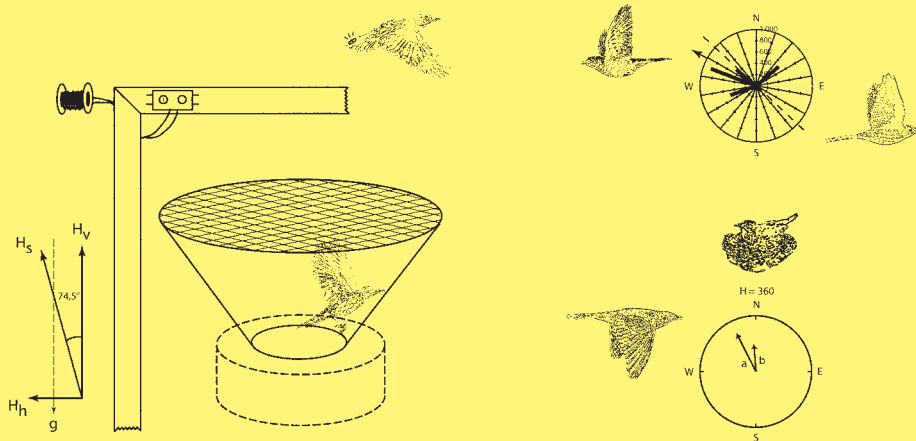


No:51

Migratory orientation and homing behaviour in thrushes (*Turdus* spp.)

by
Markku J. Huttunen



Joensuu
2007

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Migratory orientation
and homing behaviour
in thrushes (*Turdus* spp.)

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Biosciences of the University of Joensuu, for public criticism in the Auditorium M3 of the University, Yliopistokatu 7, on 30th November, 2007, at 12 noon

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Julkaisija Joensuun yliopisto, Biotieteiden tiedekunta
PL 111, 80101 Joensuu
Publisher University of Joensuu, Faculty of Biosciences
P.O.Box 111, FI-80101 Joensuu, Finland

Toimittaja FT
Editor Dr Heikki Simola

Jakelu Joensuun yliopiston kirjasto / Julkaisujen myynti
PL 107, 80101 Joensuu
puh. 013-251 2652, fax 013-251 2691
email: joepub@joensuu.fi

Distribution Joensuu University Library / Sales of publications
P.O.Box 107, FI-80101 Joensuu, Finland
tel. +358-13-251 2652, fax +358-13-251 2691
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Verkkojulkaisu <http://joypub.joensuu.fi/joypub/faculties.php?selF=11>
väitöskirjan yhteenveto-osa; toim. Markku A. Huttunen
and Tomi Rosti
ISBN 978-952-219-033-8 (PDF)

Internet version <http://joypub.joensuu.fi/joypub/faculties.php?selF=11>
summary of the dissertation; ed. by Markku A. Huttunen
and Tomi Rosti
ISBN 978-952-219-033-8 (PDF)

Sarjan edeltäjä Joensuun yliopiston Luonnontieteellisiä julkaisuja (vuoteen 1999)
Predecessor Univ. Joensuu, Publications in Sciences (discontinued 1999)

ISSN 1795-7257 (printed); ISSN 1457-2486 (PDF)
ISBN 978-952-219-032-1 (printed)

Joensuun Yliopistopaino
2007

Huttunen, Markku J.
Migratory orientation and homing behaviour in thrushes (*Turdus* spp.). – University of Joensuu, 2007, 96 pp.
University of Joensuu, PhD Dissertations in Biology, n:o 51, ISSN 1795-7257 (printed), ISSN 1457-2486 (PDF)

ISBN 978-952-219-032-1 (printed), ISBN 978-952-219-033-8 (PDF)

Keywords: magnetic field, orientation, migration, thrushes, *Turdus* spp., redwing, *Turdus iliacus*, fieldfare, *Turdus pilaris*, song thrush, *Turdus philomelos*, blackbird, *Turdus merula*, mistle thrush, *Turdus viscivorus*, migratory activity, cage experiments, release experiments, visible migration, ringing, recovery, homing, displacement, release, navigation

The ability to orient in relation to their surroundings is a fundamental property of the annual life cycle of birds. Orientation experiments have shown that migratory songbirds use the geomagnetic field, stars, the sun, and polarized light patterns to determine their migratory direction. However, the integration of these multiple directional cues is still poorly understood. Recent studies have shown that birds may transfer information from one compass system to another, for example from magnetic to celestial cues.

