Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flocking

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16 **Abstract**

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18 Flapping flight is the most energetically demanding form of sustained forwards locomotion

19 that vertebrates perform. Flock dynamics therefore have significant implications for energy

20 expenditure. Despite this, no studies have quantified the biomechanical consequences of flying

21 in a cluster flock relative to flying solo. Here, we compared the flight characteristics of homing

22 pigeons (*Columba livia*) flying solo and in pairs, using high-precision 5 Hz GPS and 200 Hz

23 tri-axial accelerometer biologgers. Paired flight increased route accuracy by ~7%, but, was

24 accompanied by an increase in wingbeat frequency of ~18%. As expected, paired individuals

25 benefitted from improved homing route accuracy, which reduced flight distance by ~7% and

26 time by ~9%. However, realising these navigational gains involved substantial changes in flight

27 kinematics and energetics. Both individuals in a pair increased their wingbeat frequency by

28 *c.*18%, by decreasing the duration of their upstroke. This sharp increase in wingbeat frequency

29 caused just a 3% increase in airspeed, but reduced the oscillatory displacement of the body by

30 ~22%, which we hypothesise relates to an increased requirement for visual stability and

31 manoeuvrability when flocking. Overall, the shorter flight distances and increased wingbeat

32 frequency in a pair resulted in a net increase in the aerodynamic cost of returning home, which

33 we estimate was ~14%. Our results demonstrate that flocking costs have been underestimated

34 by an order of magnitude and force reinterpretation of their mechanistic origin. We show that,

35 for pigeons, two heads are better than one, but keeping a steady head necessitates energetically

36 costly kinematics.

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38 **Key words**: accelerometer, biologging, energy, flocking, pigeon, stabilisation, wingbeat

39 frequency

Introduction

Across the animal kingdom many species travel in groups, from pairs to flocks, shoals, herds and swarms, some containing millions of individuals [1,2]. Indeed, the collective motion of animals produces some of the most spectacular displays of synchronisation and coordination in the world [3]. Commonly cited benefits of collective travel include an improved ability to detect and avoid predators [1,4], enhanced orientational efficiency through the pooling of navigational knowledge [5–8], and energetic efficiencies derived from fluid dynamic interactions [9–13]. Flocking in birds, in particular, has received considerable attention due to the complex aerodynamic interactions that take place between group members [11–14].

Avian flock formations can be categorised as either line formations or cluster formations [15,16]. Line formations, which include the distinctive 'V' of many long-distance migrants, are utilised by medium to large-sized birds, such as northern bald ibis (*Geronticus eremita*) and Canada geese (*Branta canadensis*), whereas cluster formations are typically observed in smaller birds, such as homing pigeons (*Columba livia*) and common starlings (*Sturnus vulgaris*), which fly in irregular three-dimensional flocks [11–16]. Birds flying in close cluster flocks in particular are able to move with near perfect synchrony, whilst making rapid directional changes in three dimensions. While birds travelling in V-formation can save energy by flying in aerodynamically optimal positioning within the V [11–13], those species flying in cluster flocks have been shown to incur an additional energetic cost in denser formations [14]. In homing pigeons, for example, a tenfold increase in the spatial density of a flock has been observed to be associated with a modest 0.1 Hz increase in wingbeat frequency, and was presumed to be accompanied by an energetic cost over the seven flights that were observed [14]. Flapping flight is the most energetically demanding form of sustained forwards

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65   locomotion that vertebrates perform [17,18], and flock dynamics may therefore have

66   significant implications for individual energy expenditure and lifetime fitness. However, no

67   studies have yet compared the biomechanical consequences of flying in a pair to flying solo,

68   so the energetic impact of this form of flocking is unknown.

69

70   To fill this fundamental gap, we recorded the body accelerations associated with every

71   wingbeat of 20 free-flying homing pigeons flying solo and in pairs as they homed from a site

72   7 km east of their loft (Fig. 1A). The birds were equipped with 5 Hz GPS trackers and 200 Hz

73   tri-axial accelerometer biologgers which allowed us to reconstruct their trajectories and

74   wingbeat patterns during each homeward flight (see Methods; Fig. 1B-F) [19,20]. The

75   experiment consisted of four phases. In Phase 1, each subject first completed 21 successive

76   solo flights (Fig. 1F), the last six of which provided the solo baseline (solo 1). During these six

77   solo flights, the median wingbeat frequency and amplitude (dorsal body displacement) for all

78   birds were 5.48 ± 0.19 Hz (grand mean of the median value of each flight $\pm$ s.d. of the individual

79   means) and 20.68 ± 1.17 mm, respectively (after accounting for the effects of airspeed, date of

80   release and weather variables including wind support, crosswind, temperature, humidity and

81   air density; Fig. 2A). These wingbeat frequencies are consistent with those measured

82   previously for solo pigeon flights [20,21]. In Phase 2, following the solo releases, birds were

83   released six times from the same – now familiar – site, but in similar-sized pairs. Pairs were

84   assigned based on similarity in body mass and structural size as measured by tarsus length [22].

85   Body size and mass are strong predictors of preferred flight speeds in birds, both at the intra-

86   and inter-specific levels, with optimal flight speeds usually assumed to be those for which the

87   cost of transport (i.e. energy expenditure per unit distance) is predicted to be at its minimum

88   [18]. Therefore, we hypothesised that for birds of different sizes either one or both birds may

89   have to adjust their wingbeat frequency and/or amplitude to stay together as a pair, which

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90   would represent an additional 'hidden' compromise cost of flying with another bird. In Phase

91   3, immediately following completion of the six similar-sized pair releases, each bird was then

92   flown in size-mismatched pairs for a further six flights (different-sized pairs), again from the

93   same site. Finally, in Phase 4, upon completion of the six size-mismatched flights, each bird

94   flew six times solo again (Fig. 2D). We compared the wingbeat characteristics of birds flying

95   in pairs relative to flying solo to determine if pigeons alter their wingbeat characteristics when

96   flying in a pair.

