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Pigeon Homing along Highways and Exits

Hans-Peter Lipp,[1,*] Alexei L. Vyssotski,[1]
David P. Wolfer,[1] Sophie Renaudineau,[2]
Maria Savini,[3] Gerhard Tröster,[4]
and Giacomo Dell'Omo[1]
[1]Institute of Anatomy
University of Zürich
CH-8057 Zürich
Switzerland
[2]Laboratory for the Neurobiology of Cognition
Unité Mixte de Recherche 6155
Centre National pour la Recherche Scientifique
Marseille
France
[3]University La Sapienza
Rome
Italy
[4]Institute for Electronics
Swiss Federal Institute of Technology
Zürich
Switzerland

Summary

Background: Anecdotal observations and early airplane and helicopter tracking studies suggest that pigeons sometimes follow large roads and use landmarks as turning points during their homeward journey. However, technical limitations in tracking pigeon routes have prevented proof.

Results: Here, we present experimental and statistical evidence for this strategy from the analysis of 216 GPS-recorded pigeon tracks over distances up to 50 km. Experienced pigeons released from familiar sites during 3 years around Rome, Italy, were significantly attracted to highways and a railway track running toward home, in many cases without anything forcing them to follow such guide-rails. Birds often broke off from the highways when these veered away from home, but many continued their flight along the highway until a major junction, even when the detour added substantially to their journey. The degree of road following increased with repeated releases but not flight length. Significant road following (in 40%–50% of the tracks) was mainly observed from release sites along northwest-southeast axis.

Conclusions: Our data demonstrate the existence of a learned road-following homing strategy of pigeons and the use of particular topographical points for final navigation to the loft. Apparently, the better-directed early stages of the flight compensated the added final detour. During early and middle stages of the flight, following large and distinct roads is likely to reflect stabilization of a compass course rather than the presence of a mental roadmap. A cognitive (roadmap) component manifested by repeated crossing of preferred topographical points, including highway exits, is more likely when pigeons approach the loft area. However, it might only be expected in pigeons raised in an area characterized by navigationally relevant highway systems.

*Correspondence: hplipp@anatom.unizh.ch

Introduction

The most widely accepted explanation for pigeon homing over distances of 20 km and more is that they rely on a "map-and-compass" strategy. It has remained undisputed that pigeons have an internal clock and an internal sense of compass direction home and that this latter sense depends on the position of the sun, if visible. Yet directional knowledge alone is not sufficient for successful homing, and so pigeons must also have a large-scale mental map containing information about their current position with regard to their loft [1]. Mechanisms of position determination and the nature of the mental map used by homing pigeons have remained controversial for decades. Supporters of the magnetic theory of pigeon homing claim a predominant role of the earth's magnetic field for both compass and map mechanisms [2]. Others propose a major role of the olfactory system and atmospheric gradients [3, 4]. Although vision is helpful yet not mandatory for successful long-distance homing [5–7], there is general agreement that pigeons rely at least partially on visual cues for flights within their familiar home range, 2–4 km around the loft [8–10]. Whether the local visual information is used by the birds for homing from distant release sites—a strategy coined "pilotage" [11]—has been equally controversial [2, 12–16].

Likewise, the nature of the objects used by pigeons for pilotage has been debated. Breeders of racing pigeons have often observed that large flocks of homing pigeons fly along major highways [17], and it is a familiar observation for most pigeon breeders that the birds often do not approach the home loft according to a straight compass direction from the release site. Early attempts to identify topographic guide-rails used by homing pigeons (e.g., roads, railways, powerlines) by means of airplane tracking have yielded equivocal results [18]. Some studies reported positive evidence [19]; helicopter tracking studies even found that pigeons were circling over road crossings [20]. However, even in these positive cases, observations were rare and anecdotal. Moreover, other, older tracking studies found little or no evidence for even occasional use of topographic leading lines [21–24], although there seems to be agreement that pigeons appear to be attracted to villages and cities [20, 24, 25]. Even the most recent and widely publicized "discovery" of pilotage along British highways [17, 26] refers, according to the experimenters, to anecdotal cases observed during short-distance releases [27, 28] or to observations from unpublished data [29].

The major obstacle to verifying navigational use of landmarks such as roads or characteristic locations has been technical. Although the angle at which an individual pigeon leaves the release site and the time at which it arrives at the loft can be easily recorded, the intermediate journey has been near impossible to follow accurately and frequently enough for statistical analysis. Even the use of route recorders monitoring angular changes in flight direction [14, 30–32] has not been able to produce the necessary data for quantitative analysis. Recently, however, new technological advances have provided the materials necessary for significant advances in the ability to record flight paths. Our lab has utilized GPS (global positioning system) technology to develop miniaturized path loggers that sit on the pigeons' backs and precisely record the entire route taken by individual homing pigeons during their flight back to the loft [33–35]. Because even the first technical studies provided single-case evidence for a road-following strategy of homing pigeons [34], we have, for the last four years, focused on employing this method to test predictions of the magnetic, olfactory, and visual hypotheses of bird orientation.

Results and Discussion

Overall Road Following

The presented analysis is based on 216 technically complete GPS tracks obtained from 34 birds during the years 2001–2003. Pigeon tracks not presented here include birds with experimental treatments or pigeons released in small flocks. All pigeons were pre-trained from five often-used and nine seldom-used release sites chosen for their ability to reveal topographic and geomagnetic impacts on homing routes. Details for the five major release sites are found in Table 1. The loggers recorded the position of the pigeons in intervals of 1 s, with an accuracy of ± 6 m [34]. The loft was located 20 km west of Rome (Testa di Lepre), at an altitude of 20 m above sea level, in a small, flat, canyon-type valley connecting with the Mediterranean sea (for details of topography and methods, see the Supplemental Data available with this article online). The nearest main road runs north-south and crosses coastal highway Nr. 1 (SS Aurelia) at highway junction 22, about 3 km south of the loft.

