

HOMING BEHAVIOUR OF REDWINGS (*Turdus iliacus*) AND FIELDFARES (*T. pilaris*)

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ABSTRACT

Homing behaviour of displaced wild birds are largely unexplored, with the exception of the orientation and homing performance of pigeons (*Columba livia*), which are well documented. Using the redwing (*Turdus iliacus*) and the fieldfare (*T. pilaris*) as an example of typical nocturnal and diurnal/nocturnal migrant species, respectively, homing movements of birds following displacements were investigated. A total of 16 colour-ringed birds were displaced over distances of 6 to 22.5 km in several directions from their nesting territories. In these displacement experiments 8 out of 12 redwings and 2 out of 4 fieldfares were observed to return to their home territories. Most of them were observed at their nest sites the following morning after the release, i. e. their return took less than one day. The pooled movement directions in cage and release experiments by individual birds showed a significant preference for the home direction. There was seemingly no difference between birds' headings under clear or overcast skies. Assumption is made that migrants returning to previously occupied nesting sites perform behaviour analogous to that of a homing pigeon. Redwings, for example, exhibit a high degree of site fidelity with respect to previous breeding sites. Therefore, it is assumed that, in general, captured redwings displaced and released in entirely unfamiliar areas could home by true navigation.

Keywords: homing, redwing, *Turdus iliacus*, fieldfare, *Turdus pilaris*, displacement, release, navigation

1 INTRODUCTION

Homing abilities of displaced wild birds are largely unexplored, with the exception of the orientation and homing performance of pigeons (*Columba livia*), which are well documented. Many studies have shown that homing pigeons usually fly directly home even when released at unfamiliar sites hundreds of km from the loft. This is the case of true navigation in which the organism is able to select the direction toward a goal when released in an unfamiliar environment (Griffin 1955, reviewed by Keeton 1974b). Homing involves various orientation mechanisms and depends to a

greater or lesser extent on individual experience (Papi 1992).

The basic orientational requirements of any bird are to orient within its own home area, and to be able to return this area if forced to leave it, for example when escaping a predator (Wiltschko and Wiltschko 1978). This would also apply to birds displaced from their current position whether it is a nest, resting place or wintering area. Most experiments documenting the homing behaviour of wild birds have been displacement tests performed during the breeding season. Less

attention has been paid to the question whether birds also home when displaced from their wintering sites (Mewaldt 1964, Benvenuti and Ioalè 1980, Ioalè and Benvenuti 1983).

Many migratory birds return to the same wintering areas year after year which has led to the hypothesis that, after visiting many stopover sites during their first migration, birds recall these intending to stop at them on subsequent migratory flights (Wiltschko and Wiltschko 1978, 1999). This can be described as *route reversal* based on an external reference. An efficient way to use landmarks is when a bird is familiar with a number of landmarks within its home area, i.e. it has an integrative picture of the spatial distribution of the landmarks, learned by individual exploration (Papi and Wallraff 1992). This would lead bird to take a more direct route, since it knows how to home from any given landmark independently of how it reached it (*pilotage*). At sites outside the familiar area this *mosaic map* is useless for homing. It has been demonstrated in many studies of homing pigeons that landmarks are normally used and that they facilitate homing and increase successful homing considerably, although the opposite findings have been reported (Arnould-Taylor and Malewski 1955, Michener and Walcott 1966, Keeton 1974a).

Birds could apply three different strategies after natural or artificial displacement (Griffin 1955): Type I is random or systematic exploration until the bird reaches familiar landmarks, Type II is flying on a particular compass direction, even in unfamiliar territory, and Type III is determining the direction to home even though home situates in an unusual direction. Type III navigation appears to be the most superior of all, as it requires a special “sense of direction” which would allow the displaced bird to choose near the correct direction of its home area even when released in a completely unknown territory. All these three methods can be used in sequence by an individual bird to find home

(Michener and Walcott 1966).

