (Carrete & Tella, 2010), and local adaptation where innately bolder birds are fitter in urban areas (Møller, 2008b). Recently, the alarming loss of biodiversity and urbanization as one of its main drivers (IPBES, 2019) have piqued interest in the conservation potential of urban areas (Lepczyk et al., 2023), making it even more important to consider fearfulness as one contributor to a species' success.

The white wagtail *(Motacilla alba)* is an omnipresent, insectivorous bird in Eurasia and parts of North Africa (Birdlife International, 2019) that has accompanied humans throughout urbanization, inhabiting versatile open habitats from natural beaches all the way to agricultural fields, parks, and city centers. Adult white wagtails have either black or grey crowns, which has been considered as a sign of sex, so that adult individuals with grey, dark grey or black crown fading to grey at neck are female while males have black crowns (e.g., Laine, 2015). The species is often described as fearless, letting humans approach as close as a few steps away (Koskimies, 2021). Some studies have inspected the FID of the white wagtail before as a part of larger interspecies research questions (Blumstein, 2006; Mikula, 2014; Møller & Erritzøe, 2014; Møller et al., 2019; Zhou & Liang, 2020; Tätte et al., 2018; Morelli et al., 2022; Bao et al., 2025). However, there has not been much focus on the other parts of its fear response, AD and ED (but see Tätte et al., 2018), on intrinsic individual traits, such as age and sex, or on it as an open habitat dweller in the urban gradient.

Aiming to increase current knowledge, I am focusing on the white wagtail as a potential biological model species for fear response in open habitats in the urban landscape. In this thesis, I assess the fear response of the white wagtail in two cities in Finland, Helsinki and Lahti, by using behavioral indicators AD, FID, and ED as a proxy for fear response. I aim to answer the following main research questions:

1. *What intrinsic factors (e.g., bird age and sex) and extrinsic factors (e.g., land use) relate with the fear response (considering AD, FID, and ED) of the white wagtail?*
2. *Are the relations of these factors different between Helsinki and Lahti?*

I predict that juvenile white wagtails will have longer AD, FID and ED than adults (meaning they are more vigilant, shyer, and overcautious), as found for FID before, for example, in barn swallows *(Hirundo rustica)* (Møller, 2014) and American robins (*Turdus migratorius*) (Eason et al., 2006), although the opposite has been observed in black redstarts (*Phoenicurus ochururos*) (Kalb et al., 2019) and black-headed gulls (*Chroicocephalus ridibundus*) (Liu et al., 2025). Additionally, if crown color signals sex, males may be bolder, having shorter AD, FID, and ED than females, as found in house sparrows *(Passer domesticus)* for AD and FID (García-Arroyo & MacGregor-Fors, 2020) and for FID in black redstarts (Kalb et al., 2019), or there will be no difference, at least in FID (Møller, 2014; Sol et al., 2018; Hall et al., 2020; McDonald et al., 2025).

Given FID is generally shorter in more disturbed environments (e.g. Ikuta & Blumstein, 2003; Samia et al., 2015; Hall et al., 2020), I predict that the fear response will be different between the two cities, so that at least FID will be lower in Helsinki either because of higher human presence facilitating habituation (e.g. Cavalli et al., 2018) or larger settlement size sustaining systemic habituation (García-Arroyo et al., 2023), compared to smaller, less populated and disturbed Lahti. Similar effects could span over to AD and ED as well. This same relation could extend to different land uses in the urban gradient, FIDs being shorter in more disturbed environments with greater amount of built cover, or in land uses with more human activity, such as commercial areas.

2 Methods

2.1 Study species

The white wagtail, sometimes also called the pied wagtail, is a small, lean bird with black, grey, and white coloring and a long wagging tail (Figure 1). It is the second most widespread bird in Finland with 400 000–600 000 pairs (Valkama et al., 2011) but has dropped from the category of least concern to near threatened in Finland between 2015 and 2019 (the Red List, 2019). The breeding population in Finland has decreased by a third after the year 2000 (Lehikoinen & Väisänen, 2023). The cause for the population decline remains unknown (the Red List, 2019). Globally, the white wagtail is categorized as least concern with 135 to 221 million mature individuals (BirdLife International, 2019).

The habitat of the white wagtail consists of open areas with scarce vegetation, including rocky, sandy, or rugged beaches, field headlands, sides of roads, yards, lawns, and industrial or storage areas (Koskimies, 2021), thus being present in diverse habitats on the urban gradient. It forages by walking and making short flights to catch flying insects (Laine, 2002). Its natural predators include at least the Eurasian sparrow hawk (*Accipiter nisus*) (Table S2 in Møller & Erritzøe, 2014).

Figure 1. Adults and juvenile of the white wagtail: a) adult male, with dark crown and bib. b) likely an adult female with grey crown and black bib. c) juvenile without black in both crown and bib. Pictures: Minna Ursin

2.2 Study area

The data was collected in Helsinki and Lahti, Finland (Table 1). Helsinki (60°10'32.16''N, 24°56'3.12''E) is a coastal capital city in Uusimaa region with 664 028 inhabitants and population density of 3 108 inhabitants per km². The whole Helsinki metropolitan area has 1 260 620 inhabitants, the urban continuum covering 314 km². Helsinki was founded in 1550 but began to widely urbanize after the 1930s through the development of suburbs (Pääkkönen, 2021). It has a hemiboreal climate and 34 percent of its area is green (Saarto, 2024). Lahti (60°58'49.44''N, 25°39'18.00''E) is the ninth largest city in Finland and the capital of the Päijät-Häme region, founded in 1905. It has 121 019 inhabitants and population density of 264,31 inhabitants per km². The municipal land area is 459,47 km², the urban continuum spans 54 km² (MacGregor-Fors et al., 2021), and 62,7 km² are green spaces (Lahden kaupunki, 2013). Lahti has a south boreal climate and shares shoreline with the lake Vesijärvi.