A large-scale motorway map (1:300,000) with all flight paths superimposed shows that the experienced pigeons accurately oriented themselves homeward on release, regardless of the position of the release site. Yet, many flight paths of pigeons released from 28 km northwest (NW) at Santa Severa (or approaching the shoreline from a northwestern release at sea), converged and ran together over long distances (Figure 1). These common pathways appear to be associated with the coastal highways Nr. A12 and the SS Aurelia, and, to a lesser extent, with the coastal railway. Tracks of pigeons released from the north converged into the flat valley leading to the loft, whereas tracks from the northeast fanned out more but finally merged with the former. Tracks from the southeast were more dispersed but aggregated approximately at the highway junction between the SS Aurelia and the valley road leading to the loft. Finally, pigeon tracks from the south also converged on this point and continued northward to the loft. Although this pattern of tracks looked suggestive, the question remained as

Table 1. Details of Release Sites

					Measurements with 100 m Squares						Measurements with 250 m Squares					
Main Release Sites	Beeline (km)	Direction	Number of Tracks	Number of Birds	Track Length[a] (km)	SEM	Actual Road Length (km)	SEM	Simulated Road Length (km)	p Value t-test[b]	Percent of Tracks for which $p < 0.05$[c]	Actual Road Length (km)	SEM	Simulated Road Length (km)	SEM	p Value t-test[b]
Cesano	19.5	N	34	19	34.4	1.7	2.2	±0.2	2.0	n.s.	5.9	5.3	±0.4	4.8	±0.04	n.s.
Marcigliana	24.9	NE	40	16	43.2	1.8	2.5	±0.2	1.7	0.0004	15.0	5.7	±0.4	4.2	±0.04	0.0009
Santa Severa	27.6	NW	36	20	45.7	2.2	4.5	±0.4	2.2	<0.0001	41.7	11.3	±0.8	6.0	±0.01	<0.0001
Via Pontina	32.2	SE	38	17	44.1	2.9	3.6	±0.3	1.8	<0.0001	47.4	7.0	±0.6	4.1	±0.10	<0.0001
Seaside	52.0	WNW	32	18	37.6	2.7	3.7	±0.4	1.7	0.0002	46.9	8.8	±0.9	4.7	±0.14	<0.0001
All pigeons		n = 34	216		39.6	1.0	3.0	±0.1	1.8	<0.0001	28.2	6.9	±0.3	4.5	±0.08	<0.0001
Random independent sample		n = 31	31		39.7	2.9	2.5	±0.3	1.5	0.0006	19.4	5.9	±0.6	3.9	±0.22	0.0018

[a] For seaside release; track length over land only is shown.
[b] Two-tailed t-test for related samples.
[c] Refers to the number of real tracks with more road-following than expected by chance as computed by simulation.

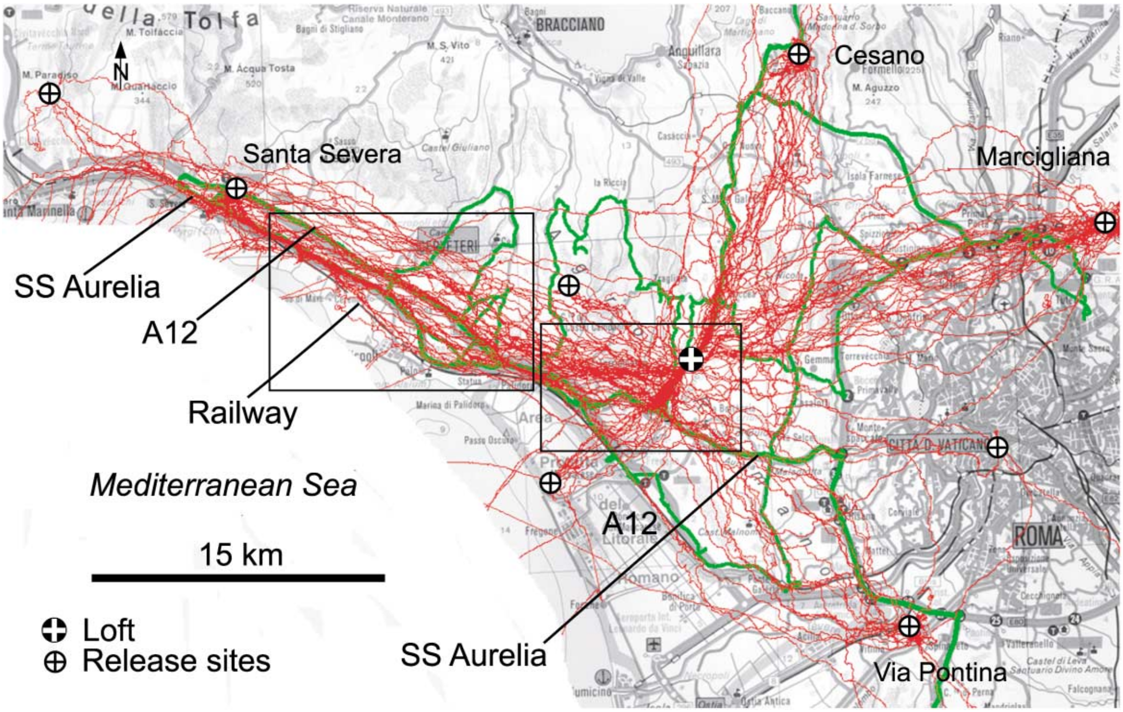

Figure 1. Tracks, in Red, of 216 GPS-Equipped Pigeon Flights Near Rome during 2001–2003

Dense strips of paths overlaying coastal highways and railway reflect pigeons released from the northwest and from the sea. Note that many pigeons arriving from the sea did not turn homeward at the shoreline but flew until they met the coastal highway running 1–2 km from the coast. Frames indicate regions of interest shown in Figures 3 and 4. Green bands show the course of highways and roads as recorded by a pigeon GPS logger placed in a car.

to what degree it may have been caused by chance and to what degree it may have been caused by a specific distribution of roads and highways in that region.

Statistical Analysis of Road-Following Behavior

The main problem for statistical testing was to define a null hypothesis for the distribution of tracks between the release site and the loft. The flight paths of homing pigeons show many peculiarities not easily addressed by geometrical models using a defined distribution of paths along the beeline (the shortest distance between the loft and the release site). Using a variant of bootstrap simulation [36], we generated a distribution of virtual flight paths by extracting the geometrical information from the available 216 tracks. In brief, we assumed that any pigeon could have used, by adjusting for distance, any of the 216 trajectories to fly home, some of these trajectories being more straightforward, others more tortuous. We also assumed that the pigeon could choose a route symmetrical to the beeline. Thus, a "virtual pigeon" could use $216 \times 2 = 432$ variants to fly home. Because the release sites had different locations and directions to the loft, trajectories from a given release site to the loft were rotated and scaled to fit any combination of release site and loft. We visualized their distribution by using density maps, which we computed by dividing the study area into a grid of 100×100 m squares (for comparison, we also divided the study area into 250×250 min squares) and then counting the number of tracks coinciding with each square. This resulted in two density maps, one containing the actual 216 tracks (Figure 2A) and the other presenting those tracks reiteratively scrambled and fitted to the same release sites (Figure 2B). For the real tracks, the same clusters as observed in Figure 1 were again seen, whereas the virtual map showed a smooth density of all possible virtual tracks within the actual observed boundaries.

