Common waxbill (*Estrilda astrild*), Rui Pereira, Santarém 2023.

Aggressive show-off: a test of how waxbills manage dominance hierarchies

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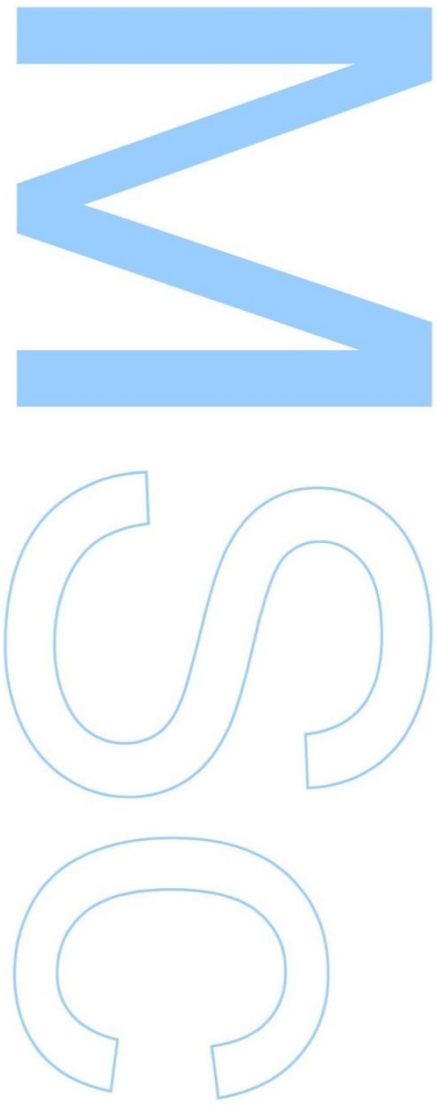
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Resumo

O equilíbrio entre os benefícios e custos da sociabilidade pode ser alcançado com informação sobre os membros do grupo, mas esta pode estar ausente ao interagir com indivíduos desconhecidos. No contexto de agressão social, surgem efeitos de audiência quando o comportamento dos indivíduos é influenciado pela presença de espetadores. Ademais, o efeito sobre os espetadores pode ocorrer se a observação de uma interação entre dois outros indivíduos influenciar o comportamento do espetador. São necessários estudos experimentais para entender a dinâmica da agressão social e estratégias usadas para transferir informação sobre agressividade. Um estudo descritivo recente com bicos-de-lacre (*Estrilda astrild*) em ambiente seminatural demostrou que existe um aumento de agressividade quando indivíduos menos familiares estão presentes na audiência, no entanto, as interações agressivas não foram direcionadas a esses indivíduos estranhos, mas sim a membros muito subordinados do bando. Isto foi interpretado como a utilização da agressão pelos bicos-de-lacre para demonstrar dominância aos espetadores desconhecidos. Com o objetivo de complementar este trabalho, conduzi ensaios em condições controladas, manipulando o contexto social de grupos de bicos-de-lacre em gaiolas e controlando o ambiente físico. O comportamento agressivo das aves foi gravado durante um protocolo padronizado de competição por comida e posteriormente analisado. Não encontrei evidência de que os bicos-de-lacre dirigissem agressão a companheiros familiares com o intuito de exibir agressividade na presença de indivíduos desconhecidos. Em vez disso, encontrei uma associação entre a quantidade de agressão recebida de indivíduos desconhecidos e a quantidade de agressão direcionada a indivíduos familiares, um padrão mais facilmente interpretado como agressão redirecionada de indivíduos não familiares para familiares. A agressão redirecionada é uma estratégia que pode ocorrer em animais gregários quando um indivíduo que foi atacado direciona a agressão a um espetador não envolvido na interação. Deste modo, os meus resultados apontam, tanto quanto sei pela primeira vez, para agressão redirecionada unidirecional apenas de indivíduos desconhecidos para familiares, mas não na direção contrária. Discuto estes resultados em contraste com os apresentados recentemente para uma população seminatural de bicos-de-lacre, à luz das diferenças metodológicas entre os dois estudos, todavia observando semelhanças nas descobertas de ambos: embora de maneira diferente, a exibição de agressão ou a agressão redirecionada de desconhecidos para aves familiares parecem ser estratégias cautelosas utilizadas pelos bicos-de-lacre para sinalizar domínio social na presença de indivíduos estranhos.

Palavras-chave: Agressão redirecionada; Estratégias sociais cautelosas, *Estrilda astrild*, Sociabilidade.

Abstract

Individuals can balance the benefits and costs of sociality with information about their group members, but this information is lacking when interacting with unfamiliar individuals. In the context of social aggression, audience effects occur when individuals behave differently depending on the presence of bystanders. Additionally, effects on bystanders may occur if observing an interaction between two others influences the behaviour of the bystander. Empirical research is needed to understand the dynamics of social aggression and the strategies for transferring information on aggressiveness. A recent descriptive study with common waxbills (*Estrilda astrild*) in a semi-natural setting found increased aggressiveness when less familiar individuals are present as bystanders in the audience, yet aggressive interactions were not directed at those unfamiliar individuals but towards very subordinate flock members. This was interpreted as waxbills using aggression to show-off dominance to the unfamiliar bystanders. To complement this work, I used experiments in controlled conditions, manipulating the social context of waxbills in cages while controlling for the physical environment. Agonistic interactions were recorded during a standard assay of competition for food and subsequently analysed. I did not find evidence of waxbills directing aggression to familiar companions to show-off aggressiveness in the presence of unfamiliar individuals. Instead, I found an association between the amount of aggression waxbills received from unfamiliar individuals, and the amount of aggression they directed to familiar individuals, a pattern most easily interpreted as redirected aggression from unfamiliar to familiar birds. Redirected aggression is a strategy that may occur in gregarious animals when an individual who has been attacked directs aggression to a bystander who was not involved in the agonistic interaction. As such, my results point towards, to my knowledge for the first time, unidirectional redirected aggression only from unfamiliar towards familiar individuals, but not vice-versa. I discuss these results in contrast with the ones recently presented for a semi-natural population of common waxbills in light of the methodological differences between the two studies, also noting similarities in the findings of both: albeit in a different manner, aggressive show-off or redirected aggression from unfamiliar towards familiar birds seem to be cautious strategies employed by waxbills to signal social dominance in the presence of unfamiliar individuals.

Keywords**:** Cautious social strategies, *Estrilda astrild*, Redirected aggression, Sociality.

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BORIS – Behavioural Observation Research Interactive Software

GLMM – Generalized Linear Mixed Model

ID – Identification

1. Introduction

1.1. Social living

Complex social systems are composed of individuals who interact with many others throughout different social contexts and over time (Freeberg et al., 2012). Sociality and gregariousness can be shaped by the advantages of group living (e.g., social information acquisition for foraging, Tóth et al., 2017; rearing young, Krama et al., 2012; or protection against predation, Sorato et al., 2012) and by costs such as conflict and competition for resources (e.g., food, Kakareko et al., 2013; Ulbrich & Henschel, 1999; or mates, Baxter et al., 2015), which in turn can result in the risk of injury, energy expenditure or decreased food intake (Baird, 2013). The outcomes of social interactions are dependent on individual decisions regarding whether and how to engage with conspecifics (Sheehan & Bergman, 2016). If individuals possess more information about their group members and social context, they may be able to better balance the costs and benefits of sociality, by reducing the uncertainty of their decisions.

1.2. Dominance hierarchies

Social interactions are influenced by how individuals evaluate their capabilities, those of group members, and the hierarchical structure within a group (Chase et al., 1994; Hobson, 2020; Hobson et al., 2021). Frequent aggressive interactions among individuals lead to the establishment of stable, asymmetric relationships (Hobson & DeDeo, 2015; Holekamp & Strauss, 2016) that form emergent social properties (i.e., dominance hierarchies, Bradbury & Vehrencamp, 2014; Chase, 1974; Drews, 1993). Aggression, despite its immediate costs, can yield rank-dependent benefits that are realized over time (Hobson & DeDeo, 2015). Such benefits may encompass enhanced access to crucial resources and opportunities like access to food, preferred spatial positions or reproductive success (e.g., Basham et al., 2022; Dewsbury, 1982; Hall & Fedigan, 1997; Ulrey et al., 2022).

Dominance hierarchies are ubiquitous among animals and structure societies in numerous species (Hobson et al., 2021; Shizuka & McDonald, 2015; Tibbetts et al., 2022). Among these species are fish (Dijkstra et al., 2009), birds (Pravosudov & Lucas, 2000; Sheppard et al., 2013), ungulates (Correa et al., 2013; Vervaecke et al., 2007), and primates (Bergman et al., 2003; Cheney & Seyfarth, 1999), including humans (Mascaro & Csibra, 2012, 2014).

After being formed, a stable hierarchy is known to decrease some of the costs of social living by decreasing aggressive interactions between conspecifics (Ward & Webster, 2016). Recognizing rank in dominance hierarchies enables individuals to strategically allocate aggression based on their hierarchical relationships (Hobson et al., 2021). Exhibiting appropriate behaviour corresponding to one's social status

also helps minimize conflicts and repeated dominance negotiations within the group (Holekamp & Strauss, 2016).

Dominance hierarchies' formation is often influenced by intrinsic factors, including body size, fighting ability, and personality traits (Araujo-Silva et al., 2023; Chase & Seitz, 2011; David et al., 2011; Funghi et al., 2015). As a result, dominance status may fluctuate over time due to variations in competitive ability and health (Holekamp & Strauss, 2016). Nepotism also affects one's position in the dominance hierarchy and is present in some primate species (Markham et al., 2015), as well as in spotted hyenas (*Crocuta crocuta*, Engh et al., 2000).

Moreover, social rank might have significant implications for various aspects of fitness in animals (Archie et al., 2012; Lewin et al., 2015; Mendonça-Furtado et al., 2014; Rozempolska-Rucińska et al., 2023; Winberg & Sneddon, 2022). High-ranking spotted hyenas, which face fewer challenges than low-ranking individuals, showed significantly greater mean telomere length than did subordinates, an important biomarker of ageing and cellular stress (Lewin et al., 2015). Dominance rank can also lead to endocrine and oxidative stress responses in individuals (Beaulieu et al., 2014; Mendonça-Furtado et al., 2014). For example, high-ranking male baboons (*Papio cynocephalus*), who appeared to escape from the immunosuppressive costs of glucocorticoids, were found to be less likely to become ill and recovered faster than low-ranking males (Archie et al., 2012).

