TRACKING CLOCK-SHIFTED HOMING PIGEONS FROM FAMILIAR RELEASE SITES

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Summary

Clock-shifted homing pigeons were tracked from familiar sites 17.1 km and 23.5 km from the home loft in Pisa, Italy, using an on-board route recorder. At the first release site, north of home, the majority of clock-shifted birds had relatively straight tracks comparable with those of control birds. At the second release site, south of home, the clock-shifted birds deflected in the direction predicted for the degree of clock shift, with many birds travelling some distance in the wrong direction before correcting their course. The possible role of large-scale terrain features in homing pigeon navigation is discussed.

Key words: navigation, pigeon, *Columba livia*, sun compass, tracking.

Introduction

The mechanism by which homing pigeons navigate from an unfamiliar place is now relatively well understood. Pigeons determine their location with respect to home using a 'map', thought to be based on olfactory cues (Papi, 1991), or other cues of unknown origin (Wiltschko, 1996) and are then able to take up the correct home direction by referring to a sun azimuth compass. This is widely known as the map-and-compass mechanism of true navigation (Kramer, 1953). Because the sun azimuth compass is time-compensated, homing pigeons can be 'clock-shifted'. If their day/night cycle is artificially shifted, when they are released from an unfamiliar site they misread the sun compass and fly in the wrong direction (Schmidt-Koening, 1958, 1960, 1961). The degree to which the bird flies in the wrong direction is predictable, and for a 6 h shift this varies from 70° to 140° depending on the time of day and year. The deflecting effect of a clock-shift has also been demonstrated at very short distances from the home loft (Graue, 1963) and at sites with which pigeons were extremely familiar (Füller et al., 1983), suggesting that the map and compass is used even when it would be possible to navigate by familiar site cues such as visual landmarks. Two experiments have suggested that pigeons can refer to familiar site cues if the map part of the map and compass is unavailable. Bingman and Ioalè (1989) found that clock-shifted birds familiar with release sites (40.4–54.8 km from home), but denied access to olfactory cues (anosmic), oriented in the home direction. Wallraff et al. (1994) performed an experiment which differed from that of Bingman and Ioalè (1989) in that clock-shifted anosmic birds received training releases around the point of experimental release (24–30 km from home) but never from the exact site until the test. They found that the mean orientation of a group of such birds was a compromise between the home direction and the clock-shift direction. However, a further study by Luschi and Dall'Antonia (1993), using the same protocol as Bingman and Ioalè (1989), found that these birds oriented in the clock-shift direction. Their conclusion was that even landmarks are encoded into the map and compass. Recent tracking experiments by Holland et al. (1999) using route recorders (Bramanti et al., 1988) have suggested further complications. When released at relatively short distances (2–10 km) from home, it was discovered that clock-shifted homing pigeons with no olfactory manipulation sometimes showed deflected tracks and sometimes straight tracks when released from a familiar site. These two different patterns could occur in different birds from the same release site on some occasions. It therefore seemed that a bird could use the sun compass at one place in the familiar area but use another independent mechanism at other places. At relatively short distances from home, however, it is possible that the birds can see the loft, which confounds the results. In the present study, we therefore performed clock-shift releases from familiar sites out of visual range of the home loft. These experiments were carried out in Pisa, Italy, using route recorders to track the homing routes of clock-shifted birds.

Materials and methods

These experiments were performed in Italy in the area surrounding Pisa, between 1 and 29 August 1996. The home loft was at the Arnino field station (43°39′N, 10°25′W) of the Dipartimento di Scienze del Comportamento Animale of the University of Pisa.

The route recorder

The device carries a traditional compass equipped with a transducer to convert the angular values into electrical resistance values. The compass consists of a pair of magnetic needles fixed to a grayscale disc with a light-emitting diode (LED) photoresistor located underneath. As the bird's heading varies, so does the position of the LED with respect to the disc, and the variation in the output of the photoresistor is recorded into a digital memory at regular time intervals (e.g. 2, 4, 6, 8 s).