For the statistical testing of road-following behavior, a pattern of roads and highways recorded by GPS tracking devices in a car was overlaid computationally with square grids of different cell sizes (100×100 min, 250×250 m, and 500×500 m), with one cell centered on the home loft. The roads included the large highways (A12 and SS Aurelia) running from northwest (NW) to southeast (SE), the large ring highway around Rome, the road in the valley of the loft, and some smaller roads running north-south, either along a flight direction or perpendicular to the flight axes from NW to SE. The number of squares crossed by a real flight track and also the number of road-containing squares crossed by the track were counted, resulting in estimates of the length of a track associated with a road and the length of the entire track. This procedure overestimated the true track length as measured by GPS by 14.6% (for squares of 100×100 m) but remained highly correlated with the GPS track ($r = 0.94$). For statistical comparison, the number of road-associated squares crossed by any of the 432 virtual tracks and their flight path length were computed similarly, giving a mean simulated flight path length and track length close to the roads. The calcula-

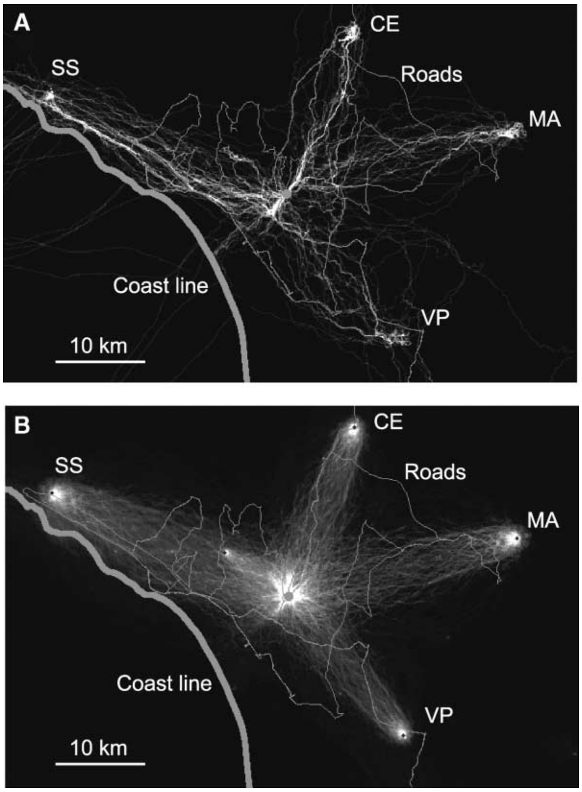

Figure 2. Actual and Simulated Density Plots

Grayscale coding indicates the probability of finding a pigeon in a specific quadrant (white = 1.0; black = 0). Dark gray lines indicate the coast, and small gray lines indicate the major motorways and smaller roads that were used in the computational analysis.

(A) Actual density (*N* releases = 216). Bright spots correspond to the major release sites and the loft (in the center).

(B) Simulated density of the null hypothesis of trajectories, with the assumption of no landmarks so that any route may be chosen.

tion of such values permitted the application of conventional statistical methods for comparing mean values of real and simulated road-following scores for different release sites. It was also possible to calculate the probability that a given real track would overlay the GPS-mapped roads by chance (see Experimental Procedures).

Table 1 shows a comparison of averaged real and simulated path lengths for all 216 tracks observed in 34 birds and respective scores for the five major release sites. Because the statistical comparison of all tracks includes a mixture of birds released only once and those released repeatedly, we randomly selected a sample of 31 tracks, each one from a different pigeon and a different date of release. Because this sub-sample included, by chance, many tracks over regions containing no marked roads, we consider it as the most conservative estimate of road-following tendency in our collection of tracks. The statistically most distinctive values were those obtained with square sizes of 100 × 100 min and were thus used for correlative statistics shown later. However, this stringent criterion clearly underestimated the road-following tendency of the birds because there is no need for road-following pigeons to fly above the road or within 50m of it. The road-following scores obtained with squares of 250 m side length (125 min on each side of the road) correspond better to the visual impression provided by inspection of tracks shown on topographical maps. We use this resolution of 250 min squares for description here; although scores based on squares of 500 × 500 m appear to match the eye-scoring best, they also increasingly include virtual tracks, diluting statistical precision.

Overall, the 216 tracks showed an average road-following score of 6.9 km as compared to 4.5 km expected by simulation, the difference being highly significant ($p < 0.0001$) and 28% of the tracks being classified as significantly road-following. The conservative sub-sample still showed a highly significant difference between real and simulated road following ($p < 0.001$). A comparison of the various release sites revealed interesting differences despite the fact that the regions contained different patterns of marked roads and highways. From the northern release site (Cesano, Figure 1), there was no difference between real and simulated track length, although many of the pigeons released there showed preferential road following from other sites. The pigeons could have followed a country road fairly coincident with the bee-line but did so only during the last kilometers before the loft, after the road descended gradually into the shallow creek of the Arrone valley. Likewise, road following from a northeastern release site (Marcigliana) was only moderate, although highly significant (5.7 km real versus 4.2 km simulated, six out of 40 tracks being considered statistically as road following). This low road-following tendency is understandable given that the pigeons needed to cross the periphery of Rome and fly above many intersecting roads. The score is certainly biased; the only road recorded by GPS in this region was the large four-to-six-lane highway around Rome. Visual inspection of maps revealed, however, that the pigeons appeared to largely ignore other minor roads leading toward their loft. This and the results from the Cesano release site suggest that the size of the road partially influences the road-following tendency of experienced pigeons.

Road following was notably more pronounced from release sites where pigeons had to fly along a NW-SE axis. From these release sites, between 40% and 50% of individual tracks were classified as road following. For further description, we concentrate specifically on these release sites.

