

Artificial mass loading disrupts stable social order in pigeon dominance hierarchies

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Dominance hierarchies confer benefits to group members by decreasing the incidences of physical conflict, but may result in certain lower-ranked individuals consistently missing out on access to resources. Here, we report a linear dominance hierarchy remaining stable over
35 time in a closed population of birds. We show that this stability can be disrupted, however, by the artificial mass-loading of birds that typically comprise the bottom 50% of the hierarchy. Mass loading causes these low-ranked birds to immediately become more aggressive and rise-up the dominance hierarchy, however, this effect was only evident in males and was absent in females. Removal of the artificial mass causes the hierarchy to return to its previous structure.
40 This interruption of a stable hierarchy implies a strong direct link between body mass and social behaviour, and suggests that an individual's personality can be altered by the artificial manipulation of body mass.

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1. Introduction

Many animals live and travel in groups [1,2]. The benefits of group living can include enhanced vigilance and predator detection [1,2], energetic saving through positive aero- or hydro-
60 dynamic interactions [3,4] and increased foraging efficiency [5,6]. Within a group, however, individual characteristics in personality, morphology and physiology can lead to conflict. A product of such conflicts can be the emergence of dominance hierarchies [7], and these dominance relationships are a frequently documented characteristic of group living [8].

65 A dominance hierarchy within a group can confer benefits to all its members by decreasing the severity and incidence of physical conflicts [9]. By reducing the time devoted to agonistic encounters, time can be invested in other important behaviours such as maintenance, vigilance and foraging [10]. Dominance hierarchies within animal societies are frequently arranged in a linear fashion; higher-ranked individuals dominate all individuals of lower rank [8]. Linear
70 hierarchies have often been linked to parameters such as body mass/size [11], and have shown to be either stable [8] and unstable [12] over time. The degree to which there is apparent temporal variation in dominance hierarchies appears linked to certain life-history traits, with animal groups either confined to a limited area or living together for prolonged periods of time favouring stable hierarchies [13].

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How dominance and body mass interact both within and between seasons is not fully understood (although see [14]). Given that body mass can vary substantially throughout the annual cycle in response to key life-history events such as breeding, moult and migration, how these changes in body mass are reflected in the stability of group hierarchies and individual
80 positions therein is likely to have significant consequences on overall group dynamics and levels of aggression. Therefore, a better understanding of how responsive – and the rapidity of

response – dominance hierarchies are to smaller-scale instantaneous changes in body mass has the potential to offer insight into both collective and individual energy expenditure.

85 Using a captive flock of homing pigeons (*Columba livia*), we tested whether (a) group dominance hierarchies were stable over successive years in a closed population, (b) whether any hierarchical structure was directly related to body mass, and, (c) if linear hierarchies were stable and correlated with body mass, whether they could be disrupted by artificial instantaneous manipulations of body mass.

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2. Material and methods

(a) Birds

Seventeen homing pigeons (8 males, 9 females) were housed at the Royal Veterinary College (Hatfield, UK). All birds were six years old, and were purchased when they were one year old.

95 Birds were kept in a pigeon loft with *ad libitum* access to food and water. No birds were added to the group during the period of the study.

(b) Dominance hierarchies

To determine the dominance hierarchies, birds were studied initially at three different points in
100 the annual cycle for three consecutive years; 2011 (November), 2012 (March, June, November), 2013 (March, June). Nineteen months after the commencement of the study, the nine birds that constituted the bottom positions in the hierarchy were artificially weighted. Artificial mass was added four hours prior to the commencement of the experiments. The mass was added using self-adhesive lead bike balancing weights (Abba, Essex, UK). The lead
105 balancing weights were available in integers of 5 g, and the additional artificial body mass added was 12% of the bird body mass, to the nearest 5 g. A value of 12% was chosen as this reflects natural body mass dynamics throughout the annual cycle in pigeons [15]. The birds

were familiar with having biologging devices attached to their backs for prior studies on flight [16]. The weights were removed immediately following the experiments. The next dominance session – unweighted – was done the day immediately after the artificial mass manipulation. Determination of dominance followed the same procedure as [17-19] (see supplementary information for full dominance protocols).