97

98   **Results**

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100   We analysed the data from all flights using Bayesian hierarchical models to account for

101   variation due to a set of environmental covariates, and the individual identity of the focal bird

102   and any partner (see Methods). Our results show that when birds flew in pairs, their median

103   wingbeat frequency increased by 1.00 Hz (95% Bayesian credible interval (CrI) [0.61, 1.38])

104   relative to flying solo, representing an increase of 18.2% (Fig. 2B-C). This was not associated

105   with greater variability in wingbeat frequency, the standard deviation of which remained stable

106   between solo and paired flight (2% lower standard deviation for size-matched pairs). Likewise,

107   the median peak-to-peak amplitude of dorsal body (DB) acceleration was similar in both solo

108   and paired flights (difference of 0.16 g, where g is gravitational acceleration; 95% CrI [-0.16,

109   0.47], where the fact that the credible interval crosses zero indicates that any difference is

110   statistically indistinguishable from zero). This combination of increased wingbeat frequency

111   and unchanged amplitude of DB acceleration resulted in a net 22.5% reduction in the median

112   peak-to-peak amplitude of dorsal body (DB) displacement (-4.65 mm, 95% CrI [-6.31, -3.06])

113   through the wingbeat, as a result of the correspondingly shorter time period over which DB

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114   acceleration is integrated to produce DB displacement (see supplementary text for further

115   analysis of the oscillatory accelerations experienced by an accelerometer).

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117   These statistical findings were consistent within and between pairs, irrespective of whether the

118   birds were flying in similar-sized or different-sized pairs (0.01 Hz increase per mm difference

119   in tarsus length between the pair; 95% CrI [-0.13, 0.16]; Fig. S1), or whether the bird was in

120   front or behind during the flight (0.01 Hz increase for travelling behind, 95% CrI [-0.10, 0.12]).

121   Moreover, the probability of whether an individual bird flew ahead in a given pair was

122   unaffected by the birds' tarsus length (0.01 per mm difference in tarsus length, 95% CrI [-2.68,

123   2.44]), solo airspeed (-0.22 per m s^{-1} difference in median solo airspeed, 95% CrI [-3.08, 2.65])

124   or body mass (0.02 per g difference in body mass, 95% CrI [-0.10, 0.15]; Fig. S4), meaning

125   there is no evidence that the larger or faster bird sets the pace by leading. Interestingly, and in

126   contrast to the closely coordinated flight of birds flying in V-formation[12], there was no

127   correspondence between the front and back bird's median wingbeat frequency (β = -0.23, 95%

128   CrI [-1.23, 0.75]; Fig. S3), indicating that their wingbeats cannot have been phase-locked

129   through most of the flight. All of these results were computed after accounting for the birds'

130   median airspeed, date of release and weather variables, none of which had an effect on

131   wingbeat frequency that was distinguishable from zero (Fig. S2, Table S1). Hence, whilst we

132   found no evidence in support of our hypothesis that birds of different sizes would specifically

133   have to adjust their wingbeat frequency or amplitude to stay together as a pair, we found clear

134   evidence that both birds in a pair increased their wingbeat frequency, independent of individual

135   size or solo flight speed.

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137   In addition to these results for all releases, one similar-sized pair and one different-sized pair

138   separated during three releases each, which means we can fortuitously compare sections of

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139   paired and solo flight within the same release. The results for these six releases clearly confirm

140   that wingbeat frequency increases as a direct result of flying in a pair, because the birds' median

141   wingbeat frequency decreased by 1.01 ± 0.30 Hz (mean $\pm$ s.d.) after they separated and flew

142   solo (raw values with no covariates; Fig. 2E-H).

143

144   As previous research has shown that pigeons increase their wingbeat frequency by up to 0.1

145   Hz as flock density increases [14], we analysed the effect of horizontal inter-individual distance

146   ranging from 0 m (i.e. directly above or below another bird) to 50 m (i.e. the cut off point for

147   flying in a pair) in a random sample of 100 wingbeats from each flight. This subsampling was

148   necessary due to the computational demands of dealing with the otherwise extremely large

149   volume of data. In total, we analysed 45,500 wingbeats from solo and paired flights. The results

150   demonstrate that birds flying with no horizontal spacing did indeed have the highest wingbeat

151   frequency (increase of 1.21 Hz relative to flying solo; 95% CrI [0.81, 1.61], 21.6%), with

152   wingbeat frequency decreasing by 0.011 Hz for every metre increase in horizontal spacing

153   (95% CrI [-0.012, -0.009]). Thus, birds flying 50 m apart had an expected wingbeat frequency

154   0.54 Hz lower than birds flying 0 m apart. Nevertheless, the act of flying in a pair still had a

155   larger overall effect than the distance between (or density of) the birds, which meant that even

156   birds flying 50 m apart increased their wingbeat frequency by 0.66 Hz (11.9%) relative to

157   flying solo. On average, birds flew with a median spacing 12.12 ± 4.76 metres (mean of the

158   means for all pairs $\pm$ standard deviation), which equates to a 1.07 Hz increase in wingbeat

159   frequency under the fitted relationship (*cf.* the 1.00 Hz increase in median wingbeat frequency

160   was over the whole flight).

