

From Compromise to Leadership in Pigeon Homing

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Summary

A central problem faced by animals traveling in groups is how navigational decisions by group members are integrated, especially when members cannot assess which individuals are best informed or have conflicting information or interests [1–5]. Pigeons are now known to recapitulate faithfully their individually distinct habitual routes home [6–8], and this provides a novel paradigm for investigating collective decisions during flight under varying levels of interindividual conflict. Using high-precision GPS tracking of pairs of pigeons, we found that if conflict between two birds' directional preferences was small, individuals averaged their routes, whereas if conflict rose over a critical threshold, either the pair split or one of the birds became the leader. Modeling such paired decision-making showed that both outcomes—compromise and leadership—could emerge from the same set of simple behavioral rules. Pairs also navigated more efficiently than did the individuals of which they were composed, even though leadership was not necessarily assumed by the more efficient bird. In the context of mass migration of birds and other animals, our results imply that simple self-organizing rules can produce behaviors that improve accuracy in decision-making and thus benefit individuals traveling in groups [3, 9, 10].

Results and Discussion

How birds traveling in groups negotiate their routes is a fundamental issue in avian navigation, and two alternative schemes have been proposed [11]. The “many wrongs” hypothesis purports that individuals average their preferred direction, leading to a compromise in route choice [12, 13], whereas in the leadership hypothesis, one or a small subset leads the group. Theoretical arguments predict that unless leaders have very different and superior information, a decision made by one or a small number of leaders is less accurate than one made by the averaging of all members' preferences [4, 5, 11].

Despite theoretical interest, few experiments have investigated group navigation by birds [1, 2]. In homing pigeons, limited experimental evidence does not provide clear support for preferring either hypothesis [14–18]. An explanation behind observations of both compromise- and leadership-based decisions may lie in

the limitations imposed by local rules for decision-making [2]. Couzin et al [3], modeled two small groups of leader individuals, each with its own preferred destination, within a much larger set of group members with no preferred direction. Individuals always followed the same local rules, but as the angle between the directions preferred by the two leader groups increased, the model identified a switch from movement in the average of these directions to movement following one of the two. The group “decision” to adopt a strategy of compromise or leadership thus emerged from the local behavior of individuals, without an explicit change in individual strategy in response to conflict [9, 10].

Technological innovations for tracking free-flying pigeons have periodically provided important advances in our understanding of bird navigation [19–21]. Most recently [22, 23], homing pigeons have been fitted with miniature GPS loggers that allow extremely precise reconstruction of the animals' movements. In addition, recent work [6–8] has shown that once familiar with a local homing task, pigeons develop individually distinct routes that they recapitulate faithfully during each subsequent flight (true navigation from longer distances over unfamiliar terrain may of course involve different navigational processes [24]). A combination of these two developments now provides a means to test different hypotheses about how conflict affects navigational decision-making on a second-by-second basis. We GPS-tracked pairs of pigeons that had established different homing routes and examined how conflict generated by the dual forces of social cohesion and attraction to one's established route was resolved. We documented all possibilities—birds taking an average trajectory, one bird acting as leader, and the pair splitting up—often as different stages of the same flight (Figure 1). Thus, these tracks do not confirm that either a leader- or a compromise-based model is clearly dominant during pigeons' paired flights.

To understand better how decision-making in pairs is determined by the degree of conflict between individuals, we developed a model based on two hypothesized forces: attraction to an established route and attraction to the partner (see the [Supplemental Data](#) available online for details of the model). The model made strong predictions concerning how the collective outcome depends on the distance between the two birds' established routes (Figure 2A): (1) At small distances between established routes, birds will average, flying an intermediate route; (2) beyond a critical between-route distance, of approximately twice the range at which individuals are maximally attracted to their established routes, birds will follow one of the two routes; and (3) splitting can occur over a wide range of interroute distances as a result of an initial, or some randomly induced, difference in the birds' path during paired flight. These results hold even if birds differ in their attraction to their established routes, but in such cases the tendency to follow the “leader” becomes stronger (Figure 2B). Most

