Year: 2008

Flock flying improves pigeons' homing: GPS-track analysis of individual flyers versus small groups

Dell'Ariccia, G; Dell'Omo, G; Wolfer, D P; Lipp, H P

Flock flying improves pigeons' homing: GPS-track analysis of individual flyers versus small groups

Abstract

The effects of aggregation in navigating animals have generated growing interest in field and theoretical studies. The few studies on the effects of group flying on the performance of homing pigeons (Columba livia) have led to controversial conclusions, chiefly because of the lack of appropriate technology to follow pigeons during their entire homeward flight. Therefore, we used GPS data-loggers in six highly pre-trained pigeons from a familiar release site first by releasing them six times individually, then six times as a group from the same site, and finally, again six times individually. Flight data showed that the homing performance of the birds flying as a flock was significantly better than that of the birds released individually. When flying in a flock, pigeons showed no resting episodes, shorter homing times, higher speed, and almost no circling around the start zone in comparison to individual flights. Moreover, flock-flying pigeons took a nearly direct, “beeline” route to the loft, whereas individually flying birds preferred to follow roads and other longitudinal landmarks leading towards the loft, even when it caused a detour. Our results show that group cohesion facilitates a shift towards more efficient homing strategies: individuals prefer navigating by familiar landmarks, while flocks show a compass orientation.

Flock flying improves pigeons' homing: GPS-track analysis of individual flyers versus small groups

GAIA DELL'ARICCIA[1], GIACOMO DELL'OMO[1], DAVID P. WOLFER[1,2] & HANS-PETER LIPP[1]

[1] Institute of Anatomy, University of Zurich

[2] Department of Biology, Swiss Federal Institute of Technology, Zurich

Short Title for Running Headline: Dell'Ariccia et al.: Flock flying improves pigeons' homing

Correspondence: G. Dell'Ariccia, Institute of Anatomy, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland. (e-mail: gaia.dellariccia@access.uzh.ch)

G. Dell'Omo, D.P. Wolfer and H.-P. Lipp, Institute of Anatomy, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.

Word count for the text: 3730

ABSTRACT

The effects of aggregation in navigating animals have generated growing interest in field and theoretical studies. The few studies on the effects of group flying on the performance of homing pigeons (*Columba livia*) have led to controversial conclusions, chiefly because of the lack of appropriate technology to follow pigeons during their entire homeward flight. Therefore, we used GPS data-loggers in six highly pre-trained pigeons from a familiar release site first by releasing them six times individually, then six times as a group from the same site, and finally, again six times individually. Flight data showed that the homing performance of the birds flying as a flock was significantly better than that of the birds released individually. When flying in a flock, pigeons showed no resting episodes, shorter homing times, higher speed, and almost no circling around the start zone in comparison to individual flights. Moreover, flock-flying pigeons took a nearly direct, "beeline" route to the loft, whereas individually flying birds preferred to follow roads and other longitudinal landmarks leading towards the loft, even when it caused a detour. Our results show that group cohesion facilitates a shift towards more efficient homing strategies: individuals prefer navigating by familiar landmarks, while flocks show a compass orientation.

Keywords: *Columba livia*, GPS tracking, group flight, homing pigeon, landmarks, leadership, "Many-wrongs principle", navigation, road following, social cohesion.

Many animals spontaneously aggregate when foraging or when travelling. Aggregation is commonly recognised to provide benefits for group members, for instance through predation avoidance or improved foraging efficiency (Krause & Ruxton 2002). Recently, there has been an increasing interest in the potential navigational advantages for animals moving in groups (Simons 2004; Conradt & Roper 2005; Couzin et al. 2005; Hancock et al. 2006, Codling et al. 2007).

According to the "Many-wrongs principle" (Bergman & Donner 1964; Hamilton 1967; Wallraff 1978; Simons 2004) group cohesion allows a more accurate navigation because individual errors are mutually corrected through information pooling. Such advantage of group navigation found further support by theoretical models showing that even experienced and informed individuals have a larger navigational error than the combined error of several inexperienced group members (Conradt & Roper 2003).

Homing pigeons provide an optimal model for navigation research owing to their well developed orientation capabilities and for the ease of their experimental manipulation (Schmidt-Koenig 1980). Experimental studies have demonstrated the existence of different orientation mechanisms (for a review see Walcott 2005). While there are conflicting theories with respect to orientation mechanisms used by pigeons, the most widely accepted notion is still Kramer's "Map-and-Compass" model (1957). It holds that displaced birds first determine their position (the map step) and then follow a homeward course (the compass step). Ideally, this is the beeline from release site to the loft. Calculation of this compass direction includes the position of the sun (if visible) and, presumably, magnetic cues.

Pigeons that are repeatedly released from the same location generally improve homing performance, reaching an asymptote after three to six releases (Graue 1965; Wallraff 2005). On the other hand, GPS tracking studies have shown that repeated releases from a familiar location entails stereotyped routes during homing (Biro et al. 2004), often along longitudinal landmarks such as highways and railroads (Lipp et al 2004).

The role of group flying on homing performance has been investigated in a limited number of studies so far, and these have led to conflicting conclusions. Some of these studies suggested that orientation in flock is more accurate than that of individual birds (Hamilton 1967), with less-scattered vanishing bearings and shorter homing times (Tamm 1980). Contrarily, other experiments failed to demonstrate any improvement in navigational accuracy of pigeons released in flocks (Keeton 1970; Benvenuti & Baldaccini 1985). Part of these contradictions may reflect that these early studies were conducted assessing directional information at the release site only, namely vanishing bearings, and homing speed as the only performance variable.

