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

the introduction of new members, even those with no prior knowledge, adds diversity that can enhance the group's behavioural solutions (Mehlhorn et al. 2015). As is often the case (Hills et al. 2015), behavioural patterns that lead to a search for improvement, whether individually, socially, or over multiple generations, involve an exploration–exploitation trade-off. In navigation problems, both solitary individuals and groups have to balance between exploiting previously acquired information necessary to navigate a known route and exploring for additional information that might allow them to approach the optimal route (Fu and Gray 2006). However, how moving collectives compromise between these tasks has received limited attention.

Understanding the exploration–exploitation trade-off is complicated by ambiguity about group leadership (Couzin et al. 2005; Garland et al. 2018). Although some collectives (*e.g.*, ants, honeybees) can allocate certain individuals to spatial exploration while others continue to exploit accumulated information (Hills et al. 2015), individuals in cohesively moving groups are highly coupled and can only benefit from compromising between exploring and exploiting if they do so in unison. If they are to stay together, the group must reach consensus between following a known route or departing from it to find better routes, foraging patches, or temporary resting locations. Elucidating whether different group members contribute differently to this process is crucial to understanding how groups compromise between exploration and exploitation.

We investigate this question in the context of navigation through natural landscapes using the homing pigeon *Columba livia* as our model system. After successive homing journeys from a given release site, pigeons develop stable idiosyncratic routes that are followed with high fidelity (Meade, Biro, and Guilford 2005; Guilford and Biro 2014). These birds rely on sequences of localized visual landmarks to recapitulate familiar yet individually distinct routes (Biro, Meade, and Guilford 2004; Meade, Biro, and Guilford 2005). Each route is learned in a gradual process starting with an exploration phase that samples new landmarks, from which the bird eventually converges upon a stable sequence of landmarks (Biro, Meade, and Guilford 2004). Experiments with paired birds show that route information can be passed from experienced birds to naïve individuals through social learning (Pettit, Flack, et al. 2013) and can be modified through information pooling when individuals with different idiosyncratic routes share information to reach a compromise between their routes (Biro et al. 2006). Although learning generally improves route efficiency, both social learning and information pooling tend to reach a plateau beyond which further improvement in efficiency is not seen. However, for birds flying together, the introduction of a naive individual in place of an experienced one effectively leads to the resumption of exploratory behaviour and further route improvement (Sasaki and Biro 2017). Yet, it remains unclear to what extent a bird's prior experience influences the balance between exploration and exploitation and how birds with potentially different route preferences jointly shape a route.

Indeed, the mechanisms underlying how different individual preferences are combined into a collective outcome is one of the key foci in studies of collective animal behaviour. Broadly, group decisions can range from despotic with a single leader to democratic in which input from different individuals is aggregated to reach consensus (Conradt and Roper 2003). Evidence of both despotic and democratic decisions exists in homing pigeons (Biro et al. 2006; Nagy et al. 2010; Jorge and Marques 2012). When leadership is defined

as disproportionate input into collective navigational decisions, either through spatial position (Pettit, Perna, et al. 2013), route similarity (Flack et al. 2012), or directional correlation delay (Nagy et al. 2010), a number of different factors have been shown to play a role in it. Leadership dynamics are influenced by individual differences among birds in fidelity to their own routes (Freeman et al. 2011), their typical flight speed (Pettit et al. 2015), their personality (Sasaki et al. 2018), as well as their level of experience (Flack et al. 2012). Moreover, equally experienced birds are known to come to a compromise by averaging their idiosyncratic routes so long as the pair's route remains within a threshold distance from each bird's favoured one – a low level of conflict. Higher levels of conflict lead instead to a splitting of the pair or to the emergence of a single leader (Biro et al. 2006). Nonetheless, experience alone is unable to fully recover the leadership structure characteristic of larger flocks (Watts et al. 2016). Spatial position offers some insight into leadership: on average, birds flying closer to the front of the flock have a stronger influence on the flock's directional choices than birds flying at the back (Nagy et al. 2010; Pettit, Perna, et al. 2013). Even so, the moment-to-moment relationship between leadership and level of experience remains unclear.

Leader–follower interactions of this sort can be accurately captured using information-theoretic measures that quantify causal relations in terms of predictive information (Butail, Mwaffo, and Porfiri 2016; Kim et al. 2018; Crosato et al. 2018; Ray et al. 2019; Valentini et al. 2020). One of these measures, *transfer entropy,* quantifies information about the future behaviour of a focal individual that can be obtained exclusively from knowledge of the present behaviour of another subject (Schreiber 2000). Transfer entropy measures information transferred from the present of the sender to the future of the receiver (Lizier and Prokopenko 2010). It explicitly accounts for autocorrelations characteristic of individual birds' trajectories (Mitchell et al. 2019) by discounting predictive information available from the sender's present that is already included in the receiver's past. Furthermore, it does not require a model of how sender and receiver interact, and it is well suited to study social interactions both over space and over time (Lizier, Prokopenko, and Zomaya 2008). Consequently, transfer entropy can capture causal interactions due not only to alignment forces (Nagy et al. 2010) but also to attraction and repulsion forces that result in temporarily unaligned states (Pettit, Perna, et al. 2013).

We study collective decision making and the exploration–exploitation trade-off using an experimental analysis of cumulative route development in homing pigeons (Sasaki and Biro 2017). In these experiments, pairs consisting of a naïve and an experienced bird were required to successively solve the same homing task a fixed number of times. This set of paired flights allowed the naïve bird to acquire knowledge of localized visual landmarks necessary for homing. The more experienced bird was then replaced with a new naïve individual and the learning process was repeated through five generations of replacement in a transmission-chain design. Route efficiency was measured as the ratio of the beeline distance between the release site and the home loft (*i.e.*, the ideal optimum) and the actual distance travelled by birds. The results showed that, although homing efficiency dropped considerably every time a new naïve bird was introduced, transmission-chain pairs continued to improve within and over generations, eventually outperforming both solo and fixed-pair controls (respectively, 0.92 efficiency versus 0.83 and 0.85). In contrast, the efficiency

of solo and fixed pairs plateaued after they had first established their idiosyncratic routes (around the 9th–10th release for the former and the 7th–8th release for the latter).

