Homing Pigeon (*Columba livia*) dominance hierarchies are stable over time and resistant to perturbation

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Abstract

Dominance hierarchies are a social dynamic common in many species, which help balance the costs and benefits of social living. Which individuals in a group occupy high ranking positions is influenced by a multitude of different intrinsic and/or extrinsic factors. While Homing Pigeons (*Columba livia*) have been studied extensively for their navigational abilities, research on their social dynamics and assessments of the determinants of dominance rank have been comparatively limited. Here we document the dominance hierarchies in two closed populations of Homing Pigeons and the physiological and behavioural factors associated with rank position including body size, metabolic rate, personality, and iridescent plumage % reflectance. Measurements of body size and resting metabolic rate all positively correlated with rank position in accordance with the performance model of energetic management. While iridescent plumage % reflectance was negatively correlated with rank, suggesting a potential cost of dominance. Attempts to alter hierarchy structure through manipulation of body mass and feather iridescence were ineffective, with hierarchy dynamics remaining stable throughout the perturbations. The inability to destabilise these dominance hierarchies demonstrates their advantage at preventing excess competition even in cases of minor changes in fitness.

Keywords: feather reflectance, mass manipulation, metabolic rate, respirometry, structural size, tarsus

Introduction

Living as part of a group is a common occurrence in many animal species (Elgar 1989). Being part of a collective group can come with many benefits, such as increased protection from predation (Bertram 1978), opportunities for social learning (Slagsvold and Wiebe, 2011), higher foraging success (Alexander 1974), energetic savings (Markham and Gesquiere, 2017) and increased mating opportunities (Ulrich et al.2018, Elgar 1989). Conferring these benefits can, however, still come at a cost. Such costs can include increased transmission of diseases

(Witte et al. 2020), food being stolen by conspecifics (Brockmann and Barnard, 1979), and an unequal sharing of resources (Alexander 1974). Due to competition, and this unequal sharing of resources, conflicts can arise in animal groupings. Heightened competition can be costly, as it typically involves high energy expenditure and the risk of injury, with potentially no pay off from the aggressive interaction if unsuccessful (Alexander 1974). In order to reduce these potential costs, individuals may avoid conflict with conspecifics they have previously lost fights with to avoid wasting energy, and this frequently leads to the formation of dominance hierarchies (Hand 1986, Drews 1993).

Dominance is a measure of status within a group and is typically – but not always – determined based on aggressive interactions. Winners can ascend to higher ranking positions and typically procure a greater proportion of resources. Dominance hierarchies can have differing structures, ranging from differing degrees of linearity to triangular or despotic arrangements, depending on the species (de Vries, Stevens and Vervaecke, 2006). When dominance hierarchies are highly linear, they can be correlated with certain physical or intrinsic traits (Beacham, 2003). Common parameters typically associated with determining rank positions include high body mass and/or structural size, which greatly aids defence of resources and can also assist in resistance to environmental stresses (Haramis et al.1986; Moreno-Opo, Trujillan and Margalida 2020). This relationship can result from a positive feedback loop whereby dominant individuals are able to maintain or increase their high body mass due to their high resource holding (Verhulst et al., 2014). This positive relationship between body mass and rank is documented in a diverse range of species such as Zebra Finches *Taeniopygia guttata* (Cuthill et al.1997), Masu Salmon *Oncorhynchus masou* (Yamamoto, Ueda and Higashi, 1998) Tuataras *Sphenodon punctatus* (Moore et al. 2007) and White-tailed Deer *Odocoileus virginianus* (Taillon and Côté 2006). Other variable factors which are reported to relate to rank position include personality traits such as boldness and neophobia, (Fox et al.2009) and metabolic rate (Bryan and Newton 1994).

Unlike the relationship between rank and body mass, the association between personality, metabolism and rank is typically more complex. Several energetic-based models predict the potential relationships between metabolic rate and personality traits, and in turn dominance, under various scenarios (Mathot, Dingemanse and Nakagawa 2019; Senar et al. 2000). The *allocation model* suggests variation in metabolic rate is not associated with changes in behaviours relating to energy gain; individuals with higher metabolic costs are less likely to invest in foraging behaviours, gain dominance, and exhibit overall boldness personality traits, due to their energetically costly nature (Mathot, Dingemanse and Nakagawa 2019). In contrast, a low metabolic rate may permit individuals to engage in costly behaviours, such as aggression, due to having a higher metabolic 'ceiling' (e.g., Peterson et al. 1990). This relationship between metabolic rate and behaviour has been observed in species such as Mosquitofish *Gambusia affinis* (Cote et al.2010), Deer Mice *Peromyscus maniculatus* (Careau et al. 2011), Ouachita Dusky Salamanders *Desmognathus brimleyorum* (Gifford, Clay and Careau 2014) and Zebra Finches (Mathot et al. 2009). In contrast the *performance model* predicts that metabolic rate correlates with increased of behaviours involved in energy gain. Under this model, individuals will have greater activity, be more dominant, and exhibit more exploratory behaviour if their metabolic rate is higher, due to that individuals higher energetic requirements (Mathot, Dingemanse and Nakagawa 2019). This interaction between behaviour and metabolism can be highly influential in the determination of dominance hierarchies, with certain personality types being more common in certain rank positions. In several species such as Common Lizards *Zootoca vivpara* (Le Galliard et al. 2013), Pied Flycatchers *Ficedula hypoleuca* (Røskaft et al. 1986), Great Tits *Parus major* (Røskaft et al.1986) and Mountain Chickadees

Poecile gambeli, for example, exploratory birds will occupy higher ranking positions, while opting to kleptoparasite subordinates instead of investing in foraging behaviours (Fox et al. 2009; Jablonski, Brown, and McCormack 2007).

Once a hierarchy has been established, aggression and ranks can remain relatively stable, with aggression levels remaining lower than before the hierarchy was formed (Hewitt, Macdonald and Dugdale 2009; Portugal et al. 2020). Part of this hierarchy stability can arise from the investment in status symbols and badges which help indicate to group members individual rank position. Status symbols can be an important part of social communication, being selected for as a symbol of rank and high fitness (Strassman 2004). These indicators help in the prevention of aggressive confrontation as a judgment may be made on the relative strength of the competitor, before initiating the conflict (Møller 1987) (Dey et al., 2013). Hierarchy stability can change over time due to factors such as seasonal modifications in physiology and behaviour (Forand, Marchinton and Miller 1985), immigration and emigration, or the death of a high-ranking member (Grossel et al. 2021). As many dominance hierarchy types can be dependent on the body condition of the individuals, any changes in body condition of a dominant individual, such as body mass, may lead to disruption of the hierarchy and group dynamics (Robinson 1986).

Signalling through plumage colourations and quality reflecting individual hierarchy position is a trait found across various species (Santos et al. 2011). Changes in badge quality can occur with sickness where opportunistic pathogens can affect the quality of signals (Lecair et al., 2014, Hamilton and Zuk 1982, Dolnik and Hoi 2010). Plumage differences in house sparrows *Passer domesticus* with higher parasite loads saw some dominant individuals receiving more challenges for rank; the cost of infection on fitness was high enough and noticeable enough to decrease the stability of the hierarchy (Hamilton and Zuk 1982, Dolnik and Hoi 2010). For example, artificial mass loading of subordinate Homing Pigeons *Columba livia* saw a disruption of hierarchy stability, with lower ranking individuals gaining rank after the increase in body mass (Portugal et al. 2020). This was despite the hierarchy being stable for a number of years prior to the artificial mass manipulation experiments. This experiment only involved one single deployment of artificial mass on the Homing Pigeons, and focused on the subordinate individuals only. Thus, it is still not fully clear how birds respond to manipulated body mass, how sensitive birds are to subtle body mass dynamics, and in turn, how these interact, temporally, with dominance hierarchies and rank position.