1.3. Conspecific assessment

The acquisition of information about conspecifics is a crucial aspect of dominance hierarchies, as it enables individuals to assess the competitiveness of rivals without engaging in agonistic interactions (Bradbury & Vehrencamp, 1998; Sheehan & Bergman, 2016). Social recognition and communication signals stand out as the two primary strategies by which animals evaluate others (López-Idiáquez et al., 2016; Mateo, 2004; Sheehan & Bergman, 2016).

Social recognition involves learning and remembering the quality or characteristics of other individuals or groups during social interactions or observations (Sheehan & Bergman, 2016). Individual recognition is typically found in species where repeated interactions occur among a limited number of individuals (Smith & Harper, 2003; Tibbetts & Dale, 2007). Information obtained via social recognition includes resource-holding potential, individual quality, and dominance (Sheehan & Bergman, 2016).

In contrast, signals provide information during first contact and do not require previous encounters (Sheehan & Bergman, 2016). Signals can convey information about a range of traits that exhibit reasonable stability and persistence (Bergman & Sheehan, 2013; Blum et al., 2022). Social recognition can be highly reliable due to the inability to bluff prior encounters, making it resistant to developmental constraints that may limit the accuracy of quality signalling (Sheehan & Bergman, 2016).

1.4. Familiarity

Individuals interact with conspecifics differently, reflecting different social preferences (Kohn, 2017; Riveros et al., 2017; Silveira et al., 2020; Ward et al., 2020). Many studies have reported social preferences for familiar over unfamiliar individuals (Gomes et al., 2022; Griffiths & Magurran, 1999; Keller et al., 2017; Kohn, 2017). Associating with familiar individuals can amplify the numerous benefits conferred by gregariousness (Ricardo et al., 2023; Siracusa et al., 2021; Swaney et al., 2001). Aggression is also affected by the familiarity between individuals, for example, territorial disputes can elicit more aggression towards unfamiliar conspecifics compared to aggression directed at neighbours (Dear Enemy effect, Amorim et al., 2022; Temeles, 1994; Tumulty, 2022), although such an effect could manifest itself with flexibility rather than in a fixed way (Jin et al., 2021). In some cases, neighbours may impose a greater threat (Godard, 1993; Olendorf et al., 2004), and individuals could elicit more aggression towards familiar neighbours (Nasty Neighbour hypothesis, Gutiérrez-Carrillo et al., 2023; Müller & Manser, 2007; Sanada-Morimura et al., 2003; Temeles, 1994; Velásquez et al., 2006).

1.5. Audience effect

Social information can also be acquired by watching the interactions of others (Bradbury & Vehrencamp, 1998; Johnstone, 2001). Hence, individuals may behave differently when other individuals are present and may observe the interaction (Hobson, 2020), a phenomenon known as audience effect (Coppinger et al., 2017; Slocombe et al., 2010; Szipl et al., 2018; Zaccaroni et al., 2013; Zuberbühler, 2008). The information carried in a signal can be altered in response to changes in the presence, composition, or characteristics of the receivers (Coppinger et al., 2017; Fichtel & Manser, 2010; Szipl et al., 2018; Zuberbühler, 2008). As a result, this social approach suggests that signallers might adapt signal production and possess an awareness of the perceptual states of their recipients (Chen et al., 2016; Townsend et al., 2017; Zuberbühler, 2008).

Audience effects have been reported in several animal species (Evans & Marler, 1994; Matos & Schlupp, 2005; Slocombe et al., 2010; Szipl et al., 2018). Birds and non-human primates are commonly used as models to study audience effects, particularly by accessing vocal signalling. In non-human primates, the presence of certain individuals in the audience, such as kin and offspring (Wheeler, 2008), dominant individuals (Chapman & Lefebvre, 1990), or important social partners (Slocombe et al., 2010), has been observed to affect behaviour. Human signallers too adjust the acoustic characteristics of their speech in response to social pressures exerted by the surrounding audience members (Coupland, 1984). Furthermore, male red-legged partridges (*Alectoris rufa)* alter their alarm calls depending on the audience, which may reduce eavesdropping and promote mate investment (Zaccaroni et al., 2013), and adult male zebra finches (*Taeniopygia guttata)* modify their songs directed at young male pupils by including more repeated elements and longer spacing between song elements, perhaps to increase attention and improve

song learning (Chen et al., 2016). Other examples include ravens (*Corvus corax*) that modulate their call rates when attacked, based on their audience containing bystanders with valuable relationships to them or their aggressors (Szipl et al., 2018).

1.6. Effect on bystanders

Not only can bystanders influence the behaviour of individuals, bystanders themselves can also be influenced by the behaviours they observe. For example, an animal that observes a dominance contest between two others may then behave differently than a non-observer when meeting the interactants (Dugatkin, 2001). Individuals can therefore minimize the costs of conflict through social eavesdropping (Danchin et al., 2004; Rieucau & Giraldeau, 2011). By discerning dominance rank through observation of social interactions and their outcomes, individuals can optimize decision-making processes, resulting in energy conservation and a reduced likelihood of injury (Hobson & DeDeo, 2015). Effects on bystanders may pose cognitive challenges, involving observing social interactions, learning and remembering individuals, associating traits, and making assumptions (Frith & Frith, 2012).

Evidence suggests that primates, including human children (Bergman et al., 2003; Cheney & Seyfarth, 1999; La Freniere & Charlesworth, 1983; Pannozzo et al., 2007), and other social mammals (Curley, 2016; Engh et al., 2005), birds (Massen et al., 2014), and fish (Murch et al., 2003) can alter their behaviour in response to what they observe in the social interactions of others. The effect on bystanders has been studied in songbirds both in the context of territorial defence (Peake et al., 2001) and mate choice (Mennill et al., 2002), revealing the use of eavesdropping to acquire information about competitors. Invertebrate behaviour can also be influenced by observing others: bumblebees are more likely to visit a flower when other pollinators are on the flower (Leadbeater & Chittka, 2007), and social eavesdropping is a key mediator of social interactions in *Polistes fuscatus* wasps (Tibbetts et al., 2020).

1.7. Showing-off as a way to manage dominance hierarchies

In a recent descriptive, non-experimental study, in an open-air mesocosm (Figure 1A), it was found that common waxbills (*Estrilda astrild,* Figure 2), became more aggressive when less familiar individuals are present in the audience, but attacking preferentially the most subordinate conspecifics (Beltrão et al., 2023). This suggests a low-risk strategy for managing dominance hierarchies: rather than attacking unknown opponents with whom there may be dominance conflicts and incurring the risk of a serious fight, waxbills appear to often show-off aggressiveness in their presence by bullying low-rank individuals. Bullying is the term used to describe patterns of aggression where attacks are directed mostly towards the very subordinate individuals (Hobson et al., 2021). This is not the most common pattern of aggression in

animals, having been reported for only a small number of mammal and bird species in a recent meta-analysis (Hobson et al., 2021).

Figure 1 – (A) Inside view of the open-air mesocosm at CIBIO's installations, where Beltrão et al. (2023) studied a population of common waxbills, Gonçalo Cardoso, Vairão 2022. (B) Cage room, at CIBIO's installations, where standard behavioural tests for this thesis were performed, Beatriz Saldanha, Vairão 2023. All photographs are reproduced with permission.

Descriptive studies cannot manipulate the social context precisely, and the finding that waxbills increase aggressiveness in the presence of unfamiliar individuals (Beltrão et al., 2023) should be confirmed experimentally. One can hypothesize that increased aggression is used as a signal of dominance, to show-off to unfamiliar conspecifics, without having interacted with them, and/or that increased aggressiveness results from waxbills redirecting aggression received from those unfamiliar individuals. The second possibility, redirected aggression, so far has no support from work with common waxbills studied in a large mesocosm environment, because waxbills were not more likely to have been attacked by less familiar individuals (Beltrão et al., 2023). However, aggressiveness in environments or contexts other than foraging was not examined, and patterns of aggression in these environments may vary (Beltrão et al., 2023). Thus, it is possible that redirected aggression could also occur in the open-air mesocosm.

1.7.1. Redirected aggression

Redirected aggression, also known as redirection or displaced aggression, occurs when an individual who has been attacked directs aggression towards a bystander who was not involved in the initial aggressive interaction (Bastock et al., 1954; Kazem & Aureli, 2005; Marcus-Newhall et al., 2000). Targets of redirected aggression can be objects (Hinde, 1952) or individuals (Aureli et al., 1993; Virgin & Sapolsky, 1997; Wittig & Boesch, 2003). This behavioural pattern has been reported in many animal species and is often investigated in gregarious animals (Cheney & Seyfarth, 1989; Engh et al., 2005; Kazem & Aureli, 2005; Øverli et al., 2004). This may be a way of managing conflict, as has been well documented in humans (Marcus-Newhall et al., 2000).

Redirected aggression was proposed to be relevant during competitive interactions to reduce aggression-induced stress (Bastock et al., 1954; Virgin & Sapolsky, 1997). It was also suggested to be important for post-conflict uncertainty reduction, since individuals who redirect aggression might reduce the cost of being attacked by becoming aggressors themselves (Kazem & Aureli, 2005; Tokuyama & Furuichi, 2014). Redirecting and showing-off aggression can both be, nonetheless, cautious strategies to manage social dominance hierarchies in the presence of unfamiliar individuals, and it could be important to understand if and when those strategies are employed.

