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

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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 on six highly 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.

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Keywords: *Columba livia*; GPS tracking; group flight; homing pigeon; landmark; leadership; many-wrongs principle; navigation; road following; social cohesion

Many animals spontaneously aggregate when foraging or when travelling. Aggregation is commonly recognized 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. This advantage of group navigation has found further support from 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, *Columba livia*, provide an optimal model for navigation research owing to their well-developed orientation capabilities and the ease of their experimental manipulation (Schmidt-Koenig 1980). Experimental studies have demonstrated the existence of different orientation mechanisms (reviewed in Walcott 2005). While there are conflicting theories with respect to orientation mechanisms used by pigeons, the most widely accepted notion is still Kramer's (1957) map-and-compass model. 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 their homing performance, reaching an asymptote after three to six releases (Graue 1965; Wallraff 2005). On the other hand, GPS tracking

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studies have shown that repeated releases from a familiar location result in stereotyped routes during homing (Biro et al. 2004), often along longitudinal landmarks such as roads and railways (Lipp et al. 2004).

The role of group flying in homing performance has been investigated in a limited number of studies, and these have led to conflicting conclusions. Some of these studies suggested that orientation in a flock is more accurate than that of individual birds (Hamilton 1967), with less-scattered vanishing bearings and shorter homing times (Tamm 1980). In contrast, other experiments failed to show any improvement in navigational accuracy of pigeons released in flocks (Keeton 1970; Benvenuti & Baldaccini 1985). Some of these contradictions may reflect the fact that these early studies assessed directional information only at the release site, 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 reassessment of the problem.

In the present study, we compared homing performances of the same pigeons successively released individually, in a flock, and again individually, always from the same site. All pigeons were highly trained from that release site to avoid increasing familiarity confounds of release repetitions. None the less, 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.

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 northwest of Rome (12.28°N, 41.93°E). There, in a traditional farm setting, local homing pigeons were housed in three 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 lived 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 up to 50 km from the loft and released in small flocks or individually. The study was licensed by the Ministero dell Salute Roma.

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 northwest of the home loft.

In this experiment we used six adult 2-year-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, 4–5% of body weight), affixed on their backs with Velcro strips to habituate them to the load. To mount dummies or loggers, we trimmed the dorsal feathers between the wings in a small area of 1.5×3 cm. A strip of rough plastic Velcro was glued on the trimmed feathers with nontoxic contact glue and we made sure that the strip and the attached dummy did not interfere with the pigeons' movements and flight. The soft part of the Velcro was glued on to the dummies and GPS loggers. We separated the load from the dorsal Velcro by inserting a flat tool between the two strips, to avoid 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 on the birds again after we retrieved the GPS at the loft. The logger took one positional fix every second, and then stored the data. Further technical information can be found in 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 at intervals of 3 days. Subsequently, the same birds were released from the same crate as a flock (F), again at intervals of 3 days for a total of six releases. This served to assess possible improvements caused by 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 analysed 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 the 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 s with GPS speed less than 5 km/h), total flying time, average distance to the beeline between the release site and the loft, and distance flown (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 for at least 500 m).

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/s, a reliable estimator of the efficiency of the orientation process already used by other authors (i.e. Biro et al. 2004).

These parameters were analysed with parametric and nonparametric procedures. In a first step, simple Pearson 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). This procedure was also applied to the other conditions to discover any effects of repeated releases.

To analyse differences between the three conditions, we averaged the values from the S1, F and S2 conditions, 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 nonparametric one-way ANOVA with three repeated factors (S1, F, S2; Friedman test for related samples, two-tailed), followed post hoc by pairwise nonparametric 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 improvement only. Thus, one-tailed significance levels were applied. For simplifying data presentation, the Friedman ANOVA values are omitted in figures and text. We analysed individual variation in the six pigeons graphically by plotting three key variables (flight speed, straightness index and road following) for each of the 18 releases.

We used the software package Statview 5.01 (SAS Institute, Cary, NC, U.S.A.). To plot GPS tracks we used MapInfo (Map Info Corp., Troy, NY, U.S.A.).