The development of small GPS data-loggers now permits precise reconstruction of the homeward journey of pigeons (Steiner et al. 2000; Von Hünerbein et al. 2000; Biro et al. 2002; Lipp et al. 2004), and thus a re-assessment of the problem.

In the present study, we compared homing performances of the same pigeons successively released individually, in flock, and again individually, always from the same site. All pigeons already were highly pre-trained from that release site to avoid increasing familiarity confounds due to releases repetitions. Nonetheless, if flock navigation is superior, one would expect an increase in homing performance in pigeons released in flocks, and a subsequent performance drop upon reverting to the individual-release schedule, even from a familiar release site. Our results, indeed, indicate that group navigation is more efficient than that of individuals, chiefly because group flight corrects the penchant of individual birds to follow suboptimal routes.

METHODS

Study Area and Facilities

Homing pigeons used for this study were kept in the facilities of the University of Zurich at Testa di Lepre, Italy, 25 km NW of Rome (12.28° N; 41.93° E). There, in a traditional farm setting, local homing pigeons were housed in 3 identical mobile lofts equipped with aviaries (formerly Swiss Army) and cared for by an experienced breeder. Pigeons of both sexes and with different flying experience were living in the same loft. Food (a mixture of various cereals, peas, corn, and sunflower seeds sold commercially for racing pigeons), grit and water were provided ad libitum. All birds were habitually allowed to fly freely outside the lofts and they underwent regular training, which entailed frequent handling. During training the birds were transported to various locations in all directions in a range of 50 km from the loft and released in small flocks or individually.

Subjects and General Procedure

All the experimental releases took place between November 2005 and April 2006 under sunny conditions, with no or light wind, from the release site Santa Severa (11.98° N; 42.03° E), 27 km NW of the home loft.

In this experiment we used six adult two-years-old pigeons (four males and two females) which had been released from Santa Severa up to 20 times before the present experiment took place and, thus, were in the asymptotic phase of their homing performance (see also Graue 1965; Wallraff 2005).

Between experimental homing-releases, the six birds always wore PVC dummy weights (22 g. 4 to 5 % of body weight), affixed on their backs with Velcro® strips to habituate them to the load. One should note that pigeons are used to carrying up to 30 g in their crop when returning from feeding sites. To mount dummies or loggers, the dorsal feathers between the wings were trimmed in a small area of 1.5x3 cm. A strip of rough plastic Velcro was glued on the trimmed feathers using non-toxic contact glue and making sure that the strip and the attached dummy did not interfere with pigeons' movements and flight. The soft part of the Velcro was glued on dummies and GPS-loggers. Separating the load from the dorsal Velcro was done by inserting a flat tool between the two stripes, thus not ripping off any feathers. Pigeons naturally lost the glued Velcro with the moult. For experiments, the dummies were replaced with GPS-loggers of the same weight (NewBehavior AG, Zurich, Switzerland) just before the release, and placed again on the birds after retrieving the GPS at the loft. The logger took one positional fix every second, and then stored the data. Further technical information can be found under Biro et al 2002 and Lipp et al. 2004.

The birds first underwent six individual releases (S1) from a starting crate to establish baseline performance. Releases took place in intervals of three days. Subsequently, the same birds were released from the same crate as a flock (F), again at intervals of three days for a total of six releases. This served to assess possible improvements due to flock navigation. Finally, they underwent six further individual releases (S2) to determine to what extent they would maintain the performance level of flock navigation.

Data Analysis

The raw data were downloaded from the logger to a computer and analyzed first for possible artefacts and irregularities of recording (program WINTRACK. Freeware D.P. Wolfer at www.dpwolfer.ch/wintrack; Steiner et al. 2000; Wolfer et al. 2001). The program then extracted the following variables: homing speed (average speed recorded by GPS-logger during flight, excluding measures of speed of less than 5 km/h), flight altitude, number and duration of rests (rests were defined as episodes longer than 5 sec with GPS speed less than 5 km/h), total flying time, average distance to the beeline between the release site and the loft, and number of km flown along the main roads and the coast (episodes of road or coast following were defined as flying parallel to or at an angle of <10° to the road/coastline at a distance of 200 m or less during at least 500m).

We also calculated the straightness index D/L for each track, in which D is the beeline distance from the starting point to the goal, and L is the path actually followed by the animal (Batschelet 1981; Benhamou 2004). This is a scale independent measure and, given the high recording frequency of one positional fix per second, a reliable estimator of the efficiency of the orientation process already used also by other authors (i.e. Biro et al. 2004).

These parameters were analyzed using parametric and non-parametric procedures. In a first step, simple Pearson product-moment correlations were used to check whether the first series of six individual releases showed any improvement over asymptotic performance during consecutive releases (x = order of releases per condition, y = averaged score of the six birds). Likewise, this procedure was applied to the other conditions to discover any effects of repeated releases.

