Long-term evaluation of the association between dominance, bib size, sex and age

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Conflict of interest statement

The authors declare no conflict of interest.

Authors' contribution

The study was initiated by C.D. and R.C., and N.J.S., L.R.S., P.B.D.A. and A.C.F. further contributed to its conceptualisation and execution. All authors contributed to the general monitoring data. L.R.S. and A.C.F. collected and processed the dominance score of the birds. N.J.S., L.R.S., A.L., R.C., and C.D. collected and processed bib data. N.J.S. developed the deep learning model. N.J.S. and P.B.D.A. produced the statistical analyses. N.J.S. led the writing of the first draft of the manuscript with contribution from all co-authors, and all authors contributed critically to the drafts and gave final approval for publication. P.B.D.A., R.C. and C.D. supervised N.J.S. for this work. R.C. and C.D. administrated the research project and acquired the funding for this work.

Data availability statement

Analyses reported in this article can be reproduced using the data provided here: https://figshare.com/s/cafa846429419e5a31bf

Abstract

Individual-based long-term datasets are needed to investigate the relationships between drivers of labile individual traits. A case in point is dominance structures, which has been shown to vary greatly across years and populations. Using an eight-year dataset, encompassing more than 700 individuals, we studied the association between the size of a melanin-based plumage trait (a black patch under the beak or 'bib'), individual attributes (age and sex) and dominance. Our study model, the sociable weaver (*Philetairus socius*), is a small passerine, which lives year-round in colonies of varying size. Bib sizes were obtained from pictures and automatically pre-processed with an object segmentation deep learning network based on YOLO. We recorded 36,346 dominance-related interactions to estimate dominance hierarchies. We then investigated the effect of sex and age on bib size, and the overall and between-year association of bib size and age with dominance for each sex. We found that bib size increased with age within individuals of both sexes. Age was a strong and consistent predictor of dominance in males, but not in females. Nevertheless, dominance was not correlated with bib size in males and not in females. Finally, these relationships did not strongly vary between years. Our results suggest that males and females may use different factors to regulate dominance interactions. Furthermore, our longitudinal dataset allowed us to show that bib size is not a badge of status under our population conditions even though its growth encodes age information, highlighting the importance of considering multiple traits over time when studying morphological signalling of hierarchy positions.

Keywords: Badge of status; Dominance; Deep learning; Long-term studies; Object segmentation; *Philetairus socius*; Social species; Status signalling hypothesis

1. Introduction

Competition over resources (e.g., food, territories, mates) often lead to aggressive interactions between individuals. These agonistic events can be very costly, sometimes leading to severe injuries or death (Clutton-Brock et al., 1979; Neat et al., 1996; Riechert, 1998; Sneddon et al., 2002). To limit these costs, many species establish dominance hierarchies (Tibbetts et al., 2022). Several traits or individual attributes, most commonly sex or age, have been found to be linked to the position of individuals in the dominance hierarchy (Tibbetts et al., 2022). However, dominance relations are likely to vary according to individual and environmental conditions and in a recent review, Tibbetts et al. (2022) argued that long-term field research is needed to deduce the factors influencing the stability of dominance hierarchies. In parallel, accumulating evidence shows that phenotypic traits and their signalling function may vary depending on external forces (e.g., availability of food, mates), which vary over time and can ultimately influence competition intensity (Kvarnemo & Ahnesjo, 1996; Lucchesi et al., 2019). Long-term studies integrate the wide ecological and social variation that characterise the environments experienced by individuals (Clutton-Brock & Sheldon, 2010a, 2010b; Cockburn, 2014) and have provided several examples where limited temporal sampling could have resulted in inaccurate generalisation of association patterns (Clutton-Brock & Sheldon, 2010a; Cockburn, 2014; Cornwallis & Uller, 2010; Doutrelant et al., 2020).

Dominance signalling relies on intrinsic competitive abilities of individuals and can be displayed through ‘badges of status’. These traits can be visual, olfactory or acoustic and correlate with the individuals’ dominance status (Rohwer, 1975, 1982; Senar, 2006; Smith & Harper 2003; Whiting et al., 2003). They therefore allow to

resolve conflicts without direct confrontation, as individuals can assess the competitive ability of others and decide how to interact with them. The signalling function of badges of status has been demonstrated both by correlational and experimental studies in a wide range of taxa (e.g., mammals (Burgener et al., 2009; Clutton-Brock & Albon, 1978), birds (Senar, 2006), reptiles (Stapley & Whiting, 2006), and insects (Tibbetts & Lindsay, 2008)).

In birds, a meta-analysis using 47 studies encompassing 23 species found that plumage was linked to dominance across species and plumage types (e.g., carotenoids, melanic), suggesting that there is overall statistical support for the status signalling hypothesis across birds (Santos et al., 2011); however, heterogeneity was high, indicating low generality of that finding across studies. Regarding melanin-based plumage patches in birds, the textbook example has been the bib size of male house sparrows *Passer domesticus*, which was found to be correlated with the fighting abilities of individuals (Nakagawa et al., 2007). However, this example was challenged in a meta-analysis conducted on 19 studies (Sánchez-Tójar, Nakagawa et al., 2018), which showed that when including unpublished studies, the overall effect size of the correlation between dominance and bib size was not different from zero, and that the overall evidence for the hypothesis in house sparrows has been declining over time. This meta-analysis revealed a strong publication bias that calls for reconsideration of the bib size-based status signalling in this species, and for further investigation of within-species variation in the relationships between badges of status and dominance rank.