(c) Analysis

We tested for linearity in each data set by calculating Kendall's coefficient of linearity [20-22], Landau's index h and the index of linearity h_0 [21,22]. Both indexes provide a value between 0 (absence of linearity) and 1 (complete linearity). Where the dominance hierarchy was found to be a significantly linear order (e.g. $A > B > C$), the matrix was reordered in such a fashion that the order of the individuals is most consistent with a linear hierarchy [21,22].

The repeatability over non-weighted sessions of (i) aggression via David's score and (ii) body mass was assessed by calculating the intraclass correlation coefficient using the rptR package in R [20,23]. The significance of repeatability was assessed using likelihood ratio tests and the 95% of repeatability was estimated using 10,000 parametric bootstraps. The stability of the linear dominance hierarchies between sessions was also assessed by Spearman rank correlations and Bonferroni-corrected regression rank comparisons between each sampling session.

Steepness of the dominance hierarchies was calculated as described in de Vries et al. [24] using the R package 'steepness' [20,25,26] (see electronic supplementary information). Any changes in the overall composition of the aggressive behaviours between weighted and non-weighted sessions was assessed using arcsine square-root transformations on percentage composition

data of the total number of recorded aggressive encounters, for each behavioural type. To assess the impact of mass manipulations, we used a linear mixed effects models with David's score as dependent variable, and mass load as a binary (i.e. whether a bird was wearing artificial mass or not) predictor variable, sex of the bird was also included as a fixed effect in an interaction with mass load. Finally, pigeon ID was included as random intercepts.

3. Results

All dominance hierarchies for non-weighted sampling sessions (N=7) over the three years were significantly linear (table 1), and strongly correlated with body mass (figure 1a; supplementary table 1,2). Taking the mean rank and body mass for each individual bird for the seven sampling periods, body mass was significantly correlated with rank position (figure 1b). David's score across the seven (not mass-loaded) trials was significantly repeatable ($R = 0.78 \pm 0.07$ (s.e.m.), 95% CI: 0.60–0.86, $p < 0.001$), as was body mass ($R = 0.96 \pm 0.02$ (s.e.m.), 95% CI: 0.91–0.98, $p < 0.001$). Spearman's Rho comparisons supported the repeatability of David's score across non-weighted sessions, with comparisons between each unweighted sampling session being significantly correlated (ρ range 0.78-0.99; table 2), indicating that rank in one (unweighted) session was a good predictor of rank the following session.

Upon application of the artificial mass, the dominance hierarchy changed significantly (table 1,2; figure 1c,d) but remained linear; the dominance hierarchy observed when nine birds were artificially weighted was significantly different than all seven non-weighted hierarchies (Spearman's Rho, ρ , range 0.04-0.09; table 2). Artificial mass loading significantly increased an individual's dominance score (LMM: DF = 118, $t = 4.52$, $p < 0.001$) by 42.85 ± 9.47 (s.e.m.) (David's score)). The nine individuals who were artificially mass manipulated significantly, on average, increased their aggression (figure 1c,d), resulting in a significant increase in their rank

(figure 1c,d). On average, individuals that were artificially mass loaded increased their number of aggressive behaviours by $134 \pm 261.6\%$ (s.d.). Not all birds increased their aggressive behaviours (figure 1c,d); the maximum decrease in aggressive behaviours observed by artificially mass loaded birds was 38.33%. Of those birds which did increase aggressive behaviours, the maximum and minimum increases were 750% and 11.3%, respectively (electronic supplementary material).