To analyse differences between the three conditions, the values from the S1, F, and S2 condition were averaged, because the number of repeated factors in a one-way ANOVA design (18 here) should not exceed the sample size (n=6). These averaged values were then used for a non-parametric one-way ANOVA with three repeated factors (S1, F, S2; Friedman test for related samples, two-tailed), followed post hoc by pair wise non-parametric comparisons (Wilcoxon test for related samples). Predictions were that the group flight condition would reveal better performance, and that comparisons between S1 and S2 should show either no differences or then improvement only. Thus, one-tailed significant levels were applied. For simplifying data presentation, the Friedman ANOVA values were omitted in graphs and text. An analysis of individual variation in the six pigeons was done graphically by plotting three key variables (flight speed, straightness index, and road following) for each of the 18 releases.

Calculations were done using the software package STATVIEW 5.01™. Plotting of GPS tracks was done with the aid of MapInfo™.

RESULTS

Overall, we conducted 107 releases out of the 108 planned (six pigeons released six times in each of the three series of releases) with the GPS data-loggers and obtained complete and technically valid tracks from all of them except for two tracks in the S1 series (p 613, p830). For the last individual release in S2, one pigeon (p811) was excluded because it had sustained injuries during the fifth release.

Figure 1 summarizes the main results in form of GPS tracks showing the first series of single releases (S1, blue tracks), the flight paths of group releases, evident as one track per group release as the pigeons flew together (F, red tracks), and the flight paths of the same pigeons when released individually again (S2, green tracks). The tracks of singly released birds, before and after group flights, were generally well oriented, but showed considerable topographical scattering to the left and right of the beeline (a direct line between release site and loft).

Prior to the group flights, this scatter was mainly towards the right side of the beeline in a region rich in longitudinal landmarks pointing home, such as roads and railways. In fact, as indicated by overlapping flight paths, the pigeons showed road following mostly along the motorway A12.

When the same pigeons were released in groups of six, they flew much closer to the beeline, but always followed somewhat different trajectories. In three of the six releases, the pigeons flew closely together, from the releasing point to the loft; in two releases the birds flew together but they split 1-3 km before the loft, following individual routes, partially along a local road. During the first group release, the flock divided after about 10 km into individually flying birds; the particular path of splitting suggests a raptor attack. However, they kept a relatively parallel course, not moving away more than one km from each other, and they again formed a cohesive flock during subsequent flight, the last pigeon to rejoin the group about seven km after the splitting. Thus, the splitting of the terminal trajectories, and during the first group release, caused minor quantitative within-group variation in the analysis of flight parameters.

In the individual releases subsequent to the group flights, S2, the flight trajectories appeared again much more scattered. A number of flights appeared to have shifted to the north into a region that does not contain structural cues leading homewards. Some overlapping of tracks (implying development of new route preferences) was noted in these regions, too, albeit less than in the S1 condition.

The comparison across the six successive releases of S1 for each individual pigeon failed to detect any systematic trend in repeated flights, indicating that the pigeons had already reached asymptotic (yet not invariant) homing performance from this familiar site. Three of the birds (601, 811,823) showed high yet not temporally ordered variability in flight speed, straightness index, and road following, while the others (613, 830, 848) performed relatively constantly (Fig. 4).

The overall comparison of flock-versus-individual releases revealed significant differences in a number of variables. When pigeons were group-released they invariably flew to the loft without any resting episode. Contrarily, when released individually some of the pigeons took a rest on the way home (Fig. 2a). Moreover, the actual flight speed recorded by GPS-loggers showed that flocks flew faster than did most of their members during individual S1 releases, with the exception of one release when pigeons 601 and 811 flew faster than the flocks (see also Fig. 4). During flock flights, speed was increasing significantly over releases ($r = 0.82$, $p < 0.05$, $n = 6$; x = order of releases, y = average speed of birds per release). Individual birds then maintained this average group flight speed during the S2 releases (Fig. 2b), possibly indicating a physical training effect.

Measures of path geometry revealed a more efficient navigation for group flights; the path to leave the start zone (defined as the distance flown before leaving a circle of 1 km radius about the release point) was significantly shorter when pigeons flew as a flock than in the two series of individual releases (Wilcoxon signed-rank test, one-tailed: $p = 0.023$ for S1 vs. F, and F vs. S2). There was no significant difference between the two series of individual releases (Fig. 2c). Likewise, the straightness index was significantly higher in flocks, indicating a more linear way home (Wilcoxon signed-rank test, one-tailed: $p = 0.014$ for S1 vs. F, and F vs. S2), than in both series of individual releases, with no statistical difference between the latter (Fig. 3a). The average distance of the track from the beeline between release site and loft was shorter when pigeons were flying as a flock than in the first series of individual releases (Wilcoxon signed-rank test, one-tailed: $p = 0.014$). Again, S2 pigeons showed an average increase of the distance to the beeline as compared to F1 condition, yet non-significantly (Wilcoxon signed-rank test, one-tailed: $p = 0.058$).

To find reasons for the prolonged flight paths of singly flying birds, we also measured the total cumulative length of flight tracks along longitudinal landmarks, such as highways, roads, and coastline (known to be followed by pigeons released from this place, Lipp et al. 2004). Individually flying pigeons in S1 flew along the main roads (particularly the highway) significantly more than flock-flying pigeons (Wilcoxon signed-rank test, one-tailed: $p < 0.07$). In the S2 condition, road-following increased non-significantly as compared to the F condition (Wilcoxon signed-rank test, one-tailed: $p = 0.058$) (Fig. 3b). An analysis of correlations, however, showed a significant reduction of road following over consecutive releases ($r = -0.87$, $p < 0.05$, $n=6$; x = order of S2 releases, y = average road-following scores per release).

No differences were observed in flight altitude.