Table 1 Characteristics of the two study cities.

City	Municipal land area	Urban continuum	Inhabitants	Location
Helsinki	214.19 km²	314 km²	664 028	60°10'32.16''N, 24°56'3.12''E
Lahti	459.47 km²	54 km²	121 019	60°58'49.44''N, 25°39'18.00''E

2.3 Field surveys

The surveys took place during morning hours, from 6 AM to 11 AM. I chose five different routes, approximately ten kilometers in length, aiming for variation in habitat and built cover. I sampled each route once in June, July, and August in a five-day period in Helsinki during 2023. Additionally, I surveyed one day in July in Suomenlinna, an island in the Helsinki region. For Lahti, I established routes with same characteristics but modified them flexibly on field to gain sufficient data for all land uses and different aged birds. I sampled the routes in a single week in early June of 2024. See routes in Figure 2. I wore neutral clothing, mainly grey or black, to minimize its influence (Zhou & Liang, 2020) and surveyed only when weather was mild with low to no precipitation and wind, as weather may change fear response (Hammer et al., 2022).

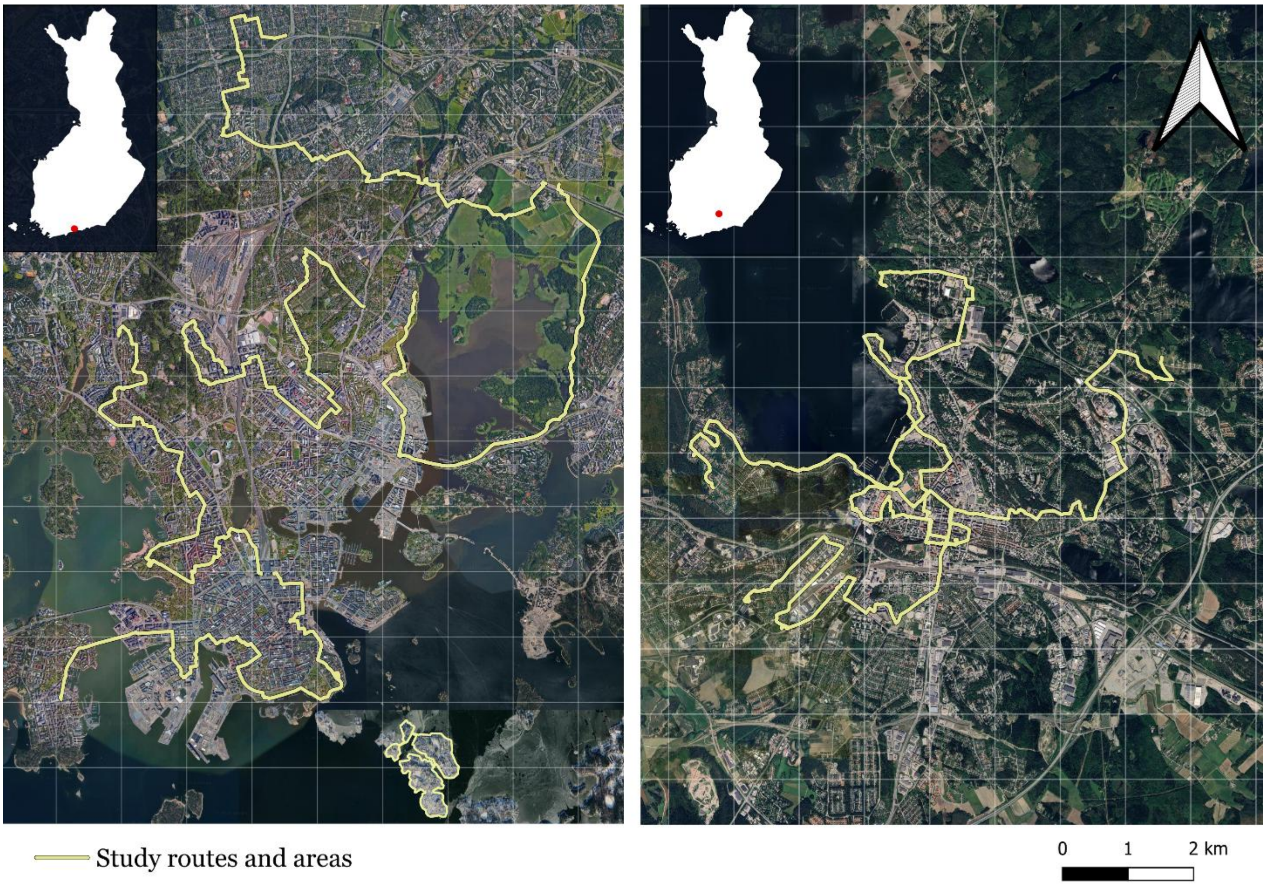

Figure 2. The locations of the cities and the map of the survey routes and areas in Helsinki (left), and Lahti (right). Map data ©2025 Google.

From each observation, I noted twelve variables: time and date of the observation, the crown color of the individual (black/grey), age (adult/juvenile), land use, conspecific flock size within 10 meters, height (if above ground level), starting distance, AD, FID, ED, distance to refuge (all in meters), escape method (run/flight), number of humans within 50 meters, and location. I determined the age of the bird based on appearance, as juveniles during the summer months have less defined plumage patterns, with less black and often yellowish facial feathers (e.g., Laine, 2015) and pronounced gape flanges.