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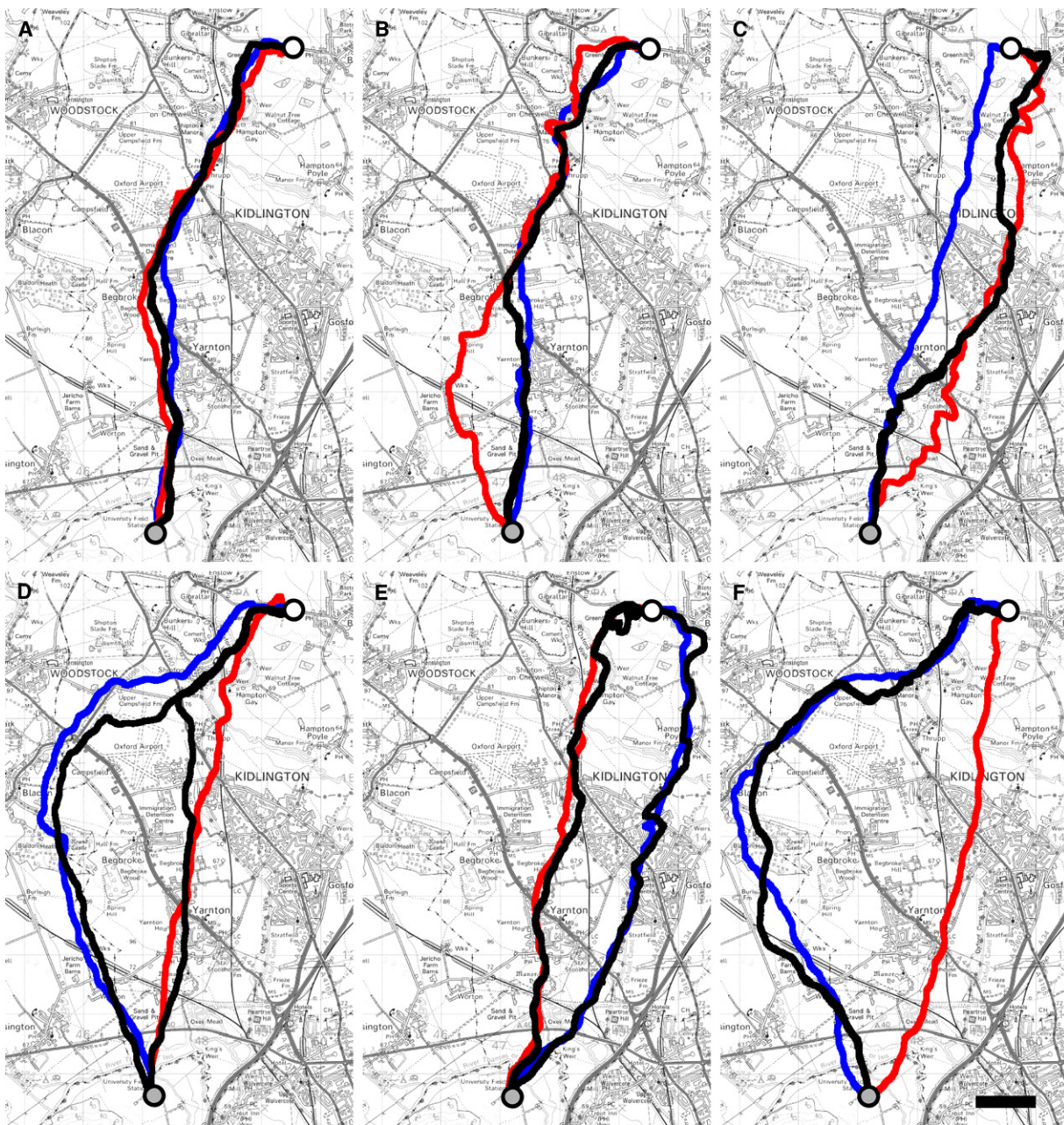


Figure 1. Examples of Flights Performed by Stably Route-Recapitulating Homing Pigeons Released in a Pair

In each panel, black lines show flights performed by birds 1 and 2 of a pair when released together. Blue and red lines indicate tracks flown singly by birds 1 and 2, respectively, in releases immediately prior to the paired flight. (A) \bar{d} (average point-by-point nearest-neighbor distance between established routes) = 147 m, and birds remain in a pair and take an intermediate route; (B) \bar{d} = 374 m, and birds remain in a pair, initially take an intermediate route, and then take one of the established routes; (C) \bar{d} = 340 m, and birds remain in a pair and switch between routes; (D) \bar{d} = 1091 m, and birds initially remain in a pair, take an intermediate route, then split up, and each returns to its established route; (E) \bar{d} = 998 m, and birds split up soon after release, each returning to its established route; and (F) \bar{d} = 1791 m, and birds remain in a pair and follow one of the established routes. All examples are taken from the Greenhill Farm release site. The release point is indicated by a white dot, the home loft by a gray dot. The scale bar represents 1 km.

