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Waiting time before release increases the motivation to home in homing pigeons (*Columba livia*)

Gaia Dell'Ariccia[1,*], David Costantini[1], Giacomo Dell'Omo[1,2] and Hans-Peter Lipp[1]

[1]Division of Neuroanatomy and Behaviour, Institute of Anatomy, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland and [2]Ornis italica, Piazza Crati 15, 00199 Rome, Italy

*Author for correspondence (gaiadellariccia@yahoo.it)

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SUMMARY

When performing homing experiments with individual releases, pigeons have to wait in a transport box for a certain amount of time before being released and hence perceive the departure of companions. Quite often, the last pigeons disappear straightforward from the release site. The question is whether this reflects improved orientation because of prolonged exposure to the release place or whether it reflects increased homing motivation. By releasing pigeons from a familiar site, we investigated the effects of the time spent at the release site on homing performance, recording pigeons' flights with GPS loggers. Our results show that, despite individual peculiarities of flight patterns, the waiting time at release site had a positive effect on homing speed and time, and reduced the time spent circling around the release point. However, the overall path efficiency as derived from GPS tracking was not influenced. These results suggest that a longer waiting time before release improves homing performance and this is related not only to increased navigational abilities but also to increased homing motivation.

Key words: *Columba livia*, GPS tracking, homing pigeon, motivation, initial orientation.

INTRODUCTION

The homing pigeon (*Columba livia* Gmelin 1789) has been intensively used as a model species to study orientation and navigational capabilities of birds. In spite of this great interest, only a few studies dealt directly with the possible influences of birds' motivation on homing performance (i.e. Del Seppia et al., 1996). However, pigeons are commonly used for racing by fanciers who have successfully developed differential strategies (i.e. food reward, manipulations of the brood or the clutch) aimed at improving the motivation to home when displaced and the homing performance during competitions. Despite this anecdotal knowledge, a systematic scientific research on this topic is missing. However, motivation to home, acting as a behavioural factor, can have a significant influence on homing and orientation performances of pigeons, as has been recently suggested in the discussion of some results (Biro et al., 2002; Dell'Ariccia et al., 2008; Schiffner and Wiltschko, 2009).

To perform homing experiments, pigeons are taken from their lofts and transported to a determined location in wicker baskets, where they stay until the moment they are released, generally individually. Immediately after release, most pigeons first circle for some time around the release sites in a radius of about 1 km before choosing a flight direction (Matthews, 1951; Biro et al., 2002; Schiffner and Wiltschko, 2009). We consistently observed that during a series of releases, the last released pigeons headed home more rapidly and circled less around the release site than the first released pigeons. Such observations suggested an influence of the duration of waiting time at the release site on subsequent homing.

Although it seems clear that circling time has a social and motivational component (Dell'Ariccia et al., 2008; Schiffner and Wiltschko, 2009; Wiltschko et al., 2007), the rapid vanishing of late-released birds could reflect improved adaptation to local navigation cues. Using GPS tracking enables the assessment of both the flight behaviour around the release site and the navigational efficiency during the entire flight home. Thus, if prolonged waiting improves navigational efficiency, one would expect that late-released birds navigate more efficiently during both the early flight segments around the release site and during the entire path homewards. Should the rapid vanishing of long-waiting birds reflect their motivational status, one ought to expect efficient orientation and fast vanishing primarily around release site and higher flight speed also during the rest of the homeward journey. At the same time, purely navigational parameters such as path efficiency and distance to the beeline should be comparable with the ones of the early starters.

MATERIALS AND METHODS

For this study, we re-analysed a set of GPS tracks from our database. We selected a series of 16 releases that took place between November 2004 and April 2005 from the release site Santa Severa, Italy, 27 km NW of the loft (11.98°N; 42.03°E). During this series only pigeons without any experimental manipulation that could alter homing capabilities were released, all individually. Moreover, it included only pigeons already very familiar with the site. High familiarity allows for the better assessment of the influence of waiting time, because of the reduced orientation uncertainty after repeated releases from the same site (Graue, 1965; Wallraff, 2005).

