2   **Overall dynamic body acceleration as an indicator of**

3   **dominance in Homing Pigeons *Columba livia***

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20   The benefits of dominance are well known and numerous, including first access to resources

21   such as food, mates and nesting sites. Less well studied are the potential costs associated with

22   being dominant. Here, the movement of two flocks of domestic homing pigeons *Columba livia*

23   – measured via accelerometry loggers – was recorded over a period of two weeks, during which

24   the birds were confined to their lofts. Movement was then used to calculate each individual's

25   daily overall dynamic body acceleration (ODBA, *G*), which can be used as a proxy for energy

26   expenditure. The dominance hierarchy of the two flocks was determined via group-level

27   antagonistic interactions, and had a significantly linear structure. The most dominant bird

28   within each flock was found to move significantly more than conspecifics – on average, *c*.39%

29   more than the individual with the next highest degree of movement – indicating a possible cost

30   to possessing the top rank within a hierarchy. Despite the dominance hierarchy being highly

31   linear, this was not the case for ODBA, suggesting that energy expenditure may be more

32   reflective of a despotic hierarchy. These results show the potential for the future use of

33   accelerometery as a tool to study the fusion of energetics and behaviour.

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36   Group living is a common way of life for many animals (Lamprecht 1986, Sheel & Packer

37   1991, Baird & Dill 1996, Hughes *et al*. 2002). The formation and persistence of these social

38   groups is driven by the interests of the individuals who comprise it, not by the interests of the

39   group as a whole (Alexander 1974). For group living to persist, therefore, it must be less costly

40   to an individual's fitness than living alone (Alexander 1974). Such fitness benefits can be

41   derived from reduced individual predation risk (Cresswell 1994), reduced time spent vigilant

42   (Bertram 1980), improved foraging efficiency (Baird & Dill 1996) and energetic savings

43   (Weimerskirch *et al*. 2001, Portugal *et al*. 2014). Living in a group, however, always comes

44   with costs which must either be tolerated or overcome (Alexander 1974). These costs include

45   increased disease transmission (Hughes *et al*. 2002), increased risk of group detection and

46   attack by predators (Alexander 1974), and increased competition for resources resulting in

47   increased aggression (Clutton-Brock *et al*. 1979).

48   One way to reduce daily aggression between members of a group is the formation of dominance

49   hierarchies (Chase 1980). Dominance hierarchies reduce the occurrence and severity of

50   aggressive interactions between individuals (Chase 1980). Hierarchies can either be linear

51   when dominance is established and then follow a transitive order (e.g., A>B>C and A>C), or

52   non-linear, when the rank order is irregular (e.g., A>B>C and C>A) (Carlini *et al*. 2006). These

53   hierarchies decide the order of access to limited resources (Chase 1980, Chase *et al*. 2002,

54   Carlini *et al*. 2006), with the most dominant taking the best resources. While being the most

55   dominant individual in a group comes with clear benefits, there can also be costs associated

56   with dominance. One such cost could be increased energy expenditure (Mathot *et al.* 2019);

57   performing regular antagonistic behaviours to maintain dominance is likely to cost energy.

58   An individual's basal metabolic rate (BMR) has long been assumed to influence behaviour,

59   and a convincing argument is that a lower BMR allows higher metabolic scope to perform

60   energy demanding activities, which may include aggressive behaviours that permit dominance

61   (Mathot *et al.* 2019). Meta-analyses of multiple studies have shown that there are significant

62   correlations between daily metabolic rate (not BMR) and traits assumed to be associated with

63   net energy gain, such as boldness and dominance; animals with higher daily metabolic rates

64   (DMR) are more dominant, bolder, and also forage at more efficient rates (Mathot *et al.* 2019).

65   Here we studied two flocks of Homing Pigeons *Columba livia* to investigate the relationship

66   between position in a dominance hierarchy and daily overall dynamic body acceleration

67   (ODBA, *G*), a proxy for energy expenditure (Gleiss *et al.* 2011). We tested the hypothesis that

68   dominant individuals within the flock will be the most active – thus most likely expending the

69   greatest energy – to assert their dominance through antagonistic behaviours.