In addition to dominance signalling through phenotypic traits, dominance hierarchies have also been shown to be associated with individual attributes, most

notably age. The hierarchies associated with individual attributes are called ‘convention-based’ hierarchies, and in these, age influences various phenotypic traits and regulates dominance interactions in many taxa (e.g., in birds (Sergio et al., 2009; Stahl et al., 2001), insects (Taylor et al., 2020), and mammals (Šárová et al., 2013)). For instance, in chimpanzees (*Pan troglodytes*), female social status is influenced by age, while males fight to gain status in the male hierarchy, which ultimately increases their reproductive success (Foerster et al., 2016).

The mechanisms regulating dominance may differ between the sexes because the benefits (and costs) of dominance are unlikely to be equivalent, and sex-biased dispersal may lead to stronger social bonds within one of the sexes. In birds, status traits have been studied mostly in males and less in females (Doutrelant et al., 2020), but some studies on mutually ornamented species found an association between dominance and a given ornament only in females (e.g., Chaine et al., 2011; Crowhurst et al., 2012; Jawor et al., 2004; Murphy et al., 2014; Watt, 1986). Hence, the selective pressures affecting these ornaments and their signalling function may be sex-specific. Finally, studies have also found evidence for a sex-dependent relationship between dominance and age (Foerster et al., 2016). However, overall sex differences in the mechanism regulating dominance remains to be explored in depth.

Long-term datasets are important because they allow to account for environmental variability. However, collecting such data can represent a challenge as it requires continuous funding to cover both logistical and human resources (Cockburn, 2014). Another challenge is the processing of the large volumes of data collected, which is very time consuming and costly when extracting information from videos or images (Weinstein, 2018). Recent approaches based on deep learning

methods (LeCun et al., 2015) can help with image processing, as they allow to conduct time-consuming and repetitive tasks much faster than humans (e.g., few milliseconds per images classification; Jocher et al., 2022) and sometimes outperforming the repeatability and performance of humans (Ditria et al., 2020). In ecology, deep learning methods are increasingly used for multiple tasks such as identification, or density estimations, among others (Christin et al. 2019). However, these methods are still rarely used for fine scale measurements of morphological traits, as it requires accurate detection and precise segmentation of the phenotypic traits of interest.

In the present study, we examine the relationship between a putative badge of status (a black plumage 'bib') and dominance, age, and sex in a highly social colonial and cooperative bird, the sociable weaver (*Philetairus socius*). To this end, we used a deep learning approach, based on object-segmentation, to automatically extract the bib size from approximately 10,000 pictures. We then calculated dominance from more than 36,346 dominance interactions collected over seven years. In this species, both male and female adults display a black melanin-based bib, with males only presenting very slightly larger bibs (+0.032 cm^2; Acker et al., 2015). Sociable weavers establish steep dominance hierarchies within their colonies with males being dominant over females (Rat et al., 2015; Silva et al., 2018) and older males have been found to be dominant over younger males (Silva master thesis, 2017). Previous short-term studies on this species found conflicting results regarding the association between dominance and bib size, with either a positive association in male-male interactions only (over two years; Rat et al., 2015), or females with larger bibs being dominant when interacting with both sexes (Silva master thesis, 2017).

Here, we first evaluated how bib size varies in relation to sex and age, and performed a longitudinal analysis to understand the within individual variation in bib size. Then, we tested how dominance related with bib size, age and sex, and whether these associations varied between years. Since dominance hierarchies in this species are structured by sex (with most males being dominant over most females), we then explored whether the traits associated with dominance were different when estimating all individual hierarchies compared to when estimating same-sex dominance hierarchies. Long-term studies on badges of status are rare and we expected that by using such a large dataset spanning across time, we could reliably assess whether bib size functions as a badge of status, as well as capture potential variation over time of the relationship between dominance, age and bib size.

2. Materials and Methods

2.1. Species and individual information

Sociable weavers are passerines endemic to the semi-arid savannahs of the Kalahari region of southern Africa. They are small sexually monomorphic birds of approximately 28g and are colonial facultative cooperative breeders (Maclean, 1973). The study was conducted at Benfontein Nature Reserve, in South Africa (-28°818S, 24°816E, 1190m asl), an area of ~15km² of open savannah where up to 15 colonies are simultaneously monitored as part of a long-term study since 2010 (some colonies collapsed during the course of the study and new ones were added to the long-term monitoring).

The study was conducted between 2013 and 2021. Dominance trials were conducted on 5 of the regularly monitored colonies, while bib pictures were taken

from all colonies. We define a year as the period between 1st of September and the 31st of August, as the birds in the study colonies are captured at the end of the Southern Hemisphere winter, generally in August-September, and the breeding season usually starts in September-November (D'Amelio et al., 2024b). Sociable weavers can form very large colonies up to approximately 500 individuals (Maclean 1973), but colonies in our study area over the years of this study varied between 7 and 82 birds (mean±SD, 38±17 individuals). Individuals are ringed with three colored rings and a numbered metal ring, allowing individual visual identification. We also take morphological measurements (mass, tarsus+intertarsal joint's length) and blood samples to sex genetically all individuals (D'Amelio et al., 2024a; Griffiths et al., 1998). Exact age is known for all individuals that were born in the studied colonies as a result of a routine breeding monitoring (these individuals constitute 77% of the males and 65% of the females in the dataset). For immigrants, which were first captured as adults, we computed the age by adding the "average minimum age" of first dispersion to the first date of identification. This average minimum age of first dispersion in days was quantified for both males and females based on the long-term capture-recapture database (mean±SD, males: 690±46 days, N=13; females: 727±291 days, N=184). All protocols were approved by the Northern Cape Nature Conservation (permit FAUNA 1638/2015, 0825/2016, 0212/2017, 0684/2019 and 0059/2021) and the Ethics Committee of the University of Cape Town (permit 2014/V1/RC and 2018/V20/RC).