At present, numerous orientation cage experiments have been carried out with passerine bird species, but very few have so far been done with thrushes, and even fewer with *Turdus* thrushes. This is also congruent with the studies on homing experiments. In this thesis I investigated for the first time the orientation and homing behaviour of different species of *Turdus*, especially of redwings *T. iliacus*, fieldfares *T. pilaris* and song thrushes *T. philomelos*. The purpose was to find out whether the behaviour of thrushes differs in any way from that of other passerines exposed to similar tests.

The main methods used were orientation cage experiments followed by release tests and visual observation of migration with respect to ringing recoveries. To further investigate the orientation capabilities of thrushes, I studied homing behaviour in two thrush species by displacement experiments from the study area in eastern Finland during two breeding seasons.

In orientation cage experiments under clear and overcast sky conditions, both magnetic and visual cues turned out to be crucial for orientation in thrushes. The results demonstrate that thrushes use a magnetic compass during the autumn migratory period, and that their magnetic compass may function as an inclination compass. Release tests indicated that thrushes' celestial compass may be recalibrated on the basis of the magnetic field experienced in the cages during the sunset hour. In an examination of orientation performance under natural conditions, for most of the *Turdus* species the visible migration records did not correspond with ringing recoveries. In general, diurnally migrating thrushes seemed to orient towards the WNW–NW sector irrespective of wind direction. Several potential explanations are discussed in the text. In the displacement experiments 10 out of 16 birds were observed to return to their home territories, usually in less than 24 hours. The mean directions in cage and release experiments by individual birds showed a significant preference for the home direction.

It can be concluded that thrushes may use information from the sun and its associated polarized light patterns, and the earth's magnetic field to adjust their migratory directions for a given season. While the uniform direction of SW in autumn is found to be dominant on the basis of orientation experiments and ringing recoveries, the directional tendencies are more sophisticated as regards the total view of the migration period and are largely unknown in the case of nocturnal migration. It can also be suggested that captured birds displaced and released in entirely unfamiliar areas could home by true navigation. The findings in this thesis support the data on many other passerine species tested experimentally, and thrushes seem not to behave differently.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, referred to in the text by their Roman numerals I–IV.

- I Huttunen MJ (2007) Magnetic and sunset orientation in migratory thrushes (*Turdus* spp.). Submitted manuscript.
- II Huttunen MJ (2004) Orientation and migratory activity of song thrushes (*Turdus philomelos*) in northern Italy: cage and release experiments under over-cast conditions. *Ring* 26, 1: 23–39.
- III Huttunen MJ (2004) Autumn migration of thrushes over eastern Finland: a comparison of visible migration and ringing recovery patterns. *Ring & Migration* 22: 13–23.
- IV Huttunen MJ (2001) Homing behaviour of redwings (*Turdus iliacus*) and field-fares (*T. pilaris*). In: *Orientation and Navigation – Birds, Humans and Other Animals*, P7: 1–10. Royal Institute of Navigation, Oxford.

Publications II–IV are reprinted with permission from the publishers. Some unpublished results are also presented.

1 INTRODUCTION

1.1 Thrushes

Thrushes are members of a cosmopolitan group of medium-sized songbirds. They are placed taxonomically in the sub-family Turdinae of the Muscicapidae, the latter being a family of the sub-order of the Oscines, also including Old World warblers and flycatchers (Sibley & Ahlquist 1990). The family Muscicapidae is composed of just over three hundred species, including the ‘true’ or typical thrushes (162 species), e.g. *Turdus* (65), *Zoothera* (36), *Monticola* (13) and *Catharus* (12) thrushes, as well as many small, so-called chat-like thrushes such as the robin (*Erithacus rubecula*), the redstart (*Phoenicurus phoenicurus*), the wheatear (*Oenanthe oenanthe*) and the stonechat (*Saxicola torquata*) (Sibley & Monroe 1990). The genus *Turdus* consists of 65 species, of which about one third can be found in the Palaearctic region (Clement & Hathway 2000). While many species are monotypic, some have large geographical variation, e.g. the island thrush (*T. poliocephalus*), which is widely scattered across a large number of islands from Indonesia to the SW Pacific, splitting into 52 races. Thrushes as a subfamily are naturally absent only from New Zealand and the polar regions.