161

162   To explore the mechanism underlying this change in wingbeat frequency, we divided each

163   wingbeat into an upstroke and a downstroke phase. We defined these phases with respect to

164   the peaks and troughs of the DB acceleration, which results from a combination of aerodynamic

165   and inertial forcing (see supplementary text for further detail). Whereas the dorsal aerodynamic

166   force is expected to peak mid-downstroke when the wing reaches its maximum flapping speed,

167   the dorsal inertial force is expected to peak at the start of the downstroke when the wing's

168   downwards acceleration is maximal. It follows that the maximum DB acceleration will be

169   reached somewhere between the start and middle of the kinematic downstroke, and similarly

170   for the minimum, which will be reached somewhere between the start and middle of the

171   kinematic upstroke. Hence, the downstroke phase, which we define as running from the point

172   of maximum to minimum DB acceleration, is expected to lag the kinematic downstroke slightly

173   (and similarly for the upstroke), but by less than a quarter of a cycle. With these definitions,

174   we found that birds reduced the median duration of the upstroke phase by 20.6% (-27.99

175   milliseconds, 95% CrI [-35.61, -19.92]) when flying in pairs, whereas the median duration of

176   the downstroke phase did not vary significantly (-3.53 milliseconds, 95% CrI [-8.35, 1.38]; 2c-

177   d). It is clear by inspection of the wingbeat acceleration traces that this decrease in upstroke

178   duration results in a less asymmetric pattern of forces between the two wingbeat phases

179   (compare red versus blue lines in Fig. 1B-E), so that this change in wingbeat frequency

180   essentially represents a switching of kinematic – if not aerodynamic – gait [24].

181

182   We hypothesise that a potential function of increasing wingbeat frequency and decreasing

183   oscillatory displacement of the body may be to enhance visual stability when attending to

184   nearby conspecifics. We therefore conducted a second experiment using head-mounted

185   accelerometers on six homing pigeons on short-range flights (950 m), flying solo and in pairs,

186   to determine if the same measured changes in wingbeat characteristics result in increased head

187   stability (see Methods). In close agreement with the first experiment, birds flying in pairs

188   increased their median wingbeat frequency by a mean of 1.10 Hz ± 0.26 relative to flying solo

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189   (6.6 ± 0.42 Hz mean ± s.d. for pairs; 5.5 ± 0.46 Hz for solo). More importantly, however, the

190   results also show that the median peak-to-peak head displacement simultaneously decreased

191   by 5.3×10^{-3} m $\pm 6.6 \times 10^{-4}$ between solo and paired flight, representing a 30% reduction in the

192   amplitude of oscillatory head displacement (Fig. 3). This substantial improvement in

193   translational head stability is expected to result in a significant reduction in the retinal slip of

194   nearby objects including flight partners.

195

196   In summary, by reducing the duration of their upstroke phase, birds flying in a pair were able

197   to accommodate one additional wingbeat per second, whilst maintaining the same peak-to-peak

198   DB acceleration and simultaneously increasing the vertical stability of the head. Intuitively, a

199   higher-frequency kinematic gait adopted in paired flight will therefore be associated with a

200   higher mechanical power input than the lower-frequency flight kinematic gait adopted in solo

201   flight. Of course, a higher mechanical power requirement in paired flight could still be

202   associated with a lower cost of transport if this increased frequency were more than

203   compensated by an increased flight speed. However, whereas birds migrating in V-formations

204   are known to increase their airspeed as flock size increases [25], the birds in our study only

205   increased their airspeed by 3.3% when flying in pairs (0.64 m s^{-1} increase, 95% CrI [0.08, 1.2]).

206   As we now explain, this increase in airspeed is much smaller than could have been expected to

207   be caused by the increase in wingbeat frequency alone, suggesting that there must have been

208   other compensatory changes in the kinematics.

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210   In cruising flight, the net thrust of the wings balances the drag on the body, which scales as

211    $\rho U^2 S_b$ where ρ is air density and S_b is body frontal area. For a 3% increase in airspeed U, it

212   follows that the time-averaged thrust can only have increased by just over 6%. In contrast, the

213   thrust on a flapping wing has been shown to scale as $T \sim \rho S_w f^2 A^2$, where S_w is wing area, f is

214   wingbeat frequency, and A is wingbeat amplitude [26]. Assuming all other things are equal, an

215   18% increase in wingbeat frequency would therefore be expected to produce about a 39%

216   increase in thrust. However, we also know that the time-averaged lift must balance the bird's

217   weight when cruising, and that lift scales as $L \sim \rho S_w U^2$ in fast forward flight when the

218   contribution of the wing's own flapping speed can be ignored. This implies that the 3% increase

219   in airspeed (i.e 6% increase in U^2) would have to have been countered by either a 6% decrease

220   in wing area, or an equivalent decrease in the proportionality constant of the scaling

221   relationship (i.e. the wing lift coefficient). Either kinematic change would be expected to

222   attenuate the thrust similarly, thereby reducing its expected increase to approximately 31%.

223   This is still significantly higher than the 6% increase in thrust estimated on the basis of the 3%

224   increase in airspeed, but the scaling $T \sim \rho S_w f^2 A^2$ implies that these figures could be brought

225   into line by an accompanying 10% decrease in wingbeat amplitude (see supplementary text for

226   further confirmation).

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228   The aerodynamic power requirement of a flapping wing has been shown to scale as

229     $P_A \sim \rho c S_w f^3 A^2$ where c is the wing chord [26]. The inertial power requirement also varies in

230   proportion to $f^3 A^2$, albeit with some further complications related to the effect of varying wing

231   span, but is an order of magnitude smaller than the aerodynamic power requirement [27,28] so

232   is neglected here for simplicity. Assuming that the 18% increase in wingbeat frequency f

233   between solo and paired flight was accompanied by a 6% decrease in wing area S_w and by a

234   10% decrease in wingbeat amplitude A as required to meet the equilibrium conditions above,

235   then the aerodynamic power requirement (in J s^{-1}) would have increased by approximately 25%

236   when flying in a pair. Given the 3% increase in airspeed, it follows that the aerodynamic cost

237   of transport (in J m^{-1}) must also have increased by some 21%. However, another key benefit

238   often ascribed to flying in flocks is the ability to pool navigational knowledge. This should

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239   improve homing route accuracy [7,8], which could offset the increased aerodynamic cost of

240   transport and increased aerodynamic power requirement by simultaneously decreasing the

241   distance and duration of the flight.