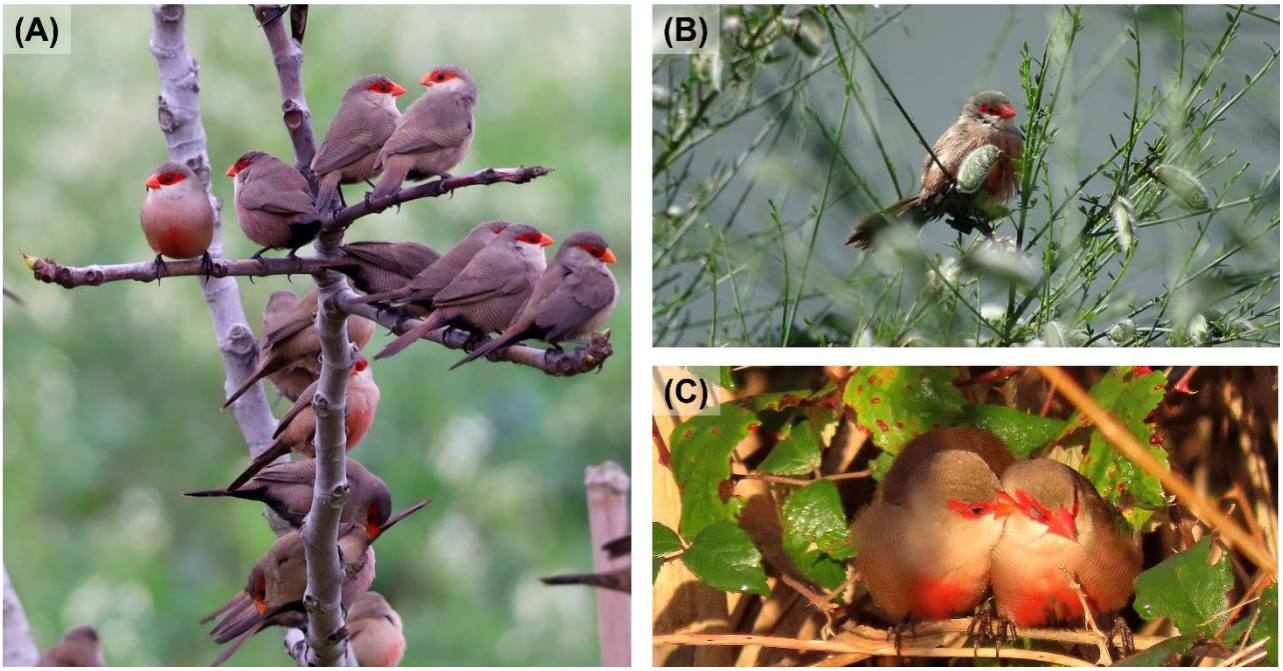

Figure 2 – (A) Group of common waxbills roosting together, Hugo Marques, Setubal 2022; (B) Waxbill perched on a branch at CIBIO's open-air mesocosm, Patricia Beltrão, Vairão 2022; (C) Two waxbills allopreening, Luís Silva, Montemor-o-Velho 2022. All photographs are reproduced with permission.

1.8. Objectives

The objective of this work is to test the hypothesis that common waxbills show-off aggressiveness to manage dominance hierarchies, in well-controlled experimental conditions (Figure 1B). I will assess how aggressiveness is affected by social context, namely the familiarity of their conspecifics, by manipulating the social environment and quantifying agonistic behaviour, while controlling for possible effects of the physical environment. I further aim to investigate if there is evidence of the use of redirected aggression in waxbills, to gain a more comprehensive understanding of the social dynamics and aggression strategies in this species.

Concretely, I will test (1) if aggressive interactions are more common when unfamiliar individuals are present, (2) if aggression is more frequently directed towards the familiar than those unfamiliar individuals, and (3) if, by showing-off aggressiveness for potentially signalling dominance, individuals reduce the

likelihood of receiving aggression from the unfamiliar companions. Additionally, I will (4) infer if redirected aggression could affect the aggression pattern of waxbills.

Based on the descriptive results by Beltrão et al. (2023), who studied the behaviour of a free-flying waxbill flock, I expect that if waxbills are showing-off aggression to manage dominance hierarchies, aggressive interactions will increase in the presence of unfamiliar individuals but will mostly be directed towards familiar birds. Furthermore, I expect that if there is an advantage of using this strategy, waxbills that show-off aggression will receive less aggression from unfamiliar conspecifics.

2. Material and Methods

2.1. The common waxbill

The common waxbill (family Estrildidae, Figure 2), hereafter waxbills, is a successful avian invader native to sub-Saharan Africa, inhabiting a wide range of grassland and woodland habitats in proximity of water (Clement et al., 1993). It is a small finch that feeds on herbaceous seeds in low vegetation and forages in flocks, roosting communally year-round (Cardoso & Reino, 2018; Clement et al., 1993; Payne, 2010). They are non-territorial and non-migratory birds, instead making vagrant movements in search of suitable habitats, known also to form fission-fusion groups and breeding pairs (Clement et al., 1993; Payne, 2010). Male and female waxbills are similarly ornamented (Cardoso et al., 2014a; 2014b) and do not display clear differences in other phenotypic traits (e.g., personality aspects, Carvalho et al., 2013; cognitive performance, Gomes et al., 2020).

This finch is an ideal species to study social behaviour as it is highly gregarious (Clement et al., 1993; Payne, 2010). It has stable individual differences in aggressiveness (Funghi et al., 2015, 2018), with waxbill groups showing dominance hierarchies with mildly steep slopes Beltrão et al., 2021b; Funghi et al., 2015), and previous studies found that the sexes are similar in social dominance and aggressiveness (Beltrão et al., 2021a; Funghi et al., 2015, 2018). Importantly, waxbills establish dominance hierarchies not only when in free-flying flocks, as found in semi-natural settings (Beltrão et al., 2021a), but also when living in small groups in bird cages (Beltrão et al., 2021b; Funghi et al., 2015).

2.2. Housing conditions

I made use of six metal cages (88.5×30 cm and 40 cm high) to house 24 adult waxbills, 12 males and 12 females, distributed in six groups composed of four birds each (two males and two females). Cages were visually but not acoustically isolated from each other (Figure 1B). Birds grouped in each cage were familiar with each other, as they had been living together for approximately 8 months. Each cage is open in the front, with a metal grid, and it has four perches in symmetrical positions (Figure 3A). *Ad libitum* food (Tropical Finches Prestige, Versele-Laga), and water were provided to the birds, using two drinkers and one long feeder per cage (Figure 3A). In addition, smashed oyster shells and sand were provided weekly in the ground of the cages for calcium supplements. Cages are located in the research aviary at CIBIO/InBIO-BIOPOLIS, Vairão, in a room with natural temperature and sunlight, complemented by a full-spectrum ceiling lamp that matched the natural light-dark cycle (lights on ca. 30 min before sunrise and off ca. 30 min after dawn). Waxbills were marked with coloured leg rings, in addition to a numbered ring. The colours chosen for the leg rings are putatively neutral for waxbills (green, white, dark blue, black) to minimize the

chances of influencing waxbill behaviour. Colours such as red, orange and yellow, which could resemble the birds' ornamental colouration and perhaps affect their behaviour, were avoided (Burley et al., 1992; Coopersmith & Burley, 1987).

2.3. Food competition assay

Each group formed per cage was composed of two male and two female waxbills (Table S1, Figure 3A). Assays of competition for food were conducted on three consecutive days per week (testing two cages per day), during four consecutive weeks, so as to allow one-week intervals between assays (Table S2). To record waxbill behaviour, I used two video cameras (Canon Legria HF M306 and Sony Handycam HDR-CX116), positioned in a net wall opposite the front of the cages. Tests took place between the 13th of September and the 7th of October, every Tuesday, Wednesday, and Thursday morning, except in one week when, due to a national holiday, the Wednesday and Thursday experiences took place one day later (6th and 7th of October, Table S2). All assays were conducted roughly from 9 am to 11:15 am, to minimize behavioural variation due to daily cycles.

I used 4 treatments: (A) a control treatment for both the social and physical environment, where I tested four individuals familiar with each other in their home cage (Figure 4A), (B) another control treatment only for the social environment, where four individuals familiar with each other where tested together, now in a neighbouring cage (Figure 4B), (C) an experimental treatment only for the social environment, where one male and one female in their home cage were tested together with an unfamiliar male and female that were moved from a neighbouring cage (Figure 4C), and, finally, (D) an experimental treatment for both the social and physical environment, where one male and one female were moved out of their home cage to be tested with an unfamiliar male and unfamiliar female in the neighbouring cage (Figure 4D). Cages were grouped in three blocks of two cages each (cages A and B, cages C and D, and cages E and F, Table S2). Birds were manipulated always in the same way, by me, in all treatments and were moved only between cages belonging to the same block (Table S2). Thus, for instance, if performing the control treatment that involved a familiar group of birds being exposed to a novel cage, all birds of cage A would be moved to cage B and vice versa (Figure 4B, Table S2). Also, for example, when a male and female from cage A were being tested with treatment C, the other male and female from cage A were receiving treatment D in cage B, and vice-versa for the birds from cage B (Figure 4C,D, Table S2). The order of the treatments was as balanced as possible, to minimize effects of potential confounding factors, such as date or order effects (Table S2). Experiments involved a food deprivation period of 2h, intended to enhance motivation to compete for food, and also to allow the birds to rest and diminish stress provoked by changing them to a neighbouring cage. After this period, I performed a behavioural assay following a standard protocol already used in this species (Beltrão et al., 2021b; Funghi et al., 2015, 2018).