The map is from the EDINA Digimap database: ©Crown copyright/database right 2006; an Ordnance Survey/EDINA-supplied service.

significantly, the model predicts a switch from “compromise” to “leadership” at a critical level of conflict.

The distance between paired birds’ established paths—and thus degree of conflict—will vary over the course of the journey home. Thus, to test the model’s predictions, we evaluated positional choices during paired flight point-by-point. In 13 of the 48 pairs tested,

birds split up prior to arrival home, with both individuals returning to recapitulate their respective established routes after the split (e.g., Figures 1D and 1E). In the remaining 35 pairs, birds stayed together for the whole journey (e.g., Figures 1A–1C and 1F), averaging an inter-individual distance of 24 m (standard deviation [SD] \pm 14 m). Splitting was associated with significantly more

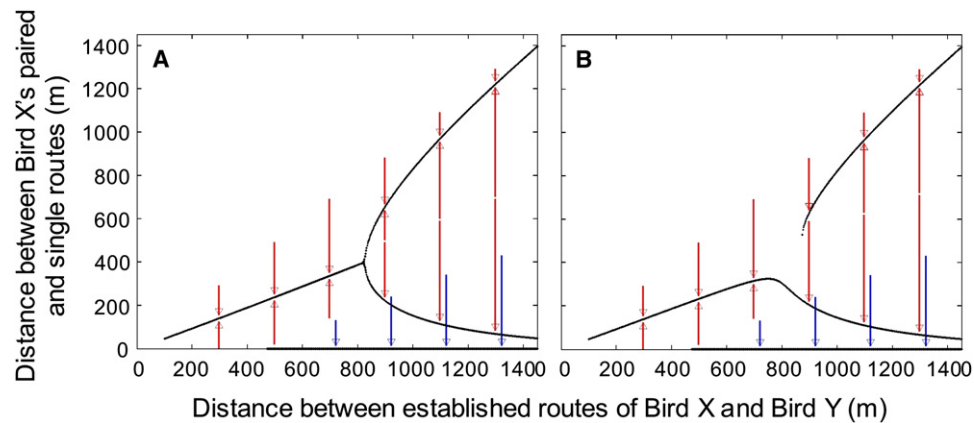


Figure 2. Predictions of the Paired Decision-Making Model

Heavy black lines indicate the stable equilibria of the position of bird X as a function of d , the distance between the targets of birds X and Y. Colored arrows show how the initial position of bird X, $x(0)$, determines its final equilibrium position. Red arrows indicate initial conditions for which the birds remain in a pair at equilibrium, and blue arrows indicate initial conditions for which the birds split and take up their established routes. Equilibria are shown for cases where (A) both birds have an equal attraction to their established route (i.e., $\beta = 1$) and (B) bird X has a slightly stronger attraction to its route than bird Y does (i.e., $\beta = 0.98$). See the [Supplemental Data](#) for details of the model.

divergent established routes: The average point-by-point distance between established routes was 1042 m (SD \pm 488 m), compared to 460 m (SD \pm 350 m) for nonsplitters (two-sample t test, $T = -3.94$, $p = 0.001$).

When pairs stayed together, the joint route depended strongly on the distance between the two birds' established routes. [Figure 3A](#) shows the distribution of distances between routes taken by individuals during their paired flight and the immediately preceding single (established) route as a function of distance between the birds' established routes at the corresponding point of the journey. Plotting the modes of these distances ([Figure 3B](#)) and analysis of kurtosis in the data ([Figure 3C](#)) reveal significant bimodality in the positions assumed by birds relative to their established routes emerging at around 575 m. Below this critical value, the distribution of distances between the birds' established and paired routes peaks at the average of the two routes, with a boundary set by the interroute distances (e.g., [Figure 1A](#)). Above the critical distance, birds become either leaders or followers, progressing down one of the established routes (e.g., [Figures 1B](#) and [1C](#)). Thus, rather than birds adopting exclusively averaging or leadership strategies, our experimental results confirm our model's prediction of a switch from compromise to leadership (compare [Figures 2](#) and [3B](#)).