Several of the *Turdus* and *Catharus* thrushes, together with some of the *Monticola* and *Zoothera* thrushes, are long-distance migrants covering up to 10,000 km, whilst others make migrations of limited duration and distance (medium- or short-distance migrants, partial residents) (Clement & Hathway 2000). The thrushes of the genus *Turdus* present a varied and interesting series of migratory patterns and behaviour, as demonstrated by the different species

studied (see e.g. Ashmole 1962, Simms 1978). Some individuals may change their status from being migrant one year to non-migrant the next.

In most of northern Europe all species are primarily migratory, and only a minor proportion remain there throughout the winter. There is a general tendency to migrate on a broad front to the south-west in autumn (Simms 1978). The wintering areas of all the European *Turdus* species overlap to a considerable extent, at least for part of the year. For example, in SW France and N Spain it is possible to find all six species wintering together (Ashmole 1962).

Both the redwing (*T. iliacus*) and the fieldfare (*T. pilaris*) are Palaearctic species. The breeding distribution of the species is roughly similar, lying mainly from northern Eurasia to Russia and Siberia (Clement & Hathway 2000). The redwing is completely migratory and Fennoscandian birds disperse widely for the winter, reaching the British Isles, south to the Mediterranean, North Africa and east up to Asia Minor. Fieldfares are mainly migratory but their movements are often variable, sometimes reaching ‘invasion’ levels, which are subject to local weather conditions. Some birds winter annually in the northern areas, but most of them move south to the British Isles, SW and S Europe.

The song thrush (*T. philomelos*) – perhaps the most familiar thrush in western Europe – breeds over a wide area of Eurasia (Simms 1978). In the northern part of its range the song thrush is a true migrant, moving southward to winter in the Mediterranean, N Africa and the Middle East regions. The mistle thrush (*T. viscivorus*) has a slightly similar breeding distribution to that of the song thrush, but it reaches further south to the Mediterranean area and N Africa (Clement & Hathway 2000). Most of the mistle thrushes in northern and central Europe migrate for the winter to SW

or S Europe.

Northern and central European blackbirds (*T. merula*) are partial migrants, the proportion of migrating individuals probably increasing from south to north and from west to east (Simms 1978). Birds from the northern population mostly spend the winter in western Europe. The numbers of blackbirds continually spreading northwards and wintering in northern Europe or arriving earlier has been increasing in recent years. This change in migration is probably connected with the recent amelioration of the climate, especially the milder winters (e.g. Burton 1995, Tøttrup et al. 2006). The ring ouzel (*T. torquatus*) has a more restricted breeding range, being a species of the western Palaearctic with a fragmented boreal-alpine distribution (Clement & Hathway 2000). Northern ring ouzels winter mainly in SW Europe and N Africa.

1.2 Mechanisms of orientation and navigation

The major cues that birds use for migratory orientation are landmarks, the sun and its associated patterns, the stars, and the geomagnetic field. Most of these cues are used widely among animal groups, both vertebrates and invertebrates (Able 1980, Horváth & Varjú 2004, Bingman & Cheng 2005, Wiltschko & Wiltschko 2005).

The use of *landmarks* is often considered to be the most primitive means of orientation (Wiltschko & Wiltschko 1978). Landmarks are utilized by birds, e.g. pigeons (*Columba livia*) and many diurnal migrants that also use other cues for orientation. In the early 1950s, Gustav Kramer discovered that *the sun* is the directional cue used by starlings (*Sturnus vulgaris*) during daytime (Kramer 1951). Associated with the sun, the E-vector of *polarized light* can be

used as an axis of orientation, but also as a reference to determine the position of the sun (e.g. sunset direction, partly cloudy sky) when the sun is not directly visible (Able 1982, Moore & Phillips 1988, Helbig 1991). Among animals, *stellar* orientation has been demonstrated only in birds, and it appears that the use of star configurations as directional cues is learned. These are used in combination with the rotation of the night sky as the polar direction, which is an innate phenomenon (Wiltschko et al. 1987).