70   **METHODS**

71   **Subjects and housing**

72   A group of 18 Homing Pigeons aged 6 – 12 months old were kept in two flocks of nine pigeons

73   each at Royal Holloway University of London (Egham UK). Flock 1 was composed of four

74   males and five females, and flock 2 was composed of five males and four females. All pigeons

75   had been housed together since approximately one month old in two flocks of varying

76   composition. Sex was determined via genetic testing of feather samples. Each flock was housed

77   in a separate loft (7ft x 6ft). The pigeons were provided with *ad libitum* access to food

78   (Johnstone & Jeff Four Season Pigeon Corn, Gilberdyke, UK), grit and water. Further details

79   on pigeon husbandry can be found in Portugal *et al.* (2017*a*, 2017*b*).

80   **Dominance hierarchies**

81   Determination of dominance hierarchies followed the precise protocols of Portugal *et al.*

82   (2017*a*, 2017*b*) (see supplemental material for full details). The total number of interactions

83   between individuals was recorded in a matrix, as initiators of aggressive acts (winners) or

84   receivers of aggressive acts (losers) from each interaction. The matrix was then used to

85   calculate a rank for each bird using David's Score (Gammel *et al*. 2003), and the linearity of

86   the hierarchy using Landau's linearity index (*h'*) (Landau 1953). Landau's index of linearity

87   (*h'*) uses the interaction matrix to calculate one value which describes the linearity of the group.

88   This value ranges from 0 to 1, where 0 indicates that each that each individual dominates an

89   equal number of other individuals, and 1 indicates complete linearity (Landau 1953).

90   *(c) Overall Dynamic Body Acceleration (ODBA)*

91   Measurement of ODBA occurred during February and March 2018. Each pigeon in both flocks

92   was fitted with a harness which held two accelerometers (23 x 32.5 x 7.6 mm, 11g, 120 Hz,

93   Axivity Ltd, Newcastle upon Tyne, UK) on the centre of their backs, for a period of two-weeks.

94   For further information regarding logger attachment, see Taylor *et al*. (2017) and Taylor *et al*.

95   (2019). One accelerometer was programmed to record for the first week, and the other was to

96   record for the second week to ensure full data capture while minimising disturbance. During

97   this time all pigeons remained within their home lofts. ODBA (*G*) for each bird was calculated

98   from the raw accelerometry data using the formula presented in Gleiss *et al.* 2011). To calculate

99   ODBA (equation1), the raw accelerometer data were first smoothed for each of the three

100   channels (surge, sway, heave) to derive static acceleration, which converts the data to dorsal

101   body acceleration (DBA). This smoothing is achieved through using a running mean over 2 s,

102   and then subtracting the static acceleration component from the raw data. The DBA values

103   were then converted to positive values, before being summed to calculate ODBA (Gleiss et al.

104   2011).

105 $$ODBA = |A_x| + |A_y| + |A_z| \qquad\qquad \text{(equation 1)}$$

106   Where A_x, A_y and A_z are the derived dynamic accelerations at any point in time corresponding

107   to the three orthogonal axes of the accelerometer. ODBA was firstly summed per hour for each

108   individual bird, before a 24-hour value was calculated.

109 Data analysis was carried out in RStudio (Team RDC 2008, Team R 2006). We ran a mixed

110 effects ANOVA on each flock separately using R package "car" with pigeon ID as fixed effect,

111 and due to the non-independence of dominance interactions, day of the study was included as

112 random intercepts. Sum of all ODBA in a day was the dependent variable. Post-hoc tests were

113 then used to investigate the variation between individual's daily ODBA in SPSS (IBM SPSS

114 Statistics, Armonk, NY: IBM Corp.). The assumptions of parametric tests used were checked

115 and met before tests were run. The relationship between dominance and ODBA was explored

116 using linear mixed effects model from R package "nlme", with dominance score as the

117 dependent variable; ODBA as a fixed effect; random effects as flock ID and day. The

118 relationship between total number of interactions (both wins and losses) and total ODBA (i.e.,

119 24-hour ODBA values summed for the duration of the experimental period, per individual) was

120 investigated via regression.