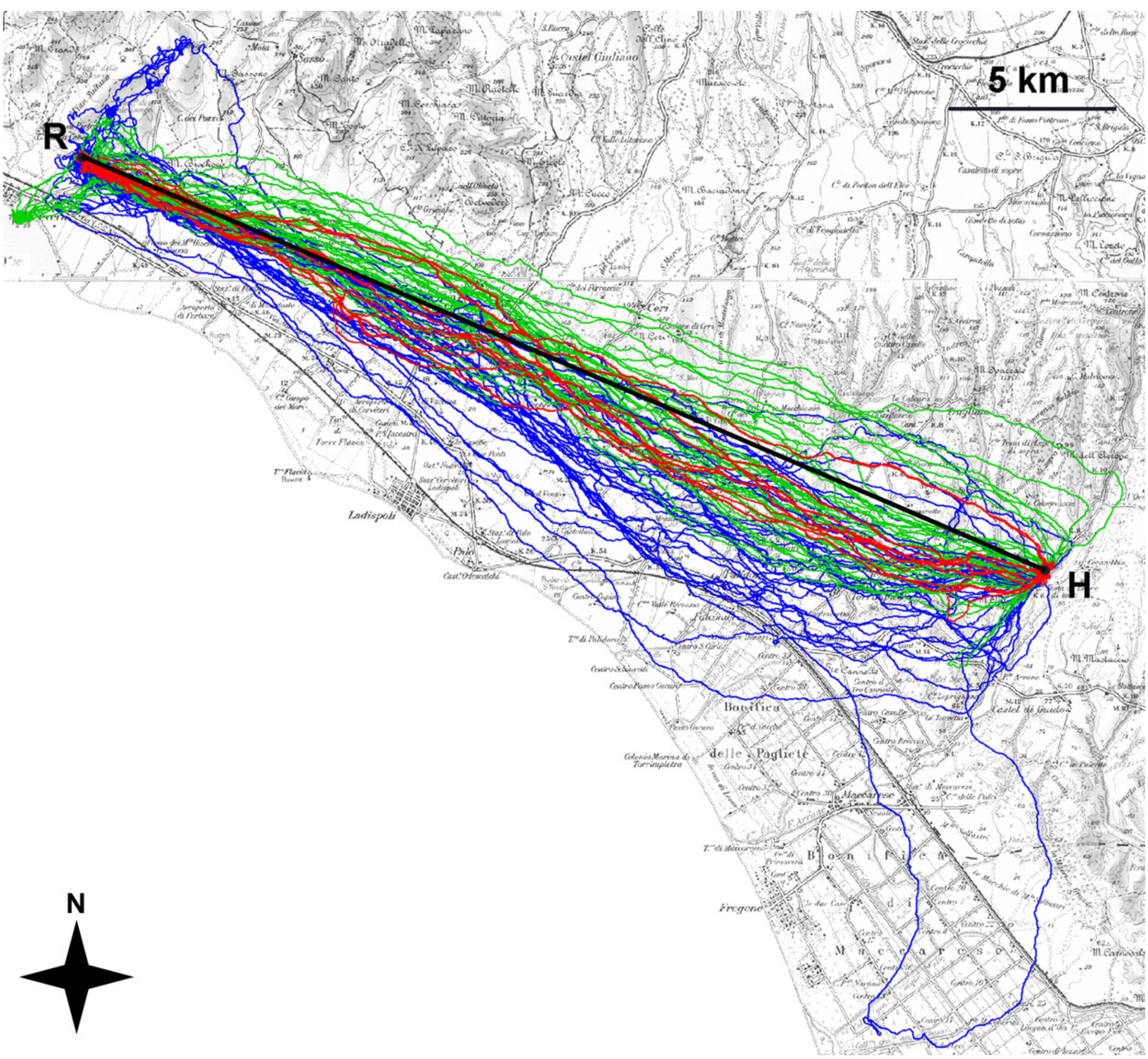