A graphical inspection of individual variation in three key variables (flight speed, straightness index, and road following. Fig. 4) largely confirmed the results of the ANOVA using averaged data, but revealed some interesting aspects. For example, two pigeons (601 and 811) showed, during the fourth S1 release, high flight speed, and a flock-like straightness index. During the following release, however, they were much slower and showed a high road following score.

Between-release variation of measures in the flock condition showed a much more homogeneous performance than for both individual-release conditions. However, a clearly lower straightness index was observed for the last of the group releases, indicating a suboptimal group trajectory on that day, although homing speed and road following were not affected. A detailed analysis of GPS tracks revealed that the flock, while following approximately the beeline, performed a series of loops and turns over the first 3 km from the release site, as it is was often observed in singly released pigeons.

The analysis of individual transitions from flock releases to individual releases showed that flight speed and straightness index dropped most distinctly during the first or second release after flock conditions, during which 4 pigeons also increased their road following score. Thereafter, four of the six pigeons (601, 613, 823, 848) regained a straightness index that was comparable or only slightly inferior to the flock condition. While this temporary impairment resulted in significant (non-parametric) group differences for the averaged values between the F and the S2 condition, it also indicates that the pigeons did not lose their ability for well-directed homing.

DISCUSSION

Our data demonstrate superior homing performance of pigeons released in small flocks as compared to pigeon released individually, even when tested in releases from a highly familiar location. In comparison to individual flights, pigeons in a flock left the release site faster, flew generally faster, made no stops, and showed improved directionality during their homeward flight. For one, this confirms the predictions of the many-wrongs principle and other models of group navigation predicting cancelling of individual navigational errors (Bergman & Donner 1964; Simons 2004; Codling et al. 2007).

In this study, the homing performance of pigeons is a compound of initial flight behaviour at the release site, actual flight speed, number of rests, and navigational accuracy during homing. It is unlikely, however, that all these parameters can be classified only as mutually cancelling navigational errors. Prolonged circling around the release site may be taken as an indicator of directional uncertainty. But, since the release site was thoroughly familiar, it is more likely to reflect the tendency of waiting for a companion bird. Likewise, stops during flight may be caused by orientation problems, by lack of flight motivation or, again, by waiting for a companion. The changes in these two variables suggest, at least in part, motivational problems associated with the individual flight condition, particularly so as they are observed after successive fast and efficient flock homing. Thus, flying in flocks appears, somehow, to increase homing motivation. This conclusion is supported by the observation that reverting from flock to individual flight condition caused a drop in homing performance during the first release of the S2 condition, while pigeons attained levels comparable to flock flight afterwards, mostly regarding homing speed.

On the other hand, the improvement in directionality observed in flock flying pigeons, and the lower variability of all measured variables, is in agreement with superior flock navigation predicted by group navigation models (Bergman & Donner 1964; Simons 2004; Codling et al. 2007). However, in such models directional errors are assumed to be random. In our case, the directional error is a systematic bias introduced by previous development of individual stereotyped routes, typically observed after repeated releases from a familiar location (Biro et al. 2004; Lipp et al. 2004). The reasons underlying development of stereotyped routes are still unclear. These directional biases cannot be qualified as actual navigational errors (the birds return reliably), but may be considered as a suboptimal homing strategy. Nevertheless, flock flying significantly reduces such individual directional biases. Based on these findings, one can probably expect larger corrections by group flights in releases from unfamiliar sites, where the probability of true navigation errors is higher.

It is important to note that, occasionally, individually flying pigeons were able to show almost perfect homing in terms of directionality and speed. This indicates that individually flying pigeons, released from a familiar site, can choose between following a rather precise compass direction, or alternatively follow landmarks providing a suboptimal but predictable way home. In the majority of cases, pigeons flying alone seem to prefer such route following, while this strategy is shown by flocks only occasionally. Thus, flying in flocks appears to shift the balance between homing strategies in favour of compass navigation that is always used by pigeons from unfamiliar sites.

Homing pigeons have an innate tendency to group when flying due to their evolution and breeding history (Schmidt-Koenig 1980), and group cohesion is actively kept. GPS tracks show that the splitting of groups rarely occurs, and if so, subgroups may separate up to 1 km before joining each other, as observed during the first group release. At least in small flocks, group cohesion prevents landing and rests of individual flock members, and also drives pigeons to adopt flight speeds they would not maintain while flying alone. Future research should investigate whether there are changes in some measurable physiological parameter, such as physical effort or stress, among pigeons released individually or in flocks.

The reasons why flock flying pigeons abandon acquired route strategies in favour of (superior) compass orientation are unknown. One possible explanation is that flock flying pigeons must pay visual attention to their companions for maintaining flock cohesion, thusly cancelling the attraction of landmarks, and possibly also the influence of other distracting visual cues. In consequence, the flock maintains the compass direction to the loft better than individually flying pigeons. This idea needs to be tested, but preliminary data from EEG recording in flock versus individually flying pigeons shows less attentional EEG responses of flock flying birds when passing familiar landmarks (Vyssotski et al. unpublished).

A possible alternative explanation of superior homing performance of flocks is the presence of a leader bird with better navigational abilities, leading the companions home. Since the precision of the GPS used did not allow testing this hypothesis directly, we checked for every release the rank order of the pigeons according to their performance. In the case of a typical leader dictating speed and direction of the flock, the leader bird should have consistent performance in individual and group flights. However, we failed to identify a pigeon with constant superior performance. This observation corresponds to previous results showing increased performance in all pigeons (Benvenuti & Baldaccini 1985, Biro et al. 2006).