I used binoculars for detecting and identifying birds if seen far away. I approached all birds in a linear manner with a standardized walking pace of 5 km/h while looking at the bird. If there were obstacles between me and the bird, or the bird was already alerted or became alerted by external forces (e.g., other by-passers) in the process, I discontinued the approach and did not include the bird in the sample. If the bird was a part of a flock, I approached the closest individual. To avoid resampling individuals, I continued the route for some time before surveying another individual. I measured distances over three meters with a TecTecTec! ULT-X laser rangefinder, visually if less due to the inaccuracy of the rangefinder at such distances. I marked starting point, alert point and escape point. Afterwards, I walked to the spot the bird escaped from, then measuring starting distance, AD, FID, ED, and distance to refuge. I determined the distance to refuge from the birds first location before approach to a potential refuge such as a tree, a bush, or a building.

On site I categorized each observation into one of four land use categories: residential, recreational, transportation, or commercial. Categories were meant to express both physical landscape traits as well as patterns of human use, as in Hall et al. (2020). Afterwards, to further describe urbanization intensity, I quantified the percentage of built cover within 50-meter radius in Google Earth Pro for each observation.

2.4 Statistical analysis

To answer my first question, I built three linear models, one for each dependent variable (i.e., AD, FID, ED), which were log-transformed with natural logarithm to obtain normality. The independent variables in the models were: age, crown color (as a proxy of sex), distance to refuge, number of conspecifics, passing pedestrians, built cover, and land use, and for ED, also escape method. For the second question, the cities were inspected separately with their own linear models for each dependent variable. I first calculated the coefficients of determination (R^2) for each linear model (rsq R-package: Zhang, 2024) and then further assessed the relative importance of variables in terms of their explanatory power using the lmg metric (relaimpo R-package: Grömping, 2006). Additionally, I created a classification and regression tree, CART, (rpart R-package: Therneau & Atkinson, 2023; rpart.plot R-package: Milborrow, 2024) for each dependent variable to reveal non-linear relationships and threshold values, complementing linear models (De'ath and Fabricius, 2000). For additional data visualization, I made a box plot with ggplot2 R-package (Wickham, 2016). Statistical analyses were run in R version 4.4.1 (R Core Team, 2024).

3 Results

3.1 Overview

I recorded 137 observations in total, 66 for Helsinki with 39 adults and 27 juveniles, and 71 for Lahti with 46 adults and 25 juveniles, respectively. Obtained observations per land use were not equal in quantity (Table 2). Individuals met in transportation land use were almost exclusively juveniles. Most birds fled by flight while 11–18 % ran away, juveniles rarely running. 60 % of birds occurred alone, 28 % in pairs, 9 % in a flock of three, and 3 % in a flock of four. The number of pedestrians ranged from zero to five in Helsinki and zero to two in Lahti. No pedestrians were present in 55 % of observations in Helsinki and in 72 % of observations in Lahti. The mean starting distance was 20.8 m, ranging between 6–39 m. Distance to refuge ranged between 0.5–28.5 meters, with a mean of 7.11 meters in Helsinki and 4.88 meters in Lahti. Since none of the birds were met above ground level, I excluded the variable "height" from analysis.

Table 2. Observations per land use.

City	Recreational	Commercial	Residential	Transportation
Helsinki	40	5	15	6
Lahti	41	13	12	5

FID varied between 2–20.6 meters, AD between 3.6–30 meters, and ED between 0.5–44.3 meters. The difference of the mean AD between cities was almost non-existent, being 11.84 meters in Helsinki and 11.74 meters in Lahti. The mean FID was slightly larger in Helsinki than Lahti, 8.15 meters and 7.14 meters, respectively. The mean ED was slightly larger in Lahti, 12.6 meters, than in Helsinki, 11.8 meters. Figure 3 showcases variation of FID per land use and age in detail.

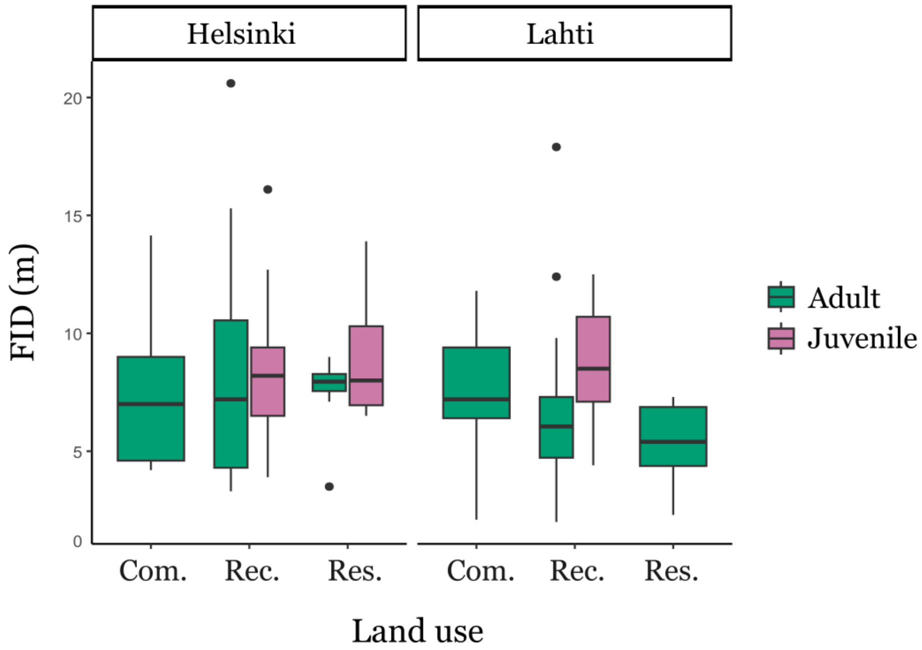

Figure 3. FID in meters by city, land use and age group. Helsinki is on the left side and Lahti on the right. Com. stands for commercial, rec. for recreational and res. for residential. The combinations of land use and age with less than five observations are not shown.

