Environmental effects on collective behaviour and social structure

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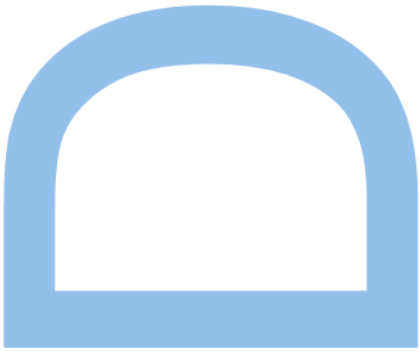

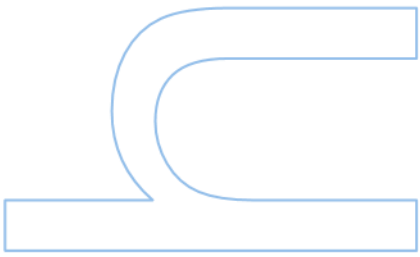

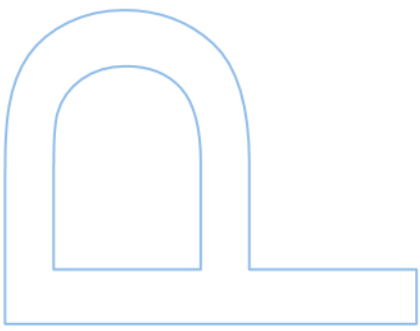

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Na elaboração desta tese, e nos termos do número 2 do Artigo 4º do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31º do D.L. 74/2006, de 24 de Março, com a nova redação introduzida pelo D.L. 65/2018, de 16 de Agosto, foi efetuado o aproveitamento total de um conjunto coerente de trabalhos de investigação já publicados ou submetidos para publicação em revistas internacionais indexadas e com arbitragem científica, os quais integram alguns dos capítulos da presente tese. Os respetivos capítulos estão elaborados de acordo com a linguagem (inglês britânico versus americano) e o estilo bibliográfico apresentados na revista onde foram ou possam vir a ser publicados. Tendo em conta que os referidos trabalhos foram realizados com a colaboração de outros autores, a candidata esclarece que, em todos eles, participou ativamente na sua conceção, na obtenção, análise e discussão de resultados, bem como na elaboração da sua forma publicada. A tese de Doutoramento da candidata foi apresentada à Faculdade de Ciências da Universidade do Porto, tendo o trabalho sido realizado sob orientação do Doutor Gonçalo Cardoso, Investigador do Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO/InBIO, Universidade do Porto).

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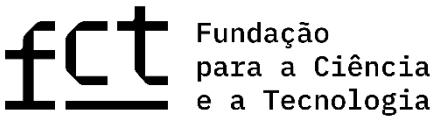

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Abstract

Gregarious animals often benefit from cooperation, protection from predators, access to mates, among other advantages. Group-living also comes with costs, such as increased competition for resources, and this conflict between individuals can lead to the emergence of dominance hierarchies. Recent research has given attention to the aggression strategies used to manage dominance hierarchies, but usually these studies do not consider the social environment, which can be crucial to understanding aggression strategies. Not only the social environment but also ecological conditions may affect social behavioural dynamics, such as conflict, cooperation or social structure. The aim of this thesis was to study how the environment, both abiotic and biotic, can affect social and collective behaviour, and for this I used as model a very gregarious bird species, the common waxbill (*Estrilda astrild*). Most of this work used waxbills living in semi-natural conditions, in a large outdoor aviary in northern Portugal, exposed to the natural climate and with abundant natural vegetation, where they could nest and show fission-fusion flocking behaviour. The birds had access to feeders equipped with radio-frequency identification (RFID) antennae that, together with an array of perches also equipped with RFID antennae, allowed to monitor their behaviour.

In chapters 2 and 3 I study nesting behaviour in relation to ecological conditions. The common waxbill is an opportunistic breeder, and its breeding phenology is known to differ geographically across its native sub-Saharan African range. Using nest monitoring in the mesocosm and field data from the waxbill invasive range in Portugal I found that, despite some year-to-year variation, in the temperate and seasonal climate of Portugal waxbills show a main peak of breeding in Spring, coinciding with that of most native birds, and that breeding can then continue until the Autumn. In the high-density condition of the mesocosm, relative to available nesting sites, I also found that waxbills not only make their typical isolated domed nests near the ground, but also often build compound structures with two or more chambers. These compound nests were mainly found off-ground, in bushes, and the different chambers could be used by the same or different pairs. Most nests that proceed to egg-laying were off-ground nests. Since the space for building off-ground nests is limited, due to a limited number of bushes, birds may have been forced to clump their nests together. Compound nest building is one type of social behaviour not reported in nature for this species, and hence it appears to be a plastic component of waxbill's behaviour that is expressed in the particular conditions of the mesocosm (i.e., constrains in space availability).

In chapters 4 to 6, I study dominance hierarchies, and how waxbill aggressive behaviour is affected by individual traits and the social environment. By manipulating testosterone levels, I found that testosterone has sex-specific effects on dominance status, with higher levels of testosterone increasing male but not female social dominance. I also showed that dominance status of waxbills is predicted by the saturation of red colour in their breast plumage, which could potentially act as a badge of status. When looking at patterns of aggression at feeders, I found a pattern of bullying, meaning that waxbills direct their aggression towards very subordinated individuals and that social environment modulated waxbills aggressiveness. Namely, birds tended to be more aggressive when socially distant individuals were present in the audience, which led me to suggest that showing-off aggression in the presence of socially distant individuals may be a safe strategy to manage the social status, without entering in a direct conflict with these less familiar individuals.

In chapters 7 and 8, I studied how the abiotic environment (food availability and the weather) affect collective behaviour. By experimentally reducing the number of feeding points in their feeding area, or decreasing their predictability, I found that waxbills became more aggressive, and foraged in smaller and more fragmented groups. Also, foraging efficiency decrease, as the birds spent less time in the feeding area and made more trips to the feeders. Although this shift in behaviour may seem to increase rather than solve the environmental challenges, it may in fact be adaptative if, in nature, these changes in collective behaviour function as a trigger to explore new regions before the local food resources are depleted. By studying natural fluctuations in weather over 5 years, I found that during colder and cloudier days, when energetic demands are higher, waxbills spent more time feeding and, on colder days, joined more and larger foraging groups, resulting in less structured social networks. During rainy days, foraging groups became briefer and more synchronous, leading to stronger associations between individuals and less structured networks. Wind appeared to act as a disturbance making foraging groups less frequent and larger, with individuals showing more aggression at the feeders. Having shown that the weather can affect social behaviour in more ways than previously expected, we can improve predictions of how gregarious animals will react to climate change. In conclusion, in this thesis I uncover different new environmental (both abiotic and social) influences on collective and social behaviour, providing insight on the ecology and social structure of gregarious animals.

Keywords: aggression, audience effects, badge of status, behaviour plasticity, bullying, collective foraging, dominance hierarchy, environmental fluctuation, food availability, gregarious animals, nest building, social behaviour, weather disturbance

Resumo

Os animais gregários frequentemente beneficiam de cooperação entre indivíduos, proteção contra predadores, acesso a potenciais parceiros, entre outros. Viver em grupo também possui custos, como aumento da competição por recursos, e por usa vez o conflito entre indivíduos pode levar ao aparecimento de hierarquias de dominância. Recentemente, tem sido publicado estudos dedicados às estratégias de agressão usadas para manter as hierarquias de dominância, no entanto, os mesmos não têm em atenção o ambiente social, que pode ser essencial para entender as estratégias de agressão. Para além do ambiente social, as condições ecológicas também podem afetar a dinâmica comportamental, como competição, cooperação ou estrutura social. O objetivo desta tese foi estudar como é que o ambiente, tanto abiótico quanto biótico, pode afetar o comportamento social e coletivo, e para isso usei como espécie de estudo uma espécie muito gregária, o bico-de-lacre (*Estrilda astrild*). A maioria do trabalho usou um sistema seminatural, onde as aves foram alojadas num grande aviário (mesocosmo), ao ar livre no norte de Portugal, expostas ao clima natural e com vegetação natural abundante, onde podiam construir ninhos e mostrar comportamentos de fusão e fissão de grupos. As aves tinham acesso a comedouros equipados com antenas de identificação por radiofrequência (RFID) que, juntamente com um conjunto de poleiros cada um equipado com 4 antenas, permitiam monitorizar o seu comportamento.

Nos capítulos 2 e 3, eu estudei o comportamento de nidificação em relação às condições ecológicas. O bico-de-lacre é um reprodutor oportunista, e sua fenologia reprodutora é conhecida por diferir geograficamente no seu habitat nativo, África subsaariana. Ao monitorizar a construção de ninhos no mesocosmo e usando dados de campo relativos à área de invasão do bico-de-lacre em Portugal, descobri que, apesar de alguma variação de ano para ano, no clima temperado e sazonal de Portugal, os bico-de-lacre têm um pico de reprodução na primavera, coincidindo com a maioria das aves nativas, e que a reprodução pode continuar até o outono. No mesocosmo, em consequência da alta densidade populacional em relação aos locais disponíveis para nidificação, também descobri que os bico-de-lacre não constroem apenas ninhos isolados em forma de bola perto do solo, mas também constroem estruturas compostas com duas ou mais câmaras. Esses ninhos compostos foram encontrados principalmente a alturas mais elevadas, em arbustos, e as diferentes câmaras podem ser usadas pelo mesmo par ou por diferentes pares. A maioria dos ninhos com postura de ovos foram encontrados em arbustos, não estando perto do solo. Como os locais para construir

ninhos fora do solo são limitados, devido a um número limitado de arbustos, as aves podem ter sido forçadas a agrupar os ninhos. Não existem relatos de ninhos compostos na natureza para esta espécie, portanto, parece que a construção de ninhos é um comportamento plástico que é expresso nas condições particulares do mesocosmo (ou seja, restrições na quantidade de locais adequados à construção de ninhos).

Nos capítulos 4 a 6, eu estudei as hierarquias de dominância e como o comportamento agressivo do bico-de-lacre é afetado pelas características dos indivíduos e pelo ambiente social. Ao manipular os níveis de testosterona, eu descobri que os efeitos da testosterona na dominância dos indivíduos diferem com o sexo, onde níveis mais altos de testosterona aumentam a dominância dos machos, mas não das fêmeas. Eu também mostrei que a dominância é prevista pela saturação da cor do peito, e deste modo, esta característica poderá potencialmente sinalizar aos conspecíficos o estatuto social. Ao analisar os padrões de agressão nos comedouros, descobri que as aves utilizam uma estratégia de *bullying*, ou seja, direcionam sua agressão para os indivíduos muito subordinados e que ambiente social afetou a agressividade. As aves eram mais agressivas na presença de indivíduos socialmente distantes, sugerindo que mostrar agressão na presença de indivíduos socialmente distantes pode ser uma estratégia segura para manter a posição na hierarquia de dominância, sem entrar em um conflito direto com esses mesmos indivíduos.

Nos capítulos 7 e 8, estudei como é que os fatores abióticos (disponibilidade de alimento e clima) afetam o comportamento coletivo. Ao experimentalmente reduzir o número de comedouros ou diminuir a previsibilidade alimentar, descobri que os bico-de-lacre se tornavam mais agressivos, procuravam alimento em grupos menores e mais fragmentados. Juntamente, a eficiência na procura de alimento diminuiu visto que as aves passavam menos tempo na área de alimentação e faziam mais viagens aos comedouros. Embora esta mudança comportamental possa parecer exacerbar os desafios ecológicos, pode ser na realidade uma adaptação, visto que na natureza, estas mudanças podem impulsionar as aves a explorar novas áreas antes que os recursos alimentares locais se esgotem. Ao estudar as flutuações naturais do clima ao longo de 5 anos, descobri que em dias mais frios e nublados, associados a maiores requisitos energéticos, os bico-de-lacre passavam mais tempo a alimentar-se e, em dias mais frios, as aves participavam em mais grupos, sendo eles também maiores, resultando em redes sociais menos estruturadas. Em dias de chuva, os grupos eram mais breves e síncronos, levando ao aparecimento de associações mais fortes entre os indivíduos e redes sociais menos estruturadas. O vento parece atuar como uma perturbação,

tornando os grupos menos frequentes e maiores, com os indivíduos mostrando mais agressão nos comedouros. Ao mostrar que o clima pode afetar o comportamento social em mais maneiras do que previamente previstas, torna possível melhorar as previsões sobre como animais gregários reagirão às mudanças climáticas. Para concluir, esta tese revela como o ambiente (social e abiótico) influencia o comportamento coletivo e social, fornecendo novas perspetivas para a ecologia e estrutura social de espécies gregárias.

Palavras-chave: agressão, *bullying*, comportamento social, construção de ninhos, disponibilidade alimentar, efeitos de audiência, flutuações ambientais, forrageamento em grupo, hierarquia de dominância, perturbações climáticas, plasticidade comportamental

Índice

Lista de Tabelas

List of Figures

List of Abbreviations

PIT	Passive Integrated Transponder
RFID	Radio-frequency Identification
T	Testosterone

Statistical abbreviations

AIC	Akaike Information Criterion
AICc	Akaike Information Criterion corrected for small sample sizes
ANOVA	Analysis of Variance
ARMA	Auto-regressive moving average
CI	Confidence Interval
CV	Coefficient of variation
df	Degrees of Freedom
DSP	Double semi-partialing permutations
GAMM	General Additive Mixed Model
GLMM	General Linear Mixed Model
GLMQAP	General Linear Model Quadradic Assignment Procedure
GMM	Gaussian Mixture Model
ICC	Intraclass Correlation
LMM	Linear Mixed Model
MCMC	Markov Chain Monte Carlo
MRQAP	Multiple Regression Quadratic Assignment Procedure
NP	Node permutations
P	*P-value*
PC	Principal Component
PCA	Principal Component Analysis
P_t	Proportion of transitive triangles
R	Repeatability
REML	Restricted Maximum Likelihood
SD	Standard Deviation
SE	Standard Error
t_{tri}	Triangle transitivity
χ^2	Chi-Square

Chapter 1 | General Introduction

Group-living species benefit from access to information on food location (Aplin et al. 2012; Tóth et al. 2017), access to possible mates (Ryder et al. 2011), protection from predators (Griesser et al. 2006), and diverse cooperative behaviours (Ward and Webster 2016; Griesser et al. 2017). When living socially, individuals are constantly affected by the behaviour of their conspecifics. Importantly, the social environment that surrounds an individual strongly affects one's behaviour. A familiar example is the teaching of meerkats pups (*Suricata suricatta*) to handle and feed on venomous scorpions (Thornton and McAuliffe 2006). However, gregariousness also comes with costs, as it can promote within-group conflict and competition. The aggression between group members often leads to the emergence of dominance hierarchies, where individuals have different priorities for access to resources (e.g., food or mates). Once established dominance hierarchies can function to reduce within-group conflict, providing stability to the social group (Ward and Webster 2016).

Dominance hierarchies

The maintenance of dominance hierarchies and individual dominance status can be done with resource to aggression (Holekamp and Strauss 2016). Increasing attention has been given to the aggression strategies used to manage dominance hierarchies, since they provide insight about how individuals perceive social information (Hobson 2020). For example, the "close competitor strategy" refers to when individuals direct aggression mostly towards conspecifics of similar dominance status to themselves, since the dominance relationship may comprise uncertainty due to both individuals having similar resource holding potential/fighting ability. This illustrates how knowledge of peer dominance status can impact to whom individuals direct aggression (Hobson et al. 2021). In social groups, the dyadic dominance interaction often occurs in a social environment, where the presence of particular conspecifics (e.g., kin, dominant individuals) may condition behaviour (Perry et al. 2004; Coppinger et al. 2017; Szipl et al. 2018). This change in behaviour can be strategic, with the new behaviour having a signalling function to the audience (Zuberbühler 2008). The study of aggression strategies and audience effects are usually done separately, not being clear on how these two parts interconnect. I aimed to address this gap in the literature, focusing on how aggression strategies can convey information to audience members.

Collective behaviour

In group-living species, we often observe collective behavioural patterns, which arise from the continuous interactions between individuals (Couzin and Krause 2003; Camazine et al. 2020). In such populations, the fitness of the individuals may be dependent on the behaviour of conspecifics, as it affects for example the coordination and synchrony of the group (e.g., Beauchamp 2015; Ward and Webster 2016). But how did these collective behaviours emerged and what drove their evolution? Challenging ecological conditions have been shown to favour sociality and cooperative strategies (Firman et al. 2020). Nevertheless, empirical studies manipulating the environment to lead to the emergence of collective behaviour can be quite difficult to implement.

Fluctuations in the social or abiotic environment often require that animals adjust their behaviour accordingly (Dingemanse et al. 2010; Snell-Rood 2013). One of the most direct consequences of environmental fluctuations is the change in food availability and predictability. Collective foraging can enhance the efficiency in exploring food resources, as individuals can share information about food locations with conspecifics (Giraldeau and Caraco 2000; Galef and Giraldeau 2001), and therefore reducing environmental uncertainty (Dall et al. 2005; Lihoreau et al. 2017). For example, under unpredictable environments, European starlings (*Sturnus vulgaris*) increase their foraging success when they had access to social information (Rafacz and Templeton 2003). However, when resources are scare, within-group competition can increase, and if the competition costs outweigh the benefits of collective foraging it could result in a decrease of social behaviour. When in periods with low food availability, orcas (*Orcinus orca*) forage in smaller groups and show more fragmented social networks (Beauchamp 2014). Little is yet known about how cooperation and competition are favoured during challenging environmental conditions. Hence, I studied which of these scenarios emerged during changes in food availability and predictability.

Fluctuations in weather can influence food availability and predictability, making it difficult to disentangle the effects of climatic factors and food availability on collective behaviour. Understanding how abiotic factors affect collective behaviour is of increasing importance, particularly when considering the rapid rate of climate change (Turner et al. 2020), as it may allow to make inferences about the future of gregarious species (Snijders et al. 2017). With the environment becoming more unpredictable, collective behaviour and particularly cooperation could be key for individuals' survival (Fisher et al. 2021). For example, in several bird species individuals roost tightly together during colder nights for preserving heat (Smith 1972), and during the breeding season under

unfavourable environmental conditions, Taiwan yuhinas (*Yuhina brunneiceps*) adopt more cooperative strategies (Shen et al. 2012). Moreover, there is a positive relation between sociality and cooperative behaviours and harsh ecological conditions (Rubenstein and Lovette 2007; Cornwallis et al. 2017; Firman et al. 2020). However, a recent study has also shown that extreme and variable temperatures can instead fragment social networks, indicating reduced cooperation (Rat et al. 2020). To resolve such contradictions, and better understand how the environment affects the functioning of animal groups, I conducted a comprehensive study that investigate how multiple environmental factors may affect different aspects of social behaviour and social structure.

Study system and model organism, the common waxbill

The work I developed during this thesis uses the common waxbill (*Estrilda astrild*) as a model organism. Waxbills can be found in grassy areas, as they feed mostly on seeds, moving in flocks through the year (Payne 2010; Cardoso et al. 2018; Silva et al. 2018). Their gregariousness allowed me to study behaviour both at the individual and group levels, including collective foraging dynamics, dominance hierarchies and social network structure. Moreover, because waxbills show fission-fusion dynamics, I could also study the effects of different social environments on individuals' behaviour. Waxbills, although not migratory, can perform vagrant movements probably is search of suitable habitats (Payne 2010), which may be important as in their native range (sub-Saharan Africa) rainfall is unpredictable, impacting food availability. This is particularly interesting as it suggests waxbills already have adaptive behavioural adaptations to deal with environmental fluctuations, as they face these challenges in their native habitat.

My work was conducted mainly using a mesocosm population of common waxbills. The mesocosm consists of a large outdoor enclosure (ca. 235 m2, and 1.30–2.70 m high), with abundant natural vegetation and exposed to the natural weather. Waxbills living in this semi-natural environment were captured from the wild, within a 20 km radius from the mesocosm which is located in Vairão, Porto (for details on the captures see (Guerra et al. 2020), or were born in the mesocosm. Birds have access to *ad libitum food* (Tropical Finches Prestige seed mixture, Versele-Laga), provided in 12 feeders, and *ad libitum* water. The feeding area was also equipped with 8 perches. Every bird had a passive integrated transponder (PIT) tag (Dorset ID, The Netherlands) on a leg ring which was then detected by a radio-frequency identification system (RFID). All the feeders were equipped with an antenna, and each perch had a set of 4 antennae

(Chapter 4, Figure 4.1). The mesocosm was connected to a small room (4 m2, 2.25 m high), through a small window, which had tall tree branches for perching. This semi-natural environment allowed waxbills to fly freely, roost communally, reproduce, show fission-fusion dynamics and social preferences. The RFID system recorded daily the individuals' arrivals and departures from the antennae, which resulted in automatic and detailed monitoring of waxbills' behaviour through time (Gomes et al. 2021). Additionally, besides the collection of large amounts of data, the mesocosm also allowed to control and to manipulate food resources, which enable to study the effects of food availability to separate from the abiotic effects. With this system, I was able to identify dominance interactions, foraging groups, and associations between individuals based on their proximity.

Thesis structure

In this thesis I aimed to shed light on how the social and abiotic environment affects group behaviour. With this purpose my thesis is directed towards 4 main topics.

1. The effects of spatial constrains on nest aggregation (chapter 3).

I studied how an environmental constrain, i.e., space, can lead to the appearance of a complex nest structure. Importantly, in some species compound nests are associated with cooperative behaviours within the social group. By studying plasticity in compound nest construction, I report a possible pathway for the evolution of this type of social organization.

2. The effects of social environment on aggression (chapter 6).

I studied the aggression strategies of common waxbill as well as the effect that audience type, depending on the social status and or social proximity, has on aggression. I was particularly interested in understanding how animals can use aggression to communicate because, as Zuberbühler (2008) noted, changing the behaviour upon an audience might reflect a strategy to convey information to audience members.

3. The effects of food availability and predictability on social behaviour (chapter 7).

Reduced food availability and predictability might either favour cooperation and social cohesion, to overcome those ecological challenges, or promote within-group conflict, due to competition for limited resources. I aimed to shed light on how cooperation or

competition is emphasized in challenging environments by experimentally manipulating food availability and predictability.

4. The effects of weather on social behaviour (chapter 8).

Multiple abiotic factors may affect different aspects of social behaviour and social structure. To gain a better understanding of how social groups behave upon environmental fluctuations, which is of increasingly importance, I attempted to gain a holistic understanding of how natural variation in weather influences various aspects of social behaviour.

The social behaviour is intimately related with seasonal changes, with the breeding season being often accompanied by changes in aggression and social structure (e.g., Mathur 2009; Johnson et al. 2017). Since the breeding phenology of the common waxbill in the Iberian Peninsula was not fully understood, I studied its breeding phenology using data from across continental Portugal and the mesocosm. Chapter 2 of this thesis thus describes the breeding phenology of the waxbill in the wild and in the mesocosm.

For three of the main thesis topics (chapters 6, 7 and 8) I was interested in understanding the different social and abiotic effects on aggression. There are different metrics to compute dominance hierarchies, and choosing which one would is most adequate depends on the dominance interactions and structure of the study group, which was insufficiently known in the beginning of my work (Funghi et al. 2015). Moreover, the RFID datastream contains information on aggressive interactions (displacements at the feeders) that, by developing and validating an algorithm to detect those events, can be used to study dominance hierarchies. Thus, in chapters 3 and 4 I studied social dominance and developed methods to assess dominance hierarchies in the common waxbill.

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Chapter 2 | European breeding phenology of the invasive common waxbill, a sub-Saharan opportunistic breeder

European breeding phenology of the invasive common waxbill, a sub-Saharan opportunistic breeder

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Abstract

Biological invasions may involve species colonising different climatic regions than those in their native ranges, and it is not straightforward to predict how breeding phenology changes in the invasive ranges. The common waxbill *Estrilda astrild* is one of the most widespread invasive birds worldwide. It is an opportunistic breeder, adapted to transient breeding opportunities in its native sub-Saharan African range, which is often climatically unpredictable. The least equatorial range of invasive waxbills is now in Europe, in the Iberian Peninsula, where they experience predictably seasonal climate. Previous reports of waxbill breeding phenology in two different regions in Iberia show a very long breeding season, but differ in whether or not peak breeding coincides with the Spring breeding of native passerines. Using field data from over 20 sites across climatically different regions in their Iberian range, we show that waxbills have a long breeding season extending until Autumn, but with a clear Spring peak around May, both in regions with hotter and milder summers. Nest monitoring in a large mesocosm with over 50 waxbills, across three years, confirmed these field observations and showed what appears to be year-to-year plasticity in phenology, which may include smaller nesting peaks outside Spring. This behavioural flexibility, together with the long breeding season of waxbills in the Iberian temperate climate, likely facilitates their invasion success.

Keywords: breeding season, climate, *Estrilda astrild*, exotic species, nests, reproduction

1. Introduction

Biological invasions, which can result from translocation of exotic species, have become increasingly frequent (Blackburn et al. 2009). Some of these species originate from biogeographic regions that are climatically and ecologically very different from where they eventually establish. In such cases, it is not straightforward to predict reproductive behaviour and phenology in the colonized areas. Nonetheless, this knowledge is important to understand the effects that invasive species may have on their novel ecosystems, and it may provide insight into the influences of plasticity vs. genetic determination for breeding phenology. For example, some invasive species may breed earlier than in their native ranges (Luna et al. 2017) or change the duration of their breeding seasons (Evans et al. 2005).

Opportunistically breeding species, i.e., species that do not breed always in the same seasons, but when the climatic conditions are favourable (Hau 2008), are interesting in this respect. They typically evolve in regions where climatic and ecological changes have a high degree of unpredictability throughout the year, such that being able to use transient breeding opportunities should be adaptive. This is the case of a very successful avian invader native from sub-Saharan Africa, the common waxbill (*Estrilda astrild,* family Estrildidae). The common waxbill, hereafter simply waxbill, is a gregarious and granivorous finch that, as typical of opportunistic breeders, has vagrant movements and in much of its native range breeds at any time of the year or in multiple seasons throughout the year (Payne 2010; Sanz-Aguilar et al. 2015). Since waxbills are easy to maintain in cages and are very colourful, with vivid red plumage and bill, they have been kept as pet birds as traded globally for several centuries (Cardoso and Reino 2018). Due to accidental escapes from captivity, in different regions, they have become established in several regions of the world, including many islands in the Atlantic, Indic and Pacific oceans, extensive areas in Brazil and Iberia (Stiels et al. 2011).

The Iberian Peninsula is now the least equatorial part of the waxbill range (Stiels et al. 2011), and where they experience very predictable and seasonal climate. Waxbills became established on the Iberian Peninsula recently, with the largest invasion having started in the 1960s, gradually occupying most of Portugal and still expanding to adjacent areas in Spain (reviewed in Cardoso and Reino 2018). Breeding phenology in this northernmost part of the waxbill range is not yet well understood. Captures of breeding females near Doñana, in southern Spain, indicate that the waxbill breeding season has a peak in April and May, similarly to that of most native passerines, but unlike native passerines they can extend breeding until November (Sanz-Aguilar et al. 2015). Captures of breeding females and juveniles in three wetlands further north, in central Portugal, suggested a similarly long breeding season, from March to December, but with the peak of breeding occurring in Autumn (Tenreiro and Petronilho 2002), and it was speculated that juveniles hatched early in the breeding season could breed later in the same year (Ferreira 1980). If this Autumnal peak of breeding is true, it could indicate extreme opportunistic breeding, with the late peak being the cumulative result of a long breeding season gradually increasing recruitment of new breeders until conditions deteriorate before winter.

These past studies were geographically restricted and used climatically different regions (Peel et al. 2007; AEMet and IM 2011). Namely, summers are hot and dry in south Spain, near Doñana (latitude 36º 56’ N), while the wetlands in central Portugal (latitudes from 40º 8’ to 40º 24’ N) are under the climatic influence of the Atlantic and have mild summers (Peel et al. 2007). The different results reported so far could thus be due to climatic differences between sites. Also, it cannot be discarded that some results are influenced by seasonal or vagrant movements of waxbills flocks (Payne 2010), which might influence the proportion of juveniles observed at certain times and habitat types. Geographically broader studies are needed to clarify the breeding phenology of waxbills in this northernmost and most seasonal part of their current range.

Here we quantify seasonal changes in the proportion of breeding females and juveniles captured with mist-netting across a large area of the waxbill biological invasion in Iberia, comprising both areas with hot and mild summers. Additionally, we closely monitored nesting phenology for 3 years of wild-caught waxbills in a large mesocosm environment near Porto, in the north of Portugal. Our detailed nest monitoring in three consecutive different years allows assessing year-to-year changes in breeding phenology. With this work, we aim to assess the length and the peak of the waxbill breeding season, evaluate whether they differ between these temperate climates with either hot or mild summers, and whether there are substantial year-to-year differences in phenology.

2. Methods

2.1. Field data

We conducted fieldwork from June to September 2010 and from March to July 2011, in 23 sites scattered throughout the invasive range of waxbills in Portugal. Sites were visited in semi-random order to avoid a correlation between date and ecological differences (Figure 2.1; see Batalha et al. 2013 and Carvalho et al. 2013 for geographic coordinates and dates of visit to each site). At each field site, we first chose a location where waxbills were observed gathering, and in the following days (usually 3 days) we set up mist-nets, capturing on average 28 waxbills per site (±14, standard deviation). Birds were aged as young juveniles or older based on bill colour (young juveniles have black bills that change to red as they mature) and on bill commissures (white swellings and fleshier in young juveniles; Payne 2010). We took a small blood sample for molecular sexing (see Carvalho et al. 2013 for sexing methods), and checked adults for the presence of a brood patch.

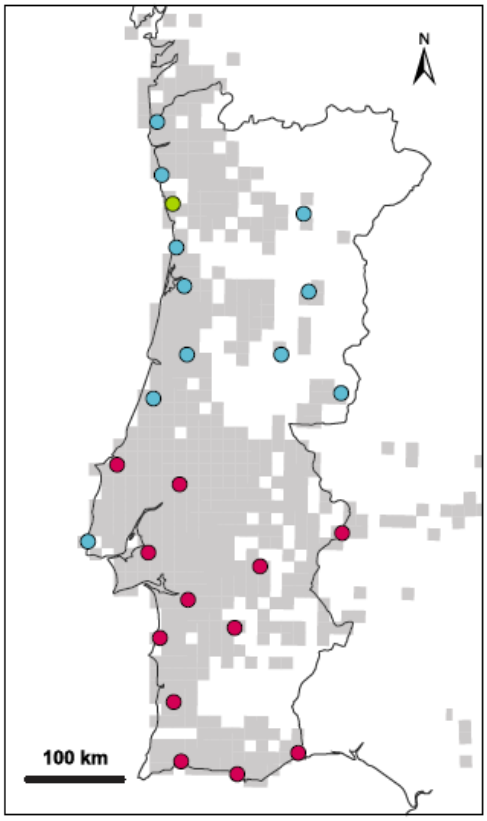

Figure 2.1. Map adapted from Batalha et al., (2013), indicating the distribution of common waxbills in Portugal (in grey), the location of the 23 field sites, and the location of the mesocosm. Half of the sites are marked in blue, corresponding to the those with milder summers, and the half marked in red correspond to those with hotter and drier summers. The location of the mesocosm in marked in green.

All birds were released after ringing with a numbered metal ring so that, in case the same individuals were re-captured, the re-captures were not counted. Here, we report the proportion of adult females that had a brood patch, and the proportion of birds captured that were young juveniles, split by calendar month. The number of captured birds for which we could confidently assign an age class was 611, and the total number of adult females captured (with or without brood patch) was 222. The field data are available in Appendix A.

2.2. Mesocosm data

In 2018, 2019 and 2020, we monitored the nesting phenology of waxbills in a large mesocosm environment near Porto, Portugal (green mark in the map of Figure 2.1). Briefly, these waxbills are housed in a large outdoor aviary covered in fine net (ca. 235 m^2, and 1.30–2.70 m high), with abundant natural vegetation and several perches and feeders, where waxbills live in semi-natural conditions. The mesocosm is connected to a dormitory (4 m^2, 2.25 m high), through a small window, with abundant tree branches for perching. These waxbills form fission-fusion groups and pairs, which build nests and breed. As reported for their native range, waxbill nests consisted of a ball-shaped chamber with a small tunnel-like opening, and in the top of the nest there could be an additional cup-like structure (“cock's nest”; Payne 2010; see Figure 2.2).

Figure 2.2. Examples of waxbill nests built in the mesocosm.

In 2018 the birds were provided with coconut fibers to build nests, but in 2019 and 2020 the only materials available were grasses and other vegetation growing naturally

in the mesocosm. Birds living in this mesocosm were captured from the wild, in nearby agricultural fields: 30 individuals (14 males and 16 females) were captured in October 2016 ca. 12 km away (near Póvoa de Varzim), and released in the mesocosm in December 2016, another 30 birds (again 14 males and 16 females) were captured in September 2017 ca. 20 km away (near Esposende) and added to the mesocosm in November 2017. Detailed methods for the capture of these individuals, phenotypic or molecular sexing, and a description of the mesocosm can be found in Gomes et al. (2020) and Guerra et al. (2020). After this initial set of 60 birds, the population fluctuated slightly through time, because of juveniles born in the mesocosm (of which 1 male from the breeding season of 2019, and 3 males and 4 females in the breeding season of 2020 survive until now), 7 additional wild-caught waxbills (3 males and 4 females) released in the mesocosm in January 2020, and 12 individuals having died or disappeared from the mesocosm in the intervening years. Therefore, at the dates of the first nest found, each year, the mesocosm contained 54 individuals (27 males and 27 females) in 2018, 50 individuals (23 males and 27 females) in 2019, and 52 individuals (25 males and 27 females) in 2020.

Each year, we started monitoring nests regularly as soon as signs of nesting behaviour were observed during the weekly maintenance of the mesocosm (see results). Monitoring was then done every 9-10 days (ranging from 7 to 12 days in exceptional cases, due to bad weather or calendar constraints) in 2018, and every 13-15 days (ranging from 7 to 15 days, as before due to some exceptional cases) in 2019 and 2020. In September of 2019, one monitoring point was skipped due to logistic constraints. Nest monitoring lasted until mid or late October, when nesting activity was already residual, and after which signs of nesting activity remained scarce or were absent.

Nest monitoring consisted of thoroughly examining the vegetation and the ground in the mesocosm and the communicating dormitory room. Each time, we noted the location of nests and categorized their status as: (1) new nests, for those that were not

present in the previous monitoring (nests in active construction, with fresh material, were also categorized as new nests); (2) nests in good conditions (e.g., Figure 2.2), for those whose nest structure remains intact and were thus potentially active (signs of a nest in good condition included an intact entrance, recent bird droppings by the entrance, new and/or fresh building material in the nest); or, otherwise, (3) destroyed nest (e.g., damaged nest structure, no nest entrance, fallen or collapsed nests). After a nest was observed as destroyed for two consecutive monitoring events, and if at a later date it was repaired and reactivated, then it was considered as a new nest. Here we report the total number of new nests at each time, and the total number of nests in good conditions (including new nests; data available in Appendix A).

2.3. Statistical analyses

We used Generalized Linear Mixed Models (GLMM) to test (1) if the peak of breeding observed with field data was statistically different from the amount of breeding in the remaining breeding season, and (2) if breeding phenology differed between climate types. Before running statistical models, we scored climate in our 23 field sites using a Principal Component Analysis (PCA) on climatic data from Carvalho et al. (2013; mean yearly temperature, yearly precipitation, variation in temperature, and variation in precipitation, the latter two computed as the standard deviation of monthly values), and then used this PCA to divide the sites in two climatic categories. The first principal component (PC1) of this PCA explained 0.63 of variance, and had strong positive loadings of yearly temperature (0.58) and variation in precipitation (0.55), and a strong positive loading of yearly precipitation (-0.60; variation in temperature loaded weakly on PC1, -0.03). High PC1 scores thus indicate hot and dry sites with strong seasonality in precipitation, and the reverse for low PC1 scores. We split our field sites into two groups, based on whether or not they were below the median PC1 score (Figure 2.1). This division resulted in a similar geographic pattern to that described by the Köppen-Geiger

climate classification (Peel et al. 2007; AEMet and IM, 2011), where northern sites are characterized by temperate climate with mild summers, due to a stronger influence from the Atlantic, while more southern sites are characterized by temperate climate with hot and dry summers.

We then used two GLMM with a binomial error distribution, coding the response variable as zeros and ones: either 0-adult female without brood patch vs. 1-adult female with brood patch, or 0-adult vs. 1-juvenile. Predictors in these models were date (i.e., day number since January 1st of that year), and squared date, both standardized, and also the two-level climate type variable. The interactions between climate and date, and between climate and squared date were also included in the models, and site was included as random factor. These models include a quadratic equation for date, and are therefore able to fit linear or curve-shaped changes through time, but not changes with more complex shapes. Therefore, we restricted these analyses to data from the month of apparent peak breeding plus two months on either of its sides (i.e., from March to July for the female brood patches, and from April to August for young juveniles; Figure 2.3a). Statistical support for a breeding peak would be a significant effect of squared date with negative signal, indicating a concave function. Statistical support for a difference in breeding phenology between climate types would be a significant interaction of climate type with either date or its square.

To test for differences in the breeding phenology between the years 2019 and 2020 in the mesocosm, we conducted a Fisher's Exact test comparing the counts of new nests in the same months between 2019 and 2020. The year of 2018 was not used in this comparison because by then most nests were built with hard coconut fibers, and can therefore last much longer than the other nests (see results).

3. Results

Data from field captures indicated a peak of breeding in May, when the percentage of females with a brood patch peaked at over 80%, and also because one month later, in June, the percentage of young juveniles peaked at ca. 45% of all captures (Figure 2.3a). Results from the two GLMMs, analysing either female brood patches or captures of young juveniles, corroborated these observations, since in both cases there was a significant effect of squared date with negative signal (Table 1), indicating a concave function. Figure 2.3a also indicates that the breeding season had started as early as March, since ca. 20% of captured females already had a brood patch by then, but the first juveniles only started being captured ca. two months later, in May. The breeding season extended until the end of fieldwork, in September, albeit with low percentages of females with brood patch (ca. 20% since July) and of young juveniles (ca. 10% since August).

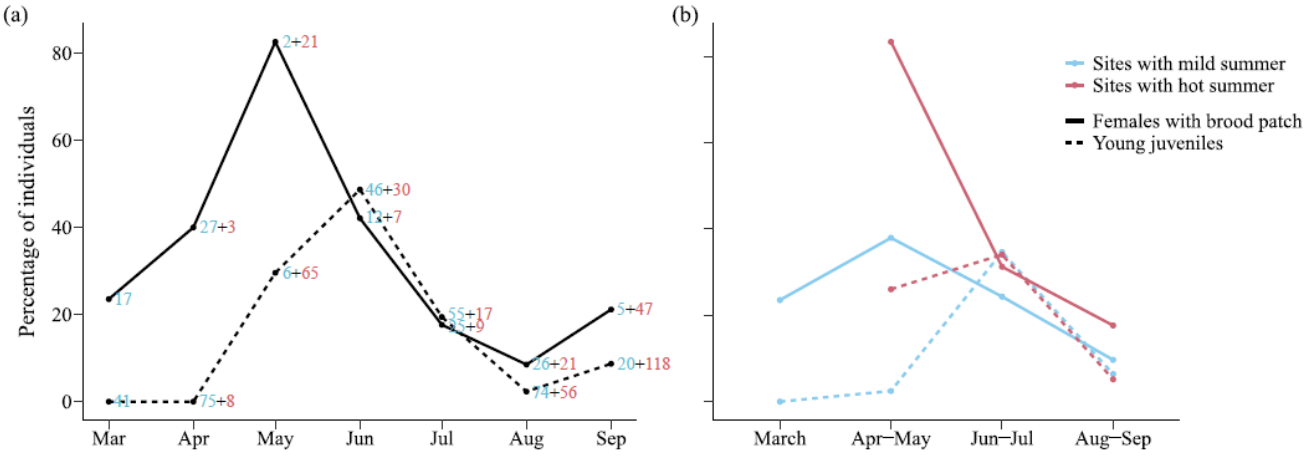

Figure 2.3. (a) Percentage of females with brood patch, relative to the number of adult females captured each calendar month, and percentage of young juveniles captured, relative to the number of individuals captured per calendar month. The sample size for each month is also shown. (b) The same data split by sites with milder or hotter summers, as shown in Figure 1; since sample sizes are smaller when split by climatic type, here we combined data per each two-month calendar period.

Splitting field data between sites with hotter vs. milder summers, the seasonal patterns of change in the proportion of females with brood patch and of captured juveniles appear identical for the two groups of sites (Figure 2.3b). This observation is

also corroborated by results of GLMMs, since none of the interactions between date and climate type were significant (Table 1). In both groups of sites, with hotter or with milder summers, the proportion of females with brood patch peaked around April-May and decreased afterwards, and the proportion of young juveniles captured peaked soon after, in June-July, and then decreased (Figure 2.3b).

Table 2.1. GlMM results for the presence of females with brood patches from March to July (123 adult females) and young juveniles from April to August (432 aged waxbills). We present the estimate (β), standard deviation (SE) and p-value (*p*) for each predictor.

	Female brood patch	Young juveniles
	β (SE; *p*)	β (SE; *p*)
Date	6.97 (2.76; 0.01) *	15.71 (6.44; 0.01)*
Date squared	-7.20 (2.81; 0.01)*	-15.53 (6.40; 0.02)*
Climate	-0.09 (1.45; 0.95)	0.80 (0.97; 0.41)
Climate * date	10.02 (13.84; 0.47)	-11.55 (9.27; 0.21)
Climate * date squared	-9.77 (12.67; 0.44)	10.79 (8.82; 0.22)

*p < 0.05

Data from nest monitoring in a large waxbill mesocosm showed a peak in the number of new nests around May-June in the three consecutive years (Figure 2.4a). Plotting the number of nests in good condition through time, instead of the number of new nests, corroborated this pattern for 2019 and 2020 (Figure 2.4b), but in 2018, when most nests were built with coconut fibers, nests remained in good condition for much longer and, therefore, the post-peak decay in number of good condition nests was not apparent (dashed line in Figure 2.4b). Figure 2.4 also shows that nest building started in different months, from late February/March in 2019 to early April in 2018. Also, the main peak of new nests varied between early May in 2020 to early June in 2018, and smaller peaks of nesting can be observed in all three years (Figure 2.4a).