To produce a track, a constant speed of $60 \, \text{km h}^{-1}$ has to be assumed, which tests have confirmed to be acceptable (Dall'Antonia et al., 1993). An MSDOS-based software program, Elabora, is used to reconstruct the track. As well as the headings, the position of the home and release sites and the wind velocity and direction on the day of release need to be known to produce an accurate track. If the angular difference between home and the final point of the track is more than $10°$, then the track is rejected; the reliability of the device is expressed by the fact that the angular difference between the home point and the end of the track is usually less than $5°$, a distance that amounts to a very small fraction of the track length (Dall'Antonia et al., 1993). The recovery of the device is essential for data retrieval.

The first device developed weighed 30 g, but a second and third generation of route recorders have now been developed with larger memory capacity (currently 32 kbytes). The third-generation device weighs 13 g. It is normally attached to the bird's back by gluing Velcro to the body of the bird and then attaching the device to the Velcro.

Subjects and training

Twenty-nine pigeons, *Columba livia* L., which had been hatched at the Arnino loft were used for the experiment. All birds used were between 2 and 3 years old and had considerable previous homing experience. The birds received 12 releases north, east and south of home (the sea coast was west, so no releases were performed in this direction) at distances ranging from 10 to 35 km from home to ensure a wide knowledge of the area in which they were to be tested and to remove the possibility of directional bias. Birds were transported to the release sites in an estate car in carrier baskets allowing adequate ventilation.

Release sites

The experimental release sites were La Costanza (43°49′N, 10°22′W, home bearing $189°$, 17.1 km from the home loft) and Orciano (43°30′N, 10°34′W, home bearing $314°$, 23.5 km from the home loft). In a previously published experiment, Benvenuti et al. (1996) released fast-clock-shifted birds from La Costanza and found that the mean vanishing bearing was deflected by $77°$ anticlockwise from the home direction. The birds used in the present experiment had not previously been released from either of the two experimental release sites, but received six releases from each of the two release sites prior to testing. These releases were randomly incorporated into the familiar area training so as to reduce any chance of directional bias.

Testing

Although 29 birds were available, only 15 route recorders were available for any one release. Thus, only half the birds could be released from a site on any day. Also, to increase the number of tracks of clock-shifted birds available, each bird was released once as a clock-shifted bird and once as a control bird. Thus, eight releases in all were performed: each bird was tracked once as a clock-shifted bird and once as a control bird from each site. Initially, birds 1–15 were clock-shifted 6 h fast (subjective day starting 6 h before dawn) for 8 days, and birds 16–29 were controls. Controls were kept in a clock-shift room under the same conditions as clock-shifted birds except that the lights in the room were switched on and off at sunrise and sunset. After a release, birds were put back in the clock-shift lofts as soon as they arrived home and were left in the clock-shift lofts for at least 2 days before a subsequent release was performed. After birds 1–15 and 16–29 had been released from both sites, they were put back in their normal loft for 8 days. Birds 16–29 were then clock-shifted 6 h fast for 8 days and birds 1–15 were kept under clock-shift room conditions with normal sunrise and sunset. Following this, the final four releases were performed.

At the release site, before each bird was released, the route recorder was started and the time noted. The device was then placed in a torpedo-shaped protective container made from plastic, which increased the mass of the bird by 16 g. The container was placed on the back of the pigeon and its time of release was noted so that the exact point at which the route recorder began logging the flight direction of the pigeon could be calculated. Vanishing bearings were taken so that these could be compared with the tracks obtained from the route recorder. Three birds of the same experimental condition (i.e. clock-shifted or control) were released singly, with a 10 min interval between each bird, before a bird of the opposite condition was released. This protocol aimed to reduce the chance that a clock-shifted bird would join a control bird, thus affecting their chosen flight directions. Wind speed and wind direction were measured at the release site to aid route reconstruction. All releases were performed under sunny conditions between 06:00 h (sunrise) and 09:00 h.