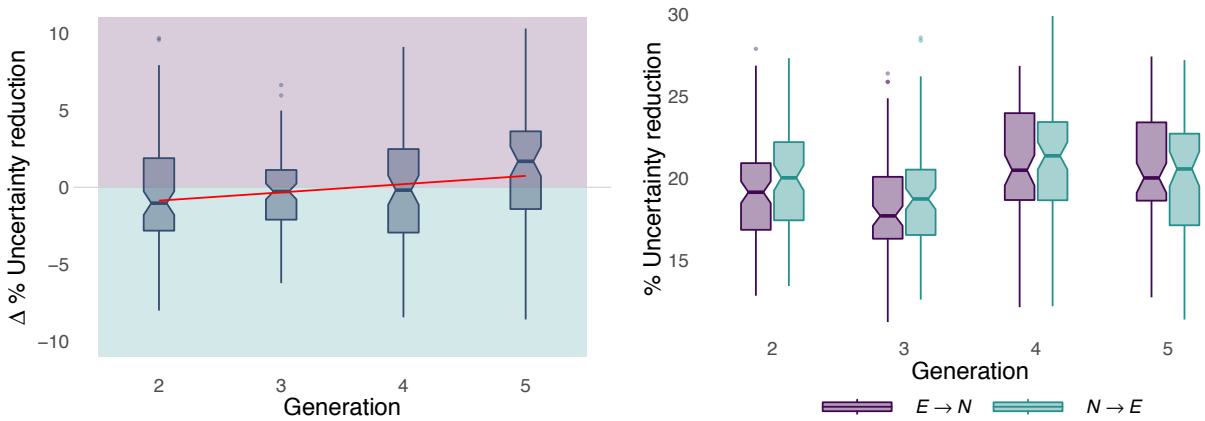
The continued improvement seen in transmission chains might result from a variety of decision-making mechanisms ranging from fully despotic to increasingly democratic. A simplified perspective of this continuum allows us to consider four alternative hypotheses. In two of these alternatives, a single despotic leader, either the naïve or the experienced bird, determines the entire homing route. Whereas evidence of social learning (Sasaki and Biro 2017) suffices to dismiss the possibility of leadership by the naïve individual, leadership by the experienced individual could still be the only process in place if social learning is unidirectional and the naïve individual merely triggers the experienced bird to resume and lead exploration. Under the other two hypotheses, birds could pool their personal information by means of democratic processes based on moment-by-moment integration of individual preferences or transient, alternating leadership (Conradt 2012). The third hypothesis entails the experienced bird contributing only its past route information and relying instead on the naïve individual for the discovery of route innovations. If this hypothesis holds, we expect the naïve bird to disproportionally lead phases of exploration. Otherwise (fourth hypothesis), both experienced and naïve birds might contribute through exploration to the discovery of new information.

We discriminated between these alternative hypotheses by using transfer entropy to reveal the extent to which birds influence each other and to investigate if relative spatial position can accurately predict leader–follower dynamics. On this basis, we studied the contribution of each bird to the exploration–exploitation trade-off over different stages of route development. This exploration–exploitation perspective of homing route development allowed us to characterize the efficiency of choices made by birds over the course of the experiment and to shed light on the superior performance of experimental pairs with respect to solo and fixed pairs controls.

Results

Birds pool information. The social-learning hypothesis under which the naïve bird passively copies the idiosyncratic route of the experienced one (*i.e.*, the despotic leader) entails a transfer of information that is unidirectional – from the experienced to the naïve bird. Instead, under the two alternative hypotheses based on democratic decision-making, the two birds rely on bidirectional information transfer to pool information and increase the efficiency of their route (Pettit, Flack, et al. 2013; Sasaki and Biro 2017). We rejected the unidirectional social-learning hypothesis by finding causal evidence of information pooling: the naïve bird actively influenced the behaviour of the experienced one for a large portion of the parameter space (Figure S1). As is common practice with these measures (Porfiri 2018), we selected the parameter configuration that maximized the total transfer of information between the two birds (one sample every 0.2 seconds, $k = 10$) . This was maximal for the shortest sampling period (*i.e.*, prediction interval) of 0.2 seconds and progressively decreased towards 0 for larger periods up to 4 seconds, indicating that the effect of an interaction between birds was transitory and lasted for a limited period of time. Using this configuration,

we compared measurements of information transfer against those of a surrogate dataset created by pairing trajectories of birds that were not flown together. We found that levels of mutual influence between birds that flew together were significantly higher than those observed in the surrogate dataset both overall and for each generation separately (Mann–Whitney–Wilcoxon, columns 2 and 3 of Table S1).



(a) **(b)**

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

During the first two generations of paired flights (Figure 2a, paired analysis), when there was a large margin to improve the efficiency of the pair's trajectory, the naïve bird was more informative than the experienced one, evidenced by a stronger influence over the latter. At generation 4 there was a balance between the two birds whereas the experienced bird eventually became the better source of predictive information in the last generation. A linear fit over generations of the paired comparison (Figure 2a, red line) showed an increasing influence of the experienced bird over the naïve one (Theil–Sen estimator, slope 0.534, $p < 0.001$). Additionally, a non-paired comparison of the same results revealed that, although the naïve bird had, on average, a marginally higher predictive power than that of the experienced one (18.7–21.4% versus 17.7–20.5%), both birds explained a large portion of each other's behaviour (Figure 2b) suggesting non-trivial leadership dynamics. These results do not show whether different levels of experience within the pair led to asymmetric contributions of birds to route development, with the experienced bird providing only its past route information and the naïve bird in charge of discovering route innovations, or if both birds contributed to the exploration for possible route alternatives. To discriminate between these remaining hypotheses, we first developed the means to evaluate leadership on a moment-to-moment basis.