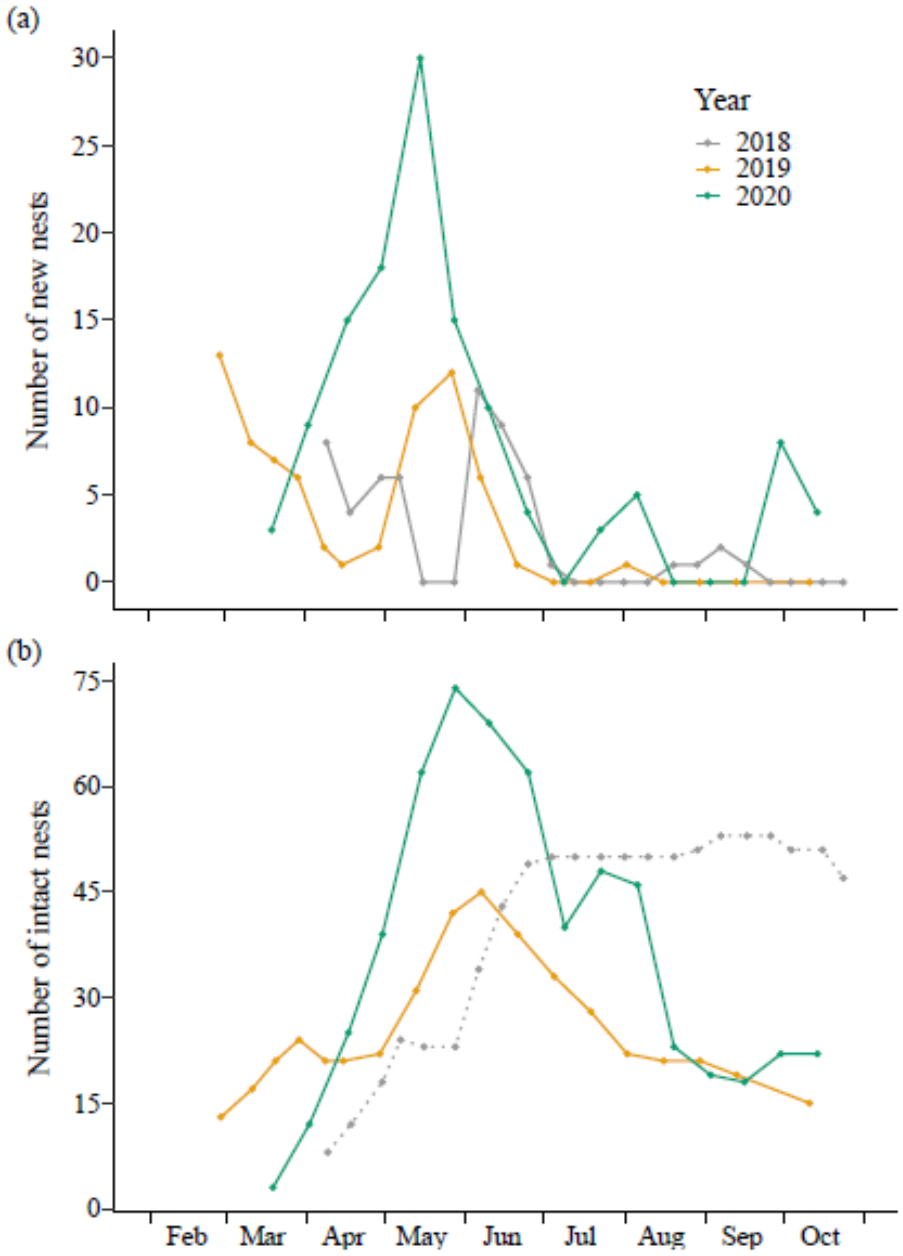

Figure 2.4. Number of (a) new nests and (b) intact nests in each of three breeding seasons. Nests in 2018 lasted much longer, even if not in use anymore, because they were mostly built of hard coconut fibers, so that the number of intact nests in 2018 stayed in a plateau rather than decreasing (dashed grey line in panel b).

Comparison of the number of new nests per calendar month, between 2019 and 2020, showed significant differences (Fisher's Exact test: $p < 0.001$), indicating that nesting phenology can vary between years.

4. Discussion

The breeding phenology of waxbills in Portugal extended from March to the end of the fieldwork, in late September, reaching a peak in May (Figure 2.3a). Figure 2.3a shows an interval of ca. one month between the peak of females with brood patch and the peak of young juveniles, which is expected because of the time taken for incubation and then for raising the young in the nest until they fledge. The incubation period of common waxbills is ca. 12 days, and the nestling period is ca. 17-19 days (Payne 2010), which sum to the 1-month delay between the peaks of females with brood patch and of young juveniles in our field data.

Our description of the breeding phenology of common waxbills across Portugal is in agreement with that by Sanz-Aguilar et al. (2015) for southern Spain, near Doñana, where waxbills breed between April and November with a peak in May. The very long breeding season of waxbills described by Sanz-Aguilar et al. (2015) and by us indicates that waxbills found a very amenable breeding environment in Iberia. Although showing a peak of breeding around May, similarly to most native passerines in Iberia, their extended breeding season can be interpreted as an axis of niche differentiation relative to the native European passerines (Sanz-Aguilar et al. 2015). This adds to other aspects of niche differentiation, such as using human-altered habitats and having dissimilar diets to those of native granivorous birds (Batalha et al. 2013; Cardoso et al. 2018). Sanz-Aguilar et al. (2015) found that, while the breeding season of native birds has evolved to overlap with the peak of availability of native food sources, in the case of the common waxbill, and of other co-occurring exotic birds, longer breeding seasons coincide with the extended period of availablilty of native and non-native food sources. For example, compared to dietary habits of the native granivorous bird species most similar in size and habitat to the common waxbill, the European serin (*Serinus serinus*), waxbills comsume more seeds from non-native, non-crop plants that are associated with agricultural

landscapes (Cardoso et al. 2018), suggesting that waxbills can have an adaptative advantage due to the exploitation of more diverse food sources.

Splitting field data between sites with hotter vs. milder summers, breeding phenology was similar in the two climate types and, importantly, towards late summer, the amount of breeding was already low in both climates (Figure 2.3b). Therefore, the apparent peak of breeding in Autumn described by Tenreiro and Petronilho (2002) is not explained by the mild summer climatic conditions of their study sites, wetlands in central Portugal, and is not supported by our results. Since Tenreiro and Petronilho (2002) used counts of females with brood patch and juveniles, rather than proportions of total captured birds, and there were more captures during Autumn months, it cannot be excluded that the apparent Autumn peak of breeding arose from vagrant movements made towards those wetlands.

The nest construction pattern in the mesocosm was congruent with the above field-based data, extending from February to October with a main peak in May-June, and we also observed smaller peaks of nesting in all three years (Figure 2.4). Comparison of new nests per calendar month between years showed a significant difference, indicating a degree of year-to-year plasticity in the time of nesting. Since the large majority of birds in aviary were the same across years, these observations suggest that individuals can make adjustments in the breeding season, perhaps due to environmental fluctuations throughout the breeding season and from one year to another (Barea and Watson 2007; Perfito et al. 2007). Year-to-year fluctuations in the optimal time for breeding, as well as plastically adjusting phenology to those fluctuations, are common in birds (de Villemereuil et al. 2020). This type of behavioural flexibility is expected from opportunistic breeding species like the waxbill, which are adapted to use transient breeding opportunities in their natural, native habitat (Payne 2010; Sanz-Aguilar et al. 2015).

In conclusion waxbills seem to show behavioural flexibility in their time of nesting, which allows them to take advantage of a large temporal window with suitable climatic conditions for reproduction. Although the breeding season of waxbills in Iberia is very long, we found a peak of breeding around May and June, consistent throughout its invasion range in Portugal and across years, and that reproduction in late Summer and Autumn is much less frequent. This peak of breeding, synchronous with that of most native passerines, likely reflects the ideal breeding conditions during Spring in temperate-climate regions, to which native European passerines are adapted in a less flexible manner than waxbills. The apparently more flexible and long breeding phenology of waxbills likely facilitated their invasion in Iberia (Cardoso and Reino 2018) and elsewhere (Stiels et al. 2011).

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Chapter 3 | Domed nests as an exaptation for compound nest construction: the case of the common waxbill

Domed nests as an exaptation for compound nest construction: the case of the common waxbill

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Abstract

Nests are essential for breeding in many birds, and differ widely in morphology across species. Only a few bird species build compound nests, with different nest chambers as part of a continuous structure. Knowing the ecological and social conditions leading to compound nest construction in species where this behaviour is not the norm can improve our understanding of their functions and evolution. We studied how limited space availability affected nest-building behaviour in a population of wild-caught common waxbills (*Estrilda astrild*), across 4 years, in a mesocosm with abundant vegetation (e.g., grass, brambles, bushes). In addition to their typical isolated domed nests, built mostly on or near ground level, we found that 141 out of a total of 423 nest chambers were in compound structures, each comprising 2 to 11 nest chambers, and that most compound nests were above the ground on bushes. Compound nests were never reported for common waxbills in nature, and we thus conclude that compound nest construction is a plastic response caused by the high density of this population relative to available nesting sites in the mesocosm. Since the morphology of domed nests resembles that of nest chambers in compound structures, domed nests may be an exaptation for high-density nesting and may facilitate the evolution of more specialized compound nest construction.

Keywords: behavioural plasticity, enclosed nests, *Estrilda astrild*, nest building, spatial distribution

1. Introduction

Nest building is essential for breeding in most bird species (Mainwaring et al. 2014). There is a wide diversity in nest morphology across species, from open to domed nests (i.e., enclosed nest chamber), the latter being common in tropical species (Collias 1964). Some birds can also build compound nests with two or more entrances, each connected to a different chamber that can be occupied by different breeding pairs (Collias and Collias 1984). Compound nests have several reported advantages over isolated nests, such as protection from challenging climatic conditions (Lowney et al. 2020), and reduced time invested in construction because of using some previously built walls of adjoining nest chambers (Gauther and Thomas 1993). Nonetheless, few bird species build compound nests. Examples include the monk parakeet (*Myiopsitta monachus*; Forshaw 2010), the Palmchat (*Dulus dominicus*; Dhondt et al. 2019) and, perhaps the most impressive, the sociable weaver (*Philetairus socius*; Maclean 1973). Sociable weavers can build very large structures with over 100 nest chambers, and they also build a common roof cooperatively, thought to confer thermal advantages (Collias and Collias 1977). Despite the interest of compound nest construction, there is yet little understanding on what may have been the initial steps in the evolutionary origin of this behaviour.

While any given bird species is characterized by a certain type of nest and of mating system, exceptional occurrences are sometimes reported. Examples of exceptional nest placement include ground nesting in the usually arboreal American robin (*Turdus migratorius*; Winnicki et al. 2022), or off-ground nesting in the usually ground nesting dark-eyed junco (*Junco hyemalis*; Yeh et al. 2007) and Canada goose (*Branta canadensis*; Shearer et al. 2022). Examples of exceptional mating system include cases of polygyny in the usually socially monogamous blue tit (*Cyanistes caeruleus*; Schlicht and Kempenaers 2021) and eastern bluebird (*Sialia sialis*; Khan 2021), and cases of cooperative breeding in species that do not normally do so (e.g., European starling, *Sturnus vulgaris*, Nichols and Arbuckle 2022; white-crowned robin-chat, *Cossypha albicapillus*, Gil et al. 2021; collared flycatcher, *Ficedula albicollis*, Laczi et al. 2021). Such exceptional occurrences might be due to behavioural plasticity, if animals change their nesting or reproductive strategy depending on ecological conditions (Snell-Rood 2013). Behavioural plasticity may be important for survival (Ducatez et al. 2020) or establishment in new areas (Ord et al. 2016). Understanding in which circumstances compound nests are built by species that normally build isolated

nests, and which species show this type of plasticity, could shed light on the function and evolution of this complex behaviour.

We studied wild-caught common waxbills (*Estrilda astrild*) living in a large outdoor mesocosm, to evaluate how limited space availability affects nest-building behaviour. Apart from a high population density for its space, this mesocosm had quite natural conditions, with abundant and diverse vegetation that allowed nesting at different strata. The common waxbill is a small, granivorous and highly gregarious passerine that moves and forages in flocks year-round (Clement et al. 1993; Payne 2010). Waxbills are described as building domed nests on or near the ground, consisting of a ball-shaped chamber with a small tunnel entrance, and nests are separated from each other (Schuetz 2005; Payne 2010; see photos of waxbill nests in Beltrão et al. 2021). Their nests may also have a small platform at the top of the chamber, named “cock’s nest” (Payne 2010), which was suggested to act as a decoy for predators (i.e., nest mimicry; Hinze 2000; Galligan and Kleindorfer 2008). Waxbills were not reported to build compound nests in nature. To gain insight on plasticity of nest building behaviour, here we describe the spatial distribution of waxbill’s nests, the frequency of compound nests during four breeding seasons in the mesocosm, and assess whether different nest chambers in compound structures are used by the same or different mating pairs. Our aim is to assess whether behavioural plasticity in high-density nesting conditions could lead to building compound nests and, thus, suggest a potential pathway for the evolution of more specialized compound nest construction.

2. Methods

2.1. Study system

We monitored nest building of common waxbills living in a mesocosm (i.e., a large outdoor enclosure with natural vegetation and exposed to the weather), during four years (2018 to 2021). The mesocosm is located in a quiet rural area near Porto, Portugal. Although the common waxbill is native from sub-Saharan Africa, it became invasive in several parts of the world, and this region is within its invasion range in the Iberian Peninsula (Cardoso and Reino 2018). The mesocosm (Figure 3.1a, b) has an area of ca. 235 m2, is covered by fine net 1.30 to 2.70 m high, and is thus exposed to the natural weather. Temperatures were similar across the four years of this study (mean annual temperatures from 2018 to 2021 were 14.6ºC, 14.3ºC, 14.9ºC, and 14.3ºC; source: Numerical Weather Prediction model, MeteoGalicia).

Figure 3.1. (a) Aereal photograph of the mesocosm, and (b) inside-view showing natural vegetation. (c) A compound nest with 2 chambers, and (d) another with 9 chambers (not all entrances are visible from this angle).

There is abundant natural vegetation, comprising an herbaceous layer, made up mainly by grasses, plus small shrubs (e.g., brambles, *Rubus* spp., rock rose, *Cistus* spp.) and taller shrubs or small trees (e.g., brooms, *Cytisus* spp., oaks, *Quercus robur*). The diversity of natural vegetation provides options for nesting at various strata and in different vegetation densities. The mesocosm is connected via a small window to an indoor room (4 m2, 2.25 m high), where tree branches with foliage had been placed for the birds to roost and also nest. Birds had water and food *ad libitum* (Tropical Finches Prestige seed mixture, Versele-Laga), the later placed in the southwest area of the mesocosm, where the vegetation was kept cut short.

Most waxbills living in this mesocosm were captured from the wild in October 2016 (14 males and 16 females), September 2017 (14 males and 16 females), October 2019 (3 males and 4 females), and October 2020 (5 males and 4 females). These birds were captured using mist-nests in agricultural fields within a 20 km radius of the mesocosm (for details see Guerra et al. 2020). During the four years of this study, the mesocosm population fluctuated due to a combination of natural mortality and births. Hence, in the beginning of the breeding seasons of 2018 (i.e., when the first nest was

identified) the mesocosms population had 54 individuals (27 males and 27 females), 50 (23 males and 27 females) in 2019, 52 (25 males and 27 females) in 2020, and 64 (33 males and 31 females) in 2021. Each bird had a small passive integrated transponder (PIT) tag on a leg ring, to allow their identification using radio-frequency identification (RFID) antennae (Dorset ID, The Netherlands).

2.2. Nest data and analyses

Once a week, starting in January, we entered the mesocosm to check for signs of nests. Once the first sign of a nest was detected, we started systematic nest monitoring every 9-10 days in 2018 (exceptionally 7-12 days, due to bad weather or other constraints), or 12-15 days in 2019, 2020 and 2021; due to logistic constraints, one monitoring point was skipped in September 2019. Nest monitoring consisted in carefully inspecting all vegetation across the mesocosm, and also in the dormitory room, searching for new nests and also noting when nests were destroyed. We noted each new nest when it had a complete chamber (i.e., completed dome with an entrance). Some nests appeared to have a "cock's nest" on top of the chamber, which was not counted as a separate nest. We considered a nest destroyed when the dome had collapsed or its walls had large holes and remained so for at least 2 monitoring rounds; any nest that appears in the same location after 2 monitoring rounds was considered as a new nest, rather than as the same old nest repaired. We noted when a compound structure was formed (i.e., two or more nest chambers sharing part of the wall, but each with its own entrance; Figure 3.1c, d). We stopped monitoring the nests when nest building behaviour became residual, usually in mid to late October (Beltrão et al. 2021), by which time new nest chambers were less than 3% of the total number. At the end of each year, during the non-breeding season, the few nests still not destroyed by winter weather were removed, in order to help us detect when novel nest construction began the following breeding season. In 2021 we also noted which nests progressed to egg-laying stage, by carefully inspecting the interior of the chamber for eggs with a thin camera probe. Finally, we measured the height at which each nest was built (from ground level to ca. 2.50 m high, which is the height of the highest shrubs or trees in the mesocosm), and noted the coordinates of each nest (i.e., distance to the east and south walls of the mesocosm).

We used a contingency table with a $\chi 2$ test to evaluate whether the number of compound structures changed over the 4 studied years, relative to the number of isolated nests, using R (R Core Team 2021). Each row represented a year of study (4 rows) and

the columns represented the different nest type (2 columns: isolated nests or compound nest structures). The null hypothesis is that the relative number of isolated nests and compound nest structures do not differ across the years. We used a Kruskal-Wallis test to compare the number of chambers per compound structure (dependent variable) across the 4 years. To test if compound nests were built earlier or later than isolated nests, we performed an analysis of variance (ANOVA) with date of nest construction (Julian date) as dependent variable and, as factors, nest type (isolated nest, or compound nest structure) and year (non-ordered). For the date of construction in a compound nest we used the date of its second nest chamber. Using data from 2021, when we noted which nests progressed to egg-laying, we also tested if progression to the egg-laying stage in each chamber was independent of nest type. For that, we used a contingency table, applying a $\chi 2$ test, with rows representing nest chambers that did or did not progress to egg-laying and the columns the nest chamber type (isolated nest vs chamber in a compound nest). Finally, we compared the height at which isolated and compound nests were built with a Mann-Whitney test, using data from all years. The height of a compound nest was computed as the mean height of all its individual nest chambers.

2.3. Identification of pairs at nest chambers

It is expected that only one pair of waxbills uses a nest chamber (Payne 2010), but we do not know whether different nest chambers in the same compound nest structure can be used by different pairs. To study this, in 2021 we placed RFID antennae around the entrances of individual nest chambers in compound nests, to identify the pair associated with each chamber. We monitored up to 4 nest chambers simultaneously, using 4 independent RFID antennae (Dorset ID). The number of days an antenna stayed at the same nest entrance varied from 3 to 29 days, depending on the abundance of compound nests. In the 2 cases when an antenna stayed in the same nest entrance for more than 15 days (22 days in one case, and 29 in the other), we divided each period in half and analysed them separately, because nest usage might have changed over such long periods of time. In total, we monitored 29 nest chambers in 7 compound nest structures from March to October 2021.

To identify the pair associated with a nest chamber, we first computed the number of 10-minute intervals in which an individual was read by the RFID antenna (hereafter, number of RFID readings), to avoid counting multiple times a single short visit. For this, we excluded RFID readings around the night period (from one hour before sunset to one

hour after dawn, using the shortest day of the study period as reference), because waxbills may gather in groups around nest areas for roosting. Then, separately for each sex, we computed the ratio of RFID readings between the first and second individuals of the same sex with the most RFID readings at a nest entrance. We considered that a nest was being used by a pair when the male and female with the most RFID readings at that nest entrance had at least 10 times more readings than the second most read bird of the same sex, and both the male and female were read at that nest at least a mean of 4 times per day. In 5 cases these conditions were true only for one of the pair members, but the pair had been previously identified in another nest chamber, and we considered the nest as being used by that pair. With this protocol we account for spurious readings from other birds at the RFID antennae, resulting from the normal daily activity in the high-density conditions of the mesocosm.

3. Results

Waxbill nests were mostly made of grass, which is a material abundant in the mesocosm. In 2018, we found a total of 56 nest chambers in the mesocosm: 52 were isolated nests (i.e., not sharing a wall with another nest), and 4 were aggregated in 2 compound nests, each with 2 chambers (Figure 3.2a). In 2019 there was a total 66 nest chambers: 60 isolated nests, and 6 aggregated in 3 compound nests with 2 chambers each (Figure 3.2b). During 2020 we found 122 nest chambers: 68 isolated nests, and 54 aggregated in 18 compound nests. The number of chambers per compound nest in 2020 ranged from 2 to 4 (Figure 3.2c). Finally, in 2021, we found 179 nest chambers: 102 isolated nests, and 77 were aggregated in 18 compound nests, of which 10 had 2 chambers, and the rest ranged from 3 to 11 chambers (Figure 3.2d).

The number of compound nests in relation to isolated nests differed significantly across the years ($\chi2$= 13.36, df = 3, P = 0.003), being higher in 2020 and 2021 (Figure 3.3). The number of individual chambers per compound nest did not differ between the studied years (Kruskal-Wallis, $\chi2$ = 3.4226, df = 3, P = 0.33). Isolated and compound nests did not differ in their average date of construction (ANOVA, effect of nest type: F1, 318 = 0.16, P = 0.69), although there was a trend for the timing of nest construction to differ between years (effect of year: F3, 318 = 2.45, P = 0.06). In 2021, only 5 isolated nests (1 in the ground and 4 off-ground) progressed to egg-laying stage, while 41 nest chambers in compound nests (all off-ground, above 25 cm) progressed at least until egg-laying stage. Progressing to egg-laying was less likely in isolated nests than in nest chambers in compound nests ($\chi2$ = 51.21, df = 1, P < 0.001).

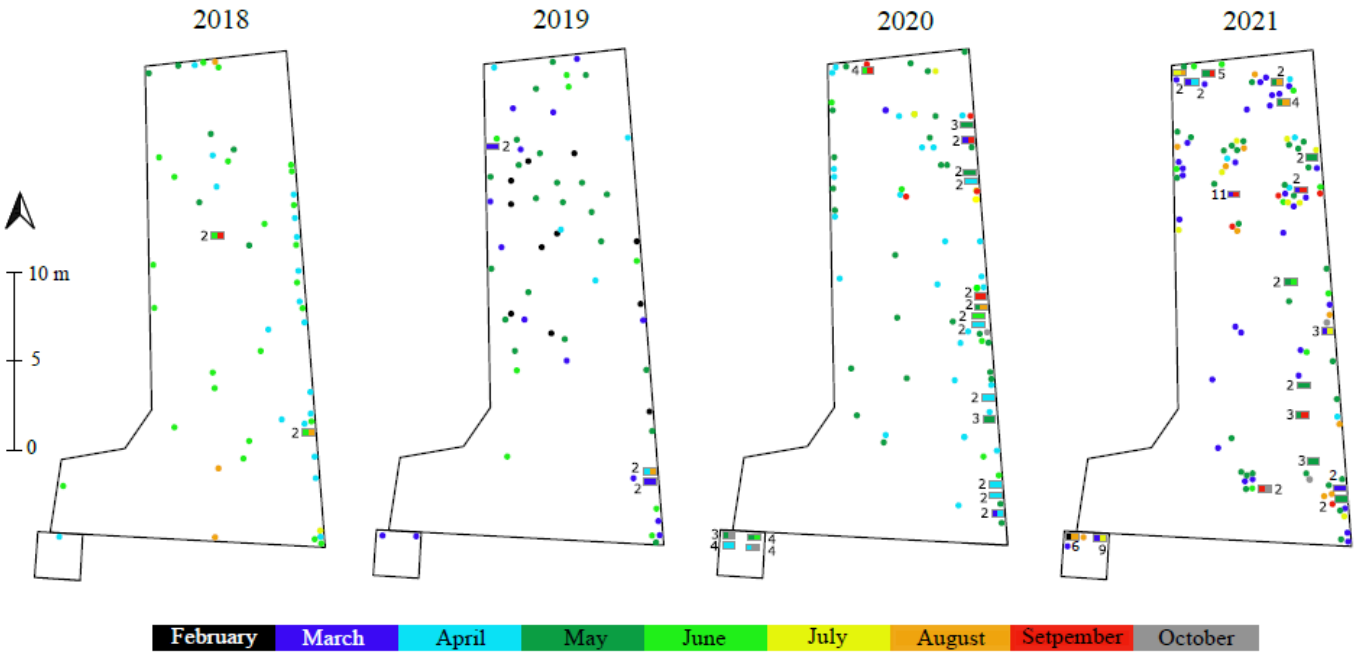

Figure 3.2. Spatial distribution of the nests in the mesocosm across the studied years. Isolated nests are represented by dots and compound nests by rectangles, with the total number of nest chambers written at the side. Colours of isolated nests show the month of nest construction. In the case of compound nests, the 2 colour scheme indicates the months when the first and last nest chamber were built.

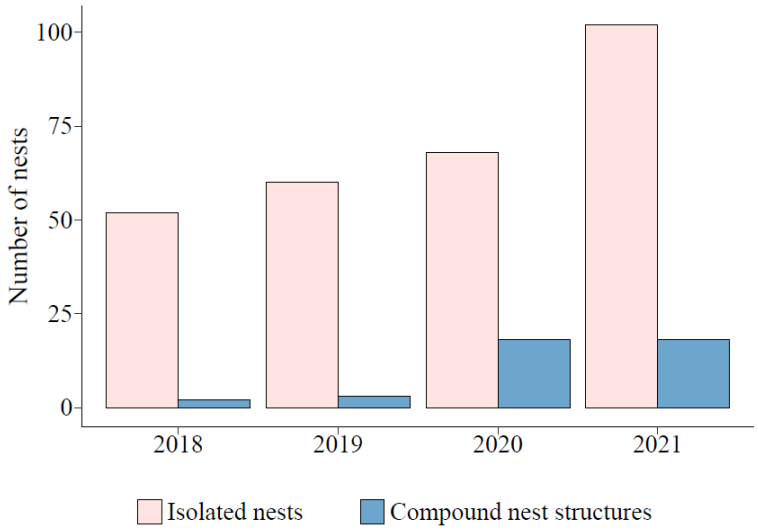

Figure 3.3. Number of isolated nests (pink) and compound nest structures (blue) built across the studied years. See also Figure 4 for the number of individual nest chambers in compound nest.

A large number of nests were built near the east wall, particularly in 2018, 2020 and 2021 (Figure 3.1), but in most years there were also areas with high nest density elsewhere in the mesocosm and in the dormitory room. Most isolated nests were built on

or near the ground, with more than half each year being below 23 cm, whereas the majority of nests in compound structures were above 50 cm from the ground (Figure 3.4). On average, isolated nests were built at lower height than compound nests (Mann-Whitney test, W = 9633, P < 0.001). In 2021, 48 out of the 49 nest chambers (isolated or in compound nest structures) with breeding activity were found above 50 cm from the ground.

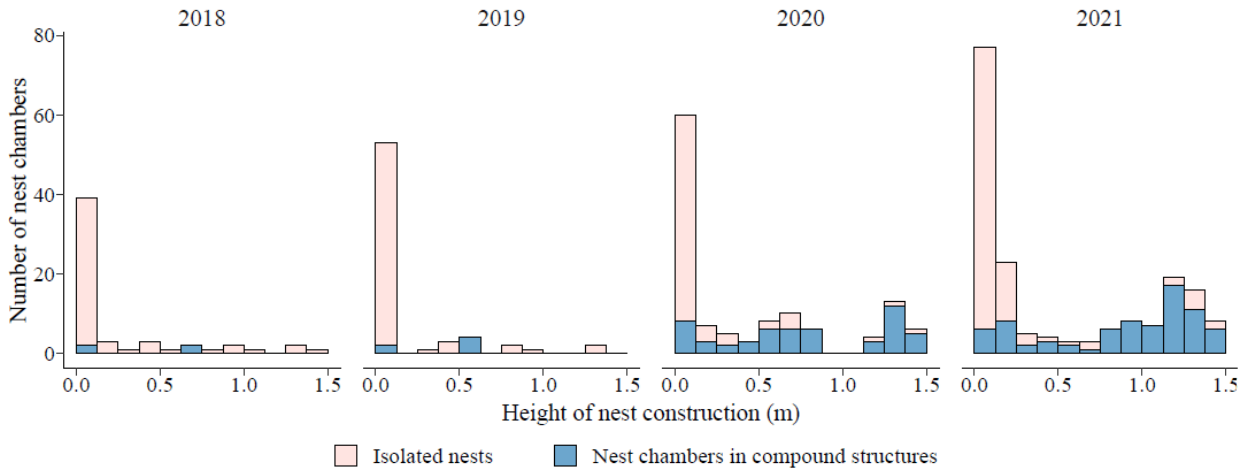

Figure 3.4. Height at which isolated nests (pink) and chambers in compound nests (blue) were built across the studied years.

Appendix B shows which pairs were identified at the different chambers in compound nests. In some cases, different pairs occupied different nest chambers simultaneously in the same compound structure (14 pairs in 5 of the compound structures monitored; e.g., C5/C6/C7 or D1/D3). In other cases, the same pair was recorded in different nest chambers in the same compound structure (2 pairs in 2 of the compound structures monitored; e.g., A5/A6 or C7/C8). The latter could be due to the proximity between the RFID antenna at different nest chamber entrances, and does not necessarily indicate simultaneous use of both nest chambers by the same pair. Finally, we also found evidence for the same pair using different nest chambers at different times in the same compound structure (e.g., A1/B4).

4. Discussion

Waxbills built many nests each breeding season, steadily increasing from 56 nest chambers in the 2018 breeding season, to 179 in 2021, the latter being ca. 3 times higher than the number of waxbills in the mesocosm. The increasing number of nests each year may have been due to increasing familiarity with the mesocosm environment and group

members, to age effects on nest building behaviour, and/or to increasing growth and density of the vegetation. In each year the number of nests was much higher than the maximum possible number of pairs in the mesocosm, and in the great majority of nests there was no egg laying. This suggests that nests are not built solely for reproduction, but may have other functions as well. Although building nests takes energy and time, several species are reported to construct more than one nest during a single breeding attempt (e.g., Australian reed warbler, *Acrocephalus australis*, Berg et al. 2006; grey fantail, *Rhipidura albiscapa*, Beckmann and Martin 2016). This behaviour could, for example, function in anti-predatory defence (Leonard and Picman 1987; Watts 1987), be related with sexual selection based on the number of nests (Garson 1980), or be a backup strategy against deterioration of older nests (e.g., because of rain or bad weather).

The spatial distribution of nests changed across the years, but there were some common patterns. There was an abundance of nests near the east wall of the mesocosm, particularly in 2018, 2020 and 2021, which is the area with most brambles, and also has other small shrubs and dense grass cover. Conversely, there were almost no nests built along the southern wall and in the southwest corner of the mesocosm, where feeders are located and all vegetation is kept cut short. These observations suggest that nest site location is influenced by the suitability of the vegetation to conceal or support the nest, at times resulting in areas of high nest density, at least in the confined conditions of this mesocosm.

The common waxbill is described as a ground-nesting species (Schuetz 2005; Payne 2010) and, accordingly, we found that isolated nests (i.e., those not part of a compound structure) were built mainly on or very near the ground. Many nests, however, were part of compound structures, usually with 2 nest chambers, but up to 11 chambers, and those compound nests were mainly built off the ground in shrubs or small trees. Both isolated and compound nest structures were built throughout the breeding season. All but one of the nests that proceeded to egg-laying stage in 2021 were off-ground, such that the likelihood of progressing to egg-laying stage was higher in compound nests than in isolated nests. This suggests that, at least in the climatic conditions of the mesocosm (Atlantic climate with frequent rainfall), off-ground nesting facilitates successful breeding. Since the number of off-ground sites (i.e., in shrubs or small trees) for nest construction in the mesocosm is limited, this may have favoured the appearance of off-ground compound nests.

Compound nests were rare in 2018 and 2019 (2 and 3 compound nests per year, respectively, with two nest entrances each), but became more common in 2020 and 2021: 18 compound nests per year, with the sum of their individual nest chambers accounting for over 43 % of the total number of nest chambers in the mesocosm. Since compound nests were not reported before for the common waxbill (Clement et al. 1993; Payne 2010), we infer that in nature they occur much less frequently than we observed here, and that the abundance of compound nests in the mesocosm could be due to the high density of the waxbill population relative to available nesting sites. While the quantity of compound nests increased throughout the years of our study, the population density remained high and approximately unchanged. This indicates that an effect of high population density, or of other conditions in the mesocosm, on compound nest construction does not make its full effect immediately, but the effect may increase through time, perhaps enhanced by periods of learning or habituation. We found that different chambers in a compound nest could either be used by the same pair or by different pairs, and that the use of different nest chambers by different pairs could happen simultaneously. Overall, these observations suggest that under high population densities, or scarcity of nesting sites, common waxbills can plasticity change nesting behaviour, from their typical isolated domed nests to compound structures that can be used by more than one pair.

While in the common waxbill compound nests in the wild should be very rare, or otherwise they would have been already described, there is small number of bird species (examples in Collias and Collias 1984) that, in the wild, are known to sometimes aggregate their nests into a compound structure ("contiguous nests" in the terminology of Collias and Collias, 1984, who reserve the term "compound" for species not normally building isolated nests). Like the common waxbill, these species are gregarious and build domed nests. It is not known why only sometimes they aggregate nests, but the hypotheses that have been proposed (Collias and Collias 1977; Anderson 2006) are consistent with our suggestion that in the common waxbill compound nest construction occurs with high population density relative to available nesting sites. For example, studying house sparrows (*Passer domesticus*) in high-latitude and cold climate, McGillivray (1980) proposed that birds aggregate their nests to create a favourable microclimate, which may be necessary because of the scarcity of thermally-suitable sites for nesting. Also, the grey-capped social weaver (*Pseudonigrita arnaudi*) aggregates nests when in trees with ants that offer security from predators (Collias and Collias 1977), and the presence of those ants can thus be viewed as a spatially-limited resource.

Domed nests offer some advantages relatively to open nests, such as more stable temperatures and protection from direct exposure to the sun and rain (e.g., Griffith et al. 2016; Martin et al. 2017; Perals et al. 2017; Perez et al. 2020; but see Medina 2019), and perhaps also protection from predators (Hall et al. 2015, but see Martin et al. 2017; Mouton and Martin 2019). Sheltering from adverse weather is also an advantage of compound nests, which should be more efficient in this regard because, in addition to being domed, they also benefit from the presence of adjacent nest chambers for thermal insulation and protection from the weather (van Dijk et al. 2013; Leighton and Echeverri 2014; Lowney et al. 2020). Finding that the common waxbill, which normally builds isolated domed nests, can in some circumstances shift to building nests aggregated to each other, forming a compound structure, suggests that domed nest construction by gregarious animals may facilitate the evolution of compound nests. If, for a certain species, compound nests are advantageous relatively to the isolated nests that it normally builds, the ability to plastically change to compound nest construction, even if rare, should expose this novel phenotype to selection. Subsequently, processes of genetic assimilation (Crispo 2007, 2008) could allow compound nest construction to become prevalent. This link between domed nests and compound nest construction, in addition to other advantages of domed nests, suggests a reason why domed nests are the ancestral state in the early oscine (songbird) lineages, and perhaps early passerine lineages as well (Price and Griffin 2017). This is because early oscines were likely highly social and even cooperative breeders (Marki et al. 2015) and, therefore, they could have benefited from domed nests in periods of high-density nesting or to evolve cooperative nest construction. We conclude that, since the morphology of domed nests is similar to that of chambers in a compound nest, domed nests can be viewed as an exaptation for high-density nesting and for subsequent evolution of more specialized compound nest building, which may involve communal structures such as roofs.

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Chapter 4 | Testosterone treatment produces sex-dependent effects in social dominance

Testosterone treatment produces sex-dependent effects in social dominance

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Abstract

Dominance hierarchies reduce the costs of competitive aggression in social animals, and testosterone is a proposed mediator of aggressive behaviour and social dominance. While the effects of testosterone on male behaviour are well studied, effects on female aggression and dominance within mixed-sex groups are less clear. We tested how short-term testosterone treatment influences aggressive behaviour and dominance hierarchies in the common waxbill, *Estrilda astrild*, a bird with mild social hierarchies. In captive mixed-sex groups, we administered intramuscular testosterone to either males or females and, using a test of competition for food, compared aggressive behaviour and social dominance to those of a control treatment (saline) with no testosterone administered. Testosterone treatment to males increased their social dominance, without increasing aggression. We observed a decrease in female aggression towards treated males, suggesting that females were reacting to subtle cues of male dominance (e.g. vocal cues). In contrast, female treatment with testosterone did not increase their dominance, which could either be due to a lack of effect on females, or because males reacted to and opposed cues of female dominance. Together, our results indicate a sex-dependent role of testosterone on social hierarchies.

Keywords: aggressiveness; Elo-rating; *Estrilda astrild*; sex differences; social dominance

1. Introduction

Sociality and gregariousness provide many benefits such as facilitating food discovery (Aplin et al., 2012; Tóth et al., 2017), antipredator behaviour (Griesser et al., 2006; Sorato et al., 2012), accessing mates (Ryder et al., 2011; Spoon et al., 2007), rearing young (Krama et al., 2012; Krams et al., 2009) and allowing for several forms of cooperation (Griesser et al., 2017; Krams et al., 2008). Gregariousness also bears costs, however (Gaglio et al., 2018; Low, 2008; Tella, 2002), as it can promote competition and agonistic interactions between group members (Brouwer et al., 2020). Dominance hierarchies are observed in many species and can help mitigate social costs, by reducing aggressive interactions and providing stability to the social group (Ward & Webster, 2016). In species with dominance hierarchies, higher dominance is generally associated with priority access to resources such as food and mates (Chiarati et al., 2010; Marra, 2000; Stahl et al., 2001).

Androgens, in particular testosterone (T), affect life history traits related to reproduction (Gerlach & Ketterson, 2013; Mills et al., 2009; Wingfield et al., 2001) and survival (Matson et al., 2016; Redpath et al., 2006; Wingfield et al., 2001), and T is important in modulating aggression and social dominance (Hunt et al., 2019; Qu et al., 2017; Whiting & Miles, 2019). In the context of reproduction, aggressive and more dominant individuals are frequently better at accessing mates, or accessing the best quality mates, and thus it can be beneficial to increase circulating levels of T during the breeding season (Mathur, 2009; Muller, 2017; Vernasco & Moore, 2020). Circulating levels of T vary through time, both seasonally and acutely, and in many species the levels of circulating T are higher during the breeding season (Gahr, 2020; Madelaire & Gomes, 2016; Schradin, 2008). Aggressive behaviour is not solely modulated by T, however, since, for example, birds do not usually have elevated basal levels of T when aggressively defending their territories in the nonbreeding season (Landys et al. 2010; Marasco et al. 2011; Soma 2006 but see Mougeot et al., 2005).

The behavioural effects of T have been widely studied in males (Ardia et al., 2010; Buchanan et al., 2010; Lacava et al., 2011). Studies with avian species, particularly in males, have established strong associations between social context, levels of circulating T and aggressive or sexual behaviour in males, with T responding to the environment (including the social environment) to then coordinate aggressive and related behaviours (the challenge hypothesis; Wingfield et al., 1999, 1990). Experimental work has shown that agonistic interactions cause an elevation of circulating T levels (e.g. Lacava et al., 2011; Ros et al., 2002, but see also Goymann et al., 2019; Wingfield et al., 2020). It has

also been shown that administering exogenous T elevates male social dominance (e.g. zebra finch, *Taeniopygia guttata*, Ardia et al., 2010; house sparrow, *Passer domesticus*, Buchanan et al., 2010; canaries, *Serinus canaria*, Vergauwen et al., 2014), and correlational work often finds associations between male T levels and aggressive or dominant behaviour (e.g. dark-eyed junco, *Junco hyemalis*, Atwell et al. 2014; spotted antbird, *Hylophylax naevioides*, Wikelski et al., 1999).

Females also have circulating T, since T is also produced, in smaller amounts, by the adrenal gland and ovaries (Staub & De Beer, 1997). The relationship between T and female aggressive behaviours or social dominance is less clear (reviewed in Rosvall et al., 2020). In some species, T levels in females follow a similar pattern to males, with higher levels of circulating T during periods of social instability, which might be advantageous for competing for resources such as territories or mates (George & Rosvall, 2018; Ketterson et al., 2005). In some bird species, exogenously increasing levels of female circulating T has been shown to increase aggressive behaviours towards other females (e.g. zebra finch, Adkins-Regan, 1999; European starling, *Sturnus vulgaris*, Sandell, 2007; tree swallow, *Tachycineta bicolor*, Rosvall, 2013) or a rise in social rank (e.g. spotless starling, *Sturnus unicolor*, Veiga et al., 2004), but not in other species (e.g. barred buttonquail, *Turnix suscitator*, Muck and Goymann, 2019). Even within the same species, such as the dark-eyed junco, exogenously increasing female T levels augmented their aggressiveness (Cain & Ketterson, 2012; Zysling et al., 2006), but natural variation among females in circulating T levels did not predict social dominance (Jawor et al., 2006). With few exceptions (Zysling et al., 2006), studies on female birds have assayed the effects of T on aggression or dominance in a sexual context, either during mate acquisition, courtship or nestbox occupation and defence. The effects of T on female aggression or dominance in a broader social environment, such as competition for food, remain poorly studied (Schwabl-Benzinger et al., 1988), although it may be particularly relevant because females often compete more directly for access to resources than for mates (Stockley & Bro-Jørgensen, 2011). Studies addressing the effects of exogenous T manipulation on male–female interactions in avian species are also scarce. Of these, some studied male–female sexual interactions (e.g. dark-eyed junco, Enstrom et al., 1997; Neudorf et al., 2002; blue tit, *Cyanistes caeruleus*, Foerster and Kempenaers, 2005) and, to our knowledge, only one study has tested how T affects nonsexual interactions between the sexes (administering T to male downy woodpeckers, *Dryobates pubescens*, in winter, which did not cause significant changes in male–female aggression, Kellam et al., 2006).

Most past work has been on the long-term effects of T on aggression and social dominance, but short-term effects are also biologically relevant. For example, a short agonistic interaction may induce a peak of circulating T that mediates an appropriate aggressive response to the agonistic challenge (e.g. Ardia et al., 2010; for review of the challenge hypothesis, see Wingfield et al., 1990, 2000). Here, to understand the effects of T in both sexes, and in a nonsexual social context, we tested how short-term exogenous administration of T influences social dominance in mixed-sex groups, using the common waxbill, *Estrilda astrild*. Common waxbills (hereafter simply waxbills) are highly gregarious, roosting communally and foraging in groups, which are larger in the nonbreeding season (Clement et al., 1993; Payne, 2010). Previous work showed consistent differences between individuals in both aggressiveness and social dominance across years and seasons (Funghi et al., 2015, 2018; Beltrão, Marques, et al., 2021). Additionally, dominance hierarchies are mild, meaning that less dominant individuals may sometimes attack more dominant ones, but hierarchies become steeper during the breeding than the nonbreeding season, perhaps because of increased competition (Beltrão, Marques, et al., 2021). We treated either males or females in mixed-sex groups with T and, using an assay of competition for food, compared their aggressive behaviour and social dominance to those of the same individuals when receiving a control treatment. We tested for sex differences in aggressiveness or social dominance, how administering T to one sex affects social hierarchies and sex differences in social dominance, and whether experimental changes in dominance are accompanied by increased aggression. If T has similar effects in males and females, we predicted that administering T to either sex will increase its aggressiveness and its social dominance relative to the other sex. This prediction follows the most common outcome in the extensive literature on the challenge hypothesis (T promotes aggressiveness and social dominance; reviewed in Welling and Shackelford, 2019; Wingfield et al., 2020), although most of this research has been on male–male interactions (see above). If effects of T on social dominance are sex specific, or partly sex specific, we expected that administering T to females would result in a different pattern. For example, previous work with waxbills did not find sex differences in social dominance and/or aggressiveness (Funghi et al., 2015, 2018; Beltrão, Marques, et al., 2021). Nevertheless, females have been reported to be less aggressive towards males than towards other females (Funghi et al., 2015), suggesting differences in how within- and between-sex aggressiveness is modulated.