Statistical analyses

The predicted direction for the degree of clock-shift was calculated from an ephemeris chart recorded during the time of the experiments.

To analyse the tracks, the straightness index was used (Batschelet, 1981). Because the path of an animal is rarely

exactly straight, it is necessary to quantify how close to a straight line the track of the animal is between the start point and the goal. The path of the animal is broken down into small sections of equal time intervals, which become vectors. If the direction of these vectors is plotted on a circle, then the vector length **r** can be calculated. An **r** value close to 1 indicates a high degree of straightness, if **r** is close to 0, then this indicates pronounced deviations from a straight line. The straightness index is an ideal measure for clock-shifted birds as it allows comparison between those birds that have deviated markedly from a straight line between the release site and home and those whose orientation has been relatively close to this line.

The Mann–Whitney *U*-test was used to test for a difference between the mean straightness indices of the control and clock-shifted groups. A one-sample *Z*-test was used to test for a difference between the mean direction at which clock-shifted birds at Orciano corrected and the distance of the release site from the home loft.

The Rayleigh test for randomness measured significant orientation of the mean bearing and vector of the experimental groups and the *V*-test measured significant orientation of mean vanishing bearings in a predicted direction.

Results

Vanishing bearings

The vanishing bearings of the control and clock-shifted groups at La Costanza and Orciano are shown in Fig. 1. Table 1 shows the results of statistical comparisons between the actual vanishing bearings and those predicted for control and clock-shifted groups at La Costanza and Orciano.

Tracks

Fig. 2 shows a selection of the tracks obtained for experimental and control birds released at La Costanza. The mean straightness indices of the two groups were as follows: controls, **r**=0.95±0.06 (mean ± S.E.M., *N*=19); clock-shifted, **r**=0.81±0.06 (*N*=20). Note that some birds tracks are not included because the birds did not return in a previous release or the data were lost. There was no significant difference in **r** between the two groups (Mann–Whitney *U*-test: *U*=413.5, *P*>0.05, *N*=39).

Table 1. *The results of* V-*tests for orientation in the predicted direction on the vanishing bearings of control and clock-shifted groups of pigeons at Orciano and La Costanza*

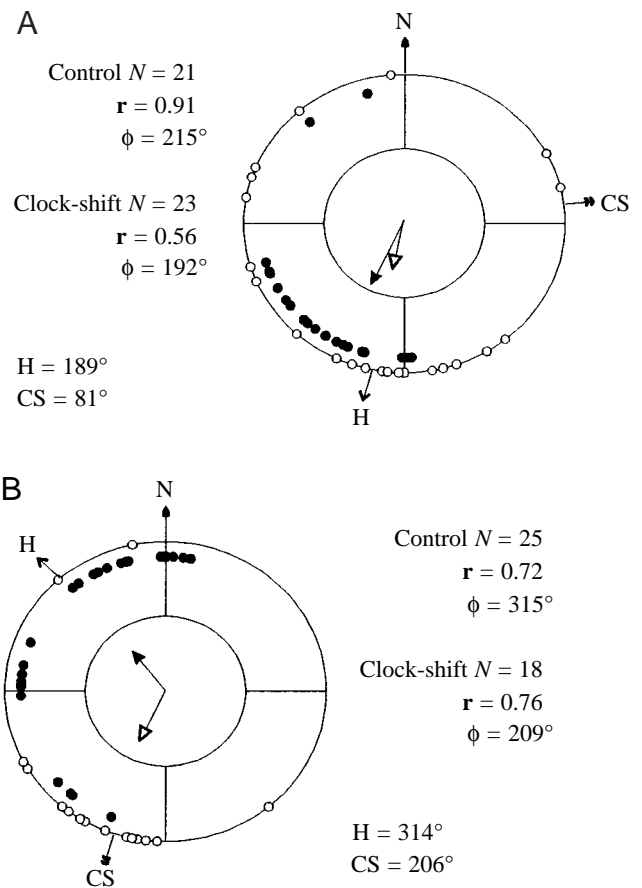|		Home-oriented	Clock-shift-oriented
La Costanza	Control (*N*=21)	*P*<0.0001	NS
	Clock-shifted (*N*=23)	*P*<0.0001	NS
Orciano	Controls (*N*=25)	*P*<0.0001	NS
	Clock-shifted (*N*=18)	NS	*P*<0.0001

NS, not significant.

