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Short Communication

Overall dynamic body acceleration as an indicator of dominance in Homing Pigeons (*Columba livia*)

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The benefits of dominance are well known and numerous, including first access to resources such as food, mates and nesting sites. Less well studied are the potential costs associated with being dominant. Here, the movement of two flocks of domestic Homing Pigeons *Columba livia* – measured via accelerometry loggers – was recorded over a period of 2 weeks, during which the birds were confined to their lofts. Movement was then used to calculate each individual's daily overall dynamic body acceleration (ODBA, G), which can be used as a proxy for energy expenditure. The dominance hierarchy of the two flocks was determined via group-level antagonistic interactions, and had a significantly linear structure. The most dominant bird within each flock was found to move significantly more than conspecifics – on average, *c.* 39% more than the individual with the next highest degree of movement – indicating a possible cost to possessing the top rank within a hierarchy. Despite the dominance hierarchy being highly linear, this was not the case for ODBA, suggesting that energy expenditure may be more reflective of a despotic hierarchy. These results show the potential for the future use of accelerometry as a tool to study the fusion of energetics and behaviour.

Keywords: biologging, *Columbia livia*, dominance, hierarchy, overall dynamic body acceleration.

Group living is a common way of life for many animals (Lamprecht 1986, Scheel & Packer, 1991, Baird & Dill 1996, Hughes *et al.* 2002). The formation and persistence of these social groups is driven by the interests of the individuals that comprise it, not by the interests of the group as a whole (Alexander 1974). For group living to persist, therefore, it must be less costly to an individual's fitness than living alone (Alexander 1974). Such fitness benefits can be derived from reduced individual predation risk (Cresswell 1994), reduced time spent vigilant (Bertram 1980), improved foraging efficiency (Baird & Dill 1996) and energetic savings (Weimerskirch *et al.* 2001, Portugal *et al.* 2014). Living in a group, however, always comes with costs, which must be either tolerated or overcome (Alexander 1974). These costs include increased disease transmission (Hughes *et al.* 2002), increased risk of group detection and attack by predators (Alexander 1974), and increased competition for resources resulting in increased aggression (Clutton-Brock *et al.* 1979).

One way to reduce daily aggression between members of a group is the formation of dominance hierarchies (Chase 1980). Dominance hierarchies reduce the occurrence and severity of aggressive interactions between individuals (Chase 1980). Hierarchies can be either linear, when dominance is established and then follow a transitive order (e.g. A > B > C and A > C), or non-linear, when the rank order is irregular (e.g. A > B > C and C > A; Carlini *et al.* 2006). These hierarchies decide the order of access to limited resources (Chase 1980, Chase *et al.* 2002, Carlini *et al.* 2006), with the most dominant taking the best resources. Although being the most dominant individual in a group comes with clear benefits, there can also be costs associated with dominance. One such cost could be increased energy expenditure (Mathot *et al.* 2019); performing regular antagonistic behaviours to maintain dominance is likely to cost energy.

An individual's basal metabolic rate has long been assumed to influence behaviour, and a convincing argument is that a lower basal metabolic rate allows higher metabolic scope to perform energy-demanding activities, which may include aggressive behaviours that permit dominance (Mathot *et al.* 2019). Meta-analyses of multiple studies have shown that there are significant correlations between daily metabolic rate (not basal metabolic rate) and traits assumed to be associated with net energy gain, such as boldness and dominance; animals with higher daily metabolic rates are more dominant, bolder and forage at more efficient rates (Mathot *et al.* 2019). Here we studied two flocks of Homing Pigeons *Columba livia* to investigate the relationship between position in a dominance hierarchy and daily overall dynamic body acceleration (ODBA, G), a proxy for energy expenditure (Gleiss *et al.* 2011). We tested the hypothesis that dominant

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individuals within the flock will be the most active – so most likely expending the greatest energy – to assert their dominance through antagonistic behaviours.

METHODS

Subjects and housing

A group of 18 Homing Pigeons aged 6–12 months were kept in two flocks of nine pigeons each at Royal Holloway University of London (Egham, UK). Flock 1 was composed of four males and five females, and flock 2 was composed of five males and four females. All pigeons had been housed together since approximately 1 month of age in two flocks of varying composition. Sex was determined by genetic testing of feather samples. Each flock was housed in a separate loft (2.1 × 1.8 m). The pigeons were provided with *ad libitum* access to food (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, UK), grit and water. Further details on pigeon husbandry can be found in Portugal *et al.* (2017a, 2017b).