Choosing and Following Highways

We chose the northwestern release site at Santa Severa to test whether pigeons would follow the compass direction home or preferentially join roads leading homeward. This was possible because they had to fly for about 20 km across a large plain (occupying 8–10 km between coast and northern hills) that is devoid of any topographical obstacles enforcing a particular flight trajectory (see altitude map and flight tracks in the Supplemental Data) and contained distinct longitudinal objects. The aggregation of flight paths over a distance of many kilometers along highways can be seen with particular clarity on a small-scale map (Figure 3) showing 72 tracks from 28

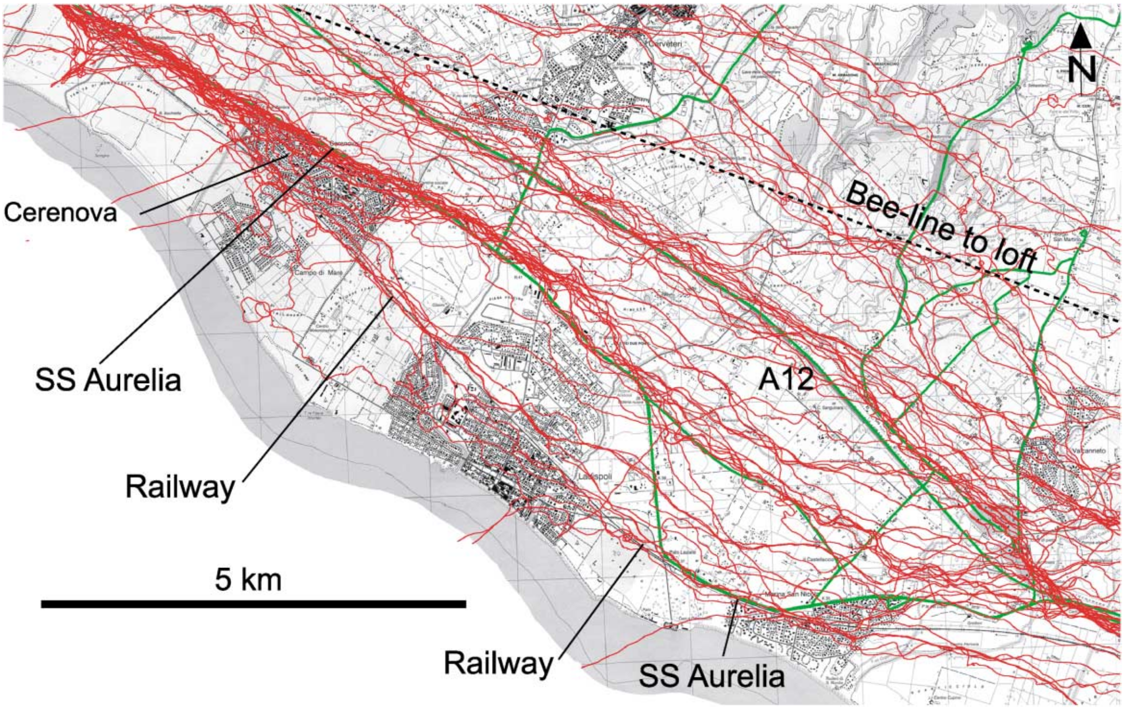

Figure 3. Pigeon Tracks along Motorways and Railway in Detail

The beeline to the loft shows the compass direction from the main release site in the northwest. Note an apparent conflict of directional strategies; pigeons appear to be attracted by both longitudinal objects in parallel to the beeline and by the proper compass direction. This conflict appears in two features; pigeons shift preferentially to the left of the highways when these turn away from the compass direction, and there are frequent break-offs of tracks subsequently aligning with the highway A12 or toward the beeline. Green lines show GPS tracks obtained by a car.

pigeons that had been released repeatedly from Santa Severa or the sea (from where the birds usually headed directly to the coast before turning homeward). A minority of tracks (10/72) loosely followed the beeline to the loft without any visible association to longitudinal features evident on a topographic map. On the other hand, most tracks (42/72) ran for the first 5 km after release in close proximity to the SS Aurelia, which was accompanied there by the coastal railway. In this segment of the journey, surprisingly few tracks (6/68) followed the A12, which passes in close proximity to the Santa Severa release site. The remaining tracks showed no clear associations with the highways. Upon approaching the village of Cerenova (Figure 3), a minority of tracks (10/72) broke off to the right by joining the railway that separated from the SS Aurelia at that point. However, the pigeons did not continually follow initially preferred objects. During the next 5–10 km, individual tracks veered from the SS Aurelia northward to join the A12, which appeared to attract increasingly more tracks or break off from the A12 toward the beeline. This trend toward the beeline may also explain why the birds had a tendency to fly on the left-hand side of the highways. Interestingly, pigeons did not join the equally distinct and easy-to-follow shoreline but rather chose to follow the man-made objects. Qualitatively, the road-following behavior was manifested most impressively at some 12–15 km after the release site. At this point, the three major longitudinal objects, A12, the SS Aurelia, and the railway, converged, and so did the pigeon tracks (Figure 3).

The quantitative analysis definitely underestimates the degree of object following because there were no GPS tracks of the railway trajectory available. Nonetheless, Figure 4 shows the estimates of road following according to the different criteria. Using a loose criterion of counting 500×500 m squares (250 m left or right from major highways), one notes that the pigeons followed highways on average for 16 km, not counting those flying along the beeline or railway. The ten tracks with the highest road-following scores ranged from 20 to 30 km (or from 12 to 20 km for the 250×250 m estimates). Given a beeline distance of 28 km from Santa Severa to the loft, these numbers are, indeed, impressive.

Road Following: Navigational Help or Human-like Road Use?

The data from all release sites show that pigeons can find the loft by using an apparently compass-based flight orientation but appear to prefer a road-following strategy along the NW-SE axis. This road-following strategy could correspond to a mechanism stabilizing a chosen flight direction (e.g., for humans, "this is my home direction and here is a long object leading roughly homewards"), or it may reflect a cognitive behavior based on a mental map (e.g., for humans, "this road is the A12 leading to Rome, I must follow it to exit 22 where I have to turn left and follow that road for three km to reach home").

The more parsimonious interpretation is that large roads leading homeward stabilize a flight direction cho-

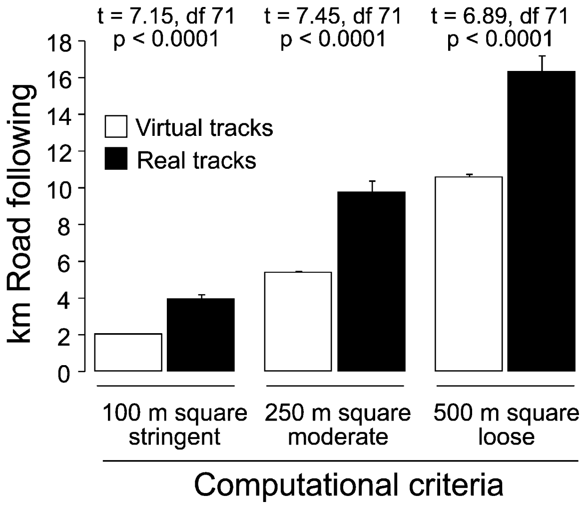

Figure 4. Road-Following Scores of Pigeons Traversing the Coastal Plain as Estimated by Different Measurement Grids