3.2 Linear models

When both cities were included (Table 3), the LM for AD ($R^2 = 0.148$) showed a significant positive relationship with distance to refuge and the number of conspecifics, and a close-to-significant trend with age, juveniles having longer ADs. The LM for FID ($R^2 = 0.182$) showed a significant positive relationship with distance to refuge, and age, juveniles having longer FIDs. The LM for ED ($R^2 = 0.295$) showed a significant relationship with age, with juveniles having higher ED, and a significant relationship with escape method, runners having lower ED. It also showed non-significant trends with land use and the number of passing pedestrians.

Table 3. The relationships between age, crown color, land use, distance to refuge, passing pedestrians, built coverage, number of conspecifics, and AD, FID, and ED for the species in both Helsinki and Lahti.

Variables	Sum of sq.	df	F	P	rel. r^2
AD (both cities)					
Age	0.49	1	3.75	0.056	0.016
Crown	0.00	1	0.03	0.866	0.006
Land use	0.55	3	1.40	0.245	0.041
Distance to refuge	0.97	1	7.36	0.007	0.039
Passing pedestrians	0.15	1	1.12	0.291	0.007
Built coverage	0.02	1	0.06	0.706	0.001
Number of conspecifics	0.70	1	5.34	0.023	0.036
Total R^2					0.148
FID (both cities)					
Age	2.05	1	13.26	<0.001	0.048
Crown	0.34	1	2.22	0.139	0.049
Land use	0.31	3	0.67	0.571	0.008
Distance to refuge	1.09	1	7.02	0.009	0.045
Passing pedestrians	0.39	1	2.53	0.114	0.015
Built coverage	0.06	1	0.30	0.518	0.005
Number of conspecifics	0.14	1	0.17	0.341	0.013
Total R^2					0.182
ED (both cities)					
Age	5.84	1	6.49	0.012	0.016
Crown	0.36	1	0.40	0.528	0.016
Land use	5.86	3	2.17	0.095	0.021
Distance to refuge	0.81	1	0.90	0.346	0.005
Passing pedestrians	2.96	1	3.29	0.072	0.014
Built coverage	0.12	1	0.13	0.715	0.004
Number of conspecifics	0.69	1	0.77	0.381	0.002
Escape method	30.79	1	34.22	<0.001	0.217
Total R^2					0.295

When Helsinki was inspected alone (Table 4), the LM of AD ($R^2 = 0.281$) had a significant positive relationship with distance to refuge, the number of passing pedestrians, and the number of conspecifics, and a non-significant trend of juveniles having longer ADs. The LM of FID ($R^2 = 0.259$) showed a positive significant relationship with the number of conspecifics, and age, juveniles having longer FIDs, and a non-significant positive trend with distance to refuge. The LM of ED ($R^2 = 0.466$) revealed a significant relationship with age, juveniles having longer ED, a significant positive relationship with the number of passing pedestrians, and a significant relationship with land use, so that birds in commercial areas escaped shorter distances, and a significant relationship with escape method, runners escaping shorter distances. It also showed non-significant trends with distance to refuge and crown color, with the grey-crowned having longer ED.

Table 4. Relationship between age, crown color, land use, distance to refuge, passing pedestrians, built coverage, number of conspecifics, and AD, FID, and ED for the species in Helsinki.

Variables	Sum of sq.	df	F	P	rel. r^2
AD (Helsinki)					
Age	0.39	1	3.02	0.088	0.023
Crown	0.02	1	0.14	0.706	0.011
Land use	0.29	3	0.76	0.520	0.069
Distance to refuge	0.58	1	4.51	0.038	0.034
Passing pedestrians	0.73	1	5.70	0.020	0.062
Built coverage	0.01	1	0.06	0.812	0.005
Number of conspecifics	0.80	1	6.21	0.016	0.077
Total R^2					0.281
FID (Helsinki)					
Age	0.74	1	4.79	0.033	0.030
Crown	0.26	1	1.70	0.197	0.040
Land use	0.10	3	0.21	0.892	0.024
Distance to refuge	0.56	1	3.64	0.062	0.029
Passing pedestrians	0.43	1	2.74	0.103	0.034
Built coverage	0.08	1	0.54	0.468	0.017
Number of conspecifics	0.85	1	5.50	0.023	0.085
Total R^2					0.259
ED (Helsinki)					
Age	7.45	1	10.29	0.002	0.038
Crown	2.86	1	3.95	0.052	0.067
Land use	6.83	3	3.14	0.032	0.083
Distance to refuge	2.09	1	2.89	0.095	0.022
Passing pedestrians	6.59	1	9.10	0.004	0.058
Built coverage	0.03	1	0.04	0.848	0.010
Number of conspecifics	1.17	1	1.62	0.208	0.009
Escape method	7.66	1	10.58	0.002	0.178
Total R^2					0.466

Lahti was different from Helsinki when inspected in isolation, showing less relationships with the independent variables and smaller explanatory power with the linear models (Table 5). The

LM of AD (R^2 = 0.189) showed a positive significant relationship with distance to refuge. The LM of FID (R^2 = 0.180) had a significant relationship with age, with juveniles again with larger FIDs. The LM of ED (R^2 = 0.264) showed a significant relationship with escape method, runners having shorter EDs than flyers, and a non-significant trend with land use.