242

243   We calculated the birds' route accuracy flying solo and in pairs using a weighted mean cosine

244   of the angle between the birds' heading and destination. Flying in a pair resulted in a 6.9%

245   increase in route accuracy relative to both the Phase 1 and Phase 4 solo releases (0.06, 95% CrI

246   [0.01, 0.10]; Fig. 1), and a 6.5% decrease in route length (Table S2). This is consistent both

247   with theory[7,8] and with previous empirical studies [5,6]. Offsetting the 21% higher cost of

248   transport when flying in a pair against the 6.5% reduction in route length, we would expect a

249   net increase of approximately 14% in the total mechanical energy expended when flying home

250   to the loft in a pair. The increase in the total metabolic energy expended could be higher or

251   lower than this, depending upon whether and how the efficiency of the flight muscles varies

252   with flapping frequency, but it is reasonable to assume that an increase in mechanical energy

253   would also be associated with an increase in metabolic energy.

254

255   Whilst these figures are necessarily approximate, the qualitative conclusion of this analysis –

256   that the energy expended returning to the loft would have been higher in paired than in solo

257   flight – is robust to the uncertainty in our estimates of the changes in wingbeat frequency and

258   airspeed. Substituting the limits of the 95% CrI's for these variables into the preceding

259   calculations leads to an estimated 4% or 24% increase in the total energy expended in paired

260   flight if the variables fall at their respective upper or lower limits, and an estimated 10% or

261   17% increase if they fall at opposite ends of their limits. These are worst-case figures for how

262   the uncertainties could combine, all of which lead to the conclusion that flying in pairs is

263   associated with a substantial net increase in energy consumption over the flight. As we now

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264   discuss, this surprising result indicates: that (*i*) the act of flying in a pair necessitates birds to

265   alter their wing kinematics to a higher-frequency kinematic gait; and that either (*ii*) the

266   navigational benefits of flying in a pair are sufficient to outweigh the increased cost of transport

267   over longer homing distances, such that flying in pairs makes sense as a general homing

268   strategy, or (*iii*) there are other benefits of paired flight that outweigh its net energetic cost even

269   over short distances.

270

271   **Discussion**

272

273   One of the most commonly cited reasons for travelling as a group is to reduce energy

274   expenditure and enhance locomotor performance [11,12]. Previous research in cluster flocking

275   pigeons has shown that the energetic cost of flocking increases slightly with increasing flock

276   density [14]. However, this study did not compare the cost of flying in a cluster flock relative

277   to the alternative of flying solo, which means, as we now show, that previous work has

278   inadvertently understated the energetic costs of cluster flocking by an order of magnitude.

279   Specifically, whereas pigeons have previously been shown to increase their wingbeat

280   frequency by a mere 0.1 Hz with increasing flock density [14], our results show that the very

281   act of flying with another bird increases a pigeon's wingbeat frequency by 1.0 Hz (18%), which

282   results in an estimated 21% increase in the aerodynamic cost of transport. Although birds flying

283   in pairs were simultaneously able to offset some of the energetic cost by flying more accurate

284   routes home, the increases in route accuracy and airspeed were insufficient to compensate for

285   the increased aerodynamic power requirements, which resulted in a net energetic loss on the

286   order of 14% when flying moderate distances (~7 km) together in a cluster formation.

287   Moreover, the fact that pigeons flying in pairs display a 18% increase in wingbeat frequency

288   over solo flight suggests that the majority of the additional cost comes merely from the act of

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289   flying with another individual, rather than from the density of the flock, the relative spatial

290   position of the bird, or the size of its partner. Indeed, the size of a bird's partner, and whether

291   that bird was a leader or follower, had almost no effect on its measured wingbeat pattern. Even

292   so, differences in inter-individual horizontal spacing did result in a 0.54 Hz difference in

293   wingbeat frequency between birds travelling 0 to 50 m apart, with this increase ranging from

294   11.9 to 21.6 %, respectively. Thus, the act of flying with a conspecific resulted in a substantial

295   alteration of the wingbeat – even the adoption of a different kinematic gait. As we now explain,

296   not only does this earlier omission mean that the costs of flocking have been massively

297   underestimated – it also means that their mechanistic origin must be re-evaluated.

298

299   Two key hypotheses have been proposed for the increase in wingbeat frequency seen in denser

300   cluster flocks: (*i*) negative aerodynamic interactions between flock members and (*ii*) increased

301   need for control and collision avoidance [14]. Whereas a focus on the small effects of spacing

302   within a flock led previous work to hypothesise a possible aerodynamic basis to the costs of

303   cluster-flocking [14], our work clearly demonstrates that both birds within a pair increase their

304   wingbeat frequency, which suggests that these effects are unlikely to have been related to

305   negative aerodynamic flow interactions, since the bird in front does not fly in the wake of the

306   bird behind. On the other hand, higher wingbeat frequencies can be used to enhance both

307   stability and manoeuvrability [14,29–31]. We therefore hypothesise that the increase in

308   wingbeat frequency is related to paired flight necessitating a greater degree of control, which

309   could come about in two different ways. First, flying with conspecifics may require enhanced

310   manoeuvrability and control because birds need to adjust their orientation continuously and

311   rapidly, both to stay together and to avoid collisions [14]. Second, birds may require enhanced

312   visual stability when flocking, in order to observe and coordinate with individuals whose

313   proximity makes the effects of motion parallax significant [32,33].

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314

315   Birds make kinematic control inputs on a wingbeat-to-wingbeat basis, so increasing wingbeat

316   frequency will increase the rate at which control inputs can be made, enhancing the bird's

317   ability to respond to the movements of others and increasing the precision of its response.