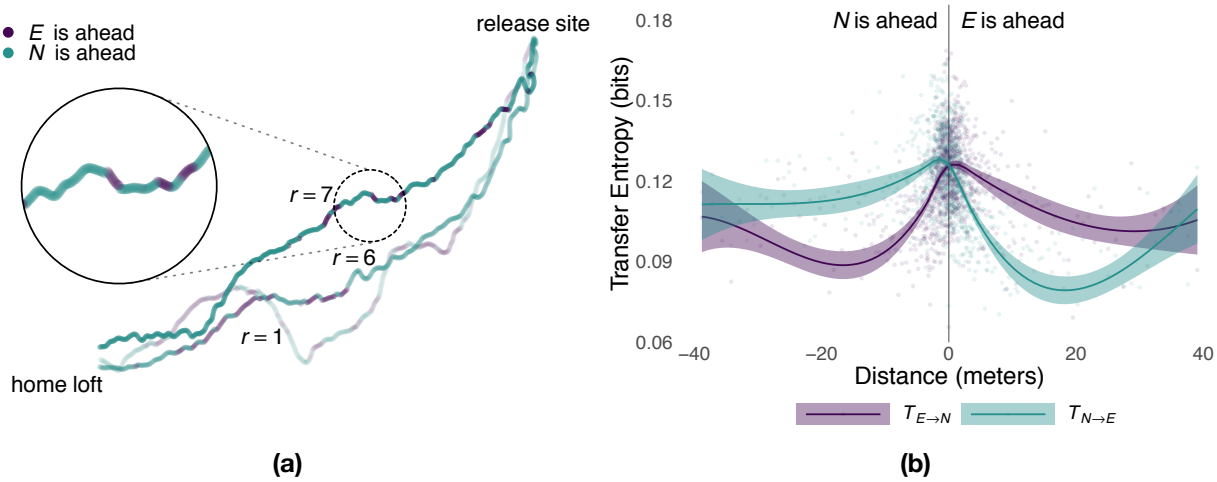


Figure 3. Panel (a) shows sample flight trajectories for a number of different releases, r, of the same pair of birds. Colors highlight which bird is ahead of the other during different segments of the route. Panel (b) shows the local transfer of information (mean and 0.95 confidence interval) between 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

by the naïve bird (Wilcoxon signed rank-test, $p = .03, V = 1851$), there was no significant difference in the proportion of a flight spent by each bird at the front of the pair (Table S3) suggesting a relatively egalitarian relation between birds despite differing levels of experience.

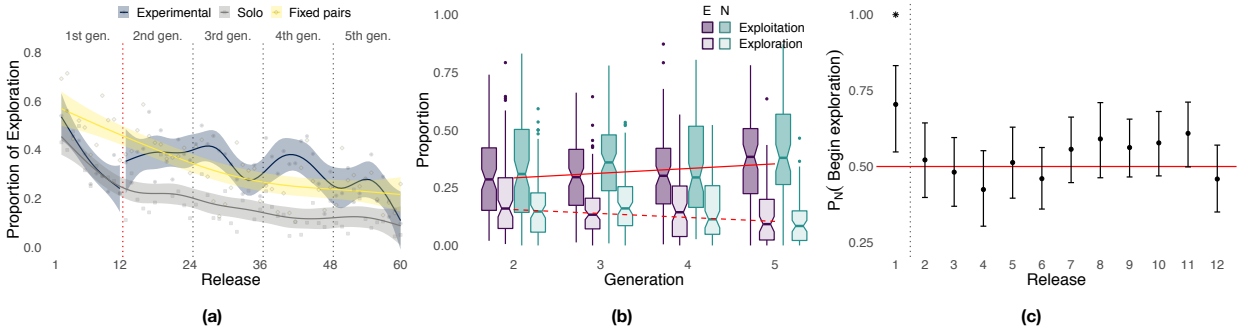


Figure 4. Panel (a) shows the proportion of exploration over releases for the experimental group (the red dotted vertical line separates solo flights at generation 1 from paired flights at generations 2-5), the solo control, and the fixed-pairs control. Smoothed lines are computed using generalized additive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

Exploration–exploitation dynamics explain flight performance. Sasaki and Biro (2017) previously showed that flight efficiency varies across treatments with experimental pairs eventually outperforming both fixed pairs of birds and solo individuals. The discovery of route innovations and, in particular, how birds with different levels of experience contribute to this task, is the key to the superior performance of experimental pairs. To understand this phenomenon and thus shed light on the pair's information pooling mechanism, we investigated how pigeons balance between exploitation of known information, closely following (< 300 meters) their most recent route, and exploration for possible route improvements. To do so, we labelled segments of flight trajectories as a function of the point-to-point distance of a focal trajectory from the immediately preceding one (*i.e.*, baseline) and compared the exploration–exploitation dynamics both across treatments and between experienced and naïve birds.

During the initial part of the experiment (Figure 4a, first 12 releases), exploration decreased steadily in all conditions with birds that flew individually in the experimental group (*i.e.*, generation 1) performing similarly to those of the solo control (respectively, 36.7% and 34.2%) whereas fixed pairs of birds explored significantly more (51.7%, Whitney–Mann–Wilcoxon, $p < .001$, Table S4). However, while exploration steadily decreased for solo and fixed pairs of birds in the successive 48 releases, experimental pairs showed a markedly different pattern of exploration oscillating over generations (Figure 4a, releases 13–60). Each time a new naïve individual was paired with an experienced one (dotted vertical lines), exploration increased for about 5 to 6 releases, reaching values well beyond those of both solo birds and fixed pairs; then exploration decreased within a few releases (2 to 4) to the same levels as those of fixed pairs. On average during generations 2 to 5, experimental pairs explored (32.9%) significantly more than both solo

(15.7%, $p < .001$) and fixed pairs of birds (29.3%, $p = .0456$). These results also held when exploration and exploitation were defined with respect to the last release of the previous generation. Under this model, differences between experimental and fixed pairs were even more pronounced, with the former characterized by 46.6% exploration and the latter by only 32.4% ($p < .001$, Table S5 and Figure S6). The inferior flight efficiency of solo and fixed pairs of birds might thus be explained, at least in some measure, by a lower likelihood to discover route improvements due to limited exploration.