Fig. 1. Circular diagram showing the vanishing bearings of control (filled circles) and clock-shifted (open circles) birds at La Costanza (A) and Orciano (B). Each bird (*N*=29) received one release as a control and one as a clock-shifted bird; some birds therefore appear in both categories. At La Costanza (A), six birds were lost before vanishing when released as controls, and eight birds were lost before vanishing when released clock-shifted. At Orciano (B), four control and 11 clock-shifted birds were lost. The mean bearings ϕ and vector lengths **r** of the two groups are shown by the arrows in the inner circle. The edge of the inner circle represents a vector length of 1. The home (H) direction is shown by the single-headed arrow on the outer circle and the clock-shift (CS) direction by the double-headed arrow. The Rayleigh test for randomness indicated that control and clock-shifted groups were highly significantly oriented in both releases (*P*<0.0001). See Table 1 for the results of statistical comparisons between mean vanishing bearings and predicted bearings.

Fig. 3 shows the tracks obtained from control and experimental birds released at Orciano between 2 and 29 August 1996. The straightness indices of the two groups were as follows: controls, **r**=0.95±0.007 (mean ± S.E.M. *N*=23); clock-shifted, **r**=0.46±0.06 (*N*=14). There was a highly significant difference between the two groups (Mann–Whitney *U*-test, two-tailed: *U*=156.5, *P*<0.00001, *N*=37).