Table 5. Relationship between age, crown color, land use, distance to refuge, passing pedestrians, built coverage, number of conspecifics, and AD, FID, and ED for the species in Lahti.

Variables	Sum of sq.	df	F	P	rel. r^2
AD (Lahti)					
Age	0.14	1	1.09	0.301	0.011
Crown	0.00	1	0.01	0.944	0.006
Land use	0.37	3	0.96	0.416	0.041
Distance to refuge	0.64	1	5.04	0.028	0.071
Passing pedestrians	0.33	1	2.59	0.113	0.034
Built coverage	0.00	1	0.02	0.884	0.002
Number of conspecifics	0.33	1	2.58	0.113	0.024
Total R^2					0.189
FID (Lahti)					
Age	1.22	1	7.67	0.007	0.064
Crown	0.04	1	0.26	0.614	0.037
Land use	0.48	3	1.01	0.393	0.028
Distance to refuge	0.36	1	2.27	0.137	0.047
Passing pedestrians	0.00	1	0.01	0.914	0.002
Built coverage	0.02	1	0.13	0.719	0.001
Number of conspecifics	0.00	1	0.04	0.847	0.001
Total R^2					0.180
ED (Lahti)					
Age	0.53	1	0.50	0.483	0.005
Crown	0.45	1	0.42	0.519	0.001
Land use	7.37	3	2.32	0.084	0.053
Distance to refuge	0.08	1	0.07	0.791	0.001
Passing pedestrians	0.03	1	0.03	0.864	0.003
Built coverage	0.01	1	0.01	0.935	0.003
Number of conspecifics	0.11	1	0.10	0.753	0.001
Escape method	14.23	1	13.46	>0.001	0.198
Total R^2					0.264

3.3 Classification and regression trees

I created CARTs for the whole dataset only. The variables included in CART analysis were age, crown color, land use, distance to refuge, number of passing pedestrians, conspecific flock size and city, and for the CART of ED, also escape method. The CARTs present scenarios where a category or a threshold of a variable leads to a certain outcome: higher or lower AD, FID or ED, also showing the proportion of data following a specific path.

In the CART of AD (Figure 4), distance to refuge was the most important splitter with a threshold value of 6.7 m. Interestingly, when the value was lower, land use, built cover and distance to refuge split the data again, while at a higher value, only the city and the number of pedestrians mattered. Age was the most important splitter in the CART of FID (Figure 5), after which built cover split the FID of juveniles while distance to refuge, conspecific flock size and city divided the adults. In the CART of ED (Figure 6), escape method split the data most, runners splitting into two groups by distance to refuge while flyers were concerned with distance to refuge, built cover, and land use.

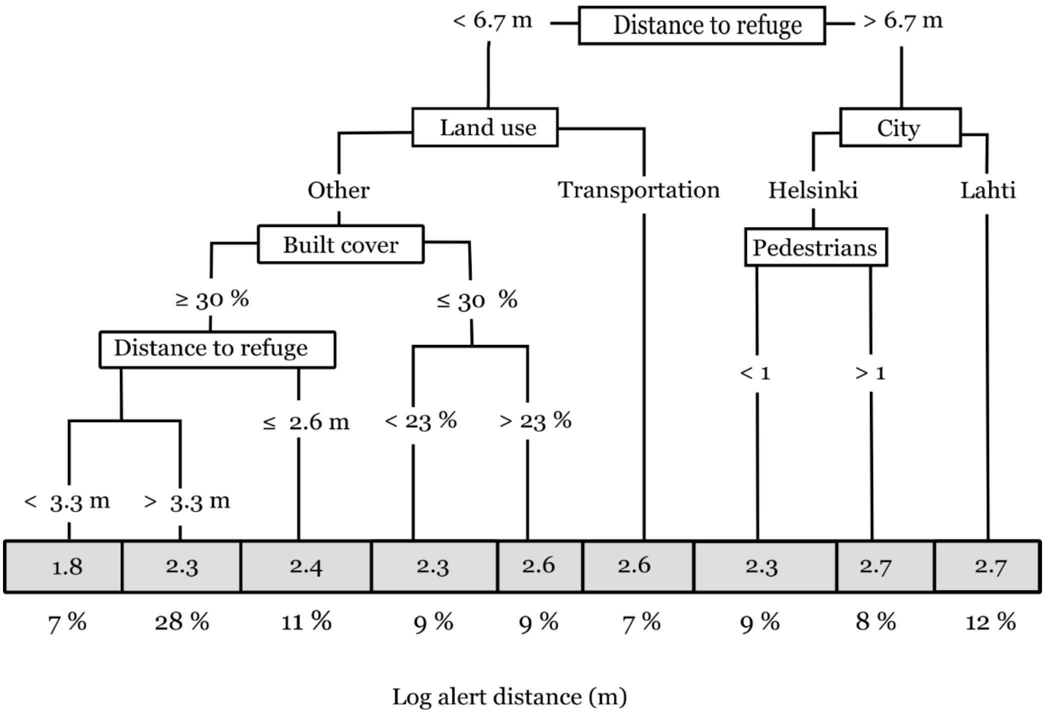

Figure 4. A classification and regression tree (CART) showing the relation of ln-transformed AD and independent variables in both cities. Percentages show the portion of birds following each possible path combination.