The superior homing performance of experimental pairs is suggested to be rooted in their ability to select novel portions of a route introduced by the naïve individual that are more efficient while discarding inefficient ones (Sasaki and Biro 2017). Under this hypothesis, we expect to observe, not only increasing homing efficiency over generations, but also an asymmetric pattern of leadership in which the naïve individual leads periods of exploration and the experienced one leads periods of exploitation. We found instead no significant difference between the contributions of the experienced bird and those of the naïve one both overall and within generations (Figure 4b and Table S7). The sole exception is represented by generation 3 during which the naïve bird contributed more than the experienced one to exploitation (Wilcoxon signed-rank test, $p = .035, V = 1871$). Experienced and naïve birds led the pair with approximately the same frequency in both exploration and exploitation, suggesting that deviations from established routes were not caused only, or even mainly, by the naïve bird (see also Figure S4, inset). We did find evidence of behavioural asymmetries, in that transitions from exploitation to exploration were marginally more likely to be initiated by naive birds (exact binomial test, $p = .042, n = 964$, Table S8); however, this result was driven by those of generation 3 ($p = .02, n = 301$) whereas no difference was detected in other generations. Transitions from exploration to exploitation were equally likely to be initiated by the two birds both overall and within each generation. However, when transitions are considered over the 12 releases composing each generation (Figure 4c), the naïve individual was more likely to initiate phases of exploration during the first release ($p < .01, n = 44$, Table S9) doing so 70.5% of the time compared to 29.5% for the experienced bird. After the first release, transitions that initiate phases of exploration were about as likely to be initiated by either of the two birds independently of their level of experience.

Discussion

For many group-living animals, searching for optimal travel routes can be a complex task as social information about routes can persist over generations regardless of its quality (Helfman and Schultz 1984; Sasaki and Biro 2017; Jesmer et al. 2018; Laland and Williams 1998). This search is inherently subject to a trade-off between the exploitation of well-established route information accumulated over time and exploration for innovations that constitute potential improvements (Hills et al. 2015). Striking a balance is fundamental as a pronounced reliance on exploitation of learned information can hinder innovations (Davies, Krebs, and West 2012) and thus promote the maintenance of potentially suboptimal behaviour

and even of maladaptive behavioural traditions (Laland and Williams 1998). Equally, an over-reliance on exploration without exploiting the rewards of beneficial innovations eventually impedes improvements in performance over time (Fu and Gray 2006; Mehlhorn et al. 2015).

We studied the causal structure of this process in flights of the homing pigeon *C. livia*, as this species is capable of both social learning and information pooling (Biro et al. 2006; Pettit, Flack, et al. 2013). Of particular interest for our study is the increase in route efficiency that results from the pairing of naïve individuals with experienced ones (Pettit, Flack, et al. 2013), including when this happens iteratively over multiple generations (Sasaki and Biro 2017). Previous work has proposed information pooling as the underlying mechanism driving this increase in flight performance (Sasaki and Biro 2017). Using transfer entropy to measure predictive information (Schreiber 2000; Pilkiewicz et al. 2020), we found quantitative evidence that supports the information-pooling hypothesis in the strength of causal interactions within pairs of birds. Experienced and naïve birds influence each other's behaviour; about 20% of the future directional choices of any individual in a pair is explained by the behaviour of the other individual. These results contrast with our expectations for unidirectional social learning that entails an asymmetric pattern of leadership with a pronounced role for experienced individuals.

Our analysis showed that, in a multi-generational transmission-chain design, the naïve bird has a higher influence than the experienced one during the early generations. In later generations, as flight efficiency increases, the experienced bird becomes the better source of predictive information. We can further hypothesize that, over generations, as birds explore an increasing portion of the search space and exhaust remaining alternatives, a newly introduced bird should become less likely to contribute productive innovations, and an increasing proportion of innovations should lead to errors instead of improvement. This theoretical reasoning is analogous to the diminishing marginal value from returning to a previous location when searching for an object in space (Stone 1976). From an information-foraging perspective (Stephens and Krebs 1986; Pirolli 2007), the time invested in harvesting innovations on the introduction of a naïve bird corresponds to the time invested in attending to a newly discovered patch; at some point, the opportunity cost of further harvesting becomes too high to justify remaining in the patch. Thus, after the introduction of a naïve bird, the information-foraging pair shifts from information-harvesting exploration back toward information-preserving exploitation, as would be expected in an optimal search problem (Stone 1976).

How do experimental pairs improve their homing routes over generations? Previous studies where leadership was defined on the basis of route similarity showed that, in pairs with a large difference in experience between birds, experienced individuals were more likely to assume leadership (Flack et al. 2012). Still using route similarity, Sasaki and Biro (2017) found evidence of social learning with naïve individuals learning routes from their experienced partners. Moreover, because newly formed pairs in the transmission-chain design also improved performance generation after generation, they proposed that naïve individuals could contribute innovations that pigeons evaluate in terms of route efficiency and prune away when inefficient. However, defining leadership in terms of causal interactions instead of route similarity allowed us to show that there is an asymmetric relation between innovators and exploiters only

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

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

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

Materials and Methods

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

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

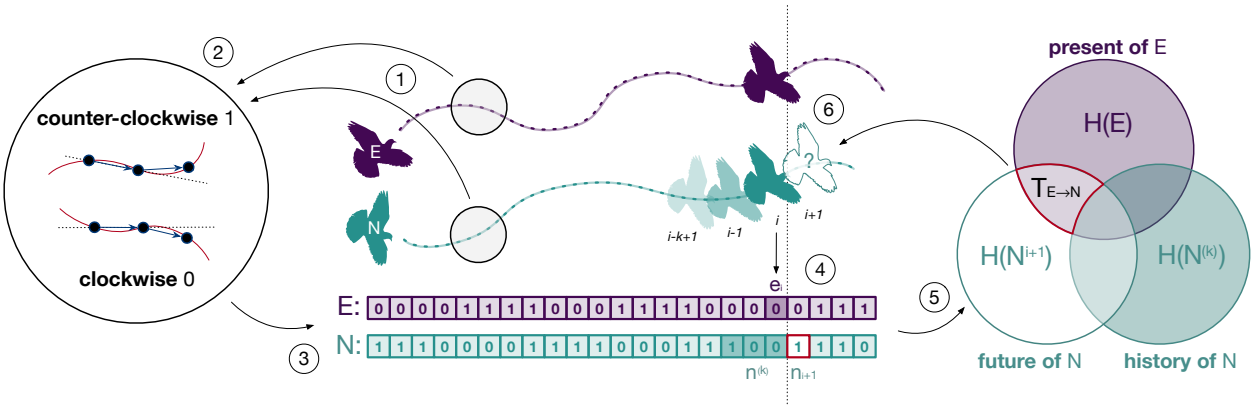


Figure 1. Illustration of the methodological approach. The spatial trajectories of an experienced (E) and a naïve (N) bird (point 1) are encoded as clockwise and counter-clockwise rotations (point 2) which we represent as discrete time series (point 3). The combination of rotations encoded in both series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