The sample includes 72 pigeons released from northwestern release sites (seaside and Santa Severa, see also Table 1). Note that the degree of real and simulated road following almost doubles with every increase in square size. The method using the largest squares provides an estimate that matches eye scoring on the maps but discriminates less (albeit still highly significantly) between simulated and real tracks. Error bars show the standard error of the mean. This graph is an exception insofar as it shows the best statistical discrimination with squares of 250 m side length. Normally, the smaller grids revealed more precise statistical discrimination.

sen by the pigeon, particularly when the birds are en route and far from the loft. The evidence for this comes from the observation that the birds break off from roads to join a course closer to the initial compass direction when the angular difference between road and loft direction is growing, but such corrections of flight course appear not to be bound to visible topographic criteria. The fact that many pigeons flew for long distances in parallel to the highways implies also that they served as visual guidance and that the birds were not relying on other motorway cues, such as heat, noise, or exhaust fumes. This is corroborated by one anecdotal case (observed during film recordings from the Santa Severa location at NW) showing that one bird held to a course along the A12 for about 10 km despite a strong and chilly side wind from the sea (50–70 km/hr, 4°C) that blew other pigeons up to the hills and beyond the beeline. Thus, the attractiveness of the highway must have been considerable. There is also some evidence that the pigeons were not following just any longitudinal object pointing homeward but seemed to make a choice. Pigeons arriving from the sea preferred to follow the SS Aurelia (associated there with the railway) and not the shore or the A12, both running parallel to the road. They also seemed to have an overall predilection for large or four-lane highways, and they apparently ignored roads in regions where they were inappropriate for navigational help. Taken together, it appears that large roads served to stabilize, during the early and middle flight segments, a course direction compatible with the homeward direction. This would not correspond to a flight behavior based on pilotage by road reading. One should also note that our releases took place maximally 50 km from the loft. Distances between 20 and 100 km pose for pigeons more orientation problems than homing from farther sites [37], presumably because long-distance gradients of geophysical or air-borne cues are better perceived when far from the loft. Hence, using roads as navigational help may be linked to this difficulty but obviously also depends on the road situation and topography of the area under study.

Approaching Home: Nodes, Beacons, and Landmarks

Within a smaller area (radius of 10 km from the loft), a cognitive component in the bird's navigational behavior was more evident. This part of the flight thus deserves a separate analysis illustrated for all pigeons approaching the loft from the NW or SE (Figure 5) and for a single case (Figure 6). The topography of the region including the final approach area without overlaying tracks can be found in detail in the Supplemental Data online. After the two coastal highways converge and cross, the SS Aurelia veers south of the loft valley until it crosses, at junction 22, a road leading up the Arrone valley. This junction at the entrance of the valley is characterized by a typical exit system associated with white supermarket buildings and a passage system painted blue. At least for humans, these are easy-to-remember spatial cues marking the motorway exit and entrance to the northern Arrone valley.

About 8–10 km from the loft, the flight tracks indicate that pigeons that had previously followed roads appeared to make a directional decision. This was often characterized by some circling (the usual behavior of pigeons at a release site during initial orientation). Such behavior took place in a zone where the two highways separated again, largely between the villages of Palidoro and Torrimpietra (their position being indicated in Figure 6). A minority of eight tracks showed a direct course toward Castello di Torrimpietra and continued from there straightforwardly to the home loft; these pigeons traversed plateaus, creeks, and valleys in order to descend to the goal, which was invisible during this approach (Figure 5). This may indicate a resetting of a compass direction, but we cannot exclude that the birds were attracted by a topographical point near the Castello di Torrimpietra (Figures 5 and 6) because this zone was also preferentially crossed by many tracks not associated with previous road following. The other tracks of the road-following pigeons either remained in proximity to the motorways A12 and SS Aurelia or made a shortcut directly toward exit 22. These pigeons reached the loft by means of a considerable detour, which added 4–7 km more to the last part of their journey. Although pigeons arriving from the west and northwest directions turned homeward in a sharp angle, 100–500 m north of exit 22, others arriving from the south and southeast crossed the SS Aurelia directly over the exit or passed close to it (Figure 5). It is noted that many pigeons were seen to circle briefly in the area between exit 22 and the entrance to the Arrone valley. Some of them took a route northward to the loft across a plateau, others followed the left valley road leading to the loft,

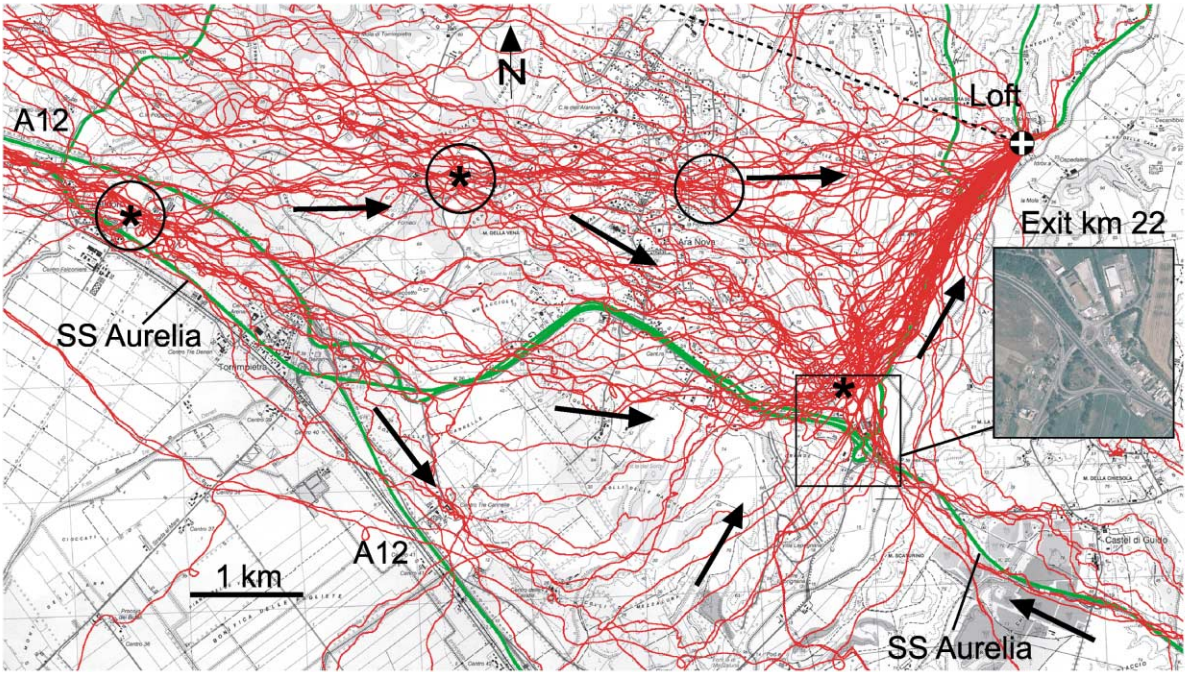

Figure 5. The Final Approach to the Loft by Direct and Indirect Routes Associated with a Landmark at Exit 22 of the Highway SS Aurelia