165 There was a significant interaction between sex and mass loading ($df = 117, t = 3.72, p < 0.001$). This relationship was driven by the males increasing their dominance score when mass loaded (Tukey posthoc test for lme in "emmeans" package: non-mass loaded males vs mass loaded males, estimate = 66.88 ± 11.1 (s.e.m.), t .ratio = 6.043, $p < 0.001$), whereas mass loaded females showed no difference to their non-mass loaded behaviour and subsequent dominance rank (estimate = -4.56 ± 15.6 (s.e.m.), $df = 117, t$.ratio = 0.292, $p = 0.991$).

The application of artificial mass resulted in an overall increase in aggression and aggressive encounters in the flock (table 1); the total number of aggressive interactions recorded during the artificial mass loading sampling session was nearly double ($N = 2580$) that of the nearest number of aggressive interactions recorded during an unweighted session ($N = 1321$, session 7; table 1; supplemental figure 1). During the artificial mass-manipulated session, the dominance hierarchy remained linear (table 1). All eight dominance hierarchies – both weighted and unweighted – had significant steepness ($p < 0.001$; table 1), indicating that the agonistic relationships of the pigeons were organized in a steep and linear fashion (the size of the absolute differences between adjacently ranked individuals in David's Score is large). The composition of aggressive behaviours remained significantly stable between sessions, and between the non-weighted and weighted trials (electronic supplementary material), with none

of the key five behaviours measured (pecking, chasing, beak grab, neck pull, wing slap) changing significantly in terms of relative contribution to overall aggressive behaviours recorded (Chi Square, all weighted to non-weighted comparisons, $p = 0.99$; electronic supplementary material).

4. Discussion

Over a 31-month period, the dominance hierarchy of the pigeon group did not significantly change, with individuals retaining their position within the hierarchy throughout the experimental period. Previously it has demonstrated that in animal groupings of less than approximately ten individuals, stable hierarchies are more commonly observed than in larger groups [27]. The linear dominance hierarchy in the pigeons was significantly related to body mass. There is no clear pattern yet determined as to why body mass is such a strong determinant of dominance in some species but not others [11,28]. It is possible that body mass is a significantly correlated with dominance in species where secondary-sexual ornamentations are less pronounced, and as a result, signalling is less clear. In such cases, body mass may become more of an important indicator of fitness. The hierarchy returning to its stable structure upon the removal of the additional mass load suggests that no carry-over or ‘memory’ effects of mass loading persist, and implies an instantaneous neurological feedback mechanism regarding changes in body mass [e.g. 29].

It is possible that the addition of the extra mass to the backs of the subordinate birds aggravated or stressed the birds, causing them to exhibit higher levels of aggression. During the addition of the artificial mass, the subordinate birds did not show any obvious signs of aggravation at the lead weights attached to them, nor did they try to peck or remove them, either on themselves or on conspecifics (S.J.P. *per. obs*), suggesting this is an unlikely explanation for their increased

aggression. Similarly, the composition of aggressive behaviours did not change between weighted and unweighted sessions, suggesting behaviours weren't more focused on the back, where the weights were attached. An alternative explanation, however, is that the addition of artificial mass – although only for a short period – increased the energetic requirements of the weighted birds, thus requiring them to be more aggressive to ensure adequate access to food [30,31]. Such a theory is akin to “lead according to need”, an idea which has previously linked to motivation and leadership in group behaviour [32].

Only males responded to the artificial mass loading by significantly increasing their aggressive behaviour, while females did not seemingly respond, suggesting that increasing aggression in response to artificial mass loading is sex specific. Previously it has been demonstrated that injections of testosterone into male pigeons did not make male pigeons more aggressive or dominant, [33], yet a perceived possible increase in physiological condition through the addition of mass in the present study did elicit a response. This sex-specific response may be linked to competition for females, with female pigeons preferentially selecting males for partnering who hold dominant positions within a hierarchy [34]. An avenue worthy of further investigation is the impact that the pairing status of an individual has on their respective rank, as it has been previously demonstrated in birds that being paired increases your rank within a hierarchy [35, 36].