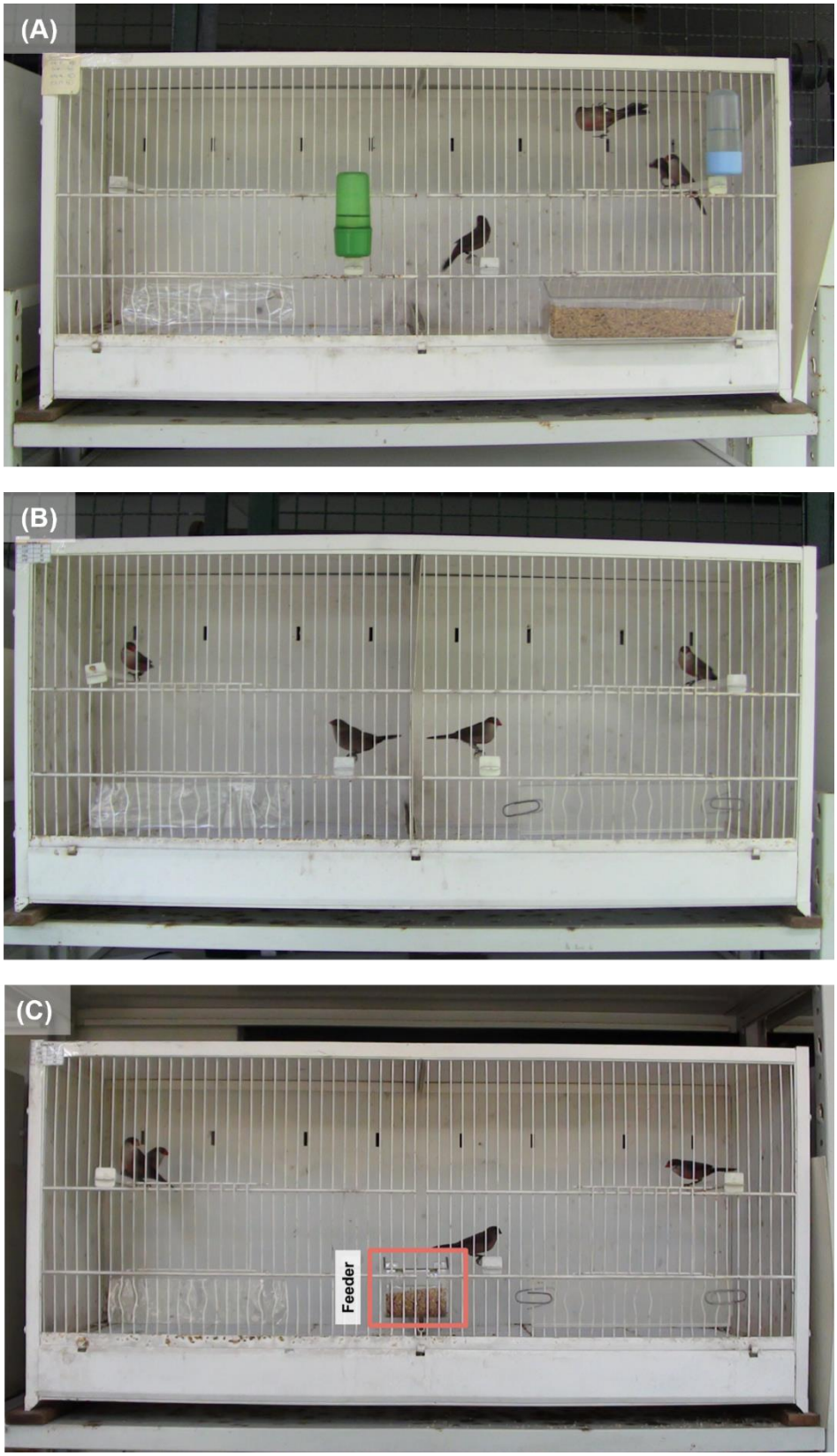

Figure 3 – (A) Bird cage housing a group of four individuals (two males and two females). (B) Before the food competition assay, the dyads (composed of a male and a female) were separated and deprived of food and water for 2 hours. (C) During the test of competition for food, a small feeder was placed in the middle of the cage. João Pacheco, Vairão 2022.

Experiments involved a food deprivation period of 2h, intended to enhance motivation to compete for food, and also to allow the birds to rest and diminish stress provoked by changing them to a neighbouring cage. After this period, I performed a behavioural assay following a standard protocol already used in this species (Beltrão, et al., 2021b; Funghi et al., 2015, 2018).

Tests of competition for food consisted of placing a small feeder in the centre of the cage attached to the front bars (Figure 3C). For the experimental treatments involving the translocation of a male and a female to a novel cage (treatments C and D), a familiar dyad of birds was placed together with a male and female from another cage. A movable and opaque partition was used to separate the two dyads during the food deprivation period so that unfamiliar birds were not able to see each other before the assay (Figure 3B). Likewise, and so that all treatments were similar in this aspect, I also used the movable opaque partition two separate the two dyads of familiar birds in treatments A and B. After the 2h of food deprivation, the partition was removed, the feeder was placed in the cages (Figure 3C) and videos were recorded for 15 minutes (plus some time for acclimation after me placing the feeder inside the cage), starting from the moment of placing the feeder, which previous work with waxbills showed to reliably reveal individual differences in aggressiveness and social dominance (Beltrão et al., 2021b; Funghi et al., 2015, 2018). The dyads of one male and one female that were moved between cages and/or kept separate during the 2h food deprivation period (Figure 4, Table S1 and S2) were consistent throughout all experimental treatments so that data on social interactions within those dyads was comparable across all treatments.

2.4. Quantifying behavioural data

For each of the 24 video recordings, I conducted focal observations on each of the four individuals, using BORIS (Behavioural Observation Research Interactive Software, Friard & Gamba, 2016), to quantify aggressive behaviours. Behavioural observations started once the birds were calm after the disturbance provoked by placing the feeder inside their cage (this took approximately 25 to 60 seconds, depending on the assay), and then lasted for 15 minutes. Videos were examined always by me, using renamed video files so that I was blind to the treatment being used. Identification of individuals was based on the combination of their leg ring colours. When analysing the video recordings, I quantified aggressive interactions (number of displays or attacks) which encompassed the number of times an individual threatens another with an aggressive display (either by opening their beak and stretching their neck, spreading their wings, or positioning the tail upwards) or an attack (which may either be chasing or flying towards another individual, or involve physical contact, such as pecking). I considered separate aggression events those that were separated in time rather than part of a continuous movement, or those that occurred in a continuous movement but in different places of the cage. For each observation of aggressive behaviour, I noted the identity of the bird behaving aggressively, and also that of the bird to whom the aggressive behaviour was directed.

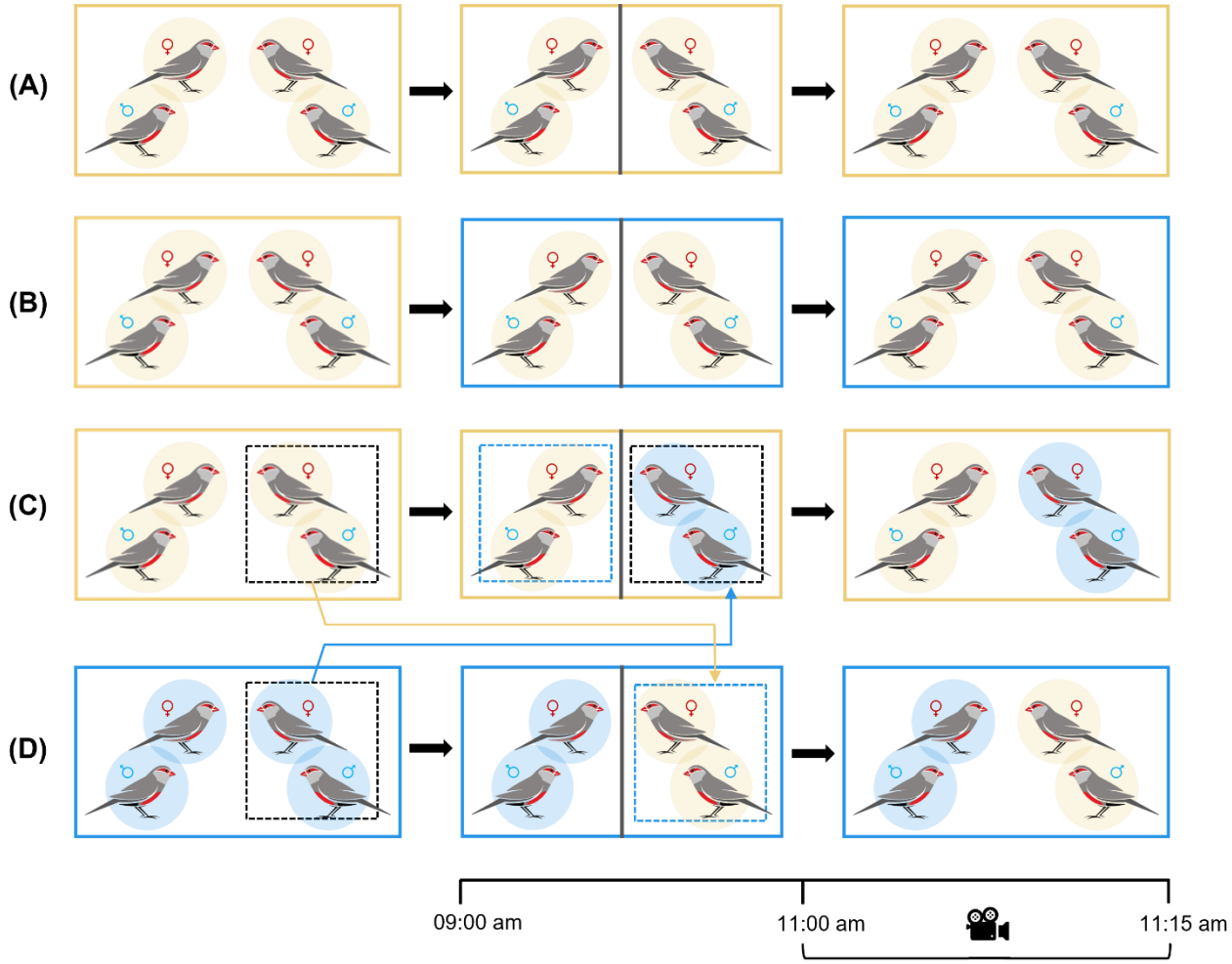

Figure 4 – Scheme representing the four treatments used. Circle colours represent familiarity and rectangles represent cages. Birds that share the same circle colour are familiar with each other and if circle colour is equal to the colour of the rectangle, then birds are in their home cages; if not, individuals are in a novel cage. (A) Control treatment, where four waxbills familiar with each other were tested in their home cage. (B) Control treatment only for the social environment, where four waxbills familiar with each other were tested in a novel cage. (C) Experimental treatment for the social environment, in which a male (♂) and a female (♀) waxbill (highlighted in blue) were tested in their home cage together with an unfamiliar dyad. (D) Experimental treatment for the social and physical environment, in which a male and a female waxbill (highlighted in blue) were tested in a neighbouring cage with an unfamiliar dyad. The food deprivation period lasted two hours (from 9 am to 11 am), during which the dyads were separated by an opaque partition. After the food deprivation period, the partition was removed, and birds were recorded for a 15-minute period (from 11 am to 11:15 am).

2.5. Statistical analyses

I ran a Generalized Linear Mixed Model (GLMM) with data from all treatments to test whether within-dyad aggression differed depending on the social or physical environment. In this GLMM the dependent variable was within-dyad aggression per bird per assay and the social environment (unfamiliar birds absent or present) and the physical environment (home cage or novel cage) were used as fixed factors and bird ID (identification) and assay ID were used as random factors. I used aggressive interactions within the dyads of individuals that were maintained together in all treatments (blue dashed squares in Figure 4) so that the data was comparable between assays that differ in social environment. I used a zero-inflated GLMM with Poisson distribution and log-link function.