Griffin’s classification is more or less outdated since Kramer (1959) proposed his *map and compass* –model. Avian navigation is viewed as a two-step process. In the first step, the position with respect to home is determined and the home direction is derived as a compass course. In the second step, this course is converted into actual direction of flight with the help of a compass.

The use of any compass system (sun, stars, magnetic field) as a directional reference allows an orientation independent of known landmarks (Wiltschko and Wiltschko 1978, 1988). Basically, an orientation to home area can be achieved by recalling the direction of the outward journey relative to the compass and then reversing for the home journey. But, in case the route for outward journey includes complicated turns and loops, the directional changes have to be integrated over time to determine the direct course home. The directionally oriented map of the course of at least two gradients (*the navigational map*) and registering their changes in relation to the respective values of the home area allow a bird to determine the home direction using this site-specific information in unknown territory (Wiltschko and Wiltschko 1978, 1999). Homing pigeons may even fix their position in relation to home by smelling odorous substances dispersed in the atmosphere (*the olfactory map*), both at the moment of release and during transportation (Papi and Wallraff 1992).

Displacement experiments were carried out to determine homing ability in two species of thrushes (*Turdus spp.*). Several basic questions were put forward first, such as how many of the displaced birds will be documented to return to their home territories, do they orient in the homeward direction after releasing them, and how long will it take for the birds to home from these relatively short displacements? Then, more demanding was to suggest whether they home by systematic search, in a given compass direction or by true navigation?

2 MATERIAL AND METHODS

Breeding adult male redwings and fieldfares were captured with mist nets in their territories in Noljakka, Joensuu (62° 37'N, 29° 41'E) in eastern Finland during the summer 1999 and 2000. The birds were captured when nestlings were at the age of approx. seven days. Before that age the nestlings have to be brooded periodically at daylight by the female. Hence, feeding visits were made only by the female during the displacement.

Birds were measured, aged and colour-ringed for individual identification. Sexes were determined by examination for brood patch and cloacal protuberance. A total of 16 birds were displaced over distances of 6 to 22.5 km in several directions from their nesting territories (Table 1, Fig. 1). The birds were carried to the release sites normally within two hours of their capture. Displacement took place by car and birds were kept in cotton bags during the displacement. Straight routes were not used and the heading was changed more than once.

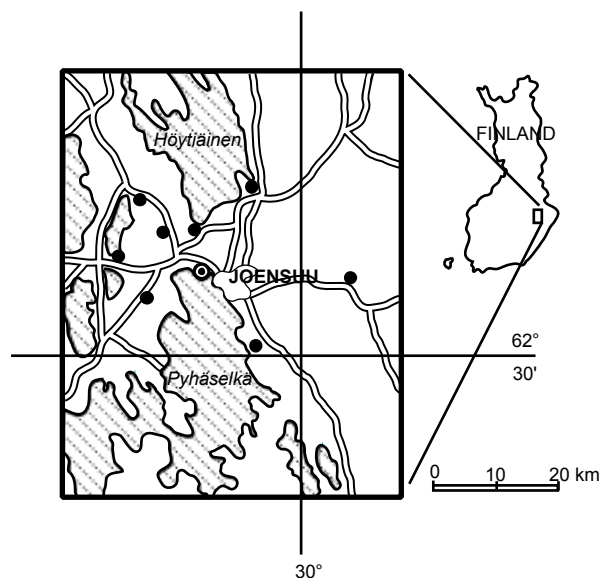


Fig. 1. Map showing the position of the study area in Joensuu ("home", white-black dot) and of the release sites (black dots). Striped areas indicate the main lake districts.