The present study demonstrates the plasticity of aggressive traits, and the rapidity with which they can be modified based on physiological condition. Fruitful future investigations would be to ascertain the attributes that lead to greater body masses in wild-type scenarios, and in turn greater dominance. The “prior attributes” hypothesis [8,27,28], for example, suggests hierarchies are predetermined by personality or physiological differences in dominance ability.

This in turn may be linked to leadership during flocking and associated energy expenditure [37-40]. How natural seasonal variations in body mass [41-43] manifest in terms of dominance and general social behaviour would further explore the interactions between individual physiology, energetics and social behaviour. Moreover, experiments which supplementary feed specific individuals over a longer period of time to increase body mass may yield different results with respect to the changes in their respective ranks. Our study focused on only one flock of birds, and to determine the full nature of these instantaneous changes in body mass, further studies are needed with larger sample sizes, both in terms of number of flocks and sampling sessions where mass was added, and ideally additional species.

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Competing interests. We declare we have no competing interests.

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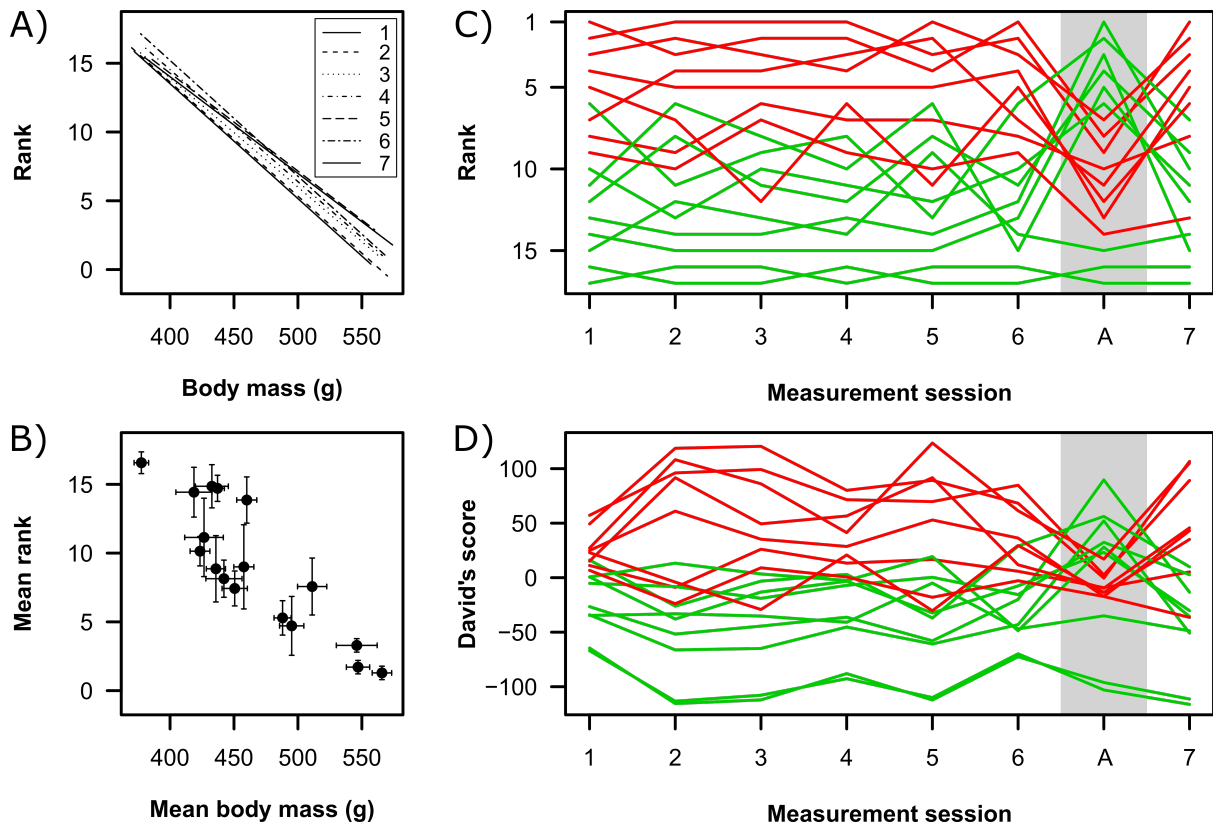