Homing Pigeons are a long established model system for the study of navigation (see Biro, 2018). Although some aspects of the social systems have been studied historically (Ritchey, 1951; Castoro and Guhl, 1958), more recently pigeons have become an emerging model species for studying social dynamics and dominance in birds (Bouchard, Goodyer and Lefebvre 2006). For example, Nagy et al. (2013) combined ground-based dominance experiments with flight-based leadership studies to determine that pigeons have context dependent hierarchies, whereby those that are dominant on the ground are not the leaders during flight-based activities. Previous investigations into the dominance hierarchies in pigeon social groups have indicated a strong linear dominance hierarchy, highly correlated with body mass (Portugal et al. 2020). However, what has been lacking from previous studies investigating dominance hierarchies, both in pigeons and species more broadly, is a holistic approach encompassing multiple phenotypic parameters that have been previously established as factors known to influence dominance. Similarly, longer-term temporal studies of dominance hierarchies on discrete populations are relatively scarce across most taxa due to the complexities of studying such behaviour over long periods of time, particularly in wild animals, thus missing how natural seasonal variation in general body condition and physiology may or may not manifest in dominance and associated rank (Sargisson et al. 2007; Strauss et al. 2022).

Using two flocks of captive Homing Pigeons, we firstly aimed to understand if certain factors – encompassing physiological (body mass, structural size, metabolic rate) and behavioural (boldness) components – contribute to an individual's position within a hierarchy. In addition, we measured feather plumage iridescent of the neck feathers of the pigeons; it has been proposed that elements of plumage iridescent play an important role in both flock social structure and breeding display behaviours (Johnston, 1992; Fankhauser 2015). We tested a series of hypotheses pertaining to these underlying traits –body mass, metabolic rate and personality – which may determine position within a rank position, before then perturbating two traits (body mass, feather iridescence reflectance) to determine how stable these rank positions are. Specifically, we first tested whether body mass, structural size, personality, resting metabolic rate and/or the degree of plumage iridescent predicted rank position. We predicted that: (*i*) body mass would be the primary determinant of rank positioning, based on prior studies, with heavier birds holding higher ranking positions, (*ii*) bolder individuals would have higher ranking positions within the dominance hierarchy, (*iii*) Homing Pigeons would follow the *allocation model* (Mathot, Dingemanse and Nakagawa 2019), whereby individuals with a low resting metabolic rate will occupy dominant hierarchy positions, due to having more metabolic scope to engage in aggressive behaviour, (*iv*) individuals, particularly males, with brighter more iridescent plumage will be more dominant, with feather quality acting as a signal of general good condition. After establishing the determinants of rank positions, we manipulated aspects of body mass and plumage reflectance, to determine whether hierarchy stability was susceptible to perturbation when these traits where artificially manipulated, or whether the dominance hierarchy was resistant to perturbation and maintain its original baseline structure. We chose body mass and plumage reflectance as these traits are comparatively more straightforward to manipulate in comparison to metabolic rate and individual personality. We predicted that (*v*) mass manipulation would disrupt the existing hierarchy, with those individuals having their mass artificially increased moving up the rankings, and (*vi*) covering the iridescence from the neck feathers of dominant pigeons, thus hiding a potential status badge, will disrupt the hierarchy, with subordinates demonstrating more aggressive behaviours directed at the previous dominant individuals.

Methods

Birds

Homing Pigeons (*n* =33) were housed at Royal Holloway University London (Egham, UK), split between two lofts (dimensions 3.6m x 2.4m). Birds had unrestricted access to food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, UK), grit and water. Loft 1 comprised seventeen individuals (8 males, 9 females) and loft 2 sixteen (8 males and 8 females). Sex was determined by genetic testing of feather samples (Animal Genetics, UK). While no birds were added to either loft during the duration of the experiment, two pigeons were omitted part way through the study period from loft 2 due to (unrelated) injuries sustained after the first dominance control study. Individual pigeons were weighed using scales (PS1C EPOS integrated scales, Swansea) to the closest 10g. Structural size was determined through measuring their tarsus length (from the elbow joint to the ankle joint) using electronic calipers (Louisware from Amazon). Tarsus length is an established method of assessing structural size in pigeons (Senar and Pascual, 1997).

Dominance hierarchies

The dominance hierarchies of each of the two pigeon flocks were determined through observing aggressive interactions, following protocols and definitions of Portugal et al. (2017a), Portugal et al. (2017b), Portugal et al. (2020) and Ricketts et al. (2021). Briefly, interactions recorded were; pecking, chasing, beak grabbing, supplantation, neck grabbing and wing slapping. Food was removed from the lofts the day before each dominance trial, at approximately 15:00. Water remained available at all times. Before each dominance trial, all birds were caught and placed into a pigeon carrier, with the carrier being kept within their home lofts. Before the first trial, each bird was labelled with back-mounted Velcro (VELCRO®) fixed in place with epoxy resin (Araldite® two-part epoxy) before the experiments began, in order to make each individual identifiable via a number on their back. Labels were replaced if any fell off during the experimental period. For each dominance trial, a single small feeder, half filled with food, was placed against the wall of the home loft opposite the carrier. The placement of the feeder against the wall removed several access points for the birds, encouraging confrontation. Ceiling-mounted cameras (GoPro Hero4 or Akaso EK7000) recorded interactions across the loft over a 60-minute period once the pigeons were released from the carrier. To begin a trial, the door to the carrier was opened, and the experimenter immediately exited the home loft. Upon completion of each dominance trial, food was returned to the loft.

The initial dominance hierarchies' trials (*n* = 10 trials) per flock were studied over a 2-week period across February and March 2021, followed by mass manipulated trials (*n* = 10 trials) in April 2021. A second control of 10 dominance trials was conducted in May and June 2021 which were undertaken to determine if any carry over effects from the first manipulation trials were evident, and to avoid these affecting the later plumage manipulation trials (*n* = 10 trials) which took place in June 2021. During dominance trials, all aggressive interactions were recorded, included pecking, chasing, wing slapping, supplantation, neck grabbing and beak grabbing (see Portugal et al. 2020 for full definitions). Which pigeon was the aggressor (winner) and which pigeon was the subject (loser) were recorded using BORIS free software (Friard and Gamba 2016). These different behaviours were summed for each bird and displayed in a matrix for each dominance trial and used to calculate rank position using David's score (see Gammel et al. 2003 for full details; Ricketts et al. (2021) for calculation equations).