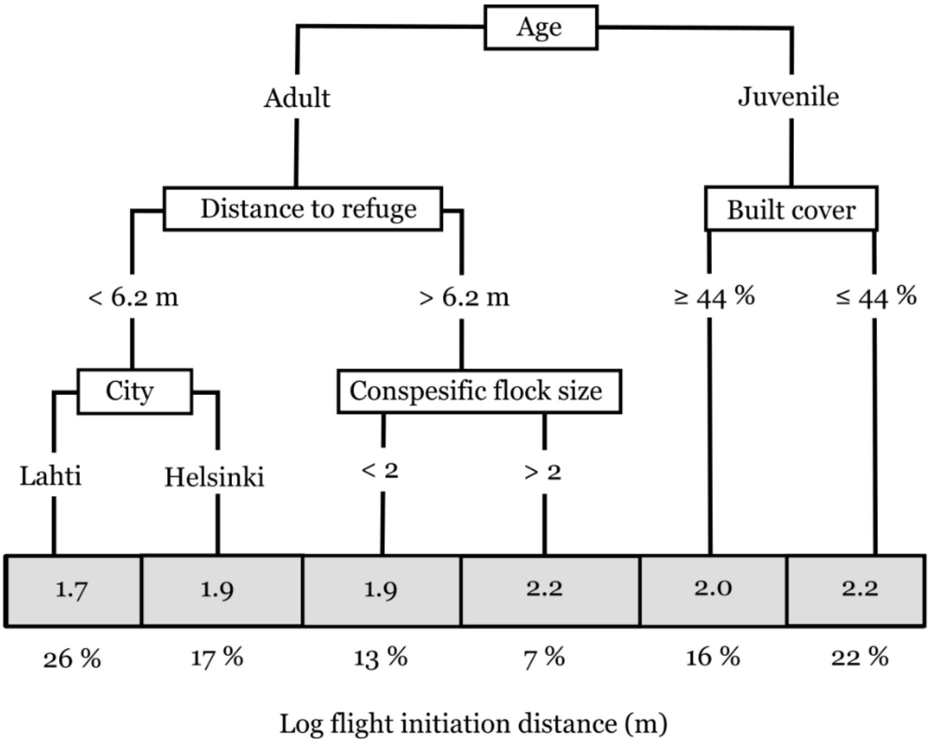

Figure 5. A CART showing the relation between ln-transformed FID and independent variables in both cities.

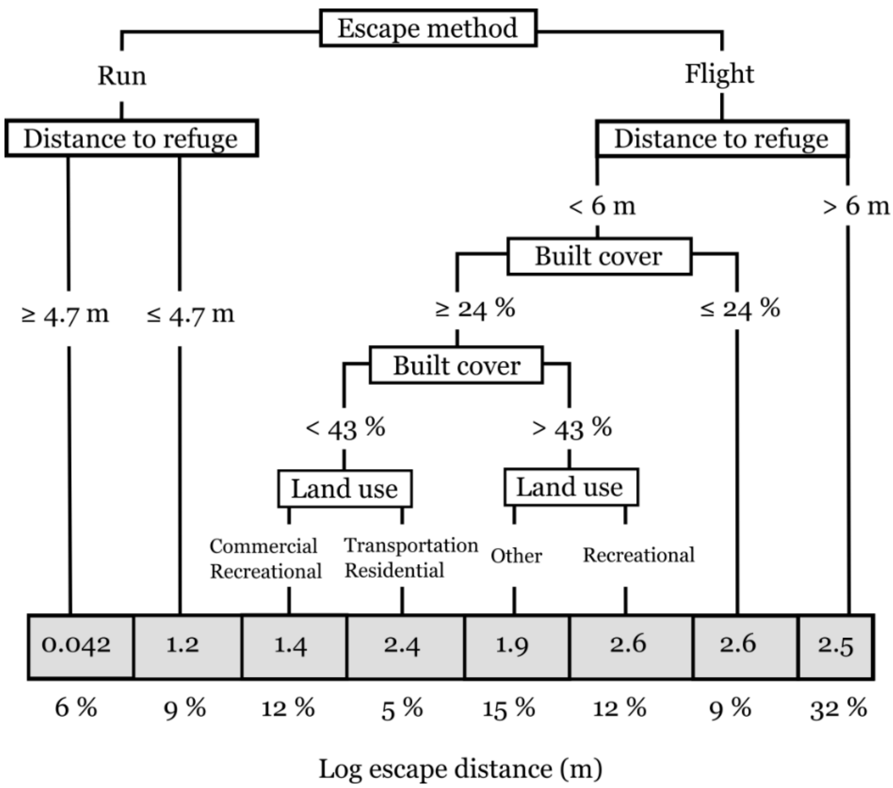

Figure 6. A CART showing the relation of ln-transformed ED and independent variables in both cities.

4 Discussion

The three indicators of fear related differently with intrinsic and extrinsic factors, giving a broader picture of how white wagtails perceive their environment and react to disturbance. It begins with the individual itself, in this case juveniles being shyer, but adjusts to immediate surroundings such as pedestrian presence and distance to refuge, while being affected by regional differences, as the cities studied here were different to a degree.