Does navigational efficiency increase as a result of pooling information from conavigating individuals? Pairs that remained together for the entire journey improved significantly compared to their performance in single flights, whereas those that split showed no such improvement ([Table S1](#); [Figure 3D](#)). Unless there is a population-level bias toward choosing routes lying to one side of the beeline home (not the case here: Of the 22 established routes, 10 lay to the left and 12 to the right), improvements in homing efficiency are a necessary consequence of averaging [1]. In fact, improvements here were not limited to cases where birds had established routes either side of the direct line home: Among those 15 nonsplitting pairs whose established routes lay on the *same* side, both birds improved in ten pairs, and one of the two birds improved in four pairs

(e.g., [Figures 1B](#) and [1A](#), respectively). Also, rather than improvement resulting from clear leadership by the more efficient bird, the pair's path was equally likely to lie nearest to either established route (19 of 35 nonsplitting pairs remained closer to the shorter of the two routes; binomial test: $p = 0.736$). Such lack of leadership by the more efficient bird is exemplified by [Figure 1F](#). In fact, leadership was determined by an entirely transitive dominance hierarchy, with no relationship to individual route efficiency (see [Figure 4](#)), suggesting a social dominance external to the navigational process (a hypothesis to be tested in future experiments).

Rather than birds adopting exclusively averaging or leadership strategies, our experimental results confirm a switch from compromise to leadership as a function of distance between the birds' established routes. This conclusion explains apparent contradictions between earlier experiments on conflict resolution in small flocks. When pairs were manipulated to induce large conflict, they tended to either split or fly in the direction preferred by one bird [17]. Meanwhile, groups of unmanipulated birds with similar preferences take an average direction of flock members [16]. Compromise versus leadership thus proves a false dichotomy. Instead, the type of decision-making outcome produced by our model and seen in the data is precisely that predicted best for fitness when target destinations differ: compromise for small differences, leadership for large [3]. In relation to current theory [2], this fits the interpretation that our birds have conflicting "interest" rather than simply conflicting "information" about the home direction. Birds do have the same final destination, home, with different information about how best to get there. However, a bird may not appreciate that its partner has the same final goal, and even if it does appreciate this, it appears that the bird's own established route provides a series of local destinations about which the two disagree (thus, a conflict of interest).

Although birds exhibited leadership, it was not correlated with efficiency. Our model shows that in pairs where individuals differ, even only slightly, in their strength of attraction to the established route, the pair

