# Naïve individuals promote collective exploration in homing pigeons

**Gabriele Valentini[1,2], Theodore P. Pavlic[2,3,4,5,6], Sara Imari Walker[1,3,6], Stephen C. Pratt[2,6], Dora Biro[7,8] & Takao Sasaki[9]**

[1] Arizona State University, School of Earth and Space Exploration, Tempe, AZ  85287, USA
[2] Arizona State University, School of Life Sciences, Tempe, AZ  85287, USA
[3] Arizona State University, Beyond Center for Fundamental Concepts in Science, Tempe, AZ  85287, USA
[4] Arizona State University, School of Computing, Informatics, and Decision Systems Engineering, Tempe, AZ  85287, USA
[5] Arizona State University, School of Sustainability, Tempe, AZ  85287, USA
[6] Arizona State University, ASU–SFI Center for Biosocial Complex Systems, Tempe, AZ  85287, USA
[7] University of Oxford, Department of Zoology, Oxford, OX1 3PS, UK
[8] University of Rochester, Department of Brain and Cognitive Sciences, Rochester, NY 14627, USA
[9] University of Georgia, Odum School of Ecology, Athens, GA 30602, USA

**Abstract.** Group-living animals that rely on stable foraging or migratory routes can develop behavioural traditions to pass route information down to inexperienced individuals. Striking a balance between exploitation of social information and exploration for better alternatives is essential to prevent the spread of maladaptive traditions. We investigated this balance during cumulative route development in the homing pigeon *Columba livia*. We quantified causal interactions within pairs of birds in a transmission-chain experiment and determined how birds with different levels of experience contributed to the exploration–exploitation trade-off. Newly introduced naïve individuals were initially more likely to initiate exploration than experienced birds, but the pair soon settled into a pattern of alternating leadership with both birds contributing equally. Experimental pairs showed an oscillating pattern of exploration over generations that might facilitate the discovery of more efficient routes. Our results introduce a new perspective on the roles of leadership and information pooling in the context of collective learning.

## Introduction

The coordinated motion of groups is a widespread phenomenon observed in multiple taxa (Vicsek and Zafeiris 2012). Among other adaptive advantages, such as increased energetic efficiency and decreased odds of predation (Krause and Ruxton 2002), collective motion also allows group members to increase their sensory and cognitive capacity (Berdahl et al. 2013; Gelblum et al. 2020) and to acquire valuable social information for navigation (Couzin 2009; Couzin et al. 2011). In many animals, this social information concerns well-established foraging or migratory routes that can, in some species, persist over successive generations (Helfman and Schultz 1984; Sasaki and Biro 2017; Jesmer et al. 2018). Knowledge and skills that accumulate over generations can provide groups with an enhanced ability to solve difficult problems (Biro, Sasaki, and Portugal 2016). Not only can later generations build on the success of earlier ones, but

42    the introduction of new members, even those with no prior knowledge, adds diversity that can enhance the

43    group's behavioural solutions (Mehlhorn et al. 2015). As is often the case (Hills et al. 2015), behavioural

44    patterns that lead to a search for improvement, whether individually, socially, or over multiple generations,

45    involve an exploration–exploitation trade-off. In navigation problems, both solitary individuals and groups

46    have to balance between exploiting previously acquired information necessary to navigate a known route

47    and exploring for additional information that might allow them to approach the optimal route (Fu and Gray

48    2006). However, how moving collectives compromise between these tasks has received limited attention.

49    Understanding the exploration–exploitation trade-off is complicated by ambiguity about group

50    leadership (Couzin et al. 2005; Garland et al. 2018). Although some collectives (*e.g.*, ants, honeybees) can

51    allocate certain individuals to spatial exploration while others continue to exploit accumulated information

52    (Hills et al. 2015), individuals in cohesively moving groups are highly coupled and can only benefit from

53    compromising between exploring and exploiting if they do so in unison. If they are to stay together, the

54    group must reach consensus between following a known route or departing from it to find better routes,

55    foraging patches, or temporary resting locations. Elucidating whether different group members contribute

56    differently to this process is crucial to understanding how groups compromise between exploration and

57    exploitation.

58    We investigate this question in the context of navigation through natural landscapes using the homing

59    pigeon *Columba livia* as our model system. After successive homing journeys from a given release site,

60    pigeons develop stable idiosyncratic routes that are followed with high fidelity (Meade, Biro, and Guilford

61    2005; Guilford and Biro 2014). These birds rely on sequences of localized visual landmarks to recapitulate

62    familiar yet individually distinct routes (Biro, Meade, and Guilford 2004; Meade, Biro, and Guilford 2005).

63    Each route is learned in a gradual process starting with an exploration phase that samples new landmarks,

64    from which the bird eventually converges upon a stable sequence of landmarks (Biro, Meade, and Guilford

65    2004). Experiments with paired birds show that route information can be passed from experienced birds to

66    naïve individuals through social learning (Pettit, Flack, et al. 2013) and can be modified through information

67    pooling when individuals with different idiosyncratic routes share information to reach a compromise

68    between their routes (Biro et al. 2006). Although learning generally improves route efficiency, both social

69    learning and information pooling tend to reach a plateau beyond which further improvement in efficiency is

70    not seen. However, for birds flying together, the introduction of a naive individual in place of an experienced

71    one effectively leads to the resumption of exploratory behaviour and further route improvement (Sasaki and

72    Biro 2017). Yet, it remains unclear to what extent a bird's prior experience influences the balance between

73    exploration and exploitation and how birds with potentially different route preferences jointly shape a route.

74    Indeed, the mechanisms underlying how different individual preferences are combined into a collective

75    outcome is one of the key foci in studies of collective animal behaviour. Broadly, group decisions can range

76    from despotic with a single leader to democratic in which input from different individuals is aggregated to

77    reach consensus (Conradt and Roper 2003). Evidence of both despotic and democratic decisions exists in

78    homing pigeons (Biro et al. 2006; Nagy et al. 2010; Jorge and Marques 2012). When leadership is defined

79    as disproportionate input into collective navigational decisions, either through spatial position (Pettit, Perna,

80    et al. 2013), route similarity (Flack et al. 2012), or directional correlation delay (Nagy et al. 2010), a number

81    of different factors have been shown to play a role in it. Leadership dynamics are influenced by individual

82    differences among birds in fidelity to their own routes (Freeman et al. 2011), their typical flight speed (Pettit

83    et al. 2015), their personality (Sasaki et al. 2018), as well as their level of experience (Flack et al. 2012).

84    Moreover, equally experienced birds are known to come to a compromise by averaging their idiosyncratic

85    routes so long as the pair's route remains within a threshold distance from each bird's favoured one – a low

86    level of conflict. Higher levels of conflict lead instead to a splitting of the pair or to the emergence of a single

87    leader (Biro et al. 2006). Nonetheless, experience alone is unable to fully recover the leadership structure

88    characteristic of larger flocks (Watts et al. 2016). Spatial position offers some insight into leadership: on

89    average, birds flying closer to the front of the flock have a stronger influence on the flock's directional

90    choices than birds flying at the back (Nagy et al. 2010; Pettit, Perna, et al. 2013). Even so, the moment-to-

91    moment relationship between leadership and level of experience remains unclear.

92        Leader–follower interactions of this sort can be accurately captured using information-theoretic

93    measures that quantify causal relations in terms of predictive information (Butail, Mwaffo, and Porfiri 2016;

94    Kim et al. 2018; Crosato et al. 2018; Ray et al. 2019; Valentini et al. 2020). One of these measures, *transfer*

95    *entropy,* quantifies information about the future behaviour of a focal individual that can be obtained

96    exclusively from knowledge of the present behaviour of another subject (Schreiber 2000). Transfer entropy

97    measures information transferred from the present of the sender to the future of the receiver (Lizier and

98    Prokopenko 2010). It explicitly accounts for autocorrelations characteristic of individual birds' trajectories

99    (Mitchell et al. 2019) by discounting predictive information available from the sender's present that is already

100   included in the receiver's past. Furthermore, it does not require a model of how sender and receiver interact,

101   and it is well suited to study social interactions both over space and over time (Lizier, Prokopenko, and

102   Zomaya 2008). Consequently, transfer entropy can capture causal interactions due not only to alignment

103   forces (Nagy et al. 2010) but also to attraction and repulsion forces that result in temporarily unaligned

104   states (Pettit, Perna, et al. 2013).

105       We study collective decision making and the exploration–exploitation trade-off using an experimental

106   analysis of cumulative route development in homing pigeons (Sasaki and Biro 2017). In these experiments,

107   pairs consisting of a naïve and an experienced bird were required to successively solve the same homing

108   task a fixed number of times. This set of paired flights allowed the naïve bird to acquire knowledge of

109   localized visual landmarks necessary for homing. The more experienced bird was then replaced with a new

110   naïve individual and the learning process was repeated through five generations of replacement in a

111   transmission-chain design. Route efficiency was measured as the ratio of the beeline distance between the

112   release site and the home loft (*i.e.*, the ideal optimum) and the actual distance travelled by birds. The results

113   showed that, although homing efficiency dropped considerably every time a new naïve bird was introduced,

114   transmission-chain pairs continued to improve within and over generations, eventually outperforming both

115   solo and fixed-pair controls (respectively, 0.92 efficiency versus 0.83 and 0.85). In contrast, the efficiency

116    of solo and fixed pairs plateaued after they had first established their idiosyncratic routes (around the 9th–

117    10th release for the former and the 7th–8th release for the latter).

118    The continued improvement seen in transmission chains might result from a variety of decision-making

119    mechanisms ranging from fully despotic to increasingly democratic. A simplified perspective of this

120    continuum allows us to consider four alternative hypotheses. In two of these alternatives, a single despotic

121    leader, either the naïve or the experienced bird, determines the entire homing route. Whereas evidence of

122    social learning (Sasaki and Biro 2017) suffices to dismiss the possibility of leadership by the naïve

123    individual, leadership by the experienced individual could still be the only process in place if social learning

124    is unidirectional and the naïve individual merely triggers the experienced bird to resume and lead

125    exploration. Under the other two hypotheses, birds could pool their personal information by means of

126    democratic processes based on moment-by-moment integration of individual preferences or transient,

127    alternating leadership (Conradt 2012). The third hypothesis entails the experienced bird contributing only

128    its past route information and relying instead on the naïve individual for the discovery of route innovations.

129    If this hypothesis holds, we expect the naïve bird to disproportionally lead phases of exploration. Otherwise

130    (fourth hypothesis), both experienced and naïve birds might contribute through exploration to the discovery

131    of new information.