The *geomagnetic field* provides both a compass (magnetic vector, for directional information) and a map (total intensity/inclination, indicating position) for birds' orientation. The birds apparently do not use the polarity of the magnetic field to determine directions. Instead, the horizontal field component provides the birds with a pole-equator axis (poleward and equatorward directions), where the pole-end is defined by the inclination of the magnetic field (Wiltschko & Wiltschko 1972, 1996). During ontogeny, celestial rotation appears to be a dominant reference system, but during migration, celestial cues appear to be controlled by the geomagnetic field (Wiltschko & Wiltschko 1990, Wiltschko et al. 1998, but see also Able & Able 1996).

For magnetoreception in birds, two hypotheses have been presented: one proposing magnetite-based mechanisms, the other suggesting radical pair processes involving photopigments (Johnsen & Lohmann 2005). Recent findings suggest that a radical pair mechanism located in the right eye provides directional information, while a magnetite-based mechanism located in the upper beak records magnetic intensity, thus providing positional information (Wiltschko & Wiltschko 2006).

Besides the cues mentioned above there are several other cues that have

been suggested as possible sources of directional information, including wind patterns, moonlight, odours (olfactory), the Coriolis effect, gravity and infrasound (e.g. Richardson 1990, Berthold 1996, Wallraff 2004).

In this study, bird orientation was examined in two behavioural contexts: (1) migration, in a specific direction (articles I, II and III), and (2) homing, including navigation to the home area (article IV). Conceptual frameworks in terminology used in studies of orientation and navigation have varied markedly during the past decades (see Able 2000, Wiltschko & Wiltschko 2003). First, one widely used definition of *migration* is, from Dingle (1980), “specialized behavior especially evolved for the displacement of the individual in space”. Orientation refers here to directed movement and is synonymous with *compass orientation*, i.e., a bird’s ability to head in a given compass direction without reference to landmarks. *Vector navigation* is used by young birds of many species on their first migration, in which they process inherited information about the direction and distance to the population-specific wintering area (contrary to the *goal-directed navigation* of experienced adults). Nevertheless, orientation mechanisms may differ between species and also within species and individuals (Emlen & Demong 1978, Sandberg et al. 1988a, Able 1990, Alerstam 1990).

In the homing process, a bird attempting to return to its nest following displacement might employ some kind of map or positioning system to fix its location relative to the familiar home area. To explain homing from distant, unfamiliar sites, I use the map and compass model of *true navigation* (e.g. Kramer 1953, 1957, Keeton 1974). This map and compass model of homing navigation can be described as a two-step process. In the first step, a displaced bird estimates its position in

space relative to the homeward direction as a compass course, e.g. “I am south of home”. In the second step, this compass is employed to identify the actual homeward direction, e.g. “that way is north”. *Map-based navigation* denotes the situation in which a bird determines its spatial position relative to the home area, or at least the direction towards home, solely on the basis of information available at the distant release site. *Gradient maps* are thought to be based on at least two gradients of some physical substrate that vary systematically over sufficiently large areas, and that a bird could learn these gradients within the familiar area (e.g. Wallraff 1991).

1.3 The objective of the study

Migratory behaviour and movements of thrushes have been studied worldwide by a variety of methods, including ringing (Ashmole 1962, Andreotti et al. 1999, 2001, Main 2002, Milwright 2002), visual, aural and radar observation (Graber & Cochran 1960, Myres 1964, Alerstam 1975, 1976, Åkesson 1993), radiotelemetry (Cochran et al. 1967, Able et al. 1984, Cochran & Kjos 1985, Cochran 1987), and cage experiments (Yong & Moore 1993, Busse 1995, Sandberg et al. 2002, Cochran et al. 2004). At present numerous orientation cage experiments are carried out with many passerine bird species, but very few have been done so far with thrushes and even fewer with *Turdus* thrushes. This is also congruent with the studies on homing experiments (e.g. Wiltschko 1992).