2. Methods

We housed 24 waxbills in six metal cages (88.5 x 30 cm and 40 cm high), two males and two females per cage, and each bird was marked with different leg ring colours. Each cage was open in the front, with a metal grid, had four perches in symmetrical positions (Figure 4.1a), and was provided with *ad libitum* food (Tropical Finches Prestige, Versele-Laga), water and mixed grit with crushed oyster shell. Cages were in the research aviary at CIBIO/InBIO, 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). Cages were visually but not acoustically isolated from each other. Birds were sexed by the colour of the undertail coverts (Cardoso et al., 2014), and were obtained from certified breeders in September 2019 (only birds that could be unambiguously sexed were purchased).

Figure 4.1. (a) Bird cages housing a group of four individuals (two males and two females) each. (b) During the test of competition for food, a small feeder was placed in the middle of the cage (yellow arrow).

Experiments were conducted in March 2020, during the morning period (0930–1300), and consisted of a food deprivation period of 2 h, administration of an experimental treatment and a behavioural test (competition for food assay). Each cage received three different treatments, each 1 week apart: (1) T to the two males and saline solution to the two females (male T treatment), (2) T to the two females and saline solution to the two males (female T treatment), (3) saline solution to the four individuals (control treatment). The order of the treatments was balanced across cages, such that the average order of all treatments was identical and all possible pairwise transitions between treatments occurred the same number of times. Treatments consisted of an intramuscular injection of a compound (20 μl saline solution or 20 μl of saline solution with 150 μg of testosterone, 86500 Sigma Aldrich). We used saline solution, as opposed to diluting testosterone in oil, to avoid potential detrimental effects of oil injections (MCS personal observation), and because injection of steroids diluted in saline solution has been shown to be effective in other studies (Binning et al., 2017; Soares et al., 2014). For the treatment to be able to influence behaviour, and without causing ill effects, we followed the testosterone dosage that Ardia et al. (2010) used when studying aggressiveness in male zebra finches, adjusted to the weight of the common waxbill. We used as dosage reference past work with male birds because experiments on T and aggressiveness have been strongly male biased, and there is little information in the literature about optimal dosages for such experiments with females. Females generally have lower levels of circulating T than males (Goymann & Wingfield, 2014), and therefore a smaller dosage might have been used for them (e.g. ca. 1/3 of the dosage used here suffices to influence female zebra finch reproductive physiology; Rutkowska et al., 2005) but it has nevertheless been shown that, in other bird species, females also respond to much higher levels of T (e.g. T-induced singing in female European starlings: Hausberger et al., 1995; T-induced ornamental plumage in female red-backed fairy-wrens, *Malurus melanocephalus*: Lindsay et al., 2016). The birds were taken from the cage individually and quickly to minimize the stress, and the treatment was administered in a contiguous separate room. We started by disinfecting the bird's chest with a cotton ball sightly humified with alcohol, followed by the injection (29G needle) with the solution at room temperature. This research was approved by the ORBEA (Organism for Animal Welfare) of CIBIO/InBIO (ethics assessment no. ORBEA_2019_Estrilda) and followed the ASAB/ABS ethical guidelines (ASAB/ABS, 2020).

Tests of competition for food started 20 min after injections, 2 h after the beginning of the food deprivation period and consisted of placing a small feeder in the centre of the cage attached to the front bars (Figure 4.1b). Behaviours were

videorecorded (Canon Legria HF M306) for a 15 min period, starting from the moment of placing the feeder, which previous work with waxbills showed to reliably reveal individual differences in aggressiveness and social dominance (Funghi et al. 2015, 2018). Previous work with waxbills, albeit with other neuroendocrinological compounds, has also shown that a 15 min interval between injection and testing is adequate to quantify behavioural effects (Silva et al., 2020). From these videos, focal observations of all four individuals were conducted by a single observer (P.B.), blind to the experimental treatments, using BORIS (behavioural observation research interactive software, Friard and Gamba 2016). The birds were identified individually by their leg ring colours. We recorded the summed number of all aggressive behaviours that each individual made during these 15 min. Aggressive behaviours consisted of the focal individual stretching the body towards a conspecific, which could be accompanied by opening the bill or flicking wings, pecking at it or displacing it by flying towards it. When a displacement by the recipient of an aggressive behaviour occurred, signalling submission, we also noted the identity of the recipient. When it was not clear that a recipient behaved submissively, then only the aggressive behaviour was noted, but not the dominant/submissive dyadic interaction (Vervaecke et al., 2000).

For each test, we inferred dominance hierarchies from the dominant/submissive dyadic interactions, using three different rating methods: Elo-rating (Elo, 1978), randomized Elo-rating (Sánchez-Tójar et al., 2018) and David's score (David, 1997). Elo-ratings and David's scores are measures of social dominance, which quantify how dominant each individual is relative to the other individuals in its group. The first method, Elo-rating, takes the order in the sequence of interactions into account, and is advisable when there is nonindependence of outcomes between consecutive interactions (Albers & De Vries, 2001), for example because they are close in time. In this method, at each sequential dominance interaction, the individual's ratings are calculated, taking into consideration the probability of that individual winning against the other (Albers & De Vries, 2001). The randomized Elo-rating method was developed recently (Sánchez-Tójar et al., 2018), while David's score has been much used in studies of dominance hierarchies (De Vries et al., 2006; Funghi et al., 2015; Stevens et al., 2007), and neither takes order of interactions into account. Randomized Elo-ratings and David's scores are therefore appropriate to infer hierarchies when the outcome of consecutively observed dyadic interactions by the same individual can be considered statistically independent (Gammell et al., 2003; Sánchez-Tójar et al., 2018). We also used the classic Elo-rating method because dyadic interactions in our experiments are close temporally (15 min test) and spatially (within a cage), which might be associated with temporal

nonindependence of interaction outcomes. From the data on dominant/submissive dyadic interactions, separately for each treatment and cage, we calculated Elo-ratings and randomized Elo-ratings with the package 'aniDom' (v. 0.1.4; as described in the Supporting Information of Sánchez-Tójar et al., 2018), and calculated normalized David's scores (De Vries et al., 2006) with the package 'EloRating' (Neumann & Kulik, 2020). In the three methods, higher ratings or scores reflect higher dominance. To assess temporal nonindependence of consecutive interaction outcomes by the same individual (i.e. being dominant or submissive in an interaction) within our 15 min behavioural tests, we ran a temporal correlogram with time–distance classes of 1 min, from]0–1 min] to]14–15 min], with the package 'ncf' (v. 1.2-9; Bjornstad, 2020), using 1000 permutations to assess the significance of autocorrelation at each time–distance class. We concatenated the data streams from all individuals to assess the overall pattern of temporal autocorrelation in our data.

We compared treatments at two levels: group and individual. At the group level, we ran a generalized linear mixed model (GLMM) with mean aggressiveness per group as dependent variable, treatment as fixed factor and group identity as random factor. To test whether sex differences in social hierarchy changed with treatment, we ran similar GLMMs using as dependent variable the difference between male and female mean hierarchy scores. After checking model assumptions, by comparing residuals for different distributions and link functions with the R package 'performance' (v. 0.4.7; Lüdecke et al., 2020), we chose a Gaussian distribution with log link function in the GLMMs for mean group aggressiveness and Gaussian distribution with identity link function in the GLMMs for hierarchy scores. We report GLMM contrasts (i.e. the simple coefficients, without having run an ANOVA on the GLMM), which test for differences between one level of the fixed factor (the control treatment) and each of the remaining levels (either male or female T treatment). At the individual level, we ran a GLMM with the number of aggressive interactions per individual as dependent variable, with treatment, sex and their interaction as fixed factors and individual identity as random factor. We also ran similar GLMMs using as the dependent variable either the hierarchy score of each individual, to test for changes in sex differences in hierarchy rank, or the number of aggressive interactions towards the opposite sex, to test for changes in between-sex aggressiveness. As before, after checking model assumptions, we chose a negative binomial distribution for the GLMMs with aggressiveness as response variable and Gaussian distributions for the GLMM with hierarchy score as response variable. As above, we report GLMM contrasts between the control and either of the T treatments. The main results of interest in these individual level GLMMs are the interactions between

treatment and sex, which test whether changes induced by a given treatment differed between females and males. We ran GLMMs using R package 'lme4' (v. 1.1-23; Bates et al. 2014) and 'lmerTest' (v. 3.1-2; Kuznetsova et al., 2017). We removed one individual from the analysis of social hierarchy in one of the treatments (male T treatment), because it did not interact with any other individual on that test and, consequently, its hierarchy score could not be computed. We estimated repeatability of individual hierarchy scores across treatments using the function 'rptGaussian' (R package 'rptR', v. 0.9.22; Stoffel et al. 2017), and the repeatability of individual aggressiveness using code available in Nakagawa et al. (2017) for negative binomial distributions, in both cases using the same models described above for individual level analyses. All analyses were conducted in R v. 3.6.3 (R Core Team, 2020). The data are available in the Appendix D.

3. Results

The correlogram in Figure 4.2 shows that the probability of being dominant or submissive in a dyadic interaction was positively and significantly predicted by previous interaction outcomes, up to almost 15 min, which is the duration of behavioural tests. The strength of temporal autocorrelation decreased for longer time intervals (Figure 4.2), suggesting that the order of interactions matters for inferring dominance hierarchies (as accounted for in the Elo-rating method). This result is opposed to assuming that the outcome of each dyadic interaction of an individual is independent of its other interactions close in time (as in randomized Elo-ratings and David's scores). Individual social dominance was significantly repeatable across treatments for all three scores of social dominance (Elo-rating: intraclass correlation, ICC = 0.58, 95% confidence interval, CI = [0.33, 0.76]; randomized Elo-rating: ICC = 0.70, CI = [0.46, 0.82]; David's score: ICC = 0.62, CI = [0.37, 0.79]) and aggressiveness was also repeatable (ICC = 0.49, CI = [0.21, 0.63]).

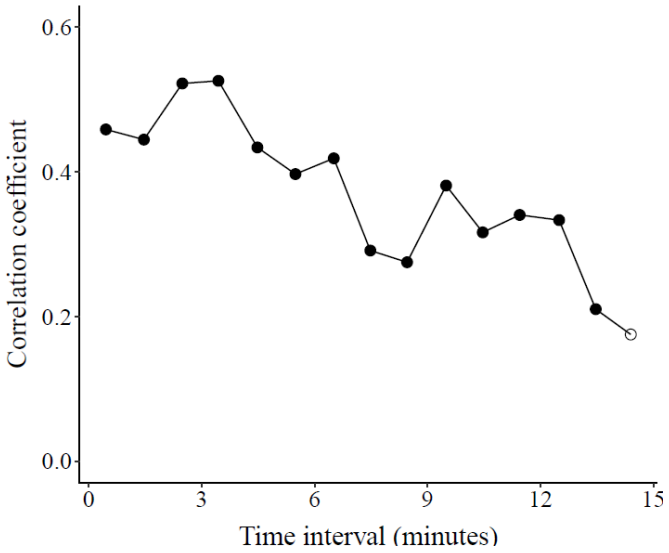

Figure 4.2. Temporal autocorrelation of the outcomes in dyadic interactions (winning or losing) of the same individual for time intervals from]0–1] to]14–15] min (behavioural tests lasted 15 min). The general pattern shown concatenates data from all individuals. Black dots indicate significant temporal autocorrelation ($P < 0.05$).

At the group level, there was a tendency for overall more aggressive behaviours in the female T treatment than in the control treatment (Appendix C Table C1). This trend was due to one group in which mean aggressiveness was ca. twice as high in the female T treatment (Figure 4.3) and without this group the tendency disappeared (female T treatment versus control: estimate = -0.06, CI = [-0.49, 0.38], P = 0.80). At the group level, we also found that sex differences in social hierarchy, evaluated with the Elo-rating method, were greater in the male T treatment relative to the control, but did not differ between the female T and control treatments (Appendix C Table C1). With the other two methods for determining social hierarchies (randomized Elo-rating and David's score) we did not find significant effects of T treatments (Appendix C Table C1).

Similar to analyses at the group level, at the individual level we found that sex differences in social hierarchy, evaluated with Elo-ratings, increased from the control to the male T treatment (Appendix C Table C2). This increased sex difference in social hierarchy scores resulted jointly from an increase in male and a decrease in female Elo-ratings (Figure 4.4). The increased sex difference in social hierarchy also involved a significant decrease in female aggression towards males when comparing the male T treatment to the control (Figure 4.5, Appendix C Table C2). Again, no effects of T treatments were detected using social hierarchy scores that do not take the order of interactions into account (randomized Elo-rating and David's score; Appendix C Table C2). Also, similar to analyses at the group level, there were no effects of T treatments on

overall aggressiveness, but males were more aggressive than females irrespective of treatment and there were no effects of T treatments on sex differences in aggressiveness (Appendix C Table C2).

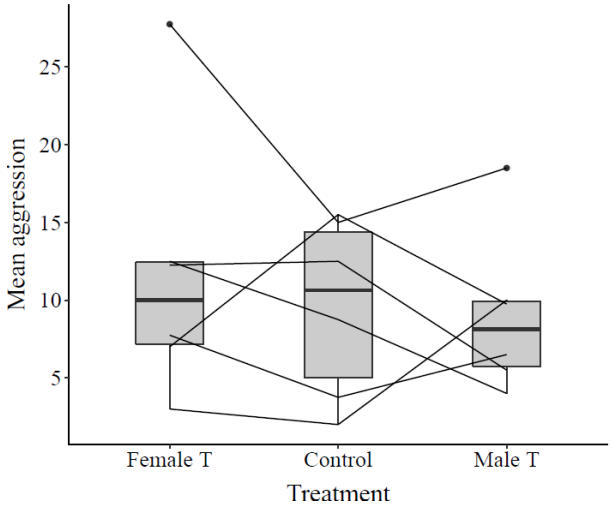

Figure 4.3. Mean number of aggressive behaviours of the four individuals per cage and experimental treatment: female T (females given testosterone and males saline solution), control (all birds given saline solution) and male T (males given testosterone and females saline solution). Each line is one of the six experimental cages. Box plots show the median and quartiles, whiskers represent the lowest and highest datum within the 1.5 × interquartile range and dots are data outside this range.

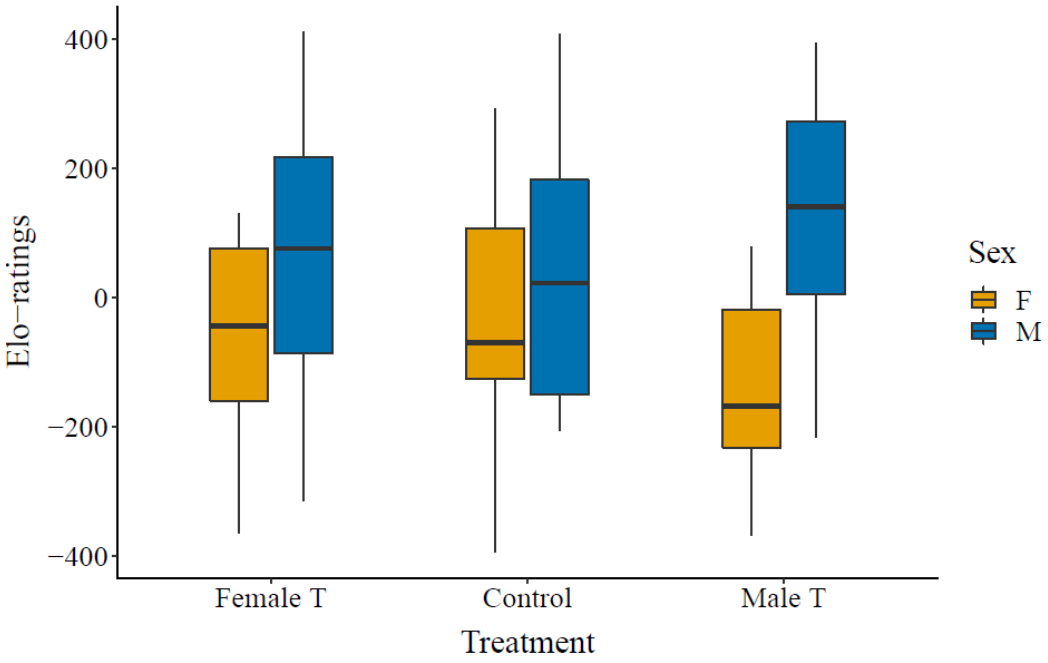

Figure 4.0.4. Elo-ratings (i.e., scores of social dominance) per individual, separated by sex, across the three experimental treatments: female T (females given testosterone and males saline solution), control (all birds given saline solution) and male T (males given testosterone and females saline solution). F: female; M: male. Box plots as in Figure 4.3.

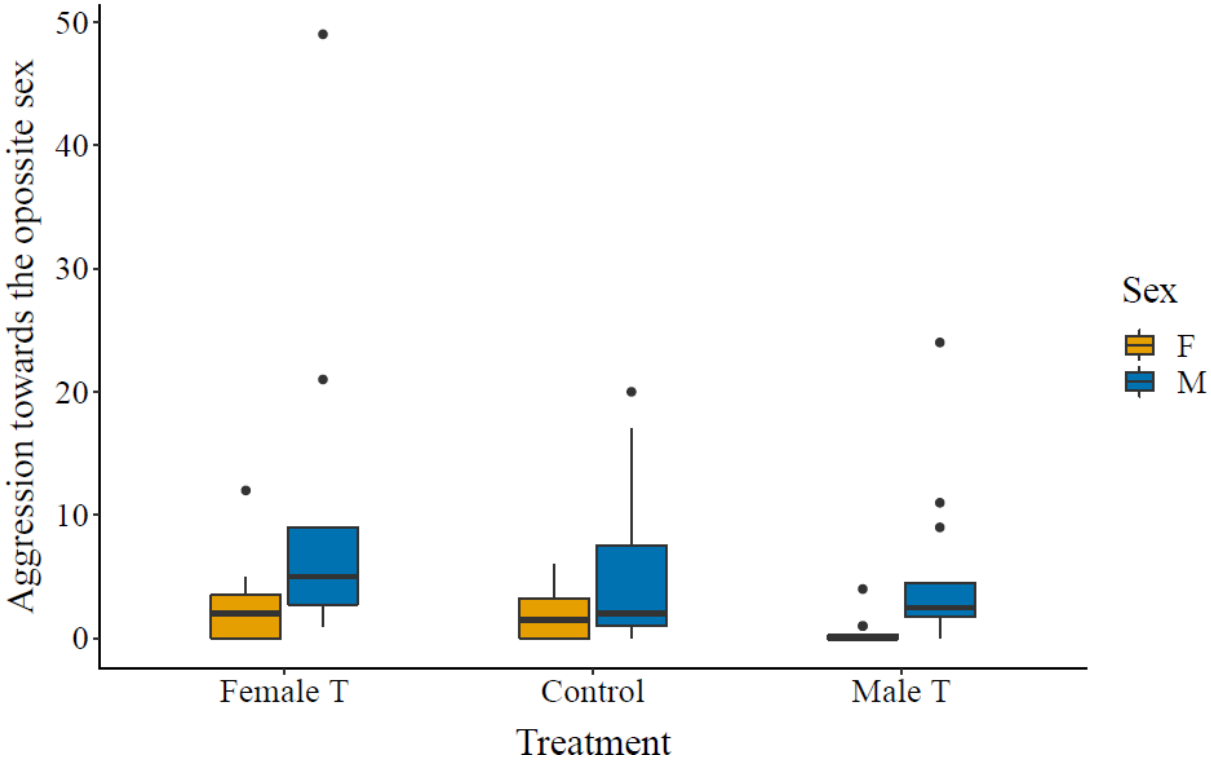

Figure 4.5. Aggressive behaviours per individual towards opposite-sex individuals, across the three experimental treatments: female T (females given testosterone and males saline solution), control (all birds given saline solution) and male T (males given testosterone and females saline solution). F: female; M: male. Box plots as in Figure 4.3.

4. Discussion

Male waxbills were on average more aggressive than females in our experiments, and we found that male T treatment increased sex differences in social hierarchy. In contrast, female T treatment did not reduce sex differences in social hierarchy, which instead remained identical to those in the control treatment. These results point to a sex-dependent asymmetric effect of T on social hierarchy. This asymmetric effect could be due to female aggressiveness and dominance not being as strongly affected by T as those of males and/or by an asymmetric contagion effect, whereby cues of female dominance induced by T are counteracted by male responses, but not vice versa.

Similar to our results, previous work with waxbills, and using behavioural tests identical to ours, showed that individual differences in aggressiveness are repeatable through time but, unlike our results, previous work had not found sex differences in aggressiveness (Funghi et al., 2015, 2018). It was only reported that female waxbills were less likely to attack males than other females (Funghi et al., 2015). Our results show more clearly that, on average, males are more aggressive than females, as has

been shown for other gregarious birds (e.g. zebra finch, Bolund et al., 2007; serin, *Serinus serinus*, and siskin, *Spinus spinus*, Senar and Domènech, 2011). The numbers of aggressive behaviours by males and females overlapped extensively, in agreement with our and earlier (Funghi et al., 2015, 2018) findings that that the steepness of waxbill social hierarchies is mild, with more dominant individuals sometimes being displaced by lower-ranking birds. Therefore, it is not unlikely that waxbill sex differences in aggressiveness are not always detected, either because of stochastic differences in the sample of individuals used, or because of methodological differences between studies. For example, our experiments took place in March, coinciding with the early breeding season of waxbills in this region, while the previous studies were conducted later in the year (July to September), towards the end of the breeding season (Beltrão, Gomes, et al. 2021; Sanz-Aguilar et al., 2015), and it is common that more aggressiveness is observed earlier in the season (Baird, 2013). In addition, we used waxbills raised in captivity, while the previous studies used wild-caught birds that, despite acclimatization to captivity, might have behaved differently if tested in their natural environment.

Male T treatment did not increase male or overall group aggressiveness, but it did increase male social dominance over females, and caused a decrease in female attacks towards males. Since T can be rapidly converted to oestradiol by the aromatase enzyme, and oestradiol can also be responsible for increasing aggressiveness (Heimovics et al., 2015), the behavioural effects of our T treatment could be caused either directly by T or by one of its metabolites, such as oestradiol. Previous studies manipulating male T, in other avian species, found that increased T is associated with more male aggression (e.g. Ardia et al., 2010; Vergauwen et al., 2014) and increased social dominance (e.g. Buchanan et al., 2010; Duckworth et al., 2004). Our finding of increased social dominance of T-treated males and reduced aggressive behaviour of females towards them, but without an increase in male aggressiveness, indicates that females' response to cues of dominance by the T-treated males is more subtle than aggressive displays and attacks. We quantified aggressive behaviour by counting the displays (i.e. stretching towards the opponent, often with open bill or flicking wings) and attacks (i.e. pecking the opponent or flying to displace it), which are clearly identifiable behaviours. There may, however, be more subtle postures, movements or other signals that communicate dominance to the birds and are undetected or difficult to quantify objectively by us. For example, waxbills are very vocal, uttering calls very frequently when interacting in groups, and perhaps these calls can be modulated in their rate, duration, sound amplitude or spectral characteristics to communicate aggressive motivation or dominance (e.g. black-capped chickadee, *Poecile atricapillus*, Baker et al.,

2012; corncrake, *Crex crex*, Ręk and Osiejuk, 2011; house wren, *Troglodytes aedon*, Krieg and Burnett, 2017). Dominance in birds might also be communicated via nonbehavioural signals, such as odours (Whittaker et al., 2018) or changed colours of bare parts (Iverson & Karubian, 2017; Murphy et al., 2009; Tarvin et al., 2016), both of which may be linked with circulating T levels (Lahaye et al., 2014; Laucht et al., 2010; McGraw et al., 2006; Whittaker et al., 2018). While odour cues can be quickly released (Whittaker et al., 2018), colour changes in avian bare parts may require hours or days (Ardia et al., 2010; Rosenthal et al., 2012; Tarvin et al., 2016). In waxbills, bill colour is not related to aggressiveness (Funghi et al., 2018), making colour signals less likely to have mediated changes in dominance in our experiment.

Based on the results of the male T treatment, which increased sex differences in social hierarchy, we would expect that female T treatment would reduce these sex differences, bringing the females' mean social dominance closer to that of males. Female T treatment, however, did not change sex differences in social hierarchy compared to controls or levels of female aggressive behaviour. Although we did not measure changes in circulating T levels, we can extrapolate that T levels were affected, since male behaviour clearly changed when compared with the control treatment. Also, females often have lower concentrations of circulating T than males (Goymann & Wingfield, 2014), so the changes in T caused by our treatment would have been more pronounced for females. Our short-term, single injection treatment mimics a situation that is common among birds: in many species it has been shown that an agonistic social challenge elicits a brief peak of high T production and circulating levels, several-fold higher than their basal circulating T level (Atwell et al., 2014; Ros et al., 2002; Wingfield & Wada, 1989), which then mediates the short-term aggressive behavioural response to the social challenge (Goymann et al., 2019; Wingfield et al., 1987). Therefore, our results with females seem to indicate either that female aggression and dominance are not strongly affected by T and/or that cues of female dominance induced by T were effectively counteracted by male responses via a mechanism akin to the challenge hypothesis. We discuss these two hypotheses in turn.

First, empirical work on whether T influences female aggression or dominance has not produced results as clear or consistent as in the case of males. For example, while aggression and T levels are positively associated in female dunnocks, *Prunella modularis* (as indicated by responses to behavioural challenge: Langmore et al., 2002) and female European starlings (as indicated by exogenous T manipulation, Sandell, 2007; but see also De Ridder et al., 2002), such a connection between T and aggression

could not be found with exogenous T manipulation in female song sparrows, *Melospiza melodia* (Elekonich and Wingfield, 2000) nor with behavioural challenges to female northern cardinals, *Cardinalis cardinalis* (DeVries et al., 2015). In both females and males, aggressive behaviour and dominance are not solely modulated by T levels, but other neuroendocrine variables also play a role, such as serotonin, corticosteroids and others (Holekamp & Strauss, 2016; Kelly & Vitousek, 2017; Kelly & Wilson, 2020). For example, bluethroat, *Luscinia svecica*, females with higher levels of oestradiol sing more towards a female intruder (Pärn et al., 2008), and in female African black coucals, *Centropus grillii*, progesterone is a central hormone modulating aggressive behaviour (Goymann et al., 2008). In females there may exist a greater need to regulate aggressiveness by co-opting neuroendocrine systems other than T, because of the negative influence of high T levels in female fertility or reproductive success (reviewed in Rosvall, 2013; Rosvall et al., 2020). For example, in zebra finches, clutch size decreases with the administration of T (Rutkowska et al., 2005).

Second, it is possible that cues of female dominance or of aggressive motivation challenged males and were effectively responded to and counteracted by male behaviour. Suggestive of this, in one of our experimental groups we observed a striking increase in aggressiveness of the group (rather than only females) during the female T treatment. This was observed in only one of six bird cages, and it is therefore an anecdotal observation from which we cannot draw clear conclusions. Since changes in dominance in our experiments involved behaviours or cues more subtle than actual aggressive displays and attacks (see above; e.g. females decreased aggression towards T-treated males in spite of these males not having increased aggressiveness), it is possible that in the other cages males counteracted female aggressive motivation in a manner more subtle than overt aggression. Our limited number of groups (six bird cages) may have contributed to a lack of statistically significant results in analyses at the group level. Future studies are needed to explore the hypothesis that subtle cues of female aggressive motivation are responded to and counteracted by males.

The results on social hierarchies that we discussed inferred social rank with Elo-ratings (Elo, 1978), because we found temporal autocorrelation on the likelihood of individuals winning or losing aggressive interactions, and the Elo-rating method accounts for such order effects in the sequence of interactions (Albers & De Vries, 2001; Gammell et al., 2003). David's scores (De Vries et al., 2006) and randomized Elo-rating (Sánchez-Tójar et al., 2018) are alternatives to score social dominance but, although they can be statistically more powerful when social hierarchies are not steep, they assume statistical

independence of consecutive observations of interaction outcomes (Gammell et al., 2003; Sánchez-Tójar et al., 2018). Interestingly, perhaps because our behavioural data on aggression show temporal autocorrelation, if we relied either on David's scores or on randomized Elo-ratings we would not be able to detect the differences in social hierarchy between treatments. This shows that, for data with temporal autocorrelation of interaction outcomes, the Elo-rating method may not only be more appropriate for addressing nonindependence of data, but also prove better able to detect biological phenomena.

In conclusion, we documented sex-specific effects of T on social hierarchies in common waxbills. As expected, male T treatment increased their social dominance relative to females, and they were attacked less by females. Interestingly, this did not involve increased male aggressiveness, indicating communication of dominance via more subtle signals than overt aggressive displays or attacks. Social hierarchies in waxbills thus appear to be maintained with a significant contribution of communication signals, reducing potentially dangerous and costly aggression. Interestingly, T treatment of females did not change their dominance relative to males. This could be due to female aggressiveness being less strongly affected by T and perhaps more strongly affected by other endocrine systems and/or due to males reacting to, and counteracting, subtle female cues of dominance or aggressive motivation. Suggestive of the latter, we found a large increase in overall aggressiveness during female T treatment in one of our experimental groups. To our knowledge, this is the first experimental demonstration, in mixed-sex bird groups, that T affects social dominance asymmetrically in males and females.

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Chapter 5 | Plumage colour saturation predicts long-term, cross-seasonal social dominance in a mutually ornamented bird

Plumage colour saturation predicts long-term, cross-seasonal social dominance in a mutually ornamented bird

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Abstract

Dominance hierarchies are known to reduce agonistic interactions between individuals and may be influenced by differences in phenotypes such as body size, personality or cognition. Colour ornamentation, especially with melanin-based colours, can also be a badge of status signalling social dominance, but status signalling with carotenoid-based colours is little understood. Here we studied whether different phenotypes, including individual differences in carotenoid-based colour ornamentation, body size, personality-, cognition- and stress-related traits, predict social dominance in the highly social and mutually ornamented common waxbill, *Estrilda astrild*. We monitored aggressive interactions of waxbills living in seminatural conditions, in a large mesocosm, using data from a radiofrequency identification system in the nonbreeding and breeding seasons over 2 consecutive years. We found the position of individual waxbills in the dominance hierarchy repeatable across seasons and years. Furthermore, the steepness of the dominance hierarchy was greater in the breeding seasons, perhaps because of increased competition over mates or breeding resources. Contrary to previous work with waxbills in birdcages, here body size did not predict social dominance, perhaps because in our more natural setting aggressive encounters were mostly airborne, where large body size may not confer a fighting advantage and may even reduce manoeuvrability. Sex, reactive-to-proactive personality differences and traits related to cognition or stress did not predict social dominance either. Finally, red colour saturation, but not the size of the red patch, strongly predicted social dominance and may thus act as a badge of status. This is one of the few studies testing whether size or saturation of carotenoid-based plumage coloration indicates social dominance and suggests that saturation may more often signal dominance.

Keywords: animal personality, badge of status, body size, carotenoid-based coloration, common waxbill, dominance hierarchy

1. Introduction

Aggressive interactions between conspecifics can arise due to competition for resources such as food (e.g. Goldberg, 2001; Kakareko et al., 2013) or mates (e.g. Ancona et al., 2010; Baxter et al., 2015) and entail costs, such as risk of injury, energy expenditure, exposure to predation or decreased food intake (Baird, 2013). Dominance hierarchies exist in many species and are known to alleviate some of these costs by decreasing aggressive interactions between conspecifics (Ward & Webster, 2016). Often, dominance hierarchies determine that more dominant individuals have privileged access to resources (Chiarati et al., 2010; Majolo et al., 2012; Yahner, 2011).

The outcome of aggressive interactions, and thus the ranking in dominance hierarchies, can be conditioned by phenotypic differences between individuals (Chase & Seitz, 2011) and, during a contest, individuals may assess the opponent's fighting ability and decide to escalate the fight or not (resource-holding potential hypothesis; Parker, 1974). Body size can indicate resource-holding potential, with several studies reporting a positive relation between body size and social dominance (Irschick et al., 2014; López-Segoviano et al., 2018; Thornton et al., 2015). Personality differences, in particular differences along a reactive-to-proactive axis (with more proactive individuals being generally faster explorers, more aggressive, active and bolder than reactive individuals; Koolhaas et al., 1999; Sih et al., 2004), have been found to correlate with social dominance, but the direction of this relation varies across studies (dominance associated with proactive personality: e.g. David et al., 2011; Dingemanse & De Goede, 2004; dominance associated with reactive personality: e.g. Fox et al., 2009; Verbeek et al., 1999). Other behavioural-related traits might also be associated with social dominance. For example, individuals may inherently differ in their levels of stress (Cockrem, 2007), and this could affect how they react to the challenges of establishing social associations and dominance hierarchies. Alternatively, occupying certain positions in dominance hierarchies (e.g. being very subordinate) could chronically affect stress levels (Cavigelli & Caruso, 2015). Cognition may also be a relevant phenotype, as social dominance has been reported to correlate positively with learning ability (Boogert et al., 2006; Fitchett et al., 2005; Langley et al., 2018; Pravosudov et al., 2003; but see also Cole & Quinn, 2012, for a negative association between dominance and problem-solving ability). Inhibitory control, for example, which is the cognitive ability of refraining from performing certain impulsive behaviours (Diamond, 1981, 2013), has been shown to be better in species with steep dominance hierarchies or with complex fission - fusion dynamics (Amici et al., 2008, 2009), perhaps because the ability to withhold aggression towards more dominant individuals avoids costly fights.

Signalling social dominance can be beneficial for both senders and receivers, and this can be achieved, for example, using badges of status (López-Idiáquez et al., 2016; Rat et al., 2015; Senar, 2006). In birds, plumage colour ornamentation can signal individual quality (Roulin, 2016; Weaver et al., 2017; White, 2020), social dominance or competitive ability (Holley, 2016; Nie et al., 2019). The badge of status hypothesis (Rohwer, 1975; Senar, 2006) predicts that individuals use signals, such as colour ornaments, to assess social dominance or fighting ability of others, thus diminishing the need for aggressive interactions to settle disputes. The most common plumage colours rely on melanin pigments, carotenoid pigments and structural colours (reviewed in Hill, 2018).

Carotenoid pigments are responsible for most of the red, orange and yellow colours, and must be obtained through the diet (Britton et al., 2008). Carotenoid-based colours are often found to be involved in mate choice, with females preferring males with more saturated plumage (Hill, 2006). There is ample evidence that melanin-based plumage can signal dominance status (reviewed in Jawor & Breitwisch, 2003; Roulin, 2016; but see Sánchez-Tójar, Nakagawa, et al., 2018), but the role of carotenoids in dominance signalling is less clear because past work on different avian species has provided mixed results. While in several avian species no evidence was found that carotenoid-based coloration is a reliable dominance signal (e.g. house finch, *Haemorhous mexicanus*, McGraw & Hill, 2000; great tit, *Parus major*, Quesada & Senar, 2007; red bishop, *Euplectes franciscanus*, Edler & Friedl, 2010), in other species carotenoid-based coloration does indicate social dominance (e.g. red-collared widowbird, *Euplectes ardens*, Pryke et al., 2001; Pryke et al., 2002; red-shouldered widowbird, *Euplectes axillaris*, Pryke & Andersson, 2003; European serin, *Serinus serinus*, Leitão et al., 2015; crimson finch, *Neochmia phaeton*, Young et al., 2016; for a meta-analysis see Santos et al., 2011).

Carotenoid-based plumage coloration comprises different components, such as the size of the coloured patch, or the saturation of the colour itself. Frequently, it is the saturation of carotenoid-based colours that has a primary role in mate choice (Hill, 2006), but for other social functions of carotenoid-based colour there is not yet a clear understanding of which colour component (size or saturation) is most important (Griggio et al., 2007; Young et al., 2016). For example, patch size is a better predictor of social dominance than colour saturation in red-shouldered widowbirds (Pryke & Andersson, 2003), while in serins only colour saturation, not patch size, predicts social dominance (Leitão et al., 2015).

Here we used a highly gregarious avian species, the common waxbill, *Estrilda astrild*, to investigate whether certain phenotypic traits (body size, personality, cognition and stress-related traits) predict social dominance, and via which components of carotenoid-based coloration (saturation or size of different colour patches) dominance may be signalled. Common waxbills (hereafter simply waxbills) have stable individual differences in aggressiveness (Funghi et al., 2015; Funghi et al., 2018), and waxbill groups show dominance hierarchies with mildly steep slopes (i.e. where dominant individuals are sometimes attacked by subordinates, Funghi et al., 2015; Beltrão, Silva, et al., 2021), as opposed to hierarchies with very steep slopes (i.e. where attacks on dominant individuals are extremely rare; Sanchez-Tojar et al., 2017). Waxbills differ in personality along a reactive-to-proactive axis, with these personality differences being repeatable through time (Carvalho et al., 2013; Funghi et al., 2015), even across seasons and when tested a full year apart (Guerra et al., 2020). Previous work using small groups of waxbills in birdcages found that larger body size, rather than differences along their reactive-to-proactive personality axis, predicted social dominance (Funghi et al., 2015). However, aggressive interactions in a confined space may be different than in a more natural setting, where birds interact in an open space and can form social groups more freely. Waxbills are also interesting for this research because we can easily study and compare colour ornamentation in both sexes, since they are similarly ornamented, with a red mask and red patch on the breast (Payne, 2010). Although males are on average more ornamented than females, the sexes overlap greatly in the extent and saturation of red coloration (Cardoso, Batalha, et al., 2014; Cardoso, Leitão, et al., 2014). In waxbills, colour ornamentation appears to influence social preferences (Cardoso, Leitão, et al., 2014), but the relation between their colour ornamentation and social dominance is not yet known. We used a waxbill population tagged with passive integrated transponder (PIT) tags for radiofrequency identification (RFID), living in a large open-air mesocosm, to study aggression and dominance hierarchies through time and across seasons, and to test whether phenotypic differences between individuals predict social dominance.

2. Methods

2.1. Study System

We monitored aggressive interactions at feeders between waxbills living in a large mesocosm, which consisted of a large seminatural environment (ca. 235 m2, ca. 1.30–2.70 m high), in a quiet rural setting near Porto, Portugal, exposed to the natural climate, covered by a fine net, and with abundant natural vegetation. This mesocosm

allowed the birds to fly freely, roost communally at night, form social groups and nest using natural vegetation (Beltrão, Gomes, et al., 2021). Birds in the mesocosm were not exposed to predation, but they continued to express appropriate behavioural reactions when, occasionally, potential predators such as jays or raptors were in the vicinity of the aviary (P. Beltrao & A. C. R. Gomes, personal observation). All birds had a metal ring on one leg with a unique number, and on the other leg a unique PIT tag embedded in a plastic ring (Dorset ID, Aalten, The Netherlands). The birds had permanent access to 12 feeders, supplying food *ad libitum*, which were placed at heights between 1.19 m and 1.54 m, mounted on the same wall near each other (maximum distance between feeders was 2.96 m). Each was equipped with an RFID antenna that automatically recorded arrivals, departures and individual identification. Birds were captured from the wild, in northwest Portugal, as adults (i.e. with a red bill, rather than the black bill of young juveniles); approximately half were captured in October 2016, and the other half in September 2017 (details on captures and the mesocosm are in Gomes et al., 2020; Guerra et al., 2020).

We monitored aggressive interactions and studied the dominance hierarchies of these waxbills in four time periods, each lasting 2 months: nonbreeding season 1 (NB1) from December 2017 to January 2018, breeding season 1 (B1) from 15 April to 15 June 2018, nonbreeding season 2 (NB2) from December 2018 to January 2019, and breeding season 2 (B2) from 15 April to 15 June 2019. There was abundant nest construction in the mesocosm during these breeding seasons (Beltrão, Gomes, et al., 2021). The mesocosm housed 54 individuals (25 males and 29 females) during NB1 and B1, 51 individuals (23 males and 28 females) in NB2, and 50 individuals (23 males and 27 females) in B2. The small differences in bird numbers between these periods were due to natural mortality. Sex was determined through genetic sexing (Gomes et al., 2020), except for four individuals that were phenotypically sexed by the colour of their undertail coverts (Cardoso, Leitão, et al., 2014). All individuals were recorded by the RFID system a minimum of 10 out of the 60 days in each 2-month period, but most individuals (88%) were recorded on more than 50 of the 60 days.

2.2. Video Observations and Identification of Aggressive Displacements

We recorded 19 videos of the feeder area during 2017 and early 2018 to observe aggressive displacements, and to develop and validate a criterion to identify these displacements from the RFID data stream. Displacements are instances when a bird leaves the feeder because of an interaction with another bird arriving at the same feeder. Video recordings were made using a camera (Canon Legria HF M306 and Sony HDRCX115EB) at different times of day (between 1000 and 1730 hours), to capture aggressive interactions throughout the year. We conducted focal observations of each bird feeding in the video recordings and measured the time each individual spent in each feeder visit (from the time it arrived at the feeder to the time it left); a total of 485 feeder visits were identified. We also measured the time difference between an individual departing from a feeder and another individual arriving at the same feeder; a total of 353 such transitions were identified from the videos (see Video S1 in the Appendix D, for examples of displacements). For each measurement, either the duration of a feeder visit or the time difference between one individual departing and another arriving at the same feeder, we noted whether or not the original individual at the feeder was displaced (i.e. it left the feeder because of a fight or because another individual was already flying towards the same feeder). From these video-based data, we constructed histograms of the duration of feeder visits and of transitions between birds, separating the cases where the focal bird left the feeder due to a displacement or not. These histograms were used to establish a temporal criterion that best identifies feeder displacements in the RFID data stream (see Results). This rationale of using video observations to identify criteria with which to then infer aggressive interactions from a RFID data stream is similar to that of Evans et al. (2018).

We identified displacements at feeders from the RFID data stream as follows. First, RFID data collected from the feeder antennae were submitted to a cleaning process that accounted for possible failures and redundancies in the system, as described in Gomes et al. (2021). Visits to a feeder by the same individual with intervals shorter than 5 s, without readings of that individual from other antennae in the RFID system or of other individuals at that same feeder, were considered as a single visit, because such gaps can occur due to temporary loss of signal in the antenna (e.g. because the bird's leg was positioned at an unreadable angle). We then identified displacements at feeders, based on the RFID data stream, as instances when the interval between the departure of a bird and the arrival of the next, at the same feeder, was less than 2 s (i.e. during the same second or an adjacent second in the RFID data stream, which has a temporal resolution of 1 s) and both birds (the displaced bird and

the one that displaced it) stayed at the feeder for a minimum of 3 s. Code for this function is available in the Appendix D. The 2 s criterion to identify displacements in the RFID data is based on the results from the video analyses (see Results). The additional requirement for continuous stays at the feeder of at least 3 s, before and after the displacement, prevents counting events where displaced and dominant roles are ambiguous, such as when birds compete for a feeder with short fights around it, which the RFID system records as rapidly switching readings between the two individuals. The interactions thus identified from the RFID data reflect a clear asymmetry of roles, where one individual is displaced from the feeder by another individual.