To test the prediction that, when in the presence of non-familiar individuals, aggression was directed mostly at familiar individuals, I used data from the treatments where non-familiar individuals were present (Figure 4C,D). I ran a GLMM with the number of aggressive interactions that each focal individual directed toward each of the other three birds per assay as dependent variable, and as fixed factors the relationship between the focal individual performing and the one receiving the aggressive behaviour (familiar or not familiar), and the physical environment (home cage or novel cage). Again, bird ID and assay ID were random factors. I used a zero-inflated GLMM with Negative Binomial distribution and log-link function.

To test the prediction that attacking familiar individuals (i.e., showing-off aggressiveness) was associated with receiving less aggression from unfamiliar individuals, I also used data from the treatments where non-familiar individuals were present. I ran a GLMM with number of aggressive interactions that each focal individual received from the non-familiar individuals in the assay as dependent variable, and three fixed factors: the number of aggressive interactions each focal individual directed toward its familiar companion in that assay, the number of aggressive interactions each focal individual directed towards the unfamiliar birds in that assay, and the physical environment (home cage or novel cage). Again, bird ID and assay ID were random factors. I used a zero-inflated GLMM with Poisson distribution and log-link function.

Lastly, I tested predictions from the hypothesis of redirected aggression using two different GLMMs, again with data from the treatments with non-familiar individuals present. In particular, I wanted to access redirected aggression from unfamiliar to familiar birds, or, conversely, from familiar to unfamiliar birds. One GLMM used as dependent variable the number of aggressive interactions each bird directed towards familiar individuals in each assay, and three fixed factors: the number of aggressive interactions each bird received from unfamiliar individuals in that assay, the number of aggressive interactions each bird received from familiar individuals in that assay, and the physical environment. Bird ID and assay ID were random factors. Redirected aggression from unfamiliar to familiar birds predicts a positive association between the number of aggressive interactions received from unfamiliar individuals and the number of aggressive interactions directed to familiar individuals, controlling for the physical environment and the number of aggressive interactions received from familiar birds. The second GLMM was similar to the previous but used as dependent variable the number of aggressive interactions directed at unfamiliar birds (rather than at familiar birds). Here, redirected aggression from familiar to unfamiliar birds predicts a positive association between the number of aggressive interactions received from familiar individuals and the number of aggressive interactions directed to unfamiliar individuals. I used a GLMM with Poisson distribution and log-link function to access redirected aggression from unfamiliar to familiar birds, and a zero-inflated GLMM with a Poisson distribution and log-link function to access redirected aggression from familiar to unfamiliar birds. The GLMM to assess redirected aggression from unfamiliar to familiar birds appeared overfitted, since assay ID was identified as causing singularity in the model (with an estimated variance of 2.419e-17); I thus opted to remove assay ID as a grouping factor in this model (Barr et al., 2013).

All statistical analyses were conducted in R v. 4.3.0 (R Core Team, 2023). The GLMM was performed using the R package ‘lme4’ (Bates et al., 2015) and zero-inflated GLMMs were run using the R package ‘glmmTMB’ (Brooks et al., 2017). Model assumptions were checked using the R packages

'performance' (Lüdecke et al., 2021) and 'DHARMa' (Hartig, 2020). To model the excess of zeros in two of the zero-inflated models (model of within-dyad aggression, and model of aggression to all other cage mates), I only used the intercept in the zero-inflation equation (Table S3). Due to model instability, in the two other zero-inflated models (model of aggression received from unfamiliar individuals, and model of aggression towards unfamiliar individuals) I had to include additional predictors in the zero-inflation equation (see predictors in Table S3).

3. Results

On average, each bird made 11.167 aggressive interactions per assay (range: 0 to 82; Figure 5A). Of these, on average 2.094 (range: 0 to 18; Figure 5B) were towards the familiar companion in the dyad that was together in all treatments.

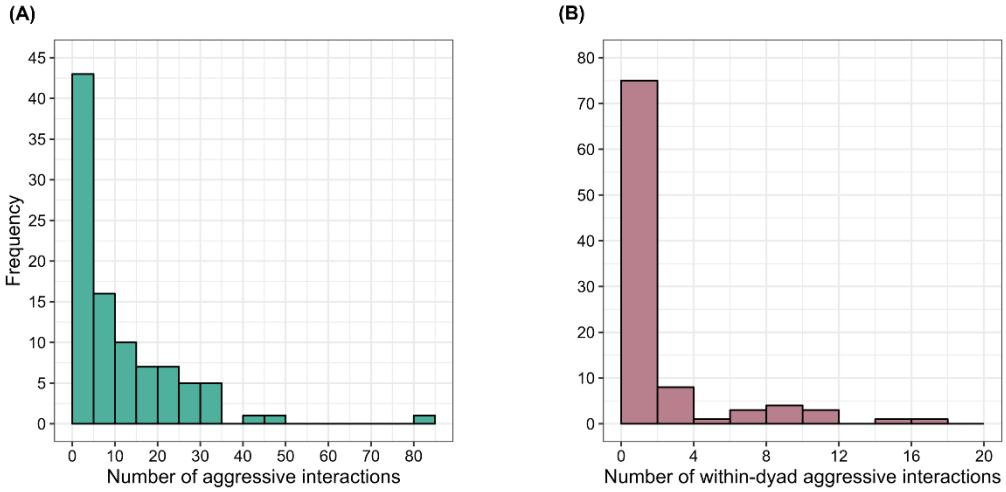

Figure 5 – Histograms of (A) the number of aggressive interactions that each bird directed towards all other cage mates, per individual per assay, and (B) the number of aggressive interactions between within the dyads that were together in all treatments, per individual per assay.

The number of aggressive behaviours, within the dyads of individuals that were together in all treatments, was lower when unfamiliar birds were present (Z = -2.362, *P* = 0.018, Table S4, Figure 6). By comparison to the effect of the social environment, there was only a smaller and non-significant trend for the amount of aggressive behaviour to be higher in a novel physical environment (home cage vs. novel cage; Z = 1.611, *P* = 0.107, Table S4, Figure 6).

When unfamiliar birds were present, aggressive behaviours were mostly directed towards these unfamiliar individuals (Z = 4.860, *P* < 0.001, Table S4, Figure 7). Additionally, there was a suggestive trend for aggression levels to be higher when birds were in a novel cage than in their home cage (Z = 1.836, *P* = 0.066, Table S4, Figure 7).

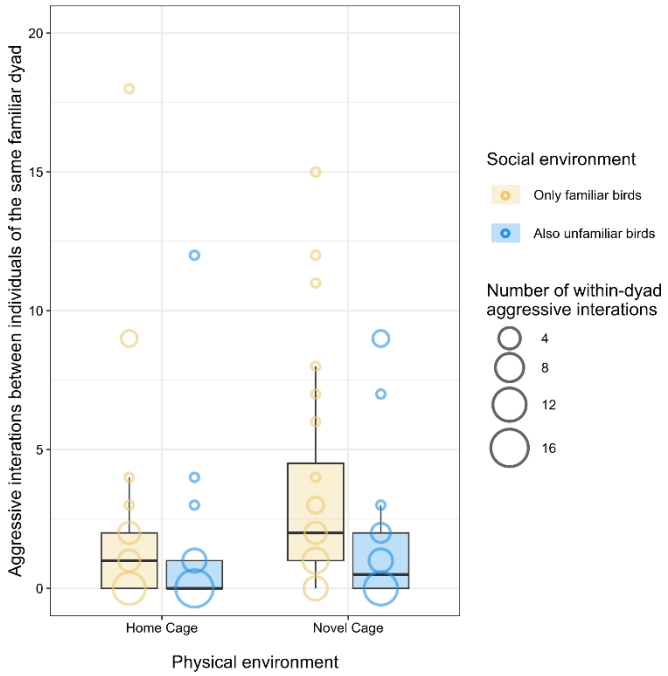

Figure 6 – Boxplot showing within-dyad aggression per individual per assay, separated by different social environments (unfamiliar individuals present or absent) and in relation to the physical environment (home cage or novel cage). Boxes show median and interquartile range (between the 25th and 75th percentiles). Circle size is proportional to the frequency of aggressive interactions per individual per assay.

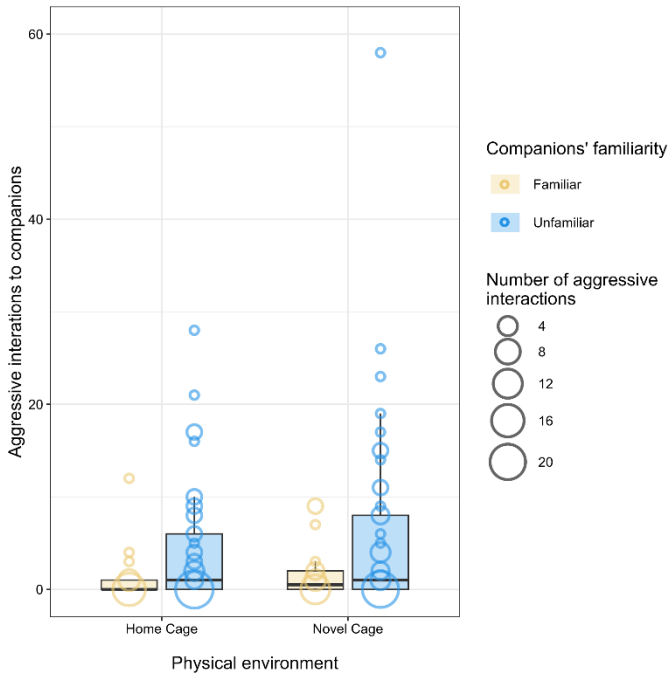

Figure 7 – Boxplot showing aggressive interactions directed to all cage mates per individual per assay, separated by companions' familiarity (aggression directed towards familiar or unfamiliar individuals) and in relation to the physical environment (home cage or novel cage). Plot details as in Figure 6.