132    We discriminated between these alternative hypotheses by using transfer entropy to reveal the extent

133    to which birds influence each other and to investigate if relative spatial position can accurately predict

134    leader–follower dynamics. On this basis, we studied the contribution of each bird to the exploration–

135    exploitation trade-off over different stages of route development. This exploration–exploitation perspective

136    of homing route development allowed us to characterize the efficiency of choices made by birds over the

137    course of the experiment and to shed light on the superior performance of experimental pairs with respect

138    to solo and fixed pairs controls.

139

140    **Results**

141

142    **Birds pool information.** The social-learning hypothesis under which the naïve bird passively copies the

143    idiosyncratic route of the experienced one (*i.e.*, the despotic leader) entails a transfer of information that is

144    unidirectional – from the experienced to the naïve bird. Instead, under the two alternative hypotheses based

145    on democratic decision-making, the two birds rely on bidirectional information transfer to pool information

146    and increase the efficiency of their route (Pettit, Flack, et al. 2013; Sasaki and Biro 2017). We rejected the

147    unidirectional social-learning hypothesis by finding causal evidence of information pooling: the naïve bird

148    actively influenced the behaviour of the experienced one for a large portion of the parameter space

149    (Figure S1). As is common practice with these measures (Porfiri 2018), we selected the parameter

150    configuration that maximized the total transfer of information between the two birds (one sample every $0.2$

151    seconds, $k = 10$) . This was maximal for the shortest sampling period (*i.e.*, prediction interval) of $0.2$

152    seconds and progressively decreased towards 0 for larger periods up to 4 seconds, indicating that the effect

153    of an interaction between birds was transitory and lasted for a limited period of time. Using this configuration,

4

154    we compared measurements of information transfer against those of a surrogate dataset created by pairing

155    trajectories of birds that were not flown together. We found that levels of mutual influence between birds

156    that flew together were significantly higher than those observed in the surrogate dataset both overall and

157    for each generation separately (Mann–Whitney–Wilcoxon, columns 2 and 3 of Table S1).

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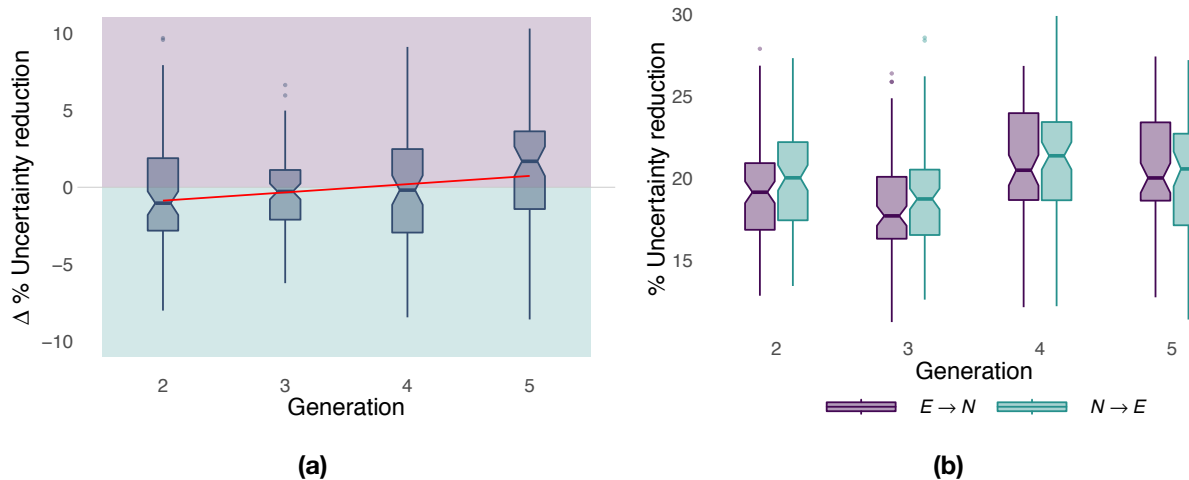


**(a)**                                    **(b)**

160 *Figure 2. Panel (a) shows the net predictive power of the two birds, $\tilde{T}_{E \to N} - \tilde{T}_{N \to E}$, over generations, where $\tilde{T}_{X \to Y} =$*
161 *$\frac{T_{X \to Y}}{H_Y} \cdot 100$ with $X, Y \in \{E, N\}$, highlighting which bird is more informative (purple for the experienced bird, green for the*
162 *naïve bird). The red line corresponds to a linear fit over generations using the Theil–Sen estimator. Panel (b) shows*
163 *the predictive power of naïve and experienced birds over generations measured as the percentage $\tilde{T}_{X \to Y}$ of uncertainty*
164 *reduction about one bird given by the other.*

165

166    During the first two generations of paired flights (Figure 2a, paired analysis), when there was a large margin

167    to improve the efficiency of the pair's trajectory, the naïve bird was more informative than the experienced

168    one, evidenced by a stronger influence over the latter. At generation 4 there was a balance between the

169    two birds whereas the experienced bird eventually became the better source of predictive information in

170    the last generation. A linear fit over generations of the paired comparison (Figure 2a, red line) showed an

171    increasing influence of the experienced bird over the naïve one (Theil–Sen estimator, slope 0.534, $p <$

172    0.001). Additionally, a non-paired comparison of the same results revealed that, although the naïve bird

173    had, on average, a marginally higher predictive power than that of the experienced one (18.7–21.4% versus

174    17.7–20.5%), both birds explained a large portion of each other's behaviour (Figure 2b) suggesting non-

175    trivial leadership dynamics. These results do not show whether different levels of experience within the pair

176    led to asymmetric contributions of birds to route development, with the experienced bird providing only its

177    past route information and the naïve bird in charge of discovering route innovations, or if both birds

178    contributed to the exploration for possible route alternatives. To discriminate between these remaining

179    hypotheses, we first developed the means to evaluate leadership on a moment-to-moment basis.

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**(a)**                                            **(b)**
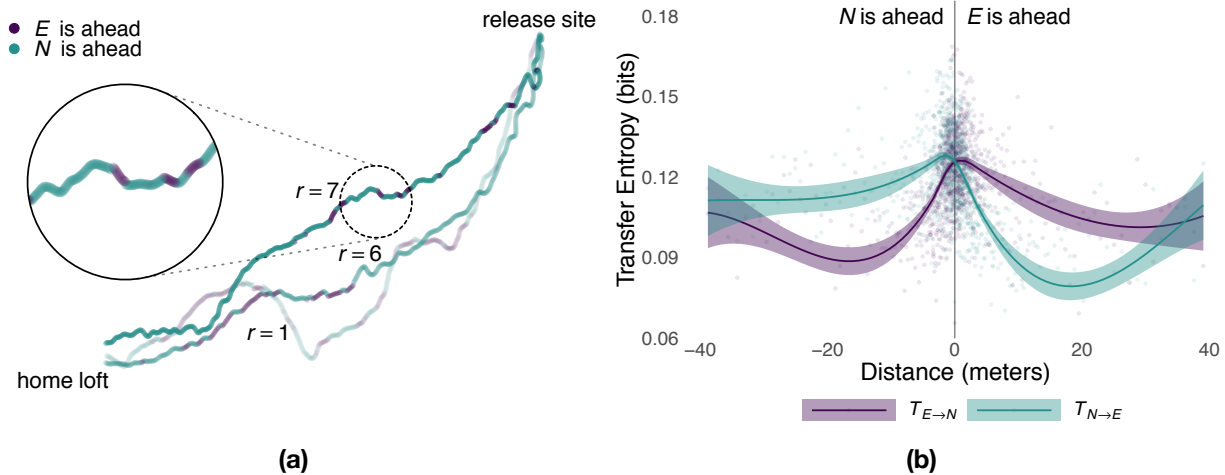
*Figure 3. Panel (a) shows sample flight trajectories for a number of different releases, $r$, of the same pair of birds. Colors highlight which bird is ahead of the other during different segments of the route. Panel (b) shows the local transfer of information (mean and 0.95 confidence interval) between the experienced bird and the naïve one as a function of their relative distance (colors represent the direction of information transfer) estimated using smoothed conditional means.*

**Relative position determines temporary leadership.** Consistent with information sharing within each pair, we found that experienced and naïve birds repeatedly switched their positions at the front and back of the pair (Figure 3a). Previous studies found evidence that birds that spent, on average, more time at the front of the flock had a tendency to assume leadership roles (Nagy et al. 2010; Pettit, Perna, et al. 2013). To see whether this average relationship between leadership and position holds at each point in time, we investigated the spatiotemporal dynamics of information transfer (Lizier, Prokopenko, and Zomaya 2008). We did so by considering the amount of predictive information obtained by each bird as a function of the distance from the experienced to the naïve bird projected over their mean direction of motion (Figure 3b). We found that within a distance of up to 30 meters, the bird flying ahead was consistently more informative than that flying in the back. This is not only further evidence that the bird flying ahead acts as the leader, influencing the path of the follower behind it, but, because of its finer grain, it also enables relative distance between birds to be used as a (more parsimonious) moment-to-moment measure of causal influence within the pair.

      The experienced and the naïve bird alternated leading segments of the route whose duration was stochastic and resembled a log-normal distribution (see Supplementary Material). Although the naïve bird flew at the front of the pair for longer segments (Whitney–Mann–Wilcoxon, $p < .047, W = 56865638$), the difference was very small (0.3 seconds) and largely driven by the flights of one generation. Indeed, for all generations but the third ($p < .001, W = 6588674$), the distribution of consecutive time spent at the front of the pair by the experienced bird cannot be distinguished from that of the naïve individual (Table S2). The tails of these distributions approach that of an exponential distribution and suggest that temporary leadership might be decided on the basis of stochastic processes (Biro et al. 2006) instead of certain rules such as fixed periods of time. Moreover, with the exception of generation 3 where 54% of the route was led

210     by the naïve bird (Wilcoxon signed rank-test, $p = .03, V = 1851$), there was no significant difference in the

211     proportion of a flight spent by each bird at the front of the pair (Table S3) suggesting a relatively egalitarian

212     relation between birds despite differing levels of experience.