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122 **RESULTS**

123 *(a) Dominance*

124 The hierarchies of both flocks were highly linear (flock 1, h' = 0.68, P = 0.006; flock 2, h' =

125 0.84, P = <0.001). David's score was found to correlate marginally significantly with sex

126 (Spearman's rank; r_s = 0.48, P = 0.04), with males being more aggressive.

127 *(b) Overall Dynamic Body Acceleration*

128 Mean ODBA per hour (*G*) showed a circadian rhythmic pattern, with peaks centred around

129 midday, and troughs throughout the night in both flocks (Fig. 1). An decrease in sum of ODBA

130 per day (i.e., 24-hour ODBA total values) was seen with a decrease in rank (here a decrease in

131 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- individual

and the next most active was at least 39% (Fig. 2). A One-Way ANOVA showed there was

significant variation in ODBA between individuals in both flocks (flock 1, $\chi2 = 329.13$, $df = 8$,

$P < 0.001$; flock 2, $\chi2 = 196.82$, $df = 8$, $P < 0.001$). Including day as a random intercept

improved the fit of the ANOVA (Flock 1: $\Delta AIC = -50.06$, Flock 2: $\Delta AIC = -43.04$). A Tukey

HSD post-hoc test showed that the most active bird in each flock was significantly more active

than all other birds, indicating they had no similarity to any other bird ($n = 1$, $P = 1$) (Fig. 2),

while all other members of the flock were found to be not significantly different from at least

three other birds. There is 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 persists when the most dominant individual in each group is removed (LME: $df = 197$,

$t = 2.804$, $P = 0.006$).

The most dominant member of each flock had the highest total number of interactions and the

highest total ODBA, compared to 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 their total ODBA value was (LM, $n = 18$, $r^2 = 0.25$, $P = 0.03$, $F = 5.461$).

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, Wilson & Shepard 2011, Fahlman *et al.*

155   2013). It had not yet, however, been used for fine-scale continuous recording of movement

156   over an extended period of time.

157   By examining the movement of the homing pigeons as a proxy for energy expenditure, it was

158   found that the most dominant pigeon in each flock showed significantly higher levels of

159   movement than its conspecifics. All other individuals within the groups all moved at similar

160   levels which were not significantly different from one another. This would suggest that there

161   is an energetic cost incurred in being the dominant which subordinates do not have to pay. Why

162   the dominants are more active and what behaviour they are performing during this time though

163   is unclear. One potential explanation for the increase in movement is that dominants may be

164   initiating the majority of agonistic interactions (e.g., Portugal *et al*. 2020). For a dominant to

165   retain its rank, and so the benefits which come with it, the individual must continue to win all

166   antagonistic encounters against other birds in the flock (Chase 1980, Chase *et al*. 2002). A pre-

167   emptive strategy, whereby the dominant bird initiates such encounters, may result in less

168   injuries to the dominant individual, and keep overall aggression levels lower within a group

169   through the prevention of usurpation attempts. An alternative explanation for why the dominant

170   individuals are so aggressive and active could be because these individuals have *higher* basal

171   metabolic rates; higher energetic requirements may force such birds to be aggressive to ensure

172   adequate access to food. Such an idea is akin to the 'lead according to need', a theory which

173   has previously linked to motivation and leadership in group behaviour (Conradt & Roper 2003,

174   Portugal *et al*. 2020). Determinants of intra-specific variation in BMR can include body

175   composition and organ mass variation, with a genetic component identified in some species

176   studied (Konarzewski & Ksiazek 2013).