2.2. Dominance status

Using an established protocol (Rat et al., 2015; Silva et al., 2018), dominance hierarchies were determined within seven colonies each year (2013-2019) by

analysing and scoring agonistic interactions between individuals feeding on an artificial food source, a plate with mixture of bird seed, placed beneath each colony. Behavioural observations were performed using a video camera (Sony Handycam HD) on a tripod 2-3m from the feeder, to record all interactions seen approximately up to 1m around the feeder. From 2014 to 2017 and in 2019 observations were conducted in September; in 2013, from September to November; and in 2018, in December. Over these seven years, we conducted approximately 4h of observations each day, usually starting between 06:45 and 12:50; and repeated later in the day, between 13:15 and 16:50, and the food provided was removed between recordings. We obtained a total of 550 hours of video and each colony was recorded approximately (mean±SD) 15±12 hours per year (mean±SD, over approximately 6±4 days per colony). Both the type and direction of agonistic interactions observed were scored (as aggressions, displacements, threats and avoidances (Table 1 in Silva et al., 2018)). A total of 36,346 agonistic interactions (6,869 acts of aggression, 14,856 displacements, 3,459 threats and 11,162 avoidances) were recorded (mean±SD, approximately 1,010±1,240 interactions per colony per season).

To assess individual rank and to obtain dominance hierarchies, we used David's score (David, 1987), which is considered as one of the most appropriate and reliable methods available (Sánchez-Tójar, Schroeder et al., 2018), as it allows to assess overall individual success in agonistic interactions (Gammell et al., 2003). Additionally, this method allows to compare results to previous studies on dominance behaviour in this species. This score is calculated using the “steepness” R package (De Vries et al., 2006) and standardized per year and colony to allow comparison between individuals of different groups.

The hierarchies produced here included the majority of the birds captured in winter for the studied colonies (85%±22% (mean±SD)). The 15% missing correspond to birds never observed interacting at the feeders or that were not alive/present at the colony at the recording time. Individuals seen in several colonies (N=29 individuals) and those seen interacting less than three times in a given colony and year (N=45 individuals) were excluded from the analyses to avoid prospecting individuals (i.e., individuals briefly visiting colonies without being part of it).

In addition to these general dominance hierarchies (both-sexes dominance hierarchies) including all individuals and interactions, we also extracted dominance hierarchies by considering i) only male-male dominance interactions (N=16,261 interactions between 256 males, the between-males hierarchies) and ii) only female-female dominance interactions (N=2,651 interactions between 267 females, the between-females hierarchies).

To obtain reliable and representative dominance hierarchies for steep dominance hierarchies, like the sociable weavers' (Silva et al., 2018), Sánchez-Tójar, Schroeder et al. (2018), proposed that the threshold ratio of total number of observed interactions to total number of individuals should have a minimum of 10. In our study site, many colonies did not fulfil this criterium. We therefore decided to run our models both with and without the colonies with a ratio inferior to 10 (except for females as one colony was not enough to run the model with colonies with ratio inferior to 10). We found that the estimates were similar between the models with and without the colonies with a ratio inferior to 10 (Table S3 to S12), and therefore decided to include the colonies with a ratio inferior to 10 in the results.

2.3. Bib size and YOLO: annotations, training bib segmentation and model validation

For all the birds captured, three top view pictures of the bib per individual were taken in the field (Rat et al., 2015). In previous works, bib size was manually analysed using image graphic editor (The GIMP Development Team, 2019 or Photoshop CS5.1 (Version 12.1), hereafter referred as “GIMP method”), which is a time-consuming task when dealing with large datasets. We improved this method by implementing a deep learning approach using YOLO (You Only Look Once; Redmon et al., 2016) to automatically detect and extract bib size from the pictures (Supplementary 1 for detailed description of the method).

We tested the repeatability of the GIMP and YOLO methods by selecting 20 individuals (300 pictures) on five different years for which bib size was measured with both methods (rptR package version 0.9.22 (Nakagawa & Schielzeth, 2010)). Results showed high repeatability and high correlations between the two methods (Table S1), indicating that the bib size measurements obtained with the deep learning model were robust. Bib size, extracted in pixels from pictures, was measured in cm^2.

2.4. Statistical analysis

All statistical analyses were conducted on R version 4.3.1, using mixed models ran with the lme4 package version 1.1-33 (Bates et al., 2014). We verified whether model assumptions were met, specifically that a) the residuals followed normality using Kolmogorov-Smirnov tests, b) the simulated dispersion of the residuals was equal to the observed dispersion, c) there were no more simulated outliers than expected, and d) there was homoscedasticity of the variance at three

quantiles (0.25, 0.5, 0.75) between the residuals and predicted values. These diagnostics were performed using the Dharma package version 0.4.6 (Hartig & Lohse, 2022), and, although not marked, some heteroscedasticity was observed and it is detailed in Supplementary 5 and 6. The plots were created with ggplot2 package version 3.4.2 (Wickham, 2014) and ggeffects version 1.3.2 (Lüdecke, 2023).