Personality assays

Individual personality was quantified by establishing individual tendency for lone exploration in an unfamiliar environment (Portugal et al. 2017a). Exploration trials took place in February and March 2021. For exploration, individual birds were taken from their home loft and placed in an animal carrier. The carrier was placed in the corner of an uninhabited loft which had been divided into 3 equal sections with tape to mark three respective zones (see Fig. 1 in Portugal et al. 2017a). The pigeon was released from the carrier and allowed to explore the loft for 30 minutes. The duration spent in the carrier, zone one (closest to carrier), zone two, zone three (furthest from carrier), as well as perches, was recorded. Five repeats were carried out per pigeon, with each repeat for each pigeon taking place approximately every 2 days; no repeats on the same pigeon occurred on the same day. Ceiling mounted camera (GoPro Hero4 or Akaso EK7000) recorded the pigeons during these trials. From footage, the duration spent in each of the three zones, as well as the duration spent on perches in each zone, was recorded using BORIS (Friard and Gamba 2016).

Spectrophotometry

Prior to any plumage manipulations (see below), feather cuttings were taken from the neck of the pigeons, using scissors to cut at the base of the quill to ensure the feature was intact. Only iridescent plumage which appeared green under natural light was sampled, from the top of the neck (McGraw 2004). Gloves were worn whenever handling feathers to prevent contamination (Meadows et al. 2011), and feathers were stored in airtight bags out of direct sunlight before spectrophotometry took place. Feathers were taped to matte black paper overlapping to replicate how they may be arranged *in situ*. Feathers reflectance was analysed using Ocean Optics spectrophotometer (Ocean Optics USB2000, Oxford, UK) measuring between 329nm – 1000nm. Prior to taking measurements the device was calibrated using a WS-1 Diffuse reflectance standard both with and without a light source. The reflectance probe and light source were held at a set distance in a reflectance probe holder at a 90-degree angle from the sample (McGraw 2004). Three repeats per feather sample were taken by placing the reflector holder on the sample at random spots on the tip of the iridescent plumage.

Respirometry

Resting metabolic rate (RMR) measurements were taken once after the initial dominance and personality control experiments had concluded, and these measurements were taken over a 2-week period in April 2021. Food was removed from the pigeons at 16:00 the day before respirometry trials were performed, to ensure pigeons were post absorptive (Mathot & Dingemanse, 2015). Starting at 09:00 the morning after food removal, pigeons were taken in groups of 3-4 from the lofts and transported to the laboratory. Per day, 5-7 pigeons had their RMR measured between approximately 09:00 and 17:00. Each pigeon was individually placed in a plastic see-through respirometry chamber (31 × 23 × 23 cm, volume 12 L) in a dark room and allowed to settle before measurements were taken. Chambers were built in-house. Oxygen (O_2) concentration was calibrated to 20.95% to match ambient air (Lighton, 2008). Initial measurements of ambient air lasting approximately 20 minutes were taken before any pigeon entered the chamber. Ambient air was pulled through the chamber at a flow rate of approximately 1700 mL min^{-1} , (SS-4 Sub-Sampler Pump, Sable Systems, Las Vegas, USA) making the flush-out rate of the chamber approximately eight minutes. After recordings for each pigeon (40 minutes) had taken place another 10 minutes of ambient air baseline took place. During recordings pigeons were kept within their thermoneutral zone (mean 20.45 ± 3.7 ºC (s.e.m.), minimum = 18.2 ºC, maximum = 23.5 ºC across all traces) (Webster and King, 1987). Air leaving the system first passed through a humidity sensor (RH-300, Sable Systems), where water vapour was removed (anhydrous indicating Drierite®, W. A. Hammond Drierite Co. Ltd, Ohio, USA) before entering the C_{O2} analyser (CA-10a, Sable Systems). C_{O2} was then removed (soda lime, Sigma Aldrich, Merck KGaA, Darmstadt, Germany) and any excess water vapour removed also, before the air then passed through an O_2 and temperature analyser (FC-10a, Sable Systems). Analysers were connected to a laptop via a UI-2 interface and data were logged in Expedata software (Sable Systems, USA).

Mass Manipulation

The relationship between body mass and structural size was determined for each of the 2 lofts (see Supplementary Fig. S1). The resultant trend line was used to artificially mass load pigeons, by using the residuals from the relationship between size and mass for those individuals below the line of best fit (see Supplementary Fig. S1). Birds who fell under the line of best fit were selected to have artificial mass administered. The resultant negative residual for each pigeon was rounded up to the nearest 5g and that amount was added to each pigeon via the addition of bike balance weights (Qiilu Wheel Weight Balance Self Adhesive, Esonline, Chiswick, London) (Portugal et al. 2020), via the back mounted Velcro used to label the pigeons. After the weights had been applied, the same protocol as for the control dominance trials was followed over 10 sessions, in April 2021. The previous study (Portugal et al. 2020) which used artificial mass manipulations chose those birds in the bottom 50% of the hierarchy to receive additional mass, rather than focusing on those individuals who were lighter for a given structural size.

Plumage Manipulation

Rank positions of all the pigeons in each loft were obtained after analysis of the first initial control trials (*n* =10 trials) using David's score (Gammel et al. 2003). The top 20% ranking birds (loft 1 *n* = 4, loft 2 *n* =4) from each loft had all their iridescent neck plumage (which were identifiable due to their colour shifting nature from pink to green and their reflection under UV) covered with black non-toxic acrylic Sharpie markers. These pigeons were habituated to this painting procedure daily, starting three days before the dominance trials were conducted. All pigeons were collected and placed into pigeon carriers. The top ranking pigeons were then separated from the carriers and then painted with the black markers until the plumage was a uniform black under natural light. A 345nm UV torch (Lepro, Birmingham, UK) was used to confirm that the plumage reflectance had been obscured (Supplementary Fig. S2). Once dry, the painted pigeons were placed in the carriers with the rest of the flock and the dominance trial was started, as previously described. Bird were painted before each dominance trial in the plumage manipulation to ensure consistent colouration in each repeat. This protocol was followed over 10 sessions in June 2021.

Statistical analysis

Statical analysis was completed using R, v. 3.6.1 (R Software, Vienna, Austria, *http://www.R-project.org*) (2013). David's score and hierarchy steepness for each set of trials for each loft was calculated using the package 'steepness'. Steepness of the dominance hierarchies was calculated as described in de Vries et al. (1995) using the R package ‘steepness’ (R Core Team 2016, de Vries, Stevens and Vervaecke 2006).

All relationships between morphological traits were assessed using linear regression (R package lme4). Correlations between David’s score across trial types were calculated using linear regression and Spearman’s Rank, respectively. Repeatability of David’s score across trials was also assessed using ‘rptR’ package (Stoffel et al. 2017) to calculate intraclass correlation coefficient, which describes the amount of variation caused by a random effect (in this case, individual variation). The significance was ascertained using a likelihood ratio test with the 95% of repeatability was estimated using 10,000 parametric bootstraps. Repeatability of exploration duration per zone in the novel environment task was also calculated in the same manner. Correlation matrices between measured traits were assessed using the package ‘corrr’. If any two traits exhibited a correlation equal to or above 0.75, one trait was removed prior to further analysis. Trait correlation was also examined for the zone duration aspects of the personality trials. The zone correlation assessments resulted in zones two and three being removed from subsequent analyses. A GLM (family: Gaussian) was used to determine what factors determined David’s score (response variable). We first ran a full model containing all non-correlated traits as predictor variables (tarsus length, RMR, % reflectance, zone 1, zone 1 plus perch, zone 2 plus perch, zone 3, carrier), then fitted all possible model combinations using the pdredge function in package ‘MuMIn’ (Barton and Barton, 2019). We retained the model with the lowest AIC (Angert et al., 2011).