Open sites were chosen as release sites to minimize the influence of nearest trees or bushes to birds' headings. Before the release, the experimental birds were placed into circular orientation cages for 20 minutes to examine the preferred direction of their movements. The tests were performed outdoors using plastic Emlen-type funnels with net cover and typewriter correction paper (Tipp-Ex paper) as the recording medium (top diameter of the funnel = 50 cm; see Sandberg and Gudmundsson 1996). A minimum of 50 scratches was set as the limit for inclusion of a particular bird in the data set. Six redwings which left less than 50 scratches were considered inactive in the funnel, whereas the remaining 10 birds were very active leaving an average of 750 scratches in the test period. When releasing initial bearings were observed with a compass. All releases were made between 7.50 and 11.20 a.m., median time (Md) being 9.40 a.m. Four birds were released under total overcast (cloud cover, cc = 8/8), seven birds under near overcast (cc = 5/8 - 7/8), and five birds under clear skies (cc = 0/8 - 2/8).

In homing experiments the main questions were 1) how much are the vanishing directions concentrated around the mean direction, and 2) how close is the mean direction (refers to cage data) to the homeward direction? We can use the equation

$$v = r \cos(\varphi - \theta_0)$$

where v is the component of the mean vector with respect to the homeward direction (*homeward component*, Batschelet 1981). It gives its highest value, $v = 1$, if all animals move exactly homeward. The homeward component even becomes negative when the difference $\varphi - \theta_0$ exceeds 90° and thus, it may well serve as a measure of homing behaviour. To test whether the mean direction deviates significantly from the home direction, confidence interval, 95 % CI, for the mean angle was used (Batschelet

1981).

Registrations from the orientation cages and initial bearings of released thrushes were subjected to vector calculation, yielding a mean heading for each individual and test (Batschelet 1981). Home directions of individually tested birds were pooled with respect to the direction 360° to obtain a home direction for a test group. Mean vectors are relative to the radius (r) of the circle = 1.

After release breeding territories of experimental birds were visited on a daily basis. All observations on the return of birds were made early in the morning before 6 a.m. Minimum time of observation was 30 minutes. Return of colour-ringed birds was documented through binoculars or telescope. Observations were stopped after the chicks had left the nest and dispersed with the adult(s).

Table 1. Data on redwings and fieldfares during homing from displacements in Noljakka, Joensuu.

Nr	Date	Species/ Ring Nr.	Release site	Distance	Direction	Home dir.	Release dir.	Mean dir.	r	Return rate (d)
1	250599	F/C2	Kon, Asemankylä	14 km	36°NE	216°	206°	215°	0.59	<4
2	280599	F/C5	Pyh, Niittylahti	15 km	144°SE	324°	220°	328°	0.21	<1
3	040699	F/C9	Lip, Lihavaisenmutka	10.5 km	246°WSW	66°	60°	341°	0.38	-
4	080699	R/A4	Lip, Vaiviontie	8 km	316°NW	136°	140°	84°	0.59	<1
5	080699	R/A7	Lip, Vaiviontie	8 km	316°NW	136°	180°	82°	0.15	<1
6	090699	R/E1	Kii, Heinävaarantie	22.5 km	94°E	274°	270°	243°	0.95	<3
7	100699	R/E3	Lip, Kuorinka	13 km	274°W	94°	10°	30°	0.31	-
8	100699	R/A2	Lip, Kuorinka	13 km	274°W	94°	350°	44°	0.39	<1
9	140699	R/E6	Kon, Puntarikoskentie	6 km	354°N	174°	80°	-	-	<3
10	140699	R/E8	Kon, Puntarikoskentie	6 km	354°N	174°	220°	-	-	-
11	010799	F/J3	Lip, Viitalahti	14 km	324°NW	144°	250°	65°	0.31	†
12	160600	R/K8	Kon, Asemankylä	14 km	36°NE	216°	290°	-	-	<3
13	070700	R/E6	Lip, Lihavaisenmutka	10.5 km	246°WSW	66°	20°	-	-	<1
14	200700	R/w	Lip, Vaiviontie	8 km	316°NW	136°	90°	165°	0.41	†,*
15	210700	R/w	Pyh, Niittylahti	15 km	144°SE	324°	30°	-	-	<1
16	210700	R/w	Pyh, Niittylahti	15 km	144°SE	324°	30°	-	-	-