(a)            (b)            (c)
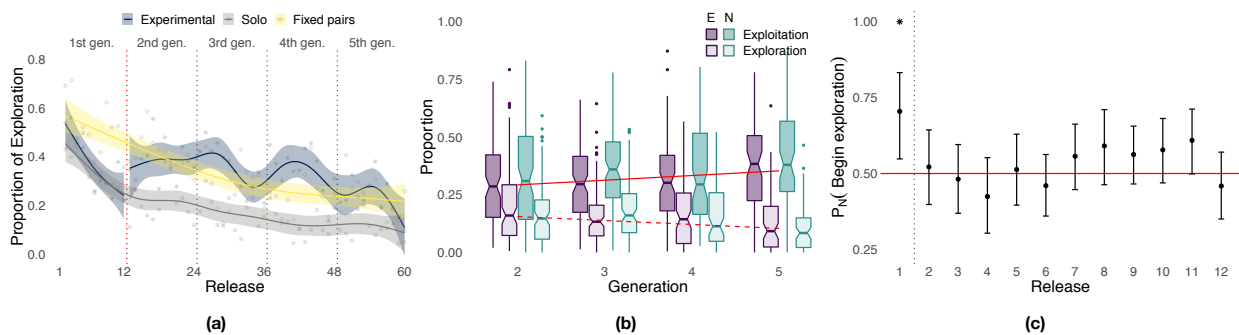
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214     *Figure 4. Panel (a) shows the proportion of exploration over releases for the experimental group (the red dotted vertical*
215     *line separates solo flights at generation 1 from paired flights at generations 2-5), the solo control, and the fixed-pairs*
216     *control. Smoothed lines are computed using generalized additive models using shrinkage cubic regression splines*
217     *(mean and standard error); points represent averages for individual releases. Panel (b) shows the proportion of a flight*
218     *led by each bird during phases of exploration and exploitation in the experimental treatment. Darker colors correspond*
219     *to exploitation, lighter colors to exploration; purple represents the experienced bird, green the naïve one; red lines*
220     *represent linear fits to data pooled from both birds using the Theil–Sen estimator (slopes and p-values: respectively,*
221     *0.0203, $p = 0$ for exploitation and $-0.0171$, $p = 0$ for exploration). Panel (c) shows the probability for the naïve*
222     *individual to initiate phases of exploration over releases (exact binomial test, $p < .01$ for release 1).*

223

224     **Exploration–exploitation dynamics explain flight performance.** Sasaki and Biro (2017) previously

225     showed that flight efficiency varies across treatments with experimental pairs eventually outperforming both

226     fixed pairs of birds and solo individuals. The discovery of route innovations and, in particular, how birds with

227     different levels of experience contribute to this task, is the key to the superior performance of experimental

228     pairs. To understand this phenomenon and thus shed light on the pair's information pooling mechanism,

229     we investigated how pigeons balance between exploitation of known information, closely following ($< 300$

230     meters) their most recent route, and exploration for possible route improvements. To do so, we labelled

231     segments of flight trajectories as a function of the point-to-point distance of a focal trajectory from the

232     immediately preceding one (*i.e.*, baseline) and compared the exploration–exploitation dynamics both

233     across treatments and between experienced and naïve birds.

234         During the initial part of the experiment (Figure 4a, first 12 releases), exploration decreased steadily

235     in all conditions with birds that flew individually in the experimental group (*i.e.*, generation 1) performing

236     similarly to those of the solo control (respectively, 36.7% and 34.2%) whereas fixed pairs of birds explored

237     significantly more (51.7%, Whitney–Mann–Wilcoxon, $p < .001$, Table S4). However, while exploration

238     steadily decreased for solo and fixed pairs of birds in the successive 48 releases, experimental pairs

239     showed a markedly different pattern of exploration oscillating over generations (Figure 4a, releases 13–

240     60). Each time a new naïve individual was paired with an experienced one (dotted vertical lines), exploration

241     increased for about 5 to 6 releases, reaching values well beyond those of both solo birds and fixed pairs;

242     then exploration decreased within a few releases (2 to 4) to the same levels as those of fixed pairs. On

243     average during generations 2 to 5, experimental pairs explored (32.9%) significantly more than both solo

244    (15.7%, $p < .001$) and fixed pairs of birds (29.3%, $p = .0456$). These results also held when exploration and

245    exploitation were defined with respect to the last release of the previous generation. Under this model,

246    differences between experimental and fixed pairs were even more pronounced, with the former

247    characterized by 46.6% exploration and the latter by only 32.4% ($p < .001$, Table S5 and Figure S6). The

248    inferior flight efficiency of solo and fixed pairs of birds might thus be explained, at least in some measure,

249    by a lower likelihood to discover route improvements due to limited exploration.

250          The superior homing performance of experimental pairs is suggested to be rooted in their ability to

251    select novel portions of a route introduced by the naïve individual that are more efficient while discarding

252    inefficient ones (Sasaki and Biro 2017). Under this hypothesis, we expect to observe, not only increasing

253    homing efficiency over generations, but also an asymmetric pattern of leadership in which the naïve

254    individual leads periods of exploration and the experienced one leads periods of exploitation. We found

255    instead no significant difference between the contributions of the experienced bird and those of the naïve

256    one both overall and within generations (Figure 4b and Table S7). The sole exception is represented by

257    generation 3 during which the naïve bird contributed more than the experienced one to exploitation

258    (Wilcoxon signed-rank test, $p = .035, V = 1871$ ). Experienced and naïve birds led the pair with

259    approximately the same frequency in both exploration and exploitation, suggesting that deviations from

260    established routes were not caused only, or even mainly, by the naïve bird (see also Figure S4, inset). We

261    did find evidence of behavioural asymmetries, in that transitions from exploitation to exploration were

262    marginally more likely to be initiated by naive birds (exact binomial test, $p = .042, n = 964$, Table S8);

263    however, this result was driven by those of generation 3 ($p = .02, n = 301$) whereas no difference was

264    detected in other generations. Transitions from exploration to exploitation were equally likely to be initiated

265    by the two birds both overall and within each generation. However, when transitions are considered over

266    the 12 releases composing each generation (Figure 4c), the naïve individual was more likely to initiate

267    phases of exploration during the first release ($p < .01, n = 44$, Table S9) doing so 70.5% of the time

268    compared to 29.5% for the experienced bird. After the first release, transitions that initiate phases of

269    exploration were about as likely to be initiated by either of the two birds independently of their level of

270    experience.

271

## Discussion

273

274    For many group-living animals, searching for optimal travel routes can be a complex task as social

275    information about routes can persist over generations regardless of its quality (Helfman and Schultz 1984;

276    Sasaki and Biro 2017; Jesmer et al. 2018; Laland and Williams 1998). This search is inherently subject to

277    a trade-off between the exploitation of well-established route information accumulated over time and

278    exploration for innovations that constitute potential improvements (Hills et al. 2015). Striking a balance is

279    fundamental as a pronounced reliance on exploitation of learned information can hinder innovations

280    (Davies, Krebs, and West 2012) and thus promote the maintenance of potentially suboptimal behaviour

281    and even of maladaptive behavioural traditions (Laland and Williams 1998). Equally, an over-reliance on

282    exploration without exploiting the rewards of beneficial innovations eventually impedes improvements in

283    performance over time (Fu and Gray 2006; Mehlhorn et al. 2015).

284    We studied the causal structure of this process in flights of the homing pigeon *C. livia*, as this species

285    is capable of both social learning and information pooling (Biro et al. 2006; Pettit, Flack, et al. 2013). Of

286    particular interest for our study is the increase in route efficiency that results from the pairing of naïve

287    individuals with experienced ones (Pettit, Flack, et al. 2013), including when this happens iteratively over

288    multiple generations (Sasaki and Biro 2017). Previous work has proposed information pooling as the

289    underlying mechanism driving this increase in flight performance (Sasaki and Biro 2017). Using transfer

290    entropy to measure predictive information (Schreiber 2000; Pilkiewicz et al. 2020), we found quantitative

291    evidence that supports the information-pooling hypothesis in the strength of causal interactions within pairs

292    of birds. Experienced and naïve birds influence each other's behaviour; about 20% of the future directional

293    choices of any individual in a pair is explained by the behaviour of the other individual. These results

294    contrast with our expectations for unidirectional social learning that entails an asymmetric pattern of

295    leadership with a pronounced role for experienced individuals.

296    Our analysis showed that, in a multi-generational transmission-chain design, the naïve bird has a higher

297    influence than the experienced one during the early generations. In later generations, as flight efficiency

298    increases, the experienced bird becomes the better source of predictive information. We can further

299    hypothesize that, over generations, as birds explore an increasing portion of the search space and exhaust

300    remaining alternatives, a newly introduced bird should become less likely to contribute productive

301    innovations, and an increasing proportion of innovations should lead to errors instead of improvement. This

302    theoretical reasoning is analogous to the diminishing marginal value from returning to a previous location

303    when searching for an object in space (Stone 1976). From an information-foraging perspective (Stephens

304    and Krebs 1986; Pirolli 2007), the time invested in harvesting innovations on the introduction of a naïve bird

305    corresponds to the time invested in attending to a newly discovered patch; at some point, the opportunity

306    cost of further harvesting becomes too high to justify remaining in the patch. Thus, after the introduction of

307    a naïve bird, the information-foraging pair shifts from information-harvesting exploration back toward

308    information-preserving exploitation, as would be expected in an optimal search problem (Stone 1976).

309    How do experimental pairs improve their homing routes over generations? Previous studies where

310    leadership was defined on the basis of route similarity showed that, in pairs with a large difference in

311    experience between birds, experienced individuals were more likely to assume leadership (Flack et al.

312    2012). Still using route similarity, Sasaki and Biro (2017) found evidence of social learning with naïve

313    individuals learning routes from their experienced partners. Moreover, because newly formed pairs in the

314    transmission-chain design also improved performance generation after generation, they proposed that

315    naïve individuals could contribute innovations that pigeons evaluate in terms of route efficiency and prune

316    away when inefficient. However, defining leadership in terms of causal interactions instead of route

317    similarity allowed us to show that there is an asymmetric relation between innovators and exploiters only

318 during the initial flight of a newly formed pair. Although leadership is ephemeral and equally shared between
319 birds during exploration and exploitation independently of their level of experience, over the course of this
320 first flight the naïve individual disproportionally initiates phases of exploration, attracting the experienced
321 bird to unfamiliar areas and triggering it to also resume the search. After that, both birds are equally likely
322 to initiate transitions between exploration and exploitation. Moreover, as it is unlikely that experimental pairs
323 were merely better than control groups at evaluating efficiency, we believe that their superior performance
324 is rooted instead in their complex exploration–exploitation dynamics that allowed them to better cover the
325 search space.