Differences in physiological traits (body mass, tarsus length, maximum % reflectance) and David’s score between sexes was assessed using two sample *t*-tests, with Cohen’s ‘d values presented for effect size. The number of interactions per repeat for each trial type was collated and compared using nonparametric Kruskal-Wallace tests; pairwise comparisons (Wilcoxon rank sum with continuity corrections) were utilised to identify where any significance lied. Kruskal-Wallace tests were also used to compare values of all measured parameters between the two lofts. FDR (Benjamini-Hochberg) corrections were applied to *p*-values where necessary (Thissen et al. 2002), due to repeated testing. The adjusted *p*-values are detailed where the test result is reported.

Results

Hierarchy stability

All measured variables for each pigeon are detailed in Table 1. There were no significant differences between the two lofts in any of the variables measured (Supplementary Table S1). Rank position and David's score remained stable across the two control trials and over the course of the two manipulation dominance trials, with David's score and rank being highly correlated between trials in both flocks, throughout (see Table 2, Table 3, for Spearman's rho and P values). In addition, David's score across all trials for both flocks were highly repeatable (loft 2, R =0.79 ± 0.09 (s.e.m.), 95% CI:0.56,0.90 $P < 0.0001$; loft 2, R =0.71± 0.10 (s.e.m.), 95% CI:0.45,0.84, $P < 0.0001$) (Fig. 1., Fig. 2).

In total, 10,599 aggressive interactions where recorded. Aggression levels between trial types varied for both flocks (loft 1 Kruskal-Wallis X^2 = 10.99, df = 3, P-value = 0.012; loft 2 Kruskal-Wallis X^2= 10.38, df = 3, P-value = 0.016) (Supplementary Table S2). Pairwise comparisons (Wilcoxon rank sum with continuity corrections) indicated this significance was between the 1st control and mass manipulation trial (P=0.03), and the mass manipulation and feather manipulation trials (P=0.006) in loft 2, and between the 1st control and mass manipulation trial (P=0.04) in loft 1. Social network diagrams for each trial type (Supplementary

Fig. S3) show similar interactions between individuals in each trial type. Though interactions in the 2nd trial (mass manipulation) for both lofts show a shift in dynamic, with a large proportion of interactions during these trials taking place between the same 5-6 birds.

Phenotypes

Body mass (g) and tarsus length (mm) were significantly correlated in both pigeon flocks combined (LM, R^2=0.34 $F_{1,29}$ = 14.95, *P*<0.001; Table 1), with males being significantly larger than females (Two sample *t*-test *t*=-2.39, df=29, *P*=0.02, Cohens '*d* = 1.69). Resting metabolic rate (RMR) was seen to increase with body mass (LM, R^2=0.23 $F_{1,29}$ = 8.53, *P*<0.001), but there was no significant difference in RMR between the two sexes (Two sample *t*-test *t*=-1.41, df=29, *P*=0.17; Cohens '*d* = 0.5).

Plumage reflectance

No significant difference in maximum feather % reflectance was apparent between the sexes when both flocks were combined (Two sample *t*-test, *t* = 0.18, df = 29, *P*= 0.86, Cohens '*d* = 0.06; after outlier removal (Cook's Distance, *D*) *t* = 1.35, df = 26, P = 0.19). RMR was significantly correlated with maximum % reflectance (R^2=0.30 $F_{1,29}$ = 11.77, *P*=0.002, after outlier removal (Cook's Distance, *D*), R^2=0.44 $F_{1,26}$ = 20.36, *P*>0.0001).

Personality and exploration

RMR was not significantly correlated with exploratory behaviour in the personality trials (Supplementary Table S4). Due to the significant relationship between body mass and structural size, only structural size was then used to investigate relationships between size and personality. Structural size was chosen as it does not vary temporally in adult birds, unlike body mass. No significant relationship between any aspects of exploration behaviour and structural size were recorded (GLM, Zone one t=-1.7, P=0.1, Zone one perch, t=0.45, P=0.66, Zone two perch, t=-1.29, P=0.21, Zone three perch, t=1.09, P=0.29, carrier, t=-1.42, P=0.17). Exploration across zones on a population level was highly repeatable: carrier; R = 0.61 ± 0.08 (s.e.m.), 95% CI:0.43,0.74 $P < 0.0001$, Zone one R =0.18 ± 0.08 (s.e.m.), 95% CI:0.02,0.33 $P < 0.01$, zone one perch R =0.69 ± 0.07 (s.e.m.), 95% CI:0.52,0.80 $P < 0.0001$, zone two perch R =0.11 ± 0.07 (s.e.m.), 95% CI:0.07, 0.26 $P = 0.04$, zone three perch R =0.22 ± 0.08 (s.e.m.), 95% CI:0.08,0.05 $P < 0.001$).

Table 1 Pigeon phenotypes for two pigeon flocks, loft 1 (n = 17 pigeons) and loft 2 (n = 14 pigeons). The two lofts are separated by a thick black line. Columns initially show; pigeon ID, sex, tarsus length (mm), body mass (g), resting metabolic rate (ml/min), mass-corrected resting metabolic rate (ml/min/g) and feather reflectance (%). Columns then present David's score (DS) and associated ranks (in brackets, in **bold**) for each behavioural dominance trial. Trials refer to baseline pre-mass manipulation trials (February-March), mass-manipulation trials (April), pre-plumage manipulation trials (May-June), and plumage manipulation trials

(June). The symbol $^{\uparrow}$ in the mass column denotes individuals that had their mass artificially manipulated. The * symbol in the reflectance column denotes individuals that had their plumage manipulated. Loft refers to which flock each bird was part; of either 1 or 2.