Data collection and pre-processing. Flight trajectories of birds were sampled at a frequency of 5 Hz using GPS loggers, converted from the geographic coordinate system to the metric system, and projected over the 2-dimensional plane (see Sasaki and Biro 2017). Each trajectory consisted of a time-ordered 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 of each flight using a binary symbolic representation where symbols 0 and 1 represent, respectively, a

clockwise and a *counter-clockwise* rotation (point 2). The direction of rotation was computed as the cross 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 when the product is negative and counter-clockwise when it is positive. We also measured the distance $d_{EN}(i)$ of the experienced bird from the naïve one projected over the current direction of motion of the pair (cf. Nagy et al. 2010 and Supplementary Material). Using this distance, we then determined the relative position of birds over time: when $d_{EN} > 0$, the experienced bird was flying ahead of the naïve bird; when $d_{EN} < 0$, it was flying behind. Previous tests using the same GPS loggers showed that these devices have a sufficient level of accuracy with a small normally distributed spatial error (SD of 0.05 meters) affecting the tracking accuracy of the direction of motion and a relatively larger error (median of 1.69 meters) affecting that of the relative position (Pettit, Perna, et al. 2013).

Measuring information transfer. We quantified the amount of information transferred between birds using information-theoretic measures (Cover and Thomas 2005; Pilkiewicz et al. 2020) estimated from the 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, point 3). We aimed to quantify causal interactions between birds in a Wiener–Granger sense by measuring the extent to which the current behaviour of one bird allows us to predict the future behaviour of the other (Bossomaier et al. 2016). Here we describe the process for predicting the naïve bird's behaviour from that of the experienced one, but we also used the same method for the opposite direction. The average amount of information necessary to fully predict the next rotation of the naïve bird is quantified by the marginal 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). This is equal to 1 bit if the flight of the naïve bird is maximally uncertain (i.e., clockwise and counter-clockwise rotations are equally likely) and to 0 bits if the flight is fully deterministic (i.e., rotations are either all clockwise or all counter clockwise). As a result of temporal autocorrelation (Mitchell et al. 2019), part of this information might be contained in the recent history of rotations of the naïve bird, $n_i^{(k)} = \{n_{i-k+1}, \dots, n_{i-1}, n_i\}$ for history length k (Figure 1, point 4, dark green entries in the naïve time series). The remaining predictive information, which is not explained by the past behaviour of the naïve bird, is quantified by the marginal entropy,

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

of its future rotations, N^{i+1}, conditioned on the outcome of the past k rotations, $N^{(k)}$ (Figure 1, Venn diagram, overlap of the white and light purple areas).

Of interest to us was how much of this remaining information (necessary to predict the future direction of rotation of the naïve bird) can be obtained by the current behaviour of the experienced bird (Figure 1, points 4–6). This is given by the transfer entropy, which estimates the time-delayed effects on the naïve bird of its interaction with the experienced one: $T_{E \to N} = H\left(N^{i+1} \middle| N^{(k)}\right) - H\left(N^{i+1} \middle| N^{(k)}, E\right)$ (Schreiber 2000). Transfer entropy is time directional, from the present of one bird to the future of the other,

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

424 $$T_{E\to N} = \sum_{n_{i+1}, n_i^{(k)}, e_i} p(n_{i+1}, n_i^{(k)}, e_i) \log_2 \frac{p\left(n_{i+1} \mid n_i^{(k)}, e_i\right)}{p\left(n_{i+1} \mid n_i^{(k)}\right)}$$

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

Supplementary Methods). In both cases, we also measured the distance $d_{EN}(i)$ between experienced and naïve birds to determine which bird was flying at the front of the pair for a given route segment.

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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.

Supplementary Information

Naïve individuals promote collective exploration in homing pigeons

Gabriele Valentini, Theodore P. Pavlic, Sara Imari Walker, Stephen C. Pratt, Dora Biro & Takao Sasaki

Methods

Relative position of birds over time. We determined the relative position of each bird within the pair using the distance d_{EF} of the experienced bird from the naïve one projected onto the direction of motion of the flock. We modified the method proposed in (Nagy et al. 2010), which gives the distance of the experienced bird from the centre of the flock, to also include the segment from the centre of the flock to the naïve bird. This is given by

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

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 velocity of the pair. The normalized velocity is computed as

$$\overrightarrow{v_{pair}}(i) = \frac{\langle \overrightarrow{\dot{x}_k}(i) \rangle_k}{\left| \langle \overrightarrow{\dot{x}_k}(i) \rangle_k \right|}.$$

As the flock is composed of two birds only, the projected distance of the experienced bird from the naïve one projected onto the direction of motion of the pair is positive, when the experienced bird is flying *ahead* of the naïve one, and it is negative when the experienced bird is flying *behind*.

Exploration–exploitation with respect to the previous generation. Our primary approach to define exploration and exploitation is based on comparing pairs of successive releases using the trajectory of the previous release as our baseline model of exploitation and then labelling newer portions of a focal route as exploration. The model of exploitation (i.e., baseline trajectory) thus varies for each focal release similarly to a moving-average window over successive releases. An alternative approach to define exploration and exploitation is to consider a constant model of exploitation for each release within a given generation. This can be obtained by setting the baseline trajectory to equal the last trajectory of the previous generation. As a consequence, exploitation is defined on the basis of the information available only to the experienced bird at the beginning of a new generation; every portion of the route within that generation that is more than 300 meters away from the baseline is considered exploration.

At the first generation of the experimental group, when birds are trained individually for the successive transmission chain experiment and there is no previous generation available to provide us with

a baseline trajectory, we consider the first release as the baseline trajectory for the remainder of the generation. In the case of solo and fixed pairs controls, for which there is no obvious definition of a generation, we considered the 60 releases in each of these experiments as formed by 5 generations, each lasting 12 releases, and used an equivalent approach to that of the experimental group to define exploration and exploitation.