In conclusion, flying in small flocks has an important positive effect on homing performance, in terms of navigational accuracy, speed, and motivation, even in releases from highly familiar release sites. GPS tracking evidences that pigeons can dynamically shift between different coexisting strategies: individually flying pigeons show a greater reliance on topographical features for homing, keeping habitual home routes, while flocks tend to adopt a compass-based navigation.

ACKNOWLEDGEMENTS

We thank Cesare & Maria Calderoni and Hans Cattin for expert care of pigeons, Phillip Hendrickson for proofreading, the Swiss Homing Pigeon Foundation for providing mobile lofts, and two anonymous referees for helpful comments on the manuscript. This work was supported by the Swiss National Science Foundation and the NCCR “Neural Plasticity and Repair”.

REFERENCES

Batschelet, E. 1981. Circular statistics in biology. London: Academic Press.

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, 229, 209-220.

Benvenuti, S. & Baldaccini, N. E. 1985. Pigeon orientation: a comparison between single birds and small flocks. *Ornis Scandinavica*, 16, 45-48.

Bergman, G. & Donner, K. O. 1964. An analysis of the spring migration of the common scoter and the long-tailed duck in southern Finland. *Acta Zoologica Fennica*, 105, 1-59.

Biro, D., Guilford, T., Dell'Omo, G. & Lipp, H.-P. 2002. How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking. *J Exp Biol*, 205, 3833-3844.

Biro, D., Meade, J. & Guilford, T. 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. *PNAS*, 101, 17440-17443.

Biro, D., Sumpter, D. J. T., Meade, J. & Guilford, T. 2006. From compromise to leadership in pigeons homing. *Current Biology*, 16, 2123-2128.

Codling, E. A., Pitchford, J. W. & Simpson, S. D. 2007. Group navigation and the "Many-wrongs principle" in models of animal movements. *Ecology*, 88, 1864-1870.

Conradt, L. & Roper, T. J. 2003. Group decision making in animals. *Nature*, 421, 155-158.

Conradt, L. & Roper, T. J. 2005. Consensus decision making in animals. *Trends in Ecology and Evolution*, 20, 449-456.

Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005. Effective leadership and decision making in animal groups on the move. *Nature*, 433, 513-516.

Graue, L. C. 1965. Experience effect on initial orientation in pigeon homing. *Animal Behaviour*, 13, 149-153.

Hamilton, W. J. 1967. Social aspects of bird orientation mechanisms. In: *Animal Orientation and Navigation* (Ed. by Storm, R.), pp. 57-71: Oregon State Univ. Press.

Hancock, P. A., Milner-Gulland, E. J. & Keeling, M. J. 2006. Modelling the many-wrongs principle: the navigational advantages of aggregation in nomadic foragers. *Journal of Theoretical Biology*, 240, 302-310.

Keeton, W. T. 1970. Comparative orientational and homing performances of single pigeons and small flocks. *Auk*, 87, 797-799.

Kramer, G. 1957. Experiments in bird orientation and their interpretation. *Ibis*, 99, 196-227.

Krause, J. & Ruxton, G. D. 2002. *Living in groups*. Oxford: Oxford Univ. Press.

Lipp, H.-P., Vyssotsky, A. L., Wolfer, D. P., Renaudineau, S., Savini, M., Tröster, G. & Dell'Omo, G. 2004. Pigeon homing along highways and exits. *Current Biology*, 14, 1239-1249.

Schmidt-Koenig, K. 1980. *Das Rätsel des Vogelzugs. Faszinierende Erkenntnisse über das Orientierungsvermögen der Vögel.* Hamburg: Hoffman und Campe Verlag.

Simons, A. M. 2004. Many wrongs: the advantage of group navigation. *Trends in Ecology and Evolution*, 19, 453-455.

Steiner, I., Bürgi, C., Werffeli, S., Dell'Omo, G., Valenti, P., Tröster, G., Wolfer, D. P. & Lipp, H.-P. 2000. A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology & Behavior*, 71, 589-596.

Tamm, S. 1980. Bird orientation: single homing pigeons compared with small flocks. *Behavioral Ecology and Sociobiology*, 7, 319-322.

Von Hünerbein, K., Hamann, H. J., Rüter, E. & Wiltschko, W. 2000. A GPS-based system for recording the flight paths of birds. *Naturwissenschaften*, 87, 278-279.

Walcott, C. 2005. Multi-modal orientation cues in homing pigeons. *Integrative and Comparative Biology*, 45, 574-581.

Wallraff, H. G. 1978. Social interrelations involved in migratory orientation of birds: possible contributions of field studies. *Oikos*, 30, 401-404.

Wallraff, H. G. 2005. *Avian Navigation: Pigeon Homing as a Paradigm.*: Springer-Verlag.

Wolfer, D. P., Madani, R., Valenti, P. & Lipp, H.-P. 2001. Extended analysis of path data from mutant mice using the public domain software Wintrack. *Physiology and Behavior*, 73, 745-753.