F = fieldfare; R = redwing; ring nr. = colour-ring number; w = white colour-ring; Kon = Kontiolahti; Pyh = Pyhäselkä; Lip = Liperi; Kii = Kiihtelysvaara; distance and direction are measured from the nest sites; r = length of the mean vector; return rate in days (colour-ring documented through binoculars or telescope); † = nest destroyed; * = bird nr. 14 was found dead on 27th Sep 2000 near its summer breeding site.

3 RESULTS

In these displacement experiments 8 out of 12 redwings and 2 out of 4 fieldfares were observed to return to their home territories. Most of them were observed at their nest sites the following morning after the release, i. e. their return took less than one day (Table 1).

Orientation cage tests resulted in a mean direction towards north-northwest, where the 95 % CI included the home direction ($\alpha = 333^\circ$, $r = 0.707$, $n = 10$, $P < 0.007$,

95% Confidence Interval: $\pm 36^\circ$; Fig. 2). In the following release tests under clear or cloudy skies, the birds selected a northern mean direction ($\alpha = 356^\circ$, $r = 0.447$, $n = 16$, $P < 0.05$, 95% Confidence Interval: $\pm 49^\circ$; Fig. 3). The two test samples did not deviate significantly from each other (Watson's U^2 -test, $U^2 = 0.120$, $U^2(\alpha) = 0.187$, $n = 10$, $m = 16$, $P < 0.05$).

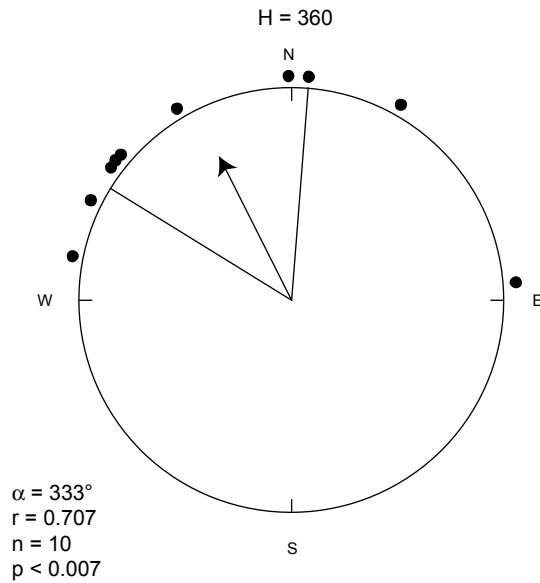


Fig 2. Orientation behaviour of displaced redwings and fieldfares in cage tests before the release. The home direction for a test group is given by the azimuth 360° outside the circular diagram. The 95 % confidence interval are illustrated by solid lines. An arrow is a sample mean vector (α) and its length is proportional to the unit radius of the circle = 1. P-values are according to the Rayleigh test (Batschelet 1981).

The angle of the home direction as given by the azimuth 360° falls in both tests into the confidence interval so the hypothesis of uniformity can be rejected, i. e. there is a preference for the home direction. The calculated homeward component was ($v = 0.624$) for the cage tests and ($v = 0.446$) for the release tests.

4 DISCUSSION

Most of the returned birds were seen within 24 hr of their capture at the nest sites. The rest of them were observed within four days of their capture. One bird which was considered as non-returned was recaptured ca. two months later near its' summer breeding site. By chance, one bird was used twice in experiments of successive years. The bird was able to home in both cases