Results

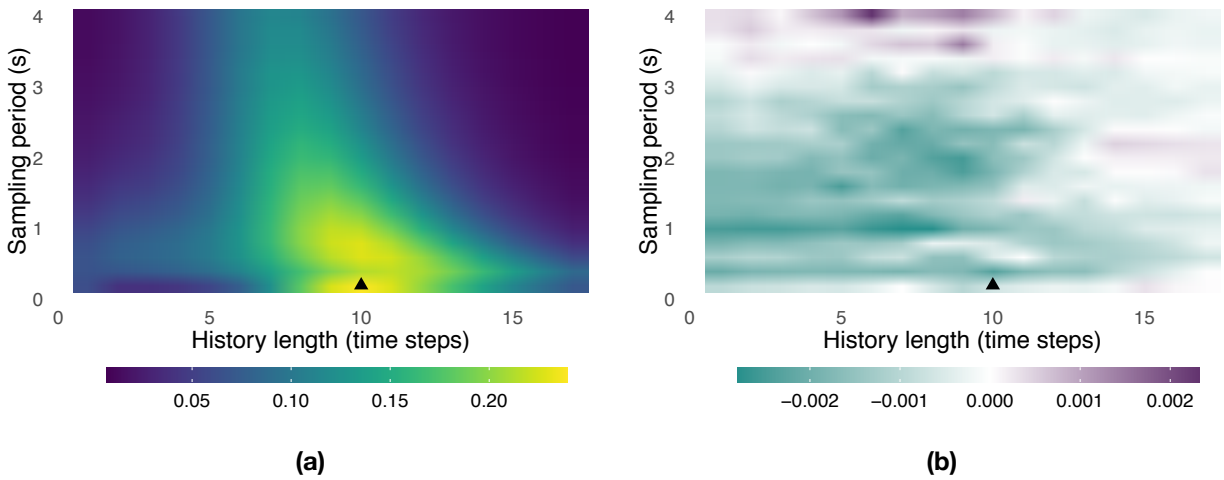


Figure S1. Landscape of information transfer as a function of the history length, $k \in \{1, \ldots, 17\}$, and of the sampling period, $\{0.2, 0.4, \ldots, 4.0\}$ seconds. Panel (a) shows the total transfer of information between the pair of birds, $T_{E\to N} + T_{N\to E}$, averaged over all releases 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.

Landscape of information transfer and choice of parameters. We first explored how information transfer between the birds varied as a function of two parameters: the sampling period (seconds) and the history length used in the computation of transfer entropy. Our original GPS data are sampled at a frequency of 1 sample every 0.2 seconds (5 Hz); we can further subsample these data by dropping samples, for example, using one sample every 0.4, 0.6, ..., 4.0 seconds as the sampling period. The history length represents the number of past rotations by the bird we want to predict that we consider when computing transfer entropy from the other bird in the pair.

The total transfer of information between the birds varies as a function of these parameters (Figure S1a). It peaks in the region delimited by history lengths of 8–10 time-steps and a sampling period between 0.2–1.2 seconds, whereas it vanishes otherwise. The total transfer of information, which is generally adopted as a measure to choose study parameters (Porfiri 2018), reaches its maximum for a history length of $k = 10$ at one sample every 0.2 seconds (black triangle in Figure S1a). We use this parameter configuration for the rest of our information-theoretic analysis. For this and for most other parameter configurations, the naïve bird is more informative about the future behaviour of the experienced one than

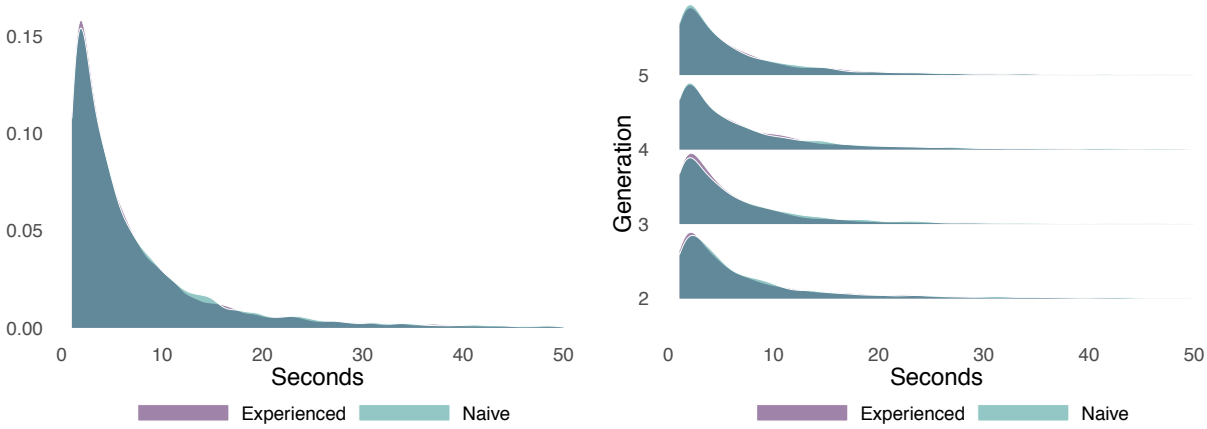
the other way around (Figure S1b). Only in two regions, both far from the point maximizing the total transfer of information, is the experienced bird more informative than the naïve one; however, the overall amount of information transferred between birds in these regions is negligible.

Comparison of information transfer with the surrogate dataset. To verify their significance, we compared our estimates of information transfer between the two birds with equivalent measurements taken from the surrogate dataset. We expect causal effects measured in the original dataset to be stronger than those found in the surrogate one. As shown in Table S1, our expectations are fully met: the original dataset shows values of transfer entropy significantly higher than those observed in the surrogate dataset, both for the entire dataset as well as for each separate generation.