In this thesis I shall explore for the first time the orientation and homing behaviour of different species of *Turdus*, especially of redwings, fieldfares and song thrushes. The main methods used were orientation cage experiments followed by release experiments, and visual

observation of migration. Based on variable migratory patterns, it is suggested that thrushes in general show a lower bias (i.e. more scatter) to the direction ratio of migration than long-distance migrants such as small passerines. The objective of this study was to find out whether the behaviour of thrushes differs in any way from that of other passerines exposed to similar orientation tests.

2 MATERIALS AND METHODS

2.1 Study areas

In article I, the test birds were captured at Höytiäinen bird observatory (ringing station) ($62^{\circ} 37'N$, $29^{\circ} 41'E$) in eastern Finland with mist nets during the autumn (from 15 September to 15 October) migration periods of 1999–2001 (Fig. 1). All the test birds were caught during the morning or evening hours and spent the time before orientation tests in individual cages in a room with windows. Orientation cage tests and release experiments were performed on the roof of the Department of Biology building at University of Joensuu, which is situated 3 km ESE of the capture site.

In article II, the test birds were captured with mist nets at the Arosio Bird Observatory, Lombardia in northern Italy ($45^{\circ} 43'N$, $9^{\circ} 12'E$) from 13 to 19 October 2000 (Fig. 1). All test birds were caught during the morning hours and were kept indoors in individual cages before the same evening's tests. Cage and release experiments were executed on the roof of the observatory main building, on the top of a low hill.

In article III, visible migration directions for nearly 28,000 thrushes were observed by a number of ornithologists in eastern Finland from 1996 to 2001. Observations were reported from the

nine municipal areas: Ilomantsi, Joensuu, Juuka, Kesälahti, Kiihtelysvaara, Kitee, Kontiolahti, Lieksa and Rääkkylä. Observations at migration watchpoints were generally made between 06.00 h and 15.00 h from 1 September to 31 October each year. In addition to this,



Figure 1 Habitats where the experimental birds were caught with mist-nets. Breeding (IV) and stopover (I) habitat at Noljakka, Joensuu, in eastern Finland (upper and middle photos by Pentti Zetterberg), and stopover (II) habitat around the Arosio bird observatory in northern Italy (lower photo by Fondazione Antonio Bana).

ringing recovery data for five species of thrushes were supplied by the Finnish Ringing Centre. Data were available for nearly 4,500 foreign recoveries of thrushes ringed in Finland during the period 1913 to 2001.

In article IV, the test birds were captured with mist nets in their territories in Noljaakka, Joensuu (62° 37'N, 29° 41'E) in eastern Finland during the summers of 1999 and 2000 (Fig. 1). These birds were displaced over distances of 6 to 22.5 km in several directions from their nesting territories. The birds were normally carried to the release sites within two hours of their capture. Displacement took place by car and the birds were kept in cotton bags during the displacement. Different release sites outside Joensuu were situated in the municipal areas of Kiihtelysvaara, Kontiolahti, Liperi and Pyhäselkä. Open sites were chosen as release sites to minimize the influence of trees or bushes on the birds' orientation.

2.2 Orientation cage and release experiments

The orientation cage technique is based on the fact that migratory birds show restlessness when confined during migration periods (Kramer 1949, Emlen & Emlen 1966, Sandberg 1990). In these conditions caged birds will repeatedly jump in their intended migratory direction. The direction of these hops and scratch marks can be recorded by registration apparatus under different environmental conditions. The orientation behaviour of birds can be compared, for example, under clear and overcast skies both in daytime and at night when different environmental cues are accessible. Test conditions can also be experimentally arranged so that birds will have conflicting information from various environmental sources.

The funnel cage design in orientation tests has undergone major development during the past decades, from a simple inkpapad-paper version (Emlen & Emlen 1966) to a modern computer connected system, which allows the sensitivity of the wall sectors to be calibrated to the size of the bird under study (e.g. Bäckman 2002). I have used a simple procedure, started by Rabøl (1979) and Beck & Wiltschko (1981) (articles I, II, IV), of lining the cage walls with typewriter correction paper, as many researchers still do in orientation studies.