Dominance hierarchies

Determination of dominance hierarchies followed the precise protocols of Portugal *et al.* (2017a, 2017b) (see Supplementary material Appendix S1 for full details). The total number of interactions between individuals was recorded in a matrix, as initiators of aggressive acts (winners) or receivers of aggressive acts (losers) from each interaction. The matrix was then used to calculate a rank for each bird using David's Score (Gammell *et al.* 2003), and the linearity of the hierarchy using Landau's linearity index (*h'*) (Landau 1953). Landau's index of linearity (*h'*) uses the interaction matrix to calculate one value that describes the linearity of the group. This value ranges from 0 to 1, where 0 indicates that each individual dominates an equal number of other individuals, and 1 indicates complete linearity (Landau 1953).

Overall dynamic body acceleration

Measurement of ODBA occurred during February and March 2018. Each pigeon in both flocks was fitted with a harness which held two accelerometers (23 × 32.5 × 7.6 mm, 11 g, 120 Hz; Axivity Ltd, Newcastle upon Tyne, UK) on the centre of their backs, for a period of 2 weeks. Further information regarding logger attachment can be found in Taylor *et al.* (2017, 2019). One accelerometer was programmed to record for the first week, and the other was to record for the second week to ensure full data capture while minimizing disturbance. During this time, all pigeons remained within their home lofts. ODBA (G) for each bird was calculated from the raw accelerometry data using the formula presented in Gleiss *et al.* (2011). To calculate ODBA (Equation 1), the raw accelerometer data were first smoothed for each of the three channels (surge, sway, heave) to derive static acceleration, which converts the data to dorsal body acceleration (DBA). This smoothing is achieved through using a running mean over 2 s, and then subtracting the static acceleration component from the raw data. The DBA values were then converted to positive values, before being summed to calculate ODBA (Gleiss *et al.* 2011).

$$\mathrm{ODBA} = |A_x| + |A_y| + |A_Z| \tag{1}$$

where A_x, A_y and A_z are the derived dynamic accelerations at any point in time corresponding to the three orthogonal axes of the accelerometer. ODBA was first summed per hour for each individual bird, before a 24-h value was calculated.

Data analysis was carried out in RStudio (R Development Core Team 2008, RStudio Team 2016). We ran a mixed effects analysis of variance (ANOVA) on each flock separately using the R package 'car' with pigeon ID as a fixed effect, and because of the non-independence of dominance interactions, day of the study was included as a random intercept. The sum of all ODBA values in a day was the dependent variable. Post-hoc tests were then used to investigate the variation between individual's daily ODBA in SPSS (IBM Corp., Armonk, NY, USA). The assumptions of parametric tests used were checked and met before tests were run. The relationship between dominance and ODBA was explored using a linear mixed effects (LME) model from the R package 'nlme', with dominance score as the dependent variable, ODBA as a fixed effect and flock ID and day as random effects. The relationship between total number of interactions (both wins and losses) and total ODBA (i.e. 24-h ODBA values summed for the duration of the experimental period, per individual) was investigated by regression.

RESULTS

Dominance

The hierarchies of both flocks were highly linear (flock 1, $h' = 0.68$, $P = 0.006$; flock 2, $h' = 0.84$, $P < 0.001$). David's score was found to correlate marginally significantly with sex (Spearman's rank; $r_s = 0.48$, $P = 0.04$), with males being more aggressive.

Overall dynamic body acceleration

Mean ODBA per hour (G) showed a circadian rhythmic pattern, with peaks centred around midday, and troughs

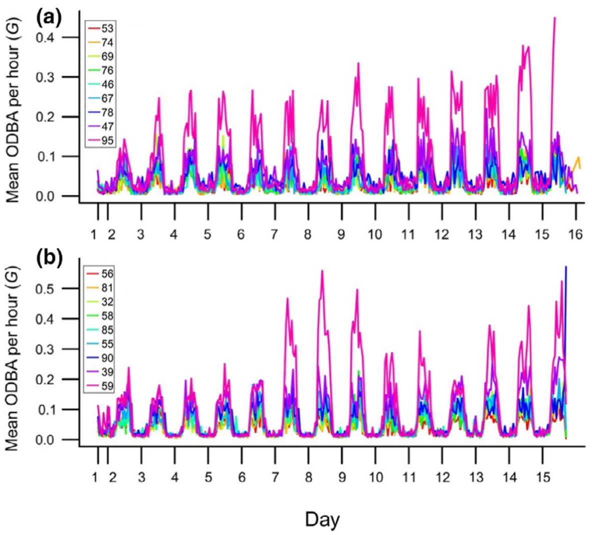

Figure 1. Mean overall dynamic body acceleration (ODBA) per hour (gravitational constant, *G*) of two pigeons flocks (flock 1 (a) and flock 2 (b)), each containing nine Homing Pigeons, over a 2-week recording period. The *x*-axis tick marks indicate 05:00 h each day, respectively, except for day 1, where the loggers were added at 17:00 h. The pink line is the number 1 ranked bird in the dominance hierarchy.