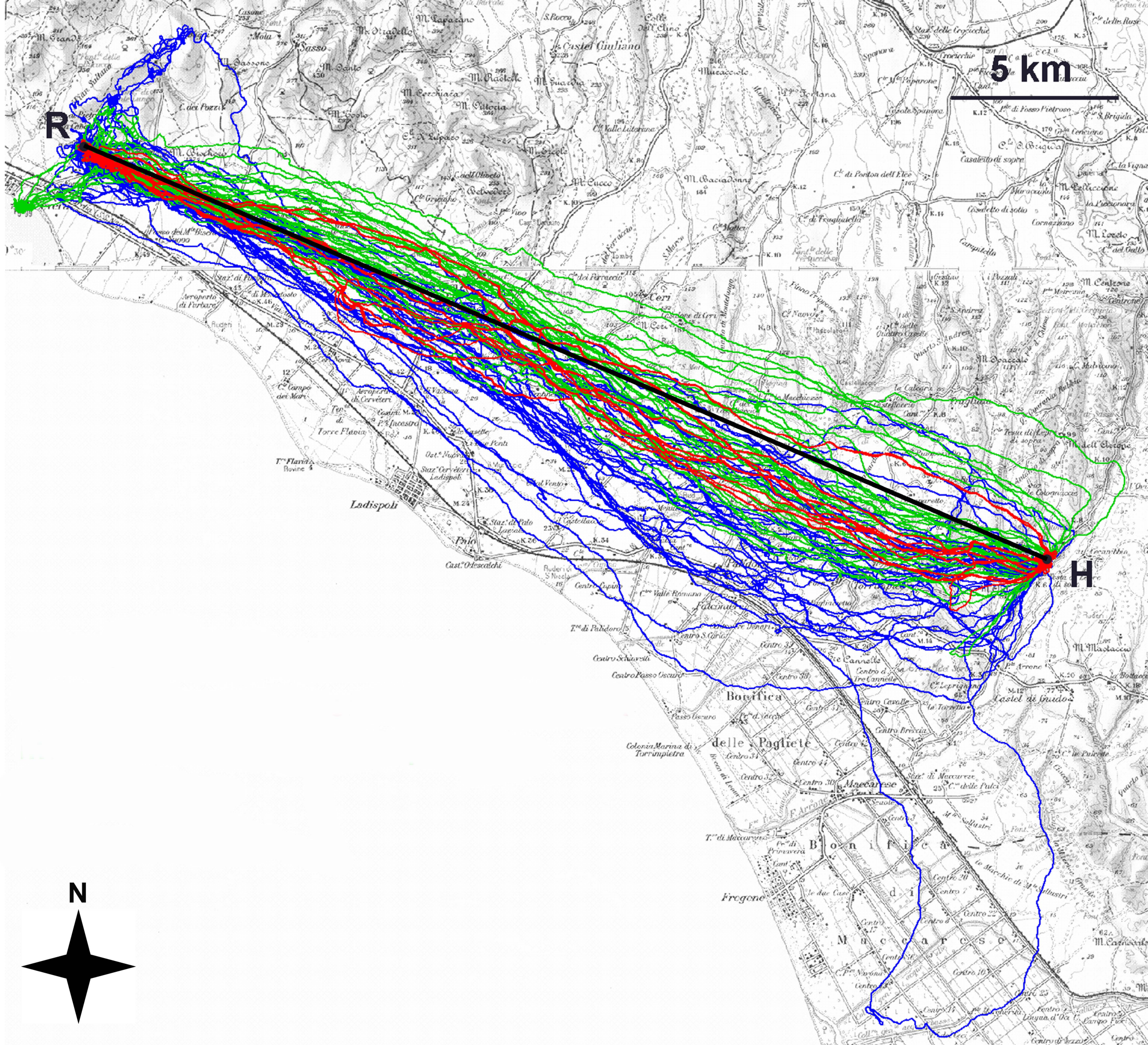
Figure legends

Figure 1. GPS tracks of homing pigeons between the release site (R) and the home loft (H). Blue tracks: 36 individual flights of six experienced pigeons released six times, condition S1. Red tracks: 6 group releases of the same six pigeons as a flock (apparent as one track per release because pigeons not split from the flock), condition F. Green tracks: 35 individual flights performed after the group releases, condition S2. Note the larger dispersal of flight paths under individual-release conditions S1 and S2. During S1, many flight paths coincide with roads. Tracks of group flight (red) do not coincide. During S2, some degree of coincidence of green tracks in regions devoid of roads pointing homewards is observed.