Bird ID	Sex	Tarsus (mm)	Mass (g)	RMR (ml/min)	RMR (ml/min/g)	Reflect. (%)	Pre-mass Baseline DS + (**Rank**)	Mass Manipu. DS + (**Rank**)	Pre-plum. Baseline DS + (**Rank**)	Plumage Manipu. DS + (**Rank**)
1	M	36.33	460$^{\uparrow}$	10.04	0.022	72.06	-39.78 **(15)**	-19.98 **(13)**	-8.09 **(10)**	45.56 **(4)**
2	F	33.25	460	13.66	0.023	90.37	-64.32 **(17)**	-59.48 **(17)**	-80.25 **(17)**	-51.07 **(16)**
3	M	36.13	500	16.03	0.032	68.43	-27.20 **(12)**	-15.16 **(10)**	-17.59 **(11)**	29.82 **(6)**
4	F	32.80	400$^{\uparrow}$	7.41	0.028	105.41	-59.04 **(16)**	-13.17 **(9)**	-21.73 **(13)**	-30.02 **(13)**
5	F	33.34	500	8.45	0.017	120.27	-13.11 **(10)**	9.66 **(6)**	22.70 **(5)**	22.49 **(7)**
6	M	35.85	470$^{\uparrow}$	14.71	0.031	79.30*	58.82 **(2)**	59.07 **(2)**	50.71 **(3)**	47.10 **(3)**
7	F	34.37	430	8.29	0.019	108.06*	38.14 **(4)**	-21.25 **(15)**	-19.28 **(12)**	-29.93 **(12)**
8	M	37.43	520	15.77	0.030	57.40*	51.97 **(3)**	62.33 **(1)**	69.10 **(1)**	49.18 **(2)**
9	M	35.74	440$^{\uparrow}$	15.63	0.035	75.85*	73.16 **(1)**	38.79 **(3)**	50.98 **(2)**	35.90 **(5)**
10	F	34.64	420$^{\uparrow}$	7.86	0.019	99.26	-29.44 **(13)**	-38.27 **(16)**	-61.48 **(16)**	-53.66 **(17)**
11	F	34.53	460	8.99	0.019	77.41	-15.63 **(11)**	-15.67 **(11)**	2.26 **(8)**	-43.43 **(15)**
12	M	36.26	480	10.74	0.022	83.30	22.11 **(6)**	35.11 **(4)**	16.77 **(6)**	52.81 **(1)**
13	M	34.15	450$^{\uparrow}$	8.52	0.019	78.37	-9.47 **(9)**	9.32 **(7)**	-26.87 **(14)**	-17.93 **(11)**
14	M	36.78	450$^{\uparrow}$	15.12	0.034	47.29	35.27 **(5)**	-8.20 **(8)**	-31.16 **(15)**	-10.76 **(9)**
15	F	32.32	410$^{\uparrow}$	9.23	0.022	143.75	-35.46 **(14)**	-21.17 **(14)**	9.77 **(7)**	-32.48 **(14)**
16	F	33.64	480$^{\uparrow}$	11.65	0.024	84.08	20.50 **(7)**	14.63 **(5)**	47.25 **(4)**	-14.56 **(10)**
17	M	36.91	500	8.4	0.017	80.36	-6.50 **(8)**	-16.57 **(12)**	-3.10 **(9)**	0.98 **(8)**
18	M	36.02	510	8.58	0.017	130.71	10.86 **(8)**	10.35 **(5)**	11.03 **(5)**	23.40 **(4)**
19	F	34.25	420$^{\uparrow}$	12.3	0.029	78.91	-48.35 **(13)**	-15.59 **(12)**	-15.48 **(11)**	13.22 **(7)**
20	F	36.32	450$^{\uparrow}$	10.16	0.022	20.36	-47.72 **(12)**	-13.92 **(11)**	-16.89 **(12)**	-21.42 **(11)**
21	M	35.44	490	10.8	0.022	99.74	4.46 **(9)**	29.22 **(2)**	36.96 **(2)**	24.77 **(3)**
22	F	34.70	530	16.32	0.031	73.07	28.18 **(4)**	21.85 **(3)**	25.48 **(3)**	20.23 **(5)**
23	M	34.80	470	13.82	0.029	80.31*	29.38 **(3)**	19.22 **(4)**	23.01 **(4)**	35.29 **(1)**
24	F	33.21	410$^{\uparrow}$	12.41	0.030	83.69	23.48 **(5)**	3.15 **(6)**	3.99 **(6)**	2.38 **(8)**
25	F	31.86	440	8.91	0.020	65.03	-62.02 **(14)**	-42.28 **(14)**	-53.65 **(14)**	-42.23 **(14)**
26	M	36.70	560	17.74	0.032	52.39*	48.56 **(1)**	49.25 **(1)**	52.42 **(1)**	30.47 **(2)**
27	M	35.12	500	9.19	0.018	105.70*	36.46 **(2)**	-0.86 **(7)**	-0.38 **(8)**	14.41 **(6)**
28	F	33.34	460	10.78	0.023	103.07	-21.26 **(10)**	-6.68 **(9)**	-11.19 **(9)**	-12.43 **(10)**
29	F	35.74	440$^{\uparrow}$	15.44	0.035	45.32	17.69 **(7)**	-11.67 **(10)**	-15.01 **(10)**	-36.00 **(12)**
30	M	33.17	380$^{\uparrow}$	7.01	0.018	146.05	21.73 **(6)**	-3.61 **(8)**	1.60 **(7)**	-11.51 **(9)**
31	F	32.50	420	6.43	0.015	71.61	-41.47 **(11)**	-38.44 **(13)**	-41.89 **(13)**	-40.58 **(13)**

Predictors of dominance

Generalised linear models for each separate flock showed no significant relationships between David’s score and any covariates (tarsus length, maximum % reflectance, resting metabolic rate, duration in zone one, zone one perch, zone two perch, zone three perch and carrier). When data for both flocks were combined, David’s score was best predicted by tarsus length (GLM, *t*= 2.17, *P*=0.04), maximum % reflectance (GLM, *t*= 2.41, *P*=0.02)(Fig. 1), and resting metabolic rate (GLM, *t*=2.51, *P*= 0.02 (Table 2). These results are additionally supported by *t*-test comparisons. The relationship between RMR and David’s score remained significant after accounting for body mass (GLM, *t*=2.53, *P*= 0.02). On average, males occupied higher ranking positions than females (Two sample *t*-test, *t* =-3.3 df = 29, *P* = 0.0002, Cohens ‘*d* = 1.2). The steepness of the dominance hierarchies remained similar throughout the dominance trials (see Supplementary Table S3).