318   Moreover, increased wingbeat frequency is expected to amplify flight stability [31], which

319   could both enhance control and visual stability. Unlike humans, birds have a limited range of

320   eye movement and therefore visual stabilisation is facilitated by compensatory motion of the

321   sophisticated avian head–neck system and is mediated by visual, vestibular and proprioceptive

322   cues [34,35]. Without image stabilisation mechanisms, birds would have difficulty

323   differentiating the motion of a target or obstacle from head or body motions, which is especially

324   problematic when viewing nearby objects or conspecifics. Our results show that dorsal body

325   displacement in reaction to the wingbeat is attenuated by 23% in the higher-frequency

326   kinematic gait adopted in paired flight (see supplementary text for theoretical analysis), which

327   should naturally translate into a reduced amplitude of head motion. Indeed, using data from

328   head-mounted accelerometers, we prove that the heads of birds flying in pairs experience

329   significantly less vertical head displacement relative to flying solo (~30%). Pigeons flying in

330   pairs have also been recorded to reduce their angular head saccades relative to flying solo,

331   which suggests either an increased focus on their partner or a decreased focus on the

332   environment [36]. Furthermore, the linearly declining effect of paired flight with increasing

333   inter-individual distance suggests that the observed changes in wingbeat frequency are less to

334   do with the local aerodynamic environment, the effects of which drop off sharply, and are

335   instead related to the coordination of flock flight, noting that the effects of motion parallax

336   decline linearly with distance. Together, our results suggest that a higher wingbeat frequency

337   may be prerequisite for flocking flight because of the increased demands for stability and

338   control.

339

340   Managing energy expenditure is critical for survival, and is a primary focus for natural

341   selection. While our results demonstrate that birds can derive navigational benefits from flying

342   in pairs even during short-range flights along familiar routes, the 7% increase in route accuracy

343   over this range was apparently insufficient to counterbalance the cost of the 18% increase in

344   wingbeat frequency, with an estimated increase in mechanical energy expenditure on the order

345   of 14%. Despite this, only six releases had to be repeated due to birds separating at the start,

346   and only twelve out of 116 pair releases (10%) resulted in separation part-way through the

347   release. Hence, the observed preference for paired flight suggests that either (*i*) the general

348   strategy of flocking is adaptive because the navigational benefits of flocking are sufficient to

349   outweigh the increased cost of transport when homing over longer distances, or (*ii*) the other

350   benefits of flocking, such as predator protection, outweigh the increase in energy expenditure

351   required to fly in pairs, even over quite short distances.

352

353   Although minimizing energy consumption may not be an especially strong selection pressure

354   for homing pigeons that have been selectively bred to return quickly to the loft, and which have

355   *ad libitum* access to feed, the results of our study nevertheless indicate that flying with

356   conspecifics entails an energetically expensive alteration to wingbeat kinematics. As many

357   other species of birds also preferentially fly in cluster flocks, our results suggest that the

358   additional benefits of flocking must outweigh any accompanying increase in energy

359   expenditure. The overall 9% reduction in homing flight time that we observed represents a 9%

360   reduction in the period over which our birds were exposed to predation risk when returning to

361   the loft. Moreover, not only does the act of flying in a pair dilute the chance of fatality during

362   a predation event by 50%, but the probability that such a predation event is successful decreases

363   as flock size increases, presumably through a combination of increased opportunity for

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364   vigilance and predator confusion effects [37]. Therefore, for pigeons, the ultimate benefits of

365   flocking, such as protection from predators and the pooling of navigational knowledge, must

366   together outweigh the energetic cost of flying with conspecifics.

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368   Over longer flight distances or circumstances where an individual has substantially less

369   navigational knowledge than the flock, it is possible that the navigational benefits of flocking

370   might be sufficient to produce a net reduction in the amount of energy expended despite the

371   increased aerodynamic power requirement that we report. In order to gain energetic savings

372   from a 21% increase in the cost of transport ($J\ m^{-1}$), the homing distance (m) would have to be

373   >17% shorter when flying in a pair to result in net energetic savings (J). In this scenario, birds

374   would experience an increased rate of energy expenditure which would be compensated by net

375   energetic savings and a reduced risk of predation. Either way, the birds in our study still opted

376   to fly in pairs despite collective travel resulting in an energetic loss at the individual level.

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378   Overall, the results of our study of a cluster flocking species stand in contrast to previous

379   studies of birds flying in V-formations [11−13]. Formation flight is typically utilised by

380   medium to large sized birds during goal-orientated movement, whereas cluster flock

381   formations are utilised by smaller birds, such as starlings, in movement ranging from orientated

382   to highly tortuous motion [15,16]. Bird size and the complexity of movement paths may both

383   contribute to the observed differences in wingbeat patterns between flock formation types.

384   Whilst birds flying in V-formations are able to fly in aerodynamically optimal positions to

385   conserve energy, the naturally higher wingbeat frequencies of smaller birds, their smaller

386   turning angles, and the rapidity of their directional changes may preclude flying in energy-

387   saving formations and instead necessitate a wingbeat pattern that facilitates a greater degree of

388   control. Thus, the demands of moving in irregular three-dimensional flocks may alter the way

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389   in which a bird flies. Overall, our results provide key new insights into both the biomechanical

390   consequences of close cluster flocking, and the energetic investments that pigeons make to gain

391   access to collective navigational knowledge and predator protection. Taken together, our

392   results demonstrate that flocking is, for pigeons, both fundamentally important and

393   fundamentally expensive.

394

395   **Materials and Methods**

396

397   a) Experiment 1

398

399   i)   Subjects

400

401   Twenty homing pigeons aged 1 or 3 years were used. Body size was quantified by measuring

402   tarsus length (mm) and body mass (g). Tarsus length was measured with callipers sensitive to

403   0.1 mm using the methods described in Sutherland et al. [22]. Body mass was measured using

404   digital scales (Salter ARC Electronic Kitchen Scales, Salter, UK; ± 1 g). All subjects completed

405   a minimum of 15 solo flights from the release site used in this study immediately preceding

406   the start of the experiment. The subjects were housed with ~120 other pigeons in two

407   neighbouring lofts at the Oxford University Field Station, Wytham, UK (51°46'58.2"N,

408   1°19'2.7"W). Access to water, grit and a standard pigeon feed mix were available ad libitum

409   at all times in the loft. The protocols outlined in this paper were approved by the Local Ethical

410   Review Committee of the University of Oxford's Department of Zoology.

411

412   ii)   Data logging

413

414   The birds were tracked using 5 Hz GPS loggers (QStarz BT-Q1300ST, 15 g) and 200 Hz tri-

415   axial accelerometers (± 16 g; Axivity AX3, 11 g), which were attached via Velcro strips glued