Juveniles showed significantly longer FIDs, confirming my first hypothesis, standing for both Helsinki and Lahti. The finding is consistent with previous studies on American robins (Eason et al., 2006) and barn swallows (Møller, 2014), although in a larger interspecies dataset, age was not significant (Sol et al., 2018), hinting it may be a species-dependent pattern. On the contrary to juvenile American robins in Eason et al. (2006), there was also a non-significant trend of juveniles having higher AD, but the difference was quite minor. Juveniles also escaped longer distances. In urban areas, humans rarely pose an actual threat to animals (Clucas & Marzluff, 2012), even less for a small, well-tolerated and even desired songbird (Liordos et al., 2020), giving the bird little reason to expect a lethal encounter. This would be learnt with age, as often suggested, leading to bolder adults (Eason et al., 2006; Møller, 2014), and reflected as decreased vigilance and short, inexpensive escape. With black-headed gulls in China, the opposite process has been observed as adults were more afraid of hand-held popguns than juveniles, potentially because of having experienced hunting (Liu et al., 2025), so similar process could occur to the opposite direction. However, the links of boldness and habituation are debated (see Diamant et al., 2023). Another explanation could be that birds with bolder innate personalities stay in urban areas as adults, while the shyer offspring hatched there will establish territories in less disturbed areas (Carrete & Tella 2010).

Crown color did not correlate with any indicators of the fear response, therefore, my hypothesis of males being bolder was not supported. All juveniles were in the grey-crowned group regardless, but running statistical analysis on adults only did not show crown color to be significant either. The result is not surprising, as sex seems to rarely relate with FID, as found in a study of 317 species across Europe and China (Sol et al., 2018), and with brush-turkeys in Australia (Hall et al., 2020), although some opposite examples exist, such as bolder male house sparrows in Mexico (García-Arroyo & MacGregor-Fors, 2020). Another possibility is that crown color is not a certain sign of sex, so grey-crowned individuals could include young males, masking the difference.

Distance to refuge correlated positively with AD and FID in the whole dataset, and with ED in Helsinki. FID being longer when refuge is farther away is consistent with previous findings (Dill & Houtman, 1989; Vincze et al., 2016; Morelli et al., 2022; but see Kalb et al., 2019), but for AD a previous study did not find such a relation in house sparrows, woodpigeons (*Columba palumbus*), blackbirds (*Turdus merula*), or magpies (*Pica pica*) (Fernandez-Juricic et al., 2001), which could be because different species traits or ways they perceive and use their environment. Presumably, reaching refuge would take a longer time, leading to increased vulnerability and heightened wariness, which makes sense in a prey species of hawks like the white wagtail. The quality of refuge and environmental structure can be linked to FID, although the relation could be species dependent as refuge could be seen either protective or obstructive (Morelli et al., 2022). Interestingly, the white wagtails did not utilize refuge, at least the one recorded closest to them, and distance to refuge did not correlate with ED, which is on the contrary to black redstarts in Kalb et al. (2019). Here, escape usually ended nearby on the ground where the bird resumed foraging.

AD increased with conspecific flock size in the whole data and in Helsinki, in contrast to the previously mentioned four species in Fernandez-Juricic et al. (2001) but in line with the house sparrows in García-Arroyo and MacGregor-Fors (2020). FID increased with flock size only in Helsinki. In previous studies, flock size has had either a positive correlation with FID (Vincze et al., 2016; Tätte et al., 2018; García-Arroyo & MacGregor-Fors, 2020; Morelli et al., 2022) or no correlation at all (Clucas & Marzluff 2012; Sol et al., 2018; Kalb et al., 2019; Morelli et al., 2023). The positive effect of flock size has been suggested to be linked to the sociability of the species, possibly stemming from shared warning cues (García-Arroyo & MacGregor-Fors, 2020). In their wintering grounds, white wagtails have been observed to operate two simultaneous social systems, both flocking and territorial behavior depending on food distribution and availability patterns (Zahavi, 1971), but here, flocks were relatively uncommon and potentially, most of the time, consisted of adults and their fledglings. In scenarios where this was the case, sociability could be enhanced. However, the reason why flock size did not increase FID in Lahti remains unknown.

Built coverage did not correlate with any of the indicators, in contrast to previous findings of FID decreasing with increasing built cover (e.g., Clucas & Marzluff, 2012; Vincze et al., 2016; Morelli et al., 2022; Morelli et al., 2023). Therefore, my hypothesis of birds being bolder in more disturbed areas was not supported. Although, higher built coverage does not necessarily equate to higher disturbance, such as higher human presence. Furthermore, built cover appeared in all CARTs, indicating a non-linear relationship, where, at a certain percentage, it either heightens fear response or dilutes it. Ultimately, the topography of the environment, such as openness, could shape the fear response more than built cover, although uniform interspecies patterns for relations with other environmental variables, such as tree height and shrub cover, have not been found, at least with AD (Fernández-Juricic et al., 2001).

Land use had a non-significant trend with ED in the whole data and Lahti, and significant in Helsinki, thus giving weak support for the hypothesis that more disturbed land uses would have bolder, less vigilant birds. However, in the CARTs of AD and ED, land use appears to split the data to a small extent, revealing a non-linear relationship. In addition, it had relatively high r^2 values within the linear models, although less so for FID or in Lahti. In this study, the land use categorization was not based on official land use data, such as the zoning plans of the cities or CORINE land cover. Rather, it was meant to grasp the characteristics of main human use in the area in question. This could mean some sites were incorrectly labelled. For example, university campuses were categorized as commercial despite this being rarely their main land use. Sample size was also small for certain land use types, as low as five. Furthermore, land use does not translate into consistent human activity. For instance, some recreational areas could be visited much more often than others. Therefore, the lack of relation could stem from methodology rather than irrelevance, but further research is needed to confirm this.

