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 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. 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.

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-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].

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 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].

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 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

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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

110   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

115   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].

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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

125   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

130   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 1*c,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

160   behaviours (figure 1*c,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 $= 66.88 \pm 11.1$ (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

170   rank (estimate $= -4.56 \pm 15.6$ (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

175   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

180   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

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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

235   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,

240   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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References

1. Elgar MA. 1989 Predator vigilance and group size in mammals and birds: a critical review

255   of the empirical evidence. *Biol. Rev*. 64, 13–33.

2. Krause J, Ruxton GD. 2002 Living in groups. Oxford University Press. UK.

3. Bill RG, Hernkind WF. 1976 Drag reduction by formation movement spiny lobsters. *Science*. 193, 1146−1148.

4. Portugal SJ *et al*. 2014 Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* 505, 399−402.

5. Brown JS. 1988 Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol*. 22, 37–47.

6. Pays O, Beauchamp G, Carter AJ, Goldizen AW. 2013 Foraging in groups allows collective predator detection in a mammal species without alarm calls *Behav Ecol*. 24, 1229–1236.

7. Chase ID, Tovey C, Spangler-Martin, D, Manfredonia M. 2002 Individual differences versus social dynamics in the formation of animal dominance hierarchies. *PNAS* 99, 5744–5749.

8. Cote SD. 2000 Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137, 1541–1566.

9. Smith SM. 1976 Ecological aspects of dominance hierarchies in black-capped chickadees. Auk 93, 95–107.

10. Brown JL. 1963 Aggressiveness, dominance and social organizations in the Steller Jay. *Condor* 65, 460–484.

11. French AR. 2005 Importance of body size in determining dominance hierarchies among diverse tropical frugivores. *Biotropica* 37, 96–101.

12. Drews C. 1993 The concept and definition of dominance in animal behaviour. Behaviour 125, 283–313.

13. Izaw, EI, Watanabe S. 2008 Formation of linear dominance relationship in captive jungle crows (*Corvus macrorhynchos*): implications for individual recognition. *Behav. Processes* 78, 44–52.

14. Wroblewski EE, Murray CM, Keele BF, Schumacher-Stankey JC, Hahn BH, Pusey AE. 2009 Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii. Anim Behav*. 77, 873–885.

15. Sargisson RJ, McLean IG, Brown GS, White, KG. 2007 Seasonal variation in pigeon body weight and delayed matching-to-sample performance. *J. Exp. Anal. Beha*v. 88, 395–404.

16. Usherwood JR, Stavrou M, Lowe JC, Roskilly K, Wilson AM. 2011 Flying in a flock comes at a cost in pigeons. *Nature*. 474, 494–497.

17. Portugal SJ, Sivess L, Martin GR, Butler PJ, White CR. 2017 Perch height predicts dominance rank in birds. *Ibis.* 159, 456–462.

18. Portugal SJ, Ricketts RL, Chappell J, White CR, Shepard EL, Biro D. 2017 Boldness traits, not dominance, predict exploratory flight range and homing behaviour in homing pigeons. *Phil. Trans. R. Soc. B Biol. Sci.* 372, 20160234.

19. Gammell MP, De Vries H, Jennings DJ, Carlin CM, Hayden TJ. 2003 David's score: a more appropriate dominance index ranking method than Clutton-Brock et al.'s index. *Anim. Behav*. 66, 601–605.

20. R Core Team. 2016 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

21. Landau HG. 1953 On dominance relations and the structure of animal societies: III The condition for a score structure. *Bull. Math. Biophys.* 15, 143–148.

22. McDonald DB, Shizuka D. 2013 Comparative transitive and temporal orderliness in dominance networks. Behav. Ecol. 24, 511–520.

23. Schielzeth H, Stoffel M, Nakagawa S. 2017 rptR: Repeatability estimation for Gaussian and non-Gaussian data. https://CRAN.R-project.org/ package=rptR.

24. de Vries H. 1995 An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim. Behav.* 50, 1375–1389.

25. de Vries H, Stevens JMG, Vervaecke H. 2006 Measuring and testing steepness of dominance hierarchies. *Anim. Behav.* 71, 585–592.

26. Leiva D, de Vries H. 2011 Steepness: testing steepness of dominance hierarchies. R package version 0.2. Available at http://CRAN.R-project.org/package=steepness.

310   27. Chiariti E, Canestrari D, Vera R, Marcos J, Baglione V. 2010 Linear and stable dominance hierarchies in cooperative carrion crows. *Ethol*. 116, 346–356.

28. Sarova R, et al. 2013 Pay respect to the elders: age more than body mass, determines dominance in female beef cattle. *Anim. Behav*. 86, 1315–1323.

29. Lind J, Jakobsson, S. 2001Body building and concurrent mass loss: flight adaptations in

315   tree sparrows. *Proc. Roy. Soc. B*. 268, 1915–1919.

30. Mathot KJ, Dingemanse NJ, Nakagawa S. 2019 The covariance between metabolic rate and behaviour varies across behaviours and thermal types: meta-analytic insights. *Biol. Rev*. Online Early.

31. Portugal et al. 2016 Associations Between Resting, Activity and Daily metabolic rate in

320   Free-living Endotherms: No Universal Rule for Birds and Mammals. *Phy. Bio. Zool.* **89**, 251–261.

32. Conradt L., Krause, J., Couzin, ID, Roper, TJ. 2009 "Leading according to need" in self-organizing groups. *Am. Nat*. 173, 304–312.