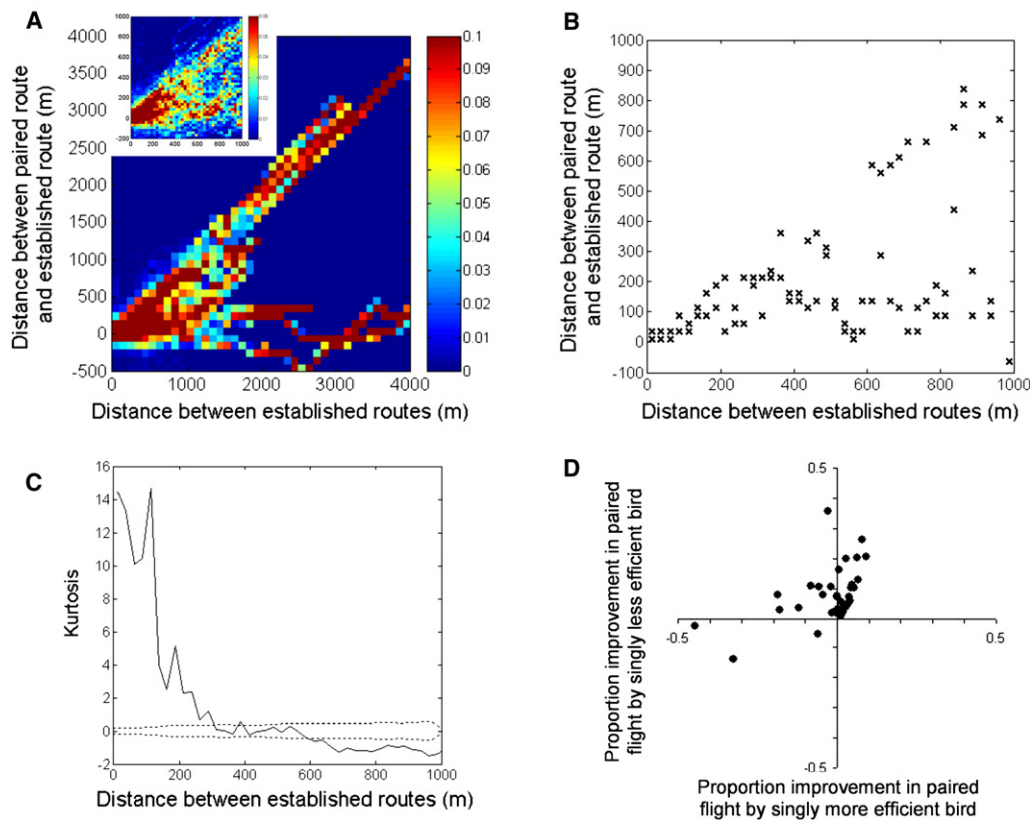


Figure 3. Analysis of Routes Taken by Pigeons Released in Pairs as a Function of the Distance between the Birds' Respective Established Routes

Data from pairs where birds split up have been excluded.

(A) Distance of birds from their own established routes during paired flights as a function of the distance between their own and their flight partner's established routes at the corresponding stage of the journey. Positive numbers on the y axis indicate positions that were assumed by the birds and lay in the direction of the flight partner's established route (i.e., within the area enclosed by the two established routes or on the far side of the partner's route); negative numbers correspond to positions in the opposite direction (i.e., away from the partner's route). Inset magnifies the 0–1000 m range.

(B) The two modes of the data shown in (A) inset.

(C) Kurtosis of the data shown in (A) inset. Dotted lines correspond to the upper and lower boundaries of the 95% confidence interval for kurtosis consistent with a normal distribution; significant bimodality in the distribution of the data begins to emerge when kurtosis drops below the lower boundary [29].

(D) Proportion improvement during paired flight by the bird with the less efficient (longer) established route as a function of proportion improvement by the more efficient bird of the pair. Proportion improvement was calculated as the difference between track length during paired flight and established route length, divided by established route length. Negative values correspond to loss of efficiency during paired flight compared to the same individual's established route.

will almost always follow the route of the individual with the stronger attraction (Figure 2B). This explains the strongly transitive nature of the hierarchy we observed, but not the lack of correlation between efficiency and hierarchy position. If the birds had modulated attraction to their established route through a judgement of that route's directness, then the pair would typically follow the more direct route, without needing a direct comparison. That pigeons did not use such a mechanism may be due to an inability to judge the efficiency of their routes or a consequence of some other benefit associated with following birds higher in the hierarchy.

Despite lack of efficient leadership in a pair, our data confirm that pairs of birds do indeed outperform single individuals. Previous evidence was equivocal regarding increased navigational efficiency as a function of group size [25–27]. Our results suggest that improvement is at least in part a consequence of the averaging of “many

wrongs” [12]. However, because birds improved even when both their routes lay on the same side of the beeline home, we cannot conclude that a simple averaging of direction home produces all the improvement. In most such pairs (nine out of ten), birds with the shorter of the two *established* routes became even more efficient in their *paired* track through a reduction in track tortuosity. Improvements on such a small spatial scale might arise either as a result of shared navigational decisions, as in our model, or through nonnavigational effects on flight decisions, such as a reduced need for vigilance in flight, but it is not possible here to distinguish the different causes.