416   to trimmed feathers on the birds' back. In total, the loggers and fastenings weighed 27 g. To

417   enable subjects to adapt to carrying the additional mass, clay weights were attached to them

418   throughout the pre-training and experimental periods, which meant the weights were attached

419   for a minimum of 43 days prior to the start of the experiment. The weights were exchanged for

420   the loggers immediately prior to each release. GPS and accelerometer data were downloaded

421   using QTravel (Qstarz International Co., Ltd., Taipei, Taiwan; version 1.48(T)) and Open

422   Movement (Om) GUI Application (Newcastle University, UK; version 1.0.0.28), respectively.

423

424   The weather, including mean wind speed per minute (ms^{-1}), a running mean of the wind bearing

425   over the previous ten minutes, temperature (ºC), humidity (%) and barometric pressure (hPa),

426   were recorded using a WS2083 Professional Wireless Weather Station with USB upload

427   (Aercus Instruments, UK) situated 5.5 m above the ground near the pigeon lofts and Cumulus

428   Weather Station Software (Sandaysoft; version 1.9.4).

429

430   iii)   Experimental procedures

431

432   The release site was located 7.06 km from the loft on a bearing of 282° (Barnard Gate;

433   51°47'48.1"N, 1°25'3.3"W). The experiment consisted of four phases: Phase 1 - six individual

434   releases (solo 1); Phase 2 - six releases with a bird of a similar size (similar-sized pair); Phase

435   3 - six releases with a bird of a different size (different-sized pair); and Phase 4 - six individual

436   releases (solo 2). Bird pairings can be found in Table S3. Releases were conducted between

437   June and September 2015, on days when the sun was visible and the wind speed was < 7 ms^{-1}.

438   Subjects participated in a maximum of two releases per day, with a minimum of three hours

18

439   between each release. The birds had to complete a minimum of one third of the flight together

440   for the flight to be included in the analysis. If the birds spent less than one third of the flight

441   together, the flight was repeated. In total, six releases out of 116 pair releases had to be

442   repeated. One different-sized pair did not complete the final pair release after repeatedly

443   separating. The Velcro failed on bird S27 after the third release with a different-sized bird

444   therefore the pairing S27 and S84 only completed three different size pair releases and S27 did

445   not complete the final solos. In addition, S13 only completed one final solo before the Velcro

446   failed, S87 completed four final solos, and S05 and S25 completed five final solos each. The

447   remaining 15 birds all completed the final solo releases.

448

449   iv)   Data processing

450

451   Data were processed using the procedures outlined in Taylor *et al*. [20]. For each GPS point,

452   the orthodromic (great-circular) distance travelled and birds' final bearing from the previous

453   point were calculated using the haversine formula and forward azimuth, respectively. The

454   dorsal accelerometer measurements were filtered by taking a running mean over three data

455   points (0.015 s). Static acceleration (or gravity) was removed by subtracting a running mean

456   over 15 wingbeat cycles (> 2 s; Fig S5). The wingbeat frequency (number of wingbeats per

457   second; Hz) and peak-to-peak dorsal body (DB) acceleration (*g*) using the dorsal acceleration

458   signal (Z-axis) were calculated for each individual wingbeat. The amplitude of the DB

459   displacement (mm) was then calculated by the double integration of dorsal accelerometer

460   measurements [14,20]. In addition, we calculated the duration of the "downstroke" from the

461   peak downstroke force (maximum *g*-force) to the lower reversal point (minimum *g*-force). The

462   "upstroke phase" duration, which included the start of the downstroke, was measured from

463   minimum *g*-force to the maximum. We used the maximum and minimum *g*-force peaks to

19

464   divide the wingbeat for consistency, as the start of the kinematic downstroke was not

465   distinguishable in the data from paired flights. See supplementary text for further analysis.

466

467   Wind support, crosswind and airspeed were calculated using the methods described in Safi et

468   al.[38] using the measurements from the weather station and speed derived from the GPS

469   devices. Humid air density (kg m^{-3}; ρ_{air}) was calculated from measures of barometric pressure

470   (hPa; P), temperature ($^{\circ}$C; T_C) and relative humidity (%; ϕ) recorded by the weather station,

471   using the following calculation derived from the ideal gas law:

472
$$\rho_{air} = \left(\frac{P_d}{R_d T}\right) + \left(\frac{P_v}{R_v T}\right)$$

473   where P_d is pressure of dry air (Pa), R_d is gas constant for dry air [287.05 J/(kg * K)], P_v is

474   pressure of water vapour (Pa), R_v is gas constant for water vapour [461.495J/(kg * K)] and T is

475   ambient temperature (K). P_v can be calculated from the saturation of vapour pressure (P_{sat})

476   and relative humidity (ϕ):

477
$$P_v = \phi P_{sat}$$

478   We used the Arden-Buck [39,40] equation to calculate P_{sat}, where P_{sat} (hPa) is calculated as:

479
$$P_{sat} = 0.61121 \exp\left(\left(18.678 - \frac{T_C}{234.5}\right)\left(\frac{T_C}{257.14 + T_C}\right)\right)$$

480   P_d can then be calculated from the barometric pressure (P) and the vapour pressure of water

481   (P_v):

482
$$P_d = P - P_v$$

483

484   The birds' route accuracy was calculated using a weighted mean cosine of the angle (θ)

485   between the birds bearing and the bearing to the loft for each timestep, where θ is equal to the

486   smallest angle difference so that θ ranged from 0 (heading directly to the loft) and 180 (heading

20

487   directly away from the loft), and the orthodromic distance between each GPS point (d) using

488   the following calculation:

$$\frac{1}{D} \sum_{i=1}^{n} d_i \cos \theta_i$$

490

491   where D is the total distance flown. Route accuracy is, therefore, on a scale of -1 (heading in a

492   straight-line away from the destination) to 1 (straight-line to the destination). For orientated

493   movement, route accuracy is >0, which means route accuracy is akin to the straight-line index

494   [41], but enables us to calculate the accuracy for sections of a flight, rather than a whole flight,

495   which is necessary if the birds separate during the flight and fly solo.