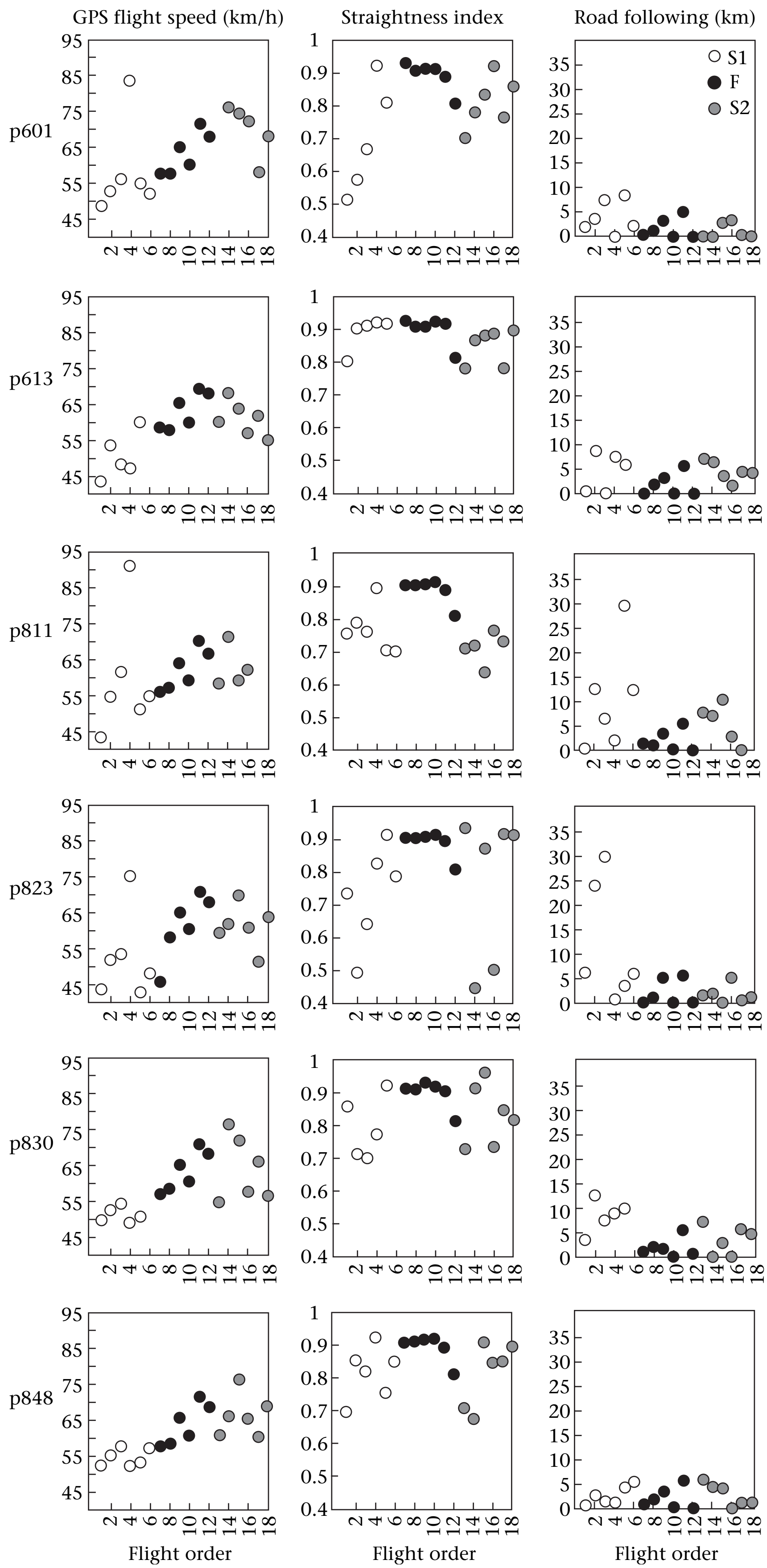