A total number of 21 homing pigeons of both sexes, 1–4 years old, participated in the selected releases. All pigeons were housed in the facilities of the University of Zurich at Testa di Lepre, Italy, 25 km NW of Rome (12.28°N; 41.93°E), where they were habitually allowed to fly freely outside the lofts, and they underwent regular training. They carried a PVC dummy the size and weight of the GPS loggers (20 g, www.technosmart.eu) to get them used to flying with the load. Dummies and loggers were attached by means of an adhesive Velcro strip glued onto the feathers on the back of the pigeon with a procedure already described in Dell'Ariccia et al. (Dell'Ariccia et al., 2008).

In the 16 releases, a different number of pigeons was used (2–13; means ± s.e.m.: 6.94±0.89). Each pigeon participated in 2–10 releases (means ± s.e.m.: 5.75±0.64) and the release order was random each time. All releases took place under at least partially sunny conditions, winds being absent or weak.

To have a standard method of measuring the waiting time of each pigeon, we set zero as the time of the first pigeon released, and we then counted the waiting time of successive pigeons until the moment of their release as being the number of minutes and seconds passed from the first pigeon released. While waiting, pigeons were in their usual transport wicker basket. Prior to release, we substituted the PVC dummy with the GPS logger, and we placed the pigeon in a small starting crate that was opened after 2–3 min. Birds were placed in the starting crate and were released in intervals of 5–10 min, only after the former pigeon had disappeared from sight. From this crate only the sky but not the surrounding landscape was visible. The loggers took one positional fix every second and then stored the data. Further technical information can be found in Biro et al. (Biro et al., 2002) and Lipp et al. (Lipp et al., 2004).

Qualitative and quantitative analyses of individual tracks were run with WINTRACK freeware (www.dpwolfer.ch/wintrack) (Steiner et al., 2000; Wolfer et al., 2001). This extracted the following variables: homing speed (HS: mean speed recorded by GPS logger during flight, excluding measures of speed of less than 5 km h^{-1}), flight altitude (ALT), flying time (FT), path (Pbeg) and time (Tbeg) until leaving the start zone (defined, respectively, as the distance flown and the time spent before leaving a circle of 1 km radius about the release point) and average track distance to the beeline between the release site and the loft (ADlin). We also calculated the straightness index (SI) for each track as D/L, in which D is the beeline distance from the starting point to the goal and L is the total path length flown (Benhamou, 2004). This is a scale independent measurement and, given the highly detailed path reconstruction at 1 fix s^{-1}, a reliable estimate of the efficiency of the orientation process.

The variables obtained by Wintrack and the SI were subsequently statistically analysed using General Linear Models in the STATISTICA package (Version 7.0, StatSoft 2004, Tulsa, OK, USA). In each model, we included 'release day' and 'individual' as random factors, the 'waiting time' as a covariate and the interaction between 'individual' and 'waiting time' to evaluate whether individual pigeons behaved in a similar way regardless of the waiting time. This also allowed us to correct for pseudoreplication due to the dependence of measurements on the same individual. The interaction had been removed from the models when non significant, and the analyses were repeated according to Engqvist (Engqvist, 2005).

The normality of distribution was checked using the Kolmogorov–Smirnov test and the Shapiro–Wilk's test. The variables that did not meet the normality criterion were log-transformed (ADlin, FT) or transformed using the reciprocal (ALT, Tbeg, Pbeg). The way of transforming the data was chosen as that which better improved the normality of distribution. Coefficients of partial correlation were calculated when we found a significant covariation.

RESULTS

Overall we analysed the tracks of 111 pigeons. Figs 1 and 2 illustrate examples of GPS tracks obtained: from the first two and last two pigeons released, after about one and a half hours, during the same release day (Fig. 1A,B) and the tracks recorded from the same pigeon during different days, when released after different waiting times, as the first one (blue) or after about 30 minutes waiting (red) (Fig. 2A,B). It appears evident that the blue tracks of early released pigeons are more tortuous around the release site (Fig. 1B; Fig. 2B) whereas there is no difference in the directedness of flight and deviation from the beeline in the subsequent flight path (Fig. 1A; Fig. 2A). Different release days and different pigeons did not always show this same clear pattern; for this reason these two factors have been inserted in the analyses to statistically assess their influence on the final output.