Figure 1. (A) Relationship between body mass and dominance rank in 17 homing pigeons for seven unweighted dominance trials covering three years (see supplementary table 1 for full regression details). All regressions were significant. (B) Relationship between mean (\pm s.e.m.) body mass (g) and mean rank (\pm s.e.m.) for seven unweighted dominance trials ($y = -0.08x + 46.4$, $r^2 = 0.77$, $F_{1,15}$, $p < 0.0001$). (C) Individual rank and thus David's score (D) was highly repeatable over unweighted measurement sessions. Individuals who were weighted for the weighted session are in green (session A, grey shaded rectangle).

Table 1. Hierarchy parameters for 17 homing pigeons. Numbers 1-7 refer to unmanipulated
 365 sampling sessions. *A* denotes the sampling session where nine birds in the bottom of the
 hierarchy were artificially mass manipulated. All hierarchies were significantly linear. *h* =
 Landau's index of linearity, *h'* = Landau's corrected index of linearity, DC = directional
 consistency index, DI = directional inconsistency index. T_N denotes the total number of
 aggressive interactions recorded amongst all individuals in the flock for each sampling session
 370 (total number of interactions = 10,906). D_{ij} refers to the steepness of the hierarchy. All
 steepness values are significant at $p < 0.001$ (after 10,000 randomisations).

	<i>h</i>	<i>h'</i>	DC	DI	Decided dyads	Zero dyads	Ties	1- way dyads	2- way dyads	I	SI	r_s	T_N	D_{ij}
1	0.47	0.53	68	16	87	48	1	56	32	4	15	0.96	991	0.34
2	0.66	71	79	11	101	32	3	78	26	2	8	0.97	1218	0.71
3	0.82	0.84	0.87	0.06	118	16	2	100	20	3	13	0.98	1285	0.66
4	0.66	0.70	0.79	11	101	32	3	78	26	2	8	0.97	1174	0.50
5	0.78	0.80	0.85	0.77	118	12	6	92	32	5	18	0.99	1268	0.47
6	0.57	0.61	0.69	15	106	29	1	68	39	6	27	0.96	1069	0.68
A	0.75	0.76	0.45	0.23	131	0	5	4	132	12	68	0.93	2580	0.51
7	0.83	0.84	0.83	0.08	120	11	5	81	44	4	18	0.98	1321	0.66

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Table 2. Regressions (r^2) between ranks within the dominance hierarchy for 17 homing pigeons measured over successive years (*shaded, left*). Numbers 1-7 refer to unmanipulated sampling sessions. *A* denotes the sampling session where nine birds in the bottom of the hierarchy were artificially mass manipulated. Spearman's Rho (ρ) comparisons between the dominance ranks of each sampling session (*right, non-shaded*). All regressions (see electronic supplementary table 2 for full regression results) and Spearman's Rho are significant at $p > 0.0001$ except for those sessions where individuals were mass manipulated (*A*).

	1	2	3	4	5	6	A	7
1	*	0.93	0.89	0.93	0.86	0.92	0.09	0.87
2	0.86	*	0.94	0.99	0.87	0.89	0.04	0.83
3	0.79	0.87	*	0.94	0.91	0.85	0.08	0.78
4	0.86	0.90	0.87	*	0.87	0.89	0.04	0.83
5	0.72	0.76	0.82	0.76	*	0.78	0.06	0.80
6	0.85	0.79	0.73	0.79	0.61	*	0.07	0.89
A	0.009	0.001	0.006	0.001	0.003	0.004	*	0.32
7	0.76	0.69	0.62	0.69	0.64	0.80	0.11	*