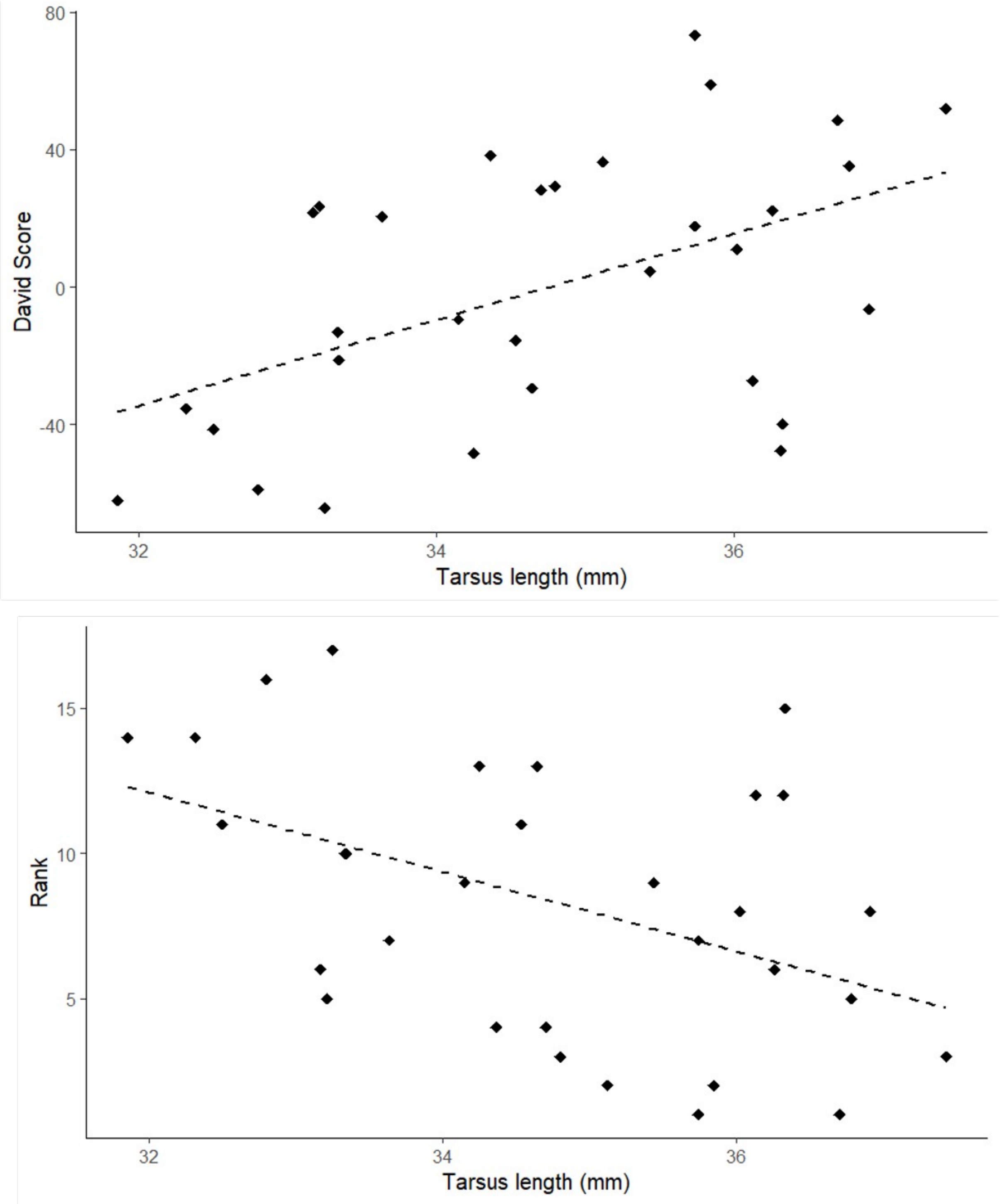

Fig. 1. Relationship between (top) David's score, rank (bottom) with tarsus length (mm) for both pigeon lofts combined ($N = 31$).

Table 2 Spearman's rank (rho) (left side; italicized and shaded) and regression (right side; unshaded) comparisons of ranks for both lofts between control dominance trials and trials with manipulated mass or plumage. *P* values (non- italicized) between trials, <0.05 suggest correlation between ranks between trials. *P* values adjusted following FDR (see Methods) to account for repeated testing for each loft. Trial number refers to (1st) control trial, prior to any manipulations, (2nd) specific individuals were weighted, (3rd) control dominance trials between manipulations and pre-plumage manipulation, and (4th) dominance trial in which the top 20% ranked birds from the 1st control from each loft had their iridescent plumage dampened resulting in decreased reflectance.

Loft 1	1st Trial	2nd Trial	3rd Trial	4th Trial	Loft 2	1st Trial	2nd Trial	3rd Trial	4th Trial
1st Trial	**X**	>0.01	0.02	0.03	1st Trial	**X**	0.01	0.01	0.02
2nd Trial	*0.70*	**X**	>0.01	>0.01	2nd Trial	*0.77*	**X**	>0.01	>0.01
3rd Trial	*0.59*	*0.75*	**X**	0.01	3rd Trial	*0.75*	*0.99*	**X**	>0.01
4th Trial	*0.58*	*0.74*	*0.65*	**X**	4th Trial	*0.65*	*0.89*	*0.89*	**X**

Table 3 Linear regressions comparing David's score between control dominance trials and manipulated mass or plumage trials for both lofts. Trial number refers to (1st) control trial, prior to any manipulations, (2nd) specific individuals were weighted, (3rd) control dominance trials between manipulations and pre-plumage manipulations, and (4th) dominance trial in which the top 20% ranked birds from the 1st control from each loft had their iridescent plumage dampened resulting in decreased reflectance. All trials were significantly correlated with each other trial, suggesting rank stability. *P*-values adjusted following FDR (see Methods) to account for repeated testing for each loft.

David's score comparison **Loft 1**	F Degrees of freedom	R^2	P	David's score comparison **Loft 2**	F Degrees of freedom	R^2	P
1st trial vs 2nd trial	$F_{1,15}=23.5$	0.61	$P=0.001$	1st trial vs 2nd trial	$F_{1,12}=19.19$	0.62	$P=0.001$
1st trial vs 3rd trial	$F_{1,15}=13.2$	0.47	$P=0.01$	1st trial vs 3rd trial	$F_{1,12}=20.06$	0.63	$P=0.001$
1st trial vs 4th trial	$F_{1,15}=5.4$	0.26	$P=0.02$	1st trial vs 4th trial	$F_{1,12}=7.702$	0.40	$P=0.02$
2nd trial vs 3rd trial	$F_{1,15}=47.8$	0.76	$P>0.0001$	2nd trial vs 3rd trial	$F_{1,12}=1116.0$	0.99	$P=0.003$
2nd trial vs 4th trial	$F_{1,15}=18.9$	0.56	$P=0.001$	2nd trial vs 4th trial	$F_{1,12}=32.8$	0.73	$P=0.002$
3rd trial vs 4th trial	$F_{1,15}=12.2$	0.45	$P=0.004$	3rd trial vs 4th trial	$F_{1,12}=36.3$	0.75	$P>0.0001$

Table 4 Generalised linear model results for both lofts combined (31 pigeons) between initial David's score (dominance) as a response variable. Original model contained structural size (tarsus length), maximum reflectance% (= maximum reflectance % of iridescent feathers), resting metabolic rate (RMR), and exploratory behaviour (zone one, zone one perch, zone two perch, zone three perch and carrier) (see *Methods*) as explanatory variables. Model presented is final model following AIC selection. Final AIC value: 306.67. All *P*-values are at a 95% confidence level. Bold denotes significant.

	Estimate	Std. Error	*t*-value	p
Intercept	-483.13	153.59	-3.14	0.004
Tarsus length (mm)	11.25	4.45	2.52	**0.017**
Maximum % reflectance	0.47	0.21	2.20	**0.036**
RMR	4.94	20.07	2.39	**0.024**