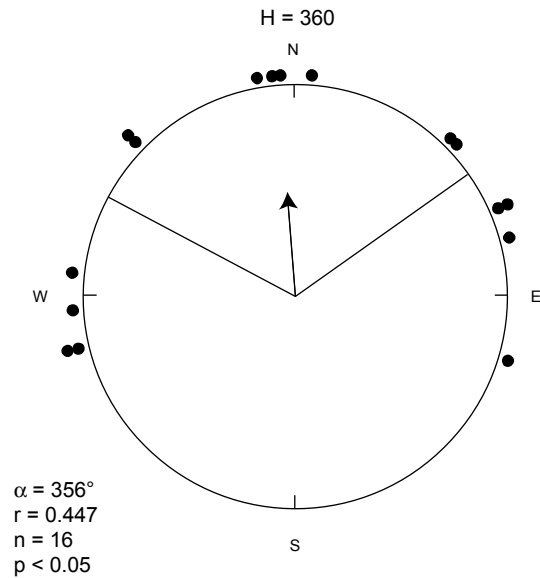


Fig 3. Orientation behaviour of displaced redwings and fieldfares in release tests after the cage experiments. All other details as in Fig. 2.

when displaced in totally different directions from it's nest site.

Most passerine species studied so far have a well-delimited reproduction territory, where they acquire a superb knowledge of the home range used e. g. for foraging or for defence from predators or weather fluctuations (Ioale and Benvenuti 1983). The hypothesis, that the adults have very much better homing performances than the sub-adults, was not confirmed in this study partly due to the limited number of test birds. Only three of the displaced birds were breeding for the first time in the study area. However, the first one homed very quickly, the second one was not observed later, and the third one which had not homed was found later at the area and may have returned soon after the displacement. It is probable that site attachment is taking place during the first autumn of birds' life and is usable in the subsequent breeding seasons (Löhrl 1959,

Sokolov et al. 1984). Moreover, true goal navigation has been performed only by individuals that had previously established a certain home area (Papi and Wallraff 1992). Some of the redwings are also faithful to their natal area (M.J.Huttunen, unpublished) though it is common for adult birds to show high site fidelity to previous breeding areas.

Two of the nests (one on both species) were destroyed by some predator during the observation period (see Table 1). Hence, a chance to demonstrate the return of the birds were lost. The behaviour of the adult birds during incubation and the fledging period varies among individuals, especially in fieldfares. For example, while redwings use to give warnings constantly, some of the fieldfares leave their nests silently without alarm and remain concealed until the danger has passed. Therefore, the homing success documented only by direct observation may include the source of uncertainty with fieldfares, though it is reliable method with redwings.

The pooled movement directions in funnel and release experiments by individual birds showed a significant preference for the home direction, even though the angular deviation appears to be rather large. The results from the initial or vanishing bearings in release tests are not always plausible, because of at least some influence by local topographical conditions to test birds (cf. Arnould-Taylor and Malewski 1955). Six redwings were considered as inactive in the funnel but still four of them were observed to have returned to their nest sites. Test birds nr. 2 and 5 (Table 1) who failed to show meaningful orientation in funnel experiments (r -values of 0.21 and 0.15, respectively) were neither well oriented when released, but still they returned in less than 24 hr. One test bird was seen jumping more in a vertical direction than against the wall from the bottom of the funnel. One of the three seemingly unhealthy or apathetic birds was observed at its nest site the following morning. Being placed in a cage means an extremely unnatural situation for wild birds.

The observed differences between test birds may reflect the ability of the individual bird to cope with this situation. Highly scattered or low activity might not mean bad orientation, but is more likely a response to stress and handling (R. Wiltschko, *in litt.*). Orientation cage tests are often used as the only test procedure in migration studies, but their results should be interpreted with caution. More reliable data are obtained if cage and release tests are used in succession.

The homing success was documented by direct observation, but still some of the birds that possibly had homed may have had a chance to avoid it. Concordantly, methods that use recapture of released birds consist probably some birds returned to the place where they had been banded, but not recaptured because they might have learned how to avoid being netted (Ioale and Benvenuti 1983).