2.4.1. Factors associated with bib size

To design and interpret the most appropriate structure for the models testing the association between bib size and dominance, we first needed to understand the relationship of bib size with age within sexes (Fig S1). These variables were found to be associated in a previous study conducted on this species (using distinct datasets: Acker et al., 2015). In addition, we included tarsus length (as a proxy of body size), to correct for a potential correlative effect between bib size and body size. We designed a linear mixed model (LMM) with bib size (in cm^2) as the response variable, and tarsus (in mm), age (in days), sex and the interaction between age and sex as fixed factors. As random factors, we controlled for year, colony and individual identity, the observer who took the photos (7 observers) and the camera model used (3 cameras). We also added random slopes to the random intercepts to estimate the link between age and bib size for every individual. We estimated random slopes uncorrelated with random intercepts, as we do not predict that individuals with larger bib size also have a higher bib size growth when getting older. We used a dataset composed of 743 individuals from 17 colonies over eight years (from 2014 to 2021, N=2,209 observations). Tarsus length was computed as the average tarsus length measured during the adult life of the individuals (by the same scorer, R.C., which measured the majority of birds, or by others if no measures by R.C. were found for that individual). Three individuals with extreme tarsus size observations were removed. The residuals

of the model using the 2,209 observations did not respect the normality assumption (Kolmogorov–Smirnov test, $P<0.001$). This non-normality of the residuals of the model were mainly due to one year photographed by one scorer. By removing this scorer from the dataset (N=647 observations), the model fitted the necessary assumptions. Estimates and effects of the different factors ranged from highly similar to identical between the two models (Table S2). Therefore, we decided to use the model containing the full dataset.

2.4.2. Overall association between dominance, sex, bib size and age

We performed a LMM using the dominance score of the individuals as the response variable and, as fixed factors, bib size, age, sex, tarsus, body index, as well as the interactions between bib size and sex, and age and sex. Body index was based on a scaled mass index (Peig & Green, 2009) that uses mass (here collected at the capture events, approximately when dominance data collection was performed) and a body size metric of an individual (here tarsus length, T) with its arithmetic mean value for the studied population (T_0). The method allows to compute a scaled mass as the predicted body mass when $T=T_0$. To visually describe the structure of our model, we designed a Directed Acyclic Graph (DAG) (Fig. S1). DAGs are visualisation tools that help to represent the links between the variables that we intend to test in a model (Wysocki et al., 2022). In this model, bib size was normalized within colony and year when analysing both-sexes dominance hierarchies, and within colony, year and sex when dealing with sex-specific dominance hierarchies. The normalisation allows us to compare relative bib size of the individuals within colonies and does not allow us to interpret bib size at the population level. Two individuals with a David score of one in different colonies might not have the same bib size but potentially be at the same bib size position in the bib size hierarchy within their colonies. Therefore, they would be

assigned the same normalized bib size. normalized bib size, body index, tarsus and age were scaled and mean-centered over the whole dataset. Body index and tarsus length were included because they are often related to dominance in other bird species (Jonart et al., 2007; Tibbetts et al., 2022). As random factors, we controlled for colony (N=7), individual identity (N=409) and year of data collection (N=7, from 2013 to 2019). We included year as a random factor since we expected potential differences in dominance between years (e.g., arising from differences in social composition, resource availability, breeding onset).

2.4.3. Between-years association between dominance, sex, bib size and age

We used the same LMM model structure as when testing the overall association between dominance and bib size, but instead of having "year" as a random categorical factor, we used it as a fixed categorical factor. Additionally, we included the interactions between year, normalized bib size and sex, as well as between year, age and sex. We then performed a post-hoc test with the emmeans package version 1.8.6 (Lenth et al., 2023) to determine if the slopes of the relationship between dominance, bib size and age were significantly different from zero between years (Table S13).

3. Results

3.1. Factors associated with bib size

We found that age and bib size were significantly positively associated (0.03±0.01 (EST±SE, used throughout the Results section except if specified otherwise), T=4.98, P<0.001; Table S2), and we estimated that between individuals

that differ by one year, the older birds have approximately 1% larger bibs. Within individuals, we found a positive association between bib size and age for 99% of the birds (Fig. 1), and this relationship was affected by sex, with bib size increasing by 0.97% per year within females and 1.98% per year within males. The variance explained by random intercepts (Table S2, V=0.012) was higher than the variance explained by random slopes (Table S2, V=0.001) suggesting that individuals vary in their average bib size but have a similar pattern of growth through time. Moreover, we found a small positive significant effect of sex (0.03±0.01, T=2.66, P=0.008; Table S2) with males having on average 1.89% larger bib size than females (mean±SD, 1.56±0.03 cm² for females and 1.59±0.03 cm² for males). Finally, we found a significant positive association between tarsus and bib size (0.02±0.00, T=3.41, P=0.001; Fig. S2; Table S2), hence larger individuals have larger bibs independently of sex.