One possible explanation for the significantly different tracks taken by clock-shifted birds released from Orciano (Table 1; Fig. 3) is that the birds correct their bearings after
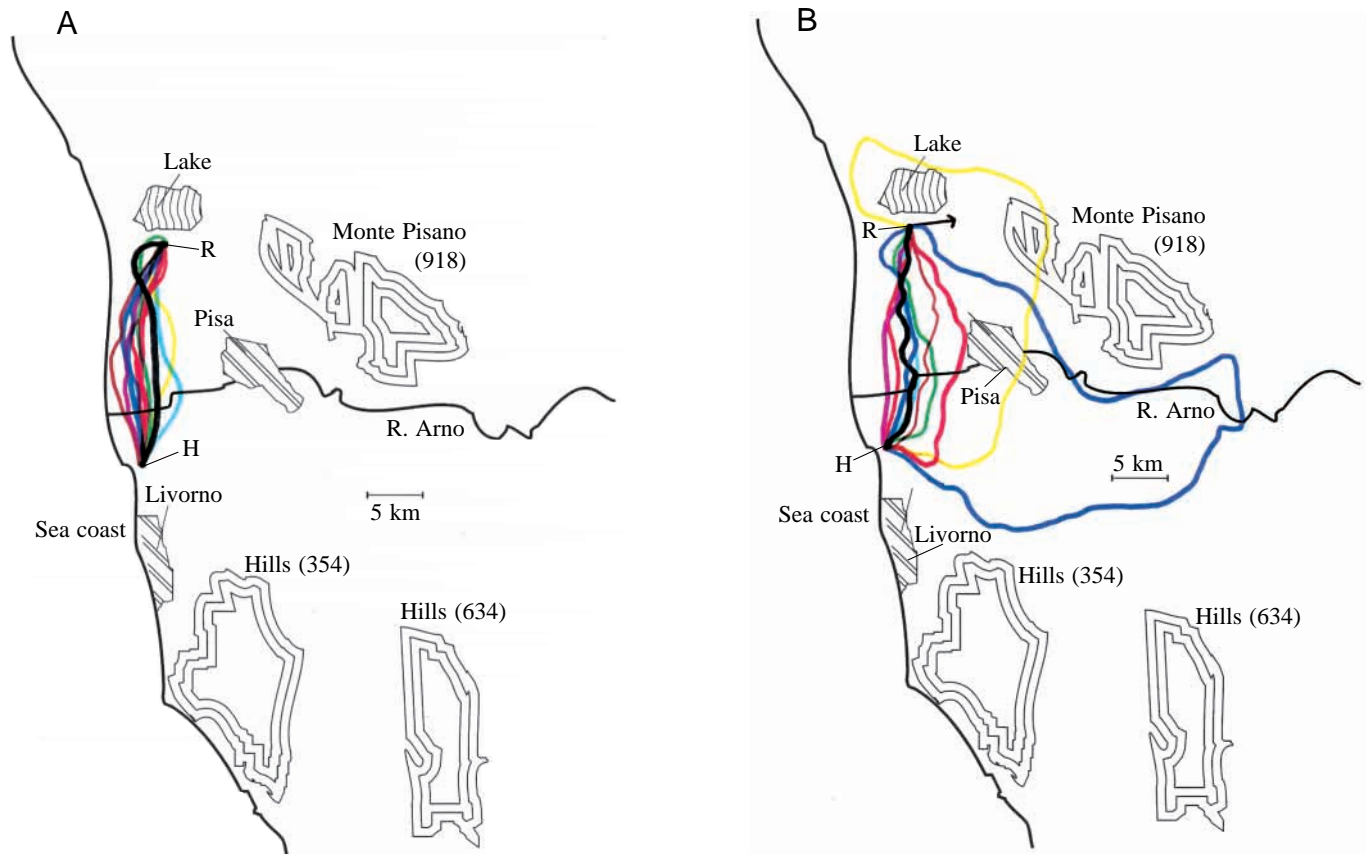
Fig. 2. A selection of tracks of birds released at La Costanza. H, home; R, release site. Large-scale topographical features are also indicated. Where hills or mountains are shown, the value in parentheses is the highest point of the feature in metres above sea level. A 5 km scale bar is shown. Tracks are presented in different colours to aid identification of individual tracks within each figure and do not represent the same bird in different figures. (A) Control birds; (B) clock-shifted birds. The black arrow shows the predicted direction for clock-shifted birds.

flying the distance of the loft from the release site (23.5 km). The distance at which birds corrected (determined as when the angular change in direction was greater than 90°) was measured and the mean distance was compared with the distance between the loft and the release site. A one-sample Z-test showed that the mean distance at which the birds corrected (24.04±1.2 km, N=14) was not significantly different from the distance from release site to loft (Z=0.03, P>0.05).

Discussion

The results of the experiments in Pisa demonstrated that pigeons may use different methods for homeward orientation at different sites. At Orciano, the clock-shift-oriented tracks indicate that the birds were using the sun compass to determine the homeward direction, whereas at La Costanza the lack of such an effect in many of the clock-shifted birds indicated some other method of homeward orientation. The fact that the mean vanishing bearing of the clock-shifted group at Orciano was significantly clock-shift-oriented shows that birds were not compromising between the sun compass and some other cue, nor occasionally choosing the home direction.

The tracks of the clock-shifted birds at Orciano indicate a possible method by which clock-shifted birds might correct their faulty orientation.

The mean distance travelled by deflected birds before making a correction to their bearings did not differ significantly from the distance between the release site and the home loft. This gives support to the suggestion of Holland et al. (1999) that pigeons might be able to assess the flight distance from a familiar site to home as well as the direction.

At La Costanza, the majority of clock-shifted birds had tracks that were comparable with those of control birds, and there was no significant difference between the straightness indices of the two groups. From Fig. 2B, it seems that a few birds deflect in the clock-shifted direction (e.g. yellow and blue tracks), but there is no evidence that all the birds compromise between the home direction and the predicted direction of clock-shift. Therefore, the pigeons must be using a sun-compass- independent method of orientation at this site in preference to the sun compass. There are several alternative explanations for the straight tracks of clock-shifted birds at this site which are discussed below.