The number of aggressive behaviours an individual directed towards its familiar companion predicted positively the number of aggressive behaviours it received from unfamiliar individuals ($Z = 2.196$, $P = 0.028$, Table 1, Figure 8A). The number of aggressive behaviours directed towards unfamiliar individuals did not

predict the aggression received from them (Z = 0.432, *P* = 0.666, Table 1, Figure 8A), and the aggression received from unfamiliar individuals was lower in novel cages (i.e., in the home cage of the unfamiliar individuals; Z = - 4.025, *P* < 0.001, Table 1, Figure 8B).

Table 1 – Conditional model of a zero-inflated GLMM relating aggression received from unfamiliar companions per individual per assay with aggression directed at familiar and unfamiliar companions per individual per assay and the physical environment, considering data only from the experimental treatments.

	β	SE	Z	*P*
Aggression received from unfamiliar individuals				
Aggression to familiar individuals	0.085	0.039	2.196	**0.028**
Aggression to unfamiliar individuals	0.005	0.013	0.432	0.666
Physical environment	- 0.515	0.128	- 4.025	**< 0.001**

Reference levels: home cage for the physical environment. Coefficients (β), standard errors (SE), Z and P-values.
Bold indicates significance.

The amount of aggression an individual directed towards its familiar companion was positively predicted by the aggression it received from unfamiliar birds in the same assay (Z = 2.744, *P* = 0.006, Table 2, Figure 9A). The aggression an individual directed to the familiar companion was not predicted by the aggression received from that familiar companion (Z = 0.496, *P* = 0.620, Table 2, Figure 9A), and was higher when in a novel cage (Z = 2.921, *P* = 0.003, Table 2, Figure 9B).

The amount of aggression towards unfamiliar birds was not predicted by the number of aggressive behaviours received either from familiar or unfamiliar birds (Z = -0.899, *P* = 0.369, and Z = 0.317, *P* = 0.752, respectively, Table 2, Figure 10A). This model also indicated that aggression directed at unfamiliar birds was higher when in a novel cage (Z = 2.967, *P* = 0.003, Table 2, Figure 10B).

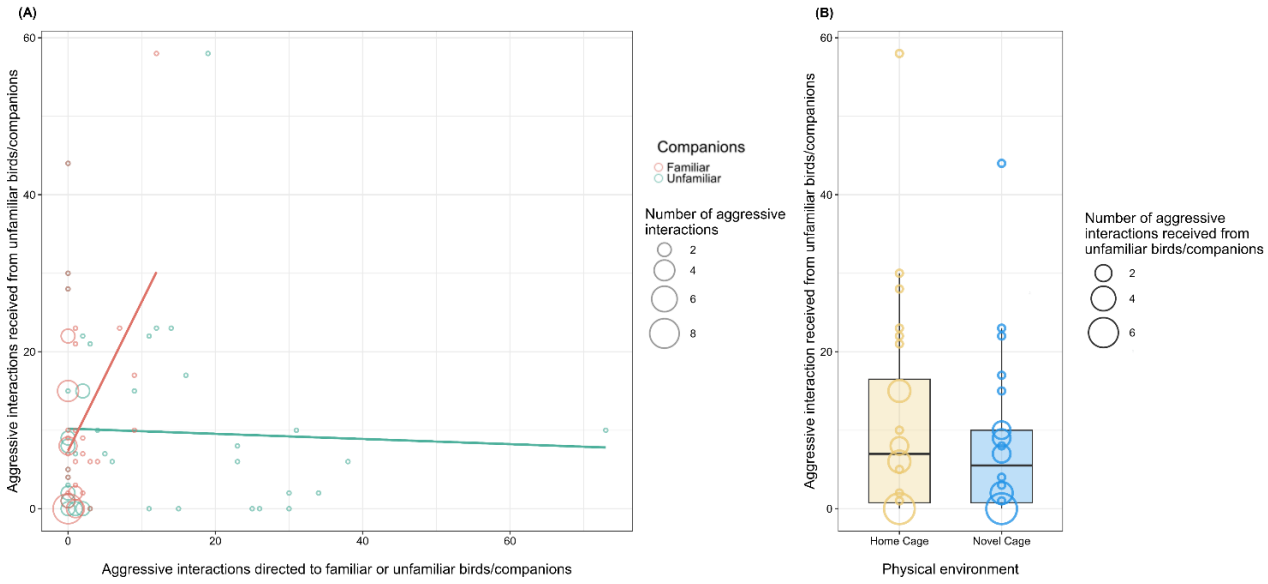

Figure 8 – (A) Scatterplot relating aggressive interactions received from unfamiliar companions per individual per assay with aggressive interactions towards companions (either familiar or unfamiliar) per individual per assay. Solid lines represent simple linear regressions used only to demonstrate the relationship between aggressive interactions directed at familiar companions and aggressive interactions received from unfamiliar companions (orange) and between aggressive interactions directed at unfamiliar companions and aggressive interactions received from unfamiliar companions (green). (B) Boxplot showing aggressive interactions received from unfamiliar companions per individual per assay in relation to the physical environment (home cage or novel cage). Plot details for panel A and B as in Figure 6.

Table 2 – GLMMs results of the relation between received and directed aggression, both per individual per assay, and the physical environment, considering data only from the experimental treatments.

	β	SE	Z	*P*
Aggression to familiar individuals				
Aggression received from familiar individuals	0.035	0.071	0.496	0.620
Aggression received from unfamiliar individuals	0.051	0.018	2.744	**0.006**
Physical environment	0.968	0.332	2.921	**0.003**
Aggression to unfamiliar individuals *				
Aggression received from familiar individuals	-0.057	0.063	-0.899	0.369
Aggression received from unfamiliar individuals	0.006	0.018	0.317	0.752
Physical environment	0.471	0.159	2.967	**0.003**

Reference levels: home cage for the physical environment. Coefficients (β), standard errors (SE), Z and P-values. **Bold** indicates significance. * - Conditional model of a zero-inflated GLMM.

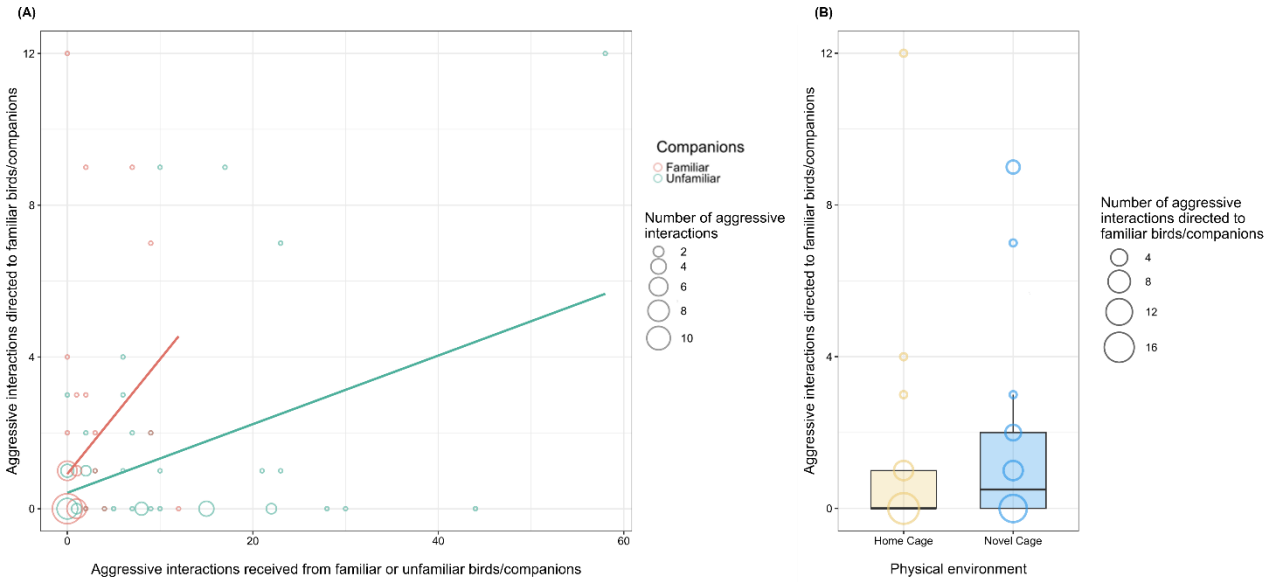

Figure 9 – (A) Scatterplot relating aggressive interactions directed towards familiar companions per individual per assay with aggressive interactions received from companions (either familiar or unfamiliar) per individual per assay. Solid lines represent simple linear regressions used only to demonstrate the relationship between aggressive interactions received from familiar companions and aggressive interactions directed at familiar companions (orange) and between aggressive interactions received from unfamiliar companions and aggressive interactions directed at familiar companions (green). (B) Boxplot showing aggressive interactions directed towards familiar companions per individual per assay in relation to the physical environment (home cage or novel cage). Plot details for panel A and B as in Figure 6.

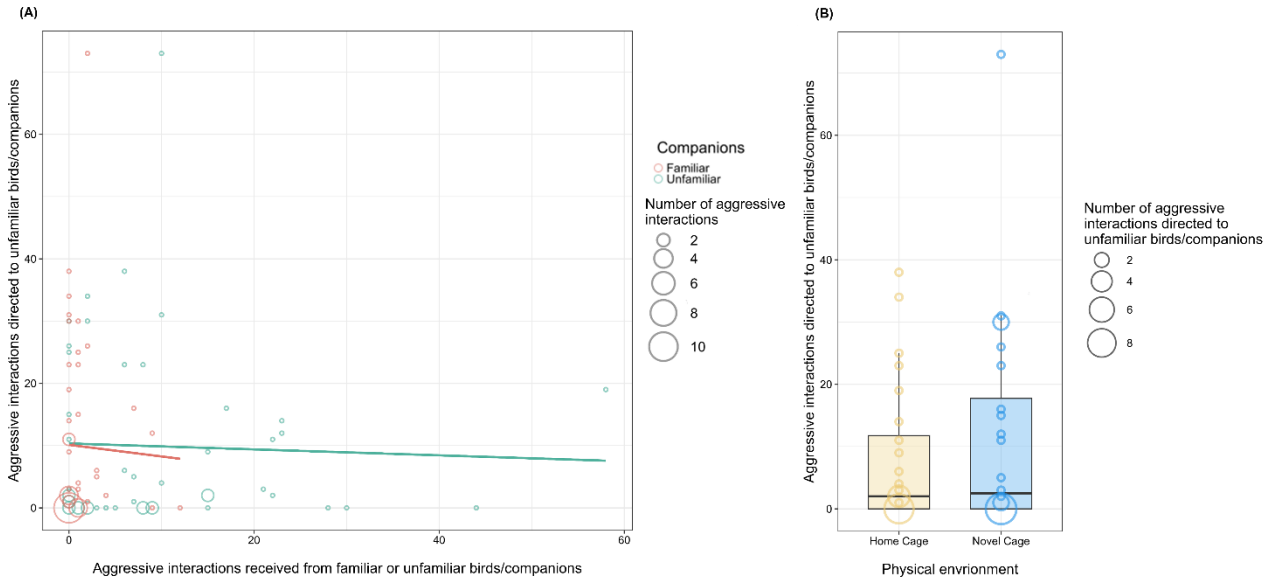

Figure 10 – (A) Scatterplot relating aggressive interactions directed towards unfamiliar companions per individual per assay with aggressive interactions received from companions (either familiar or unfamiliar) per individual per assay. Solid lines represent simple linear regressions used only to demonstrate the relationship between aggressive interactions received from familiar companions and aggressive interactions directed at unfamiliar companions (orange) and between aggressive interactions received from unfamiliar companions and aggressive interactions directed at unfamiliar companions (green). (B) Boxplot showing aggressive interactions directed to unfamiliar individuals per individual per assay in relation to the physical environment (home cage or novel cage). Plot details for panel A and B as in Figure 6.