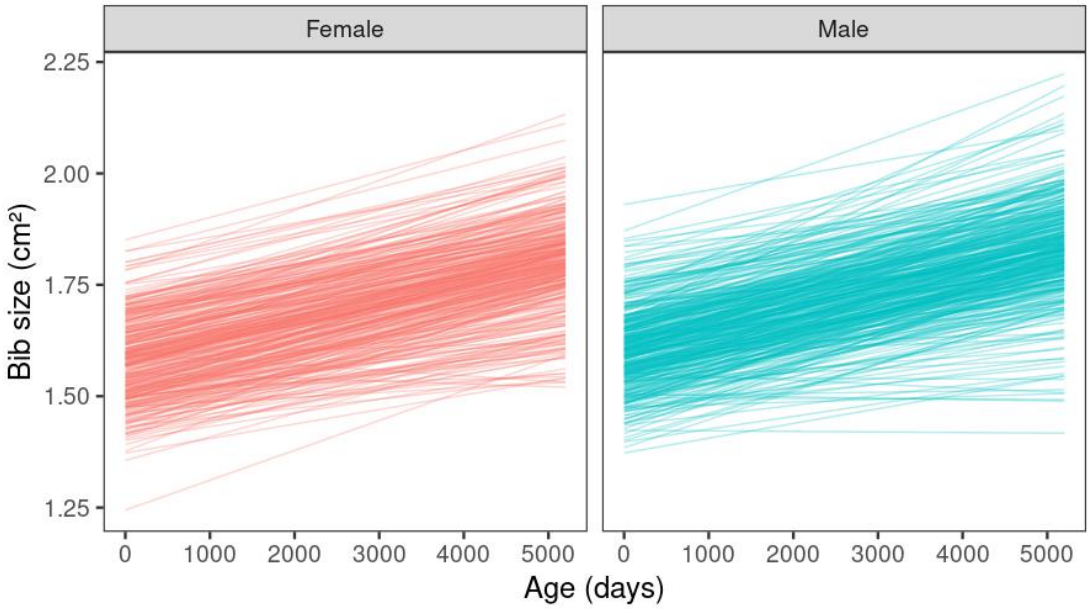

Figure 1: Linear regression of bib size as a function of age. The random slopes and intercepts of the 743 individuals (344 females (red) and 399 males (blue)) were used

to simulate bib size development every 200 days between one to 5,201 days old (i.e., more than 14 years).

3.2. Overall association between dominance, bib size, age and sex

Dominance in relation to bib size and sex. We found no significant association between normalized bib size and dominance in the datasets considering both-sexes dominance hierarchies (0±0.01, T=0.19, P=0.852; Table S3; Fig. 2.A) and between-males dominance hierarchies (-0.02±0.01, T=-1.69, P=0.092; Table S5; Fig. 2.C). However, we found a small positive significant correlation between bib size and dominance in between-females dominance hierarchies (0.04±0.02, T=2.34, P=0.020; Table S7; Fig. 2.E). Females being ranked 25% higher in the normalized bib size ranks have an estimated 8% higher dominance score. However, the between-years analysis bellow shows that the relationship is mainly influenced by two years with very low sample size (Table S13) and when removing these two years the correlation is weak and non-significant (0.02±0.02, T=1.06, P=0.290, Table S14).

Dominance in relation to age and sex. In both-sexes dominance hierarchies, we found a strong significant link between sex and dominance, indicating that males are approximately two times more dominant than females (0.30±0.02, T=18.61, P<0.001; Table S3). We also found a strong association between dominance and the interaction of age and sex (0.11±0.02, T=7.2, P<0.001; Table S3), indicating a different relationship between age and dominance for males and females (Fig. 2.B), specifically a much steeper slope for males. Dominance score is 1.36% higher in females and 9.39% higher in males when comparing individuals that differ by one year (Table S3). This was found also in the sex-specific interactions' datasets, where

we observed a different correlation between age and dominance, with a positive, strong and significant association in between-males dominance hierarchies (0.16±0.01, T=11.77, P<0.001; Table S5; Fig. 2.D), while there was no statistically significant relation in between-females dominance hierarchies (-0.01±0.02, T=-0.35, P=0.725; Table S7; Fig. 2.F).