326    Personally acquired information allows solo individuals to improve flight performance (Meade, Biro, and
327 Guilford 2005) but only to discover routes moderately efficient (consistently within $0.8$–$0.85$ efficiency
328 across a large number of experiments, reviewed in Guilford and Biro 2014) because solo individuals rapidly
329 reduce their exploration efforts to seek out novel information. Experimental and fixed pairs of birds on the
330 other hand explore more and thus outperform solo individuals. Together, two birds have superior sensory
331 and cognitive capacities compared to single birds (Krause, Ruxton, and Krause 2010) which facilitates the
332 discovery of better routes that are then learned collectively (Biro, Sasaki, and Portugal 2016; Kao et al.
333 2014). The reasons why pairs explore more than solo individuals might lie partly with the conflicts
334 characteristic of newly formed pairs (Biro et al. 2006) if the resolution of conflict, *e.g.*, through averaging
335 individual inputs, indirectly prompts pairs to explore more and discover route innovations. This hypothesis
336 could also explain why experimental pairs outperform fixed pairs. Differently from fixed pairs that undergo
337 a process of mutual habituation as they develop a stable route that likely reduces conflicts, the introduction
338 of a naïve individual at the start of each generation repeatedly creates an experience imbalance in the
339 newly formed pair. This experience imbalance could be the source of new conflicts possibly explaining why
340 experimental pairs reach levels of exploration generally higher than those of fixed pairs. The process of
341 gradually settling on a joint route over the course of a generation following this initial perturbation is also
342 reminiscent of the transient effects observed when an ant with outside information joins a group of
343 nestmates transporting an object: the new information temporarily steers the collective in the right direction
344 but its effects on collective motion vanish quickly (Gelblum et al. 2015, 2016, 2020).

345    Adopting an explicit exploration–exploitation perspective to study search strategies and doing so
346 through the use of predictive information to quantify causal interactions has the potential to advance our
347 understanding of collective navigation in larger flocks. The conceptual framework of exploration and
348 exploitation as well as the methods we proposed can also benefit researchers studying other taxa that
349 move in groups with the potential to learn from previous experiences, such as shoaling fish or certain
350 primates. In principle, this information-theoretic approach could also be applied to the study of information
351 transfer between the environment and the individuals within a group. The ability to quantify causal
352 interactions of this sort could shed light on broader questions in ecology involving animals moving in a
353 group and their environment such as the impact of visual landmarks on navigation or the effects of terrestrial
354 migration on the environment (Bracis and Mueller 2017; de Guinea et al. 2021).

355

## Materials and Methods

357
358 Data and source code are available in (Valentini et al. 2021).

359
360 **Experimental subjects and procedure.** Data were taken from a previous study on cumulative route
361 development in the homing pigeon *Columba livia* (Sasaki and Biro 2017). Pairs of birds composed of an
362 *experienced* and a *naïve* bird were released together from the same site and allowed to fly back to the
363 home loft. Pairs were created and released over 5 successive generations of a transmission chain, each
364 generation lasting 12 consecutive releases of the same pair, according to the following procedure: initially,
365 at generation 1, a naïve bird was released alone 12 times, allowing it to develop its own idiosyncratic route
366 to the home loft. This bird, now experienced, was then paired with a new (naïve) bird at generation 2, and
367 together they performed another 12 flights. This process was then repeated in the next generation with a
368 new pair of birds composed of the former naïve bird and of a new naïve one. Data were gathered for a total
369 of 10 independent transmission chains, each lasting 5 generations (see Sasaki and Biro 2017 for details).
370 Birds flying at an average linear distance greater than 250 meters from each other were not considered as
371 pairs and were thus excluded from the analysis, leaving 343 flights with a mean ± SD flight duration of
372 $8.65 \pm 1.33$ minutes. Additionally, in two control conditions, nine solo birds and six pairs (all initially naïve)
373 were released from the same site for a total of 60 releases (the equivalent of $5 \times 12$ releases for the
374 transmission chains).
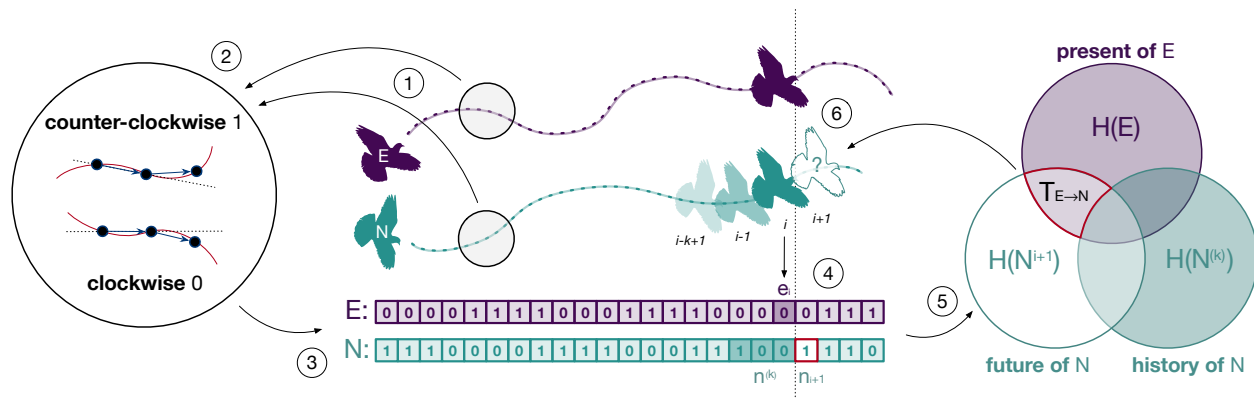


375
376 *Figure 1. Illustration of the methodological approach. The spatial trajectories of an experienced (E) and a naïve (N) bird*
377 *(point 1) are encoded as clockwise and counter-clockwise rotations (point 2) which we represent as discrete time series*
378 *(point 3). The combination of rotations encoded in both series (point 4) is used to estimate the probabilities required to*
379 *compute transfer entropy (point 5) and to determine the influence of one individual over the future behavior of the other*
380 *(point 6). This example illustrates transfer entropy from experienced to naïve, but we also computed it for the opposite*
381 *direction.*

382 **Data collection and pre-processing.** Flight trajectories of birds were sampled at a frequency of 5 Hz
383 using GPS loggers, converted from the geographic coordinate system to the metric system, and projected
384 over the 2-dimensional plane (see Sasaki and Biro 2017). Each trajectory consisted of a time-ordered
385 series of positions in space, $(x_i : (x^1, x^2)_i, i \geq 1)$, see Figure 1 (point 1). We encoded the pattern of rotations
386 of each flight using a binary symbolic representation where symbols $0$ and $1$ represent, respectively, a

11

387  *clockwise* and a *counter-clockwise* rotation (point 2). The direction of rotation was computed as the cross

388  product $\overrightarrow{x_{i-1}x_i} \times \overrightarrow{x_i x_{i+1}}$ between the motion vector at time $i$ and that at time $i + 1$. The rotation is clockwise

389  when the product is negative and counter-clockwise when it is positive. We also measured the distance

390  $d_{EN}(i)$ of the experienced bird from the naïve one projected over the current direction of motion of the pair

391  (cf. Nagy et al. 2010 and Supplementary Material). Using this distance, we then determined the relative

392  position of birds over time: when $d_{EN} > 0$, the experienced bird was flying ahead of the naïve bird; when

393  $d_{EN} < 0$, it was flying behind. Previous tests using the same GPS loggers showed that these devices have

394  a sufficient level of accuracy with a small normally distributed spatial error (SD of 0.05 meters) affecting

395  the tracking accuracy of the direction of motion and a relatively larger error (median of 1.69 meters)

396  affecting that of the relative position (Pettit, Perna, et al. 2013).

397

398  **Measuring information transfer.** We quantified the amount of information transferred between birds

399  using information-theoretic measures (Cover and Thomas 2005; Pilkiewicz et al. 2020) estimated from the

400  series of rotations of the experienced, $E = (e_i, i \geq 1)$, and of the naïve, $N = (n_i, i \geq 1)$, birds (Figure 1,

401  point 3). We aimed to quantify causal interactions between birds in a Wiener–Granger sense by measuring

402  the extent to which the current behaviour of one bird allows us to predict the future behaviour of the other

403  (Bossomaier et al. 2016). Here we describe the process for predicting the naïve bird's behaviour from that

404  of the experienced one, but we also used the same method for the opposite direction. The average amount

405  of information necessary to fully predict the next rotation of the naïve bird is quantified by the marginal

406  entropy of its series of rotations $H(N^{i+1}) = -\sum_{n_i} p(n_i) \log_2 p(n_i)$ (Figure 1, Venn diagram, lower-left set).

407  This is equal to 1 bit if the flight of the naïve bird is maximally uncertain (i.e., clockwise and counter-

408  clockwise rotations are equally likely) and to 0 bits if the flight is fully deterministic (i.e., rotations are either

409  all clockwise or all counter clockwise). As a result of temporal autocorrelation (Mitchell et al. 2019), part of

410  this information might be contained in the recent history of rotations of the naïve bird, $n_i^{(k)} =$

411  $\{n_{i-k+1}, \dots, n_{i-1}, n_i\}$ for history length $k$ (Figure 1, point 4, dark green entries in the naïve time series). The

412  remaining predictive information, which is not explained by the past behaviour of the naïve bird, is

413  quantified by the marginal entropy,

414
$$H(N^{i+1}|N^{(k)}) = -\sum_{n_i^{(k)}, n_{i+1}} p(n_i^{(k)}, n_{i+1}) \log_2 \frac{p(n_i^{(k)}, n_{i+1})}{p(n_i^{(k)})},$$

415  of its future rotations, $N^{i+1}$, conditioned on the outcome of the past $k$ rotations, $N^{(k)}$ (Figure 1, Venn

416  diagram, overlap of the white and light purple areas).

417      Of interest to us was how much of this remaining information (necessary to predict the future

418  direction of rotation of the naïve bird) can be obtained by the current behaviour of the experienced bird

419  (Figure 1, points 4–6). This is given by the transfer entropy, which estimates the time-delayed effects on

420  the naïve bird of its interaction with the experienced one: $T_{E \to N} = H(N^{i+1}|N^{(k)}) - H(N^{i+1}|N^{(k)}, E)$

421  (Schreiber 2000). Transfer entropy is time directional, from the present of one bird to the future of the other,

12

422 and considered for this reason a measure of information transfer (Lizier and Prokopenko 2010). It is defined

423 as

$$T_{E \rightarrow N} = \sum_{n_{i+1},\, n_i^{(k)}, e_i} p(n_{i+1}, n_i^{(k)}, e_i) \log_2 \frac{p(n_{i+1} \mid n_i^{(k)}, e_i)}{p(n_{i+1} \mid n_i^{(k)})}$$

425 and formally measures the reduction of uncertainty of the future rotation $N^{i+1}$ of the naïve bird given by

426 knowledge of the current rotation $E$ of the experienced bird at the net of possible autocorrelations in the

427 naïve bird's past $N^{(k)}$ (Figure 1, Venn diagram, area with red border). The logarithmic part of the above

428 equation is known as local transfer entropy and measures over time whether the interaction at time $i$

429 (Figure 1, point 4, dark green and dark purple entries) was informative (positive) or misinformative

430 (negative) (Lizier, Prokopenko, and Zomaya 2008).