496

497   The data were trimmed within a 200m radius around the release site and the loft to remove

498   take-off and landing. When analysing the pair tracks, sections of flight where the birds were ≥

499   50 m apart was excluded. In addition, if the birds swapped front-vs-back positions, the bird

500   who spent the majority of the flight in front based on GPS positioning was identified and the

501   rest of the data from when the other bird was in front was excluded.

502

503   v)   Data analysis

504

505   We analysed the data using Bayesian hierarchical models, which are analogous to mixed

506   models in frequentist methods and enabled us to account for the effects of each bird both as an

507   individual and a partner in a specific pair. The median wingbeat frequency ($\overline{W}_{i,j}$) for the pair

508   (i, j) was assumed to be normally distributed,

509

510    $$\overline{W}_{i,j} \sim N(\delta_0 1_{pair} + \delta_1 \|T_i - T_j\| + \omega_i \mu_i + (1 - \omega_i)\mu_j + \gamma X, \sigma)$$

511

512   where 1_{pair} is an indicator variable equal to 1 if the bird flew in a pair, and 0 for solo flights.

513   δ_0 is the difference in wingbeat frequency between the solo and paired flight. δ_1 is the

514   difference in wingbeat frequency for every mm absolute difference in tarsus length (T) between

515   the pair (i, j). For solo flights, the term involving δ_1 equals zero. The expression $\omega_i \mu_i + (1 -$

516     $\omega_i)\mu_j$ represents a weighted average of the solo wingbeat frequency (μ) of birds i and j with a

517   mixing weighting (ω_i), which determines the weight placed on the bird's own solo wingbeat

518   frequency (μ_i) relative to that of its partner (μ_j). For solo flights, this weighted average equals

519   bird i's solo wingbeat frequency (μ_i). The weighting is bounded to lie between 0 and 1 and

520   was determined by a logistic sigmoid function of the absolute difference in tarsus length,

521     $$\omega_i = logit^{-1}(\eta_1 + \eta\|T_i - T_j\|)$$

522   However, across all cases, there was no consistent effect of tarsus difference on the mixing

523   weighting.

524

525   Finally, γX represents the effect of the covariates, which accounts for median wind support (m

526   s^{-1}), median crosswind (m s^{-1}), median temperature (°C), median humidity (%), humid air

527   density (kg m^{-3}) and the date of release treated as a categorical variable. The birds' median

528   airspeed (m s^{-1}) was also added as a covariate on all models except for models of airspeed. We

529   used airspeed rather than ground speed as a covariate because ground speed and wind support

530   were correlated (Fig. S5). In terms of the response variable, there was almost no difference

531   between the models of airspeed and ground speed as the model accounts for the effect of wind

532   (0.64, 95% CrI [0.08, 1.20] compared to 0.69, 95% CrI [0.10, 1.28]). For consistency with the

533   covariates, we present the results of the model for airspeed. A covariate indicating whether the

534   bird was a leader or follower was also added to the model in a secondary analysis to determine

535   the effect of the birds' position on wingbeat frequency.

22

536

537   In addition to modelling the median values, we also took a random sample of 100 individual

538   wingbeats to analyse the effect of horizontal distance between birds in pairs. We analysed

539   horizontal distance rather than three-dimensional distance because GPS precision is generally

540   poorer in the vertical than the horizontal [42]. Horizontal distance (m) was added as a covariate

541   to the paired data, along with a categorical covariate identifying the specific bird and flight to

542   account for the repeated measures of 50 wingbeats from one flight. In total, 44,500 wingbeats

543   from 454 unique bird and flight combinations were analysed.

544

545   To investigate whether the birds were flying in phase, we used the following model to identify

546   whether the median wingbeat frequency of the follower ($\bar{W}_F$) is related to the leader ($\bar{W}_L$) in

547   pair (P):

548 $$\bar{W}_F \sim N(\alpha_P + \beta_P \bar{W}_L + \gamma X, \sigma')$$

549

550   We also investigated whether the difference between the leader and follower's tarsus length,

551   body mass or solo airspeed (S) predicted why the bird was a leader (L) in the pair using a

552   Bernoulli regression:

553 $$L_i \sim Bernoulli(\alpha_P + \beta_P S_i)$$

554

555   The model priors were centred on the null hypothesis using the mean, standard deviation and

556   square root standard deviation of the solo data (Table S4). Eight Markov chain Monte Carlo

557   (MCMC) chains were run simultaneously, each with 12,500 warm-up and 12,500 model

558   iterations, which resulted in 100,000 samples for each posterior distribution. For the model

559   involving raw wingbeat data, the model was run for 10,000 samples due to the size of the

560   model. Across all estimated models and parameters, we detected convergence in the sampling

561   distribution as determined by using a criterion $\hat{R} \leq 1.1$ on all parameters[43]. The number of

562   divergent iterations was 0.0-1.3% of the total sample size. The code for the wingbeat frequency

563   model and the model output can be found in the Supplementary Materials.

564

565   In addition to these results, one similar-sized pair (birds B01 and B82 with a tarsus length of

566   32.4 mm and 33.3 mm, respectively) and one different-sized pair (birds B01 and B07 with a

567   tarsus length of 32.4 mm and 35.2 mm, respectively) split and flew solo for more than 30% of

568   the flight for three of their six releases. As the sample size is low, only descriptive statistics

569   can be performed comparing the paired (< 50 m distance between birds) and solo flight (> 300

570   m distance).

571

572   We approximated the number of wingbeats difference between the solo and paired flight using

573   the total flight distance (excluding the 200m take-off and landing) and the model results from

574   route accuracy, airspeed and wingbeat frequency (Table S2). We calculated the number of

575   wingbeats difference as not all of birds completed 100% of the paired flights together or with

576   one leader.