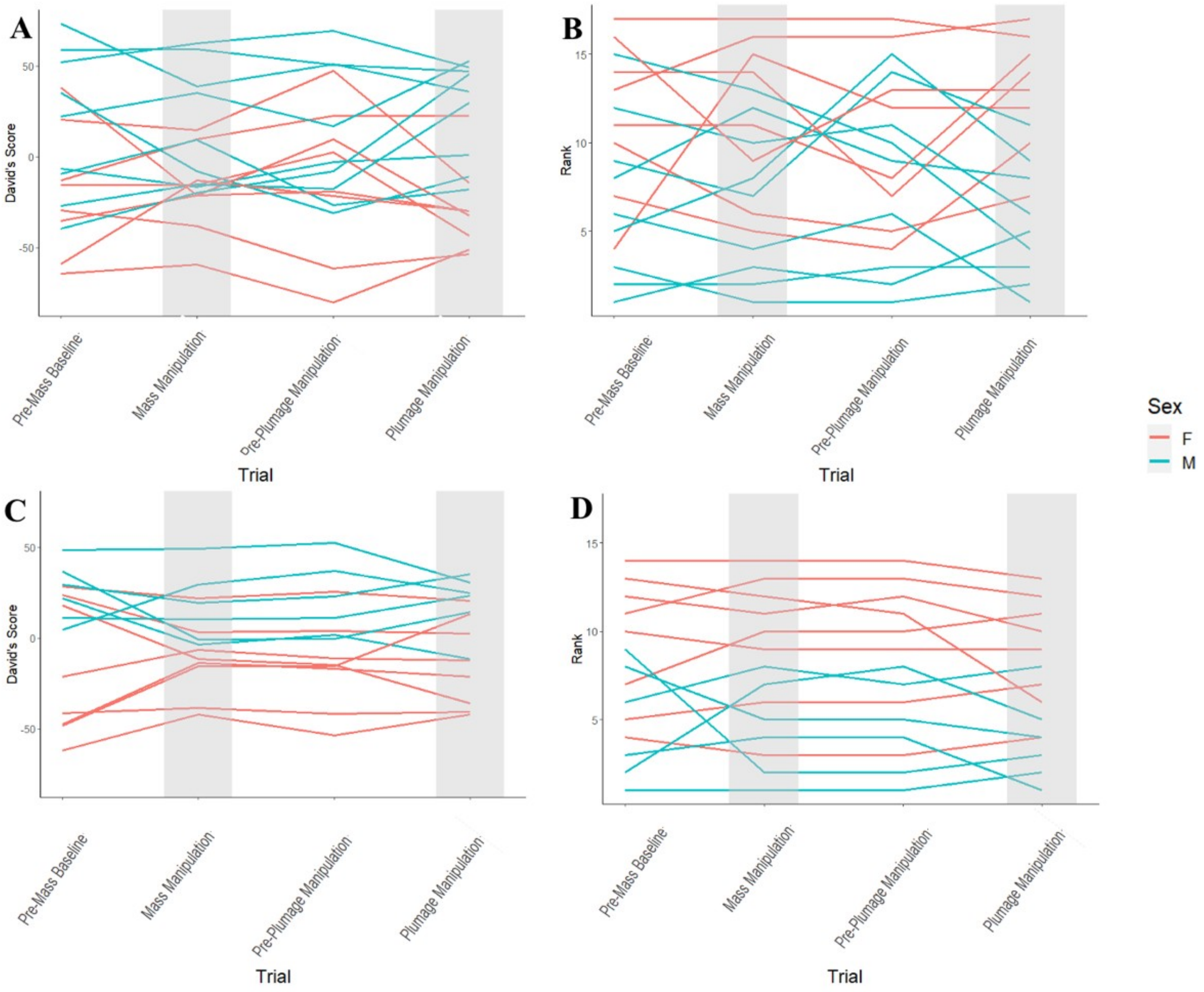

Fig. 2 David's score and rank over the two control trials (1 and 3 denoting the 1st and 2nd control respectively on x-axis) for two flocks of pigeons (loft 1, *n*=17; loft 2, *n* = 14). The mass manipulations and plumage manipulations are denoted by grey shaded area. A and B detail loft 1 and C and D present loft 2. Colours represent male and female pigeons (see inset legend).

Discussion

We aimed to firstly determine what traits – physiological and/or behavioural – dictated an individual's position within a dominance hierarchy. We then aimed to establish how stable these dominance hierarchies where, and how resistant they were to experimental perturbations. Over the four dominance trial types conducted, the hierarchies for both pigeon flocks remained stable across all experimental conditions and were not destabilised by any experimental perturbations. Analysis of morphological traits revealed a clear positive relationship between rank (via David's score) and body size and resting metabolic rate (RMR). Additionally, there was a negative relationship between RMR and iridescent plumage % reflectance.

Hierarchy stability

Between all dominance hierarchy trials conducted there was no significant change in rank, with neither attempts to perturb hierarchy organisation being successful. This suggests that pigeon dominance hierarchies are highly stable over time and resistance to major disruption. This may particularly be the case in larger groups of more than 10 individuals, as previously observed in Carrion Crows (Chiarati et al. 2010) and Lake Tanganyika Cichlids *Neolamprologus pulcher* (Taborsky et al. 2005)

Artificially increasing mass of lighter individuals did not significantly affect hierarchy structure, which could indicate perhaps that body size is a more important trait for asserting dominance than mass (Márquez-Luna et al. 2019, Brown and Maurer, 1986). Given that Homing Pigeons have context dependant hierarchies (Nagy et al. 2013), this relationship between size, RMR and rank and the associated rank stability is likely different when navigating during flight. Watts et al. (2016) indicated that leaders during flight lose influence over flock mates when they have inaccurate information. In those scenarios the consequence for spreading misinformation is much higher, compared to on the ground. The fact that the ground-based hierarchy was able to remain stable despite perturbations suggests none of the altered traits were manipulated sufficiently, or the traits that were focused upon don't contribute to hierarchy stability. Given that hierarchy formation reduces group aggression, it is understandable why hierarchies remain stable.

Most empirical evidence suggests dominance hierarchies are usually highly stable, with reported instability only occurring when there is a change in group composition through emigration or immigration (Grossel et al. 2021). In the present study, the two populations remained stable except for loft 2 where, due to an unrelated incident, two pigeons were removed. While the overall flock hierarchy structure did not significantly change as a result of this, there is some evidence to suggest there was some instability caused by this change with one or two members changing more than 2 ranking positions. Whether this was caused by the flock changes or just seasonal variation is unknown, as similar occurrences were visible in loft 1, which in contrast had a stable undisturbed population over all 40 dominance trials.

Intrinsic Traits and David's score

Previous research on Homing Pigeons (Portugal et al. 2017a; 2017b) reported a strong relationship between body mass and rank position. This is prevalent across multiple taxa, potentially indicating that larger body sizes and masses – the two typically being correlated – are important factors for resource holding, likely due to the increased ability to exclude and intimidate smaller individuals if you are bigger and heavier (Brown and Maurer 1986; Márquez-Luna et al. 2019). Such a scenario likely contributes to a positive feedback loop, as the already heavier, more dominant, birds obtain a larger quantity of resources, which in turn assists in body mass maintenance and mass gains. As such, our finding that structural size and body mass where strong determinants of rank within a dominance hierarchy matches that which was found previously. Body mass and structural size were significantly correlated in the pigeons, as has also been observed previously.

RMR and behaviour

Resting metabolic rate predicted aggressive behaviour (David's score), even when body mass was accounted for which is in accordance with the *performance model* (Mathot, Dingemanse and Nakagawa 2019). As previously described, the *performance model* suggests individuals with higher RMRs perform a higher amount of energetically costly behaviours, in addition to behaviours which result in net energy gain (Mathot, Dingemanse and Nakagawa 2019). In contrast to the relationship with David's score, RMR was not predictive of an explorative personality, which directly contradicts the aforementioned *performance model*. In this case, the results suggests that investment in aggressive behaviour (leading to higher David's score) contributed to a net gain of energy due to better access to food resources (Careau et al. 2008).

No relationship between any of the recorded personality traits and David's score were observed. Similar studies have reported a variety of contrasting and corroborating results. Some studies indicate a relationship between heightened boldness and social rank position, such as negative relationships in captive Black-capped Chickadees *Poecile atricapillus* with boldness being a trait more prevalent in subordinate birds (MacDougall-Shackleton et al. 2011). In contrast, other species and populations exhibit no relationship between rank and personality, such as that seen in wild Black-capped Chickadees (Devost et al. 2016) and Common Waxbills *Estrilda astrild* (Funghi et al. 2014).