The released birds usually landed to nearest trees or bushes after a short flight, although release sites were chosen as open as possible to minimize the tree effect. After short resting time some of the birds were seen heading into expected home direction. Observation of one test bird delineate well the homing behaviour at the release site: "*When released the test bird landed after a short flight on the ground, began to clean its feathers, looked around for a while, and finally after another short flight continued on its way jumping towards the 'home site' at the distance of 22.5 km. During the first 10 minutes the bird has moved on ca. 100 metres.*" It succeeded to reach its nest site in less than 3 days. The behaviour at the release point suggests that it possess sufficient information for homing. One possible explanation for homing might be that after the bird has determined the right direction it "migrates" in short steps as long as it reaches the familiar area.

Homing experiments performed with wild birds generally show that they are able to return to their nesting site after the displacement (Able 1980, Wiltschko 1992), but the timing differs between species. Some

species of sea birds and swallows have been reported to perform rapid homing flights from long distances (see Wiltschko 1992) which may not be surprising for active fliers that spend most of their time in the air. Longer homing flights might be interpreted as an indication that birds need a certain period of time at a given site to obtain necessary information that will enable them to return (Baker 1978).

In nearly all reported cases of homing by displaced passerine birds, the time interval between displacement/release and recovery at the home site has been so long that simple searching cannot be ruled out, suggesting no direct flight. Given the very slow rates (up to 12 days) at which wood thrushes (*Hylocichla mustelina*) travelled in the study of Able et al. (1984), they would have been unable to preclude the possibility of homing by random search if they had not been radio tracking the birds' movements (the distribution of directions was significantly oriented). This may indicate that displaced wild birds, besides homing, must be concerned about searching for food and performing other daily activities at an unfamiliar site. Moreover, because the physiological state of a migrant species is different outside the migration season, they are not prepared to undertake extended flights longer than used in their usual daily activities (R. Wiltschko, *in litt.*).

Is there some motivational factor unrelated to navigation in behaviour of the tested birds? How the displaced birds are motivated to return from the unknown environment towards the home site depends possibly on the stage of the breeding season that has been reached and the time period birds are kept confined before the release. For example, individuals displaced early in the breeding season may show a higher percentage of return than individuals displaced toward the end of the breeding season. Furthermore, if birds are kept long time in captivity their motivation to return may decrease. It is suggested that a higher proportion of the redwings and the fieldfares,

like birds in general, are motivated to return to their home site if displacement takes place at the right time in relation to the breeding season (see also Baker 1978, for "removal migration threshold").

In this study only male birds were displaced. Among passerine birds parental care investment to brooding is considered to be larger in the female, whereas investment to nest site defence is dominated by the male. No significant differences in homing ability between males and females of some passerine species to a wintering area were observed in the study of Ioale and Benvenuti (1983).

There was seemingly no difference between birds' headings under clear or overcast skies. It has to be reminded that the position of the sun may be clearly visible to the birds even under nearly total overcast, i.e. under the 7/8 cloud cover depending on the thickness of the cloud and the degree of polarization pattern which the birds may be able to perceive. Able et al. (1984) observed that wood thrushes moved in a series of short flights performed primarily at dawn before the sun was visible above the horizon, a behaviour that cannot be explained reasonably. However, it can be stated that neither a view of the sun at the time of release nor visual information during the displacement are necessary for the birds to orientate towards home.

The data in this study do not give much information on the orientational mechanisms used in homing. The only proof of homing ability was taken to be the documentation of the colour-ringed birds at their home territories. The obvious shortcoming of this method is that nothing is known of the route taken by the test birds after their release. There seemed not to be any difference in homing performances from various localities situated approx. within the same distance from home but in different directions.

How the birds then know the right direction for homing? After flying on its expected home direction for the adequate amount of time, the displaced bird would

arrive at the breeding area where it may use a map of landmarks and a map of gradients. The final step, *bicoordinate navigation*, is considered to be type III navigation. If the sun is visible birds could use it as a compass by deducing their position in relation to home from the sun's altitude and the rate of its change. In this case the sun would itself act as a positional and directional external reference (Papi and Wallraff 1992).