4. Discussion

Waxbills' aggressive behaviour differed with their social environment. Contrary to the prediction that waxbills would attack familiar individuals to show-off social dominance to strangers, aggression was lower when non-familiar individuals were present, and waxbill aggression was mostly directed towards those unfamiliar birds rather than towards familiar ones. These results differ from those reported by Beltrão et al. (2023), where waxbills became more aggressive in the presence of unfamiliar bystanders, directing their aggression not towards those unfamiliar individuals but mostly towards subordinate individuals in what appears to be a show-off of social dominance. Also contrary to the prediction that showing-off by attacking familiar individuals would reduce aggression received by strangers, I found a positive, rather than negative, association between aggression towards familiar individuals and aggression received from unfamiliar individuals. More aggression received from unfamiliar birds predicted more aggression directed at familiar individuals, but aggression received from familiar individuals did not predict aggression directed at unfamiliar birds, suggesting redirected aggression only from unfamiliar to familiar individuals but not vice-versa. In common with the results of Beltrão et al. (2023), this indicates a cautious way of managing conflict with strangers. I next discuss these different results in light of the methodological differences between the two studies: here assays of competition for food in a confined space after a period of food deprivation, and in Beltrão et al. (2023) monitoring a free-flying flock of common waxbills at a feeding station.

4.1. Impact of the social environment on waxbills' aggressive behaviour

Because Beltrão et al. (2023) found that waxbills showed-off aggressiveness in the presence of unfamiliar birds, not by attacking them directly but by attacking subordinate individuals, I predicted that waxbills would increase aggression, especially between dyads of familiar individuals, when experimentally placed in the presence of unfamiliar birds. Contrary to this prediction, aggression within the dyads of familiar individuals was lower in the presence of non-familiar birds, and aggression was also mostly towards these unfamiliar birds.

Waxbills in a stable population in an open-air mesocosm (Beltrão et al., 2023) face different challenges from those imposed in the context of these essays, where birds were maintained in small groups in cages and where the social context was manipulated. In the experimental assays, waxbills were deprived of food and water to be motivated to feed in a small feeder, used to promote close contact between them, and were confined to the small space of the cage. In contrast, Beltrão et al. (2023) studied agonistic interactions of waxbills living and flying freely, recorded at a feeding station in a large open-air mesocosm (ca. 235 m2), where birds had *ad libitum* access to food. All birds were acquainted with the environment, be it social or physical. These methodological differences could help explain the contrasting results between our works.

I found that the agonism exchanged between dyads of familiar individuals was lower when in the presence of unfamiliar waxbills, while in the open-air mesocosm the opposite was true: increased aggression when non-familiar individuals were present in the audience (Beltrão et al., 2023). Lower levels of aggression exchange between dyads of familiar individuals in a novel social environment, compared to a familiar one, could be interpreted as a social buffering response to novelty-induced stress, where group cohesion is prioritized over agonistic behaviour (Doran et al., 2019), differing from what was found for a semi-natural waxbill population, maybe because birds were knowledgeable about their social setting. When there is a lack of social stability, this response of intragroup conflict could be important in mediating group formation and dynamics of fission-fusion societies (Doran et al., 2019), as is the case for waxbill populations (Clement et al., 1993; Payne, 2010).

Prior research (Beltrão et al., 2021b) demonstrated that aggressive interactions among waxbills in cages are temporally correlated and not separate events, as waxbills may be unable to flee socially unfavourable situations due to a lack of cover or space. Therefore, the chance of aggressive retaliation between individuals is probably higher in cages, and additional aggressive interactions between individuals after first contact are anticipated to be more prevalent. As a result, the small space and correlated aggression events may have contributed to forcing aggressive interaction with non-familiar conspecifics, leading to increased aggression towards these individuals. As is the case here, most often conflict over dominance is expected to be more common between individuals that are less familiar with each other, where dominance relationships may not be well (Meese & Ewbank, 1973; Moss, 1978)Clique ou toque aqui para introduzir texto.. Pigs (Meese & Ewbank, 1973; Moss, 1978), rabbits (Andrist et al., 2012; Gerencsér et al., 2019), bats (Ancillotto & Russo, 2014), as well as other animals (Asensio et al., 2008; Riveros et al., 2017; Silveira et al., 2020), have shown increased aggression towards unfamiliar individuals. This result, however, contrasts with Beltrão et al. (2023), where birds tended to avoid behaving aggressively towards unfamiliar conspecifics.

Food deprivation in the standard assays could also help explain the different results obtained here and in Beltrão et al. (2023), where food was always available. Feeding motivation might have led to an overall increase in aggression in cages as brief periods of food deprivation might reduce sociability (Killen et al., 2016; Krause, 1993) and, in the short term, individuals may become more aggressive and competitive for food (Webster & Hart, 2006). While aggression within a familiar dyad of birds was lower in the presence of non-familiar waxbills, feeding motivation coupled with a confined physical environment could have led individuals to aggress mostly these unfamiliar birds, shifting towards a strategic focus on securing one's resource-holding potential (i.e., access to food) against individuals whom dominance relations are less clear.

Since restrictions upon aggression did not exist in Beltrão et al. (2023) – birds could move freely and determine how, when and whom they interacted with – it may be for that reason that waxbills prefer to not interact aggressively with non-familiar conspecifics, instead using a cautious strategy (i.e., aggressive show-off) to signal social dominance to these non-familiar individuals. This low-risk social strategy does not require prior interactions with unfamiliar birds (Beltrão et al., 2023) and was instead found to be more of a

proactive than a reactive approach. Because in the particular setting of my experiments aggression was found to be less common between dyads of familiar individuals when in the presence of non-familiar waxbills, but mostly directed at those non-familiar waxbills, aggressive show-off does not seem to play a role in modulating waxbills' aggression patterns when tested in the confines environment of bird cages.

If at all, the effect of being in a familiar or unfamiliar physical environment (home cage vs. novel cage) was smaller than that of social familiarity, as there was only a non-significant trend for aggressiveness within the same dyads of birds to increase in a novel physical environment. Nonetheless, in tests using smaller datasets (only the assays where strange birds were present), aggression was found to be higher when individuals were placed in a novel cage. Heightened aggression in a novel physical environment could stem from a stress-induced reaction (Honess et al., 2004; Honess & Marin, 2005, 2006; Lendvai et al., 2011), or alternatively, it might serve as a coping strategy employed to manage the potential adverse physiological and psychological impacts of novelty (Baker & Aureli, 2000; Koolhaas et al., 1999; Wechsler, 1995).

4.2. Associations between received and directed aggression

Aggressing preferentially familiar individuals could be advantageous if it deterred aggression received from non-familiar individuals. I did not find evidence for such a function, at least in the confined context of these experiments. On the contrary, I found a positive association between the amount of aggression directed towards familiar companions and the aggression received from unfamiliar individuals. This could be due to either of two phenomena: social eavesdropping and preventive attacks towards aggressive individuals or redirected aggression.

First, unfamiliar birds could be using social eavesdropping (Earley & Dugatkin, 2002; Otter et al., 1999) by observing the aggressive interaction among dyads of familiar waxbills. With this information, they might identify which individuals are aggressive and might pose a threat to their own social standing in order to attack or threaten those aggressive individuals preventively, as a means of safeguarding or asserting one's social rank. Aggressing individuals could in fact be considered a bigger threat by their conspecifics since it was found in a previous work studying waxbills in cages that more aggressive individuals tented to occupy higher ranks in dominance hierarchies (Funghi et al., 2015). However, this hypothesis (eavesdropping which individuals are aggressive and attacking them preventively) would also predict that aggression directed towards an unfamiliar individual would also cause preventive aggression received from the other unfamiliar individual, which is not consistent with my finding that aggression towards unfamiliar individuals did not predict the aggression received from them. Moreover, preventive aggression towards aggressive individuals is not well supported in the literature. On the contrary, following aggressive encounters, it is the recipients of aggression that often face subsequent agonism (Kazem & Aureli, 2005; McFarland & Majolo, 2011; Schino & Marini, 2011). Similarly, for instance, both male Siamese fighting fish (*Betta splendens*, Oliveira et al., 1998) and great tits (*Parus major*, Peake et al., 2002) respond differently

towards perceived “losers” and “winners” of eavesdropped contests by being more cautious in approaching and displaying towards the latter.