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

			Original vs surrogate dataset	
Generation	$T_{E\to N} - T^{s}_{E\to N}$	$H_1: T_{E\to N} > T^{s}_{E\to N}$	$T_{N\to E} - T^{s}_{N\to E}$	$H_1: T_{N\to E} > T^{s}_{N\to E}$
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 ($n = 69, n^s = 4761$)	$\mu = 0.0111$	$\boldsymbol{p <.001}$ ($W = 214258.5$)	$\mu = 0.0075$	$\boldsymbol{p =.002}$ ($W = 197618.5$)

Analysis of time spent by each bird at the front of the pair. We divided each flight into different segments, with each segment representing a consecutive portion of the route with either the experienced or the naïve bird at the front of the pair, and then measured the segment durations (Figure S2). The distribution of segment durations resembles a log-normal distribution for both the entire dataset and for individual generations. Experienced and naïve birds are characterized by very similar distributions closely overlapping each other. Overall, the naïve bird spent significantly longer periods of time at the front of the pair (Table S2), but the difference is small and largely driven by that of generation 3 (the only generation showing significant differences). With the exception of generation 3, the experienced and the naïve bird spent, on average, an approximately equal portion of the route at the front of the pair (Table S3). At generation 3, the naïve bird was at the front of the pair for a significantly larger portion of the route with 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 ($n = 69$)	$\mu = 0.49, \sigma = 0.2$	$\mu = 0.51, \sigma = 0.2$	$p = .95$ ($V = 1219$)

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

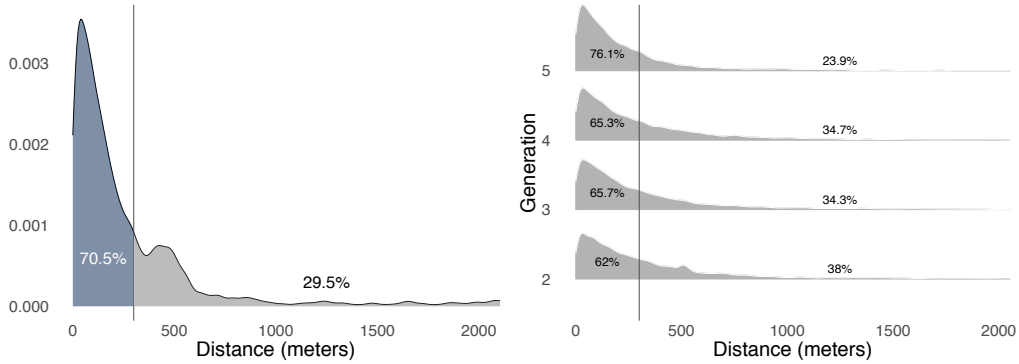


Figure S3. Distribution of minimum distances between the pairs of consecutive flights. Panel (a) shows the results for the trained birds during the first generation of the experiment. Panel (b) shows the results for the pair of birds during all remaining generations of the experiments. Vertical lines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

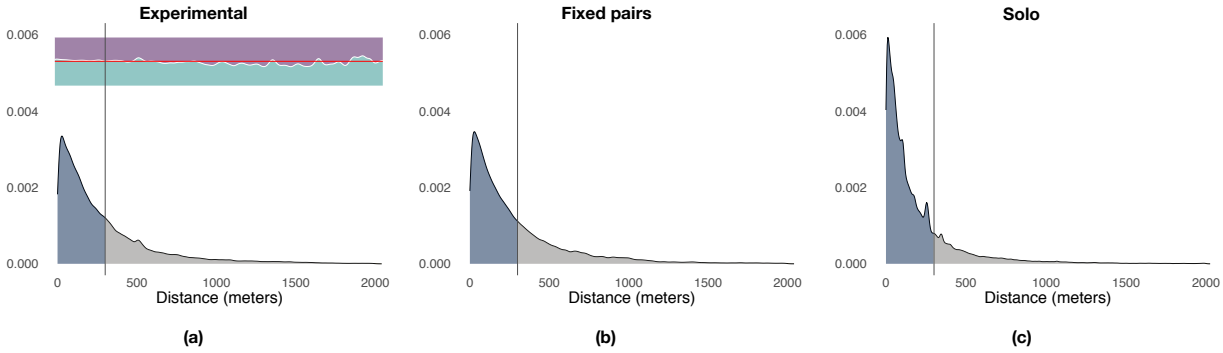


Figure S4. Illustration of the distribution of point-to-point distances between pairs of consecutive flights highlighting the 300 meter threshold that demarks the end of exploitation and the beginning on exploration. Panel (a) reports the results for experimental pairs over generations 2–5, panel (b)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

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

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

Table S4. 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). 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: 36.7% vs 63.3% Col: 34.2% vs 65.8% $p = .55$ ($W = 5288$)	Row: 36.7% vs 63.3% Col: 51.7% vs 48.3% $\boldsymbol{p <.001}$ ($W = 2230$)
	Solo control	–	Row: 36.7% vs 63.3% Col: 34.2% vs 65.8% $\boldsymbol{p <.001}$ ($W = 1837$)
13 to 60	Experimental (gen. 2-5)	Row: 32.9% vs 67.1% Col: 15.7% vs 84.3% $\boldsymbol{p <.001}$ ($W = 94108.5$)	Row: 32.9% vs 67.1% Col: 29.3% vs 70.7% $\boldsymbol{p =.0456}$ ($W = 50472$)
	Solo control	–	Row: 15.7% vs 84.3% Col: 29.3% vs 70.7% $\boldsymbol{p <.001}$ ($W = 31517$)