The number of pedestrians has been observed to increase FID in blackbirds in Spain (Martín et al., 2008) and in Europe for 16 species (Morelli et al., 2018) but decrease it in a larger interspecies study in Latin America (Morelli et al., 2023). Here, more pedestrians related with increased AD and ED only in Helsinki. The number of pedestrians was relatively low in both cities, even more so in Lahti, which could explain the absence of relations there. The presence of pedestrians could make birds more vigilant, in case any of them become disturbing, while longer escape could be tied to avoiding other pedestrians in the close vicinity, along the approacher.

Escape method correlated with ED, with the median ED being four times larger for flyers than runners, which is in line with an interspecies study including the white wagtail in Estonia (Tätte et al., 2018). Juveniles almost exclusively flied away. A similar tendency to escape by flight has been recorded before in juvenile blackbirds (Martín et al., 2008). Running uses less energy than flying, allows staying at the foraging ground, and reduces the chance of overestimating the risk, making it a cheaper escape method (Martín et al., 2008). This could further signal adults are capable of more accurate risk assessments or consist of individuals with bolder personalities.

By nature, biology, and behavioral ecology as its branch are complex to study as living organisms are constantly affected by countless abiotic and biotic factors (Møller & Jennions, 2002). Capturing everything in a singular study and controlling field conditions is not possible, potentially leaving some significant factors in the shadows. For example, noise pollution may change fear response in one direction or another (Sweet et al., 2022; Abou-Zeid et al., 2024). Even something trivial at first glance, such as the color of the observer's clothing, can be significant (e.g., Zhou & Liang 2020). Without the control of variables, causation cannot be proven, thus, this study can only assess relations. One should be careful when interpreting results or generalizing, since contrasting patterns between species and environments are evident across literature. Another limitation comes from confining heterogenous environmental variables into categories suited for analysis, which can lead to the oversimplification of the real field surroundings. For instance, the amount of built coverage characterizes only a fraction of change urbanization brings upon environments. Moreover, in this study, the sample size was low for certain land use and bird age combinations. Nevertheless, the study's models were sufficient in capturing major trends, but future studies could focus on these finer scale questions.

The white wagtail as a species seems to be well-suited for modelling fear ecology. Its wide distribution across the globe and habitats through the urban-rural gradient make it well available for further studies, allowing comparison between regions. The white wagtail is not endangered globally and does not seem to be bothered by approaches, as it most often resumes its activities soon, thus, relieving ethical concerns of inducing stress on wildlife (Gaynor et al., 2021). Relatively short AD, FID, and ED make assessing their changes more tangible. Since according to this study, sex is irrelevant and juveniles distinguishable from adults, we can control for some intrinsic factors. Finding white wagtails is relatively easy as they can be detected far away, tend not to hide and have distinct calls. However, its appearances can be sporadic and congregated to certain habitats, raising the risk of resampling same individuals and putting pressure on gathering sufficient sample size, which can become an issue depending on study design.

More generally, if we do not consider AD, FID, and ED as mere results of risk perception and assessment, they could reflect how the animal feels about its environment. For example, in the case of the white wagtail, it seems to feel more comfortable in areas where distance to refuge is shorter, reflected as shorter distances in all indicators. Fear can be used as a non-lethal tool to both deter unwanted animals from certain areas (Gaynor et al., 2021), but vice versa, it can help to design areas where animals feel safe, aiding conservation. However, the link between behavioral indicators and physiological stress markers, such as corticosterone levels, is not straightforward but go hand in hand for some cases, such as in the urban-rural binary, urban birds being bolder with lower corticosterone levels (Tablado et al., 2021). Therefore, using behavioral indicators as a proxy of stress may not be ideal in all cases. Nevertheless, if we wish to conserve biodiversity or invite it into urban areas, it could be beneficial to consider behavior and fear response alongside offering ecologically suitable and functional habitats, to ensure population health.

Many aspects of fear response are situational and depend on species and the environment, as previously covered. Further studies are needed for different species and regions before moving to practical applications, preferably conducted with the target environments and species. A holistic approach helps to see the bigger picture: fear builds up from evolutionary history and phylogenetical and morphological traits, being further shaped by individual personalities, finally adjusting to immediate, situational and regional environmental traits. Fortunately, using behavioral indicators is intuitive and relatively cost-effective, making uncovering the web of fear feasible, piece by piece.

5 Conclusion

In this thesis, I studied what intrinsic and extrinsic factors relate with the fear response of the white wagtail (*Motacilla alba*) when considering AD, FID, and ED, and if these relations were different between Helsinki and Lahti. The assessed white wagtails were alerted faster in larger flocks and farther from refuge, fled faster if they were juveniles or if refuge was farther, and juveniles and flyers escaped longer distances compared to adults and runners. Additionally, in Helsinki, the white wagtails were alerted faster in higher pedestrian presence, fled faster in larger flocks, and fled farther with higher pedestrian presence, but fled closer in commercial land use. In Lahti, the white wagtails were alerted faster if distance to refuge was higher, fled farther if they were juveniles, and fled farther when flying. Built cover was related to their fear response non-linearly. Therefore, fear transforms, being situation-, place-, and bird-specific.

6 Ethics statement

Only birds foraging or otherwise “relaxed” were approached, while already alerted or nesting birds were not, as in Blumstein (2003). No birds were harmed or caught. The distances were collected in a few minutes, after which the observer continued to another place. Most birds quickly resumed their previous activity close-by, showing no obvious signs of distress. As the study took place in urban areas, it could be assumed the birds are relatively well-adjusted to human disturbance and face no long-term consequences from a brief and single approach, hardly different from other pedestrian activity. The white wagtail is not classified as endangered in Finland.

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