33. Lumia AR (1972). The relationships among testosterone, conditioned aggression, and

325   dominance in male pigeons. *Horm. Behav*. 3, 277–286.

34. Burley N. (1981). Mate choice by multiple criteria in a monogamous species. *Am. Nat.* 117, 515–528.

35. Hepp GR. & Hair, J.D. (1984). Dominance in wintering waterfowl (Anatini): Effects of distribution of sexes. *Condor* 86, 251–257.

330   36. Poisbleau et al. (2006). Social dominance correlates and family status of wintering dark-bellied brent geese, *Branta bernicla bernicla*. *Anim. Behav*. 71, 1351–1358.

37. Sankey DWE, Shepard ELC, Biro D, Portugal SJ. 2019 Speed consensus and the "Goldilocks principle" in flocking birds (*Columba livia*). *Anim. Behav.* 157, 105–119.

38. Sankey DWE, Portugal SJ. 2019 When flocking is costly: reduced cluster-flock density over long-duration flight in pigeons. *Sci. of Nat*. 106, 47.

39. Nagy M, Akos Z, Biro D, Vicsek T. 2010 Hierarchical group dynamics in pigeon flocks. *Nature*. 464, 890–893.

40. Nagy M, Vasarhelyi G, Pettit B, Roberts-Mariani I, Vicsek T, Biro D. 2013 Context-dependent hierarchies in pigeons. *P.N.A.S.* 110, 13049–13054.

41. Portugal, SJ., Green, JA, Butler, PJ. 2007 Annual changes in body mass and resting metabolism in captive barnacle geese: the importance of wing moult. *J. Exp. Biol.* 210, 1391–1397.

42. Piersma, T. 2002 Energetic bottlenecks and other design constraints in avian annual cycles *Int. Comp. Biol*. 42, 51–67.

43. Lima SL. 1986 Predation Risk and Unpredictable Feeding Conditions: Determinants of Body Mass in Birds. *Ecology*. 67, 377–385.
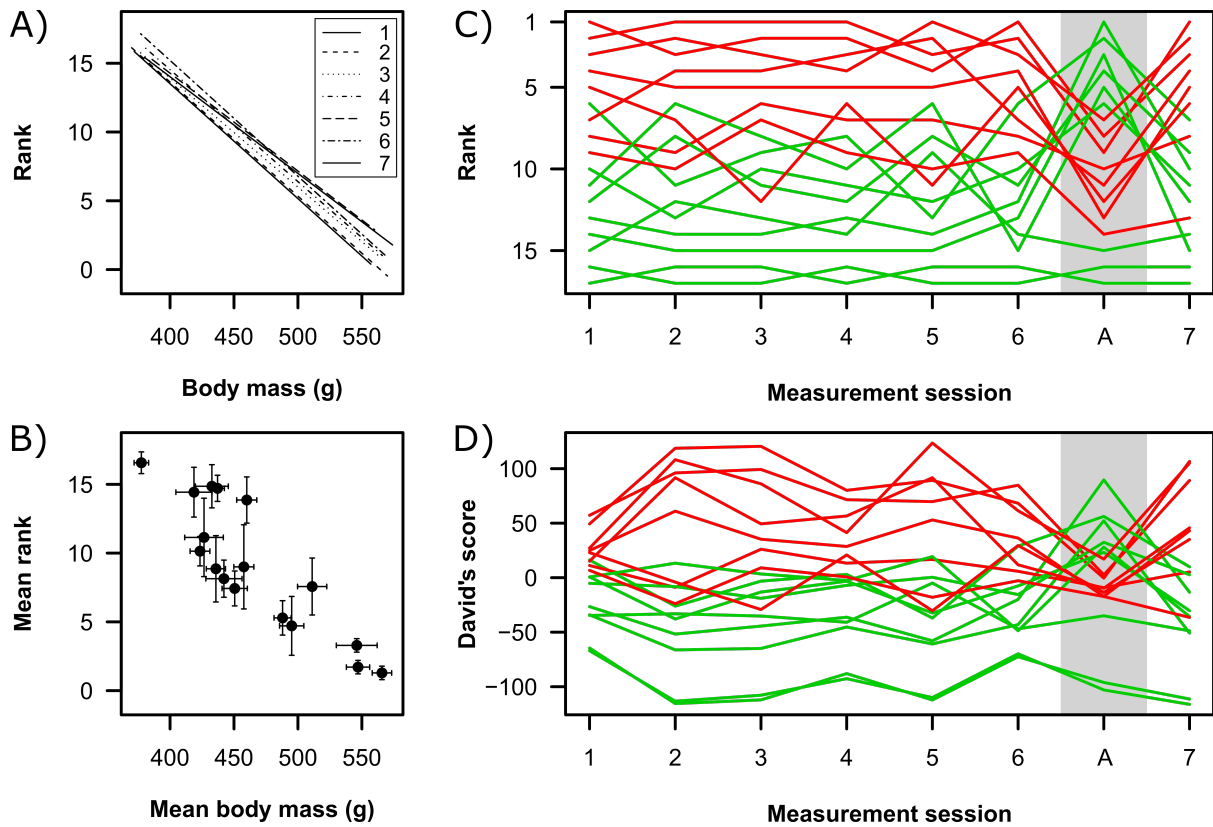
Figure 1. (A) Relationship between body mass and dominance rank in 17 homing pigeons for seven unweighted dominance trials (see supplementary table 1 for full regression details). All regressions were significant. (B) Relationship between mean (± s.e.m.) body mass (g) and mean rank (± s.e.m.) for seven 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 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 (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).

	h	h'	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

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	*