The modified cage design of Sandberg & Gudmundsson (1996) has been used in the studies described in articles I, II and IV. In article I, the use of magnetic and sunset cues by three thrush species was studied in orientation cage experiments under clear and overcast sky conditions. The availability of magnetic cues was manipulated with the help of magnetic coils, by deflecting or inverting the normal magnetic field (for technical details, see I). According to preliminary expectations, it was predicted that the test birds would use directional information from the geomagnetic field or the sunset sky to select an appropriate compass direction for their migratory journeys. To do this, they would need to respond in a consistent way to experimental deflections of the magnetic field (Fig. 2), or to adjust their preferred direction according to the azimuth of the setting sun. Most of the experiments were conducted under natural sky conditions, either clear or overcast, but sometimes the visual cues were controlled with the help of Plexiglas, to create an artificial overcast. No restriction screens were used during the experiments, and there was thus a view of the clear horizon or sunset sky, when available.

Plexiglas sheets were measured at the Department of Physics, University

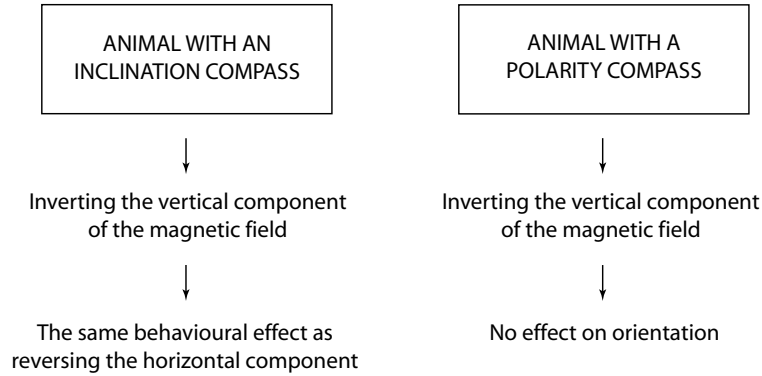


Figure 2 The effect of inverting the vertical component of the magnetic field on test animals possessing either an inclination compass or a polarity compass.

of Joensuu, using three different angles of light geometry: (1) 0° , (2) 45° TE- (transverse electric) and (3) 45° TM- (transverse magnetic) polarization. These translucent plastic sheets (thickness 3 mm) permitted 33% of the diffuse natural light to pass through, but only 4% of the incoming polarized light. For example, if the diffuse natural light is polarized to 5%, the test bird would see it polarized perhaps only to 0.2% (Dept. of Physics, Univ. of Joensuu; I).

The test birds were placed in orientation cages during the time of sunset. After one hour registration in the cages, the birds were released with small lightsticks attached to their tails (see methods in I and II) to be able to observe their flight directions after dark. The released birds are usually considered to have successfully taken off on their migratory flights if they gain considerable height and disappear from view without descending or landing (Ottosson et al. 1990, Sandberg et al. 1991).

Article II deals with the orientation behaviour and migratory activity of test birds under overcast conditions close to the wintering area. No mag-

netic or visual manipulations were used in this study; instead I investigated how thrushes would orient at different time periods, namely before, during and after the sunset. To find out how the amount of stored fat possibly influences the choice of direction or the birds' activity, the visually estimated fat classes were compared for the test birds used in orientation cage experiments (I, II).

Orientation studies yield data points that are distributed on a circle. These data were analyzed by circular statistics, the details of which are given in Mardia (1972) and Batschelet (1981). In all studies, each individual was tested only once under a given experimental condition. In cage tests, the number of scratches left on the typewriter correction paper was the criterion for activity (Table 1). For evaluation, the funnel paper was divided into 24 equal 15° sectors and the number of scratches was counted for each bird. In release tests, differences in the take-off and vanishing times of experimental birds were investigated. Registrations from the orientation cages and the vanishing bearings of released thrushes were sub-

Table 1 Summary of the number of thrushes captured at the study sites and tested in orientation cage and release experiments during the test periods (I, II, IV).

	Active	Inactive	Disoriented*	Landed	Total (n)
Cage tests	144	24	21	–	189
Release tests	130	–	–	62	192

* Unclearly oriented, but otherwise active test birds

jected to vector calculation, yielding a mean heading for each individual and test. The mean headings obtained under each test conditions were then pooled to calculate sample mean vectors and axes of orientation according to Batschelet (1981).