Figure 1. GPS tracks of homing pigeons between the release site (R) and the home loft (H). Blue tracks: 36 individual flights of six experienced pigeons released six times, condition S1. Red tracks: six group releases of the same six pigeons as a flock (apparent as one track per release because pigeons did not split from the flock), condition F. Green tracks: 35 individual flights performed after the group releases, condition S2.



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

RESULTS

Overall, we conducted 107 releases 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 but two tracks in the S1 series (p613, 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 the form of GPS 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 close together, from the release 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 more than 1 km from each other, and they again formed a cohesive flock during subsequent flight, the last pigeon rejoining the group about 7 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 (p601, p811, p823) showed high but not temporally ordered variability in flight speed, straightness index and road following, while the others (p613, p830, p848) performed relatively constantly (Fig. 2).

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 periods of resting. In contrast, when released individually some of the pigeons took a rest on the way home (Fig. 3a). Moreover, the actual flight speed recorded by the 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 p601 and p811 flew faster than the flocks (see also Fig. 2). During flock flights, speed increased significantly over releases (Pearson correlation: $r_4 = 0.82$, $P < 0.05$; x = order of releases, y = average speed of birds per release). Individual birds then maintained this average group flight speed during the S2 releases (Wilcoxon signed-ranks test, one-tailed: $T = -2.2$, $N = 6$, $P = 0.014$ for Sl versus F and Sl versus S2; Fig. 3b), 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 ($T = -1.99$, $N = 6$, $P = 0.023$ for S1 versus F and F versus S2). There was no significant difference between the two series of individual releases (Fig. 3c). Similarly, the straightness index was significantly higher in flocks, indicating a more linear way home ($T = -2.2$, $N = 6$, $P = 0.014$ for S1 versus F and F versus S2), than in both series of individual releases, with no statistical difference between the latter (Fig. 4a). 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 ($T = -2.2$, $N = 6$, $P = 0.014$). Again, S2 pigeons showed an average increase of the distance to the beeline compared to the F1 condition but this was not significant ($T = -1.57$, $N = 6$, $P = 0.058$).

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 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 motorway) significantly more than flock-flying pigeons ($T = -2.2$, $N = 6$, $P = 0.014$). In the S2 condition, road following showed a nonsignificant tendency to increase compared to the F condition ($T = -1.57$, $N = 6$, $P = 0.058$; Fig. 4b). An analysis of Pearson correlations, however, showed a significant reduction of road following over consecutive releases ($r_4 = -0.87$, $P < 0.05$; x = order of S2 releases, y = average road-following scores per release). No differences were observed in flight altitude.

Figure 2. 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 Figs. 3b, 4a and b. 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). (Pigeons p613 and p830 have five S1 releases because of a corrupted track recorded by GPS; p811 has five S2 releases because it sustained injuries.)

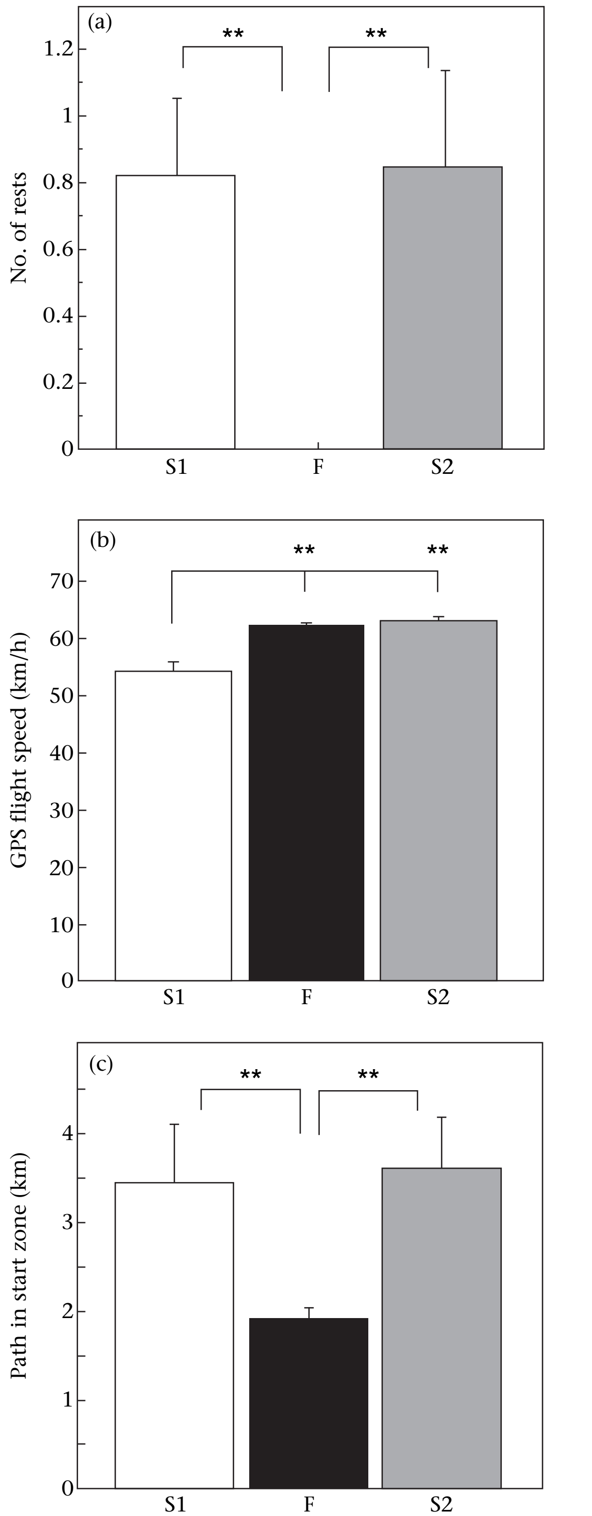


Figure 3. (a) Average number of rests during flight. (b) Average homing speed recorded by the GPS logger. (c) Path to leave start zone (defined as the distance flown before leaving a circle of 1 km radius around the release point). Bars indicate means + SEM. $^{**}P < 0.025$. S1: individual flights; F: group flights; S2: individual flights after group releases.