177   By observing antagonistic interactions, other members of the group can gain information about

178   which individuals they are, and are not, capable of dominating, thus reducing the number of

179   repeated interactions needed to maintain their place in the hierarchy. This reduced number of

180   interactions needed to maintain the hierarchy, particularly in a static group, could explain why

181   the rest of the flock showed highly homogenous levels of movement at a lower level compared

182   to the dominant. While the social hierarchy is highly linear, the distribution of energy

183   expenditure within both flocks is reminiscent of a despotic society (Chase *et al*. 2002), with

184   one individual spending energy policing the flock, while the subordinates move considerably

185   less, and at a more similar level. The true cost of dominance could, therefore, be that to retain

186   dominance and gain its benefits, dominants are need to maintain high activity levels for the

187   maintenance of the hierarchy and to keep overall group aggression low. For example, removing

188   dominant individuals from deer leks led to an increase in fighting between males, likely due to

189   the disruption of the social hierarchy (Apollonio *et a*l. 1989). Similarly, hierarchy stability has

190   been shown to decrease in response to abiotic factors, such as rapid changes in environmental

191   conditions, when the dominant individual reduces aggression levels (e.g., Sneddon *et al*. 2005).

192   During the study period, all birds were kept inside and confined to their social hierarchy;

193   behaviours were limited to feeding, sleeping, preening and social interactions. Previously it has

194   been established that ground-based dominance hierarchies do not match that of leadership

195   during flights (Nagy *et al*. 2010, Nagy *et al*. 2013). An interesting further avenue of research

196   would therefore be to determine how ODBA compares for ground-based dominant birds and

197   flight leaders, as leaders during flights typically have to make fewer adjustments to their

198   trajectories than followers (Nagy *et al*. 2010), particularly as overall, flying in a flock has been

199   shown to come at a cost in pigeons (Usherwood *et al*. 2011). Similarly, how ODBA, flight

200   duration and flock composition interact would provide useful insight into the energetics and

201   compromises involved in group travel (Sankey & Portugal 2019, Sankey *et al*. 2019).

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

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213 **ETHICS STATEMENT**
214 All experiment protocols were approved by the RHUL local Ethics and Welfare Committee.

215 **DATA ACCESSIBILITY STATEMENT**
216 Data available from the Dryad Digital Repository: http://dx.doi.org/*** [*].

217 **AUTHOR CONTRIBUTIONS**

218 Conceptualisation and methodology, R.L.R, D.W.S. and S.J.P. resources, S.J.P.; data collection, R.L.R, B.P.T.,
219 J.B. and J.F.D.; analysis, R.L.R and D.W.S.; writing – original draft, R.L.R. and S.J.P; writing, reviewing and
220 editing, R.L.R,. D.W.S., B.P.T., J.B., J.F.D. and S.J.P.

221 **COMPETING INTERESTS**
222 We declare we have no competing interests.