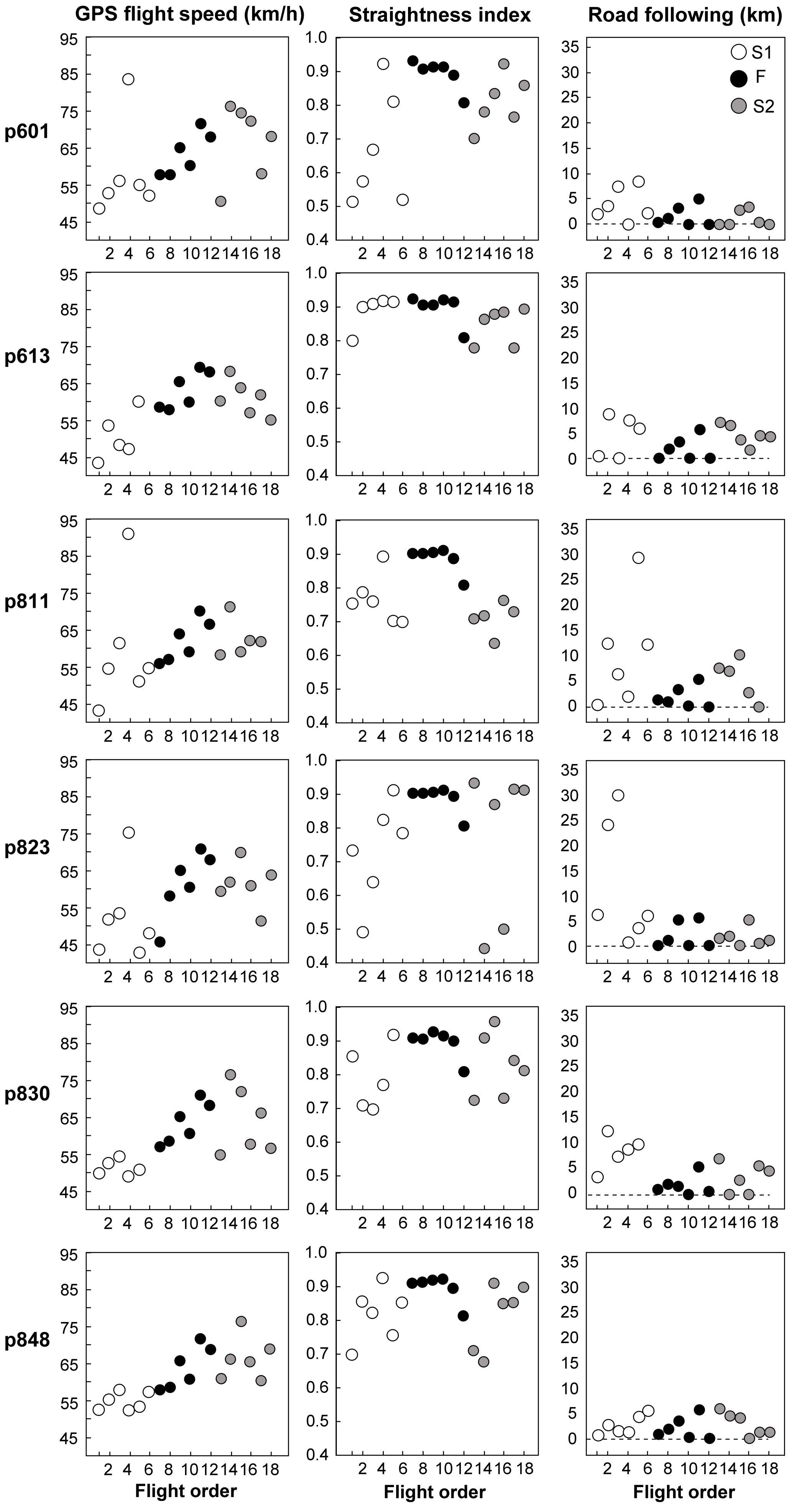
Figure 2. (a) Average number of rests during flight. Flock-flying pigeons never stopped, but individually released pigeons did so, both before and after the group flights. (b) Average homing speed recorded by the GPS-logger. Flock flying improved homing speed with respect to individual releases; after flying in flocks pigeons maintained the higher flight speed in the S2 condition. (c) Path to leave start zone (defined as the distance flown before leaving a circle of 1 km radius around the release point). Individually released birds fly significantly more within the start zone before leaving. Bars indicate means and S.E.M. ** $p < 0.025$. S1: individual flights; F: group flights; S2: individual flights after group releases.

Figure 3. (a) Straightness index. Flock flying pigeons maintained a straighter course homewards. (b) Road following scores showing loss of road and coastline following during group flight, resulting in improved directionality homewards. After the flock flights, the routes of individually released pigeons (S2) appeared to be shifted to the north (see Fig. 1) where conspicuous longitudinal landmarks such as roads pointing homewards are scarce. Bars indicate means and S.E.M. ** $p < 0.025$. S1: individual flights; F: group flights; S2: individual flights after group releases.