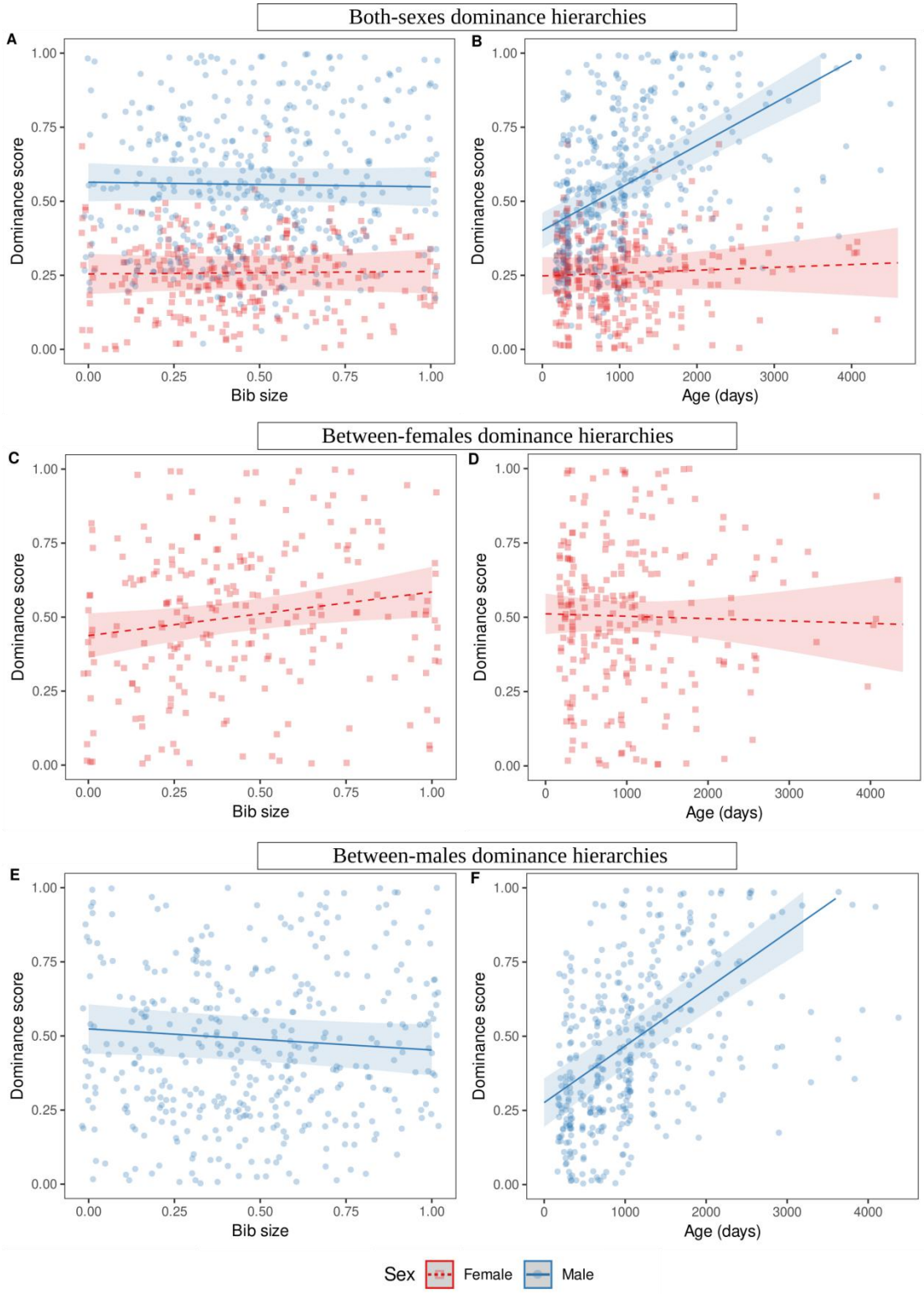

Figure 2: Association between: (A,C,E) dominance and normalized bib size; and (B,D,F) dominance and age. Results were obtained using both-sexes dominance hierarchies (A,B), between-females dominance hierarchies (C,D) and between-males dominance hierarchies (E,F). Dominance score was standardized within colony and

year of data collection, and bib size has been normalized within colony and year of data collection. Females are represented in red (square dots and dashed line) and males are represented in blue (circle dots and solid line).

3.3. Between-years association between dominance, bib size, age and sex

Dominance in relation to bib size, sex and year. We found no evidence that the relationship between dominance and normalized bib size varied between years, with a few exceptions. Out of the seven years used in each analysis, the only significant associations we found were a slightly negative relationship for one year in males in both-sexes dominance hierarchies (-0.06±0.03, T=-2.18, P=0.030; Table S13; Fig. 3.A in year 2016), a slightly negative relationship for one year in between-males dominance hierarchies (-0.06±0.03, T=-2.04, P=0.042 in year 2014; Table S13; Fig. 3.E), and positive relationships for two years in between-females dominance hierarchies (0.14±0.06, T=2.34, P=0.020 in year 2013, and 0.17±0.08, T=2.25, P=0.026 in year 2016; Table S13; Fig. 3.C). However, the sample size was limited for these latter years, with respectively 19 and 12 individuals only (the other years presenting between 17 and 84 individuals, Table S13), and so these relationships remain unclear.

Dominance in relation to age, sex and year. We found no between-years variation in the association between dominance and age in both-sexes dominance hierarchies and in between-males dominance hierarchies, with dominance being positively associated with age in all years for males and never associated for females (Table S13; Fig. 3.B and 3.F). In between-females dominance hierarchies, dominance

was negatively associated with age in one year only (-0.07±0.03, T=-2.15, P=0.033; Table S13; Fig. 3.D in year 2017).