throughout the night in both flocks (Fig. 1). A decrease in sum of ODBA per day (i.e. 24-h ODBA total values) was seen with a decrease in rank (here a decrease in rank is from 1 to 10 as 1 is the highest ranked individual and 10 the lowest; Fig. 2). There was a substantial decrease between the top-ranked bird – with respect to dominance and total ODBA – and the next most active bird. The percentage difference between the top-ranked individual and the next most active was at least 39% (Fig. 2). A one-way ANOVA showed significant variation in ODBA between individuals in both flocks (flock 1, $\chi^2 = 329.13$, df = 8, $P < 0.001$; flock 2, $\chi^2 = 196.82$, df = 8, $P < 0.001$). Including day as a random intercept improved the fit of the ANOVA (flock 1: $\Delta\text{AIC} = -50.06$, flock 2: $\Delta\text{AIC} = -43.04$). A Tukey honest significant difference post-hoc test showed that the most active bird in each flock was significantly more active than all other birds, indicating that they had no similarity to any other bird ($n = 1$, $P = 1$; Fig. 2), whereas all other members of the flock were found to be not significantly different from at least three other birds. There was a significant relationship between dominance score (David's score) and ODBA (LME: df = 227, $t = 8.893$, $P < 0.001$). This relationship between dominance and ODBA persisted when the most dominant individual in each group was removed (LME: df = 197, $t = 2.804$, $P = 0.006$).

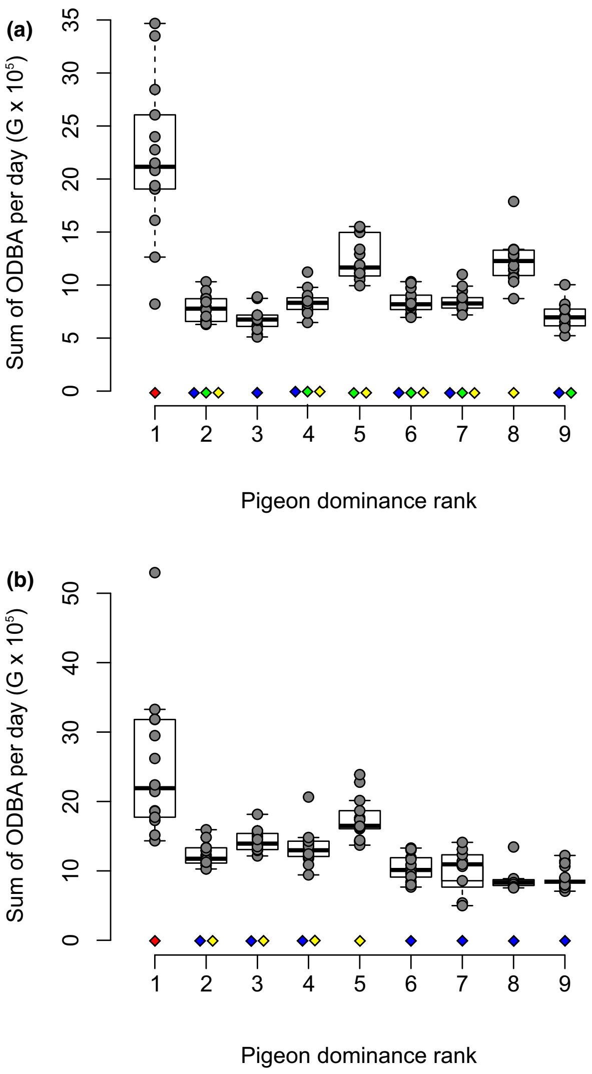

Figure 2. The sum of overall dynamic body acceleration (ODBA) (gravitational constant, *G*) for each complete day of the recording period for all pigeons in (a) flock 1 and (b) flock 2. Filled diamonds indicate the homogeneous subsets calculated with a Tukey honest significant difference post-hoc test. (a) Blue: subset 1, $n = 6$, $P = 0.97$; green: subset 2, $n = 6$, $P = 0.069$; yellow: subset 3, $n = 6$, $P = 0.082$; red: subset 4, $n = 1$, $P = 1$. (b) Blue: subset 1, $n = 7$, $P = 0.197$; yellow: subset 2, $n = 4$, $P = 0.302$; red: subset 3, $n = 1$, $P = 1$.

The most dominant member of each flock had the highest total number of interactions and the highest total ODBA, compared with all other members of their respective flocks. The relationship between total number of interactions (both wins and losses) and total ODBA showed a positive relationship for both flocks combined; the more overall interactions an individual took part in, the higher was their total ODBA value (LME: $n = 18$, $r^2 = 0.25$, $P = 0.03$, $F = 5.461$).