Top arrows: shortcut across creeks and plateaus by birds arriving from the northwest or from the encircled area between motorways. These birds could not see the loft during their approach. All other pigeons follow the routes marked by arrows and pass nearby or through exit 22. The loft is not visible from this point, either. Note that the motorway veers downhill and southeast to the right immediately before the exit, which becomes visible for pigeons only when they enter the framed area. Most pigeons arriving from the west thus cut the corner at the exit. Pigeons arriving from the south and southeast pass over the exit and avoid the valley's right side, leading to the loft. Inset: satellite view of exit 22. Circles show "traffic nodes" where pigeons appear to make decisions for taking directions. Asterisks indicate zones where pigeons were frequently observed to circle, typically a sign of navigational incertitude. Green lines mark the highway and road to the loft as revealed by GPS tracking with a car. For detailed topography, see also the Supplemental Data.

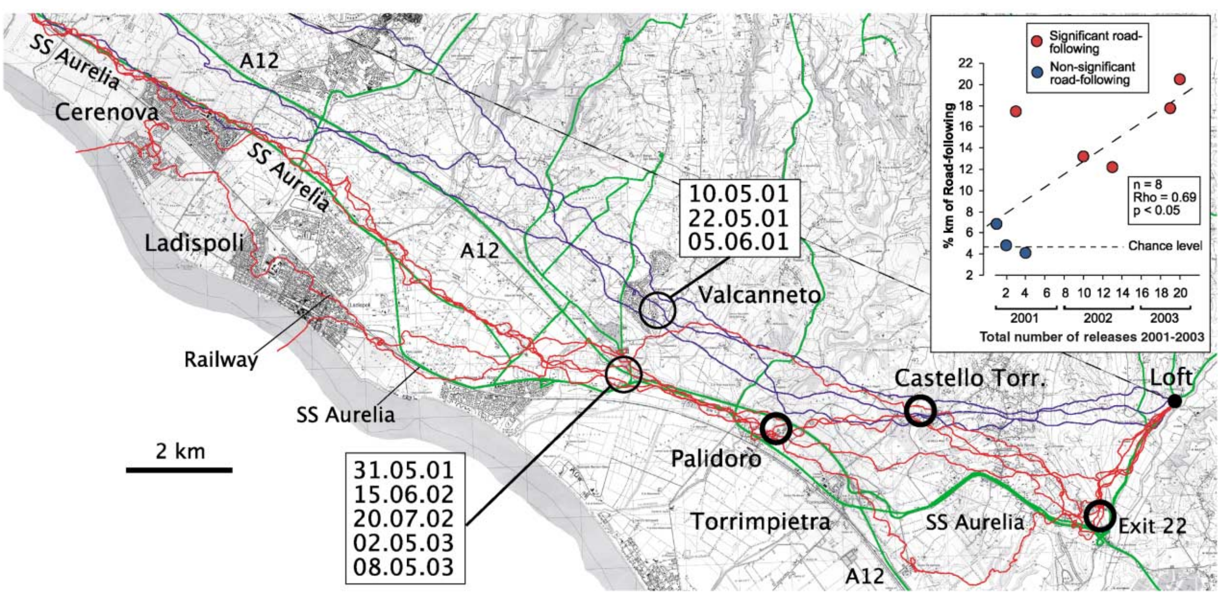

Figure 6. Learning of Road Following by an Individual Bird, Pigeon Nr. 9

The eight tracks recorded span a period of 3 years, with a total of 20 releases from different sites. The graph shows a significant correlation between the consecutive number of releases the pigeon has experienced and the relative road following (expressed as percentage of the entire flight track). Red tracks have been classified statistically as road following above chance level (4.5%, see graph). Large circles indicate topographical regions ("traffic nodes") passed regularly by the pigeon. Thicker circles indicate points of apparent navigational decision-making. Note the bifurcation point at Castello di Torrimpietra, from where the later flights (2002 and 2003) veered to the southeast in order to pass near exit 22.

and a few tracks joined a smaller road at the right rim of the valley (Figure 5). Exit 22 appeared to be a highly attractive point because many of the more northern tracts passing near the Castello di Torrimpietra veered southward to approach it, distinctly away from the home direction. Thus, the larger home area appears to be characterized by at least three geographical points, which the pigeons pass repeatedly and where they seem to make directional decisions. The most important geographical attractor was highway exit 22, which could not have been seen by pigeons approaching via highways from the SE or NW or directly from Torrimpietra, but it could possibly have been seen from Castello di Torrimpietra.

Individual pigeons frequently passed other geographical locations that cannot be seen on the map in Figure 5. Taken together, the ensemble of tracks and analysis of individual birds strongly suggests that the larger home area (up to 10 km) contains familiar geographical locations resembling traffic nodes, a concept associated with home-range patrolling of rodents [38]. These points may serve as beacons, i.e., as distantly perceived attracting objects permitting pilotage in the form of beacon-hopping homeward, most likely spotted over many kilometers. This would imply what is called taxon learning in animal psychology [39]. Although there might be some other beacons (inconspicuous to human observers) above the rim of the valley marking the position of the loft, both exit 22 and the loft itself are not visible for many birds because they are hidden in the Arrone valley. Making a detour to reach one invisible point via another invisible point, however, only makes sense if the birds have memorized that the loft can be safely reached by passing through the intersection of the SS Aurelia with the Arrone valley, this location being marked by a conspicuous object, exit 22 and adjacent buildings. In addition, they must have learned somehow that this invisible point can be found by following highways, preferentially the SS Aurelia. In this case, the location of exit 22 would represent a landmark in its navigational sense, namely a memorized object used to determine an invisible goal location, as for the Morris water maze task in which rodents are required to find a submerged platform by using extramaze navigational cues [40]. This conclusion, however, depends on the demonstration that road following is a learned strategy.