An alternative to the model of a learned map of gradients states that birds do not use site-specific information but instead they measure all angular accelerations during the outward journey based on inertial mechanisms, followed by a double integration to determine the home direction (Barlow 1964). Several clock-shift experiments regarding this, however, have not supported the hypothesis (cf. Keeton 1974b, Able 1980). Whether birds could accumulate information during the outward journey in displacement experiment and use it later in homing is not known, but cannot be totally excluded (Able 1980).

It is most likely that birds build up their map sense by learning landmarks. Birds have an advantage in that while flying or migrating they can get a wide view of the landscape below. For instance, at 1000 m altitude the range of vision is over 100 km where a bird could theoretically survey over 30 000 square kilometres (Alerstam 1990). However, birds do not normally fly that high; they do so only during migration. It is not clear whether birds could use this to head home from unknown areas or if they even have mechanisms to handle this kind of information while breeding or returning after displacement. Michener and Walcott (1966) found no definite reactions to landmarks in homing pigeons further than 5 miles from the loft. Moreover, could birds that live in very restricted territories showing high site fidelity be familiar with an area of many hundreds or thousands of square kilometres? However, almost nothing is known about local movements of single birds to confirm the familiar area. Data from some passerine

species suggest that postbreeding movements within the breeding area are rather limited (see Able et al. 1984, for references).

Examples which hold uncertainty concerning the familiar area of an individual or the possibility of direct sensory contact with home area should be assumed explicable without invoking true navigation until proved otherwise (Able 1980). However, many birds are obviously able to return home from distant sites by determining their home course, so the possibility of such an ability cannot be generally excluded (R. Wiltschko, *in litt.*).

The level of homing performances in different species is determined by navigational ability and motivational factors, such as those connected with inter-individual competition at the release site and the suitability of the release site environment, which all may affect each species in a different way (Ioale and Benvenuti 1983). Assumption is made that migrants returning to previously occupied nesting sites perform behaviour analogous to that of a homing pigeon, apart from previous training flights in pigeons. Homing pigeons have been selected since many generations by pigeon breeders for a strong urge to home and for flying speed (Wiltschko and Wiltschko 1978). Current homing ability in pigeons is a product of intensive training, behaviour not seen in the wild rock dove (*C. l. livia*). However, a comparison between the races indicates that difference lies in the flying ability and the motivation to return, not in the orientation capabilities (Papi and Wallraff 1992).

Redwings and fieldfares are medium-sized (weight ca. 65 g and 100 g, respectively), strong fliers that migrate several thousand km each year. A well developed navigational map of gradients for homing would be expected in displaced thrushes. Among the two species studied, the Redwing has high percentage of returns to its breeding area, so that, after allowing for the mortality rate of the species and the

observation efficiency it seems likely that nearly all the surviving individuals are able to return to the home site. Given (1) the data showing that redwings lack fidelity to the wintering sites, (2) the hypothesis that winter quarters of the species may depend on the prevailing winds, and (3) the ringing recoveries showing that one and the same redwing could in one year winter in west Europe and in the other winter close the Near East (Alerstam 1990), we can easily expect that the Redwing possess real navigational abilities for homing.

Although quite short displacements were used in this study, homing ability did not seem to decrease with increasing distance from home. Therefore, the possibility that homing is based on a search for the familiar site by systematic exploration of the region was excluded. Moreover, this study shows that the displaced birds have sense of the home direction even in cage conditions under overcast skies before any release has been made. The results from the funnel and release experiments suggest that the homing starts out first in a certain compass direction, and, if the course proves incorrect, the birds either stop flying or make a turn to a well-directed homeward course. Finally, it is assumed that, in general, captured redwings displaced and released in entirely unfamiliar areas could home by true navigation, which requires both directional and positional information.

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