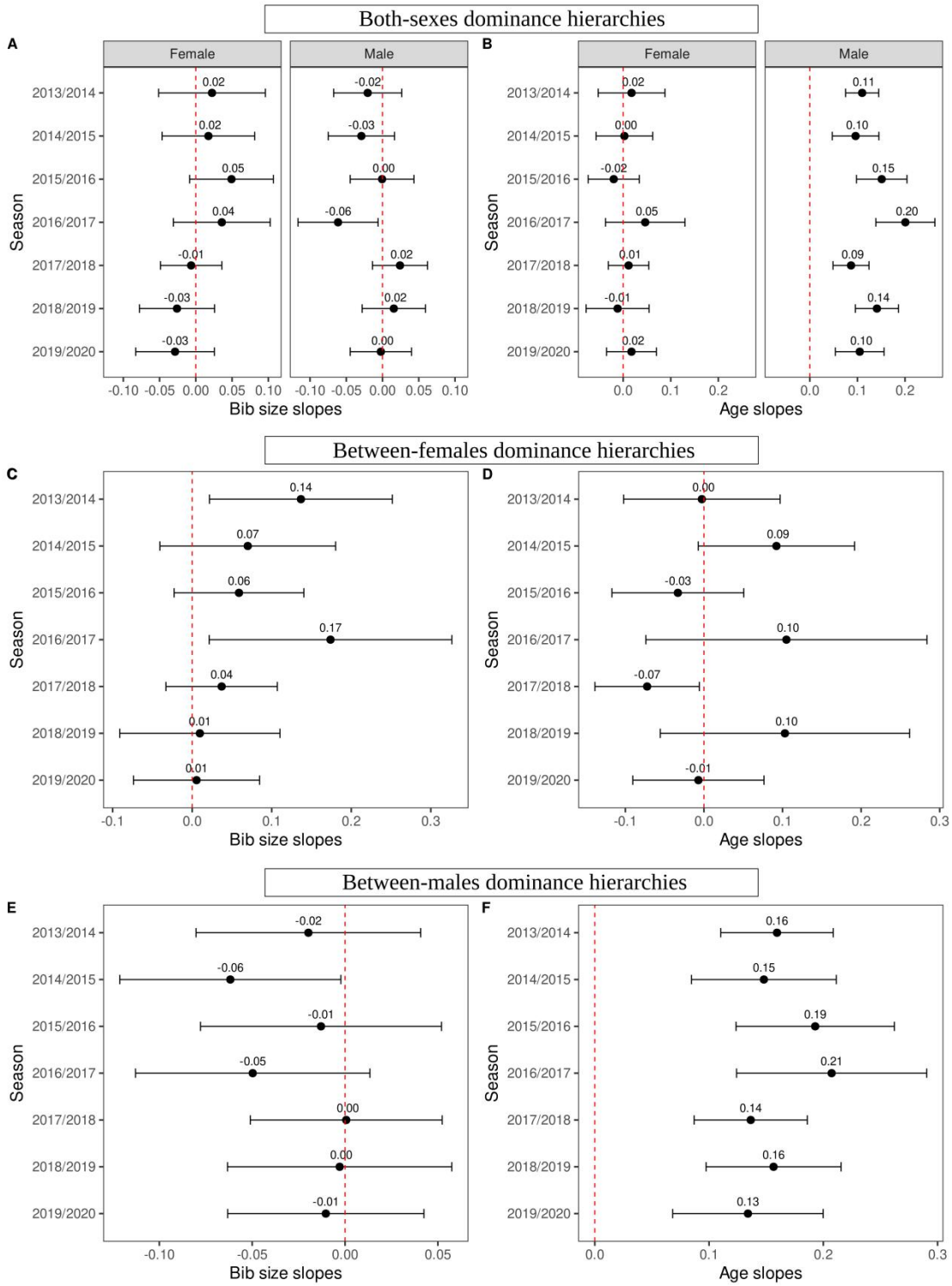

Figure 3: Slopes of the association between: (A,C,E) dominance and normalized bib size; and (B,D,F) dominance and age. Results were obtained from the models using

both-sexes dominance hierarchies (A,B), between-female dominance hierarchies (C,D) and between-male dominance hierarchies (E,F). Dots represent the estimated means of the relationships and bar are the confidence intervals.

4. Discussion

We examined whether bib size and age relate to dominance at artificial feeders in sociable weavers and how these relationships vary between sexes and years. We found that, in both sexes, bib grows with age, and that larger birds have larger bibs. We also confirmed that males were dominant over females. However, normalized bib size was not found to be associated with dominance in any of the hierarchies (except in between-females dominance hierarchies for two years, but based on very low sample size). In addition, we confirmed that age was strongly associated with dominance in males a pattern that was consistent between years. In contrast, age was not found to be associated with female dominance. Our study is one of the largest long-term studies investigating correlates of dominance with a potential badge of status, providing robust results to understand the association between dominance and bib size, and the variation in its associated dominance correlates, given the low uncertainty in the variation obtained between years (see also Parker (2013); Sánchez-Tójar, Nakagawa et al. (2018); Tibbetts et al. (2022)). While previous studies found positive associations between dominance and bib size with only one year (included in this study (season /2014); Silva master thesis, 2017) and two years of data (not included in this study; Rat et al. 2015), our analyses, on a much larger dataset, led to very different conclusions. Finally, this study showed a strong sexual difference in the factor used to regulate dominance interactions

4.1. Association between dominance, bib size and sex

Relative bib size was clearly not associated with dominance, whether when considering all birds or only males, and this did not change between years. We found an association within females, but the association was weak and unclear, with small effect sizes, and we had a smaller number of female-female interactions in the hierarchies (32 out of 33 colonies were below the recommended threshold of ratio of 10 of interactions to number of individuals in the group; Sánchez-Tójar, Schroeder et al. 2018). In addition, this association was only present in two years, which had among the lowest sample sizes of all years tested here (respectively N=19 and N=12 females). When these two years are removed there is no longer evidence of an association between relative bib size and dominance in females. If confirmed, these results would add to the growing number of studies showing that badges of status might function only in females but not in males (e.g., Chaine et al., 2011; Crowhurst et al., 2012; Jawor et al., 2004; Murphy et al., 2014; Watt, 1986), but more studies on both males and females are needed to better understand the possible functions of badges of statues in both sexes (Doutrelant et al., 2020).

Several factors might explain why bib size does not function as a badge of status in this population. First, the sampling period could influence our results, as the association between bib size, age and dominance being potentially used by the birds only in some parts of the season or some seasons only depending on the social and environmental contexts. A density-dependent effect in the association between badge of status and dominance has been found in the black-crested titmouse (*Baeolophus atricristatus*), where males with larger black crests had more access to feeding