Simulation models, based on the same principles as our model but with more than two individuals, demonstrate that our current results should scale up to larger groups and longer distances [3]. In particular, these models show that small numbers of individuals with

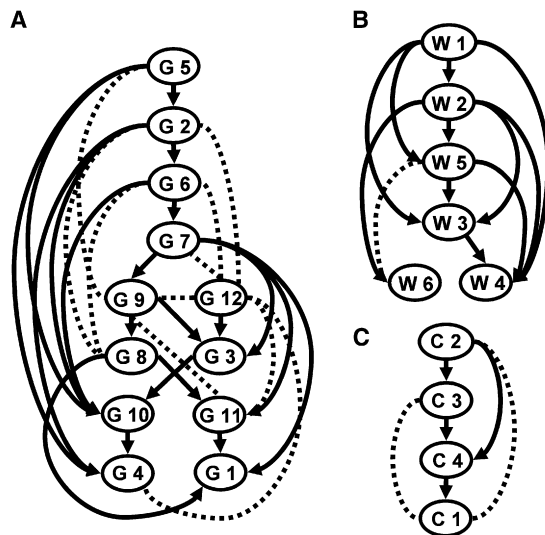


Figure 4. Outcomes of Specific Pairings of Individuals at the Three Release Sites

Shown are (A) Greenhill Farm, (B) Weston Wood, and (C) Church Hanborough. Ellipses indicate individual birds. Letters within ellipses denote release sites, and numbers correspond to the relative rank attained by each bird at that site in terms of homing efficiency during single flights (1 = most efficient). Solid arrows point from the winner of a pair to the loser; identity of the winner was established as the bird that remained closer to its respective established route during a paired flight. Dotted lines indicate pairs that split up. Note that the plots imply an entirely transitive dominance hierarchy at all three sites in that they contain no cycles. Position in the hierarchy is unrelated to individual homing efficiency (correlation coefficients between birds' ranks in homing efficiency versus proportion of paired flights led: -0.200 , $n = 4$, and $p = 0.800$ at Church Hanborough; 0.771 , $n = 6$, and $p = 0.072$ at Weston Wood; and -0.245 , $n = 12$, and $p = 0.443$ at Greenhill Farm).

strong directional preferences could lead large groups of less-well-informed individuals without losing group cohesion. We would predict that large migratory groups traveling over long distances can, as they navigate over terrain where the relative forces of attraction to landmarks and conspecifics change, switch dynamically between averaging and leadership in their directional choices.

Experimental Procedures

Subjects and Experimental Protocols

We used 22 adult homing pigeons, trained to carry miniature GPS logging devices. Each subject was assigned to one of three release sites: twelve subjects to Greenhill Farm (distance to home: 8.6 km, direction to home: 197°), six to Weston Wood (10.7 km, 221°), and four to Church Hanborough (5.3 km, 129°). At each site, subjects were released singly 20 times in succession, over the course of not longer than three weeks. By the end of this training phase, GPS data indicated that birds had developed individually distinct, stable homing routes, which were recapitulated on every subsequent release: mean \pm SD perpendicular distances between the penultimate and final training tracks for each subject were 105 ± 82 m at Church Hanborough, 107 ± 90 m at Greenhill Farm, and 91 ± 85 m at Weston Wood.

Having completed training, birds were assigned to pairs at random and released from their respective training sites simultaneously with their partner. To minimize problems of pseudoreplication, on subsequent releases, we again chose pairs randomly, with the constraint that no bird had the same partner more than once. After each

paired release, birds were given at least two single flights and, provided that they continued to recapitulate their established route, were then assigned a novel partner. Birds that did not demonstrate satisfactory route recapitulation after a paired release did not participate any further. Most birds participated in three to six pairs; one completed two paired flights, and another completed seven. A total of 48 paired releases were performed across the three sites.

GPS Devices and Data Handling

GPS trackers (24 g) were attached to the subjects' backs by a Velcro strip glued to clipped feathers, and they logged geographical longitude and latitude at 1 Hz, with data downloaded upon recapture (see [6, 28] for details). Subjects' flight tracks during paired releases were evaluated with reference to single flights immediately preceding the paired flight. Using code written in Matlab (The MathWorks Inc.), for each point on a given single track, the distance to the nearest neighboring point on the same bird's subsequent paired track was calculated. In addition, for the nearest point on the paired track thus identified, the distance to the nearest neighbor on the flight partner's paired track was calculated. For each flight, track length was calculated as total distance traveled to reach home (the sum of the distances separating all consecutive points of a track) and homing efficiency as straight-line distance between release site and home divided by track length. Track tortuosity was calculated as average number of degrees turned per meter traveled.

Supplemental Data

Supplemental Data include Experimental Procedures and one table and are available with this article online at: <http://www.current-biology.com/cgi/content/full/16/21/2123/DC1/>.

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