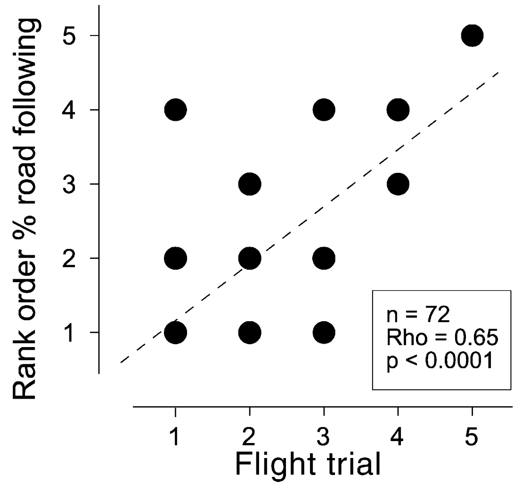

Figure 7. Learning to Follow Roads across the Coastal Plain

The plot indicates the flight trial (number of the release) at given sites (Santa Severa, the sea, and a more distant location northwest). In order to equalize differences in distance and locations as well as individual propensities of the pigeons, road following is expressed as rank order for an individual bird. This presentation is biased by a disproportionate amount of cases that have only one or two releases but illustrates that all birds having had several repeated releases show a ranking of road-following scores according to flight trial.

Learning to Follow Roads and Landmarks

The analysis of possible learning effects was hampered by the fact that all pigeons had been pretrained at least twice with GPS dummies from any new release site, that pigeons had undergone different numbers of releases and had different experience, and that we had no release information from old birds except that they were experienced long-distance racers. That pigeon routes are learned is most easily demonstrated by comparison of the first release from an unfamiliar site with the subsequent ones [14], but this carries the risk of frequent losses of GPS devices.

The releases from the NW (Santa Severa and the sea) were the focus of the analysis because they included the largest number of birds ($n = 24$) with repeated tracks (total 72) along the coastal plains. A single case analysis could be conducted with pigeon Nr. 9, having mastered 20 releases in three years, 8 of them along this axis, albeit with different track lengths. By plotting the degree of road following as a function of releases in chronological order, one can clearly see that the bird developed a significant habit of road following over time. During the first year, three out of four tracks were rather remote from roads, whereas during the following two years, the remaining five tracks were increasingly associated with the course of the A12 and SS Aurelia. All birds released from the NW were then analyzed, with individuals being ranked by their road-following score and these ranks being plotted against the number of the release (flight trial; Figure 7). This revealed a significant correlation between flight trial and road-following rank (Rho = 0.65, $p < 0.0001$). This crude correlation analysis is limited by the fact that there were many birds with one to three GPS releases, but it nevertheless distinctly shows that practically all pigeons improved their road-following score with more releases over time.

In order to verify these results, we then selected, from the entire sample of 216 tracks, 22 birds that had experienced three or more GPS-tracked releases and plotted their averaged road-following scores against the total number of releases (Figure 8). This clearly showed that the degree of road following was a matter of experience; the more releases the birds had done (and with it the more kilometers the birds had flown), the better were the road-following scores (Rho = 0.59, $p < 0.01$). This correlation was not a function of age because it was also shown by yearlings (Figure 8), provided they made several flights.

We then ran a similar analysis to check whether the pigeons arriving from the NW had learned to pass near exit 22 in order to reach the loft. For each pigeon, we

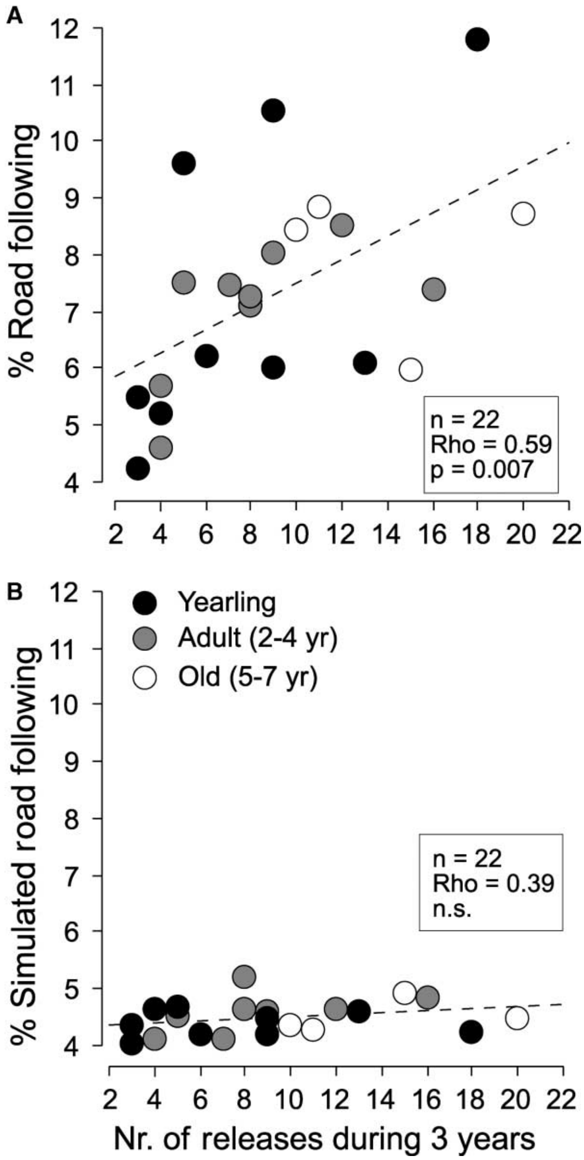

Figure 8. Learning and/or Optimization of Road-Following Scores for Individual Pigeons as Assessed from All Release Sites. The Plots Show Birds that Had at Least Three Releases

The X-axis shows the number of releases for a given pigeon. As in the inset of Figure 6, it corresponds roughly to the total flight distance covered by the pigeons.

(A) Significant correlation with actually observed road-following scores.

(B) Control plot with simulated road-following scores

calculated the minimal distance to the center of exit 22 and found a moderate yet significant correlation (Rho = 0.31, n = 72, $p < 0.01$) between the number of releases the bird had experienced and the pigeon's proximity to exit 22. Thus, both road-following and using landmarks appears to be learned, or at least optimized, with time and release number.