stations when competition was high but did not display such advantages when population density decreased and competition was low (Queller & Murphy, 2017). Here, the dominance scores were always computed at the end of winter, most of the time before the onset of the breeding season. Therefore, the association between dominance and bib size should be investigated at another moment of the year and over a longer time scale to confirm the results obtained here. Second, here we only tested the size of the bib, while other bib features could signal the dominance abilities of the individuals (e.g., Santos et al., 2011). For instance, in black-capped chickadees (*Poecile atricapilla*), high-ranking males exhibit darker plumages than subordinates (Poston et al., 2005). Finally, when facing known opponents, animals are expected to use information on the opponents' previous behaviour (i.e., their 'reputation') to decide how to interact (Senar, 2006; Tibbetts & Dale 2007). For instance, Chaine et al. (2018) experimentally manipulated plumage patch size of golden-crowned sparrows (*Zonotrichia atricapilla*) and showed that manipulation only affected interactions between unknown individuals. Sociable weaver groups live together all year long, interacting on a daily basis, and this increased familiarity between individuals, could remove the need badges of status. In addition, male sociable weavers are philopatric, therefore knowing each other since birth. A previous study showed that the number of aggressive interactions between two individuals was negatively correlated with relatedness (Rat et al., 2015). Therefore, the social system of sociable weavers might not promote the use of badges of status in males. However, badges of status might still be important for individuals that move between colonies, especially females, which disperse to reproduce in other colonies (Covas et al., 2006; van Dijk et al., 2015). Badges of status could also play a more important role among the residents of very large colonies where individuals might not be able to keep track of all residents.

Specifically, some sociable weaver colonies house several hundreds of birds (Maclean, 1973), while our study was conducted in colonies that varied in size between 7 and 82 residents.

4.2. Association between dominance, age and sex

We found a strong sexual difference in the association between age and dominance. Evidence of age-based dominance hierarchies (also referred to as social queuing) is common in many taxa and has particularly been found in species that form long-term associations with relatives (Tibbetts et al., 2022), like sociable weavers. In ungulates, for instance, individuals, that are young and more inexperienced learn to be subordinates to older and stronger individuals, and do not challenge the hierarchy when getting older, resulting in age-based hierarchies (Favre et al., 2008; Thouless & Guiness, 1986). In sociable weavers, males know each other since birth and a mechanism similar to the ungulates could explain their age-based hierarchy. In contrast, females disperse to reproduce and therefore may not be able to use previous information about the status of dominant or subordinate of their opponents. Females may resort to alternative cues to infer fighting abilities of other females to decide how to interact with them, or may not need to enter in competition with them. However, it is important to note that because of this natal dispersion of the females, our estimation of age for this sex is less accurate than for the males.

Social queuing has been suggested to also arise when the costs of reaching a higher position in the hierarchy are higher than the benefits of reaching that position (Broom et al., 2009). For instance, in chimpanzees, dominant males benefit from higher mating and reproductive success, therefore males fight for higher ranks

(Foerster et al., 2016). However, females do not obtain fitness benefits from higher dominance rank in the hierarchy and intense fights would only bring fitness costs, resulting in age-dominance hierarchies in females (Foerster et al., 2016). In sociable weavers, males of the same colony are more related to each other than females and, within males' fights could either bring direct fitness costs (if the fight is lost), but also indirect fitness costs (if the fight is won against a related individual). This could suggest that, for males, the fitness costs of reaching a higher dominance rank might not be compensated by the fitness benefits of reaching this rank, leading to age-based dominance hierarchies within males. In male sociable weavers, dominant individuals are more likely to access food and reproduce (Rat, 2015; Silva et al., 2018), but further information of the exact fitness costs and benefits on the long-term for the individuals are needed to explore the origin of the age-based dominance hierarchies in males.

4.3. Association between bib size, age and sex

In agreement with a previous study (Acker et al. 2015), we found that bib size increases with age in both sexes. Age-related changes in adult plumage have been described in several species (e.g., Dreiss & Roulin, 2010; Wiebe & Vitousek, 2015). However, the bib size growth between years is small, only 1% and 2% growth per year for females and males respectively, and the perception by the individuals of such difference is questionable. Interestingly, we found that the growth rate of the bib is very similar between individuals, but individuals vary in bib size, indicating that the mechanisms behind bib size first growth varied between individuals. This last result is in line with the strong determination that genetics and development are expected to

have on bird melanic patches (Roulin & Ducrest, 2013). Finally, we detected an effect of sex, with a difference of approximately +0.03cm² (approximately +2%) for the bib size of males compared to females. This sexual difference is in line with the one found previously in this species (Acker et al., 2015), but again, the perception of this difference by the birds would need to be demonstrated.

4.4. The growing importance of artificial intelligence in ecology

Finally, our methodology for automatically measure thousands of bibs from pictures adds to the growing examples that illustrate the effectiveness and accuracy of deep learning-based methods to detect and quantify morphometrical traits, and how this can facilitate the process of extracting large amounts of data from images. This approach can be used in different taxa, from museum specimens (Miele et al., 2020), to live ones (He et al., 2023), but it is still rarely used for such tasks in evolutionary ecology. While in many cases developing deep learning methods would be too demanding technically or too time consuming, data extraction from existing long-term datasets, as was the case here, is particularly well suited to be processed automatically (i.e., here the mode processed 124 times faster than a human's; based on 30 pictures).

5. Conclusion

In this study we found no convincing evidence that bib size functions as a badge of status in sociable weavers, although for female-female interactions further investigation is needed. These results align with the previous recommendation of re-evaluating the status signalling hypothesis of melanic patches as well as evaluating the temporal variation of the correlates with dominance. By using multiple years of

data, we were able to reach stronger conclusions regarding the stability of the correlates (i.e., bib size and age) with dominance in our species. The sexual differences in the association between dominance and age for the two sexes suggest that male and female dominance interactions are potentially not regulated by the same factors. These results show the importance of conducting analyses on both sexes when trying to understand the role of phenotypic traits on dominance, and suggest that males and females may be subjected to different selective pressures.

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