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

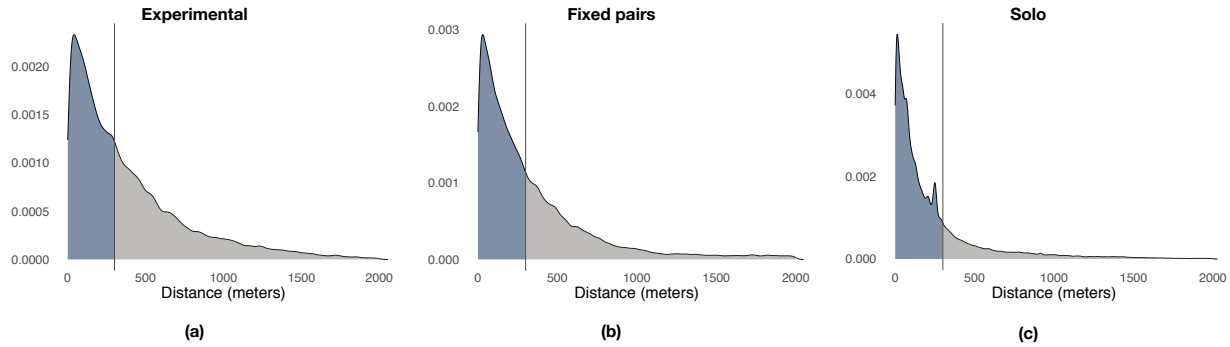


Figure S5. Illustration of the distribution of point-to-point distances between each flight of a generation (focal trajectories) and the last flight of the previous generation (baseline trajectory). Colors and vertical lines highlight the 300 meter threshold that demarks the end of exploitation and the 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% Col: 55.8% vs 44.2% $p = .11$ ($W = 5592$)	Row: 61.5% vs 38.5% Col: 82.9% vs 17.1% $\boldsymbol{p <.001}$ ($W = 1721$)
	Solo control	–	Row: 55.8% vs 44.2% Col: 82.9% vs 17.1% $\boldsymbol{p <.001}$ ($W = 1163$)
13 to 60	Experimental (gen. 2-5)	Row: 46.6% vs 53.4% Col: 18.9% vs 81.1% $\boldsymbol{p <.001}$ ($W = 103095$)	Row: 46.6% vs 53.4% Col: 32.4% vs 67.6% $\boldsymbol{p <.001}$ ($W = 60502$)
	Solo control	–	Row: 18.9% vs 81.1% Col: 32.4% vs 67.6% $\boldsymbol{p <.001}$ ($W = 30744$)

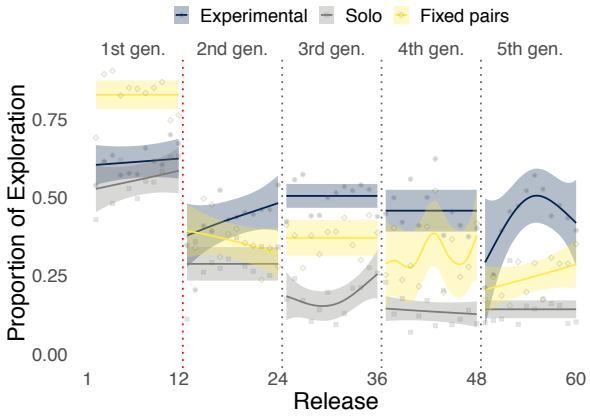


Figure S6. Illustration of the proportion of exploration (respectively, one minus the proportion of exploitation) over releases when considering the last release at the previous generation as the baseline trajectory. Results are shown for

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

The role of leadership during exploration and exploitation. Using this distance-based mechanism, we label each segment of a flight as either exploration or exploitation. For each segment, we keep track of which bird, experienced or naïve, is leading the pair. We then compute the proportion of time spent by the experienced bird and by the naïve one leading the pair during either an exploration or exploitation phase (Table S6). The combined proportion of time of both birds in either exploration or exploitation gives instead the corresponding contribution of the pair. Overall, each bird spends approximately 16.5% of the time leading the pair during an exploration phase and 33.5% of the time leading the pair during an exploitation phase. With the exception of exploitation phases in generation 3, there is no significant difference between the proportion of time spent by the two bird in an exploration or exploitation phase (Table S7).

Table S6. Proportion of a flight led by each of the two birds, calculated separately for exploration and exploitation phases. 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 led, respectively, by the experienced and the naïve bird for the case of exploration. Columns 4 and 5 give the mean and the standard deviation of the proportion of a flight led, respectively, by the experienced and 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 $(n = 69)$	$\mu = 0.13, \sigma = 0.13$	$\mu = 0.1, \sigma = 0.1$	$\mu = 0.37, \sigma = 0.17$	$\mu = 0.4, \sigma = 0.21$

Table S7. Statistical comparison of leadership by experienced vs. naïve birds, tested separately for exploration and exploitation over all generations and over separate generations. Column 1 reports the generation and sample size. Columns 2 and 3 report the results of two-sided paired Wilcoxon signed-rank tests with continuity correction (p-value and V statistic) for differences in proportion of flight led between experienced and naïve birds for exploration and 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 $(n = 69)$	$p = .22$ $(V = 1187)$	$p = .8$ $(V = 1131)$

Transitions between phases of exploration and exploitation. Although once initiated, phases of exploration and phases of exploitation are led in equal manner by the experienced and the naïve bird, the experience unbalance within the pair might affect the likelihood of a bird to initiate transitions from one phase of the exploration–exploitation process to other. To investigate this question, we measured transition probabilities for both birds over generations (Table S8) and over releases (Table S9). Transitions from exploration to exploitation are not significantly different between experienced and naïve birds, but transitions from exploitation to exploration are significantly (albeit marginally) more likely to be initiated by naïve birds. However, this result seems driven by the data of generation 3, where the naïve individual is marginally but significantly more likely than the experienced one to initiate exploration phases, while in all other generations both birds are equally likely to initiate changes in either direction. When looking at transition probabilities over releases, we found a similar trend except for the first release where the naïve bird is much more likely to initiate exploration phases.

Table S8. Statistical comparison of the proportion of transitions from exploitation to exploration and from exploration to exploitation led by the experienced and by the naïve bird over generations. Column 1 reports the generation number. Columns 2 and 4 report the estimated probabilities that transitions are led by the experienced bird, P_E, and by the naïve bird, P_N, for transitions, respectively, from exploitation to exploration and from exploration to exploitation. Columns 3 and 5 give the results of exact binomial tests (p-value and sample size n) of the null hypothesis that the probability P_E 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	$P_E = 0.45, P_N = 0.55$	$p = .18$ $(n = 200)$	$P_E = 0.522, P_N = 0.478$	$p = .57$ $(n = 203)$

Table S9. Statistical comparison of the proportion of transitions from exploitation to exploration and from exploration to exploitation led by the experienced and by the naïve bird over releases. Column 1 reports the release number. Columns 2 and 4 report the estimated probabilities that transitions are led by the experienced bird, P_E, and by the naïve bird, P_N, for transitions, respectively, from exploitation to exploration and from exploration to exploitation. Columns 3 and 5 give the results of exact binomial tests (p-value and sample size n) of the null hypothesis that the probability P_E that 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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