RMR and Personality

In addition to the lack of relationship between personality and David’s score, a similar lack of relationship was observed between resting metabolic rate and personality traits. Careau and Garland (2012), in addition to Mathot and Dingemanse (2015), reviewed empirical research which found relatively few correlations of boldness or exploration with metabolic rate in avian species. Two studies in Great Tits have indicated negative correlations between risk taking behaviour and basal metabolic rate (BMR) (Mathot et al. 2014), in addition to exploration and BMR specifically in females (Bouwhuis et al. 2014). Both of these studies were conducted with wild populations where individuals are subject to different selection and resource pressures. In contrast, the Homing Pigeons in the present study are domesticated and kept in captivity, where access to food and water were unlimited, and the birds were safe from being predated upon when in their home loft. This difference in overall selection pressures could have impacted general motivation and willingness to explore during trials (Montiglio et al. 2018, Poranen, and Ruuskanen 2021). An interesting further avenue of study would be to repeat the experiments with wild Feral Pigeons or Rock Doves, to determine if they match the behaviours of the captive pigeons. In the present study, pigeons explored an unfamiliar loft alone. It is possible that in the case of Homing Pigeons, navigation and flight exploration could be a more reliable indicator of boldness (Portugal et al. 2017a), as opposed to ground-based experiments. Group flight is an energetically costly activity (Taylor et al. 2019; Sankey et al. 2019; Sankey and Portugal, 2019) and captive Homing Pigeons will experience similar predation threats during homing flights that wild populations encounter. Under these circumstances, exploratory flight and RMR may be linked in Homing Pigeons to a greater extent than loft based explorations.

Previous work establishing the links between metabolic rate, dominance and individual personality traits have not been ubiquitous. In the present study, it is possible that time of day was potentially impacting personality. Personality trials took place throughout the day between 09:00 and 17:00, and the time of day at which individuals had their personalities assessed could have been influenced by their natural behavioural circadian rhythms. Typically, pigeons are less active in the afternoons (Ricketts et al. 2021). Thus, birds who had repeat trials in the afternoons may exhibited reduced activity levels and a lowered willingness to explore. Individuals may have also been influenced by the external temperatures; personality assays were undertaken in February and March 2021, where temperatures averaged 8◦C and ranged from 16◦C to -2 ◦C. These low temperatures may have affected motivation for exploration leading to variation in activity (see Paladino, 1995).

A consistent issue raised by prior studies is that of measuring personality in a social species with isolated individuals (Funghi et al. 2014). Several studies on Zebra Finches indicate that individuals exhibit decreased neophobia when solitary, compared to social contexts which can appear counter intuitive (Schuett and Dall, 2009, Mainwaring, Beal and Hartley 2011, Kerman, Miller and Sewall 2018). Zebra Finches with higher basal metabolic rates were also more likely to adopt the scrounger role as a foraging strategy in groups (Mathot et al. 2009). As personalities of individuals of social species can be so different when isolated in contrast to within a group, a more accurate measure of personality may be to assess neophobic tendencies of individuals during both solitary and group settings. This method may reveal more about individual behavioural syndrome and social standing (Funghi et al. 2014).

RMR and Iridescent feather % reflectance

In our study maximum % reflectance of iridescent neck feathers was seen to decrease with increasing RMR. This suggests a potential energetic cost of either producing or maintaining the brightness of iridescent plumage. On a genetic level, sequencing of both iridescent and non-iridescent plumage related genes of Superb Starlings (*Lamprotornis superbus*) indicated non-iridescent feathers are associated with higher metabolic gene expression compared to iridescent plumage (Rubenstien et al. 2021). These different plumage types not only differ in production but also greatly differ in maintenance. A study on the iridescent plumage of Mallards *Anas platyrhynchos* indicated iridescent feathers were less hydrophobic and less efficient at self-cleaning, due to the difference in barbule structure (Eliason and Shawkey 2011). This functional difference could suggest that individuals have to invest a greater amount of time preening iridescent feathers to maintain structurally coloured plumage, which is likely to come at an energetic cost (Viblanc et al. 2011). The negative relationship between (assumed) feather quality and David's score has been reported in other species. Dominant Coal Tits *Periparus ater* produced lower quality feathers that grew at a slower rate than subordinates, thought to be a trade off with the costs of increased territory size, resources and mate choice (Hay et al. 2004).

Though our GLM results indicated a significant relationship between maximum % reflectance of plumage and David's score, this does not necessarily suggest that feather reflectance is a dominance signal in Homing Pigeons, as no significant change in rank position occurred when feathers and associated plumage were altered. The lack of significant overall aggressive interactions towards plumage altered birds suggests birds were still recognising each other despite the painting of certain feathers. This is corroborated by studies which have demonstrated that individual recognition in pigeons is more focused on their 'face' than their body

(Shimizu 1998). Furthermore, the observed relationship between dominance position and reflectance was negative, which would be unusual for a dominance signal; dominance signals are commonly highly investing ornamental traits.

While in the present study altering plumage signals had no significant effect on positioning within the hierarchy, dampening experiments on Blue Tits did show that reflectance was used to gauge attackers rank, but only during initial encounters. Once the birds were familiar with each other, subsequent interactions ended the same as the first confrontation, regardless of any reversal in UV plumage alterations (Vedder et al. 2010). This reliance on first interactions for determining dominance could suggest that because the pigeons in the present study had been living together for many years, the alteration of this signal were ineffective in disrupting hierarchies. Plumage brightness in House Finches *Carpodacus mexicanus* was negatively associated with dominance, with drab males being more aggressive and having poorer access to food. McGraw and Hill (2000) suggested this could be due to birds having to attack more to make up for their poor plumage and diet to obtain resources. Dominant individuals usually initiate more aggressive interactions and retreat less than subordinates, spending a proportionally larger time in combat (Hay et al. 2004). These birds also predominately have higher activity levels (Ricketts et al. 2021) and this could be attributed to their higher metabolic costs.

Conclusion

Overall, our results indicate rank position in Homing Pigeons is positively correlated with tarsus length and resting metabolic rate. In addition, a negative relationship was observed between iridescent plumage reflectance and David’s score, suggesting a link to the further cost of dominance traded off against the high investment costs of iridescence. The dominance hierarchies of the Homing Pigeons were highly resistance to experimental perturbations, indicating how their formation in social species is highly beneficial through decreasing aggression levels and maintaining stable group dynamics.

Our study focused on only one species, held in captivity with food provided *ab libitum*, and comparative safety from being predated upon. Therefore, to understand better the mechanisms behind dominance and their respective interactions with the traits we recorded (size, metabolic rate etc), wider investigations are required that ideally; (*1*) study these parameters for a number of years within the same population, (*2*) explore these relationships across a wider range of species, (*3*) work with a variety of social systems, including closer-knit family groups, fission-fusion societies, and species which exhibit winter group roosting behaviours but do not breed communally.

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AUTHOR CONTRIBUTIONS

Amaia A. Urquia-Samele: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Writing-original draft (lead); Writing-review & editing (equal).

Steven J. Portugal: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (lead); Supervision (lead); Writing original draft (supporting); Writing-review & editing (equal).

COMPETING INTERESTS

We declare we have no competing interests.

Data availability statement

All data are available within the tables provided in the main text and supplementary information.

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