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225 **REFERENCES**

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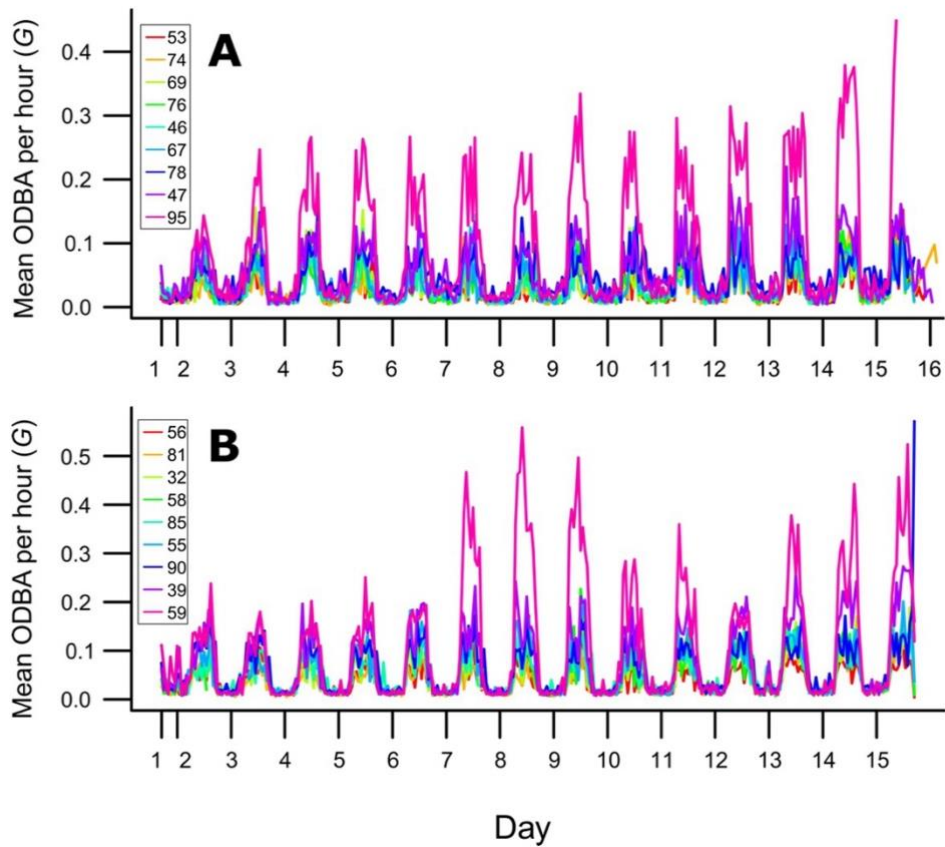
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302 **Figure 1.** Mean ODBA per hour (gravitational constant, *G*) of two pigeons flocks (A and B),

303 each containing nine homing pigeons, over a two-week recording period. The x-axis tick marks

304 indicate 05 00h each day, respectively, except for day 1, where the loggers were added at 17