431 The above information-theoretic measures were computed in R 3.6.1 using the rinform-1.0.2

432 package (Moore et al. 2018) by estimating probabilities separately for each flight. To test whether causal

433 interactions were significant, we also evaluated a surrogate dataset artificially created by pairing

434 trajectories of birds that were not flown together: the trajectory of each experienced (or naïve) bird was

435 paired with that of the naïve (or experienced) one from every other pair of birds not containing the same

436 subjects.

437

438 **Measuring exploration and exploitation.** Pairwise analysis of successive routes from the last three flights

439 of the experienced bird during training (generation 1) showed that, once established, the bird largely

440 remained within a point-to-point distance of 300 meters from its idiosyncratic route (Figure S3a). Therefore,

441 we used 300 meters as a threshold to differentiate flight segments between those exploring new solutions

442 and those exploiting known ones. We then compared the trajectories of consecutive flights for the same

443 subjects to label each segment in the experimental and control datasets. For each focal trajectory that we

444 aimed to label, we considered the trajectory of the previous release as a baseline trajectory for the

445 comparison. In the case of paired birds (i.e., both experimental and fixed-pairs control), we considered the

446 trajectory of the pair defined by the mean position of the two birds over time. For the first release of each

447 generation in the experimental group, we used as baseline trajectory the last release of the previous

448 generation because in this case there was no previous flight of the same pair to compare with. This

449 approach to define exploration and exploitation led to a model of exploitation (*i.e.*, the baseline trajectory)

450 that varied over successive releases. Because the introduction of a naïve bird at each generation was likely

451 to affect the baseline model of exploitation in a more pronounced manner than that of solo and fixed pairs

452 of birds, this model might have been susceptible to differences between the experimental design of

453 transmission chain experiments with respect to those of the two controls. To control for this scenario, we

454 also explored an alternative approach where exploitation was defined on the basis of only information

455 available to the experienced bird at the beginning of a new generation. In this case, the last release of the

456 previous generation was used as the baseline trajectory for all releases within a given generation (see

457     Supplementary Methods). In both cases, we also measured the distance $d_{EN}(i)$ between experienced and

458     naïve birds to determine which bird was flying at the front of the pair for a given route segment.

459

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613

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## Author contributions statement

GV and TS designed the study with input from all authors. TS and DB provided data. GV analysed data with feedback from all authors. All authors contributed to the writing of the manuscript.

## Additional information

**Competing interests:** The authors declare no competing interest.

1  # Supplementary Information

2

3  ## *Naïve individuals promote collective exploration in homing*
4  ## *pigeons*

5
6  **Gabriele Valentini, Theodore P. Pavlic, Sara Imari Walker**, **Stephen C. Pratt, Dora Biro &**
7  **Takao Sasaki**
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13  ## Methods

14  **Relative position of birds over time.** We determined the relative position of each bird within the pair using

15  the distance $d_{EF}$ of the experienced bird from the naïve one projected onto the direction of motion of the

16  flock. We modified the method proposed in (Nagy et al. 2010), which gives the distance of the experienced

17  bird from the centre of the flock, to also include the segment from the centre of the flock to the naïve bird.

18  This is given by

19
$$d_{EN}(i) = \left(\overrightarrow{x_E}(i) - \overrightarrow{x_N}(i)\right) \cdot \overrightarrow{v_{pair}}(i) \cdot 2,$$

20  where $\overrightarrow{x_E}(i)$ and $\overrightarrow{x_N}(i)$ are the positions of the experienced and the naïve bird and $\overrightarrow{v_{pair}}(i)$ is the normalized

21  velocity of the pair. The normalized velocity is computed as

22
$$\overrightarrow{v_{pair}}(i) = \frac{\langle \overrightarrow{x_k}(i) \rangle_k}{\left| \langle \overrightarrow{x_k}(i) \rangle_k \right|}.$$

23  As the flock is composed of two birds only, the projected distance of the experienced bird from the naïve

24  one projected onto the direction of motion of the pair is positive, when the experienced bird is flying *ahead*

25  of the naïve one, and it is negative when the experienced bird is flying *behind*.

26

27  **Exploration–exploitation with respect to the previous generation.** Our primary approach to define

28  exploration and exploitation is based on comparing pairs of successive releases using the trajectory of the

29  previous release as our baseline model of exploitation and then labelling newer portions of a focal route as

30  exploration. The model of exploitation (i.e., baseline trajectory) thus varies for each focal release similarly

31  to a moving-average window over successive releases. An alternative approach to define exploration and

32  exploitation is to consider a constant model of exploitation for each release within a given generation. This

33  can be obtained by setting the baseline trajectory to equal the last trajectory of the previous generation. As

34  a consequence, exploitation is defined on the basis of the information available only to the experienced bird

35  at the beginning of a new generation; every portion of the route within that generation that is more than 300

36  meters away from the baseline is considered exploration.

37  At the first generation of the experimental group, when birds are trained individually for the

38  successive transmission chain experiment and there is no previous generation available to provide us with

1

39    a baseline trajectory, we consider the first release as the baseline trajectory for the remainder of the

40    generation. In the case of solo and fixed pairs controls, for which there is no obvious definition of a

41    generation, we considered the 60 releases in each of these experiments as formed by 5 generations, each

42    lasting 12 releases, and used an equivalent approach to that of the experimental group to define exploration
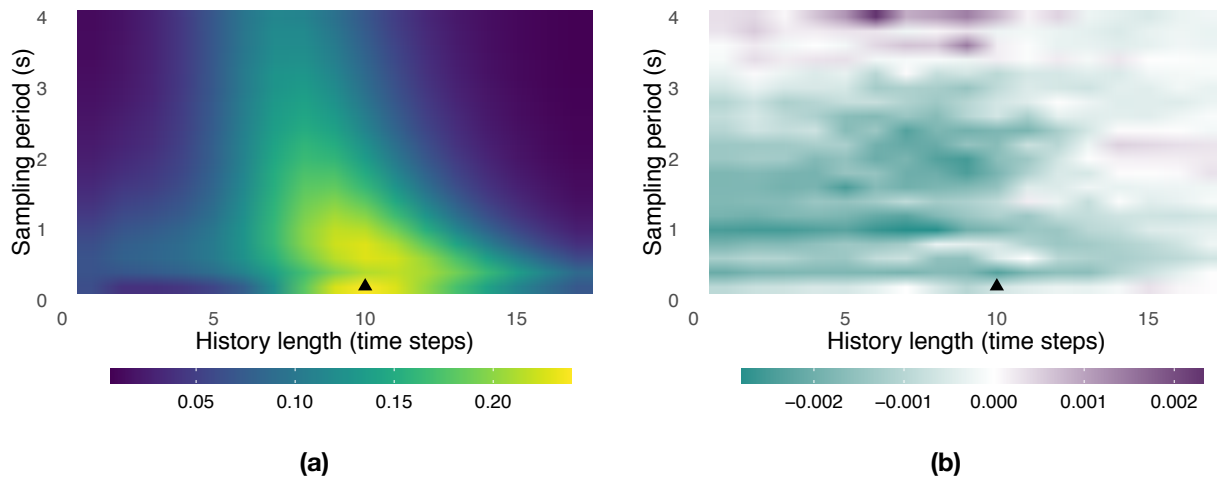
43    and exploitation.

44

45    **Results**

46



(a)        (b)

*Figure S1. Landscape of information transfer as a function of the history length, $k \in \{1, ..., 17\}$, and of the sampling period, $\{0.2, 0.4, ..., 4.0\}$ seconds. Panel (a) shows the total transfer of information between the pair of birds, $T_{E \to N} + T_{N \to E}$, averaged over all releases and generations. Panel (b) shows the net transfer of information between the pair of birds, $T_{E \to N} - T_{N \to E}$, averaged over all releases and generations. Positive (respectively, negative) values represent configurations where the experienced (naïve) bird is more informative than the naïve (experienced) one. The triangle represents the configuration with maximum total transfer of information.*

47    **Landscape of information transfer and choice of parameters.** We first explored how information

48    transfer between the birds varied as a function of two parameters: the sampling period (seconds) and the

49    history length used in the computation of transfer entropy. Our original GPS data are sampled at a frequency

50    of 1 sample every 0.2 seconds (5 Hz); we can further subsample these data by dropping samples, for

51    example, using one sample every 0.4, 0.6, ..., 4.0 seconds as the sampling period. The history length

52    represents the number of past rotations by the bird we want to predict that we consider when computing

53    transfer entropy from the other bird in the pair.

54       The total transfer of information between the birds varies as a function of these parameters (Figure

55    S1a). It peaks in the region delimited by history lengths of 8–10 time-steps and a sampling period between

56    0.2–1.2 seconds, whereas it vanishes otherwise. The total transfer of information, which is generally

57    adopted as a measure to choose study parameters (Porfiri 2018), reaches its maximum for a history length

58    of $k = 10$ at one sample every 0.2 seconds (black triangle in Figure S1a). We use this parameter

59    configuration for the rest of our information-theoretic analysis. For this and for most other parameter

60    configurations, the naïve bird is more informative about the future behaviour of the experienced one than

61     the other way around (Figure S1b). Only in two regions, both far from the point maximizing the total transfer

62     of information, is the experienced bird more informative than the naïve one; however, the overall amount

63     of information transferred between birds in these regions is negligible.

64

65     **Comparison of information transfer with the surrogate dataset.** To verify their significance, we

66     compared our estimates of information transfer between the two birds with equivalent measurements taken

67     from the surrogate dataset. We expect causal effects measured in the original dataset to be stronger than

68     those found in the surrogate one. As shown in Table S1, our expectations are fully met: the original dataset

69     shows values of transfer entropy significantly higher than those observed in the surrogate dataset, both for

70     the entire dataset as well as for each separate generation.