2.3. Dominance Hierarchies

We quantified dominance hierarchies based on the dyadic displacement interactions identified in the RFID data stream. It may not be correct to consider each dyadic interaction as an independent event, because the outcomes of interactions close in time may be positively related, for example, due to winner - loser effects. For waxbills observed in cages, the probability of an individual being dominant or submissive in an aggressive encounter is predicted by the outcome of previous interactions close in time, as shown by a decreasing strength of temporal autocorrelation as aggressive interactions are further apart in time (Beltrão, Silva, et al., 2021). To assess temporal autocorrelation in the outcome of aggressive dyadic interactions in our RFID data stream, we ran correlograms for each individual, separately for each of the four time periods, with three temporal resolutions: 2 min (up to 1 h), 10 min (up to 2 h) or 1 h (up to 24 h). We used the R (v. 4.0.2; R Core Team, 2020) function ‘correlog’ (package ncf, v. 1.2-9; Bjornstad, 2020) to compute autocorrelations. We found no evidence for decreasing temporal autocorrelation, since in none of the four time periods did correlograms show decreasing autocorrelation as time intervals increased (Appendix D Figure D1).

Since interaction outcomes did not show temporal autocorrelation, we could use methods to infer dominance hierarchies that assume independence of interaction outcomes. We therefore chose to describe dominance hierarchies using the randomized Elo-rating (Sánchez-Tójar, Schroeder, et al., 2018), a recently developed method that, contrary to the original Elo-rating (Elo, 1978), does not consider the order of the interactions, but is one of the most powerful to study social hierarchies that are not very steep (Sánchez-Tójar, Schroeder, et al., 2018), as has been reported for common waxbills (Beltrão, Silva et al., 2021; Funghi et al., 2015). We computed randomized Elo-ratings for each individual, separately in each of the four time periods, with the function

'elo_scores' (R package 'aniDom', version 0.1.4; Farine & Sánchez-Tojar, 2019), and setting the argument 'n.rand' to 1000. The dataset with randomized Elo-ratings per individual, per time period, is provided in Table S1. We estimated hierarchy uncertainty using the repeatability of these randomized Elo-ratings (with the function 'estimate_uncertainty_by_repeatability' of the 'aniDom' package), which is a good indicator of the steepness of the social hierarchy and is independent of sampling effort (Sánchez-Tójar, Schroeder, et al., 2018). To further describe the structure of social hierarchies, we also calculated transitivity, which is a measure of orderliness that is not biased by unknown dyads (Shizuka & McDonald, 2012). For this, we first calculated the proportion of transitive triads (Pt, the number of transitive triads, divided by all triads; in a random population Pt is expected to equal 0.75), and then computed triangle transitivity (ttri, a scaled measured of Pt, varying between 0 and 1) as described in Shizuka and McDonald (2012), using the package Elorating (with the function 'transitivity', version 0.46.11; Neumann & Kulik, 2020). Finally, to evaluate sampling effort we computed the ratio of interactions to individuals (number of interactions divided by the number of individuals), which helps to evaluate whether inferred dominance hierarchies were reliably described (Sánchez-Tójar, Schroeder, et al., 2018).

2.4. Body Size and Behavioural Traits

Following the capture of the birds in the wild but prior to releasing the birds in the mesocosm (i.e. during the autumn of 2016 or of 2017), we measured several morphological and behavioural traits, as described in Gomes et al. (2020), and these measurements are in the supplementary material of Gomes et al. (2020). Below we provide a summary of each trait studied here.

2.5. Body size

Body size was quantified as the first principal component (PC) of a principal component analysis (PCA) on tarsus length and head-plus-bill length. The first PC explained 64% of the variance, with high loadings for both skeletal measurements (0.80 in both cases).

2.6. Mirror test

Mirror tests, which evaluate personality type along a reactive-to-proactive axis in common waxbills (Carvalho et al., 2013), were made twice to each individual with an

interval of ca. 6 weeks. Tests were video recorded and had a duration of 10 min, 5 min with the mirror covered with cardboard and 5 min with the mirror exposed. Based on previous studies (Carvalho et al., 2013; Funghi et al., 2015), we quantified four behaviours that reflected a social response to the mirror: (1) time facing the mirror; (2) time in fast movement; (3) activity; and (4) number of vocalizations. These four behaviours, during the period with the mirror exposed, were summarized in a PCA whose first PC explained 62% of the variation (loadings: time facing the mirror, –0.77; time in fast movement, 0.84; activity, 0.85; number of vocalizations, 0.69). High values on this PC indicate more proactive individuals that vocalize and move more in response to the mirror image, and lower values indicate more reactive individuals that are less active inside the cage and look more in the direction of the mirror image. We used the mean value of the two mirror tests as the behavioural measure for each individual. Guerra et al. (2020) showed that individual differences in this test are repeatable, even when retested across seasons or a year apart.

2.7. Tonic immobility

Tests of tonic immobility, a measure of stress or anxiety, were also conducted twice, after each mirror test, and consisted of placing the bird dorsally on top of a platform, in a state of tonic immobility. We measured the time (s) it took the bird to leave tonic immobility and fly away, up to a maximum of 60 s, and then averaged the two durations. Guerra et al. (2020) also showed that individual differences in this test are repeatable in the short and long term.

2.8. Breath rate

Breath rate, which can also be an indication of stress or anxiety, was quantified from the first 5 min of the mirror test, which were video recorded with the mirror covered, by monitoring belly movements indicative of breathing. These data were then cleaned for outliers using an algorithm developed in Gomes et al. (2021), and again we used the mean breath rate over the two tests. Gomes et al. (2020) showed that individual differences in this measurement are repeatable.

2.9. Detour-reaching performance

Detour-reaching performance, an aspect of cognitive performance related to inhibitory control (Boogert el al., 2011; Diamond, 1981), was tested using the detour-

reaching cylinder task adapted from Boogert et al. (2011). This consisted of training the birds to feed from an opaque cylinder, and then testing them with a transparent cylinder. Successful trials are those where the bird detours towards the sides of the transparent cylinder to reach the seeds inside, and unsuccessful trials are those where the bird did not inhibit the behaviour of pecking directly at the walls of the transparent cylinder. Detour-reaching performance was quantified as the proportion of successful trials, in a total of 15 trials.

2.10. Colour Ornamentation

Individual waxbills differ noticeably in the extent and saturation of colour ornamentation (Figure 5.1a; see also Figure 1 of Cardoso, Leitão, et al., 2014). We measured the extent of red colour in the breast and mask using digital photography, and red colour saturation in the breast using reflectance spectrophotometry, adapting methods from previous work on this species (Cardoso, Batalha, et al., 2014). As in previous work, we did not measure red colour saturation in the mask, since reflectance spectrophotometry of the small erect mask feathers is strongly confounded by skin reflectance in live specimens (G. C. Cardoso, personal observation). Photographs and measurements were taken 1–7 days before release into the mesocosm.

We used an Ocean Optics usb4000 spectrophotometer with a PX-2 xenon light source, calibrated between 0% (using opaque black velvet) and 100% reflectance (using an Ocean Optics WS-1-SL white standard; Ocean Insight, oceaninsight.com). Breast reflectance was measured with the reflectance probe perpendicularly to the feathers, at four points where red colour appeared more vivid. We flattened low reflectance values to 1% reflectance, as small and spurious inaccuracies near 0% can strongly affect colour metrics, and log10-transformed the reflectance measurements, since a ratio scale of reflectance is more biologically meaningful (Cardoso & Gomes, 2015). Red saturation of each colour spectrum was computed as the difference between the mean log-transformed reflectance at wavelengths from 600 to 700 nm (where red reflects the most) and the mean log-transformed reflectance across wavelengths from 320 to 700 nm (the bird-visible range of wavelengths; Montgomerie, 2006). For each individual, we then averaged the four saturation measurements from the breast.

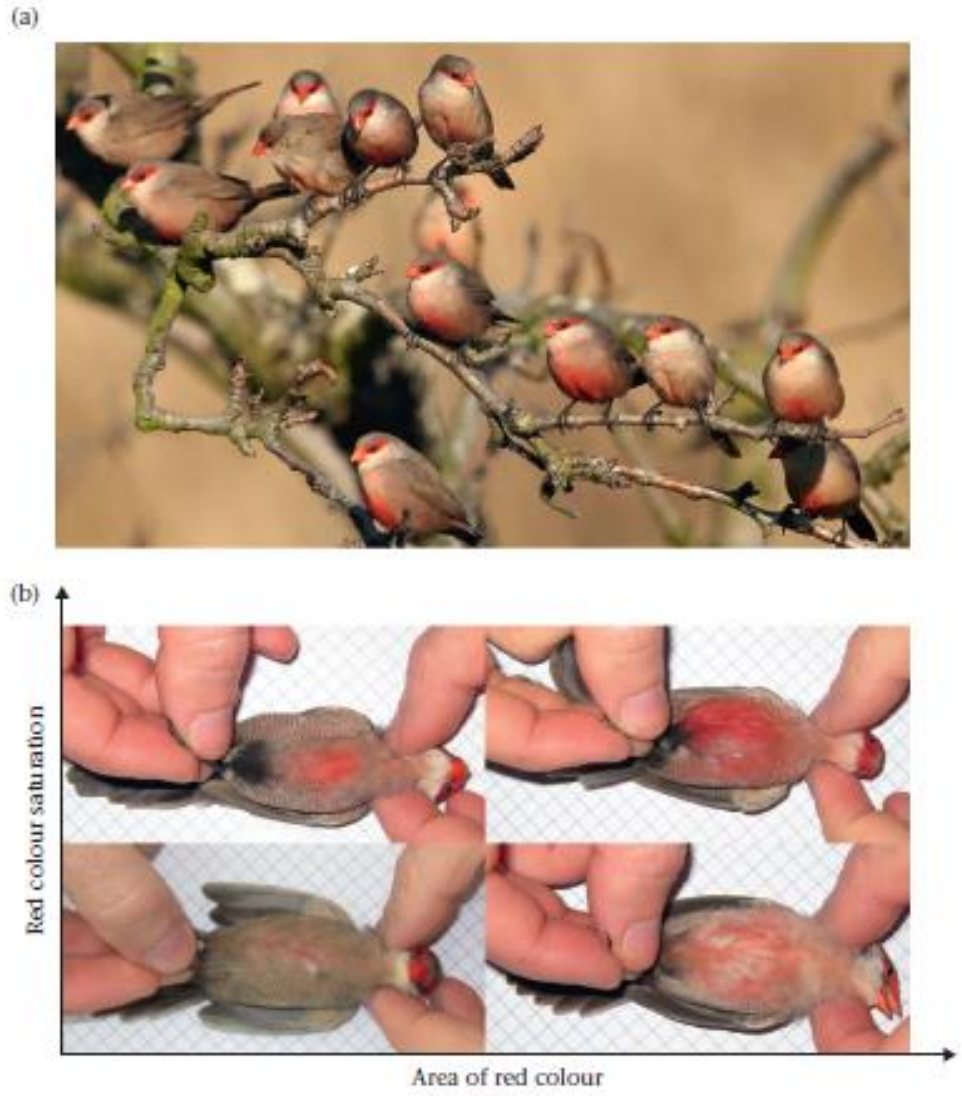

Figure 5.1. (a) A flock of common waxbills in the wild, showing individual differences in colour ornamentation. Photo: Pedro Olivença (https://commons.wikimedia.org/wiki/File:Bico_de_Lacre_(Estrilda_Astrild).jpg) licensed under a CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0/deed.en). (b) Examples of common waxbills differing in the saturation and area of red in the breast. The top row shows birds with more saturated red than the lower row, and the right column shows birds with a larger area of red than the left column.

To quantify the extent of red in the breast and mask, birds were photographed in ventral and lateral positions, on both the right and left side of the head, as described in Cardoso, Batalha, et al. (2014). The photographs included a metric scale on the background that allowed us to convert pixel counts to cm2. Areas were measured as number of pixels, using GIMP's (version 2.10.6) free selection tool, which allowed manual delineation of the red area in the breast or mask. This area was then converted to cm2 based on the number of pixels along 4 cm of the metric scale in the same photograph. We averaged the mask area for the left and right sides of each individual.

Area measurements were all made by the same person (A.C.R.G.), who later repeated the measurements for a set of 20 randomly selected individuals, blind to the earlier measurements. The intraobserver correlation coefficients of these repeated measurement were 0.94 (SE = 0.03; confidence interval, CI = [0.87; 0.98]; $P < 0.01$) for the breast, and 0.95 (SE = 0.02; CI = [0.89; 0.98]; $P < 0.01$) and 0.96 (SE = 0.02; CI = [0.90; 0.98]; $P < 0.01$) for the left and right sides of the red mask, respectively. Repeatability was computed with the 'rptGaussian' function from R package 'rptR' (version 0.9.21; Stoffel et al., 2017), including measurement replicate as the factor and individual identity as a random effect; normality and homogeneity of residuals were checked with histograms and QQ plots.

Individual differences in the saturation of red breast colour, and in the areas of red in the breast and mask, were found to be repeatable across years (Gomes et al., n.d.). Correlation coefficients between the extent of red in the mask, extent of red in the breast and red breast colour saturation were significant but not very high ($0.38 < rp < 0.52$, N = 54 birds, all $P < 0.01$). For example, even the correlation between red breast area and saturation, which pertain to the same colour patch, was only 0.52, meaning that these two aspects of colour ornamentation are not strongly linked (examples in Figure 5.1b).

2.11. Statistical Analyses

For each individual, in each of the time periods (i.e. NB1, B1, NB2 and B2), we computed the rate of displacements as the number of times that an individual displaced another, divided by the total time (min) it spent on the feeders. We estimated individual repeatability of displacement rates across the four time periods using the function 'rptGaussian' (version 0.9.22; Stoffel et al., 2017), after log(x+1) transformation to correct the right-skew distribution in these data. To test for differences in displacement rates between time periods we conducted a generalized linear mixed model (GLMM; Gaussian distribution with log link function) with displacement rate as the dependent variable (after an x+1 transformation to avoid zeros), time period as a predictor and individual identity as a random factor. To test whether dominant individuals are more aggressive, as opposed to simply being less attacked by others, we computed Spearman rank correlations between rate of displacements and randomized Elo-rating, separately for each time period. To understand the relation between the rate of displacements and randomized Elo-ratings, we computed Spearman correlations across individuals, separately for each time period.

We also estimated individual repeatability of randomized Elo-ratings using the function 'rptGaussian'. First, we estimated repeatability using each individual's randomized Elo-ratings in each of the four time periods. Then, to test repeatability from the first year to the second year, irrespective of seasonality, we first averaged each individual's randomized Elo-ratings in NB1 and B1, and in NB2 and B2, and then tested the repeatability across years. To test repeatability between the breeding and nonbreeding seasons, we averaged each individual's randomized Elo-ratings in B1 and B2, and in NB1 and NB2, and then tested the repeatability across seasons.

Since randomized Elo-ratings were found to be repeatable across time periods (see Results), we averaged the individual's randomized Elo-ratings computed for each time period, resulting in one single value per individual. For this, we first standardized randomized Elo-ratings from each time period (i.e. sample mean of 0 and standard deviation of 1), and then computed the mean randomized Elo-rating for each individual across time periods. Standardizing the randomized Elo-ratings per time period was necessary to avoid biased mean values, as four birds were not present in all time periods. Before running the models below, all continuous variables were standardized by subtracting the mean and dividing by two times their standard deviation, as recommended by Gelman (2008), to allow comparison between model estimates from dichotomous predictors (i.e. sex and capture year) and estimates from continuous predictors (all others).

We used an AIC-based multimodel inference approach (Burnham & Anderson, 2002) to test which phenotypic traits best predicted randomized Elo-ratings. We ran linear models with each individual's mean randomized Elo-rating as the dependent variable and, as predictors, different combinations of sex, capture year and the measured phenotypic traits (i.e. body size, behavioural and ornamental measurements; see below for excluded traits). We ran models with all combinations of these predictors up to a maximum of five predictors, to avoid overparameterization for our sample size (Burnham & Anderson, 2002; Harrell, 2001), and with no interactions or quadratic terms because, unlike for the main effects of predictors (see Introduction), we had no a priori expectations for interactions between predictors affecting social dominance. We then computed the AICc values (Akaike information criterion corrected for small sample sizes) of each model. For model averaging, we considered those models with a ΔAICc (difference in AICc) lower than 6 from the best model (Richards, 2005, 2008). Model averaging was weighted by Akaike weights, setting to zero the weights of predictors not included in each model, as recommended for the purpose of evaluating which predictors

have the strongest effect on social dominance (Burnham & Anderson, 2002; Grueber et al., 2011). We report model-averaged standardized coefficients (βst), its standard error (SE), z and P values. AIC-based model selection was performed with the R package 'MuMIn' (version 1.43.17; Barton, 2020).

In the AIC-based model selection approach described above we did not include two phenotypes. (1) We did not include red area in the breast because, as part of another work, it was experimentally manipulated after the first year. To test for associations between red breast area and social dominance, we used the data from only the first year analysed (i.e. NB1, B1) in an AIC-based multimodel inference approach similar to that described above, which now also included the red breast area as an additional predictor. (2) The main analyses also did not include detour-reaching performance, since nine of the 54 individuals in our data set had not completed this test (see details in Gomes et al., 2020). We none the less report results of a simple regression of randomized Elo-ratings on detour-reaching performance for the 45 birds that did complete the detour-reaching test. For all models with ΔAICc <6, we checked model assumptions with the package 'performance' (version 0.4.8; Lüdecke et al., 2020), and no violations of assumptions were detected. Variance inflation values, computed using the package 'performance', were below 3 indicating no problems of multicollinearity among predictors (Zuur et al., 2010). The randomized Elo-ratings can be found in the Appendix, Table A1.

2.12. Ethical Note

This research followed the ASAB/ABS ethical guidelines and work with wild animals was done under permits 690/2016/CAPT and 57/2017/CAPT from the Instituto da Conservação da Natureza e das Florestas.

3. Results

Based on video observations, the distribution of durations of feeder visits were very similar for visits that terminated with a displacement and those that terminated without a displacement (Figure 5.2a). Therefore, the duration of feeder visits did not allow us to distinguish between displaced and nondisplaced visits. In contrast, Figure 5.2b shows that the distributions of intervals between one individual departing from the feeder and another arriving at the same feeder were very different for feeder visits that

terminated with a displacement and those that did not. Intervals after a displacement were shorter than 2 s in 99.6% of the cases (227 of 228), while only 8% of intervals after nondisplaced feeder visits were shorter than 2 s (only 10 of 125). Therefore, intervals shorter than 2 s indicate with a great degree of certainty that a displacement from the feeder occurred in our system, and we used this criterion to identify displacements in the RFID data stream.

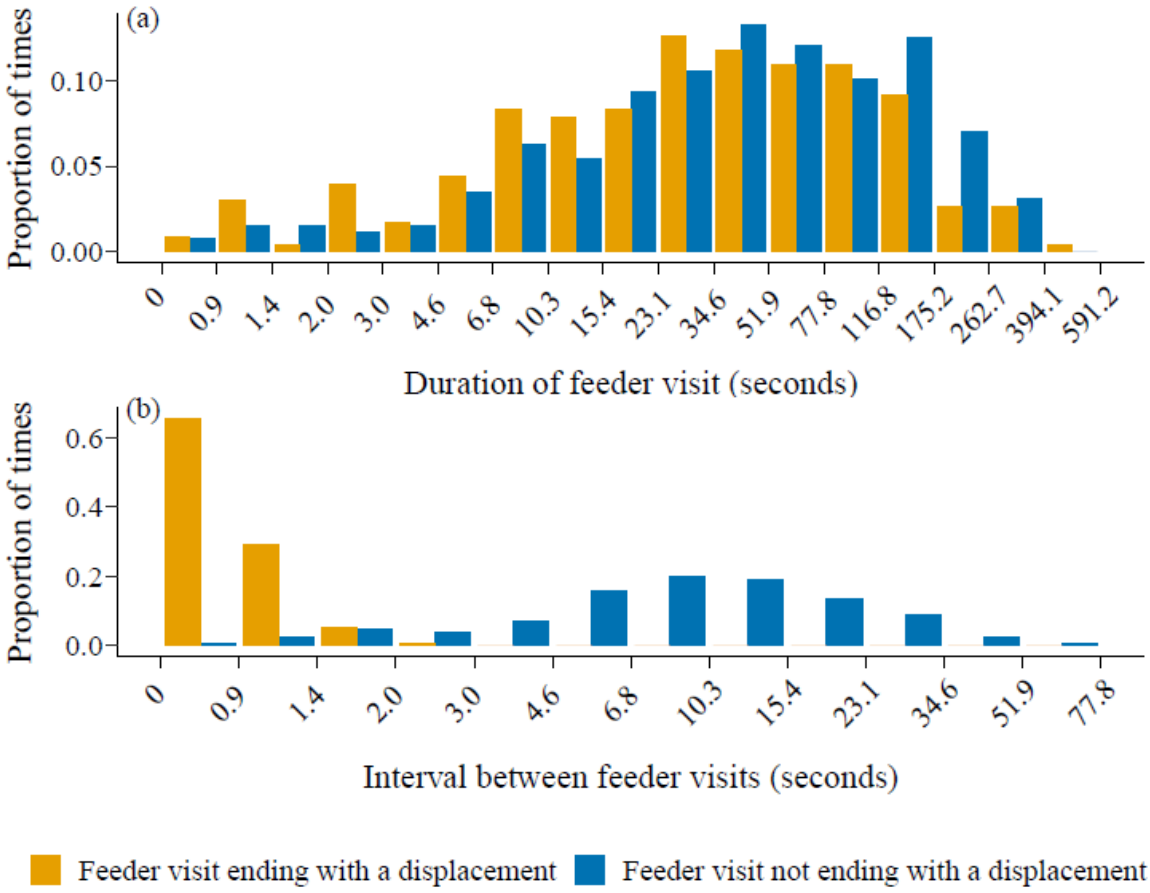

Figure 5.2. Histograms for (a) the duration of feeder visits and (b) the time interval between one individual departing and another arriving at the same feeder, separately for instances where leaving the feeder was due to a displacement and where it was not.

Based on the RFID data, the rate of displacements differed between seasons (GLMM of displacement rate on time period: $\chi^2_3 = 245.31$, $P < 0.001$). Inspection of Figure 5.3 shows that this difference between seasons is mostly due to displacements occurring more frequently in the nonbreeding than in the breeding seasons. Despite these seasonal differences, the rate of feeder displacements by different birds was repeatable across the four time periods ($R = 0.38$, $P < 0.001$). The correlations between

randomized Elo-ratings and rate of displacements were statistically significant in all time periods (NB1: rS = 0.75, N = 54; B1: rS = 0.86, N = 54; NB2: rS = 0.70, N = 51; B2: rS= 0.82, N = 50; P < 0.001 in all cases).

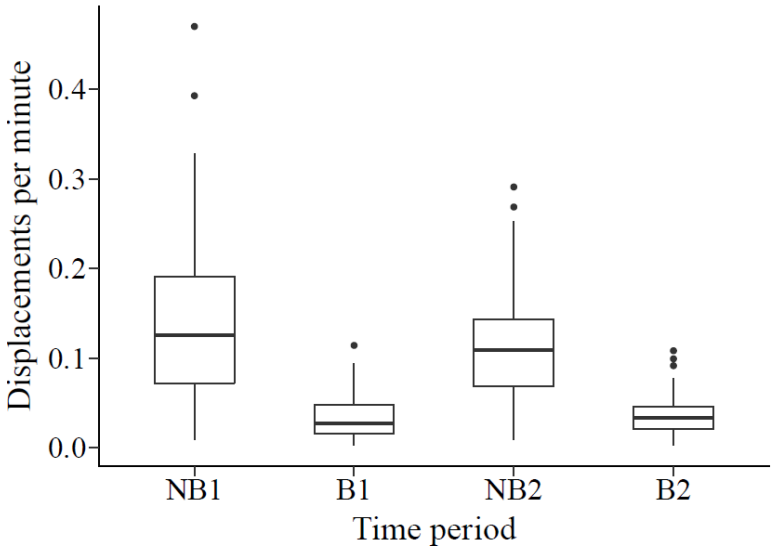

Figure 5.3. Number of displacements/min across all four time periods (NB1, B1, NB2, B2). Boxes show the median and interquartile range (between the 25th and 75th percentiles), whiskers represent the data range up to 1.5 the interquartile difference above or below the box and dots represent individuals outside this range.

Randomized Elo-ratings were repeatable across the four time periods (R = 0.68, P < 0.001), and mean randomized Elo-ratings of each individual were also repeatable between the first and second years (R = 0.74, P < 0.001) and between breeding and nonbreeding seasons (R = 0.80, P < 0.001). In calculating randomized Elo-ratings, the ratio of interactions to individuals (a measure of sampling effort) was 148.6 for NB1, 45.4 for B1, 129.1 for NB2, 27.9 for B2, indicating that dominance hierarchies were reliably inferred (ratio > 20 in all cases; Sánchez-Tójar, Schroeder, et al., 2018). The slopes of dominance hierarchies were not steep in either of the seasons (0.34 ≤ R ≤ 0.56), indicating that there were instances where more dominant individuals could sometimes be displaced by less dominant individuals, and hierarchies appeared milder in the nonbreeding seasons (NB1, R = 0.43; NB2, R = 0.34) and steeper in the breeding seasons (B1, R = 0.56; B2, R = 0.48). Transitivity of dominance was statistically significant in all time periods (comparison of triad transitivity with the random expectation: NB1: Pt = 0.88, ttri = 0.52, P < 0.001; B1: Pt = 0.91, ttri = 0.64, P < 0.001; NB2: Pt = 0.83, ttri = 0.32, P < 0.001; B2: Pt = 0.84, ttri = 0.36, P < 0.001).

The model selection approach, to test which individual phenotypes predict social dominance, resulted in 68 models within 6 ΔAICc from the best, which together included

eight predictors: breast saturation, mask area, capture year, sex, body size, breath rate, mirror and tonic immobility tests. Breast saturation was present in all but four of these top models and on average it was strongly and positively associated with randomized Elo-ratings (Table 1, Figure 5.4). No other predictor had a statistically significant effect on social dominance, and effect sizes of the remaining predictors were low (Table 1). Using data from the first year only, to include the size of the red breast area as predictor, resulted in 60 models within 6 ΔAICc from the best. In this smaller analysis, we only found two predictors showing positive tendencies, breast saturation as before and tonic immobility (Table 2). The association with tonic immobility, however, should be taken cautiously because it was not present in the larger analysis with all data (Table 1). Although in this smaller analysis breast saturation had a βst that was not too different from that in the main analysis, its association with social dominance was statistically weaker (Table 2) than in the main analysis (Table 1, Figure 5.4). Breast saturation was included in 50 of the 60 top models.

Table 5.1. Model averaging results of the relation between randomized Elo-ratings and predictors

Predictor	β_{st}	SE	*z*	*P*
Capture year	0.23	0.16	1.43	0.15
Sex	0.04	0.11	0.38	0.70
Body size	0.02	0.08	0.31	0.76
Mirror test	0.05	0.10	0.49	0.63
Tonic immobility test	0.08	0.12	0.68	0.50
Breath rate	–0.05	0.10	0.47	0.64
Breast saturation	0.40	0.15	2.55	0.01*
Mask area	–0.005	0.06	0.08	0.93

Standardized coefficient (βst), standard error (SE), z and P values. Positive values of βst for sex indicate male > female.
*$P < 0.05$.

The nine birds that did not interact with the detour-reaching apparatus (Gomes et al., 2020) were not randomly distributed with regard to social dominance or ornamentation, but tended to be more dominant and have more saturated breast colour (yellow points in Figure 5.4). We, therefore, did not remove these individuals from the model selection approach above, because removal of such nonrandom data would bias tests. None the less, a simple regression of mean randomized Elo-ratings per individual on detour-reaching performance, for those 45 birds that did complete the detour-reaching test, did not suggest any relation (βst = 0.14, SE = 0.16, P = 0.37).

Table 5.2. Model averaging results of the relation between randomized Elo-ratings and predictors, considering only data from the first year of the study (i.e. NB1 and B1)

Predictor	β_{st}	SE	*z*	*P*
Capture year	0.21	0.15	1.36	0.17
Sex	0.08	0.14	0.52	0.60
Body size	–0.01	0.06	0.18	0.86
Mirror test	0.08	0.13	0.66	0.51
Tonic immobility test	0.26	0.15	1.77	0.08
Breath rate	–0.004	0.05	0.07	0.94
Breast saturation	0.30	0.18	1.67	0.09
Mask area	–0.02	0.08	0.30	0.76
Ventral area	–0.003	0.06	0.06	0.95

Standardized coefficient (βst), standard error (SE), z and P values. Positive values of βst for sex indicate male > female.

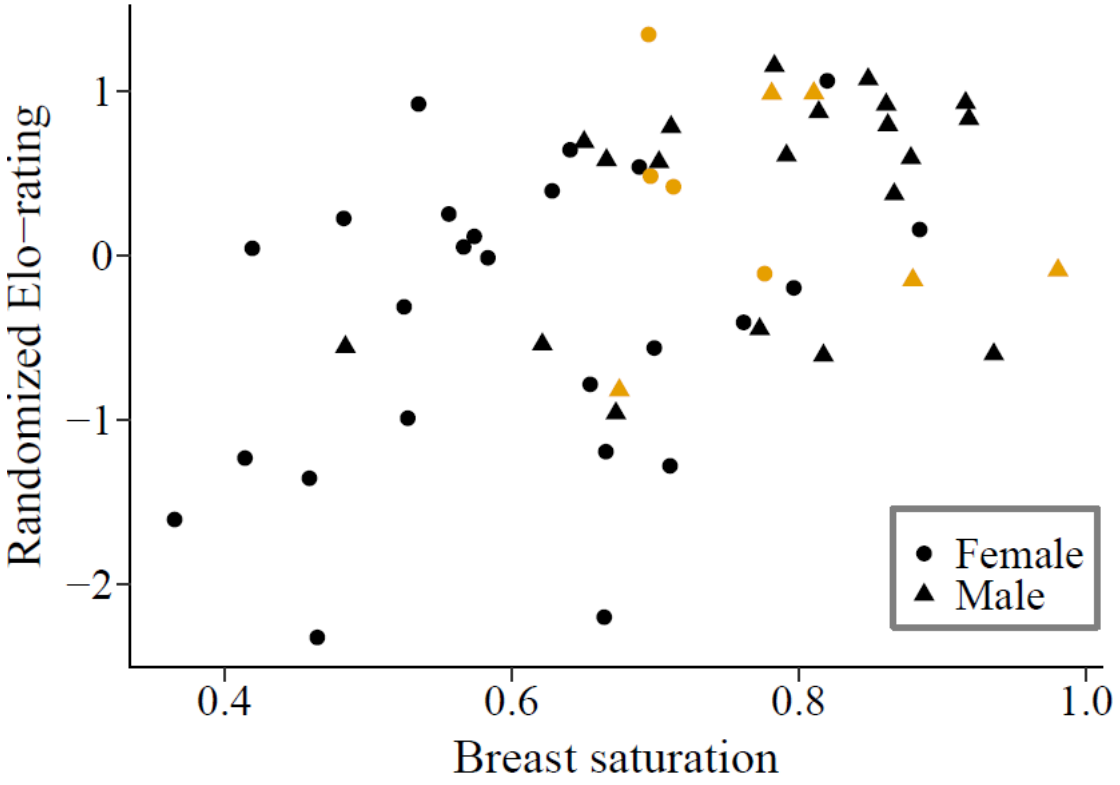

Figure 5.4. Scatterplot of the mean randomized Elo-rating of each individual, as a function of its red breast saturation. The yellow points, grouped mostly on the right upper part of the figure, are the nine individuals that did not complete the detour-reaching task, showing that they are not randomly distributed with regard to social dominance or ornamentation.

4. Discussion

By monitoring aggressive dyadic interactions (displacements from feeders) in a mesocosm population of common waxbills during two nonbreeding and two breeding seasons, we arrived at four main results. First, we found transitive and mildly steep hierarchies (steeper during breeding seasons) where, despite seasonal changes in the rate of aggressive interactions, dominance ratings of individuals were repeatable across seasons and years. Second, we found that waxbill social dominance was not predicted by personality differences along a reactive-to-proactive axis, similarly to previous results (Funghi et al., 2015), and not predicted by individual differences in stress-related traits or in inhibitory control. Third, contrary to previous observations of waxbills confined to birdcages (Funghi et al., 2015), here we found that social dominance was not related to larger body size. Finally, we found that social dominance was predicted by colour ornamentation, specifically by the saturation rather than the area of waxbills' red plumage. We discuss these results in turn.

Similarly to results of a previous study with common waxbill groups in birdcages (Funghi et al., 2015), we found that the steepness of common waxbills dominance hierarchies was mild, indicating that more subordinate individuals may sometimes win against more dominant individuals. The dominance ratings of each bird were strongly repeatable, including between the first and second year, and between breeding and nonbreeding seasons, which means that social dominance is a stable individual phenotype. Despite this stability in social dominance, we observed steeper dominance hierarchies during the breeding seasons. This may perhaps be due to mate guarding or other forms of competition throughout the breeding season (Harts et al., 2016), since high-competition contexts have been shown to promote steeper hierarchies (Barrett et al., 2002). Even though breeding seasons probably entail more competition, we observed a reduced rate of displacements at feeders at that time. This might be an effect of the steeper dominance hierarchies, since clearly defined hierarchies can reduce the number of aggressive interactions (Holekamp & Strauss, 2016; Ward & Webster, 2016; e.g. Silk et al., 2019), or alternatively, because waxbill flocks are smaller and more dispersed during the breeding season (Clement et al., 1993), there might be fewer opportunities for aggressive interactions.

Waxbill personality differences along a reactive-to-proactive axis did not predict social dominance. The literature on the relation between animal personality and social dominance has produced conflicting results across passerine species. In some species, more proactive individuals have higher dominance (e.g. zebra finch, *Taeniopygia guttata*;

David et al., 2011); in others it is the more reactive individuals that are reported to be more dominant (mountain chickadees, *Poecile gambeli*; Fox et al., 2009), or no relation between personality type and social dominance was found (e.g. black-capped chickadees, *Poecile atricapillus*; Devost et al., 2016). Conflicting results were also reported within the same species (great tit; Dingemanse & De Goede, 2004; Verbeek et al., 1999). In waxbills, reactive-to-proactive personality differences are not related to body size, nor to other morphological traits that could reflect condition or competitive ability (Carvalho et al., 2021; Gomes et al., 2020), which helps to explain why personality does not predict social dominance either in birdcages (Funghi et al., 2015) or in our study.

The stress-related traits that we studied (tonic immobility and breath rate) did not predict social dominance, providing no support for an important role of stress in dominance relations. Associations between stress levels and social dominance, however, could be further studied by measuring physiological indicators of stress (e.g. corticosterone levels) in relation to actual agonistic interactions (e.g. Poisbleau et al., 2005; Yang & Wilczynski, 2003). The cognitive trait that we studied here, inhibitory control, was not related to social dominance, unlike recent findings with hyaenas, *Crocuta crocuta*, living in large groups, where low-ranking individuals had higher inhibitory control (Johnson-Ulrich & Holekamp, 2020). Our results, however, do not imply that other cognitive traits do not influence dominance hierarchies in waxbills, and, in fact, in other species, dominance status has been associated with individual differences in traits such as memory (e.g. Pravosudov et al., 2003) and learning (e.g. Kar et al., 2017).

While previous work, on waxbill groups in birdcages, found that large body size was associated with social dominance (Funghi et al., 2015), we found no association between body size and dominance. An important difference in relation to the previous study is that we studied waxbills interacting mostly when in the air, around feeders placed over 1 m high on a wall, whereas in birdcages they had little room to fly and interacted mostly on perches or on the cage floor. Waxbills are very light (ca. 8 g) and acrobatic, and in nature they mostly feed perched on the stems of grasses (Cardoso et al., 2018; Goodwin, 1982; Oren & Smith, 1981; Sullivan et al., 2015), so that most of their interactions occur in the air. Larger weight or body size may confer fighting advantages when animals interact on the ground, but not necessarily in aerial interactions. On the contrary, a lighter body may be advantageous for aerial manoeuvrability (Hedenström & Rosén, 2001; Van Den Hout et al., 2010). The contrasting results in Funghi et al. (2015)

and here, therefore, indicate that a fighting advantage of large body size is context specific, and does not apply to aerial interactions in a more natural environment.

Most traits we studied, including personality, stress, cognition, morphology and sex, did not predict social dominance, and therefore we still do not fully understand why some individuals and not others are more aggressive and become dominant. None the less, colour ornamentation did predict social dominance, since the saturation of red in the breast was strongly and positively associated with dominance rating and may, therefore, function as a badge of status signalling dominance. Unlike morphological or personality traits, which could causally explain individual differences in aggressiveness and dominance, coloration can only function as a signal, perhaps allowing a safe assessment of aggressiveness or fighting ability without entering into direct conflict. We found that the association with social dominance was specific to the saturation of red plumage, not to the size of red plumage patches. Waxbills also have vividly coloured red bills, which we did not study in this long-term analysis because bill colour is plastic (Funghi et al., 2018), it can change depending on short-term ecological conditions (Freitas et al., 2021) and, unlike for plumage colour traits, between-individual differences in bill colour are not repeatable in the long term (Gomes et al., n.d.). Also, previous work showed that waxbill bill colour saturation does not predict individual differences in aggressiveness (Funghi et al., 2018), further indicating that a role in signalling dominance is specific to plumage colour saturation. Our results help to explain social preferences that were previously found in laboratory choice experiments with common waxbills: females preferred individuals with more saturated red plumage and, controlling for coloration differences, they approached males more than other females, suggesting a sexual preference for saturated red plumage (Cardoso, Leitão, et al., 2014). Considering our results, this preference might be due to fitness advantages of pairing with dominant individuals, as is commonly found in other species (e.g. Komers & Dhindsa, 1989; Pizzari & Birkhead, 2000; Ratcliffe et al., 2007). Males, in contrast, were found to prefer less saturated red plumage when interacting with other males (Cardoso, Leitão, et al., 2014), which, in light of our results, could be a strategy to avoid aggressive individuals.

Badges of status like colour ornamentation are potentially falsifiable, such as when subordinate individuals are able to develop and express them (Senar, 2006), but several studies none the less showed that coloration can be a reliable signal of social dominance (reviewed in Santos et al., 2011). Most of these studies are on melanin-based colours (e.g. López-Idiáquez et al., 2016; Rat et al., 2015; Roulin, 2016), whose

expression is generally strongly modulated by testosterone and, since testosterone also regulates aggressiveness, in this way may reliably signal dominance (reviewed in Bókony et al., 2008; Roulin, 2016). Although carotenoid-based coloration is not related to social dominance in many species (e.g. Edler & Friedl, 2010; McGraw & Hill, 2000; Quesada & Senar, 2007), some studies have found that, similarly to our results, carotenoid-based colours can indeed signal dominance (e.g. Leitão et al., 2015; Murphy et al., 2009; Pryke et al., 2002; Young et al., 2016). Carotenoids can have antioxidant and immune functions, such that diverting carotenoids from these functions into plumage coloration might create a cost that helps to maintain the honesty of carotenoid-based colours as a signal of quality or condition (Pérez-Rodríguez, 2009; Simons et al., 2012; Svensson & Wong, 2011). Supporting this, carotenoid- or antioxidant-rich diets allow female common waxbills to express more saturated red bill colour (Freitas et al., 2021). Moreover, work on other species suggests that carotenoid-based coloration can signal parasite resistance, an indicator of immune status (Koch & Hill, 2018; Koch et al., 2017; Weaver et al., 2018).

Since carotenoid-based colours can be signals of quality, mate preferences have often been found for either the size or, especially, the saturation of carotenoid-based colour patches (Hill, 2006). High colour saturation requires mobilizing, metabolizing and depositing a larger amount of carotenoid pigments (Saks et al., 2003), which may explain the sexual preferences for colour saturation as a signal of individual quality. Equally suggestive that the saturation of ornamental colours may more often be a sexual or social signal than the size of these colours, it has been found that, on average, gregarious estrildid species have more saturated plumage colours than solitary species, but not a larger extension of ornamental coloration (Gomes et al., 2016). Only three studies (Leitão et al., 2015; Pryke et al., 2002; Pryke & Andersson, 2003) have tested whether the size or the saturation of plumage coloration is the most informative aspect of carotenoid-based signals of dominance. In red-collared and red-shouldered widowbirds, both plumage colour and the size of the red coloured patch indicate social dominance (Pryke et al., 2002; Pryke and Andersson 2003) but, in the red-shouldered widowbird, patch size is the most reliable signal (Pryke & Andersson, 2003). In contrast, in European serins it is the colour saturation of the yellow crown, rather than its size, that indicates social dominance (Leitão et al., 2015). Our results with common waxbills indicate that the saturation rather than the size of red coloration indicates dominance, perhaps pointing to a pattern similar to that from studies on mate preferences (Hill, 2006), whereby the saturation of carotenoid-based colours is often the most relevant signal.

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Chapter 6 | Bullying as an advertisement of social dominance in common waxbills

Bullying as an advertisement of social dominance in common waxbills

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Abstract

Bullying consists of preferentially attacking individuals lowest in the dominance hierarchy, and its functions are unclear because the most subordinate individuals do not pose social challenges to the aggressor. Instead, conflict is expected mostly between individuals of similar dominance rank or socially-distant (i.e., weakly associated), among whom dominance relationships may not be well established. A possible function of bullying is that it may be used as a low-risk strategy of showing-off dominance to relevant third parties. To study this hypothesis, we monitored aggressions during feeding, the composition of audiences, dominance hierarchy and social network of common waxbills (*Estrilda astrild*) in an open-air mesocosm, and tested 1- whether their aggressions show a pattern of bullying, and 2- whether audience effects influence aggressiveness. Waxbills showed bullying, most often attacking the lowest-ranking individuals rather than socially-distant individuals or those of similar dominance rank, and aggressions increased when the audience included socially-distant individuals, indicating a signalling function of bullying. Showing-off dominance in the presence of socially-distant individuals may be a strategy to manage dominance hierarchies, avoiding direct fights with potentially dangerous opponents in the audience. We suggest that bullying is a safe manner of managing dominance hierarchies, by signalling dominance status to potential opponents.

Keywords: Aggression strategies, audience effects, dominance hierarchies, *Estrilda astrild*, social dominance pattern, social networks

1. Introduction

Gregariousness and animal sociality can facilitate, for example, foraging (e.g., [1,2]) or defence against predators (e.g., [3,4]), but it may also increase agonistic interactions between group members [5]. Dominance hierarchies may emerge as a result of within-group conflicts, and being able to recognize the dominance rank of other individuals may decrease overall aggression [6,7]. Recognizing dominance rank and other aspects of social organization requires notable cognitive abilities, in the form of acquiring, processing, retaining and using information from the social environment [8]. For example, dominance status of other individuals may be perceived through direct interactions with them or by observing their interactions with others [9,10]. The information can then be memorized and shape future interactions [11].

Recognizing dominance rank may be based on the evaluation of signals or cues of dominance, and/or on individual recognition combined with previous knowledge of their dominance status [10]. For example, experimental manipulation of badges of status in golden-crowned sparrows (*Zonotrichia atricapilla*; their black and gold crown patches) affected how unfamiliar individuals evaluated their dominance, but not how familiar birds reacted to them [12]. Similar results were found for the green anole (*Anolis carolinensis*), where the colour of eyespots function as a badge of status, but mostly in contests with unfamiliar individuals [13]. These results show that both badges of status and individual recognition can be used to evaluate the dominance rank of others.