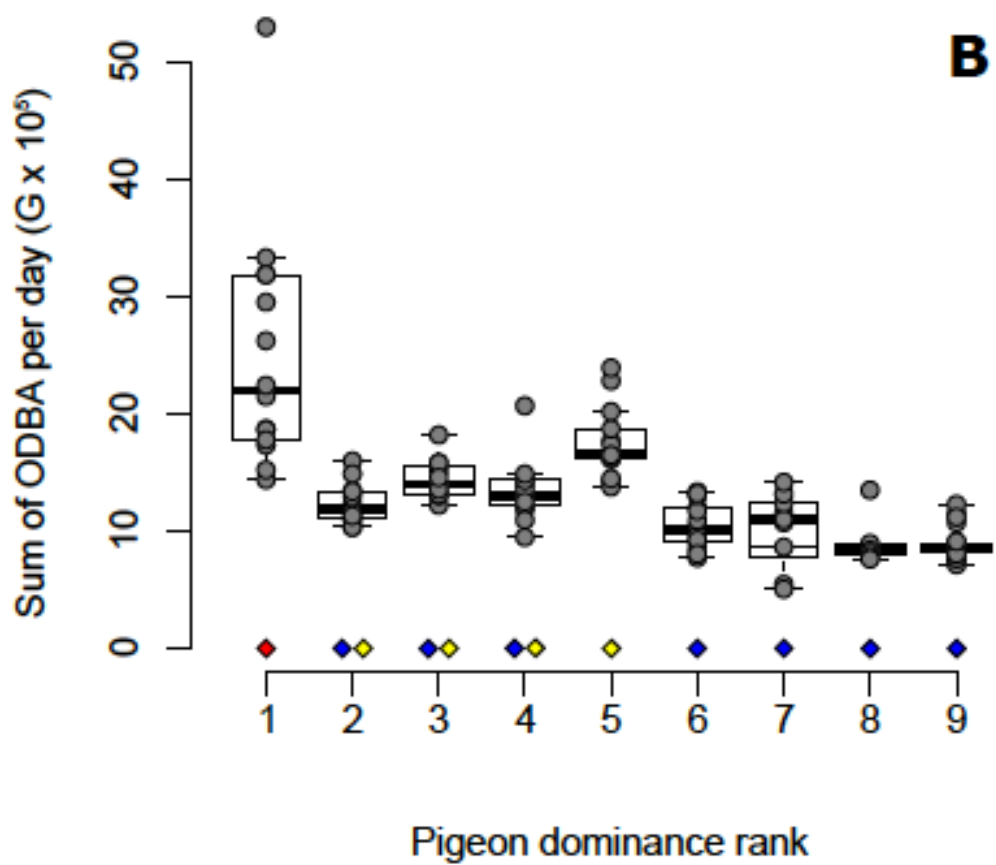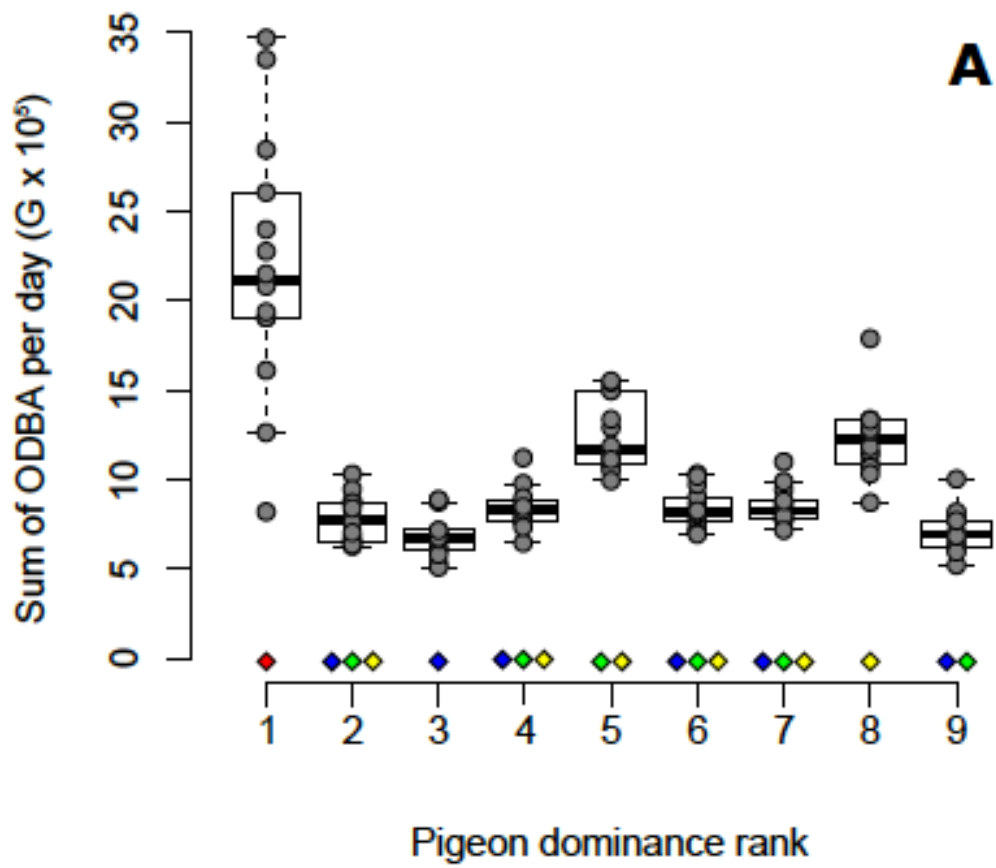305 00h. The pink line is the number 1 ranked bird in the dominance hierarchy.

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317 **Figure 2.** The sum of ODBA (gravitational constant, G) for each complete day of the recording

318 period for all pigeons in **A**) flock 1 and **B**) flock 2. Filled diamonds indicate the homogenous

319 subsets calculated with a Tukey HSD post-hoc test. a) Blue; subset 1, n = 6, P = 0.97, green;

320 subset 2, n = 6, P = 0.069, yellow; subset 3, n = 6, P = 0.082, red; subset 4, n = 1, p = 1. b)

321 Blue; subset 1, n = 7, P = 0.197, yellow; subset 2, n = 4, P = 0.302, red; subset 3, n = 1, P = 1.