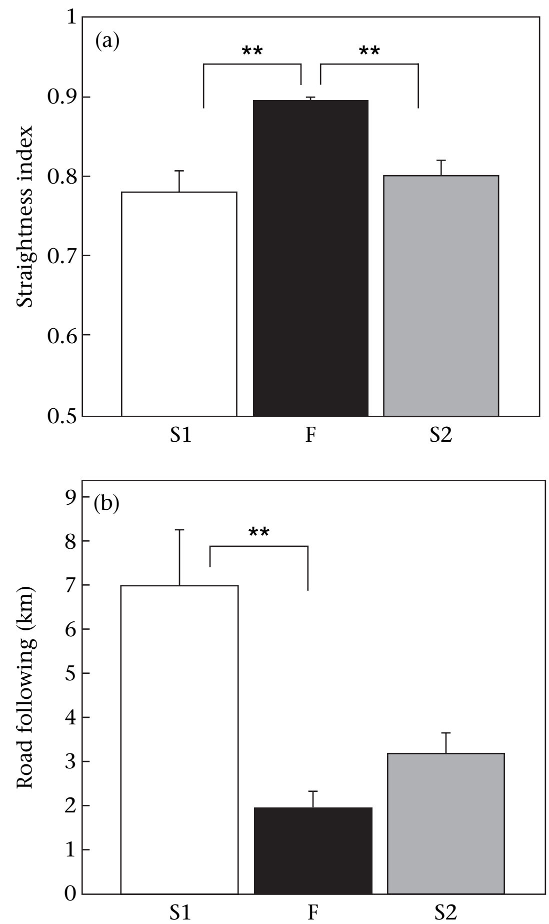


Figure 4. (a) Straightness index. (b) Road-following scores. Bars indicate means + SEM. $^{**}P < 0.025$. S1: individual flights; F: group flights; S2: individual flights after group releases.

A graphical inspection of individual variation in three key variables (flight speed, straightness index and road following; Fig. 2) largely confirmed the results of the ANOVA using averaged data, but revealed some interesting aspects. For example, two pigeons (p601 and p811) 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 had 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 approximately following the beeline, performed a series of loops and turns over the first 3 km from the release site, as 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 four pigeons also increased their road-following score.

Thereafter, four of the six pigeons (p601, p613, p823, p848) regained a straightness index that was comparable or only slightly inferior to the flock condition. While this temporary impairment resulted in significant (nonparametric) 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 results demonstrate superior homing performance of pigeons released in small flocks compared to pigeons 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. 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 was 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 to wait for a companion bird. Similarly, 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 as they were 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 reduced 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 was 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 actual navigational errors (the birds return reliably), but may be a suboptimal homing strategy. Nevertheless, flock flying significantly reduced 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.

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 and following landmarks providing a suboptimal but predictable way home. In the majority of cases, pigeons flying alone seemed to prefer such route following, whereas this strategy was only occasionally shown by flocks. Thus, flying in flocks appears to shift the balance between homing strategies in favour of compass navigation which is always used by pigeons from unfamiliar sites.

Homing pigeons have an innate tendency to group when flying because of their evolution and breeding history (Schmidt-Koenig 1980), and group cohesion is actively kept. GPS tracks show that groups rarely split, and, if they do, 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 individual flock members landing and resting 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.

Why flock-flying pigeons abandon acquired route strategies in favour of (superior) compass orientation is unknown. One possible explanation is that flock-flying pigeons must pay visual attention to their companions to maintain flock cohesion, thus 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 recordings in flock- versus individually flying pigeons shows less attentional EEG responses of flock-flying birds when passing familiar landmarks (Vyssotski et al. 2007).

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 us to test 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 the 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 shows that pigeons can shift dynamically between coexisting strategies: individually flying pigeons rely more on topographical features for homing, keeping habitual home routes, whereas flocks tend to adopt a compass-based navigation.

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