Individuals may identify the dominance status or aggressiveness of others [11], as has been found in taxonomically diverse species (e.g., mammals: [14,15]; birds: [16,17]; fishes: [18,19]). Recognizing the dominance rank of others allows individuals to adopt a “rank-informed aggression strategy”, directing aggression depending on dominance relationships [20]. Dominance hierarchies are frequently shaped by differences in resource holding potential [7,21], or the ability to win fights [22]. Therefore, due to their discrepancy in fighting ability, we expect that interactions between individuals of very different dominance ranks are stable and not agonistic, with subordinates avoiding or not challenging dominant individuals [7]. This contrast with interactions between individuals similar in rank, where the similarity in fighting ability may cause aggressive disputes to compete for resources or to clarify dominance relationships (e.g., [23,24]). There are, nonetheless, exceptions to these general predictions. For example, a bullying pattern of aggression, where attacks are preferentially directed towards the most subordinated individuals, is observed in some species or populations [20], including

monk parakeets (*Myiopsitta monachus*), especially towards group members that had been absent [25].

Aggression rates can also be affected by social relationships between individuals [26], namely in gregarious species where individuals associate non-randomly in social networks depending on social preferences [27]. We expect that individuals prefer to associate with others from whom they receive less aggression, resulting in fewer aggression rates between socially-close (i.e., higher strength of associations) than socially-distant individuals (i.e., lower strength of associations; e.g. [28,29]; but also see [30]). Another reason to predict more aggressiveness between socially-distant individuals is that there could be more uncertainty in the perception of their relative dominance ranks, due to less frequent interactions.

Not only the social relationships between interacting individuals, but also relationships with individuals in the audience, may affect aggressiveness and other social behaviours [32–34]. The presence of dominant individuals in the audience can affect different behaviours [31,32], including decreasing aggressiveness by subordinates [33,34]. For example, female spotted hyenas are less likely to participate in coalitionary aggression when higher-ranking hyenas are present in the audience, likely to avoid the risk of being attacked by those dominant individuals [35]. Social proximity to the audience can also change one's behaviour, and studies with corvids and primates have shown that individuals behave differently in the presence of socially-close or socially-distant bystanders (e.g., [36,37]). Namely, white-faced capuchins monkeys (*Cebus capucinus*) solicit help from allies socially-closer to themselves than to the opponent [37], and during fights common ravens (*Corvus corax*) call for help more often when in the presence of kin [36]. If aggressiveness can change depending on the composition of audiences, we expect that the predictions explained earlier (more aggression towards individuals similar in social rank, or towards individual that are socially-distant to each other) can also apply to audience effects. Namely, we expect that individuals show-off more aggression in the presence of bystanders that are of similar dominance rank to themselves, or in the presence of socially-distant bystanders, to help clarify dominance relationships between them. It is however difficult to evaluate these hypotheses because there are yet few studies on how bystander dominance rank [33,34] or social proximity [36,37] may affect aggressiveness.

We studied group-level patterns of aggression in a highly gregarious bird, the common waxbill (*Estrilda astrild*), to test whether aggression rates are higher towards individuals of similar dominance rank, towards individuals more distant in the social

network, or in the presence of bystanders of similar dominance rank or socially-distant. We studied aggression when foraging because, in species that forage in groups, this can be an important context for socialization and for establishing dominance hierarchies [7]. In the common waxbill (hereafter simply waxbill), males and females do not differ in social dominance, on average [38], and dominance hierarchies have mildly steep slopes (i.e., where sometimes subordinates can win over more dominant individuals) that are stable through time, even across seasons and between consecutive years [38,39]. Waxbills also form stable social networks, with non-random and long-lasting associations among individuals [40], suggesting good individual recognition abilities that could help avoid conflicts [41]. We studied waxbills with passive integrated transponder (PIT) tags, living in a large open-air mesocosm equipped with an array of radio-frequency identification (RFID) antennae in perches and feeders (Figure 1). This system allows us to monitor aggressive interactions at feeders [38], proximity-based social networks [42], and the composition of audiences with great detail. Using RFID data, we characterized the dominance hierarchy, and test how they modulate aggressiveness depending on the social rank and social proximity of those attacked and also of audience members, with the goal of understanding their strategies to manage social dominance hierarchies.

2. Methods

2.1. Study system, aggressive behaviour, social hierarchy and social network

We studied waxbills living in a large open-air mesocosm covered by fine net (ca. 235 m2, net ceiling at 1.30 to 2.70 m high), with abundant natural vegetation and exposed to natural climate (Figure 5.1a,b). A total of 12 feeders and 8 perches (15.5 cm-long) were located in an area of ca. 10 m2 (Figure 5.1b,c,d). Each feeder had a RFID antenna, and each perch had a row of 4 RFID antennae (Dorset ID, The Netherlands). The birds had *ad libitum* access to food (Tropical Finches Prestige, Versele-Laga) and water. Waxbills had been captured from the wild, and all were living in the mesocosm for at least a year by the time this study started. All individuals had a PIT tag (Dorset ID) on a leg ring, and the array of RFID antennae continuously recorded arrival and departure times of each individual to the feeders and perches. For details on the mesocosm and capture of wild waxbills see [43]. Common waxbills were captured under the permits 690/2016/CAPT, 57/2017/CAPT, 127/2019/CAPT and 112/2020/CAPT from Instituto da Conservação da Natureza e das Florestas (ICNF). All applicable national and institutional guidelines for the handling and care of the birds were followed.

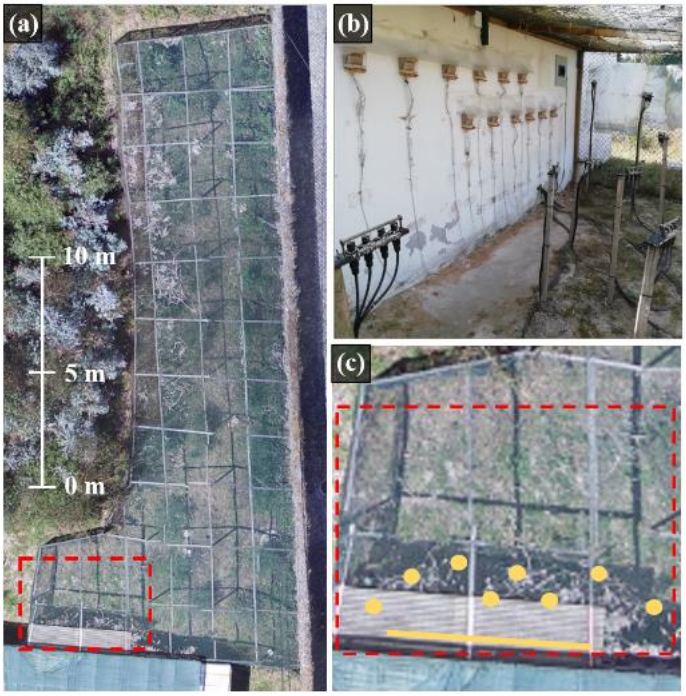

Figure 6.1. (a) Aerial photograph of the mesocosm, with the feeding area marked in red, (b) perspective of the feeding area containing 12 feeders and 8 perches equipped with radio-frequency identification (RFID) antennae, and (c) aerial detail of the feeding area showing the location of the 8 perches (yellow dots) and the set of feeders along the wall (yellow line). Aggressive displacements at the feeders were identified from the RFID datastream, and used to characterize the dominance hierarchy [38]. The RFID datastream was also used to monitor audiences of those aggressive events, and to infer the social network of the flock based on proximity among individuals [42].

We used 4 months of RFID data, from October 2018 to January 2019 [44], to identify aggressive interactions among the 52 waxbills in the mesocosm at that time (24 males and 28 females), to describe their dominance hierarchy and social network. Four months of RFID data in this system provides abundant information to robustly infer the social network [42] and dominance hierarchy ([38]; see also the results, below). It is also useful that these 4 months are in the non-breeding season [44], when sex roles should be more similar [40], because we can analyse social behaviour and group structure without confounding effects of reproduction. The RFID data went through an automated curation process, described in [42], to correct reading redundancies or failures of the RFID antennae. Aggressive displacements at the feeders were then automatically identified from the RFID datastream (code available in [38]). Briefly, [38] showed that aggressive displacements are reliably identified when the time period between one individual leaving a feeder and the other individual arriving there is inferior to 2 seconds in the RFID datastream. The criterion to identify displacements also implies that the two birds, the displaced one and the one staying afterwards, remained in the feeder for a minimum of 3 seconds, in order to avoid ambiguous interactions where one individual does not displace the other (e.g., quick fights recorded by the RFID system as a series of rapid switches between the two individuals).

Also as described in [38], we used displacements at feeders to infer dominance hierarchies by computing randomized Elo-ratings [45]. Randomized Elo-ratings are scores of social dominance, on a continuous scale, and were shown to be among the most robust to infer dominance hierarchies with slopes that are not very steep [45], as is the case in our study species [38,39]. In a dominance hierarchy with mildly steep slope there may be several individuals quite similar in dominance, and therefore it is useful to use dominance scores on a continuous scale, as opposed to ordinal ranks of dominance, so as not to lose information on the distances in dominance between individuals. Elo-ratings are computed by iterative updating of dominance scores, weighting more heavily wins against more dominant individuals and losses against more subordinate individuals [46]. We computed randomized Elo-ratings with the function “elo-scores” in the R (v. 4.0.2 [47]; package “aniDom”, v. 0.1.4 [48]). We also computed the repeatability of Elo-ratings (function “estimate_uncertainty_by_repeatability” in the “aniDom” package), which is a measure of uncertainty and steepness of the hierarchy, transitivity (function “transitivity” in the package “EloRating”, v. 0.46.11 [49]), which analyses linear dominance relationships within triads of individuals and is a measure of orderliness in the hierarchy [50], and, finally, the ratio of interactions (number of interactions divided by the total number of individuals) as a measure of sampling effort to evaluate if the dominance hierarchy was inferred based on sufficient data [45].

Previous social network analyses comprising this time period in the mesocosm, as well as data from three additional seasons, tested different proximity-based criteria to identify associations, and found that the criterion better able to reveal network structure is based on the time that two individuals are at the same time in antennae less than 40 cm from each other (Figure E1 in [40]). Therefore, similarly to [40], we used as index of association the total duration of time that a pair of individuals was together at up to 40 cm from each other, divided by the sum of durations that each of the two individuals was in the RFID datastream. This index ranges from 0 to 0.5 and is otherwise similar to the occurrence-based simple ratio index [51]. We tested whether the social network was significantly non-random, by comparing the structure of the observed network (coefficient of variation of the strength of associations, and network entropy [42]) to a null distribution model. This model was based on cumulatively permuting pairs of individual observations, between gathering events, 1,000,000 times, within the same days, and at each 1000 steps computing a social network, in order to obtain a null distribution of statistics (see [42]). The observed social network structure was significantly higher than the ones from the random null model (coefficient of variation of the strength of associations = 0.687, two-tailed $P < 0.001$; network entropy = 11.060, two-tailed $P < 0.001$). Details and code

for the analyses in this section are found in [42]. All the birds were recorded in the RFID system more than 70% of the days the work lasted, with the exception of one individual that was only recorded in 30% of the days and, therefore, we did not include it in the following analyses.

2.2. Aggression towards individuals similar in dominance status

In this and the remaining analyses we used both permutation-based and parametric statistical tests, following [40]. We report results from the parametric regression models in the main text, but we also report methods and results for the permutation-based approach in the Appendix E.

We tested the prediction that aggressiveness should be higher towards individuals of similar dominance rank, using a multimembership model with a Markov chain Monte Carlo (MCMC) approach [52]. The response variable in this model was the rate of aggression per dyad of individuals, computed as the total number of aggressive displacements in the dyad divided by the time (in seconds) the two individuals were simultaneously in the feeding area (i.e., in any of the feeders and nearby perches with RFID antennae; Figure 5.1b). This variable was log transformed, as ln(x + 0.0001), to approach normality. Log-transformation is advisable also on biological grounds [53], because perception of quantities in animals is generally logarithmic rather than linear [54,55]. As predictor, we used the absolute difference of dominance ratings (i.e., Elo-ratings) between the two individuals in a dyad. This is a measure of dissimilarity in social dominance, where small differences indicate individuals similar in social dominance. We also included as covariate the total time each member of a dyad was at the feeders, in order to control for potential bias of recording some individuals more than others [56], despite it being unlikely that our data collection is substantially biased because all individuals feed from the same feeders with RFID antennae (see also [40]). All variables were centred and standardized. The model also included a random effect, a multimembership grouping term in which each individual in a dyad enters as a random term, to account for dyad identity [57,58]. We used the MCMCglmm R package (v. 2.32; [59]) with 110000 iterations in order to attain a recommended effective sample size over 10000 [60]. The degree of belief parameter (nu) was set to zero, and the expected variance (V) to 1. We used a thinning interval of 10 and discarded as a burn-in the first 3000 iterations. Model convergence was achieved and no autocorrelation was detected (verified using functions in the coda package, v.0.19-4 [61]).

To distinguish whether the effects of dissimilarity in dominance rank on aggressiveness are due to more dominant individuals attacking subordinates or vice-versa, as follow-up analyses, we ran two more models. These models are as described above, except that as response variable we now use either (1) the aggression rate from the more dominant individual towards the more subordinate individual in each dyad (aggressions downwards in the dominance hierarchy), or (2) the aggression rate from the subordinate towards the dominant individual in each dyad (aggressions upwards in the dominance hierarchy).

The response and predictor variables (respectively, aggression rate in a dyad, and difference in dominance ratings in the dyad) are computed from the same type of data: aggressive displacements at the feeders. This should not pose a problem of circularity because the dominance rating for an individual uses information from all aggression involving it, and not only from a specific dyad. Nonetheless, we confirmed all results from this section by re-running the same 3 models, after having split the RFID data into two parts: data from the even days (counting from the onset of the study) to calculate aggression rates, and data from the odd days to compute dominance ratings. In all cases, these additional analyses (see Appendix E for methods and results) confirmed the results reported in the main text.

2.3. Aggression towards individuals distant in the network

We tested the prediction that aggressiveness should be higher between individuals distant in the social network using, as in the analysis above, a multimembership model. As before, we used aggression rate in each dyad as the response variable (log transformed as above), but now we used as a predictor the index of association among individuals. Also as before, we included as covariate the total time each member of a dyad was at the feeders, individual identity as a random term (i.e., multimembership grouping term), and all variables were centred and standardized. We used the same burn-in and total iteration number as before, and checked that the model converged.

2.4. Interaction between similarity in social dominance and distance in the network

In addition to the above models, testing separately whether similarity in social dominance or distance in the social network affect aggression, we also tested if

aggression is affected by the interaction between social proximity and distance in the network. We used a multimembership model with aggression rate in each dyad as the response variable (log transformed as above), and as predictors we included the absolute difference of dominance ratings (i.e., Elo-ratings) between the two individuals in a dyad, the index of association between those individuals, and the interaction term. Again, we also included as covariate the total time each member of a dyad was at the feeders, and individual identity as a random term (i.e., multimembership grouping term). All variables were centred and standardized. We used the same burn-in and total iteration number as before, and checked that the model converged.

2.5. Effect of audience size

It is expected that aggression rates increase with audience size, either because of an audience effect per se (i.e., individuals becoming more aggressive when perceiving a larger audience), or simply because with larger groups there are less feeders available per individual and, thus, greater need to aggressively displace others from the feeders. To study this effect, we first identified discrete groups of individuals in the timeline of the array of RFID antennae at the feeders and perches (Figure 5.1b), using Gaussian mixture models (GMM) that identify temporal bursts of activity ("gathering events" in the terminology of [62,63]) along the timeline of RFID readings. Following [51], we applied a double GMM to allow fine-scale detection of gathering events. The first GMM identifies coarse-scale bursts of activity within each day; the second GMM then analyses data within each of those coarse-scale time intervals to fine-tune or split it into more than one gathering event (adapted code in [42]). We computed audience size as the number of individuals present in each gathering event, as identified by the double GMM, minus one (i.e., minus the focal individual whose aggressive behaviour is being analysed).

We then used a Generalized Linear Mixed Model (GLMM) to test if aggressiveness was affected by the size of the audience. The dependent variable was the number of aggressive displacements that each individual made during each gathering event. Individual ID was included as random factor because data from each bird is used several times (once for each gathering event where it was present). Predictors were audience size, the duration of that gathering event (in minutes), and also the time that the focal individual was detected in that gathering event. The time that the focal individual was in a gathering event was included to account for the fact that more time in a gathering event gives more opportunity to make aggressive displacements. The duration of each gathering event was also included because mean rates of aggression

may depend on the duration of gathering events, for example if aggressive interactions are more frequent when the birds arrive and decrease afterwards. Hereafter we refer to this model as the “basic GLMM”.

In this basic GLMM, and also in the following models, we set a lower limit of 10 audience members in order for a gathering event to be included in the analysis, so that audience composition is largely independent of opponent identities (e.g., in the extreme case of an audience size of 1, audience identity would always coincide with opponent identity). Also, in this and later models, predictors were centered and standardized, we used a Poisson distribution, and, after running the model, checked the distribution of residuals and that there was no zero-inflation or overdispersion of the data as no autocorrelation (variance inflation factor was smaller than 2.5 in all models). These model assumptions were verified using the package “performance” (v. 0.4.8; [64]).

2.7. Effect of the audience’s social dominance on aggressiveness

To test if aggressiveness changed depending on mean similarity in dominance rank between each focal individual and its audiences, while accounting for the potentially confounding effects noted in the previous section, we ran the basic GLMM with one additional predictor: the mean of the absolute differences in dominance scores (i.e., Elo-ratings) between the focal individual and each of the audience members in a gathering event (low values indicate that the audience contains bystanders similar in dominance rank to the focal individual).

Since waxbills often move in large groups, this test may not be able to detect audience effects caused by the presence of bystanders particularly close in dominance rank to the focal individual, because this proximity in rank can be much diluted when computing mean similarity with the entire audience. Likewise, effects of the presence of very dominant or very subordinate individuals in the audience might also not be captured when using as predictor the mean similarity of the entire audience to the focal individual. We therefore ran another GLMM similar to the previous one but, instead of using as predictor the mean similarity in dominance rank of the focal individual to its entire audience, we used three other predictors: mean similarity in dominance rank of the focal bird to the 10% audience members most similar to it, to the 10% most subordinate audience members, and to the to the 10% most dominant audience members. The first of these predictors, computed as the mean of the absolute differences in Elo-rating between the focal bird and the 10% audience members most similar to it, serves to test if aggressiveness was affected by the presence of very similar-rank individuals. Low

values of this predictor indicate that the audience contains individuals that are very similar in rank in relation to the focal bird. The second predictor, computed as the mean difference in Elo-ratings between the focal bird and the 10% audience members with lowest Elo-ratings, serves to test if aggressiveness was affected by the presence of very subordinate individuals. High values of this predictor indicate that the audience contains individuals that are very subordinate in relation to the focal bird. Likewise, the third predictor was computed as the mean difference in Elo-ratings between the focal bird and the 10% audience members with highest (not lowest) Elo-ratings, and serves to test if the aggressiveness was affected by the presence of very dominant individuals. Low values of this predictor (i.e., strongly negative values) indicate that the audience contains individuals that are very dominant in relation to the focal bird. As in all other models, no zero-inflation, overdispersion or autocorrelation were detected.

2.6. Effect of social proximity to the audience on aggressiveness

To test if aggressiveness was affected by the social proximity (i.e., strength of association) between each focal bird and its audiences, we ran the basic GLMM with one additional predictor: the mean social network proximity of the audience to the focal bird. This was computed as the mean value of the focal bird's strength of association to all audience members in a gathering event (higher values indicate higher social proximity between the focal individual and the audience).

Again, since waxbills can move in large groups, this test may not be able to detect audience effects caused by the presence of individuals socially very close to the focal bird, or the presence of individuals very socially-distant, whose presence can be diluted when computing social proximity to the entire audience. Therefore, we ran another GLMM similar to the previous one but, instead of using as predictor the mean social network proximity of the focal bird to all audience members, we instead used two other predictors: the mean social network proximity of the focal bird to 10% audience members socially-closer to it, and to the 10% audience members more socially-distant to it, in each gathering event. The first of these predictors (high values indicating that the audience contains socially-close individuals to the focal bird) tests if aggressiveness was influenced by the presence of socially-close individuals in the audience, and the second predictor (low values indicating that the audience contains socially-distant individuals to the focal bird) tests if aggressiveness was influenced by the presence of socially-distant individuals. As before, we checked that statistical model assumptions were met.

3. Results

As shown earlier for this species [38], we found a dominance hierarchy with mildly steep slope (R = 0.305), meaning that waxbills of lower dominance rank sometimes displaced higher-ranking individuals. The dominance hierarchy was significantly transitive (P_t = 0.846, t_{tri} = 0.385, P < 0.001), meaning that the hierarchy is more ordered than random [50], and the ratio of interactions per individual was 226.2, much higher than the minimum recommended (>10) to reliably infer hierarchies [45].

Aggressive displacements were not random with respect to similarity in social dominance, with aggression rates being higher in dyads of individuals with larger differences in dominance ratings (effect of difference between ratings: posterior mean = 0.22, 95% confidence interval, CI = [0.16, 0.28], Figure 5.2a; effect of time at the feeder: posterior mean = 0.20, CI = [0.01, 0.39]). When restricting the analysis only to aggression downwards in the dominance hierarchy (i.e., the more dominant dyad member displacing the more subordinate), we again found higher aggression rates in dyads with larger differences in dominance ratings (difference between ratings: posterior mean = 0.33, CI = [0.27, 0.39], Figure 5.2b; time at the feeder: posterior mean = 0.17, CI = [0.003, 0.34]). When restricting the analysis to aggression upwards the dominance hierarchy (i.e., the more subordinate displacing the more dominant) the opposite was true: lower aggression rates in dyads with larger differences in dominance (difference between ratings: posterior mean = -0.11., CI = [-0.17, -0.05], Figure 5.2c; time at the feeder: posterior mean = 0.12, CI = [-0.04, 0.27]).

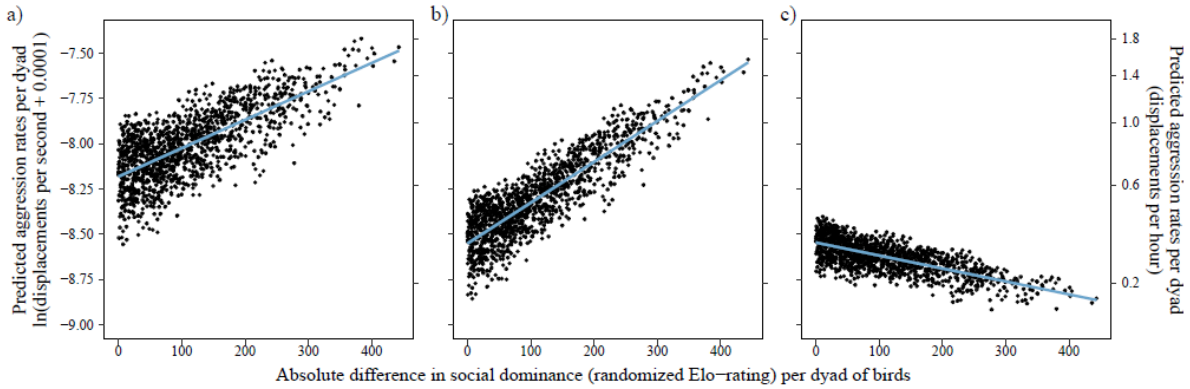

Figure 6.2. Predicted aggressive displacement rates as a function of absolute difference in social dominance in each dyad of birds. (a) All aggressive displacements, (b) displacements by the most dominant individual in a dyad, (c) displacements by the less dominant individual in a dyad. Shown are the predicted values of aggressive displacement rate at feeders, per dyad of birds, controlling for the potential confounding factors, in this case the duration that each dyad member was at the feeders [56]. The Y axis shows log-transformed aggression rates (left axis) and, for ease of interpretation, also rates as displacements per hour (right axis).

Regarding social proximity, aggression rates did not differ between dyads of birds that were socially-closer or socially-distant in the network (effect of association strength in the network: posterior mean = 0.03, CI = [-0.04, 0.10], time at the feeder: posterior mean = 0.17, CI = [-0.004, 0.34]).

We found no significant interaction effect of social proximity and similarity in dominance on the aggression rate within dyads, when including both these factors in the same model (effect of interaction: posterior mean = -0.004, 95% confidence interval, CI = [-0.05, 0.05], time at the feeder: posterior mean = 0.18, CI = [-0.02, 0.37]). As in the previous model testing for an effect of differences in social dominance, aggression rates were again found to be higher between dyads with larger differences in dominance (posterior mean = 0.25, 95% confidence interval, CI = [0.19, 0.31]). But now, controlling for differences in social dominance, we could detect higher aggression rates within dyads of individuals more closely associated in the social network (posterior mean = 0.12, 95% confidence interval, CI = [0.04, 0.19]).

The audience sizes analysed here varied between 10 and 50 (audiences smaller than 10 were not analysed; see methods) with a mean size of 27.60 (± 10.39 standard deviation, SD), corresponding to gathering events at the feeding area with a mean duration of 4 minutes and 45 seconds (± 4 min. SD; Figure E1). The number of aggressive displacements made by each individual was positively related to audience size across gathering events (GLMM: effect of audience size: $\beta = 0.496 \pm 0.017$ SE, $z = 29.496$, $P < 0.001$), negatively related to the duration of those gathering events (effect of duration of the gathering event: $\beta = -0.108 \pm 0.017$ SE, $z = -6.428$, $P < 0.01$), and negatively related to the duration of time that the focal individual was present in the gathering event (effect of duration in the gathering event: $\beta = 0.392 \pm 0.008$ SE, $z = 46.513$, $P < 0.001$).

Aggressiveness (i.e., the number of displacements at feeders) was not predicted by the mean similarity in dominance rank between each focal bird and their entire audiences ($\beta = 0.019 \pm 0.038$ SE, $z = 0.508$, $P = 0.612$; complete GLMM results in Table E1). The same was true in the second model that focused on the similarity to the 10% audience members most similar in dominance rank with each focal individual ($\beta = -0.025 \pm 0.033$ SE, $z = -0.754$, $P = 0.451$; predicted values from the model in Figure 5.3a, complete GLMM in Table E2). This second model (Table E2) also showed that waxbills behaved less aggressively as the dominance difference between them and the most dominant audience members increased (i.e., more negative values for the difference in Elo-ratings between the focal bird and the 10% more dominant audience members; β =

0.280 ± 0.062 SE, z = 4.527, P < 0.001; Figure 5.3b). Moreover, waxbills behaved more aggressively as the dominance difference between them and the most subordinate audience members increased (i.e., larger values for the difference in Elo-ratings between the focal bird and the 10% more subordinate audience members; β = 0.141 ± 0.039 SE, z = 3.580, P < 0.001; Figure 5.3c).

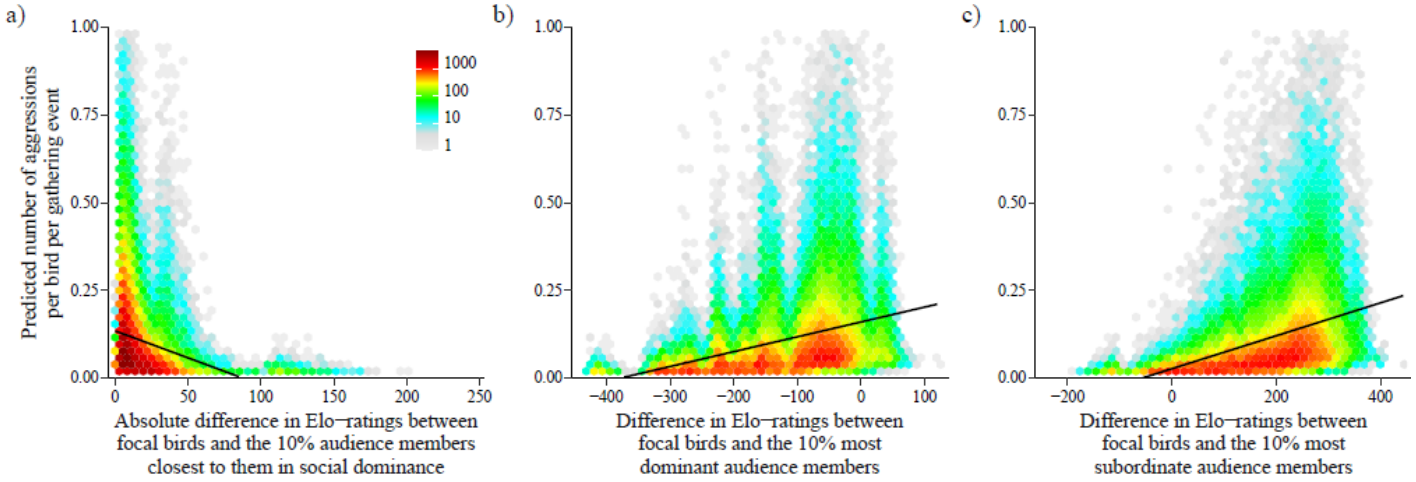

Figure 6.3. Density plots for the predicted numbers of aggressive displacements per bird per gathering event (i.e., group visit to the feeding area), as a function of similarity in dominance rank (randomized Elo-rating) with audience members. Predicted densities, controlling for other factors in each model, are shown by the colour scale, and regression lines are shown in black. Aggressions (a) decreased with increasing mean absolute difference of the focal bird to the 10% audience members most similar in dominance to focal birds, (b) decreased with decreasing mean difference of the focal bird to the 10% most dominant audience members (i.e., more negative values in the X axis, indicating bystanders more dominant relative to focal birds), and (c) increased with increasing mean difference of the focal bird to the 10% most subordinate audience members (i.e., more positive values in the X axis, indicating bystanders more subordinate than the focal birds). For ease of viewing, here and in Figure 4 the axes are truncated thus excluding some data points; for complete figures see Figures E2 and E3.

Aggressiveness of focal individuals did not co-vary with mean social proximity to their entire audiences (β = -0.010 ± 0.052 SE, z = -0.202, P = 0.84; complete GLMM in Table E3), nor in the presence of audience members very closely associated with them (i.e., stronger associations, on average, between the focal bird and the 10% audience members more closely associated with it; β = 0.038 ± 0.042 SE, z = 0.909, P = 0.364; Table E4). But waxbills did behave more aggressively in the presence of audience members very distantly associated with them (i.e., weaker mean strength of associations between the focal bird and the 10% audience members more distantly associated with it; β = -0.060 ± 0.024 SE, z = -2.545, P = 0.011, Figure 5.4; complete GLMM in Table E4).

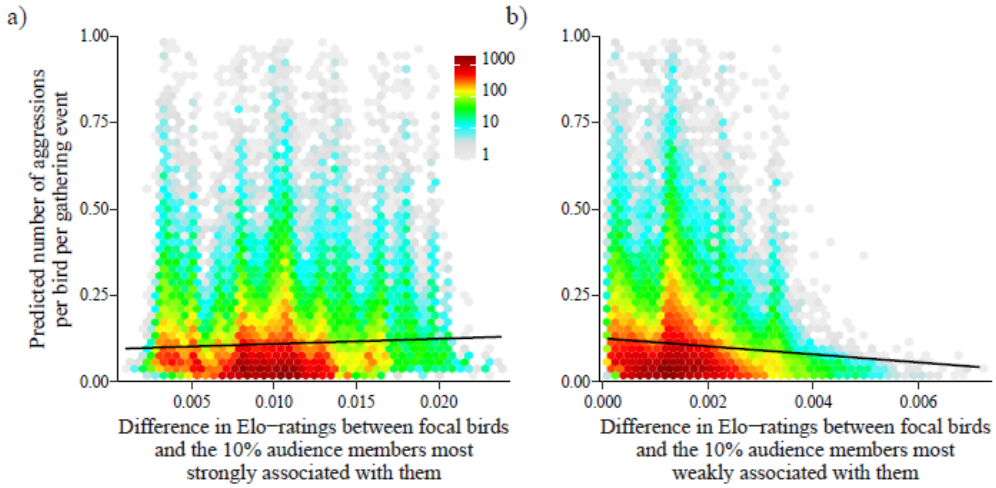

Figure 6.4. Density plots for the predicted numbers of aggressive displacements per bird per gathering event, as a function of proximity in the social network. Aggressions (a) did not change significantly as a function of mean association strength of the focal bird to the 10% audience members most strongly associated with it, but (b) increased with decreasing strength of association to the 10% audience members most weakly associated with the focal birds (i.e., values in the X axis closer to zero).

4. Discussion

We found no evidence for the prediction that waxbills should direct aggression preferentially towards others similar in social dominance to themselves, in order to resolve conflict regarding dominance relationships. Instead, waxbills attacked individuals very subordinate to them more than those weakly subordinate to them. This indicates bullying, as opposed to other more common patterns of aggression, such as “downward heuristic” (i.e., aggressing uniformly all subordinate individuals subordinate to self) or “close competitors” (i.e., aggress mostly individuals weakly subordinate to self) [20]. We also found no evidence for the prediction that waxbills would be more aggressive towards more socially-distant individuals, with whom there could be uncertainty regarding dominance relationships. We found evidence that waxbills are aware of their dominance relationships with audience members, since they behaved less aggressively when bystanders much more dominant than themselves were present in the audience and, conversely, behaved more aggressively when much more subordinate bystanders were present. The latter result, aggressiveness augmenting in the presence of bystanders very subordinate to themselves, is consistent with, and may be related to, the pattern of bullying in waxbill aggressions (i.e., attacking mostly those very subordinate to themselves). Likewise, reducing aggressiveness when there are bystanders in the audience much more dominant than oneself could be a strategy to prevent receiving aggression from those individuals.

Waxbills behaved more aggressively when very socially-distant bystanders were present in audiences. This indicates that, rather than attacking directly potentially dangerous opponents, like those socially-distant bystanders, waxbills instead show-off aggressiveness in their presence, mostly by bullying subordinate individuals. In gregarious species like the common waxbill, with long-term social associations [40], it should be advantageous for individuals to recognize group members individually [21,41], and to monitor and memorize their dominance status, to avoid conflict. However, by definition the frequency of interactions declines with social distance, which diminishes the opportunities to monitor dominance status and could also affect memory reliability [26,65]. Therefore, and since aggressiveness is highly correlated with social dominance in waxbills [38,39], showing-off aggressiveness in the presence of socially-distant bystanders could be a reliable signal that helps clarify the social dominance status of the signaller. Using bullying as a signal of social dominance to socially-distant individuals may be advantageous, by sending a message that it is not safe to attack the signaller, and at the same time should be a safe strategy because the risk of harmful retaliation by the most subordinate individuals is small. In nature, waxbills have fission-fusion group dynamics, by foraging in flocks of varying sizes and making vagrant movements in search of food and suitable habitat [66,67]. This fluidity in their social system causes encounters with unknown or socially-distant individuals, whose dominance status may not be well known. By showing-off aggression as a signal of dominance status, using a low-risk strategy like bullying, waxbills may to some extent avoid the risk and potential costs of engaging in serious fights with those socially-distant individuals.

Bullying 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 (9 mammal and 7 bird species, out of 85 [20]). Our finding that aggressiveness, including bullying, increases in the presence of potentially dangerous opponents (less closely associated individuals) bears some resemblance to another phenomenon, redirected aggression, that has been described for diverse species (e.g. mammals, birds, fish; reviewed in [68]). Unlike bullying, redirected aggression is time-sensitive and consists of, after losing an aggressive contest with an opponent, attacking a bystander (“scapegoat”) that is usually socially subordinate [69]. Redirected aggression may either be a non-adaptive physiological consequence of relieving stress caused by losing a fight [70], or it may actually convey information to bystanders that alleviate detrimental social effects of being seen losing the fight [68]. Although we did not study time-sensitive aspects of aggression, our results do not suggest redirected aggression because aggression rates were not higher within dyads of less closely associated individuals (on the contrary, they

were lower when controlling for differences in social dominance). Therefore, waxbills were not more likely to have been attacked when less familiar individuals were in the audience. Also, waxbills did not increase aggressiveness when the audience contained very dominant individuals or individuals of similar dominance rank to themselves, despite those being the opponents with whom losing fights and more serious fighting could happen. Thus, our results do not suggest that waxbills increase aggressiveness because of losing fights. Instead, the mere presence of less familiar individuals in the audience appears to have triggered an increase in aggressiveness, mostly in the form of bullying. Nonetheless, we did not study aggression in other places or contexts besides foraging, where patterns of aggression may differ, and we do not exclude that redirected aggression may also occur to some extent.

It is not straightforward to understand the adaptive function of bullying, because very subordinate individuals do not pose a social problem to the aggressor. Our results suggested that bullying could have a signalling function to bystanders, which agrees with the observation that, in humans, school-aged children and adolescents perform bullying more often in the presence of an audience [71–73]. These human bystanders can assume different roles, for example encouraging or joining the bully, intervening to help the victim, or watching passively. The latter is the most common [73] but encouraging the bully is also observed [74], suggesting that those bystanders are trusted peers of the aggressor rather than distantly associated peers [75,76]. This is in apparent contradiction to our results with waxbills, where bullying increased in the presence of distantly associated individuals to whom the aggressor may need to show-off dominance. The apparent contradiction can be resolved if we consider that close peers of school-aged humans can be simultaneously the most important competitors for, for example, social status [77]. We may therefore hypothesize that, similarly to waxbills, bullying in humans may also be used to show-off dominance to potentially serious competitors in the audience, possibly in an unconscious manner. This hypothesis predicts that, in humans, the effect of audiences promoting bullying will be more pronounced when there are motives for within-group competition, or when known competitors are present in the audience. This line of enquiry may prove a useful addition to the current efforts for understanding and intervening in peer dynamics to prevent bullying in schoolchildren and other vulnerable groups [78–80].

Although ours was the first study showing that the presence of potentially dangerous bystanders increases bullying of third parties, perhaps similar results will be uncovered in various other species, because several taxa possess the cognitive abilities

for adjusting behaviour depending on the composition of audiences. For example, chimpanzees (*Pan troglodytes*) and ravens (*Corvus corax*) are more likely to emit cries of help during fights when the audience contains individuals that can assist them [36,81]. Detecting effects of audience-composition on common waxbill aggressiveness and bullying was made possible by tracking a large number of individuals and monitoring their aggressive displacements automatically. We expect that, as automated tracking technologies are increasingly used to study animal social behaviour [82], we will keep improving our understanding of the strategies and cognitive abilities that social animals employ to manage dominance hierarchies.

5. References

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Chapter 7 | Collective foraging: experimentally-increased competition decreases group performance exploiting a permanent resource

Collective foraging: experimentally-increased competition decreases group performance exploiting a permanent resource

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Abstract

1. Foraging collectively offers advantages, such as access to social information on food locations, but it may also intensify competition for local resources. Social information may be most advantageous during ecologically challenging conditions, when food sources are scarce or unpredictable, which predicts more collective foraging during such conditions. Alternatively, higher within-group competition when resources are scarce might destabilize social groups and reduce collective foraging.

2. To evaluate these effects, we experimentally decreased the number and predictability of food sources (feeders with *ad libitum* seeds) available to wild-caught common waxbills (*Estrilda astrild*) living in a large open-air mesocosm.

3. Compared to control periods, in the treatment with few food sources competitive aggressiveness at feeders increased, the social network became more fragmented, with on average weaker associations between individuals, and foraging groups became smaller. Foraging groups also spent less time per visit to the feeding area, individuals spent less time at the feeders per group visit and had to make more visits to the feeding area per day, all of which indicate less efficient exploitation of the food sources. These effects were also observed when the number of feeders changed unpredictably across days.

4. Even though the collective behaviour of waxbills appeared to exacerbate, rather than mitigate, the ecological challenges of reduced or unpredictable food sources, we suggest that, in nature, this increased aggressiveness and fragmentation of the social network may function adaptively as an early trigger to explore alternative foraging locations before local food sources are severely depleted.

Keywords: Aggression, common waxbill, food availability, food predictability, foraging efficiency, group behaviour, social tolerance

1. Introduction

Group-living animals continuously interact with each other, which leads to the emergence of various types of collective behaviour, including collective decision making, synchronization of activity and collective foraging (Camazine et al., 2020; Couzin & Krause, 2003). Gregariousness and collective behaviour can offer protection from predators (Ioannou, Guttal, & Couzin, 2012), increase performance in problem-solving tasks (Biro et al., 2016), and give access to new environmental information (Sumpter, 2006), among other benefits. Animals must collect information about the environment, namely pertaining to vital resources such as food location (Dall et al., 2005). Collective foraging can greatly improve how efficiently this type of information is shared socially and, therefore, how efficiently animals exploit food resources (Galef & Giraldeau, 2001; Giraldeau & Caraco, 2000).

By promoting greater efficiency exploring food resources, collective foraging can reduce detrimental effects of environmental uncertainty and should therefore be particularly useful in unpredictable or ecologically challenging environments (Dall et al., 2005; Hancock & Milner-Gulland, 2006; Lihoreau et al., 2017). For example, experiments with European starlings (*Sturnus vulgaris*) showed that having access to social information allows higher foraging success, but only when the environment is unpredictable (Rafacz & Templeton, 2003). Also, sociality and cooperative behaviours have often evolved in unpredictable or extreme environments (e.g., Firman et al., 2020; Rubenstein & Lovette, 2007; Shen et al., 2017). Therefore, we might expect that ecological challenges related to foraging, such as reduced or unpredictable food sources, could lead social animals to be cooperative and adopt a more cohesive social structure to benefit from social information on food sources.

However, sociality encompasses both cooperation and conflict, and social foraging could increase within-group competition over food, especially if food resources are scarce, and therefore creating conflict. When the competition costs outweigh the benefits of collective foraging, social behaviour might actually be reduced. For example, during periods of low food availability, orcas (*Orcinus orca*) show more fragmented social networks and are organized in smaller groups (Foster et al., 2012), likely because individuals in smaller groups can gather a larger share of the limited local resources (Beauchamp, 2014). Food-deprived animals can become more aggressive (e.g., Edmunds et al., 2021), and larger foraging groups experience higher within-group competition when compared to smaller ones (Amano et al., 2006; Beauchamp, 2014; Markham et al., 2015), so that breaking into smaller groups could be an adaptive strategy

to reduce conflict when food availability is limited. But little is yet known about how cooperation or competition are emphasized in changing or challenging environments (Firman et al., 2020).

Here we aimed to experimentally test which of the above scenarios (more cohesive and cooperative foraging, vs. competition and a breakdown of social structure) is more likely under different types of ecological challenges. We experimentally reduced the number or the predictability of food sources available to wild-caught common waxbills (*Estrilda astrild*) living in a large open-air mesocosm, and monitored their social behaviour, including aggressiveness, social network properties, feeding patterns, and collective behaviour of the foraging groups. Common waxbills are very gregarious birds, foraging and moving in flocks throughout the year (Clement et al., 1993), mostly in open areas where they feed preferentially on grass seeds (Cardoso et al., 2018; Silva et al., 2018; Sullivan et al., 2015). Waxbills are not migratory but they can perform vagrant movements, possibly in search of suitable habitat or resources (Payne, 2010), which appears especially adaptive in much of their native sub-Saharan African range where rainfall and the availability of local resources can be unpredictable. If, upon experiencing ecological challenges such as reduced or unpredictable food sources, waxbills change their behaviour to better use social information, we expect to observe more pro-social collective behaviour. This could be manifest, for example, in larger foraging groups or stronger associations among individuals. If, on the contrary, fewer or more unpredictable food sources increase competition and destabilize social groups, then we would expect to observe, for example, increased aggressiveness or a more fragmented social network.