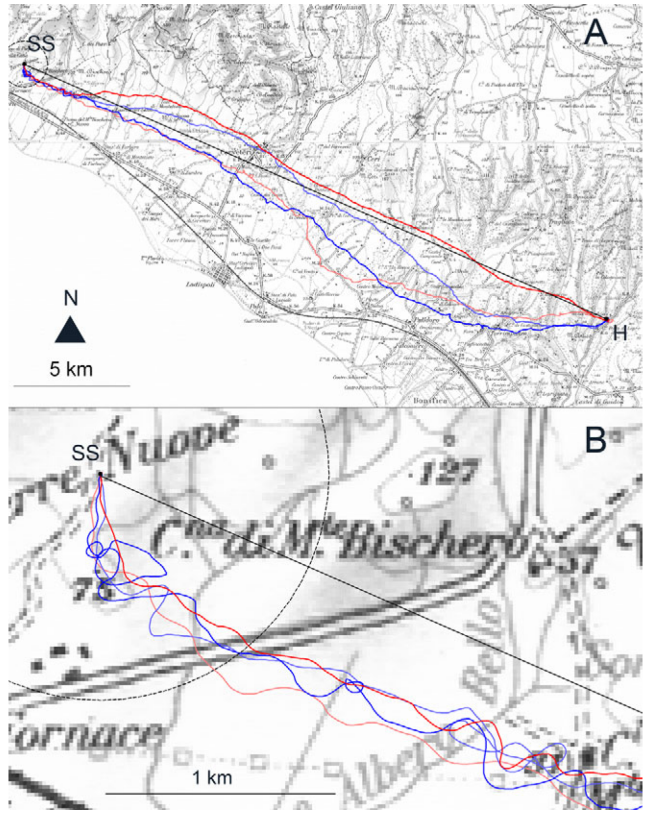

Fig. 1. (A) Examples of GPS tracks obtained during the same release day from the first two (blue) and the last two (red) released pigeons. (B) Detail of the release site of A, showing the increased circling of early released birds. The circle shows the start zone of 1 km radius. SS=release site. H=home loft.

The pattern of covariation between the waiting time and each of the flight variables was similar across pigeons (individual × waiting time: all P-values ≥0.25). Therefore, the interactions were removed and the analyses were repeated (see Table 1 for a list of the final models). All of the examined variables showed significant differences between individuals, indicating that homing performance was influenced by individual behavioural tendencies. Despite these individual differences in performance, our analyses show a positive covariation between the waiting time and the HS (partial R=0.48) (Fig. 3A), a negative covariation between the waiting time and the log-transformed FT (partial R=–0.46) (Fig. 3B) and a slight positive covariation between the waiting time and the reciprocal of both Tbeg (partial R=0.22) and Pbeg (partial R=0.22) (Table 1). The SI, the ALT and the ADlin did not significantly covary with the waiting time (Table 1). The HS and ALT differed significantly between