Second, and more likely, there could be redirected aggression from unfamiliar to familiar individuals, whereby being threatened or attacked by an unfamiliar bird causes aggression directed towards a safer target, such as a familiar companion. Waxbills could be using this strategy to reduce the stress provoked by receiving aggression from unfamiliar cage mates (e.g., Øverli et al., 2004; Virgin & Sapolsky, 1997). For instance, olive baboons (*Papio anubis*) exposed to the stress of subordinance were found to redirect aggression (Virgin & Sapolsky, 1997). In addition, individuals may use redirection toward their familiar companions to divert their attention away from the initial aggressors and place it on their familiar conspecifics (e.g., Itani, 1963). The transfer of aggression from unfamiliar to familiar individuals could also be of particular importance in reestablishing social standing, after receiving aggression (Kazem & Aureli, 2005). Redirected aggression is thought to be useful, at least in the long term, to reduce costs or gain advantages if it communicates dominance and reduces received aggression (Tokuyama & Furuichi, 2014). For example, victims of attacks in some primate species who then redirected aggression were found to lessen their likelihood of receiving renewed aggression (Aureli & van Schaik, 1991; Kazem & Aureli, 2005; Tokuyama & Furuichi, 2014). Indeed, a signalling function for this aggression pattern was already previously proposed (Kazem & Aureli, 2005). Thus, redirected aggression could effectively combine elements of conflict management approaches and social dominance signalling, either to the initial aggressor (Schino & Marini, 2014) and/or to other bystanders (Ito et al., 2018; Tokuyama & Furuichi, 2014).

Interestingly, no evidence was found for redirected aggression in the opposite direction, from familiar to unfamiliar birds. To my knowledge, this unidirectional pattern of redirection – from unfamiliar towards familiar individuals but not vice-versa – had not yet been described. Some other species have also been found to redirect aggression non-randomly, albeit in different manners than what I found in the common waxbill. For example, in some species aggression is redirected towards the original aggressor’s kin (i.e., indirect retaliation, (Aureli et al., 1992; Cheney & Seyfarth, 1989), implying a perception, to some degree, of the relations of their opponents.

Redirecting aggression from unfamiliar to familiar individuals is a different strategy from the one reported by Beltrão et al. (2023), working with a free-flying flock of waxbills. Although different, both strategies have in common that they are cautious ways of dealing with unfamiliar individuals. The two social strategies seemed to aim to minimize contact with non-familiar conspecifics, between whom dominance relations are not well established, and possibly avoid future harmful encounters. Also, in both, aggression towards other individuals appears to be used as a means of signalling social dominance, again avoiding the need for close agonistic interactions with the unfamiliar individuals. Aggressive show-off and redirection from unfamiliar to familiar birds can thus be strategies used by waxbills to signal dominance to non-familiar individuals and/or the remaining audience.

In the previous study of Beltrão et al. (2023), who monitored aggression of a free-flying flock of waxbills at feeders in a large mesocosm, waxbills were not more likely to be attacked by unfamiliar individuals, but they still increased aggression towards third parties in the presence of unfamiliar

bystanders. Thus, unlike my result studying waxbills in confined bird cages, aggression towards third parties did not appear redirected from aggression received from non-familiar birds. Perhaps redirected aggression is more effective or needed for signalling dominance in the confined cage environment of my study, or in other contexts of close proximity where direct interactions with the unfamiliar individuals are difficult to be avoided. Conversely, showing-off aggression may be more advantageous in more open spaces and with the presence of larger audiences (the audience sizes analysed by Beltrão et al., 2023, varied between 10 and 50), because more bystanders become informed of the social status of signalling individuals with a reduced signalling effort.

5. Concluding remarks

The importance of empirical studies is long recognized to explore thoroughly the ways in which animals perceive and react to their social environment. Here, I found evidence that waxbills may use redirection to modulate aggression and dominance. The identification of redirected aggression in waxbills from unfamiliar towards familiar individuals, to my knowledge, represents a novel finding in research regarding redirected aggression, perhaps also serving as a low-risk social strategy for status signalling. Moreover, this finding highlights the role of familiarity in shaping group and agonistic behaviour and also adds to the accumulating evidence of the influence of the social environment on signalling behaviour (Beltrão et al., 2023; Dugatkin, 2001; Johnstone, 2001; Peake et al., 2001; Peake & Mcgregor, 2004; Szipl et al., 2018). Finally, the present work, together with the work of Beltrão et al. (2023), sheds light on complex and cautious social strategies used by a gregarious bird species, which could also be present in other social animals. It further points towards the significance of considering methodological differences when studying patterns of aggression and social strategies, illustrated by contrasting results regarding waxbill's aggression in cages versus in an open-air mesocosm (Beltrão et al., 2023). When viewing the results of both works, it is coherent that redirection can be important in modulating aggression in this gregarious finch, and not solely a by-product of methodological constraints that may arise.

Future research in waxbills should focus on the timing of attacks, as here, aggression data retrieved did not encompass a sequential component and redirected aggression is a time-sensitive conflict management strategy. A bigger sample size (i.e., observational time) should also help to better assess this aggression pattern. The use of redirection could be more or less reliable, depending on social dominance rank, and examples exist where redirection is more common towards weaker, more subordinate individuals (Kazem & Aureli, 2005; Tokuyama & Furuichi, 2014). Thus, it may be interesting to associate individuals' social dominance while studying redirected aggression. Of significant importance, a crucial question to address is if indeed redirection is used to signal social status in waxbills, who are the signalling targets of such displays: the initial aggressor, bystanders or the general audience?

6. References

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7. Supplementary material

Table S1 – Experimental setup information regarding cage, dyad and individuals' identification and sex.

Cage ID	Dyad ID	Individuals' ID	Sex
Cage A	A1	BA/M01	F
		SA/PP	M
	A2	SA/Vesc06	F
		A/Vesc17	M
Cage B	B1	PB/M07	F
		P/M13	M
	B2	SA/Vesc12	F
		A/Vesc11	M
Cage C	C1	B/M02	F
		A/M08	M
	C2	Vesc19/SA	F
		P/M09	M
Cage D	D1	B/M10	F
		AB/M15	M
	D2	SA/Vesc09	F
		PV/M16	M
Cage E	E1	AB/M04	F
		SA/SA	M
	E2	B/M03	F
		P/M06	M
Cage F	F1	AA/Vesc10	F
		PB/Vesc7	M
	F2	B/M12	F
		P/M11	M

Sample sized: 24 individuals, 12 males and 12 females.

Table S2 – Distribution of treatments for each round/ week of tests.

Round/ week	Day	Cage	Dyads tested	Treatments
1[a]	13/09/2022	A	A1 and A2 stayed in home cage	Control (SPe)
		B	B1 and B2 stayed in home cage	Control (SPe)
	14/09/2022	C	C1 and C2 moved to cage D	Control (Se)
		D	D1 and D2 moved to cage C	Control (Se)
	15/09/2022	E	E1 stayed in home cage	Treatment (Se)
			E2 moved to cage F	Treatment (SPe)
		F	F1 stayed in home cage	Treatment (Se)
			F2 moved to cage E	Treatment (SPe)
2[a]	20/09/2022	A	A1 stayed in cage A	Treatment (Se)
			A2 moved to cage B	Treatment (SPe)
		B	B1 stayed in cage B	Treatment (Se)
			B2 moved to cage A	Treatment (SPe)
	21/09/2022	C	C1 stayed in cage C	Treatment (Se)
			C2 moved to cage D	Treatment (SPe)
		D	D1 stayed in cage D	Treatment (Se)
			D2 moved to cage C	Treatment (SPe)
	22/09/2022	E	E1 and E2 moved to cage F	Control (Se)
		F	F1 and F2 moved to cage E	Control (Se)
3[a]	27/09/2022	A	A1 moved to cage B	Treatment (SPe)
			A2 stayed in cage A	Treatment (Se)
		B	B1 moved to cage A	Treatment (SPe)
			B2 stayed in cage B	Treatment (Se)
	28/09/2022	C	C1 and C2 stayed in home cage	Control (SPe)
		D	D1 and D2 stayed in home cage	Control (SPe)
	29/09/2022	E	E1 moved to cage F	Treatment (SPe)
			E2 stayed in cage E	Treatment (Se)
		F	F1 moved to cage E	Treatment (SPe)
			F2 stayed in cage F	Treatment (Se)
4[a]	04/10/2022	A	A1 and A2 moved to cage B	Control (Se)
		B	B1 and B2 moved to cage A	Control (Se)
	06/10/2022	C	C1 moved to cage D	Treatment (SPe)
			C2 stayed in cage C	Treatment (Se)
		D	D1 moved to cage C	Treatment (SPe)
			D2 stayed in cage D	Treatment (Se)
	07/10/2022	E	E1 and E2 stayed in home cage	Control (SPe)
		F	F1 and F2 stayed in home cage	Control (SPe)

Sample size: 24 individuals, 12 males and 12 females. Control (SPe) – control treatment for the social and physical environment; Control (Se) – control treatment for the social environment; Treatment (Se) – experimental treatment where a dyad was tested in a novel social environment; Treatment (SPe) – experimental treatment where a dyad was tested in a novel social and physical environment.

Table S3 – Zero-inflated models of zero-inflated GLMMs.

	β	**SE**	**Z**	***P***
Within-dyad aggression [a]	-1.813	0.605	-2.998	**0.003**
Aggression to all other cage mates [b]	-20.860	6240.370	-0.003	0.997
Aggression received from unfamiliar individuals [b]				
Aggression to familiar individuals	0.104	7832	0.000	1.000
Aggression to unfamiliar individuals	0.090	942.100	0.000	1.000
Aggression to unfamiliar individuals [b]				
Aggression received from unfamiliar individuals	0.014	0.061	0.230	0.818
Physical environment	- 16.511	7482.256	- 0.002	0.998

Reference levels: home cage for the physical environment. Coefficients (β), standard errors (SE), Z and P-values. **Bold** indicates significance. [a] – data used from all treatments; [b] – data used only from the experimental treatments.

Table S4 – Conditional models of zero-inflated GLMMs relating within-dyad aggressive interactions per individual per assay with the social and physical environment and also aggressive interactions towards all other cage mates per individual per assay with companions' familiarity and the physical environment.

	β	**SE**	**Z**	***P***
Within-dyad aggression [a]				
Social environment	-0.915	0.388	-2.362	**0.018**
Physical environment	0.408	0.253	1.611	0.107
Aggression to all other cage mates [b]				
Companions' familiarity	1.144	0.235	4.860	**< 0.001**
Physical environment	0.319	0.174	1.836	<u>0.066</u>

Reference levels: familiar context composed of all familiar individuals for the social environment, home cage for the physical environment and aggression towards familiar companions for companions' familiarity. Coefficients (β), standard errors (SE), Z and P-values. Suggestive results are <u>underlined</u>. **Bold** indicates significance. [a] – data used from all treatments; [b] – data used only from the experimental treatments.