2. Methods

2.1. Study system

We conducted experiments in a large open-air mesocosm, consisting of a large area of ca. 235 m^2 covered by fine net 1.30 to 2.70 m high, with abundant natural vegetation (Figure 7.1a), and housing 66 waxbills (33 males and 33 females) by the time experiments began (October 25th, 2020). Of these 66 waxbills, 8 were born in the mesocosm (1 in 2019 and 7 in 2020) and the remaining had been captured from the wild and were living in the mesocosm since October 2016 (23 birds), September 2017 (19 birds), October 2019 (7 birds) or October 2020 (9 birds). Guerra et al. (2020) gives detailed descriptions of the mesocosm and of methods for capturing wild waxbills, which in all years used mist-netting in agricultural sites within a 20 km radius from the mesocosm.

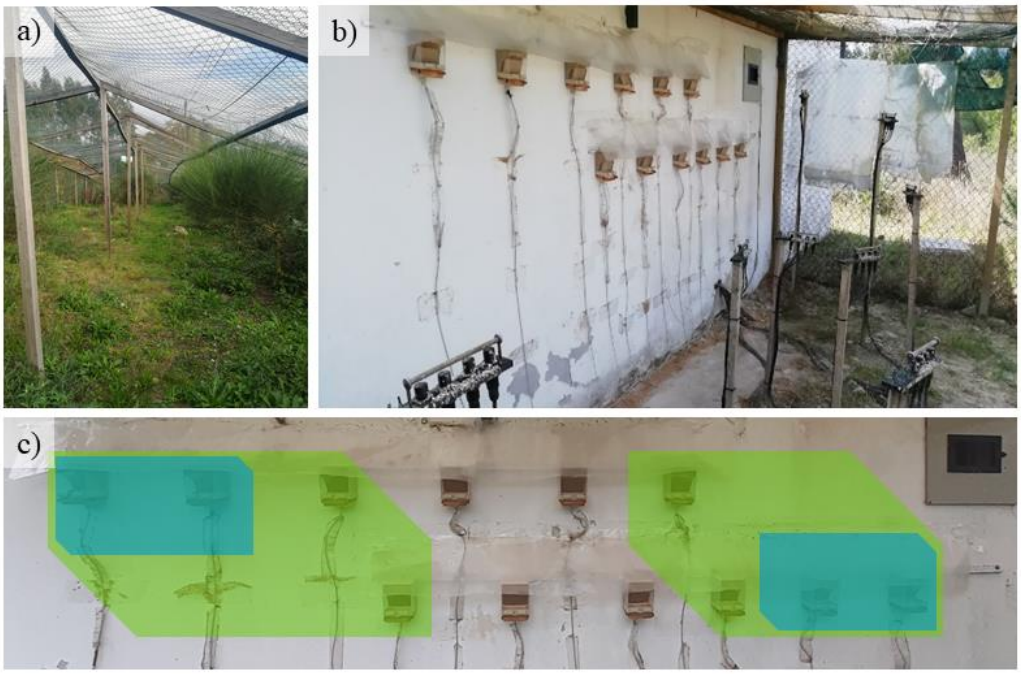

Figure 7.1. (a) Partial view of the mesocosm showing its natural vegetation, and (b) the feeding area showing feeders and perches equipped with RFID antennae. (c) Close-up of the feeders, with blue shading indicating the 4 feeders available during the treatment with 1/3 of feeders, and also during some days of the unpredictable treatment, and green shading indicating the 8 feeders available during the treatment with 2/3 of feeders.

All birds had a passive integrated transponder (PIT) tag (Dorset ID, The Netherlands) on a plastic leg ring for radio-frequency identification (RFID). An array of RFID antennae (Dorset ID) in the feeding area of the mesocosm allowed monitoring the arrival and departure times of each individual. The array of RFID antennae consisted of one antenna in each of 12 feeders, placed between 1.20 and 1.55 m high on a wall (Figure 7.1b), and a row of 4 antennae under each of 8 long wooden perches (15.5 cm long, place on wooden poles between 0.90 to 1.70 m high; Figure 7.1b). The feeders and perches with RFID antennae were within an area of approximately 9 m^2 (see Gomes et al., 2021 for details). Waxbills in the mesocosm fed almost exclusively from the feeders, which provided seeds *ad libitum* (Tropical Finches Prestige seed mixture, Versele-Laga), since the availability of naturally growing grass seeds was very limited. Water was also provided *ad libitum* away from the feeding area.

2.2 Food manipulation experiment

The food manipulation experiment lasted from October 25th 2020 to February 5th 2021, i.e., outside the breeding season of waxbills in this region (Beltrão, Gomes, et al.,

2021). There were three food manipulation treatments and four control periods. The first control period lasted 16 days, the second and third control periods lasted 12 days and separated the three treatments, and the fourth control lasted 16 days (see Figure SI1 in Supporting Information). In these control periods all 12 feeders were available, as usual in the mesocosm. The three food manipulation treatments lasted 16 days each. In the first treatment, only 1/3 of the feeders were available (the 4 feeders marked with blue shade Figure 7.1c), and the entrance to the other feeders was covered with a cardboard so that the birds could not access the seeds. In the second treatment, the number of available feeders changed unpredictably between 4 and 12, so that the mean number of feeders available was 8. For this, during the night, we placed or removed the cardboards on all feeders except the 4 marked blue in Figure 7.1c, at intervals ranging from 1 to 3 nights apart (see Figure SI1). In the third treatment 2/3 of the feeders were available (the 8 feeders marked with green shade; Figure 7.1c) and the entrances of the remaining feeders were covered. We chose to cover entrances to the feeders, which we did during the night, rather than to remove feeders, so that the overall environment in the feeding area remained unchanged and all RFID antennae continued functioning. During the course of the experiment, 2 out of 66 waxbills died, likely due to natural age causes.

2.4 Social networks

Separately for each treatment period and each control period, we inferred social networks based on the time overlap between individuals in the RFID datastream: following Ferreira et al. (2020), the value of each edge was the time that a pair of individuals was associated, divided by the sum of times that each was in the RFID array. We chose spatial-temporal criteria for identifying proximity-based associations using methods in Gomes et al. (2021). Briefly, this approach compares networks computed either using the number of co-occurrences in the same gathering events (*sensu* Psorakis et al., 2012, 2015) as the criterion for association between individuals (here identifying gathering events with a double Gaussian mixture model; Ferreira et al., 2020), or using different combinations of a spatial association criterion (maximum distance between individuals to consider them associated) and a temporal association criterion (time asynchrony allowed to compute time overlaps between individuals). These comparisons allow finding an association criterion that is efficient at filtering random associations and, thus, revealing the most network structure (i.e., low network entropy and high coefficient of variation of edge values; Gomes et al., 2021).

In all 7 time periods (3 treatment and 4 control periods), and similarly to Gomes et al. (2021; 2022), the criteria that maximised network structure was the combination of the most restrictive spatial association criterion (less than 40 cm between individuals), and no asynchrony allowed when computing time overlap between individuals (see Figure SI2). We thus chose this criterion to identify proximity-based associations for network analyses. Gomes et al. (2022) found that this procedure results in consistent choices of association criteria in our waxbill mesocosm, irrespective of season or year, while an alternative procedure (optimization of association criteria based on roosting location) does not always provide consistent results. To test if network structure was significantly non-random, separately for each of the 7 networks (3 treatments and 4 controls), we computed null distributions for the CV of the strength of associations, and null distributions for network entropy, using 1,000,000 cumulative permutations of pairs of individuals, as described in Gomes et al. (2021). Comparison with these null models showed that all 7 social networks had significantly stronger structure than random (in all cases, $P < 0.001$). Code for computing social networks, selecting association criteria and testing the significance of network structure is available in Gomes et al. (2021).

2.5 Metrics

We studied aggressiveness, feeding patterns and social network properties. Aggressive interactions consisted of an individual displacing another from the uncovered feeders, and these aggressive displacements were automatically detected in the RFID datastream following methods in Beltrão, Marques, et al. (2021). Briefly, aggressive displacements were diagnosed by a time difference between one individual leaving the feeder and the other arriving of less than 2 seconds, when both the displaced and aggressor birds stayed for a minimum of 3 seconds in the feeder before and after the displacement, respectively. Comparing RFID data with video recordings, Beltrão, Marques, et al. (2021) showed that this method reliably identifies aggressive displacements. With these data, we computed (1) aggression rate at the feeders (i.e., the number of aggressive displacements per individual divided by the total time, in minutes, that it spent in the uncovered feeders, then averaged across all individuals), and (2) the steepness of the social dominance hierarchy (i.e., whether individual differences in dominance are more or less pronounced). To compute steepness of the dominance hierarchy, and also following Beltrão, Marques, et al. (2021), we used the function “estimate_uncertainty_by_repeatability” from the “aniDom” R (R Core Team, 2021) package (v. 0.1.5; Farine & Sánchez-Tojar, 2021), which computes the

repeatability of randomized Elo-ratings and gives a good indication of the steepness of the dominance hierarchy. This method, based on randomized Elo-ratings, is reliable to study dominance hierarchies that are not very steep (Sánchez-Tójar et al., 2018), as is the case with common waxbills (Beltrão, Marques, et al., 2021; Funghi et al., 2015).

Pertaining to feeding patterns, we computed (1) the mean foraging group size, (2) the number of foraging groups per day, (3) the mean time, in minutes, at the feeding area per foraging group, (4) the mean number of foraging groups in which each individual was present per day, and (5) the mean time, in seconds, each individual spent at the open feeders per foraging group. Foraging groups were determined using a double Gaussian mixture model, which identifies gathering events from the RFID datastream, as explained above (Ferreira et al., 2020; Psorakis et al., 2012, 2015).

Pertaining to social network properties, we computed: (1) the mean strength of associations in the network, (2) network entropy, and (3) the coefficient of variation (CV) of the strengths of associations in the network. Low network entropy and high CV of strengths of associations both indicate heterogeneous strengths associations in the network (i.e., more structured networks), whereas the reverse indicate more random or homogeneous networks (Gomes et al., 2021). The code to compute network entropy and the CV of the strengths of association is available in Gomes et al. (2021). Metrics were computed separately for each treatment period and for their corresponding control periods (see below).

2.6 Statistical analysis

To understand if the experimental treatments affected collective behaviour, we compared the above metrics between each treatment period and their corresponding control periods. For most metrics, we used as control for a given treatment the combination of the previous and following control periods. In this manner, we account for any bias that could arise due to longitudinal changes in behaviour that might occur during the course of the experiments. In the case of social network metrics (the mean strength of associations, network entropy, and the CV of the strengths of associations), we compared the treatment period with the previous control period and, separately, with the following control period, because this type of social network properties should be compared using networks with similar sampling efforts (Farine, 2018).

We used, separately for each treatment period and its corresponding control, non-parametric bootstrap (i.e., random sampling with replacement) to obtain a

distribution of 1,000 bootstrapped replicates (Efron & Tibshirani, 1993) for each of the above metrics. For the metrics foraging group size and time at the feeding area, which were calculated per foraging group and then averaged across those foraging groups, bootstrap was made by randomly sampling foraging group values with replacement and then averaging them. For the metrics aggression rate at the feeders and time each individual spent at the open feeders per foraging group, which were calculated per individual and then averaged across individuals, bootstrap was made by randomly sampling individual values with replacement and then averaging them. For the metrics number of foraging groups and number of foraging groups in which each individual was present, which were calculated per day and then averaged across days, bootstrap was made by randomly sampling daily values with replacement and then averaging them. For social network metrics calculated per network, bootstrap was made by randomly sampling association values in the network with replacement, and then re-computing the respective social network metric. Finally, for the steepness of the social dominance hierarchies, we used parametric bootstrap instead, because steepness was computed with the function “rptGaussian” (package rptR, v. 0.9.22; Stoffel et al., 2017; incorporated in the function “estimate_uncertainty_by_repeatability”), which already gives an output bootstrapped replicates. Separately for each metric, we then assessed the statistical significance of comparisons between each treatment and its corresponding control by determining the overlap between the 2 bootstrapped distributions using the package overlapping (v. 1.6; Pastore, 2018); overlaps of less than 5% indicate significantly different distributions (i.e., $P < 0.05$ for the null hypothesis that the two mean values are identical). We report the overlap value between the bootstrap distributions (*p*-value).

2.7 Ethical note

The work with wild animals was done under permits 690/2016/CAPT, 57/2017/CAPT, 127/2019/CAPT, 112/2020/CAPT from the Instituto da Conservação da Natureza e das Florestas.

3. Results

The aggression rate at feeders increased significantly in all treatments, compared to their respective controls (i.e., the periods of time before and after the treatment; Figure 7.2a; Table 1). There were no significant differences in the steepness of the social dominance hierarchy between treatments and their controls (Figure 7.2b; Table 1).

Table 7.1. Comparison of behaviour in each treatment with its control. Shown is the proportion of overlap between the bootstrap distribution of each treatment period with that of its control, which corresponds to the *P*-value for the null hypothesis that their means are identical. Unlike for aggressiveness and feeding patterns, where each treatment was compared to the combination of the previous and following control periods, for behaviours involving social network analysis two values are presented, corresponding to comparison with the control period before or after the treatment, because social network properties should be compared using networks of similar sampling effort.

	1/3 F	Unpredictable	2/3 F
Aggressiveness			
Aggression rate at the feeders (per minute)	< 0.001*	0.027*	0.007*
Steepness of dominance hierarchy	0.646	0.816	0.183
Feeding patterns			
Foraging group size	< 0.001*	< 0.001*	0.300
Number of foraging groups per day	< 0.001*	0.008*	0.002*
Time at the feeding area per foraging group (min)	0.021*	0.044*	0.103
Number foraging groups an individual was present per day	< 0.001*	0.026*	< 0.001*
Time an individual spent at the feeders per foraging group (sec)	< 0.001*	< 0.001*	0.320
Social network			
Mean strength of association	< 0.001*; < 0.001*	< 0.001; < 0.001	0.196; 0.003*
Entropy	0.062; 0.134	0.042*; 0.670	0.001* 0.089
CV	0.058; 0.491	0.356; 0.314	< 0.001*; 0.040*

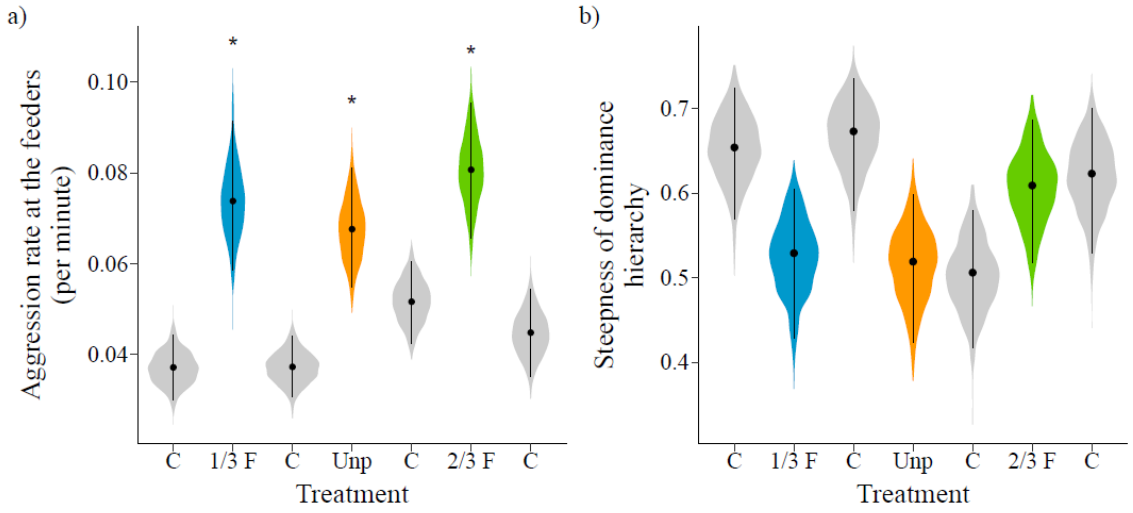

Figure 7.2. (a) Aggression rate at the feeders, in the form of aggressive displacements, and (b) steepness of the dominance hierarchy during treatments with 1/3 of feeders available (1/3 F), unpredictable number of feeders (Unp), 2/3 of feeders available (2/3 F), and each control period (C). Black dots are the observed values, violin plots are bootstrapped distributions, and vertical lines are the 95% confidence intervals from each bootstrap distribution (i.e., interval from the 2.5 to the 97.5% percentiles of the distribution). Asterisks mark significant differences of a treatment relative to its control (i.e., reunion of the following and preceding control periods).

Regarding feeding patterns, foraging group size decreased significantly in the treatment with 1/3 of feeders available, and also in the unpredictable treatment, compared to their controls, but not in the treatment with 2/3 of feeders available (Figure 7.3a; Table 1). The number of foraging group visits per day increased in all treatments compared to their controls (Figure 7.3b), as did the number of foraging groups in which each individual was present per day (Figure 7.3d; Table 1). The time at the feeding area per foraging group visit also decreased in the 1/3 of feeders and unpredictable treatments compared to their controls, but not in the treatment with 2/3 of feeders (Figure 7.3b; Table 1). Finally, the time each individual spent at feeders per foraging group visit decreased in the 1/3 feeders and unpredictable treatments, but no changes were observed in the treatment with 2/3 of feeders (Figure 7.3e; Table 1).

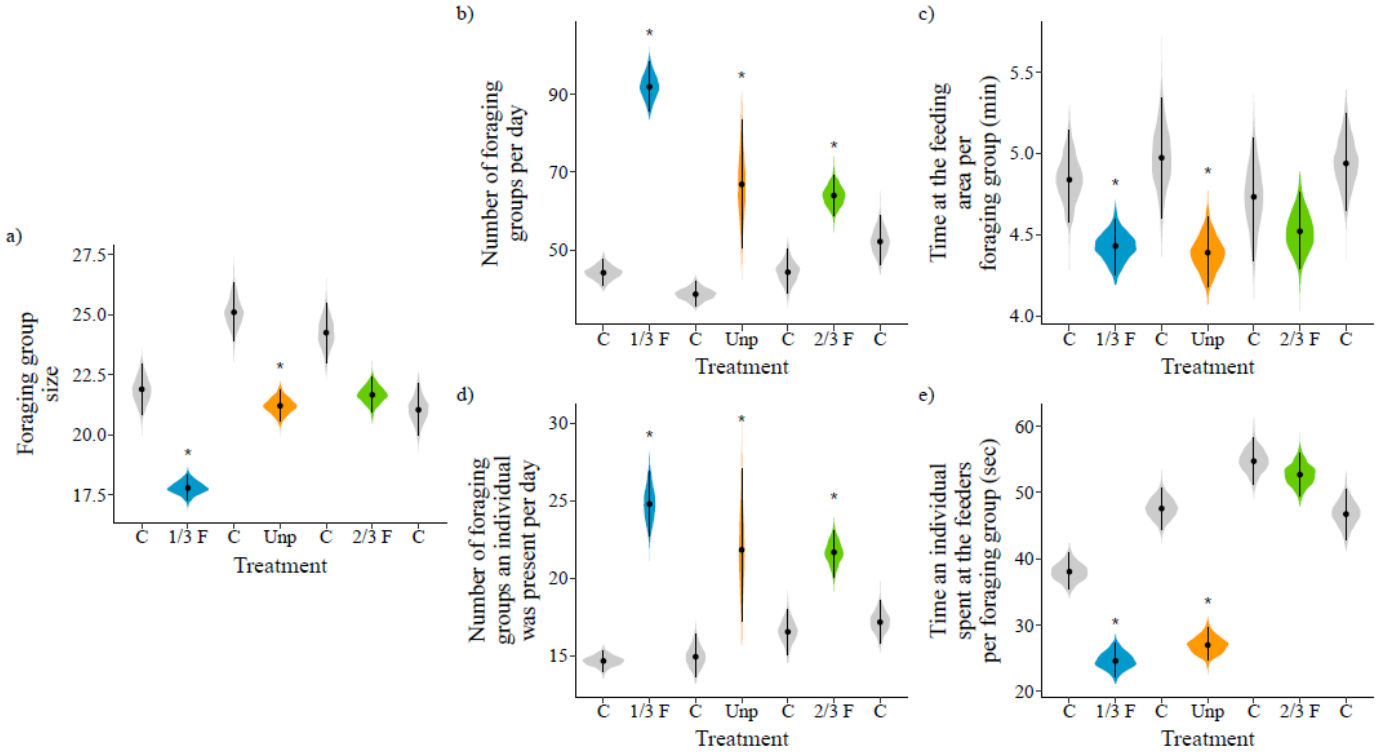

Figure 7.3. (a) Mean number of individuals in each foraging group, (b) number of foraging groups per day, (c) mean time at the feeding area per foraging group, (d) mean number of foraging groups in which each individual was present per day, and (e) mean time each individual spent at the open feeders per foraging group, for each control and treatment period. Plot details as in Figure 7.2.

The mean strength of associations between individuals decreased when compared to both their controls (i.e., control before or after each treatment) in the treatment with 1/3 of feeders and also in the unpredictable treatment. In the treatment with 2/3 of feeders, the mean strength of associations did not change from the control before but increased relative to control after (Figure 7.4a; Table 1). Finally, regarding whether social networks became more structured (less random and uniform) or less structured (more random and uniform), neither the CV of strengths of associations nor network entropy differed significantly between the treatment with 1/3 of feeders and its controls (Figure 7.4b,c; Table 1). There was also no evidence of network structure increasing or decreasing in the unpredictable treatment, since only network entropy differed from the control period preceding it, but not the one following it (Figure 7.4b,c; Table 1). However, during the treatment with 2/3 of feeders network structure decreased relative to its controls, as indicated by a lower CV of strengths of associations and also, relative to one of its controls, higher network entropy (Figure 7.4b,c; Table 1).

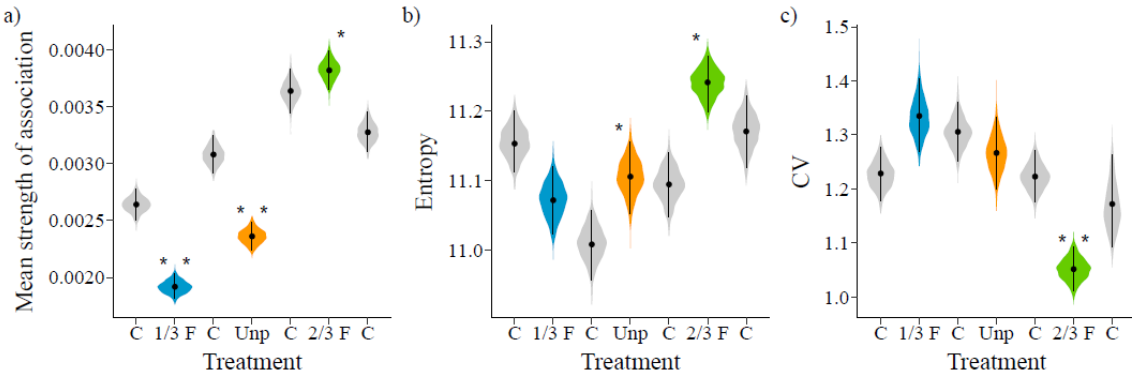

Figure 7.4. (a) Mean strength of association, (b) network entropy and, (c) coefficient of variation of the strength of association (CV), for each control and treatment period. Plot details as in Figure 7.2. Asterisks mark significant differences of a treatment relative to its preceding (asterisk on the left side) or following (asterisk on the right side) control period.

4. Discussion

We tested if changes in the number of available food sources, or in their predictability, affected common waxbill collective behaviour and social structure. We equated two contrasting sets of predictions: first, since social information and collective foraging can help find food sources and thus mitigate ecological challenges, we hypothesized that waxbills could behave more pro-socially when challenged with fewer or more unpredictable food sources; second, since fewer food sources can also increase within-group competition, this could lead to increased aggressiveness and perhaps weaken pro-social and collective behaviour. Our results supported the second scenario. The aggression rate at feeders increased both when there were fewer feeders available or when the number of feeders was unpredictable and, perhaps as a consequence of this, in treatments with the fewest or an unpredictable number of feeders, the size of foraging groups decreased, among-individual associations in the social network became weaker, and foraging behaviour appeared to have become less efficient. The decrease in foraging efficiency was because group visits to the feeding area were shorter, with individuals spending less time feeding at the feeders per visit and, likely because of that, waxbills had to make more visits to the feeding area per day. These results indicate that, rather than increasing pro-social behaviour when challenged with a reduced or unpredictable number of food sources, waxbills became more aggressive, less gregarious, and, in the mesocosm conditions of this study, foraged less efficiently. We next discuss the mechanisms that may interconnect these results, and implications for when waxbills face foraging challenges in their natural habitats.

When foraging in groups, individuals must tolerate the presence of conspecifics, by having low aggression rates in close proximity to other individuals nearby food (Cronin & Sánchez, 2012). Despite the possibility of cooperation in foraging being more advantageous when food sources are scarce or uncertain, waxbills increased aggression rates when we experimentally reduced the number or predictability of food sources. The steepness of the waxbill dominance hierarchy did not differ between treatment and control periods, but the rate of aggressive displacements at feeders approximately doubled in experimental treatments by comparison to controls. This increased in aggression could be due to waxbills lowering their social tolerance or, alternatively, simply reflect a greater rate of encounters when the number of feeders is reduced. Interestingly, aggression rates were very similar when the reduction in the number of feeders was more or less severe (cf. treatments with 1/3 and 2/3 feeders in Figure 7.2a), rather than aggression being higher in the more severe treatment. Likewise, aggression rates were similar whether the reduction of feeders was permanent or intermittent (c.f. treatment with 1/3 feeders and unpredictable treatment in Figure 7.2a), rather than being higher in the permanent treatment. This suggests that increased aggression rates did not merely reflect higher encounter rates when feeders are fewer, but involved a more permanent reduction in social tolerance around the periods when waxbills experienced any type of challenge associated with their usual food sources.

Perhaps as a consequence of the increased aggressiveness, the dynamics of foraging behaviour became less efficient, especially in the treatments with the number of feeders more severely reduced or unpredictable. In those treatments, foraging groups became smaller, waxbills had to make more visits to the feeding area and spent less time there per visit, despite the feeders providing seeds *ad libitum*. Since the birds had to go more often to the feeding area to obtain their required amount of food, they moved more and spent more energy foraging, meaning that foraging efficiency decreased. This lower foraging efficiency should be interpreted in the context of the mesocosm environment in which these waxbills lived, where dispersal to other foraging areas is not possible. A more complete understanding of how the changes in collective behaviour that we observed affect foraging efficiency could be gained by monitor foraging in the natural environment, where food sources are spread over multiple and/or wider areas. This could allow, for example, testing to which extent alternative foraging areas allow group fragmentation without a decrease in foraging efficiency.

In nature, the behavioural changes observed here may affect foraging efficiency in different manners. Waxbills in nature make vagrant movements in search of suitable

habitat or resources and, although they roost communally, during the day they move and forage in flocks of varying sizes (Clement et al., 1993; Payne, 2010), meaning that they have fission-fusion dynamics (Silk et al., 2014). The increased aggression and reduced collective foraging that we observed here, when waxbills faced ecological challenges, will likely change fission-fusion dynamics in ways that may or may not hinder foraging performance. These changes will hinder foraging performance if they simply make access to food more difficult for the group or some of its members (e.g., more subordinate individuals). But, in nature, this increased aggressiveness and fragmentation of foraging groups might improve collective performance overall, if it functions as an early trigger to explore new areas that may offer better foraging conditions at that time, before local food sources are depleted and the carrying capacity of the environment is exceeded. In this manner, a larger number of smaller sub-groups could gain foraging experience over a wider geographic area, and then pass this information socially to the wider group via their usual fission-fusion dynamics. In the wild, this ability to explore and disperse to suitable areas should be important, since the common waxbill is adapted to unpredictable ecological condition, such as rainfall and resulting availability of grass seeds, in much of its sub-Saharan native range (Cardoso & Reino, 2018; Stiels et al., 2011).

During the treatment with the number of feeders mildly reduced, changes in collective foraging appear not to have been as severe as in the other two treatments. In this treatment, we did not find significant changes relative to the control in foraging group size, in the duration of group visits, nor in the time each individual spent in feeders per group visit. We only found changes in the number of foraging group visits per day and in the number of groups in which each individual participated. For these behaviours, the degree of behavioural changes appeared to reflect the severity of the different treatments very closely. The control periods had ca. 50 foraging group visits per day, which increased to ca. 90 when the number of feeders was more severely reduced, and in the treatments with the number of feeders mildly reduced or unpredictable the number of foraging group visits per day was intermediate, at ca. 70. Moreover, the treatment with unpredictable number of feeders also showed more variability in the number of foraging group visits per day (Figure 7.3b), likely reflecting its oscillations in the number of feeders from day to day. The number of foraging groups in which each individual was present also followed the exact same pattern (Figure 7.3d). Such a close match with the severity of treatments could suggest that behavioural changes were simply short-term reactions to the immediate conditions that birds found each day. For example, since the birds spent less time at the feeders per group visit during the treatments, they remained hungry and thus had to return to the feeding area more often. But, as was also the case for

aggressiveness, the intensity of changes in foraging behaviour did not always follow the severity of treatments. For example, some behavioural changes were similar when the number of feeders was severely reduced in permanence or intermittently (unpredictable treatment; Figure 7.3c,e), indicating that the latter did not cause intermittent behavioural changes, but more profound or longer-term changes in collective foraging around the periods when there were foraging challenges.

The social network property that changed the most during the experiment was the mean strength of associations between individuals, which decreased in treatments with the number of feeders more severely reduced or unpredictable (but not in the treatment with the number of feeders mildly reduced). This is consistent with the smaller, more fragmented foraging groups found during those treatments. We found no strong evidence for erosion of the network structure (i.e., for a decrease in the heterogeneity of strengths of association) during experimental treatments. Only in one of the treatments, with the number of feeders mildly reduced, did network structure decrease, as indicated by a lower coefficient of variation in the strength of associations compared to the previous and subsequent control periods. This result, however, should be interpreted with caution because no such decrease in social network structure was observed in more severe treatments used earlier. We cannot exclude that this latter result was due to some disturbance (e.g., climatic), or due to cumulative memories of previous, more severe treatments, leading the birds to react in excess. In the sleepy lizard (*Tiliqua rugosa*), similarly to our results, social network remained stable and resilient to environmental fluctuations, but during more challenging conditions the mean strength of associations between males and females was found to be decreased (Godfrey et al., 2013). In our study, despite the fragmentation into smaller foraging groups and consequent decrease in the strength of associations among individuals, social network structure was not eroded, meaning that waxbills continued to show as well-defined social preferences as in the control periods. In line with this, previous work with common waxbills showed that preferences in their social network are stable in the long term (Gomes et al., 2022). The resilience of waxbills' social preferences and network structure may allow them to remain associated with familiar individuals, which in turn is known to offer advantages such as reduced aggression or increased competition (Maldonado-Chaparro et al., 2018; van Boekholt et al., 2021; Ward & Webster, 2016).

In conclusion, changes in the collective behaviour of waxbills appear to have exacerbated rather than mitigated the challenges of reduced or unpredictable food sources, since their increased aggressiveness and fragmentation into smaller foraging

groups resulted in overall less efficient exploitation of a food resource that was permanently available. But, since waxbills are adapted to unpredictable environments where they may often need to search for and switch to alternative foraging areas, we suggest that in nature these behaviours may actually be adaptive responses to ecological challenges. This study thus offers novel insight on whether challenging environments foster more competition or cooperation in gregarious animals: although we found support for increased competition and less pro-social behaviour, in nature this apparent non-cooperative behaviour might actually be useful for the group by adjusting its fission-fusion dynamics in a manner that helps to explore and colonize areas with better current conditions.

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Chapter 8 | Multiple effects of weather on collective behaviour

Multiple effects of weather on collective behaviour

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Abstract

1. Fluctuations in weather can be challenging for wildlife. It is important to understand how animal groups respond to weather because social animals often adapt to the environment at the group level, and, in turn, social structure can influence their ecology. The influence of weather on collective behaviour, however, is currently poorly understood, especially when considering multiple aspects of weather, controlling for seasonality, or controlling for indirect effects (such as changes in food availability).

2. We investigated how weather (temperature, rain, humidity, cloud cover, wind) affects behaviour in a gregarious species by monitoring, during five years, individual and flock behaviour of common waxbills (*Estrilda astrild*) in a semi-natural environment with constant food availability. We first described seasonal patterns in the social network, aggressiveness, and collective foraging, and then, controlling for seasonality, studied associations between weather and behaviour.

3. Regarding seasonality, foraging groups became more frequent and smaller during breeding seasons, aggression rates decreased, dominance hierarchies became steeper, and the social network became more structured, with weaker mean strengths of association. In most cases, the seasonal pattern showed a main peak during Spring and a smaller peak in late Summer.

4. Controlling for seasonality, we found individual- and group-level changes in behaviour related to increased energy demands on colder or cloudier days, such as spending more time feeding and, on colder days, more frequent and larger foraging groups that resulted in less structured social networks. Other changes appear as adjustments to weather-related disturbances. For example, on rainy days foraging group journeys became briefer and more synchronous, resulting in stronger associations between individuals and less structured networks, and on windy days foraging groups were less frequent and larger, with individuals behaving more aggressively to access food.

5. Since different aspects of weather affect collective foraging and social structure in multiple ways, we conclude that the weather is an important influence on the sociality of gregarious animals. Understanding these weather-related effects can improve predictions of how gregarious animals will react to environmental and climate changes.

Keywords: aggression, climate change, environmental fluctuations, gregarious animals, seasonality, social behaviour, social networks, weather disturbances

1. Introduction

Weather and other environmental fluctuations can be challenging for animal life. To cope with them, animals may use different strategies that affect physiology, morphology, and behaviour. Examples include changes in urine concentration and volume (Schwimmer & Haim, 2009), changes in coat colour and thickness (Blix, 2016), and moving to sunlight or shade for thermoregulation (Cloudsley-Thompson, 2012). Endothermic species can be active across a wide range of environmental conditions, but maintaining their body temperature has energetic costs (Geiser, 2021). Behavioural changes for coping with low temperatures or with other conditions that increase energetic needs include increasing food intake (e.g., Youngentob et al., 2021) or reducing activity (e.g., Riek et al., 2017).

In the case of gregarious animals, behavioural effects of environmental changes may occur not only at the individual but also at the group level. The effects of weather on collective behaviour have received relatively little attention (Fisher et al., 2021), but this is an important research topic because social structure and interactions within social groups can affect fitness (e.g., Kerth, 2010; Snijders et al., 2017; Taborsky, Cant, & Komdeur, 2021). Studies have shown that ecological conditions may affect the expression of social behaviour, such as cooperation (Firman et al., 2020; Shen et al., 2017), the strength of associations between individuals (Foster et al., 2012; Pilakouta et al., 2023) or social structure (Welklin et al., 2023). Few studies have, however, attempted to gain a holistic understanding of how the environment influences various aspects of social behaviour and social structure (reviewed in Fisher et al. 2021). Now that changes in climate are happening at an unprecedented rate (Turner et al., 2020), studying the effects of temperature and other aspects of weather on different facets of collective behaviour can help us predict how gregarious animals will react to ongoing ecosystem changes.

Collective patterns of behaviour are driven by local interactions between individuals (Camazine et al., 2020; Couzin & Krause, 2003), which in turn can be influenced by environmental factors (e.g., predator density, Herbert-Read et al., 2017; food availability, Beltrão et al., 2022 and weather, Firman et al., 2020; Welklin et al., 2023). Temperature is perhaps the most studied abiotic influence on animal behaviour (e.g., Edwards et al., 2015; Funghi et al., 2018) because it affects energetic requirements. For example, in several bird species, individuals preserve heat by roosting tightly together during colder nights (Smith, 1972). Although less studied, weather conditions other than temperature may also influence social behaviour (Sapolsky, 1986;

Shen et al., 2012). For example, on rainy days, animals may lose more heat (McCafferty et al., 2011; Wilson et al., 2004), affecting the energy they allocate to social activities, including aggressive behaviours (Shen et al., 2012).

Beyond affecting a single aspect of social behaviour (e.g., roosting, aggression), challenging environments may have broader and more multifaceted implications for sociality. For example, challenges like unpredictable rainfall and harsh temperatures have been suggested to promote within-species cooperation (Firman et al., 2020; Rubenstein & Lovette, 2007), perhaps because aggression is energetically demanding (Hardy & Briffa, 2013) and the costs of within-group conflict become less bearable in challenging environments (Shen et al., 2012). Nonetheless, some empirical work finds that environmental challenges, including extreme and variable temperatures and reduced or unpredictable food availability, can instead increase aggressiveness and fragment social networks, indicating reduced cooperation (Beltrão et al., 2022; Foster et al., 2012; Rat et al., 2020). To resolve such contradictions and to better understand how the environment affects the functioning of animal groups, we need comprehensive studies investigating how multiple environmental factors may affect different aspects of social behaviour and social structure.

To investigate how abiotic factors affect collective behaviour, here we asked how different weather components, including not only temperature but also rain, humidity, cloud cover and wind, affect social structure and social behaviour in the common waxbill (*Estrilda astrild*). Common waxbills are highly gregarious, foraging in flocks year-round (Clement et al., 1993; Payne, 2010). They are an eclectic species that can live in various climates and weather conditions, both in their native distribution range in sub-Saharan Africa and their invasive ranges worldwide (Stiels et al., 2011). We studied a waxbill population in a large open-air mesocosm exposed to natural weather, and with abundant natural vegetation, for five years, from January 2018 to December 2022. Each waxbill had a passive integrated transponder (PIT) tag, and an array of radio-frequency antennae allowed monitoring of their social network and various aspects of social behaviour, including collective foraging, aggressiveness, and the social dominance hierarchy (Beltrão, Marques, et al., 2021; Gomes, Beltrão, et al., 2022). In our study system, food was available ad libitum, allowing us to study the effects of abiotic factors on collective behaviour, not confounded by indirect effects mediated by food availability. For example, studies on how weather affects social behaviour often find stronger social bonds during the wet season (e.g., Nandini et al., 2017; Prehn et al., 2019), but since the weather can also affect food availability and predictability, it is unclear to which

factors social behaviour is responding. Moreover, with our long-term data, we can better disentangle seasonal from the non-seasonal association of different aspects of weather with multiple behaviours, providing an unprecedentedly detailed study of how the environment influences the functioning of animal groups.

2. Methods

2.1. Study system

We studied common waxbills living in a large open-air mesocosm (ca. 235 m2), exposed to the natural climate, with abundant natural vegetation, and with access to water and food *ad libitum* (Tropical Finches Prestige seed mixture, Versele-Laga). In this seminatural environment, birds fly freely, roost communally, form social groups, nest and reproduce (details in Beltrão, Gomes, et al., 2021; Gomes et al., 2022). All birds had a passive integrated transponder (PIT) tag on a leg ring (Dorset ID, The Netherlands) for radio-frequency identification (RFID). The mesocosm had 8 to 13 feeders placed ca. 0.90 to 1.55 m high on a wall, each equipped with an RFID antenna (Figure 8.1). A small roof (ca. 1.40 m by 4.40 m) above the mesocosm in that area protected the feeders from direct rain. There were also eight wooden perches 15.5 cm long and 0.90 to 1.70 m high, each with an array of four antennae, placed near the feeders (from ca. 0.65 to 4.65 meters from the feeders; Figure 8.1).

Figure 8.1. At the left, the mesocosm with its natural vegetation during winter. At the right, the feeding area showing the different perches and feeders equipped with RFID antennae.

We monitored the behaviour of waxbills for five years, from January 2018 to December 2022. Birds were captured from the wild in a week during the Autumn of 2016 (14 males and 16 females) or 2017 (14 males and 16 females). At the beginning of 2018, the mesocosm housed 54 birds (25 males and 27 females). Every year in October, at the end of the breeding season (Beltrão, Gomes, et al., 2021), we captured the birds to check their PIT tags and to ring the juveniles born in that year. The total number of birds

in mesocosm at these annual checks was 52 birds in October 2018, 47 in 2019 (including one juvenile), 66 in 2020 (seven juveniles), 67 in 2021 (nine juveniles), and 65 in 2022 (17 juveniles). Additionally, 25 wild birds were introduced in the mesocosm during these five years to compensate for natural mortality and maintain a stable population size. All waxbills introduced to the mesocosm were captured using mist-nests in nearby agricultural sites within a 20 km radius (for details on the capture methods, see Guerra et al., 2020).

Out of the 1826 days of these five years, we removed 128 days of RFID data because of interventions in the mesocosm (e.g., days in which new birds entered the mesocosm, when annual recaptures were being conducted or when feeders were closed for maintenance or for experiments; see Beltrão et al., 2022), or because of occasional technical problems with the RFID system. These data omissions were scattered through the five years and never involved more than five days in a row.

2.2. Metrics of individual and collective behaviour

We studied the amount of feeding, collective foraging, social network properties, and social aggressiveness. The average amount of feeding per bird was approximated by computing the mean time that individuals spent at the feeders per day (total time that all birds spent at the feeders, in seconds, divided by the number of individuals recorded by the RFID system). To validate this metric as a proxy for the amount of seeds consumed, we weighted the seeds that the birds consumed from the feeders every week for one year (22/07/2021 to 27/07/2022); due to calendar constraints, in exceptional cases, seeds were weighted at intervals between 3 and 11 days. These weekly means (seed weight divided by the number of days) were strongly correlated with the mean time individuals spent at the feeders during the same sampling period ($r = 0.73$, $P < 0.01$, $N = 53$), indicating that the time spent at the feeders is a good proxy for feeding.

Regarding collective foraging, we used the same methods as Beltrão et al. (2022) to calculate (1) the number of foraging groups per day, (2) the mean duration, in minutes, of foraging groups per day, and (3) the mean size of foraging groups per day. For this, we identified waxbill foraging groups using a double Gaussian mixture model (GMM; Ferreira et al., 2020; Psorakis et al., 2012; Psorakis et al., 2015) to find bursts of activity in the RFID data stream of the feeders and nearby perches (see Beltrão et al., 2022).

We characterised social network properties by computing, per week, (1) the mean strength of associations between individuals, (2) the coefficient of variation (CV) of the

strengths of associations, and (3) network entropy. The last two metrics are robust indicators of the network structure (Gomes et al., 2021) but, as noted next, are not equivalent or redundant. High CV values indicate non-random and well-structured networks with heterogeneous association strengths, while low CV values indicate more homogeneous associations. High entropy values indicate unpredictable association strengths, typically found in networks with unstable or incompletely differentiated subgroups, and lower values indicate more predictable strengths of association. More predictable strengths of association can be either because associations become more homogeneous overall (in which case both entropy and CV are low), or because subgroups in the network become more cohesive and differentiated (i.e., associations become more homogeneous only within subgroups, in which case only entropy but not CV is low; Ramos-Fernandez et al., 2018). Social networks were computed based on the RFID data stream, using a proximity-based criterion to identify associations among individuals; we used as criterion the synchronous time overlap between individuals visiting perches or feeders less than 40 cm apart, which was previous shown to best distinguish between weak and strong network associations on this system (Beltrão et al., 2022; Gomes et al., 2022, 2021). The strength of association between every two individuals was then calculated as the time those two individuals were associated divided by the sum of times each was in the RFID data stream. Social networks were computed per week, using only weeks with RFID data from 4 or more days.