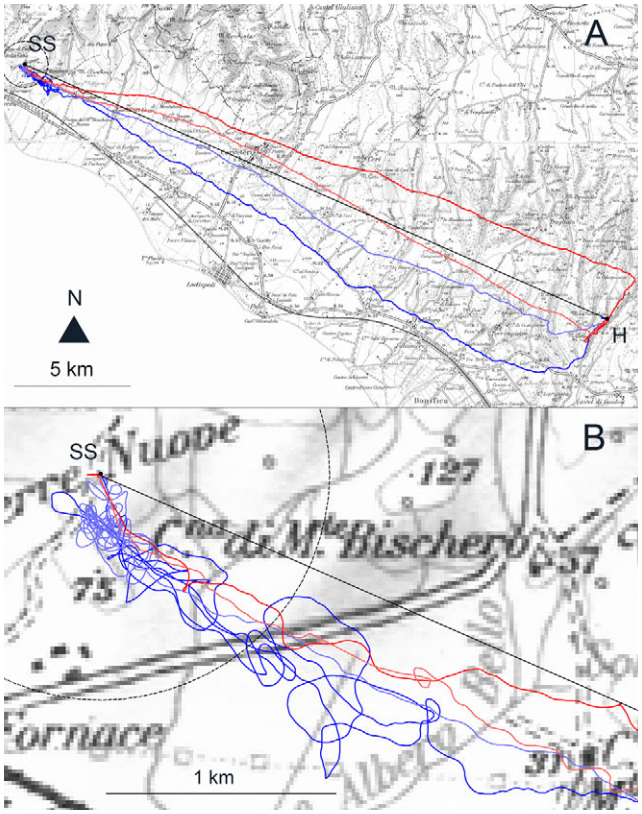

Fig. 2. (A) Examples of GPS tracks obtained from the same pigeon, during different release days, when released as the first one (blue) or after about 30 minutes waiting (red). (B) Detail of the release site of A, showing the increased circling of the bird when released as first one. The circle shows the start zone of 1 km radius. SS=release site. H=home loft.

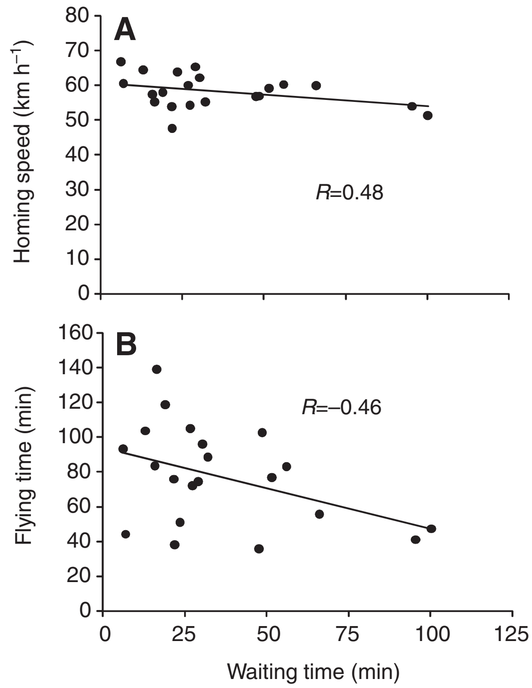

Fig. 3. The longer pigeons waited in the transport basket, the quicker they flew (A) and the shorter they homed (B). Mean-pigeon values are shown (N=21) to correct for pseudoreplication.

different releases, indicating an influence of the release day on such parameters (Table 1).

DISCUSSION

Our results showed that the waiting time before release has an influence on homing behaviour, even if there are individual tendencies in homing performances blurring this effect.

Individual behaviour influenced all examined variables, underlining that every pigeon had its own homing characteristics. This could reflect both different orientation capabilities and different motivation to home. Wallraff attributed individual variability in orientation to stochastic noise and not to consistent differences among individuals (Wallraff, 1994). According to his study, a high homing speed in one flight does not generally indicate high performance level of the individual bird but the existence of other factors influencing orientation, even if he did not identify the nature of such factors. In our case, individual differences in homing behaviour could also reflect the development of individual stereotyped routes, as it often happens when pigeons are repeatedly released from the same release site (Biro et al., 2004).

Despite these individual differences, our results show an effect of waiting time at the release site on homing speed, the time and path length until leaving the start zone and the total homing time, while the other navigational variables were not influenced. This suggests that there is no improvement in navigational capabilities: flight efficiency and the average deviation from the beeline were not influenced by the waiting time nor was the flight altitude. On the contrary, the longer a pigeon waited the faster it flew home and, consequently, the shorter was its homing time. A faster homing speed without an improvement in flight efficiency suggests an influence of homing motivation that appears to be enhanced by the wait.