First, visual landmarks may have a role. Braithwaite and Guilford (1991) demonstrated that vision is important for
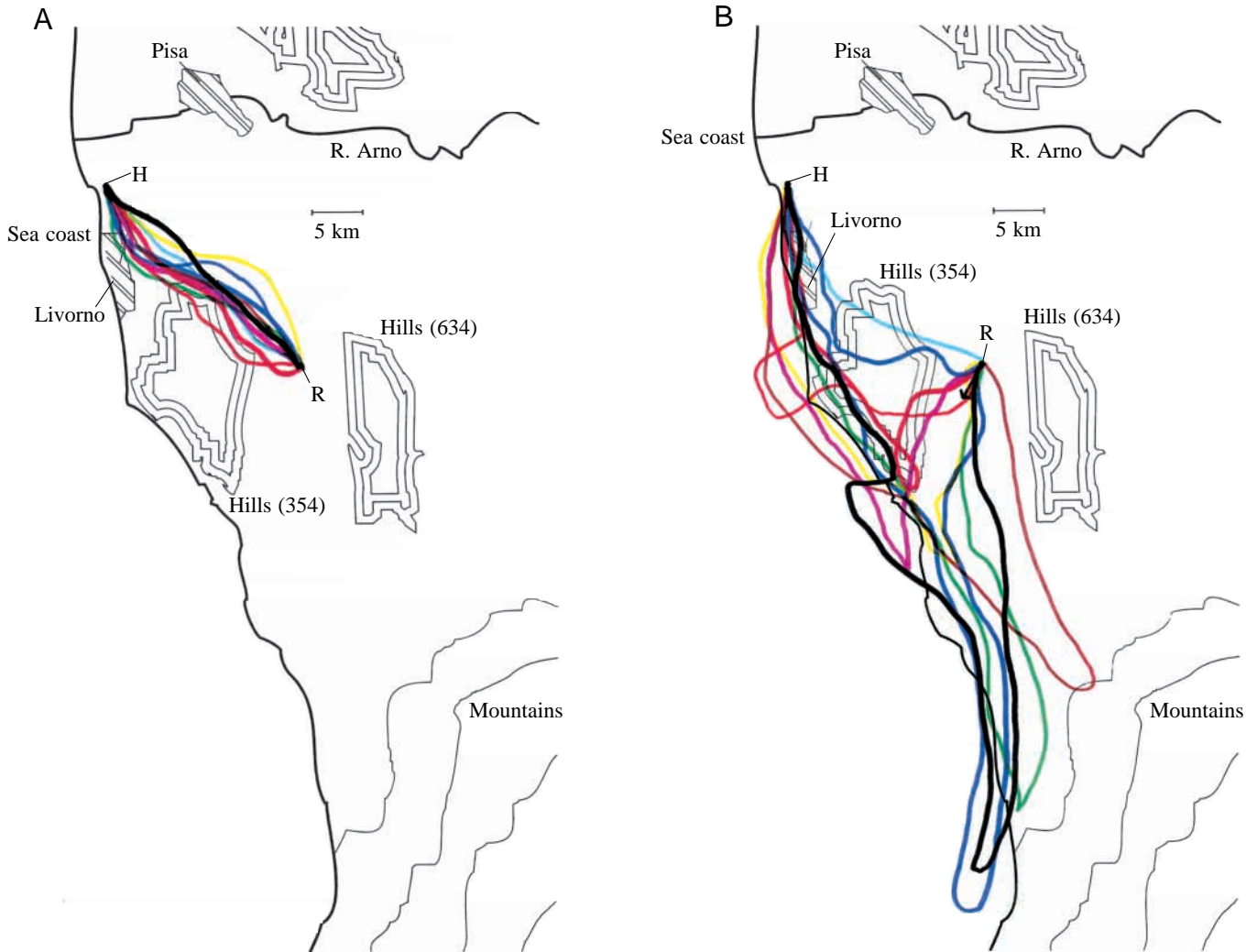
Fig. 3. A selection of the tracks of birds released at Orciano. (A) Control birds; (B) clock-shifted birds. Other details are as in Fig. 2.