Aggressiveness was studied based on aggressive displacements at the feeders, detected during the five years in the RFID data stream using the methods of Beltrão, Marques, et al. (2021). Briefly, aggressive displacements were diagnosed by a time difference inferior to 2 seconds between one individual leaving the feeder (the one displaced) and the other arriving, combined with a minimum period of stay at the feeder of 3 seconds by each bird. Beltrão, Marques, et al., (2021) showed, using video recordings, that this criterion accurately detects aggressive displacements at the feeders in this system. Thus, following Beltrão, Marques, et al., (2021), we computed (1) the aggression rate at the feeders per day (number of aggressive displacements by each individual, divided by the total time it spent at the feeders, in minutes, then averaged across the population) and (2) the steepness of the dominance hierarchy per week. The latter metric was calculated, estimating the repeatability of randomised Elo-ratings (social dominance scores) with the R (R Core Team, 2021) package “aniDom” (v. 0.1.5; Farine & Sánchez-Tojar, 2021), which (Sánchez-Tójar et al., 2018) showed to reliably infer the steepness of dominance hierarchies. The randomised Elo-rating method is advisable for computing dominance hierarchies when their slopes are not very steep

(Sánchez-Tójar et al., 2018), as in common waxbill (Beltrão, Marques, et al., 2021; Funghi et al., 2015). Steepness of the dominance hierarchy was only computed for weeks with a minimum of 4 days of RFID data.

2.3. Climate data

We obtained three different datasets of climatic data as we were not sure which would be the most reliable for the mesocosm location. For each one of these datasets, we extracted their estimated temperature and relative humidity and compared them to in situ, actual measurements, using a Taylor's diagram. The first dataset consisted of climatic readings obtained hourly in a meteorological station ca. 10 km from the study site (Pedras Rubras; IPMA). The other two datasets were obtained from the Weather Research and Forecasting (WRF) model operated by the Regional Meteorological Agency MeteoGalicia, either with a 4 km and 12 km resolution, for the location of the mesocosm. The WRF model runs operationally twice a day, with an hourly time resolution. In all cases, the hourly data were averaged within each day, because in our subsequent analyses we will use daily or weekly means, rather than hourly values. We compared these three datasets with temperature and humidity recorded by a thermometer and hygrometer datalogger (EL-USB-2-LCD+, LASCAR) every 30 minutes at the study site. This datalogger was exposed to natural climate but placed in a shaded area, covered from rain, next to the mesocosm to avoid the effect of direct sun and rain exposure, and its data were also averaged per day.

Taylor's diagrams in Figure G1 show that all three datasets are in good agreement with measurements made in situ. For temperature, all three datasets showed correlations higher than 0.95 with measurements in situ, and their amplitude of variation (standard deviation) was also very close to that of in situ measurements. For humidity, all three datasets also showed high and similar correlations with in situ measurements (r = ca. 0.90) and a standard deviation between ca. 0.70 and 1.30 in relation to that of in situ measurements. We, therefore, chose to use data from the prediction model MeteoGalicia at 4km because it was slightly better than MeteoGalicia at 12km, and did not contain missing values as the meteorological station data from IPMA.

We selected weather variables based on their potential biological relevance. At the same time, we tried to avoid those that were highly correlated and thus would not bring independent information to the analyses. We thus chose to study mean temperature (ºC), as it should influence the energetic demands of organisms. Maximum and minimum temperature, as well as surface downwelling short and longwave radiation,

were not considered because they are related to and correlated with mean temperature (r = 0.60 and r = 0.66, respectively). We also studied mean cloud cover (%) as it affects the amount of solar radiation directly reaching individuals. We studied mean precipitation (kg/m2), mean wind speed and mean relative humidity (%)because they may affect the heat loss (McCafferty et al., 2011; Schouten et al., 2010; van Dyk et al., 2019). In addition, precipitation and wind speed may also disturb flight and affect collective behaviour. Correlations among the five weather variables studied here were not strong (all |r| < 0.64; Table G1).

2.4. Breeding phenology

We collected data on the number of intact nests in the mesocosm during each breeding season. Nest monitoring was usually conducted at nine to 15 days intervals, except in 2022, when it was done monthly. It consisted of searching the mesocosm for nests and noting their condition. We considered a nest intact and complete when the ball-shaped nest chamber was complete and a nest destroyed when its dome had collapsed, or the walls had large holes. We started nest monitoring at the first signs of nesting behaviours (late February/March) and stopped monitoring in mid to late October, as nest building was residual by then (details in Beltrão, Gomes, et al., 2021).

2.5. Statistical analyses

To evaluate seasonality in the behavioural traits studied, we computed a Generalized Additive Model (GAM) with Gaussian distribution in R (“mgcv” package, v. 1.8-38; Wood, 2011) for each behavioural trait (response variable). Seasonal effects were tested by applying a cyclic cubic smoothing spline to either the day of the year for the models with behavioural variables computed per day (time spent at the feeders, aggression rate at feeders, number of foraging groups per day, their mean duration and size), or to the week of the year, for the models with behavioural variables computed per week (steepness of dominance hierarchies, and all social network properties). We considered “year” as a categorical variable, which allows us to test for seasonal effects while accounting for differences in behaviour among years. Additionally, we included a categorical variable indicating changes or experimental procedures that occurred in the mesocosm during this study (Table G2) to control for any effects those may have on behaviour. In these models, we used restricted maximum likelihood estimation (REML) to select the parameter that controls the amount of smoothing in the model (Wood, 2017). To account for temporal autocorrelation in the data, these GAM included an auto-regressive moving average (ARMA) model (Table G3). We experimented different combinations of values (between 0 and 4) for parameters p and q (Zuur et al., 2009),

which determine the number of backward time steps (days or weeks) to account for in the ARMA. We assessed different combinations of p and q by comparing AIC values and choosing the model with the lower value. In cases where the AIC values were similar (ΔAIC < 4), we applied a generalised likelihood ratio test (Zuur et al., 2009) to test if the two models were statistically different and choose the most parsimonious model when the null hypothesis was not rejected. We used the function “gam.check” to obtain diagnostic plots of model assumptions and the function “ACF” to confirm that the autocorrelation of the data was correctly accounted for.

To test for associations between climate and behaviour, controlling for seasonal effects, we ran a linear mixed-effect model (“nlme” package, v. 3.1-153; Pinheiro et al., 2021) for each behavioural trait, each including an ARMA model as explained above (Table G3). As a random effect, we included a non-ordered categorical variable separating all 60 months of the study; this categorical random factor was further broken down when changes occurred in the mesocosm that had to be controlled for (Table G2). This random effect controls for seasonality, for long-term changes that could affect behaviour (e.g., habituation of birds to the mesocosm, changes in the vegetation), and focuses the statistical tests in shorter-term, within-month associations between climate (predictor variables) and behaviour (response variable). As predictors, we included daily or weekly means (for models of behaviours computed per day or week, respectively) of temperature (in degrees Celsius), cloud cover (%), precipitation (kg/m2), wind strength (m/s) and relative humidity (%). In the model with aggression rate as a response variable, we also included the mean size and the duration of foraging groups as predictors because previous work showed that they influence aggressiveness (Beltrão et al. in preparation). All variables were centred and standardised. We checked the assumptions for all the models using the package “performance” (Lüdecke et al., 2020) and confirmed that the variance inflation factor of each predictor was smaller than 4 (Harrison et al., 2018).

3. Results

3.1. Seasonality

We found statistically significant seasonal patterns in all studied behavioural traits (all $P < 0.05$, Table G4). For the amount of feeding, the birds spent more time at the feeders from around mid-February to late April (Figure 8.2a,b), which corresponds to their early breeding season (Figure 8.2c,d), and less time around August to late October. Despite the cyclical, seasonal pattern, for this and the remaining behaviours, we

observed some year-to-year variation in the height and timing of the peaks (c.f. blue line in Figure 8.2a, showing the running average for the time at the feeders).

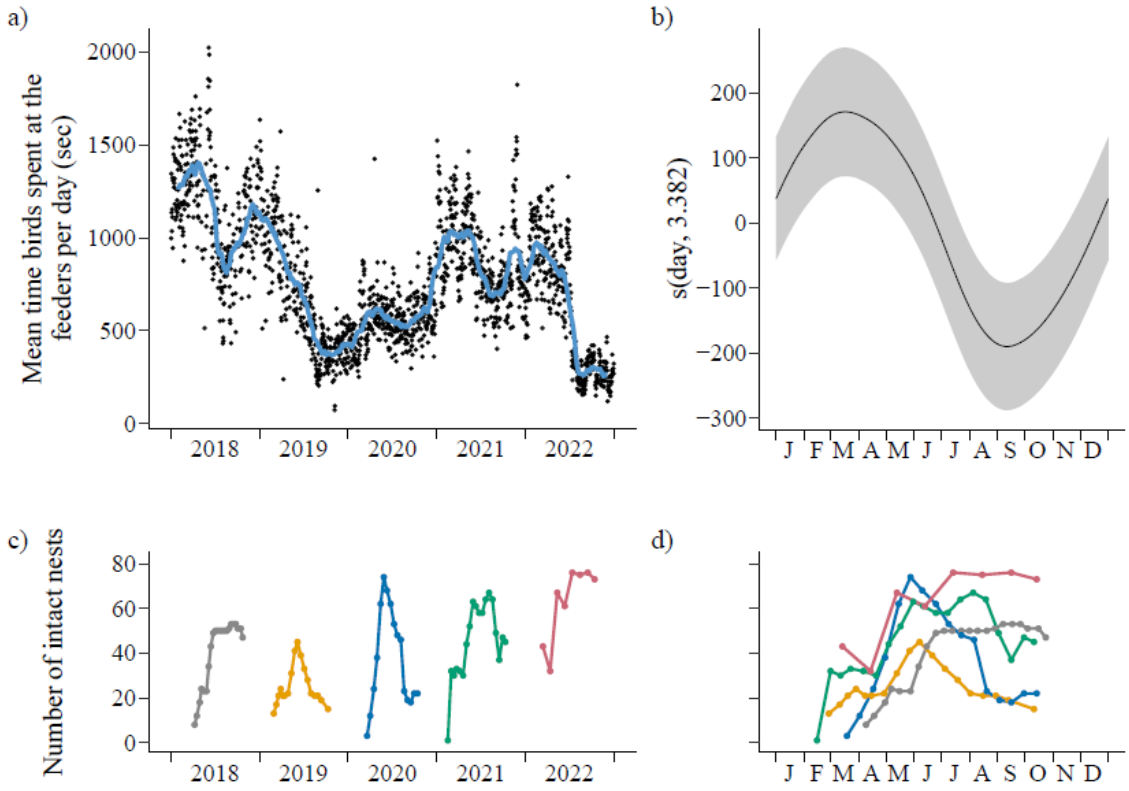

Figure 8.2. Seasonality of time spent at the feeders. a) Mean time spent at the feeders per bird for each day across the five years of the study; the blue line indicates the running average over 60 days. b) Estimated smooth function from the GAM model, with the grey area representing the 95% credible interval. c and d) Number of intact nests during nest monitoring in the five breeding seasons; each colour refers to one year.

Regarding collective foraging, the number of foraging groups per day and the duration of those foraging groups were higher around May and had a second peak around early October (Figure 8.3a-d). The size of foraging groups showed the exact inverse seasonal pattern, with the periods around May and, to a lesser extent, around October corresponding to smaller foraging groups (Figure 8.3e,f). These peaks in May coincide with peak breeding, as shown by the number of new intact nests in the mesocosm (Figure 8.2c,d).

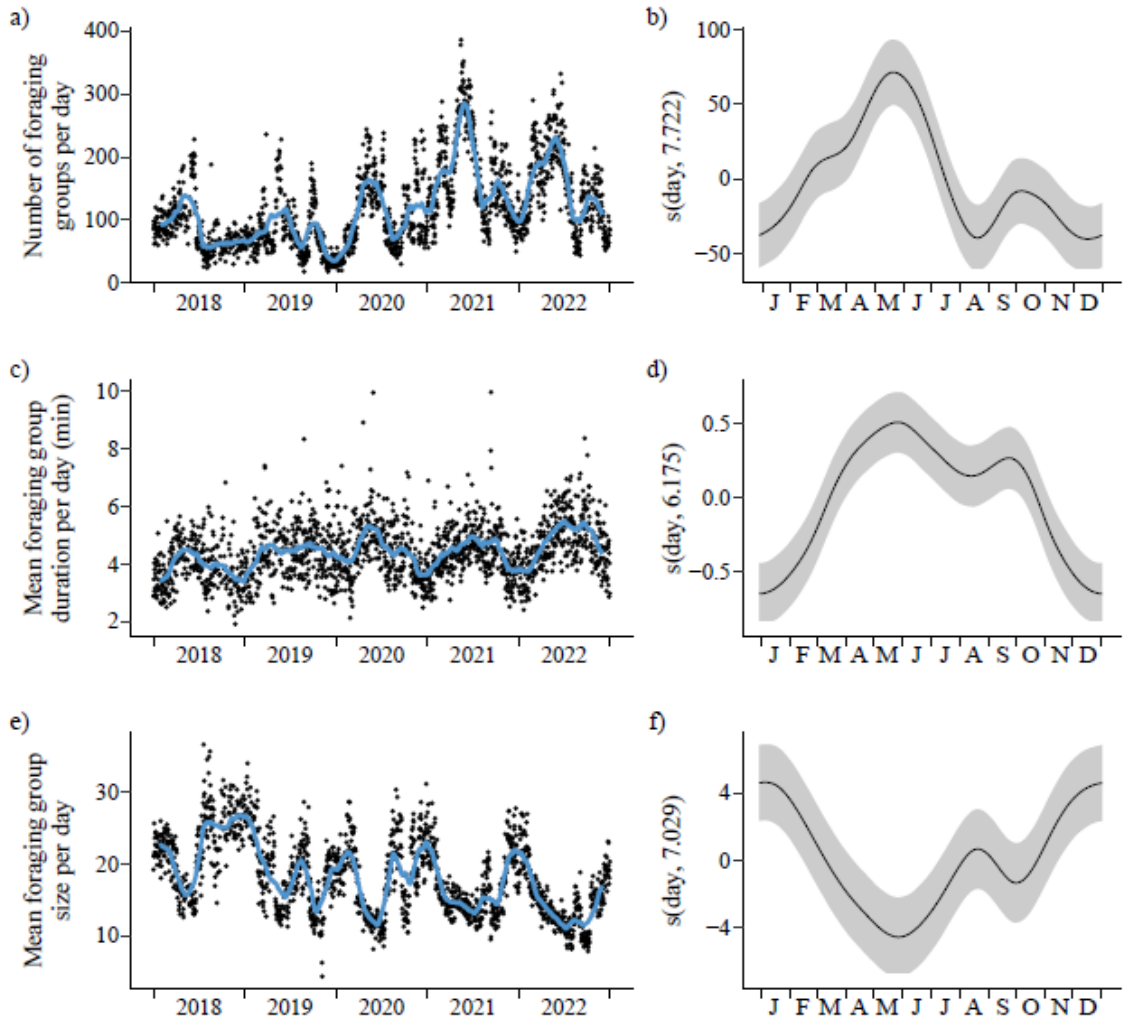

Figure 8.3. Seasonality and GAM functions for (a) the number of foraging groups, (b) the mean duration of foraging groups, and (c) the mean size of the foraging groups. Plot details as in Figure 8.2a,b.

The mean strength of associations was lower around May and had a second smaller peak of weak associations around October (Figure 8.4a,b). The two peaks of weaker associations corresponded with peaks of higher CV and lower entropy in the strengths of association (Figure 8.4c-f), indicating more heterogeneous and predictable strengths of association, respectively, which together imply that subgroups are better differentiated in the social network (Ramos-Fernandez et al., 2018). The two peaks of weaker associations also corresponded with peaks of lower rate of aggressive displacements at the feeders (Figure 8.5a,b) and of a more steep social dominance hierarchy (Figure 8.5c,d).

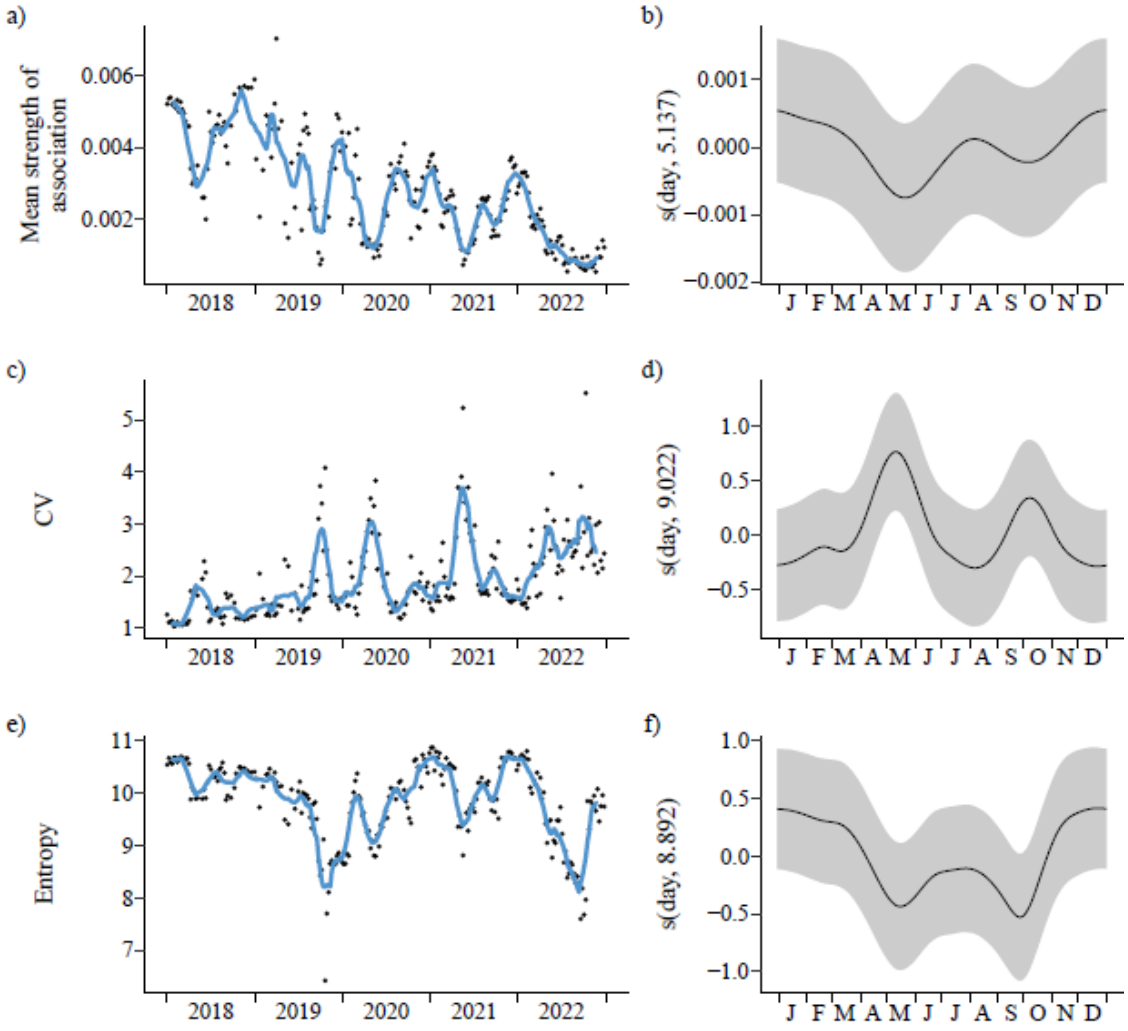

Figure 8.4. Seasonality and GAM functions for (a) strength of associations, (b) coefficient of variation of the strength of association, and (c) network entropy. Plot details as in Figure 8.2, except that the running average (blue line) is calculated over eight weeks.

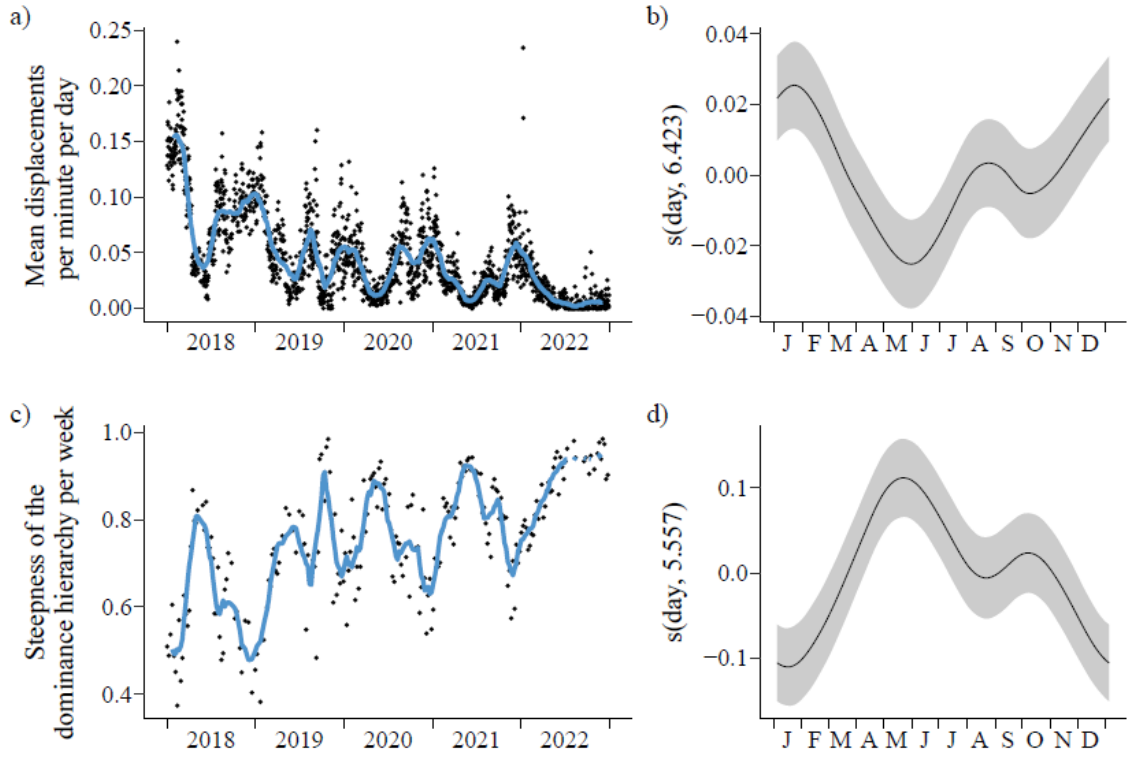

Figure 8.5. Seasonality of (a) the aggression rate, and (b) the steepness of the dominance hierarchies per week. Plot details as in Figure 8.2, except that in b) the running average (blue line) is calculated over eight weeks.

3.2. Associations with weather

Controlling for seasonality and month-to-month variation, we found that four aspects of weather significantly predicted the time spent at the feeders. Low temperature and high cloud cover were associated with more time spent at the feeders (Figure 8.6a, Table 8.1). While higher precipitation was associated with more time at the feeders, higher relative humidity was associated with less time at the feeders (Figure 8.6a, Table 8.1).

Regarding collective foraging, we found that the number of foraging groups per day was negatively associated with temperature and wind speed (Figure 8.6b, Table 8.1). The duration of those foraging groups was positively associated with temperature and negatively associated with cloud cover and precipitation (Figure 8.6c, Table 8.1). Finally, the size of the foraging groups was negatively associated with temperature and positively associated with wind speed (Figure 8.6d, Table 8.1).

The strength of association in the social network was negatively associated with temperature and positively associated with precipitation (Figure 8.6e, Table 8.1). Precipitation was also the only significant predictor of the CV of the strength of association, predicting more homogeneous strengths of association in the social network

(Figure 8.6f, Table 8.1). Network entropy was instead negatively associated with temperature, indicating more predictable strengths of associations (Figure 8.6g, Table 8.1).

Finally, controlling for group size and duration, only wind speed was positively associated with aggression rate (Figure 8.6f, Table 8.1). As expected, group size and duration were both associated with aggression rate (positively and negatively, respectively; Table 8.1). The steepness of the dominance hierarchy was not significantly predicted by any aspect of weather, although there was a marginally significant positive association with wind speed (Table 8.1); of the two confounding factors, group size and duration, group size was negatively associated with the steepness of the hierarchy (Table 8.1).

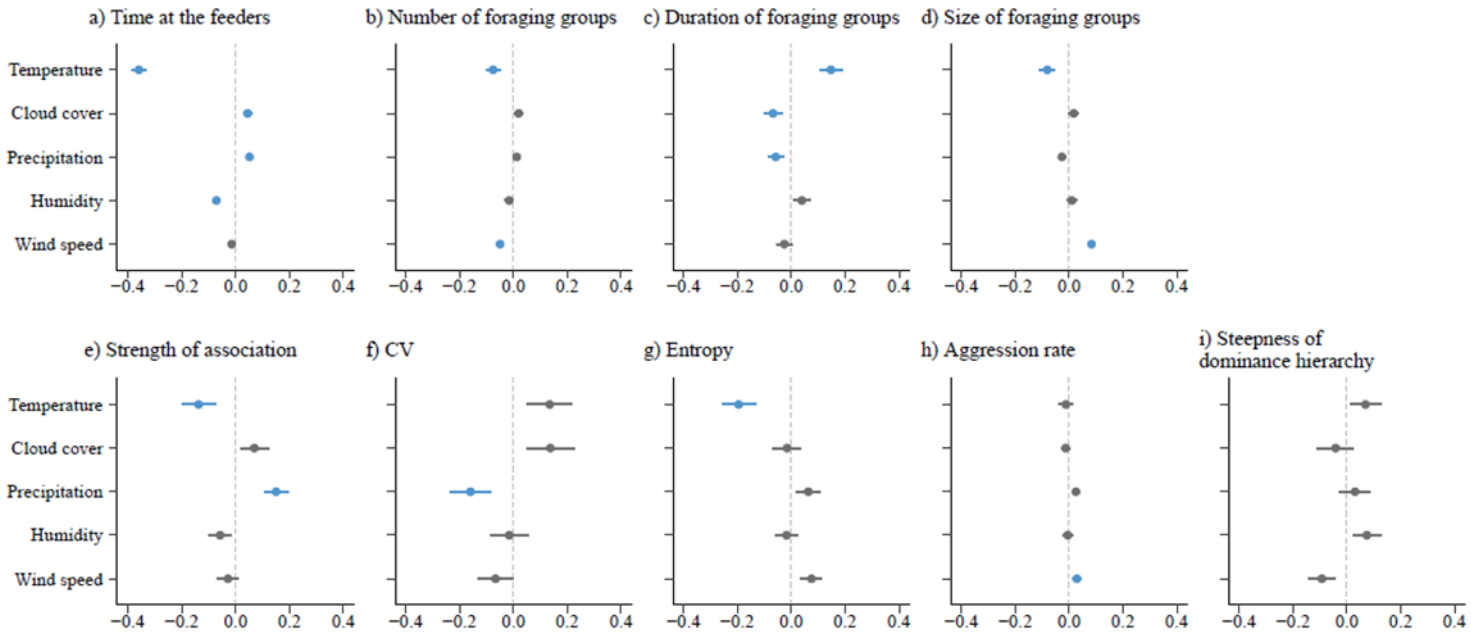

Figure 8.6. Estimates and standard deviation of the predictors included in the model averaging approach for each studied response variable. Blue colour marks significant effect sizes.

Table 8.1 Results of models relating one behaviour to a set of climatic predictors. We present the standardised coefficient (β_{std}) ± the standard error (SE) and the p-value (*P*) for each predictor.

Predictor	Time spent at the feeders	Number of foraging groups	Duration of foraging groups	Size of foraging groups	Strength of association	Coefficient of variation	Entropy	Aggressiveness	Steepness of dominance hierarchy
Temperature	-0.360 ± 0.026 < 0.001*	-0.076 ± 0.027 0.005*	0.147 ± 0.041 <0.001*	-0.081 ± 0.028 0.004*	-0.138 ± 0.062 0.027*	0.134 ± 0.082 0.103	-0.196 ± 0.062 0.002*	-0.012 ± 0.025 0.638	0.069 ± 0.057 0.232
Precipitation	0.051 ± 0.012 < 0.001*	0.012 ± 0.013 0.156	-0.058 ± 0.028 0.041*	-0.027 ± 0.014 0.055	0.150 ± 0.045 0.001*	-0.160 ± 0.074 0.031*	0.063 ± 0.043 0.146	0.025 ± 0.013 0.060	0.030 ± 0.056 0.591
Relative humidity	-0.072 ± 0.015 < 0.001*	-0.016 ± 0.016 0.311	0.039 ± 0.031 0.215	0.010 ± 0.017 0.574	-0.058 ± 0.042 0.172	-0.016 ± 0.069 0.811	-0.018 ± 0.041 0.657	-0.005 ± 0.016 0.737	0.074 ± 0.053 0.162
Wind speed	-0.015 ± 0.013 0.246	-0.050 ± 0.014 <0.001*	-0.026 ± 0.028 0.355	0.083 ± 0.015 <0.001*	-0.029 ± 0.040 0.461	-0.067 ± 0.066 0.313	0.075 ± 0.039 0.056	0.029 ± 0.014 0.035*	-0.093 ± 0.051 0.070
Cloud cover	0.044 ± 0.015 0.004*	0.019 ± 0.016 0.242	-0.068 ± 0.034 0.043*	0.017 ± 0.018 0.343	0.069 ± 0.052 0.190	0.137 ± 0.087 0.116	-0.016 ± 0.052 0.757	-0.013 ± 0.016 0.416	-0.042 ± 0.067 0.527
Foraging group size								0.340 ± 0.022 <0.001*	-0.683 ± 0.060 <0.001*
Foraging group duration								-0.072 ± 0.012 <0.001*	0.078 ± 0.050 0.160

*Significant values ($P < 0.05$)

Error degrees of freedom is 1619 in models for behaviours computed per day (time at feeders, number, duration and size of foraging groups, and aggressiveness), 165 in models for most behaviours computed per week (strength of association, coefficient of variation and entropy), and 153 in the model for the steepness of dominance hierarchy (computed per week, but for which due to insufficient data, the sample size was smaller).

4. Discussion

We found seasonal patterns in all aspects of social and collective behaviour that we studied, with foraging groups becoming smaller and more numerous during the breeding season, the mean strength of association between individuals and aggression rates decreasing, and dominance hierarchies becoming steeper. Controlling for those seasonal patterns, we found that different aspects of weather predicted many changes in collective behaviour, encompassing collective foraging dynamics, social network structure and aggressiveness. Some of these associations suggest individual- and group-level adaptations to manage varying energy requirements, such as associations between temperature and foraging dynamics. Other associations suggest effects of weather-disturbing behaviour, such as associations between wind speed and network structure or aggressiveness. Overall, we show that several aspects of weather affect collective behaviour differently, which, as we discuss next, suggest various ways in which weather-related changes in sociality can influence the ecology of gregarious animals.

4.1. Seasonality

Despite year-to-year differences in behaviour, perhaps because of habituation or year-to-year changes in vegetation density, clear seasonal patterns were present in all studied behaviours. During winter (December to March), birds increased the time spent feeding, reaching a maximum around the end of winter and the beginning of the breeding season (March/April). This could result from the low temperatures in winter when birds need more energy to maintain body temperature. Other passerine species are known to gain body fat reserves for the energetic demands of the breeding season (e.g., starling, *Sturnus vulgaris*, Meijer et al., 1994; zebra finch, *Taeniopygia castanotis*, Rozman et al., 2003). If this happens in the common waxbill, it could also help explain the winter increase in feeding prior to the breeding season.

During the breeding season, which in the region of the study usually starts in February or March and peaks around May-June (Figure 8.2c,d, and Beltrão, Gomes, et al., 2021), foraging groups were smaller, and more foraging groups visited the feeders per day. This could result from changes in social dynamics due to reproduction, with individuals focusing more on following the pair rather than aggregating in larger social groups. Despite foraging groups being smaller and the birds spending less time at the feeders during the breeding season, the foraging groups actually spent more time in the feeding area per visit. This suggests that, in the breeding season, during encounters at the feeding, birds are engaged in other activities besides feeding, perhaps including

courtship, mate-guarding, or competition for mates. Perhaps increased competition in the breeding season could even contribute to the decrease in the size of the foraging groups since a previous experiment showed that increased competition (in that case, for food) can decrease waxbill group sizes (Beltrão et al., 2022).

There was also a decrease in the mean strength of association between individuals in the breeding season, accompanied by an increase in network structure, meaning more diversity in the strength of association across the social network. Similar results were reported by Gomes et al. (2022) in this study system. Again, these changes likely reflect the social dynamics of breeding, with some associations remaining strong or becoming stronger (e.g., within-pair associations). In contrast, most other associations weaken, making the social network less cohesive.

Aggression rates at the feeders decreased in the breeding season, and the dominance hierarchy became steeper, meaning that attacks of more subordinate to more dominant individuals became rarer. This could be a consequence of foraging groups being smaller during the breeding season and, therefore, the opportunities for aggression decreasing. In contrast, the large groups outside the breeding season often comprise many more birds than the number of feeders. Individuals spend more time feeding, which requires frequent aggressive displacements to access the feeders. In those circumstances, there may often happen aggressive displacements to access a feeder that is random concerning the dominance hierarchy, thus decreasing the steepness of the hierarchy.

While the seasonal pattern for feeding was simple, with an increase towards around March and a decrease towards around October, the seasonal patterns in the other behaviours all had two peaks in the breeding season: one main peak around May, coinciding with peak breeding, and, when behaviours were already moving in the direction of the non-breeding season, a second peak of smaller magnitude around October, near the end of the breeding season for waxbills in this region (Beltrão, Gomes, et al., 2021). This complex seasonal pattern with two peaks suggests that often there is a second increase in breeding behaviour towards autumn, which is also supported by the presence of nestlings in October during at least 3 of the studied years (PB, BS personal observation). This scenario is possible because waxbills are opportunistic breeders (i.e., can reproduce when environmental conditions are suitable rather than in fixed periods of the year; Hau et al., 2008), and breeding phenology differs greatly across the common waxbill geographic range (Sanz-Aguilar et al. 2015). We suggest that, with the climatic conditions of our study, environmental conditions at the beginning of autumn

are favourable for resuming breeding behaviour, perhaps because, typically, the weather remains warm but no longer as dry as in the summer. Previous work with waxbills reported a small increase of juveniles or females with brood patches in September/October (Beltrão, Gomes, et al., 2021; Sanz-Aguilar et al., 2015). Our data on the number of intact nests did not detect such an increase in breeding by September/October (Figure 8.2d; see also Beltrão, Gomes, et al., 2021), possibly because birds were reusing the nests.

4.2. Associations with weather

Controlling for seasonality and, more generally, for any month-to-month changes in behaviour, we found that waxbills spent more time at the feeders when temperatures were low, or cloud cover was high. Since we also found that time at the feeders predicted the amount of seeds consumed, feeding increased in colder weather or cloudy days, the latter of which diminishes the amount of heat received by direct solar radiation. Increased feeding is expected on those days because individuals should increase their metabolic rate to maintain body temperature (Huey et al., 2012). Therefore, temperature and cloud cover affected feeding behaviour due to energetic needs.

Precipitation was also associated with more time spent at the feeders, which could either be because of rain increasing heat losses and, thus, requiring more energy for the thermoregulation (McCafferty et al., 2011), or simply because waxbills remained for longer at the feeders where they protected from direct rain. We cannot discard this latter possibility because the humidity was associated with less time (rather than more time) at the feeders, which does not support the hypothesis that humidity, and perhaps rain, substantially increased heat loss and required more energy for thermoregulation (O'Connor & Vézina, 2019). Nevertheless, humidity can make heat loss more difficult when temperatures are high, which perhaps contributed to its unexpected association with reduced food intake. Hence, precipitation may have affected feeding behaviour due to energetic needs or may also influence space use, including time at the feeders, due to the disturbance it causes.

Collective foraging was also affected by temperature. Fewer and smaller groups visited the feeding area on hotter days, in line with higher temperatures diminishing energetic requirements. Only the duration of foraging groups increased with temperature, perhaps to compensate for fewer visits to the feeders. This compensation, however, was only partial since, on hotter days, the birds spent less time at the feeders. The duration of foraging groups became shorter on rainy days, likely to reduce exposition

to rain. Foraging groups became larger, and the number of group visits to the feeding area decreased on windy days. Thus, while the wind did not change the time birds spent at the feeders, it changed how waxbills moved collectively. On windy days waxbills may wait for periods with less wind speed to fly away from refuges in the vegetation and visit the feeding area to avoid disturbances in flight manoeuvring and wind-related increased energy expenditure of flight (Ortega-Jimenez et al., 2014; Shepard et al., 2016). As a result, birds would forage more synchronously, in larger groups and with fewer group visits to the feeding area.

The strength of association between birds increased during colder and rainy days, meaning that their spatial proximity increased. In both cases, the social network also became less structured: in the case of precipitation, the lowered CV of the strengths of associations indicates a more homogeneous social network; in the case of low temperatures, higher network entropy is accompanied by a tendency for lower CV of strengths of associations similarly indicates less differentiated subgroups in the network. Although cold temperature and high precipitation had different effects on collective movement, they both decreased the duration of foraging groups, implying that groups moved more synchronously (i.e., foraging group members are less spread out in time). Greater synchrony can contribute to increasing spatial proximity among individuals and, thus, their strength of associations. In addition, it is possible that on cold and rainy days, birds stayed next to each other when on the perches in the feeding area for thermoregulation or to minimise the amount of rain received, further contributing to an increase in the strength of associations. Such cooperative behaviour often exists in social species (Gilbert et al., 2010), especially during rainy days (e.g., Anctil et al., 2014; Campbell et al., 2018; Ward & Webster, 2016). The cold- and rain-related increase in the strength of associations was more pronounced among individuals normally not very strongly associated because it resulted in the observed lessening of network structure. On colder but not rainy days, waxbills also foraged in larger groups. That proximity among individuals not usually together could have contributed to the observed increase in the mean strength of associations and decrease in network structure.

Finally, wind speed was associated with more aggression at the feeders, controlling for other effects of wind on group size and duration. Waxbills in the mesocosm often have to wait for the feeders to become available or displace another bird from a feeder (i.e., feeder availability is limited). Since the area near the feeders is exposed to the wind, with perches but no trees or shrubs, waxbills may more likely decide to displace another bird rather than wait to avoid wind-related disturbance. The wind-associated

increase in aggression was accompanied by a decrease in network structure (higher network entropy) and a tendency to decrease the steepness of the dominance hierarchy. This suggests that aggressions associated with disturbance by the wind tend to be more random than normal, not following the dominance hierarchy as much and perhaps compromising social network structure. In nature, since waxbills feed from seeds in grass heads, which can be very unstable on windy days, disturbance by the wind may be even more accentuated than here and perhaps influence waxbill behaviour in additional ways.

4.3. Conclusion

Our results confirmed some behavioural effects of weather that were expected and had been documented in other species (e.g., increased feeding in colder weather, Bonter et al., 2013; Zuckerberg et al., 2011; smaller foraging groups in warm weather, Funghi et al., 2019), and showed various weather-associated changes in collective behaviour not reported or anticipated before (Fisher et al., 2021). For example, increased aggression on windy days due to disturbance. Finding that the weather affects collective behaviour and social structure in multiple ways suggests that gregarious species like the common waxbill have diverse strategies to face environmental fluctuations and climatic differences. To our knowledge, our study is the first to assess the effects of natural weather variation on social behaviour without the confounding effect of food availability and predictability, which in nature depend on weather. Having standardised access to food, we showed that weather alone can affect collective behaviour profoundly, notwithstanding other indirect effects that it may have via changes in food availability or predictability (e.g., Beltrão et al., 2022; Foster et al., 2012).

Since weather-dependent changes in collective behaviour can be pervasive, they will likely influence various ecological processes in gregarious animals, such as range expansion, adaptation to climate change, or behavioural ecology. By knowing how collective behaviour differs between weather conditions, we may better understand the dynamics of range expansions in climatically heterogeneous landscapes because some changes in collective behaviour will influence movement and dispersal (e.g., smaller and more numerous foraging groups should facilitate spatial exploration and dispersal). Regarding adaptation to future climates, the adjustments in social behaviour observed in response to weather fluctuations give clues as to the long-term adjustments in response to climate change. If some of the predicted social changes concern species with a fragile conservation status, then this knowledge can inform conservation efforts (Snijders et al., 2017). Regarding behavioural ecology, the social environment can

influence the fitness of different behaviours or personality types and, thus, their evolutionary change over time (Oh & Badyaev, 2010; Regan et al., 2022; Rudin et al., 2018). In a recent biological invasion of common waxbills, some personality differences that are not predicted by age, sex, morphology, nor invasion stage, differ geographically according to weather stability (Carvalho et al., 2013, 2021) suggesting that more stable or unstable environments select for different personality types. Our results now indicate that this does not necessarily result from the degree of stability in the abiotic environment, but may also arise from the social environment that causes geographic patterns in animal personality. We hope that the findings of multiple effects of weather on collective behaviour, and the potential implications of such changes to the ecology of gregarious animals, foster research into how species with different ecological requirements react to environmental change.

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Chapter 9 | General discussion

Waxbill reproduction and dominance hierarchy

The breeding season in birds is accompanied by changes in behaviour (Ward and Webster 2016), and it is thus important to account for this variation when studying the effects of climate or other environmental effects on social behaviour. Therefore, in Chapter 2, I studied the breeding phenology of the common waxbill in continental Portugal, the northernmost part of its range, where the empirical work for the rest of my thesis also took place. I found that waxbills breed from March to late September/October, with a peak around May. Although continental Portugal encompasses different climates, particularly regarding summer temperatures (Peel et al. 2007), the breeding phenology was similar across the different sites across the country. The nest building behaviour in my study mesocosm followed the same breeding phenology as in nature. I was also able to detect year-to-year plasticity regarding the starting date for nest building, which suggests that waxbills can make adjustments to their breeding phenology, possibly in response to the environmental conditions.

Another important part of the structure of an animal society, particularly in a gregarious species, is the dominance hierarchy. In chapter 5, I characterized the dominance hierarchy of common waxbills living semi-freely in the mesocosm, showing that this species had mildly steep hierarchies (i.e., the subordinate bird may sometimes win a fight with a more dominant individual). This agrees with studies of dominance hierarchies with waxbill groups confined when to bird cages (Chapter 4 and Funghi et al. 2015). Moreover, I found that the dominance rank of individuals was repeatable across time and seasons, such that social dominance can be viewed as a stable phenotype for waxbills. Finally, I showed that personality, stress and body size did not affect the dominance status of an individual. Instead, the saturation of the breast patch was correlated with social dominance, indicating that ornamental red colour might be used as a badge of status.

Methodological contributions

Deciding on the most appropriate method to quantify dominance hierarchies is important to understand dominance interactions in a population and to better detect biological phenomena. In Chapter 4, I showed that choosing an inadequate method can lead to wrong conclusions. I found temporal autocorrelation on the likelihood of individuals winning or losing aggressive interactions, possibly due to space constraints. The Elo-rating method accounts for this non-dependence by considering the sequence

of interactions (Albers and De Vries 2001). Only when using the Elo-rating method, I was able to detect differences in social dominance when males were treated with testosterone. Unlike in Chapter 4, where waxbill groups were housed in bird cages, when studying waxbills in the semi-natural environment of the mesocosm (Chapter 5) dominance interactions were no longer autocorrelated through time and I could use statistically more powerful methods, such as the Randomized Elo-rating, to infer dominance hierarchies (Sánchez-Tójar et al. 2018).