577

578   Data processing and analysis were conducted using MATLAB (MathWorks, Natick, USA;

579   version R2015a) and the open-source software R (version 3.4.2) [44]. Bayesian models were

580   written in Stan [45] using the R interface RStan (version 2.16.2) [46].

581

582   *b) Experiment 2*

583

584   i)   Subjects

585

586   Six homing pigeons aged 3 to 10 years old were used. The pigeons were held under the same

587   conditions as outlined above and all had experience of experimental releases and the release

588   site. The protocols outlined in this paper were approved by the University of Oxford's Zoology

589   Animal Welfare Ethical Review Board (No. APA/1/5/ZOO/NASPA/Biro/

590   PigeonsHeadmountedsensors).

591

592   ii)   Data logging

593

594   We used a custom-built 'p-Sensor' to simultaneously record head movement and position. The

595   p-Sensor included an IMU with a combination of a tri-axial gyroscope, tri-axial accelerometer

596   and tri-axial magnetometer recording at 60 Hz, and a GPS logger recording at 10 Hz. The IMU

597   was mounted using double-sided tape onto a custom-made and custom-fitted wire mask

598   designed to fit each bird's head. The GPS logger, SD card, battery and microcomputer were

599   placed in an elasticated backpack on the birds back. The instrumentation, mask, and backpack

600   weighed 28.1 g and constituted 4.9 % of the body mass of the smallest bird, of which the IMU

601   unit on the bird's head only weighed 1 g. For more details, see Kano et al. [36].

602

603   All birds were habituated to wearing the custom-made mask for at least seven days prior to the

604   flight. For each day of habituation, the bird was fitted with a mask and carefully monitored for

605   two hours within its home loft for signs of discomfort and abnormal patterns of locomotion.

606   After seven days of habitation in the loft, the pigeons were released outside the loft and allowed

607   to fly freely under close observation.

608

609   iii)   Experimental procedures

610

611   The release site was located 0.95 km from the loft on a bearing of 199° (Wytham Woods;

612   51°46'29.4"N, 1°19'18.7"W). The experiments were conducted on the 23rd July 2017.

613   Releases were only conducted when the wind was low (<5 m s^{-1}) and the sun's disc was visible.

614   For the day of testing, the birds were fitted with a mask and allowed to habituate to wearing

615   the mask in the home loft before being transported to the release site by car. The birds were

616   released once solo and once in a pair on the same day. The release order was randomised.

617

618   iv)   Data processing and analysis
619

620

621   The data processing was conducted as outlined in Taylor et al. [20]. Vertical (Z-axis)

622   accelerometer measurements were smoothed by taking a running mean over five datapoints

623   (0.083 s) and then filtered using a 4th order high-pass Butterworth filter with a cut-off frequency

624   of 1 Hz. The peak-to-peak vertical head displacement was calculated by the double integration

625   of the vertical accelerometer measurements. We compared the median peak-to-peak vertical

626   head displacement between solo and paired releases for each bird.

627

628   The raw data will be available on data dryad after acceptance.

629

639

640   **References**

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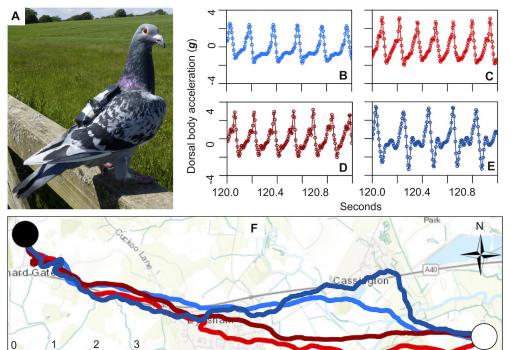
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750

Figure 1. Examples of accelerometer and GPS data recorded during solo and paired flights. A, Bird S30 carrying an accelerometer (top) and GPS sensor (bottom) attached via Velcro strips. **B-E**, Dorsal body (DB) acceleration recorded by the accelerometer during S30's final release in each of the four conditions: **B**, solo flight (blue); **C**, paired flight with a similar-sized bird (red); **D**, paired flight with a different-sized bird (dark red) and **E**, solo flight (dark blue). Accelerometer data has been filtered and gravity removed (see Methods). Note the higher wingbeat frequency when the bird is flying in a pair. **F**, Routes flown by S30 during the final release of each of the four conditions (same flights as those shown in **B-E**). Note the straighter trajectory, and hence greater route accuracy, of the paired flights. Black circle corresponds to the release site and white circle corresponds to the home loft. Map designed

31

761   using ArcGIS 10.4.1 (Esri Inc., Redlands, USA) using the World Topographic Map[23]. Scale

762   bar shows 3 km.

763

764   **Figure 2. Wingbeat frequency as a function of flight number. A-D**, Median wingbeat

765   frequency (raw data with no covariates) for all 20 birds during each of the four experimental

766   phases: **A**, six individual releases (solo); **B**, six releases with a similar-sized bird (similar-sized

767   pair); **C**, six releases with a different-sized bird (different-sized pair); and **D**, six individual

768   releases (solo). **E-H**, Raw wingbeat frequency data for birds which flew in a pair (< 50 m

769   distance) and solo (> 300 m) during the same flight. **E** and **G** are from the similar sized pair of

770   birds B01 and B82, respectively (pictured). **F** and **H** are from the different-sized pair B01 and

771   B07 (pictured). Boxplots show the median and upper and lower quartiles, and whiskers

772   correspond to 1.5 times the interquartile range.

773

774   **Figure 3**. Boxplot of median vertical peak-to-peak head displacement across six birds, each

775   flying once solo and once in a pair. Bottom and top edges of the box indicate the 25th and 75th

776   percentiles and the whiskers extend to the most extreme data points. Note that there is no

777   overlap between the median head displacements in the two conditions.

A — photograph of a pigeon with a tracking device.
B, C, D, E — Dorsal body acceleration (**g**) plotted against Seconds (120.0–120.8+).
F — map showing routes: Solo 1, Similar-sized pair, Different-sized pair, Solo 2.