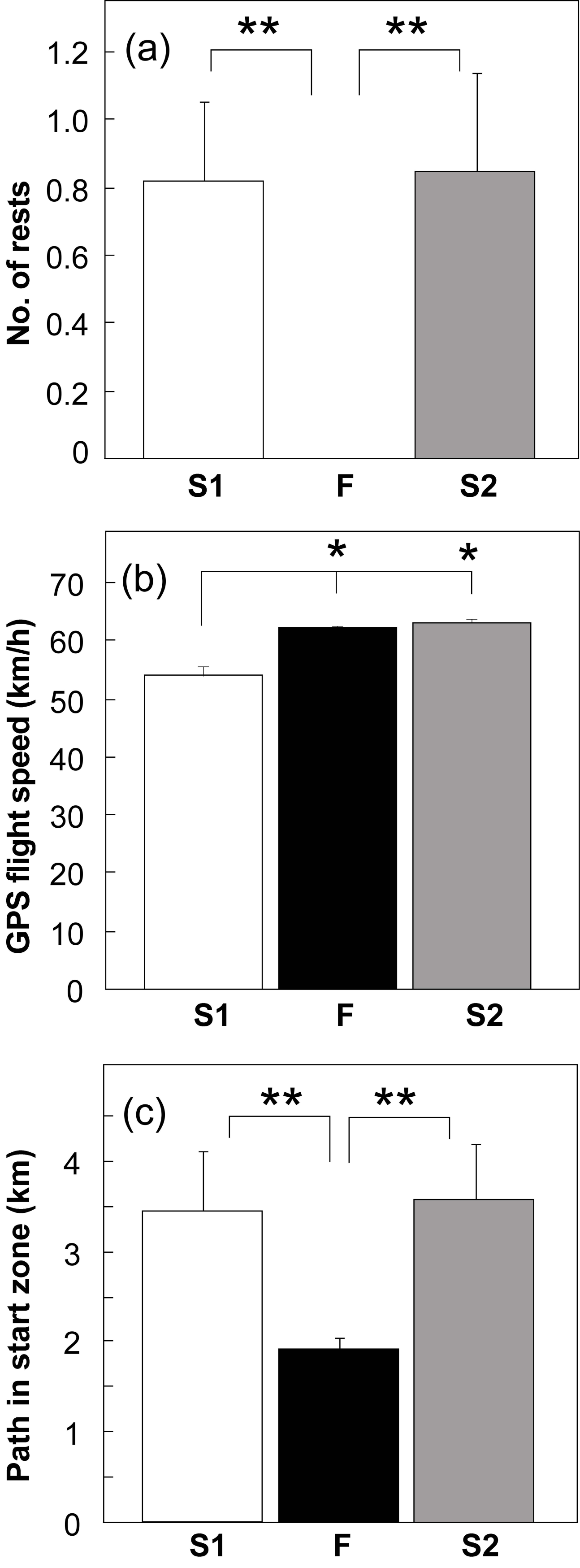
Figure 4. Individual scores for homing speed, straightness index, and road following across different releases plotted for the six pigeons (p601, p613, p811, p823, p830, p848). The corresponding but averaged values per condition and related statistics are shown in Figures 2b, 3a, and 3b. All Y-values show the same scale for comparison. White dots: first series of individual releases (condition S1). Black dots: flock releases (condition F). Grey dots: second series of individual releases, performed after the flock releases (condition S2). (p613 and p830 have five S1 releases condition because of a corrupted track recorded by GPS; p811 has five S2 releases because it sustained injuries).



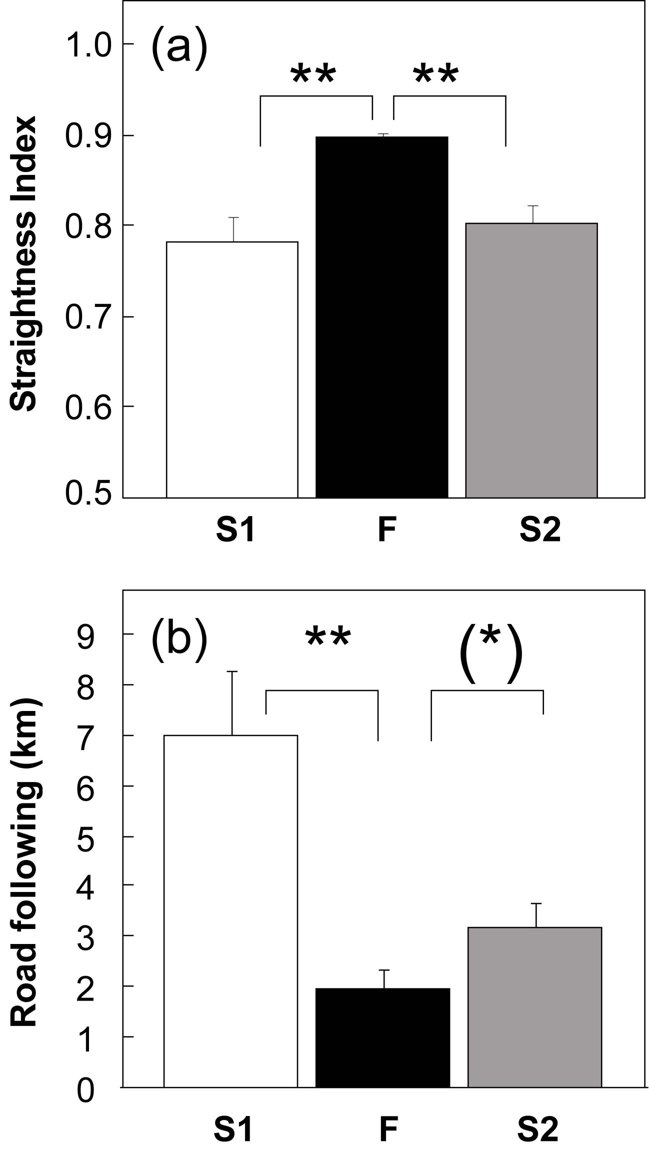
5 km
R
H
N
Ladispoli
Bonifica
delle Pagliete
Maccarese
Fregene
Palo
Ceri
Castel di Guido



GPS flight speed (km/h)
Straightness index
Road following (km)
S1
F
S2
p601
p613
p811
p823
p830
p848
Flight order
Flight order
Flight order



(a)
No. of rests
0
0.2
0.4
0.6
0.8
1.0
1.2
**
**
S1
F
S2
(b)
GPS flight speed (km/h)
0
10
20
30
40
50
60
70
*
*
S1
F
S2
(c)
Path in start zone (km)
0
1
2
3
4
**
**
S1
F
S2


(a)
Straightness Index
1.0
0.9
0.8
0.7
0.6
0.5
**
**
S1
F
S2
(b)
Road following (km)
9
8
7
6
5
4
3
2
1
0
**
(*)
S1
F
S2