Studying dominance interactions in the long term is greatly facilitated by automated monitoring of behaviour, such as RFID data on aggressive displacements at the feeders in the mesocosm. Automatically detecting these aggressive displacements, however, requires developing and validating a method to extract dominance interactions from the RFID datastream. In chapter 5, I followed an approach similar to that of Evans et al. (2018), using video recordings to determine temporal criteria that reliably identify aggressive displacements at the feeders, which could then be applied in the RFID datastream. I found that displacements at the feeder could be reliably identified as events where 1) a bird lands on a feeder less than 2 seconds after the previous bird leaves, and 2) both birds stay a minimum of 3 seconds at the feeder. With these 2 criteria, I created an algorithm that automatically identified displacements at the feeders in the RFID datastream, allowing me to study the environmental effects on social dominance and aggression.

Environmental effects on social behaviour

My work focused on the effects of the environment on various aspects of collective and social behaviour, using the common waxbill as a model. I found effects of both the social and non-social environment. The main environmental effects were, first, that upon limited space availability waxbills can build compound nests, which sheds light on a potential pathway in the evolution of this complex behaviour. Second, regarding the influence of the social environment, I found that waxbills show a bullying strategy in foraging groups, because they direct most of aggression towards very subordinated individuals. Moreover, waxbills became more aggressive in the presence of less familiar individuals, suggesting that bullying is used so as to show-off aggression in the presence of potential competitors (i.e., less familiar individuals). Third, when focusing on the effects of reduced food availability and unpredictability, in both cases waxbills became more aggressive and foraged in smaller groups, appearing to have reduced social tolerance. Finally, different climatic conditions had distinct effects on collective behaviour, some of

which had not been documented before. For example, precipitation seemed to promote prosocial behaviour, and stronger winds increased aggressive behaviour.

I reported, for the first time in this species, that waxbills can build compound nests (Chapter 3). These nests were mainly found off-ground, and the majority of nests that progressed to egg-laying were in compound structures. In the climatic conditions of the mesocosm (i.e., Atlantic climate), building nests near or on the ground might be less adequate to achieve reproductive success, perhaps due to the high humidity at the grass layer (personal observation). In these conditions, building off-ground nests seems to be more advantageous. Space available for nest construction off-ground in the mesocosm was limited. Hence, birds may have been constrained to clump their nests together when building nests off-ground. I showed that waxbills can plastically change their nest-building behaviour, and perhaps this improves their breeding success. Interestingly, different nest chambers in the compound structure could be occupied by different pairs simultaneously. If upon certain ecological conditions a bird species starts to clump their nests together plastically, and if the compound nest poses more advantages that the isolated nest, the new phenotype may become prevalent in that population and facilitate genetic evolution of more elaborate communal nests. Hence, this study could illustrate the earlier steps in the evolution of compound nests or even communal nesting.

Waxbills showed a bullying pattern (Chapter 6), directing aggression preferentially towards very subordinate individuals. This finding indicates that, by using a rank-informed aggression strategy, waxbills perceive their dominance status in relation to their group members, and use that information to benefit themselves (Hobson et al. 2021). For example, by attacking a very subordinate conspecific, waxbills reduce the risk of injury as the risk of retaliation is unlikely. The observed bullying pattern is intriguing because the dominance relationship between individuals very far apart in the dominance hierarchy should be clearly established, leading to the question of why to attack the very subordinated individuals. I found that waxbills became more aggressive in the presence of less familiar individuals, suggesting that bullying is used as a safe strategy to signal dominance status to those less familiar birds, with whom the dominance relationship may not be clearly defined. By attacking very subordinated individuals the risk of retaliation is small and allows the bird to safely signal dominance status, especially because dominance status and aggressiveness are highly correlated in waxbills (Chapter 5). In nature, waxbills show fission-fusion dynamics, which implies that birds will often encounter unknown or less familiar individuals. A strategy of signalling social dominance

by showing-off aggression could allow the birds to avoid entering in potentially dangerous fights with unknown or less familiar individuals.

Rank-informed aggression strategies, such as bullying, emerge when individuals have the knowledge about their dominance status in relation to conspecifics (Hobson 2020). These are considered to be used by high information societies as they can require the access and usage of detailed information, including information on dominance status and individual recognition (Hobson 2020). I want to highlight a result from Chapter 5, where I show that the saturation of the breast patch could function as a signal of dominance status. Therefore, we could argue that birds may not specifically recognise the dominance status of conspecifics but could target birds with an absent or slightly red-coloured breast patch. In this case, birds would not use individual recognition, but instead they would take advantage of the information provided by a badge of status (i.e., saturation of breast patch). Although this is a possible explanation, literature combined with previous knowledge on waxbills suggests another hypothesis, individuals can recognize each other as well as their dominance status. Individual recognition is probable to occur when individuals encounter and interact with each other repeatably (Tibbetts and Dale 2007), which is the case of our study system. Additionally, breast saturation could be functioning as a badge of status only for unfamiliar birds, similarly to golden-crowned sparrows (Chaine et al. 2018) or green anole (Korzan et al. 2007). Whereas for other conspecifics already acquainted, individual recognition combined with previous knowledge of their dominance status could be used. Previous work also suggests that waxbills can recognize their conspecifics, as the temporary removal of individuals (ca. 3 months) did not affect social preferences. In gregarious species, recognizing group members as well as their dominance status should be advantageous to avoid agonistic interactions, being also a reliable way, as it is not cheatable, to infer the conspecific status.

I used the controlled conditions of the study system, namely its controlled food availability, to study experimentally the effects of food availability and predictability. Upon lower and unpredictable food resources, waxbills increased aggression, suggesting decreased social tolerance, and perhaps because of this they also decreased the size of foraging groups (Chapter 7). Although fragmentation of a social group may seem disadvantageous, for waxbills it could function as an adaptive response to ecological challenges. Waxbills, in nature, show fission-fusion dynamics and are adapted to unpredictable environments, making vagrant movements in search of suitable habitats (Clement et al. 1993; Payne 2010). Fragmenting into smaller groups may function as a

trigger to explore new patches with more suitable foraging conditions, before exceeding the carrying capacity of the environment. By forming more subgroups, perhaps individual explore cover more areas, gaining knowledge on food availability and then transmitting that information to conspecifics through their fission-fusion dynamics.

Because in the mesocosm food availability is not determined by seasonality or weather conditions, I was also able to study the effects of abiotic stressors on social behaviour, without the confounding effect of food availability (Chapter 8). I found multiple effects of weather on social behaviour, namely through energetic requirements and disturbances. For example, in colder days birds were found to forage more often and during longer periods. While on windy days foraging groups were less frequent and larger, possibly to avoid periods of the day with higher wind, with individuals behaving more aggressively to access food. In a more holistic approach, the different weather conditions may be expected to affect different ecological processes such as range expansion, adaptation to climate change and behavioural ecology. I hope that this work aids to build-up and improve predictions of how gregarious animals will respond when facing environmental changes.

To conclude, my main goal was to understand how different environmental conditions could shape social behaviour. I would like to highlight how some of the discovered behavioural patterns, including the bullying strategy or the fragmentation of the foraging groups, seemed to be well aligned with the social dynamics of the group, the fission-fusion dynamics. I would also like to note how upon a challenging environment, individuals can increase conflict and pro-sociality, suggesting that living socially comprises a complex behavioural axis between these two behaviours not simply being one or another. Moreover, including the ecology of the species is particularly important when studying the effects of different environmental conditions.

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Appendices | Appendix A to G

Appendix A

Data. Field data (i.e., date, location, climate, sex, age, brood patch) and nest data (status of each nests per date of nest monitoring) are available online at https://doi.org/10.1007/s10211-021-00376-9

Appendix B

Table B1. Pairs identified at the nest chambers (numbered from 1 to 10) of different compound nests (labelled from A to G) across time in 2021. The identity of each member of a pair, separated by a slash, is indicated by 2 alphanumeric characters. Different colours in the same compound nest structure indicate different pairs.

Data. Data used in the analysis is available online at https://doi.org/10.1007/s00265-022-03264-9

Table B1. Pairs identified at the nest chambers (numbered from 1 to 10) of different compound nests (labelled from A to G) across time in 2021. The identity of each member of a pair, separated by a slash, is indicated by 2 alphanumeric characters. Different colours in the same compound nest structure indicate different pairs.

Dates	A1	A2	A3	A4	A5	A6	A7	A8	A9
09/03 - 12/03		No ID	No ID						
12/03 - 16/03		No ID	No ID						
31/03 - 06/04	34/D2	No ID	No ID						
06/04 - 13/04	34/D2	No ID	No ID						
13/04 - 23/04	34/D2	No ant.	No ID						
24/04 - 04/05	No ID	No ant.	No ID	No ant.					
17/05 - 25/05	No ant.	No ant.	No ant.	No ant.	49/86	49/86		No ant.	
25/05 - 31/05	No ant.	No ant.	No ant.	No ID	No ant.	No ant.		No ant.	
11/06 - 25/06			No ant.		49/86	49/86	87/6B	No ant.	No ID

	B1	B2	B3	B4	B5	B6
01/03 - 05/03	No ID	EC/33				
09/03 - 12/03	No ant.	No ant.		34/D2	E8/7C	
12/03 - 16/03	No ant.	No ant.		34/D2	E8/7C	
16/03 - 23/03	No ID	EC/33		No ID	E8/7C	
23/03 - 31/03	No ID	No ID		No ID	E8/7C	
13/04 - 23/04	No ant.	No ant.		No ID	No ant.	
24/04 - 04/05	No ant.	No ant.		No ID	No ant.	
25/05 - 31/05	No ant.	No ant.	No ant.	No ant.	No ant.	No ID

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10
07/05 - 17/05	No ant.	71/8A	71/8A	No ID	No ID					
31/05 - 04/06		No ant.	No ant.	No ant.	71/8A	57/26	73/49			No ant.
01/07 - 08/07		No ant.		No ID	No ID	57/26	1C/9B			No ant.
08/07 - 22/07		No ID		No ant.	No ant.	No ID	1C/9B	1C/9B		No ant.
23/07 - 06/08		No ID		No ant.	No ant.	No ID	1C/9B	1C/9B	No ant.	No ant.
19/08 - 02/09		No ID		No ant.	No ant.	No ant.	No ID	No ID	No ID	No ant.

	D1	D2	D3	E1	E2
04/05 - 07/05	49/A1				
04/06 - 07/06	49/A1	No ant.	C4/ 3E	C4/3E	No ant.
05/08 - 19/08	49/A1	No ant.	No ID	No ant.	No ant.

	F1	F2	F3	G1	G2
07/06 - 11/06	1C/9B	29/54		08/2B	
25/06 - 29/06	No ID	29/54	2C/87	No ant.	No ant.
29/06 - 01/07	No ant.	No ID	No ant.	No ID	9C/11C

No ID – No pair was identified on the nest chamber
No ant. – Nest chamber without RFID antenna
Empty cell – Nest chamber did not exist

Appendix C

Table C1. GLMM contrasts comparing group aggressiveness or sex differences in dominance score (Elo-rating, David's score, or Randomized Elo-rating). The reference level for the factor treatment is "control".

Table C2. GLMM contrasts comparing individual aggressiveness, dominance score (Elo-rating, David's score, or Randomized Elo-rating) or aggression towards the opposite sex. The reference level for the factor treatment is the "control" and for the factor sex is "female".

Table C1. GLMM contrasts comparing group aggressiveness or sex differences in dominance score (Elo-rating, David's score, or Randomized Elo-rating). The reference level for the factor treatment is "control".

	Estimate	95% CI	*P*
Mean aggressiveness			
Intercept	2.11	[1.67, 2.54]	<0.01
Female T	0.30	[-0.02, 0.61]	0.07
Male T	-0.04	[-0.41, 0.33]	0.82
Sex difference in Elo-rating			
Intercept	96.1	[-59.5, 251.6]	0.26
Female T	32.7	[-94.2, 159.6]	0.63
Male T	144.4	[17.5, 271.3]	0.05*
Sex difference in David´s score			
Intercept	0.39	[-0.15, 0.92]	0.19
Female T	0.15	[-0.31, 0.60]	0.54
Male T	0.23	[-0.22, 0.68]	0.35
Sex difference in Randomized Elo-rating			
Intercept	152.4	[5.18, 299.7]	0.08
Female T	47.9	[-90.8, 186.6]	0.51
Male T	78.9	[-59.8, 217.6]	0.29

T: testosterone treatment. Contrasts use the control treatment as reference level. Positive estimates indicate a higher value relative to the reference level. The 95% confidence intervals (CI) and P values of the estimates are shown, as well as the estimate for the effect of the intercept in each model. The asterisk indicates a significant value ($P < 0.05$).

Table C2. GLMM contrasts comparing individual aggressiveness, dominance score (Elo-rating, David's score, or Randomized Elo-rating) or aggression towards the opposite sex. The reference level for the factor treatment is the "control" and for the factor sex is "female".

	Estimate	95% CI	*P*
Aggressiveness			
Intercept	1.28	[0.68, 1.88]	<0.01
Female T	0.03	[-0.57, 0.62]	0.93
Male T	-0.30	[-0.93, 0.33]	0.35
Male	1.06	[0.26, 1.87]	0.01*
Female T * Male	0.26	[-0.52, 1.04]	0.52
Male T * Male	0.49	[-0.32, 1.31]	0.24
Elo-rating			
Intercept	-48.0	[-155.6, 59.6]	0.39
Female T	-15.8	[-111.7, 80.2]	0.75
Male T	-85.7	[-184.6, 13.2]	0.10
Male	96.1	[-56.1, 248.2]	0.22
Female T * Male	32.7	[-103.0, 168.4]	0.64
Male T * Male	158.7	[20.9, 296.5]	0.03*
David´s score			
Intercept	1.31	[1.01, 1.60]	<0.01
Female T	-0.07	[-0.33, 0.19]	0.58
Male T	-0.22	[-0.49, 0.05]	0.12
Male	0.39	[-0.03, 0.81]	0.08
Female T * Male	0.15	[-0.22, 0.51]	0.44
Male T * Male	0.27	[-0.11, 0.64]	0.17
Randomized Elo-rating			
Intercept	-76.6	[-166.8, 13.6]	0.12
Female T	-23.6	[-96.2, 49.1]	0.53
Male T	-53.8	[-128.7, 21.2]	0.17
Male	152.4	[24.8, 280.01]	0.03*
Female T * Male	47.9	[-54.9, 150.7]	0.37
Male T * Male	89.4	[-15.0, 193.8]	0.10
Aggressiveness towards the opposite sex			
Intercept	0.12	[-0.71, 0.96]	0.77
Female T	0.31	[-0.42, 1.03]	0.40
Male T	-1.40	[-2.45, -0.36]	0.01*
Male	1.04	[-0.05, 2.14]	0.06
Female T * Male	0.26	[-0.65, 1.18]	0.57
Male T * Male	1.34	[0.14, 2.54]	0.03*

T: testosterone treatment. Contrasts use the control as reference level for the factor treatment and female as reference level for the factor sex. Statistics as in Table A1. Asterisks indicate significant values ($P < 0.05$).

Appendix D

Figure D1. Temporal correlograms over increasingly longer time intervals, separately for NB1, B1, NB2, B2.

Video. The video illustrating examples of displacements at the feeders is available at https://doi.org/10.1016/j.anbehav.2021.09.011

Code and data. The code and data used to produce the research article are available at https://doi.org/10.1016/j.anbehav.2021.09.011

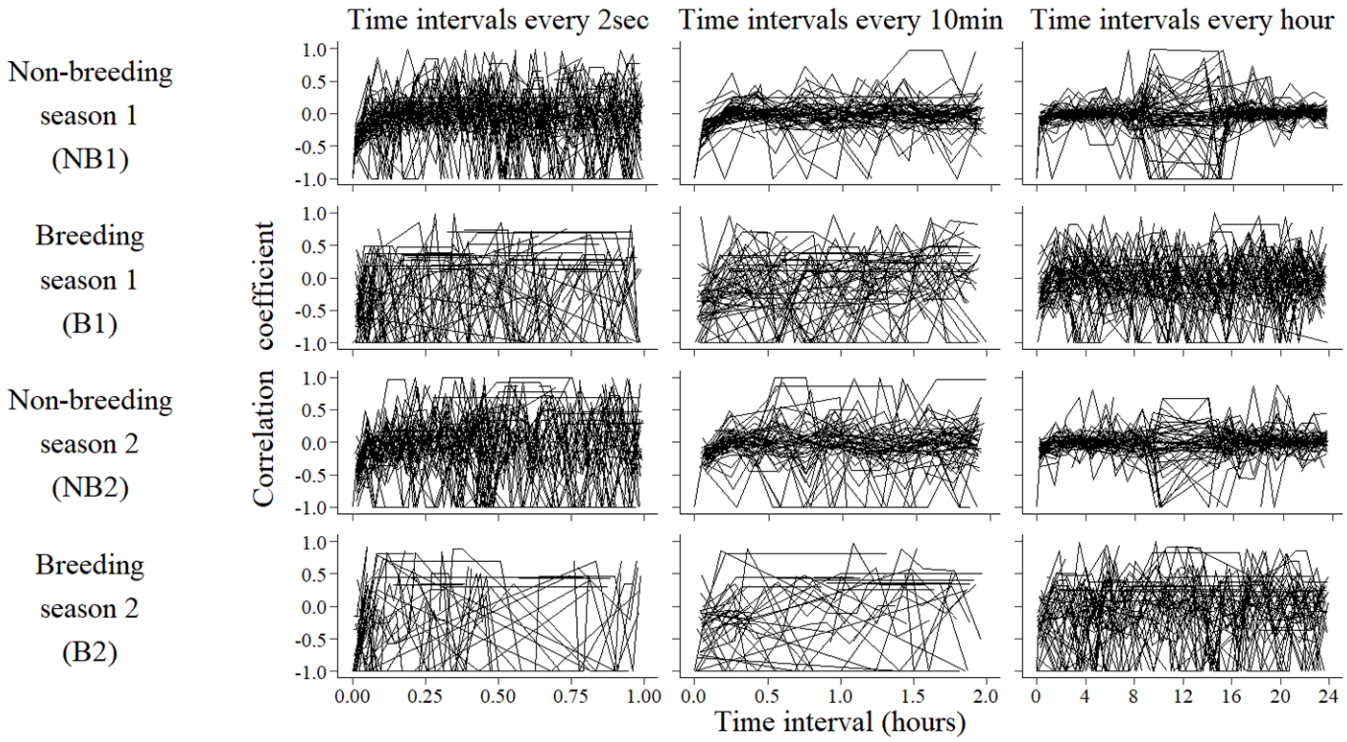

Figure D1. Temporal correlograms over increasingly longer time intervals, separately for NB1, B1, NB2, B2.

Appendix E

Supplementary Methods

Table E1. GLMM results of the relation between number of displacements per individual and the mean absolute difference in dominance ratings between the focal individual and the audience.

Table E2. GLMM results of the relation between number of displacements per individual and the mean difference in dominance ratings between the focal individual and 10 % most similar in rank, most dominant or subordinate members in the audience.

Table E3. GLMM results of the relation between number of displacements per individual and the mean network proximity of the audience.

Table E4. GLMM results of the relation between number of displacements per individual and the mean difference in network proximity between the focal individual and 10 % of the audience members socially-closer or most socially-distant to the focal.

Figure E1. Histograms of the (a) audience size, (b) time of a gathering event, and (c) time an individual was detected in a gathering event.

Figure E2. Density plots for the predicted numbers of aggressive displacements per bird per gathering event (i.e., group visit to the feeding area), as a function of similarity in dominance rank (randomized Elo-rating) with audience members. Predicted densities, controlling for other factors in each model, are shown by the colour scale, and regression lines are shown in black. Aggressions (a) decreased with increasing mean absolute difference of the focal bird to the 10% audience members most similar in dominance to focal birds, (b) decreased with decreasing mean difference of the focal bird to the 10% most dominant audience members (i.e., more negative values in the X axis, indicating bystanders more dominant relative to focal birds), and (c) increased with increasing

mean difference of the focal bird to the 10% most subordinate audience members (i.e., more positive values in the X axis, indicating bystanders more subordinate than the focal birds).

Figure E3. Density plots for the predicted numbers of aggressive displacements per bird per gathering event, as a function of proximity in the social network. Aggressions (a) did not change significantly as a function of mean association strength of the focal bird to the 10% audience members most strongly associated with it, but (b) increased with decreasing strength of association to the 10% audience members most weakly associated with the focal birds (i.e., values in the X axis closer to zero).

Data. The data used to produce the research article are available through Dryad Digital Repository https://doi.org/10.5061/dryad.brv15dvd8

Supplementary Methods

Permutation-based procedures

The statistical significance of analyses in this article was evaluated using both parametric tests (main text) and permutation-based tests (here), as in Gomes et al. (2022).

Aggression towards similar-rank individuals

We used two different permutation-based procedures. For the first approach, we conducted a Multiple Regression Quadratic Assignment Procedure (MRQAP) that, similarly to the multimembership model described in the main text, uses the rates of aggression per dyad as response variable and as predictor used the absolute difference of dominance ratings (Elo-ratings) between the two individuals in each dyad. We made 50,000 node permutations (NP) on the individual-by-individual response matrix (matrix of aggression rates per dyad), by randomly permuting, each time, all individual identities (nodes) while maintaining the edges fixed (Croft et al. 2008, 2011; Farine and Whitehead 2015). Each permutation constructs a new random individual-by-individual matrix ("rmperm" from the sna package, v. 2.6; Butts 2019), from the observed non-permuted matrix, which is then used in the MRQAP ("mrqap.custom.null" from the asnipe package, v. 1.1.16; Farine 2013) to create a posterior distribution of regression coefficients for the null model.

As a second permutation based approach, we made a Generalised Linear Models Quadratic Assignment Procedure (GLMQAP; Franks et al. 2021) with a Poisson distribution, using the R function "glmqap" from the package "aninet" (v. 0.0.0.9000; Weiss 2020). As response variable we used a matrix with the number of aggressive displacements between dyads, including the logarithm of the time a dyad spent together as argument "offset", to allow the modelling of displacement rates (Weiss 2020). We also included two predictors: a dissimilarity matrix of the absolute differences between the dominance ratings for individuals of a dyad (same as described in the previous approach), and an undirected individual-by-individual matrix of the dyads' total time at the feeders (i.e., the sum of the time that each individual spent at the feeders), to control for the potential bias of observing some individuals more than others (Franks et al. 2021). To assess the statistical significance of the effects of this model, we applied the double semi-partialling (DSP) permutation method (Dekker et al. 2007), included in the "glmqap" function (Weiss 2020), based on the permutation of residuals to create posterior

distributions of a pivotal statistic (z-value) for the null model. We used 50,000 permutations and checked that this number of permutations was sufficient for the P-value to stabilize, as advised by Farine (2017), and report two-tailed P-values.

Contrary to the results of the procedure in the main text, when considering all aggressive events (from the more to the less dominant dyad member, and vice-versa) we found no evidence that the rate of aggressive displacements differed depending on the similarity of dominance ratings in dyads (MRQAP with NP: $\beta = -8.58*10-8$, $P = 0.72$; GLMQAP with DSP: $\beta = 8.74*10-5 \pm 1.16*10-4$, $z = 0.75$, $P = 0.87$, effect of time spent in the feeders: $\beta = 3.78*10-6 \pm 2.70*10-7$ SE, $z = 14.00$, $P = 0.14$). Similarly to the results in the main text, repeating this model using only aggressions from the more to the less dominant dyad member showed higher aggression rates in dyads with larger differences in dominance ratings (MRQAP with NP: $\beta = 3.42*10-7$, $P = 0.02$; GLMQAP with DSP: effect of ratings similarity: $\beta = 0.002 \pm 1.36*10-4$ SE, $z = 14.04$, $P = 0.01$, effect of time spent in the feeders: $\beta = 3.89*10-6 \pm 3.42*10-7$ SE, $z = 11.38$, $P = 0.11$). Also in agreement with the main text, using only aggressions from the less to the more dominant dyad member showed that aggression decreases as the difference in ratings between the individuals increase (MRQAP with NP: $\beta = -4.28*10-7$, $P < 0.01$; GLMQAP with DSP: effect of ratings similarity: $\beta = -0.004 \pm 2.26*10-4$ SE, $z = -17.38$, $P < 0.01$, effect of time spent in the feeders: $\beta = -3.49*10-6 \pm 4.38*10-7$ SE, $z = 7.97$, $P = 0.24$).

Aggression towards individuals distant in the network

To study if the number of aggressive displacements was higher towards socially-distant individuals, we used similar models to those described above, but using a different predictor: the social proximity (i.e., an individual-by-individual matrix of strengths of association in each dyad). The MRQAP approach used the rate of aggressive displacements per dyad as a response variable (as described above), and the social proximity as predictor. We applied 50,000 node permutations on the matrix of aggression rates and of social proximity to create a posterior distribution of the test statistic (Farine 2017). The GLMQAP used the number of aggressive displacements per dyad as response variable (as described above) and, as predictors, the social proximity and the dyadic matrix of the times at the feeder (as described above). As before, we performed 50,000 permutations, the argument “offset” was set as the logarithm of the time a dyad spent together, the argument “family” as Poisson, and the argument “permutation” as DSP (double semi-partialling permutation).

Similarly to the results on the main text, we found no evidence supporting that the rate of aggressive displacements differed depending on the social proximity in dyads of individuals (MRQAP with NP: β = -0.001, P = 0.95; GLMQAP with DSP: effect of social proximity: β = -2.13 ± 2.71 SE, z = -0.79, P = 0.92, effect of time spent in the feeders: β = 3.78*10-6 ± 2.69*10-7 SE, z = 14.03, P = 0.14).

Additional tests of aggression towards similar-rank individuals

Analyses of aggression based on the similarity in social dominance among individuals use the same type of data (aggressive displacements at the feeders) to compute both the response (aggression rate in each dyad) and predictor variables (difference in dominance ratings in each dyad), which should not pose a problem of circularity because dominance ratings use information from all aggression events an individual was involved in it, rather than events per dyad. Nonetheless, we confirmed all results (both from the parametric multimembership model using Markov chain Monte Carlo, MCMC, approach, and from the permutation-based MRQAP with NP and GLMQAP with DSP approaches) after having divided the RFID datastream into two sets. We used RFID data from the even days (counting from the onset of the study) to infer dominance ratings, which were then used to compute the predictor variables as described in the main text methods. And we used data from the odd days to compute the aggression between individuals in each dyad, used to compute the response variable also as described in the main text methods.

After dividing the dataset into two sets to account for possible circularity in analysis, the results remained similar. We again found higher aggression towards the very subordinated individuals using the multimembership model (posterior mean = 0.17, CI = [0,11 0.23]; time at the feeder: posterior mean = 0.19, CI = [0.02, 0.35]), but no significant relation using the permutation-based procedures (MRQAP with node permutation: β = -8.05*10-8, P = 0.737; GLMQAP with double semi-partialing permutation: effect of ratings similarity: β = 1.39*10-4 ± 1.68*10-4 SE, z = 0.82, P = 0.82), effect of time spent in the feeders: β = 7.34*10-6 ± 7.58*10-7 SE, z = 9.69, P = 0.14). Moreover, when studying aggression downwards the dominance hierarchy, we found higher aggressiveness as the differences in the dominance ratings increased (multimembership model: posterior mean = 0.28, CI = [0.22, 0.35]; time at the feeder: posterior mean = 0.16, CI = [0.01, 0.31]; MRQAP with node permutation: β = 3.76*10-7, P = 0.01; GLMQAP with double semi-partialing permutation: effect of ratings similarity: β = 0.002 ± 1.97*10-4 SE, z = 10.90, P = 0.005, effect of time spent in the feeders: β =

7.06*10-6 ± 9.62*10-7 SE, z = 7.34, P = 0.14). When studying aggression upwards the dominance hierarchy, we found the opposite result, lower aggression as the differences in the dominance ratings increased (multimembership model: posterior mean = -0.13, CI = [-0.19, -0.07]; time at the feeder: posterior mean = 0.11, CI = [-0.02, 0.25]; MRQAP with node permutation: β = -4.56*10-7, P < 0.001; GLMQAP with double semi-partialing permutation: effect of ratings similarity: β = 0.004 ± 3.29*10-4 SE, z = -12.95, P < 0.001, effect of time spent in the feeders: β = 7.67 *10-6 ± 1.23*10-6 SE, z = 6.24, P = 0.19).

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Table E1. GLMM results of the relation between number of displacements per individual and the mean absolute difference in dominance ratings between the focal individual and the audience.

Predictor	βst ± SE	*z*	*P*
Mean similarity in dominance ratings	0.019 ± 0.038	0.508	0.612
Audience size	0.497 ± 0.017	29.445	< 0.001 *
Gathering event duration	-0.109 ± 0.017	-6.447	< 0.001 *
Time spent per gathering event	0.392 ± 0.008	46.494	< 0.001 *

Standardized coefficient (β_{st}), standard deviation (SE), *z*- and *P*-values

* Significant results: $P < 0.05$

Table E2. GLMM results of the relation between number of displacements per individual and the mean difference in dominance ratings between the focal individual and 10 % most similar in rank, most dominant or subordinate members in the audience.

Predictor	βst ± SE	*z*	*P*
10 % most similar audience members	-0.025 ± 0.033	-0.754	0.451
10 % most dominance audience members	0.280 ± 0.062	4.527	< 0.001 *
10 % most subordinate audience members	0.141 ± 0.039	3.580	< 0.001 *
Audience size	0.502 ± 0.017	28.810	< 0.001 *
Gathering event duration	-0.118 ± 0.017	-6.928	< 0.001 *
Time spent per gathering event	0.392 ± 0.008	46.419	< 0.001 *

Standardized coefficient (β_{st}), standard deviation (SE), *z*- and *P*-values

* Significant results: $P < 0.05$

Table E3. GLMM results of the relation between number of displacements per individual and the mean network proximity of the audience.

Predictor	βst ± SE	*z*	*P*
Mean proximity	-0.010 ± 0.052	-0.202	0.84
Audience size	0.496 ± 0.017	29.230	< 0.001 *
Gathering event duration	-0.108 ± 0.017	-6.407	< 0.001 *
Time spent per gathering event	0.392 ± 0.008	46.501	< 0.001 *

Standardized coefficient (β_{st}), standard deviation (SE), *z*- and *P*-values

* Significant results: $P < 0.05$

Table E4. GLMM results of the relation between number of displacements per individual and the mean difference in network proximity between the focal individual and 10 % of the audience members socially-closer or most socially-distant to the focal.

Predictor	βst ± SE	*z*	*P*
10 % socially-closer	0.038 ± 0.042	0.909	0.364
10 % most socially-distant	-0.060 ± 0.024	-2.545	0.011 *
Audience size	0.482 ± 0.018	27.315	< 0.001 *
Gathering event duration	-0.105 ± 0.017	-6.215	< 0.001 *
Time spent per gathering event	0.392 ± 0.008	46.471	< 0.001 *

Standardized coefficient (β_{st}), standard deviation (SE), *z*- and *P*-values

* Significant results: $P < 0.05$

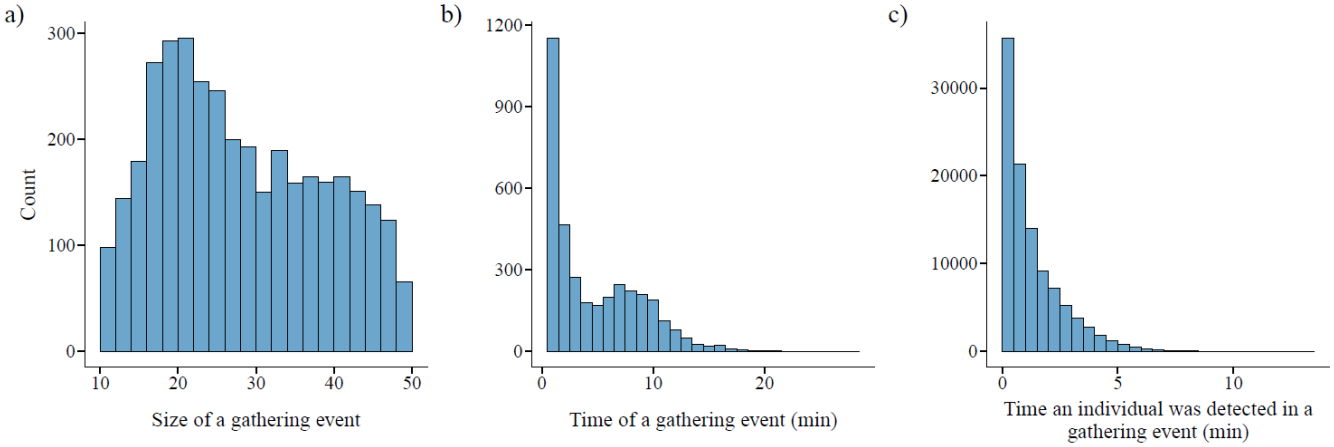

Figure E1. Histograms of the (a) audience size, (b) time of a gathering event, and (c) time an individual was detected in a gathering event.

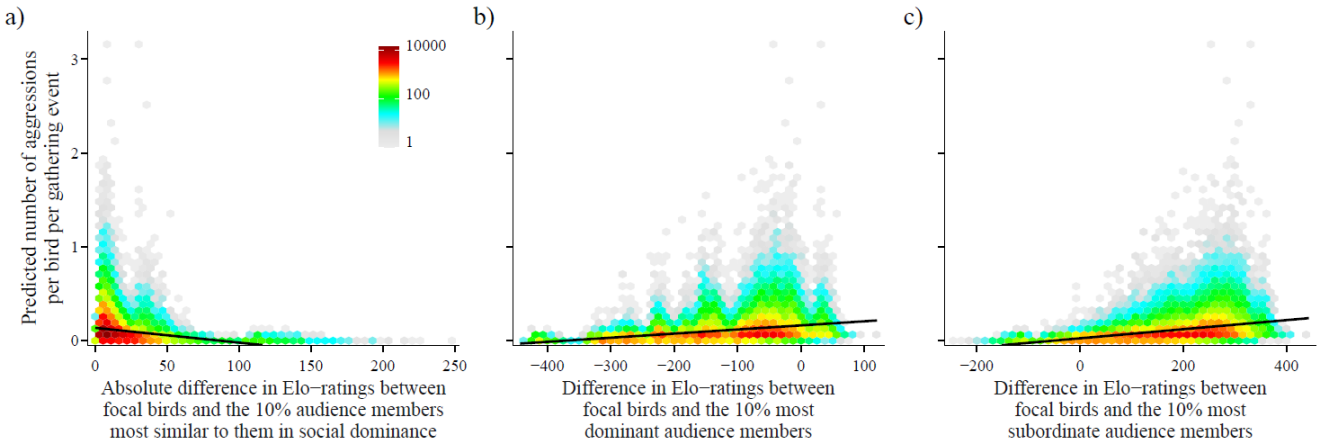

Figure E2. Density plots for the predicted numbers of aggressive displacements by each focal bird per gathering event (i.e., per group visit to the feeding area), as a function of similarity in dominance rank (randomized Elo-rating) with audience members. Aggression as a function of (a) mean absolute difference of the focal bird to the 10% audience members most similar in rank to it, (b) mean difference of the focal bird to the 10% most dominant audience members, and (c) mean difference of the focal bird to the 10% most subordinate audience members.

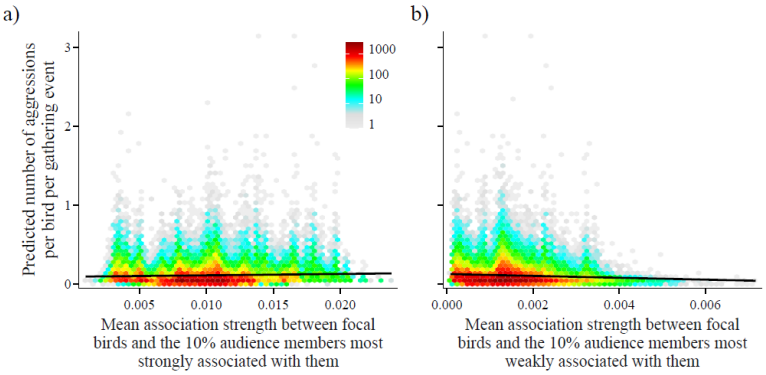

Figure E3. Density plots for the predicted numbers of aggressive displacements by each focal bird per gathering event, as a function of proximity in the social network. Aggression as a function of mean association strength of the focal bird (a) with the 10% audience members most strongly associated with it, and (b) with the 10% of the audience members most weakly associated with it.

Appendix F

Data. The data used to produce the research article are available through Dryad Digital Repository https://doi.org/10.5061/dryad.vq83bk3vq

Appendix G

Table G1. Correlation coefficients between the weather predictors used in analyses.

Table G2. Date intervals corresponding to changes or experimental procedures in the mesocosm during the 5 years of this study, which were controlled for.

Table G3. Auto-regressive moving average parameters (p, q) used in GAM and LMM for each behaviour studied.

Table G4. Smooth terms for seasonal patterns in each behaviour studied. Shown are the effective degrees of freedom (edf), F-statistic, and the p-value (P).

Figure G1. Taylor's diagrams comparing daily mean a) temperature and b) relative humidity between in situ measurements (white dot) and data from a meteorological station 10 km from the study site (pink), or from MeteoGalicia with 4km or 12 km resolution (blue and yellow, respectively).

Table G1. Correlation coefficients between the weather predictors used in analyses.

	Temperature	Cloud cover	Precipitation	Relative Humidity	Wind speed
Temperature		-0.20	-0.17	-0.23	0.11
Cloud cover			0.55	0.64	0.49
Precipitation				0.33	0.61
Relative Humidity					0.21
Wind speed					

Table G2. Date intervals corresponding to changes or experimental procedures in the mesocosm during the 5 years of this study, which were controlled for.

Date	
01/01/2018 – 10/04/2018	F8 – 8 feeders available in the mesocosm
11/04/2018 – 23/10/2019	F12 – 12 feeders available in the mesocosm
24/10/2019 – 03/02/2020	E1 – Experimental procedure
04/02/2020 – 09/11/2020	F12 – 12 feeders available in the mesocosm
10/11/2020 – 25/11/2020	F4 – 4 feeders available in the mesocosm
26/11/2020 – 07/12/2020	U – Unpredictable number of feeders (4 or 12 feeders available)
24/12/2020 – 04/01/2021	F12 – 12 feeders available in the mesocosm
05/01/2021 – 20/01/2021	F8 – 8 feeders available in the mesocosm
21/01/2021 – 28/04/2021	F12 – 12 feeders available in the mesocosm
29/04/2021 – 07/11/2021	F13 – 13 feeders available in the mesocosm
08/11/2021 – 28/11/2021	E2 – Experimental procedure
29/11/2021 – 12/06/2022	F13D – A small barrier was added to an isolated perch
13/11/2022 – 03/12/2022	E3 – Experimental procedure
28/11/2022 – 31/12/2022	F13D – A small barrier was added to an isolated perch

Table G3. Auto-regressive moving average parameters (p, q) used in GAM and LMM for each behaviour studied.

Behaviour	GAM	LMM
Time spent at the feeders	(4, 3)	(3, 3)
Number of foraging groups	(3, 1)	(3, 1)
Duration of foraging groups	(1, 1)	(1, 1)
Size of foraging groups	(1, 1)	(1, 1)
Strength of association	(3, 3)	(0, 3)
Coefficient of variation	(1, 1)	(1, 0)
Entropy	(1, 1)	(1, 0)
Aggressiveness	(2, 1)	(1, 2)
Steepness of dominance hierarchy	(1, 0)	(1, 0)

Table E4. Smooth terms for seasonal patterns in each behaviour studied. Shown are the effective degrees of freedom (edf), F-statistic, and the p-value (P).

	Time spent at the feeders	Number of foraging groups	Duration of foraging groups	Size of foraging groups
s()	3.382 1.65; <0.001*	7.722 4.308; <0.001*	6.175 4.731; <0.001*	7.029 2.348; <0.001*

Strength of association	Coefficient of variation	Entropy	Aggressiveness	Steepness of dominance hierarchy
5.137 0.843; 0.005*	9.022 2.297; <0.001*	8.892 1.842; <0.001*	6.423 2.089; <0.001*	5.557 2.821; <0.001*

*Significant values ($P < 0.05$)

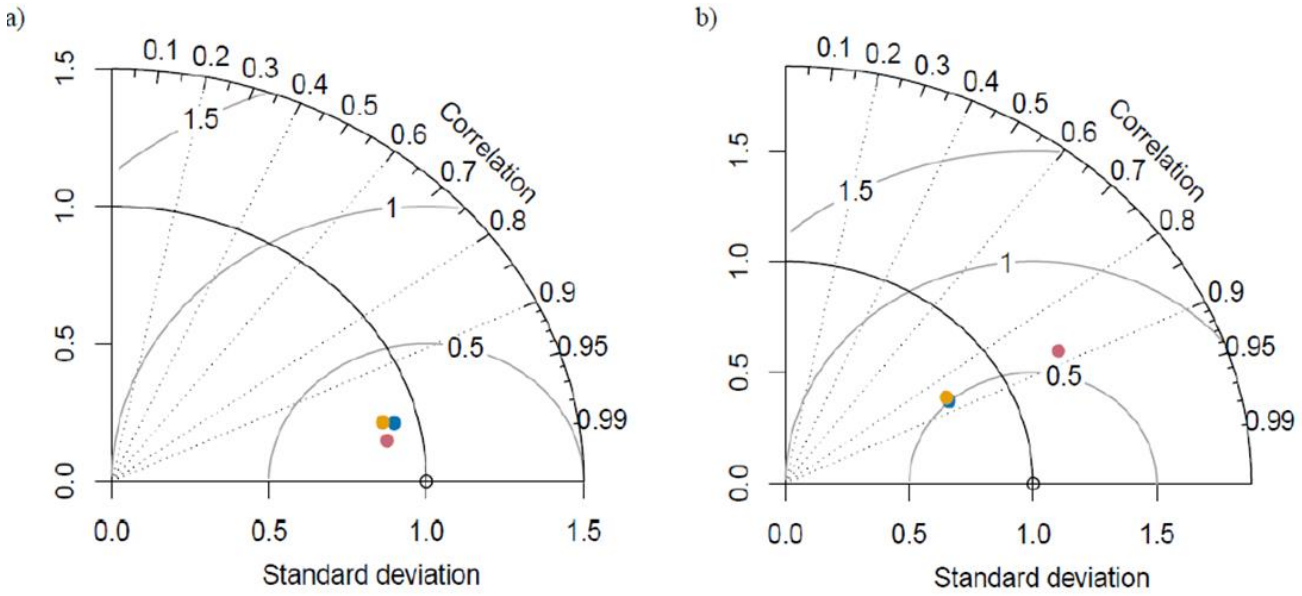

Figure G1. Taylor's diagrams comparing a) mean temperature and b) relative humidity between in situ measurements (white dot) and data from a meteorological station 10 km from the study site (pink), or data from MeteoGalicia with a 4km and 12 km resolution (blue and yellow, respectively).