The Cost of Detours

Following roads and targeting specific landmarks causes the pigeons to deviate from a flight path along the beeline which, in theory, should be the most economical homing strategy. But why were the birds adding mileage to their journey and even refining this behavior over time? One could argue that roads convey both directional and positional information, but the pigeon is then required to evaluate certainty of orientation against costs of flight – a non-trivial task even for humans. We tried to clarify the problem by calculating correlations of road-following scores with scores obtained with conventional track analysis providing additional information contained in the flight paths [34]. We carried out the analysis again by using the data from the 72 tracks from NW and verified it for the entire sample of 216 tracks. The somewhat surprising result was that the mean flight path length did not increase with road following, showing even a slight yet nonsignificant reduction (Rho = −0.19). A second and also unexpected finding was a moderate negative correlation of road following with average ground speed (Rho = −0.27, $p < 0.05$) and a positive correlation with path tortuosity (Rho = 0.30, p = < 0.025). In addition, we found a significant negative correlation of road following with altitude of flight as measured with GPS. However, it is necessary to evaluate the functional significance of this correlation by calculating altitude above ground level rather than above sea level. Thus, flight paths along roads were, perhaps, lower, and the birds tended to fly more slowly and more tortuously; they often swung regularly along the highways (for examples, see also Figure 6). On the other hand, flights across the countryside or hills were higher, faster, and more straightforward, but these were apparently associated with occasional yet substantial imprecision in directionality. Thus, road following appeared, overall, cost neutral in terms of energy, at least if one assumes that the energy costs were equal per kilometer of flight. Should road following permit a form of energy-saving flight style, this would explain why the pigeons developed a preference over time; such incremental learning usually requires a reward. Alternatively, if energy costs were equal for both road-following and non-following flights, the reinforcement of road-following could be familiarity; the pigeons might prefer to fly along known or at least familiar-looking objects instead of joining a compass direction across an unfamiliar countryside. Avoiding the unknown is a widespread rule among animals and humans and is probably the main source of habits, that is, behavioral acts developing without visible reinforcement and showing little extinction over time. From an ethological point of view, habit formation frees an animal's brain from a need to consciously attend to the once-difficult task and thus permits them to use their processing time and power for competing tasks such as watching for predators.

Do Pigeons Follow Roads Everywhere?

Our findings have served to clarify a long-standing debate concerning whether experienced pigeons can systematically use topographical guide-rails such as highways and specific landmarks to steer their home course. Historical tracking studies have found occasional evidence for such a strategy, including the observation that pigeons had a tendency to briefly visit previous release sites (see Introduction). On the other hand, there have been many observations of pigeons ignoring such cues. Wagner [20, 25] performed detailed helicopter tracking studies by using different lofts and following pigeons from unfamiliar release sites across a broad variety of topographical constellations, and these studies have suggested that homing pigeons appear to be attracted chiefly by topographical features resembling their loft situation (e.g., type of village, type of landscape, patterns of roads). This appears to be the case here also; we assume that the behavior we observed is unlikely to be shown by pigeons that have not grown up in, and been trained to return to, a loft located close to major highways.

It is also clear that demonstration of road following requires a rather unique set of features, namely multiple guide-rails imperfectly aligned with the home direction. This was clearly the case for our study, but we realize that this prerequisite is rare. A study using compass-based route recorders [14] shows tracks that might have run along the northern coastal highway A12 from La Spezia to Pisa, and possibly along roads crossing a mountain between release site and loft. For technical reasons (assumption of a constant flight speeds that routes could be calculated from angular changes in flight direction), these loggers do not have the necessary precision to verify proper following of roads. Nonetheless, the region would lend itself to study with GPS path tracking.

Whether GPS tracking of real long-distance (>200 km) flights by homing pigeons will reveal similar orientation principles remains to be determined. Preliminary observation of Belgian racing pigeons over distances up to 380 km has shown similar temporary road-following behavior, albeit less pronounced than that shown here (unpublished data). Finally, we would like to agree with Walcott [41] that homing pigeons appear to have a remarkable ability to shift from one homing strategy to another, and thus we caution against uncritical generalization of our findings.

Experimental Procedures

GPS Loggers

We constructed the loggers or obtained them from NewBehavior AG, (Hardturmstrasse 76, CH-8005 Switzerland, http://www.newbehavior.com). The technical features of the processors used are described in full detail elsewhere [34]. The main difference between this and the earlier version is a reduced weight and the placement of a flexible rechargeable battery below the logger. The loggers had a battery capacity to record for 3 hr with a frequency of positional fixes of 1 Hz.

Pigeons

Birds of both sexes were used. They were 1–7 years old, and all individuals had undergone numerous training flights. All pigeons were bred locally and belonged to a line adapted to the location. Pigeons were housed in former Swiss Army mobile lofts obtained from the Swiss Homing Pigeon Foundation, as well as in a local loft used to keep racing pigeons. They were allowed to breed and raise chicks. Experimental pigeons carried a PVC dummy of the size and weight of the GPS loggers throughout the experimental season. Dummies and loggers were attached by means of an adhesive Velcro strip glued onto the feathers on the back of the pigeon [42]. Pretraining with dummies was necessary to habituate the birds to carry the weight (19–27g) of a GPS logger. From any release site, each pigeon was pretrained twice, once in the form of a group release, once by a single release. Between releases, pigeons were allowed daily spontaneous (free) flights near the loft. Repeated GPS tracking of such free-flying pigeons (in a flock) revealed that the birds were practically always flying in a radius of maximally 500 m around the loft. Only once, two veteran birds (aged 5 and 7 years) were observed to fly straightforwardly 10 km south to the shore, where they spent 20 min walking at the beach, presumably to collect sand for digestion. Afterward, they returned straightforwardly north to the loft. We assume that these two birds had a detailed knowledge of this north-south route.

Releases and Release Sites

Releases took place in the months from February to September of the years 2001–2003. All birds were released under at least partially sunny conditions, winds being absent or weak. Transport to release sites took place in a well-ventilated car. For releases from the sea, the pigeons underwent an additional journey in normal transport crates. They were allowed to adapt for at least half an hour to the release site in transport crates permitting them to see the horizon [43]. Prior to release, GPS loggers were activated, and the pigeon was placed in a small starting crate that was opened after 2–3 min. Birds were released in intervals of about 10 min or until the former pigeon had disappeared.

Analysis of Tracks

Qualitative and quantitative analyses of individual tracks were run with FUGAWI software (Northport Systems, 95 St. Clair Av. West, Toronto, M4V 1N6, Canada), MAP INFO (One Global View, Troy, NY 12180) and WINTRACK shareware (http://www.dpwolfer.ch/wintrack). Mathematical-statistical models were computed with MATLAB (Mathworks, 3 Apple Hill Drive, Natick, MA 01760-2098).

Standard Statistics

Mean values of track lengths and related scores for real and simulated scores were analyzed with related t tests. Analysis of correlations used the (nonparametric) Spearman's Rho test.

Probability Calculations for Single Tracks

We counted the probability of observing a given road-following score by counting the number of virtual tracks that had equal or higher road-following scores (e.g., an actually observed score higher than all 431 simulated scores would have a probability of 1/432 [$p = 0.0023$]).

Supplemental Data

Additional figures, including black-and-white versions of Figures, 3, 5, and 6, for printing with non-color printers, are available at http://www.current-biology.com/cgi/content/full/14/14/1239/DC1.

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