71

72     *Table S1. Statistical comparison of information transfer between the original and the surrogate dataset over all*
73     *generations and over separate generations. Column 1 reports the generation and sample sizes. Columns 2 and 4 report*
74     *the differences between the mean value of transfer entropy of the original dataset and that of the surrogate dataset.*
75     *Columns 3 and 5 report the results of one-sided two-sample Whitney–Mann–Wilcoxon rank-sum tests with continuity*
76     *correction ($p$-value and $W$ statistic) testing if the original dataset has significantly higher transfer entropy than the*
77     *surrogate one. Significant $p$-values are reported in bold.*

*Original vs surrogate dataset*

| Generation | $T_{E\rightarrow N} - T^s_{E\rightarrow N}$ | $H_1: T_{E\rightarrow N} > T^s_{E\rightarrow N}$ | $T_{N\rightarrow E} - T^s_{N\rightarrow E}$ | $H_1: T_{N\rightarrow E} > T^s_{N\rightarrow E}$ |
|---|---|---|---|---|
| All ($n = 343, n^s = 29035$) | $\mu = 0.0089$ | $\boldsymbol{p <.001}$ ($W = 6145522$) | $\mu = 0.0088$ | $\boldsymbol{p <.001}$ ($W = 6126284$) |
| 2 ($n = 94, n^s = 7912$) | $\mu = 0.0062$ | $\boldsymbol{p <.001}$ ($W = 445262$) | $\mu = 0.0074$ | $\boldsymbol{p <.001}$ ($W = 452733$) |
| 3 ($n = 99, n^s = 9801$) | $\mu = 0.0094$ | $\boldsymbol{p <.001}$ ($W = 615721.5$) | $\mu = 0.0119$ | $\boldsymbol{p <.001}$ ($W = 645665.5$) |
| 4 ($n = 81, n^s = 6561$) | $\mu = 0.0071$ | $\boldsymbol{p =.006}$ ($W = 308433.5$) | $\mu = 0.0057$ | $\boldsymbol{p =.015}$ ($W = 303085.5$) |
| 5 ($n = 69, n^s = 4761$) | $\mu = 0.0111$ | $\boldsymbol{p <.001}$ ($W = 214258.5$) | $\mu = 0.0075$ | $\boldsymbol{p =.002}$ ($W = 197618.5$) |

78

79     **Analysis of time spent by each bird at the front of the pair.** We divided each flight into different

80     segments, with each segment representing a consecutive portion of the route with either the experienced

81     or the naïve bird at the front of the pair, and then measured the segment durations (Figure S2). The

82     distribution of segment durations resembles a log-normal distribution for both the entire dataset and for

83     individual generations. Experienced and naïve birds are characterized by very similar distributions closely

84     overlapping each other. Overall, the naïve bird spent significantly longer periods of time at the front of the

85     pair (Table S2), but the difference is small and largely driven by that of generation 3 (the only generation

86     showing significant differences). With the exception of generation 3, the experienced and the naïve bird

87     spent, on average, an approximately equal portion of the route at the front of the pair (Table S3). At

88     generation 3, the naïve bird was at the front of the pair for a significantly larger portion of the route with

89     respect to the experienced bird (respectively, 54% versus 46%).
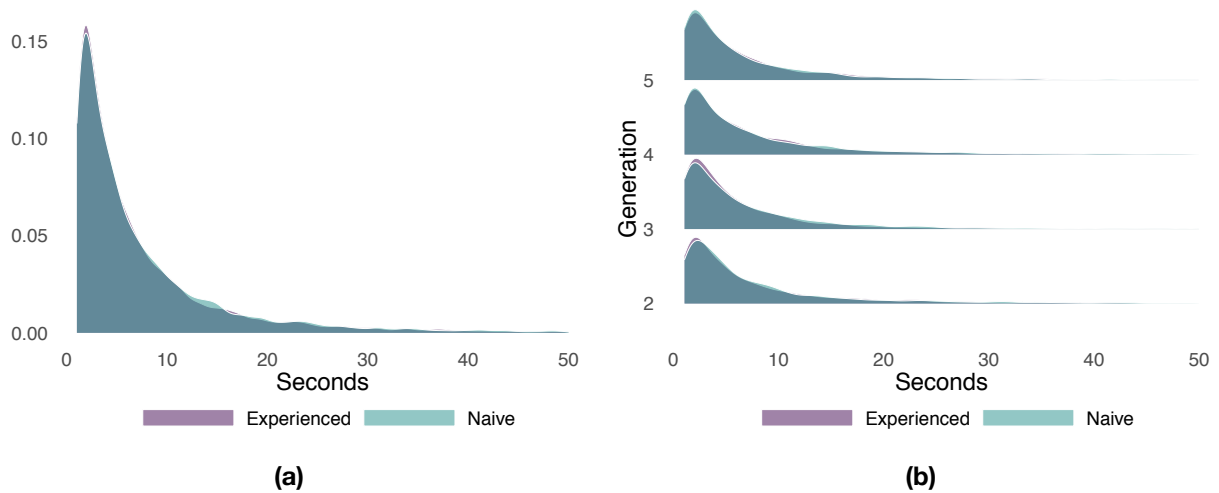
**(a)**                    **(b)**

Figure S2. Probability density function of the duration of flight segments with either the experienced or the naïve bird at the front of the pair. Panel (a) shows the results aggregated over all generations. Panel (b) shows the results separately for each generation.

Table S2. Statistics about the duration of flight segments with either the experienced or the naïve bird at the front of the pair. Column 1 reports the generation and sample sizes. Columns 2 and 3 give the mean duration and the standard deviation of segments for the experienced and for the naïve bird. Column 4 reports the results of two-sided two-sample Whitney–Mann–Wilcoxon rank-sum tests with continuity correction ($p$-value and $W$ statistic) testing differences between the distribution of the duration $D$ of flight segments for the two birds. Significant $p$-values are reported in bold.

| Generation | Experienced | Naïve | $H_1: D_E \neq D_N$ |
|---|---|---|---|
| All ($n^E = 10725, n^N = 10773$) | $\mu = 7.93, \sigma = 12.92$ | $\mu = 8.23, \sigma = 14.12$ | $\boldsymbol{p =.047}$ ($W = 56865638$) |
| 2 ($n^E = 2512, n^N = 2492$) | $\mu = 8.89, \sigma = 17.51$ | $\mu = 8.81, \sigma = 13.55$ | $p = .13$ ($W = 3052262$) |
| 3 ($n^E = 3690, n^N = 3737$) | $\mu = 6.83, \sigma = 9.08$ | $\mu = 7.96, \sigma = 14.51$ | $\boldsymbol{p <.001}$ ($W = 6588674$) |
| 4 ($n^E = 2297\ n^N = 2283$) | $\mu = 8.63, \sigma = 13.65$ | $\mu = 8.55, \sigma = 14.23$ | $p = .86$ ($W = 2630132$) |
| 5 ($n^E = 2226, n^N = 2261$) | $\mu = 7.98, \sigma = 11.23$ | $\mu = 7.73, \sigma = 13.93$ | $p = .23$ ($W = 2568854$) |

Table S3. Statistics about the proportion of a flight with either the experienced or the naïve bird at the front of the pair. Column 1 reports the generation and sample size. Columns 2 and 3 give the mean and the standard deviation of the proportion of a flight with either the experienced or the naïve bird at the front of the pair. Column 4 reports the results of two-sided paired Wilcoxon signed-rank tests with continuity correction ($p$-value and $V$ statistic) testing differences between the distribution of the proportion $P$ of a flight for the two birds. Significant $p$-values are reported in bold.

| Generation | Experienced | Naïve | $H_1: P_E \neq P_N$ |
|---|---|---|---|
| All ($n = 341$) | $\mu = 0.49, \sigma = 0.2$ | $\mu = 0.51, \sigma = 0.2$ | $p = .46$ ($V = 27817.5$) |
| 2 ($n = 92$) | $\mu = 0.51, \sigma = 0.23$ | $\mu = 0.49, \sigma = 0.23$ | $p = .69$ ($V = 2243$) |
| 3 ($n = 99$) | $\mu = 0.46, \sigma = 0.17$ | $\mu = 0.54, \sigma = 0.17$ | $\boldsymbol{p =.03}$ ($V = 1851$) |
| 4 ($n = 81$) | $\mu = 0.5, \sigma = 0.2$ | $\mu = 0.5, \sigma = 0.2$ | $p = .84$ ($V = 1705$) |
| 5 ($n = 69$) | $\mu = 0.49, \sigma = 0.2$ | $\mu = 0.51, \sigma = 0.2$ | $p = .95$ ($V = 1219$) |

4

106 **Exploration versus exploitation with respect to successive releases.** We used a distance-based
107 mechanism to label portions of a focal route as either exploration or exploitation depending on their point-
108 to-point distance from the baseline trajectory at the previous release. To determine a suitable threshold, we
109 compared successive trajectories flown by the experienced bird towards the end of training (generation 1,
110 last three flights) and studied the distribution of distances between successive trajectories (Figure S3a).
111 The distribution of distances is right-skewed and approximately exponential. A threshold of 300 meters
112 captures a large portion of the probability mass, about 70.5%, whereas larger distances are progressively
113 less likely. On this basis, we set a threshold of 300 meters to distinguish between phases of exploitation
114 ($< 300$ meters) and phases of exploration ($\geq 300$ meters). Figure S3b shows the distribution of distances
115 between consecutive flights observed during each generation whereas Figure S4a shows the same results
116 aggregated over all generations as well as the proportion of time (inset) that each bird is leading as a
117 function of the same distance. Figures S4b and S4c show similar results for fixed pairs of birds and solo
118 individuals. Whereas fixed pairs are characterized by a distribution similar to that of experimental pairs, solo
119 birds have a markedly shifted distribution towards exploitation at the expense of exploration.



(a)  (b)
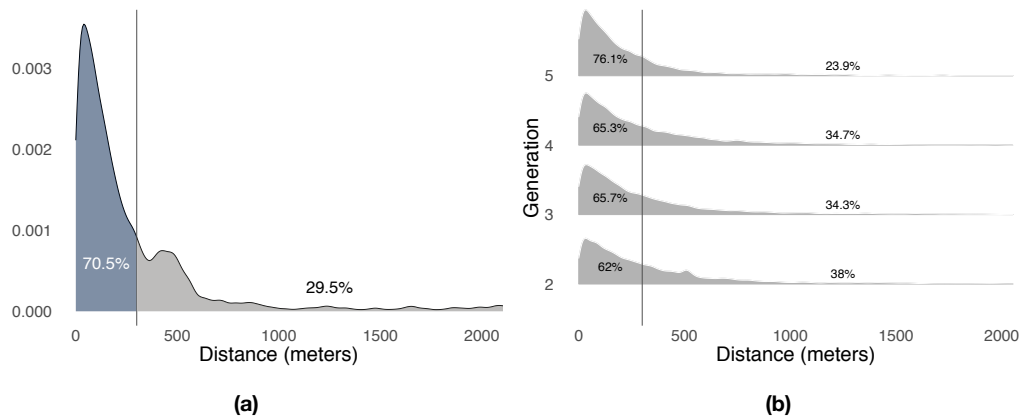
120
121 *Figure S3. Distribution of minimum distances between the pairs of consecutive flights. Panel (a) shows the results for*
122 *the trained birds during the first generation of the experiment. Panel (b) shows the results for the pair of birds during all*
123 *remaining generations of the experiments. Vertical lines highlight the division of the probability mass between*
124 *exploitation (left) and exploration (right) defined by a 300 meters threshold.*