In addition the analysis of the initial phase of homing flight supports the motivation hypothesis. Pigeons, when released, spent some time flying around the release point, or just nearby, before heading home (Matthews, 1951; Schiffner and Wiltschko, 2009). This initial phase of flight has been mainly explained as a gathering

Table 1. The results of the GLM test to examine the influence of 'release day', 'individual' and 'waiting time' on the different variables

	Circling time (Tbeg)		Circling path (Pbeg)		Homing speed (HS)		Flying time (FT)		Straightness index (SI)		Deviation from beeline (ADlin)		Flight altitude (ALT)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Release day	1.261	0.24871	1.271	0.24160	26.538	**0.00000**	1.653	0.07999	0.932	0.53356	1.592	0.09631	5.516	**0.00000**
Individual	2.226	**0.00765**	2.494	**0.00270**	4.119	**0.00001**	2.638	**0.00154**	30.31	**0.00033**	3.471	**0.00006**	6.443	**0.00000**
Waiting time	3.901	**0.05195**	3.685	**0.05869**	17.694	**0.00007**	20.350	**0.00002**	2.133	0.14833	2.017	0.15972	2.441	0.12243

Significant (P″ 0.05) and slightly significant (0.1>P>0.05) values are highlighted in bold.

of navigational information at the site (Biro et al., 2002; Spott, 1993) or a technical preparation to the flight (Schiffner and Wiltschko, 2009). Therefore, we can suppose that this cannot reduce below a certain threshold. However, the reduced time and flight path in the start zone evidenced in our results are in accordance with the hypothesis of a motivational and social component influencing this initial phase, not excluding the orientation function (Dell'Ariccia et al., 2008; Schiffner and Wiltschko, 2009; Wiltschko et al., 2007). The time spent in the start zone is dependent on the flight speed and on the flight path length. The flight speed resulted increased by the waiting while the path length was reduced indicating that pigeons headed earlier towards home. This could reflect an increased determination to reach the home loft after the wait in the basket or a decreased circling to look for flight companions. This last point being even truer for the very last pigeon of the release: it remained alone in the basket so it was probably aware that no other pigeons can be released to join it on its homeward trip.

Because no particular landscape preview at the release site was given to our pigeons, we can exclude the possibility that recognition of familiar landmarks accounted for the better performance at the release site, as was found in previous studies in which pigeons that were allowed to preview the landscape at the release site circled less around the release area compared with pigeons to which such a preview was denied (Biro et al., 2002; Braithwaite and Newman, 1994). Moreover, in our case the homing speed during the whole flight was influenced and increased gradually with the increment of waiting time.

A different explanation could be that pigeons waiting for longer have more time to receive and process olfactory and magnetic information (for a review, see Wallraff, 2005). This could have helped pigeons at the moment of release to make a faster departure. This idea should be directly verified; however, we can suppose that a pigeon better informed about its position and the direction to take will head home not only faster but also more efficiently in respect to a pigeon that had gathered less information. This we found to be the case during the initial phase but not during the rest of the flight, suggesting that overall navigation was not influenced. To better explore this topic, future studies could also investigate if there are differences in performance when the whole group of pigeons waits for a long time before the first pigeon is released. Such studies could help to assess if the waiting time alone has an influence on subsequent homing or if there are also other influencing factors, such as the hearing of previous companions being released.

The day of the release affected only the homing speed and the flight altitude. This could be a consequence of slightly different meteorological conditions, such as the intensity and direction of the wind and the visibility over different days. These environmental factors however did not preclude a significant effect of the waiting time.

In conclusion, our study shows that homing motivation can influence navigation behaviour and homing performance of pigeons. Longer waiting time before release seems to enhance the homing motivation. The influence of motivation on homing behaviour deserves further investigation to better understand and evaluate its actual role and should be taken into account when conducting homing pigeons experiments.

LIST OF ABBREVIATIONS

ADlin	average distance to beeline between release site and loft
ALT	flight altitude
D	beeline distance from starting point to the goal
FT	flight time
HS	homing speed
L	total path length flown
Pbeg	path length to leave the start zone
SI	straightness index
Tbeg	time to leave the start zone

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