DISCUSSION

Using biologging technology, this study has demonstrated the potential link between dominance and the degree to which a bird moves. Within the last decade, ODBA has been put forward as a proxy for energy expenditure (Gleiss *et al.* 2011, Fahlman *et al.* 2013). It had not, however, been used for fine-scale continuous recording of movement over an extended period of time.

By examining the movement of the Homing Pigeons as a proxy for energy expenditure, it was found that the most dominant pigeon in each flock showed significantly higher levels of movement than its conspecifics. All other individuals within the groups moved at similar levels, which were not significantly different from one another. This would suggest that there is an energetic cost incurred in being the dominant individual, which subordinates do not have to pay. Why the dominants are more active and what behaviour they are performing during this time though is unclear. One potential explanation for the increase in movement is that dominants may be initiating most agonistic interactions (e.g. Portugal *et al.* 2020). For a dominant to retain its rank, and so the benefits that come with it, the individual must continue to win all antagonistic encounters against other birds in the flock (Chase 1980, Chase *et al.* 2002). A pre-emptive strategy, whereby the dominant bird initiates such encounters, may result in fewer injuries to the dominant individual, and keep overall aggression levels lower within a group through the prevention of usurpation attempts. An alternative explanation for why the dominant individuals are so aggressive and active could be because these individuals have *higher* basal metabolic rates, and higher energetic requirements may oblige such birds to be aggressive to ensure adequate access to food. Such an idea is akin to the 'lead according to need', a theory that has previously been linked to motivation and leadership in group behaviour (Conradt & Roper 2003, Portugal *et al.* 2020). Determinants of intra-specific variation in basal metabolic rate can include body composition and organ mass variation, with a genetic component identified in some species studied (Konarzewski & Ksiazek 2013).

By observing antagonistic interactions, other members of the group can gain information about which individuals they are, and are not, capable of dominating, thus reducing the number of repeated interactions needed to maintain their place in the hierarchy. This reduced number of interactions needed to maintain the hierarchy, particularly in a static group, could explain why the rest of the flock showed highly homogeneous levels of movement at a lower level compared with the dominant individual. While the social hierarchy is highly linear, the distribution of energy expenditure within both flocks is reminiscent of a despotic society (Chase *et al.* 2002), with one individual spending energy policing the flock, while the subordinates move considerably less, and at a more similar level. The true cost of dominance could, therefore, be that to retain dominance and gain its benefits, dominants need to maintain high activity levels for the maintenance of the hierarchy and to keep overall group aggression low. For example, removing dominant individuals from deer leks led to an increase in fighting between males, probably due to the disruption of the social hierarchy (Apollonio *et al.* 1989). Similarly, hierarchy stability has been shown to decrease in response to abiotic factors, such as rapid changes in environmental conditions, when the dominant individual reduces aggression levels (e.g. Sneddon *et al.* 2005).

During the study period, all birds were kept inside and confined to their social hierarchy; behaviours were limited to feeding, sleeping, preening and social interactions. Previously it has been established that ground-based dominance hierarchies do not match that of leadership during flights (Nagy *et al.* 2010, 2013). An interesting further avenue of research would therefore be to determine how ODBA compares for ground-based dominant birds and flight leaders, as leaders during flights typically have to make fewer adjustments to their trajectories than followers (Nagy *et al.* 2010), particularly as overall, flying in a flock has been shown to come at a cost in pigeons (Usherwood *et al.* 2011). Similarly, how ODBA, flight duration and flock composition interact would provide useful insight into the energetics and compromises involved in group travel (Sankey & Portugal 2019, Sankey *et al.* 2019).

The results of this study show that the long-term use of accelerometers is a viable method of determining individual differences in movement, and thus energy expenditure, within groups of animals. Dominants within flocks of pigeons show higher levels of movement, suggesting they either have a larger metabolic budget (Portugal *et al.* 2016, Mathot *et al.* 2019) to allow such increased movement, or take on this extra movement as a cost worth paying for continued dominance.

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AUTHOR CONTRIBUTIONS

Rhianna Ricketts: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead);

Methodology (equal); Writing-original draft (equal); Writing-review & editing (equal). **Daniel Sankey:** Conceptualization (equal); Formal analysis (equal); Methodology (equal); Software (supporting); Visualization (supporting); Writing-review & editing (supporting). **Bryce Tidswell :** Investigation (equal); Methodology (supporting); Writing-review & editing (supporting). **Josh Brown:** Investigation (equal); Methodology (supporting); Writing-review & editing (supporting). **Joseph Deegan:** Investigation (equal); Methodology (supporting); Writing-review & editing (supporting). **Steven Portugal:** Conceptualization (equal); Funding acquisition (lead); Investigation (equal); 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

Data available from the Dryad Digital Repository: https://datadryad.org/stash/share/H92RZ_N8RoZnkcxbLm-Z7PzTxStEjlPvQVNuf9seAGg.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. A detailed method describing the measurement of dominance hierarchies.