125



(a)  (b)  (c)
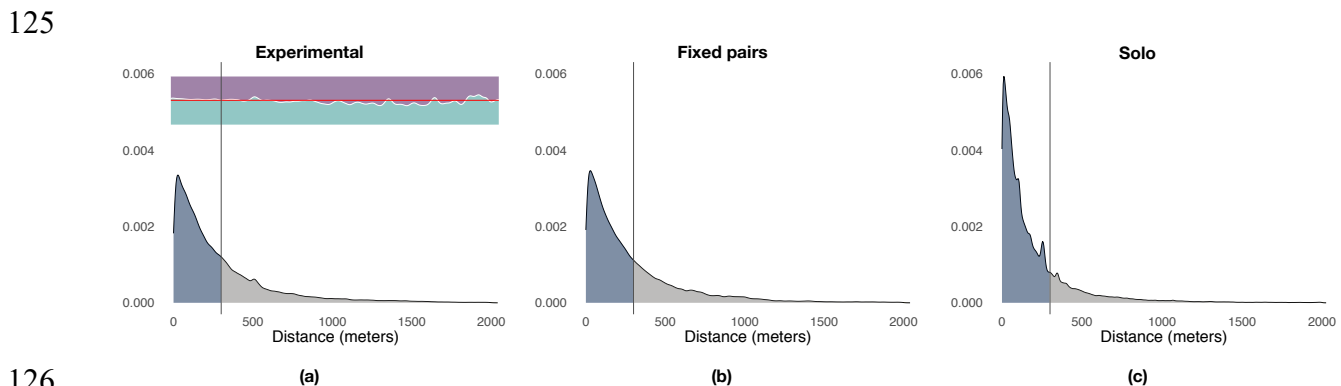
126
127 *Figure S4. Illustration of the distribution of point-to-point distances between pairs of consecutive flights highlighting the*
128 *300 meter threshold that demarks the end of exploitation and the beginning on exploration. Panel (a) reports the results*
129 *for experimental pairs over generations 2–5, panel (b) reports those for the fixed pairs control, and panel (c) those for*

5

130 *the solo control. The inset in panel (a) shows the proportion of times each bird is leading the flock as a function of the*
131 *distance between current and previous trajectory (purple represents the experienced bird, green the naïve one).*

132 We compared the proportion of exploration and exploitation across experimental conditions before the
133 beginning (*i.e.*, generation 1) and during transmission chain experiments (*i.e.*, generation 2 to 5). During
134 the first 12 releases (Table S4), individuals from the experimental group that flew solo during generation 1
135 could not be distinguished from birds in the solo control whereas fixed pairs of birds showed levels of
136 exploration significantly higher than those of solo birds. During releases 13 to 60, that is, when naïve
137 individuals are iteratively introduced in the transmission chains at the beginning of each generation,
138 experimental pairs showed instead significantly higher levels of exploration than both solo and fixed pairs
139 of birds, with these former exploring much less than birds that flew in pairs.

140
141 *Table S4. Statistical comparison of mean proportions of a flight spent exploring versus exploiting across treatments*
142 *(experimental pairs, solo and fixed pairs controls) for the first 12 releases (generation 1) and for releases 13 to 60*
143 *(generation 2 to 5). Entries report the proportion of exploration vs exploitation for pairs of treatments as well as the*
144 *results of two-sided two-sample Whitney–Mann–Wilcoxon rank-sum tests with continuity correction ($p$-value and $W$*
145 *statistic) for differences in proportion of exploration. Significant $p$-values are reported in bold. Results of testing for the*
146 *proportion of exploitation are equivalent and not repeated below.*

| *Releases* | *Dataset* | Solo control | Fixed pairs control |
|---|---|---|---|
| 1 to 12 | Experimental (gen. 1) | Row: 36.7% vs 63.3%<br>Col: 34.2% vs 65.8%<br>$p = .55$ ($W = 5288$) | Row: 36.7% vs 63.3%<br>Col: 51.7% vs 48.3%<br>$\boldsymbol{p <.001}$ ($W = 2230$) |
| | Solo control | – | Row: 36.7% vs 63.3%<br>Col: 34.2% vs 65.8%<br>$\boldsymbol{p <.001}$ ($W = 1837$) |
| 13 to 60 | Experimental (gen. 2-5) | Row: 32.9% vs 67.1%<br>Col: 15.7% vs 84.3%<br>$\boldsymbol{p <.001}$ ($W = 94108.5$) | Row: 32.9% vs 67.1%<br>Col: 29.3% vs 70.7%<br>$\boldsymbol{p =.0456}$ ($W = 50472$) |
| | Solo control | – | Row: 15.7% vs 84.3%<br>Col: 29.3% vs 70.7%<br>$\boldsymbol{p <.001}$ ($W = 31517$) |

147

148 **Exploration versus exploitation with respect to the previous generation.** In addition to the exploration–
149 exploitation analysis with respect to successive releases, we also performed a similar analysis where
150 exploitation is defined with respect to the previous generation (see supplementary Methods above) in order
151 to validate the robustness of the main results obtained with our primary approach. The distributions of point-
152 to-point distances between baseline and focal trajectories (Figure S5) resembled those observed when
153 comparing successive releases (Figure S4). Differences across experimental and control treatments (Table
154 S5) were much more pronounced under this model but in line with the results obtained above (Table S4).
155 Moreover, the overall exploration trends reported in Figure S6 showed the same signatures of the analysis
156 over successive releases (Figure 5a). Exploration decreased over generations in all experimental
157 conditions with experimental pairs exploring more than both fixed pairs of birds and solo individuals.

158

159

160

**(a)**         **(b)**         **(c)**
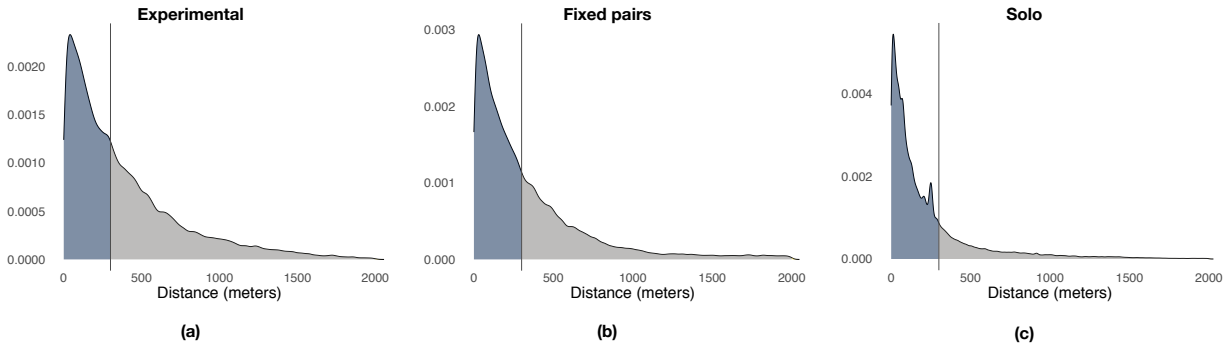
*Figure S5. Illustration of the distribution of point-to-point distances between each flight of a generation (focal trajectories) and the last flight of the previous generation (baseline trajectory). Colors and vertical lines highlight the 300 meter threshold that demarks the end of exploitation and the beginning of exploration. Panel (a) reports the results for experimental pairs over generations 2–5, panel (b) reports those for the fixed pairs control, and panel (c) those for the solo control.*

*Table S5. Statistical comparison of mean proportions of a flight spent exploring versus exploiting across treatments (experimental pairs, solo and fixed pairs controls) for the first 12 releases (generation 1) and for releases 13 to 60 (generation 2 to 5) when considering the last release at the previous generation as the baseline trajectory. Entries report the proportion of exploration vs exploitation for pairs of treatments as well as the results of two-sided two-sample Whitney–Mann–Wilcoxon rank-sum tests with continuity correction ($p$-value and $W$ statistic) for differences in proportion of exploration. Significant $p$-values are reported in bold. Results of testing for the proportion of exploitation are equivalent and not repeated below.*

| *Releases* | *Dataset* | Solo control | Fixed pairs control |
|---|---|---|---|
| 1 to 12 | Experimental (gen. 1) | Row: 61.5% vs 38.5%<br>Col: 55.8% vs 44.2%<br>$p = .11$ ($W = 5592$) | Row: 61.5% vs 38.5%<br>Col: 82.9% vs 17.1%<br>$\boldsymbol{p < .001}$ ($W = 1721$) |
| | Solo control | – | Row: 55.8% vs 44.2%<br>Col: 82.9% vs 17.1%<br>$\boldsymbol{p < .001}$ ($W = 1163$) |
| 13 to 60 | Experimental (gen. 2-5) | Row: 46.6% vs 53.4%<br>Col: 18.9% vs 81.1%<br>$\boldsymbol{p < .001}$ ($W = 103095$) | Row: 46.6% vs 53.4%<br>Col: 32.4% vs 67.6%<br>$\boldsymbol{p < .001}$ ($W = 60502$) |
| | Solo control | – | Row: 18.9% vs 81.1%<br>Col: 32.4% vs 67.6%<br>$\boldsymbol{p < .001}$ ($W = 30744$) |
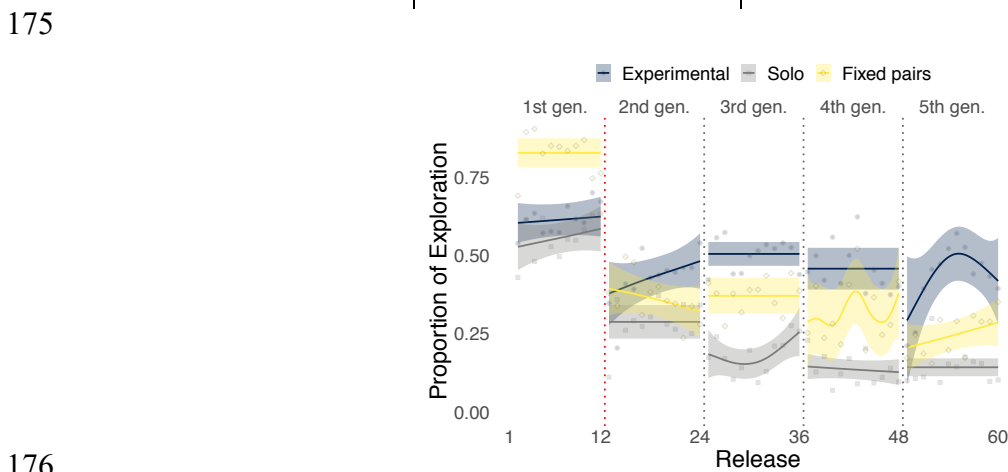


*Figure S6. Illustration of the proportion of exploration (respectively, one minus the proportion of exploitation) over releases when considering the last release at the previous generation as the baseline trajectory. Results are shown for*

7

179     *the experimental group, the solo control, and the fixed pairs control. The red dotted vertical line delineates the end of*
180     *the experimental group's training phase. Smoothed lines are computed with generalized additive models using*
181     *shrinkage cubic regression splines (mean and standard error); points represent averages for individual releases.*

182     **The role of leadership during exploration and exploitation.** Using this distance-based mechanism, we

183     label each segment of a flight as either exploration or exploitation. For each segment, we keep track of

184     which bird, experienced or naïve, is leading the pair. We then compute the proportion of time spent by the

185     experienced bird and by the naïve one leading the pair during either an exploration or exploitation phase

186     (Table S6). The combined proportion of time of both birds in either exploration or exploitation gives instead

187     the corresponding contribution of the pair. Overall, each bird spends approximately 16.5% of the time

188     leading the pair during an exploration phase and 33.5% of the time leading the pair during an exploitation

189     phase. With the exception of exploitation phases in generation 3, there is no significant difference between

190     the proportion of time spent by the two bird in an exploration or exploitation phase (Table S7).