short-distance homing, but the exact mechanism by which pigeons can use visual landmarks for orientation has yet to be determined. Large-scale terrain features may be used as beacons (Baker, 1984); alternatively, pigeons may use a learned representation, i.e. a cognitive map of the area (O'Keefe and Nadel, 1978).

Second, the magnetic compass could be used. It is possible that, on comparing the magnetic compass direction and the sun compass direction, and finding them to be in conflict, the pigeons switch to the magnetic compass. However, Wolff (1997) found that clock-shifted pigeons which had their magnetic compass disrupted by Helmholtz coils were not impaired in their ability to return to the home loft.

Third, there may be a site-specific effect of terrain features. Luschi and Dall'Antonia (1993) suggested that non-deflected bearings in clock-shifted birds might be due to a site-specific effect such as the presence of a mountain range in the direction of clock-shift. Pigeons are known to prefer to fly around these than over them (Wagner, 1972). The presence of a mountain range in the predicted clock-shift direction at La Costanza

would therefore explain our results. However, in the only critical test of such an effect, Bingman and Ioalè (1989) released clock-shifted birds unfamiliar with the release sites used in their study, and these birds had a mean vanishing bearing in the predicted clock-shifted direction, thus ruling out a non-specific effect of the terrain. In addition, a previous release from La Costanza using birds unfamiliar with the area (Benvenuti et al., 1996) obtained a mean vanishing bearing in the predicted direction for the degree of clock-shift.

Thus, although complete evidence is lacking, it seems that the most likely reason that the majority of the birds at La Costanza did not use the sun compass is because it was in conflict with the directional information that they obtained from visual landmarks, which most birds decided to use instead. So why did the birds at Orciano not use the same strategy? One possibility is the distance of the release sites from the loft. It is possible that the boundary at which pigeons use visual landmarks independently to provide directional information lies between 17.1 and 23.6 km from the loft. Purely on the basis of initial orientation performance, Matthews

(1963) concluded that homing pigeons use visual landmarks up to a distance of approximately 23 km, but attempts to replicate those results have failed (Schmidt-Koenig, 1966; Graue, 1970). Furthermore, Bingman and Ioalè (1989) found that anosmic clock-shifted pigeons had a mean homeward-oriented bearing even 54.8 km from the home loft. A more likely explanation seems to be the presence of large-scale terrain features. For example, at La Costanza, if the birds used the shifted sun compass, then this would involve flying away from the sea coast and towards mountains. Presumably, from past experience, the birds know that they have to fly towards the sea and away from the mountains to reach home. At Orciano, the terrain features did not indicate the home direction so clearly. The release site was surrounded by hills, and the shifted sun compass still indicated to them that the home direction was towards the sea coast. This proposal suggests that certain landscape features are 'better' for the formation of a topographical map than others, and this would mean that the homing mechanism that a pigeon used would depend upon the availability of relevant visual cues at the release site. Chappell and Guilford (1997) have considered this possibility on the basis of results obtained in a small-scale arena experiment.

A question that has yet to be answered is whether the topographical map is used only when the sun compass is known to be faulty or whether it is preferred at sites where the relevant cues are available. To answer this question, it would be necessary to manipulate landmarks in some way, which has so far proved beyond the bounds of field homing experiments on a large scale.

The results of these experiments suggest that pigeons can orient from a familiar release site by using the map and sun compass but, if this conflicts with other directional information, they may then ignore the sun compass in favour of this other information. It is suggested that large-scale terrain features may provide such cues.

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