191

192     *Table S6. Proportion of a flight led by each of the two birds, calculated separately for exploration and exploitation*
193     *phases. Column 1 reports the generation and sample size. Columns 2 and 3 give the mean and the standard deviation*
194     *of the proportion of a flight led, respectively, by the experienced and the naïve bird for the case of exploration. Columns*
195     *4 and 5 give the mean and the standard deviation of the proportion of a flight led, respectively, by the experienced and*
196     *the naïve bird for the case of exploitation.*

| | Exploration | | Exploitation | |
| --- | --- | --- | --- | --- |
| *Generation* | *Experienced* | *Naïve* | *Experienced* | *Naïve* |
| All $(n = 341)$ | $\mu = 0.17, \sigma = 0.15$ | $\mu = 0.16, \sigma = 0.13$ | $\mu = 0.32, \sigma = 0.18$ | $\mu = 0.35, \sigma = 0.2$ |
| 2 $(n = 92)$ | $\mu = 0.2, \sigma = 0.17$ | $\mu = 0.17, \sigma = 0.14$ | $\mu = 0.31, \sigma = 0.2$ | $\mu = 0.32, \sigma = 0.21$ |
| 3 $(n = 99)$ | $\mu = 0.16, \sigma = 0.13$ | $\mu = 0.19, \sigma = 0.13$ | $\mu = 0.3, \sigma = 0.16$ | $\mu = 0.36, \sigma = 0.17$ |
| 4 $(n = 81)$ | $\mu = 0.18, \sigma = 0.16$ | $\mu = 0.16, \sigma = 0.13$ | $\mu = 0.32, \sigma = 0.18$ | $\mu = 0.34, \sigma = 0.22$ |
| 5 $(n = 69)$ | $\mu = 0.13, \sigma = 0.13$ | $\mu = 0.1, \sigma = 0.1$ | $\mu = 0.37, \sigma = 0.17$ | $\mu = 0.4, \sigma = 0.21$ |

197

198     *Table S7. Statistical comparison of leadership by experienced vs. naïve birds, tested separately for exploration and*
199     *exploitation over all generations and over separate generations. Column 1 reports the generation and sample size.*
200     *Columns 2 and 3 report the results of two-sided paired Wilcoxon signed-rank tests with continuity correction (p-value*
201     *and V statistic) for differences in proportion of flight led between experienced and naïve birds for exploration and*
202     *exploitation, respectively. Significant p-values are reported in bold.*

| | Experienced vs Naïve | |
| --- | --- | --- |
| *Generation* | *Exploration* | *Exploitation* |
| All $(n = 341)$ | $p = .44 \ (V = 28820)$ | $p = .13 \ (V = 26240)$ |
| 2 $(n = 92)$ | $p = .17 \ (V = 2490)$ | $p = .71 \ (V = 2048)$ |
| 3 $(n = 99)$ | $p = .08 \ (V = 1891)$ | $\boldsymbol{p = .035} \ (V = 1871)$ |
| 4 $(n = 81)$ | $p = .36 \ (V = 1767)$ | $p = .79 \ (V = 1603)$ |
| 5 $(n = 69)$ | $p = .22 \ (V = 1187)$ | $p = .8 \ (V = 1131)$ |

203
204 **Transitions between phases of exploration and exploitation.** Although once initiated, phases of
205 exploration and phases of exploitation are led in equal manner by the experienced and the naïve bird, the
206 experience unbalance within the pair might affect the likelihood of a bird to initiate transitions from one
207 phase of the exploration–exploitation process to other. To investigate this question, we measured transition
208 probabilities for both birds over generations (Table S8) and over releases (Table S9). Transitions from
209 exploration to exploitation are not significantly different between experienced and naïve birds, but
210 transitions from exploitation to exploration are significantly (albeit marginally) more likely to be initiated by
211 naïve birds. However, this result seems driven by the data of generation 3, where the naïve individual is
212 marginally but significantly more likely than the experienced one to initiate exploration phases, while in all
213 other generations both birds are equally likely to initiate changes in either direction. When looking at
214 transition probabilities over releases, we found a similar trend except for the first release where the naïve
215 bird is much more likely to initiate exploration phases.
216
217 *Table S8. Statistical comparison of the proportion of transitions from exploitation to exploration and from exploration to*
218 *exploitation led by the experienced and by the naïve bird over generations. Column 1 reports the generation number.*
219 *Columns 2 and 4 report the estimated probabilities that transitions are led by the experienced bird, $P_E$, and by the naïve*
220 *bird, $P_N$, for transitions, respectively, from exploitation to exploration and from exploration to exploitation. Columns 3*
221 *and 5 give the results of exact binomial tests ($p$-value and sample size $n$) of the null hypothesis that the probability $P_E$*
222 *that transitions are led by the experienced bird equals 0.5. Significant $p$-values are reported in bold.*

| | Exploitation → Exploration | | Exploration → Exploitation | |
|---|---|---|---|---|
| Generation | $P_E$ versus $P_N$ | $H_1: P_E \neq 0.5$ | $P_E$ versus $P_N$ | $H_1: P_E \neq 0.5$ |
| All | $P_E = 0.467, P_N = 0.533$ | $\boldsymbol{p = .042}$ ($n = 964$) | $P_E = 0.513, P_N = 0.487$ | $p = .42$ ($n = 966$) |
| 2 | $P_E = 0.494, P_N = 0.506$ | $p = .9$ ($n = 247$) | $P_E = 0.52, P_N = 0.48$ | $p = .56$ ($n = 244$) |
| 3 | $P_E = 0.432, P_N = 0.568$ | $\boldsymbol{p = .02}$ ($n = 301$) | $P_E = 0.483, P_N = 0.517$ | $p = .6$ ($n = 300$) |
| 4 | $P_E = 0.5, \quad P_N = 0.5$ | $p = 1$ ($n = 216$) | $P_E = 0.539, P_N = 0.461$ | $p = .28$ ($n = 219$) |
| 5 | $P_E = 0.45, P_N = 0.55$ | $p = .18$ ($n = 200$) | $P_E = 0.522, P_N = 0.478$ | $p = .57$ ($n = 203$) |

223
224 *Table S9. Statistical comparison of the proportion of transitions from exploitation to exploration and from exploration to*
225 *exploitation led by the experienced and by the naïve bird over releases. Column 1 reports the release number. Columns*
226 *2 and 4 report the estimated probabilities that transitions are led by the experienced bird, $P_E$, and by the naïve bird, $P_N$,*
227 *for transitions, respectively, from exploitation to exploration and from exploration to exploitation. Columns 3 and 5 give*
228 *the results of exact binomial tests ($p$-value and sample size $n$) of the null hypothesis that the probability $P_E$ that*
229 *transitions are led by the experienced bird equals 0.5. Significant $p$-values are reported in bold.*

| | Exploitation → Exploration | | Exploration → Exploitation | |
|---|---|---|---|---|
| Release | $P_E$ versus $P_N$ | $H_1: P_E \neq 0.5$ | $P_E$ versus $P_N$ | $H_1: P_E \neq 0.5$ |
| 1 | $P_E = 0.295, P_N = 0.705$ | $\boldsymbol{p < .01}$ ($n = 44$) | $P_E = 0.477, P_N = 0.523$ | $p = .88$ ($n = 44$) |
| 2 | $P_E = 0.478, P_N = 0.522$ | $p = .81$ ($n = 69$) | $P_E = 0.522, P_N = 0.478$ | $p = .81$ ($n = 67$) |
| 3 | $P_E = 0.519, P_N = 0.481$ | $p = .83$ ($n = 81$) | $P_E = 0.575, P_N = 0.425$ | $p = .22$ ($n = 80$) |
| 4 | $P_E = 0.576, P_N = 0.424$ | $p = .27$ ($n = 66$) | $P_E = 0.6, P_N = 0.4$ | $p = .14$ ($n = 65$) |
| 5 | $P_E = 0.487, P_N = 0.513$ | $p = .91$ ($n = 76$) | $P_E = 0.519, P_N = 0.481$ | $p = .82$ ($n = 77$) |
| 6 | $P_E = 0.54, P_N = 0.46$ | $p = .48$ ($n = 100$) | $P_E = 0.465, P_N = 0.535$ | $p = .55$ ($n = 99$) |

| | | | | |
|---|---|---|---|---|
| 7 | $P_E = 0.443, P_N = 0.557$ | $p = .34 \ (n = 88)$ | $P_E = 0.494, P_N = 0.506$ | $p = 1.0 \ (n = 89)$ |
| 8 | $P_E = 0.409, P_N = 0.591$ | $p = .18 \ (n = 66)$ | $P_E = 0.597, P_N = 0.403$ | $p = .14 \ (n = 67)$ |
| 9 | $P_E = 0.438, P_N = 0.562$ | $p = .22 \ (n = 112)$ | $P_E = 0.496, P_N = 0.504$ | $p = 1 \ (n = 115)$ |
| 10 | $P_E = 0.422, P_N = 0.578$ | $p = .17 \ (n = 90)$ | $P_E = 0.522, P_N = 0.478$ | $p = .75 \ (n = 92)$ |
| 11 | $P_E = 0.391, P_N = 0.609$ | $p = .053 \ (n = 87)$ | $P_E = 0.453, P_N = 0.547$ | $p = .45 \ (n = 86)$ |
| 12 | $P_E = 0.541, P_N = 0.459$ | $p = .52 \ (n = 85)$ | $P_E = 0.482, P_N = 0.518$ | $p = .83 \ (n = 85)$ |

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