2.3 Migratory orientation at departure

The majority of passerine birds, including thrushes, migrate at night. However, they may make some of their movements during the daytime, for example, by continuing their nocturnal migration after dawn (Myres 1964, Alerstam 1975). In article III, I investigated the directional behaviour of diurnally migrating thrushes in eastern Finland, with respect to the ringing recovery locations of Finnish-ringed thrushes. I was able to collect considerable data on the migratory movements of thrushes for comparisons, thanks to extensive field observations by many ornithologists in eastern Finland during the six years of the study. Data on wind conditions for the same period were obtained from the Finnish Meteorological Institute.

Besides the main wintering areas, recoveries of ringed thrushes have also shown different degrees of fidelity to these areas (e.g. Ashmole 1962, Andreotti et al. 2001), but how widespread this behaviour might be still remains unresolved. For ringing recov-

ery comparisons in this study, Finland was geographically divided into six regions according to ringing site, and additionally, into two longitudinal areas. The selection of ringing recoveries was mainly based on the following criteria: all foreign recoveries, ringed in Finland and recovered at least 50 km from the ringing site were included.

Ringing recoveries and flight directions of migrating thrushes were subjected to vector calculation, yielding a mean heading for each species (Batschelet 1981). In circular statistics, mean vectors are relative to the radius (r) or diameter (r_2) of the circle and are relative to 1.0, so that a vector of zero would mean a totally random circular distribution, 0.5 would suggest a more concentrated mean orientation, and 1.0 would mean that all the birds orient in exactly the same direction. These were used to analyse whether the birds' mean visible migration direction differed from the mean direction of ringing recoveries, according to Batschelet (1981).

2.4 Homing experiments

To further investigate the orientation capabilities of thrushes, I studied homing behaviour in two thrush species from the study area in eastern Finland by displacement experiments during two breeding seasons (IV). The test birds were measured, aged and colour-ringed (read-rings) for individual iden-

tification. After having displaced breeding male thrushes to various distances and directions from their nest sites, I first conducted orientation cage experiments to find out whether the birds could still orient properly towards their home sites. In these cases, the birds were placed in circular cages for only 20 minutes (cf. one hour registration, I and II). Then, immediately after the cage tests, I released the birds at test sites, which were assumed to have been completely unknown to them, given their strong fidelity to the previous year's breeding sites (Huttunen, *unpublished data*). During the release tests, the birds' behaviour and directions were observed carefully. The cage and release tests were made under various open sky conditions (clear, nearly overcast and total overcast).

The main questions addressed in the homing study were: (1) how many of the displaced birds were documented as having returned to their home territories, (2) did they orient in the homeward direction after their release, and (3) how long did it take for the birds to home from these relatively short displacements? Then, suggestions were made as to whether they homed by systematic search, in a given compass direction, or by true navigation?

3 RESULTS AND DISCUSSION

3.1 Magnetic orientation in thrushes (*Turdus* spp.): evidence of a compass mechanism use in orientation tests

In contrast to the technical compass used by humans, the avian magnetic compass works as an 'inclination compass', based on the inclination of the Earth's magnetic field lines rather than their polarity (Wiltschko & Wiltschko 1996). This means that birds do not distinguish

between magnetic north and south as indicated by polarity, but between poleward and equatorward, along the axial course of the magnetic field lines and their inclination in space.

In orientation cage experiments, under clear and overcast sky conditions, both magnetic and visual cues turned out to be crucial for orientation in thrushes (Fig. 3; I). Deflection of the horizontal or vertical component of the magnetic field by different arrangement of magnetic coils, however, sometimes resulted in an unclear mean orientation, not corresponding to the expected shift.

In the control experiments, with no manipulations under clear sky conditions, redwings oriented towards SW, which is the appropriate migratory direction for the season, according to ringing recovery data (Ashmole 1962; III). The results from the reversed vertical magnetic field under overcast skies showed that redwings can use an inclination compass during their autumn migration period. Song thrushes showed unexplained axial orientation during control tests, but responded consistently to the CCW-shifted horizontal magnetic field. Fieldfares responded to this shift only to some a degree. Unfortunately, given the low number of test birds within the test conditions, the interpretation of the results is difficult. However, there was some indication that song thrushes and fieldfares respond to magnetic field deflections, especially under overcast conditions, even though the effect of skylight polarization patterns on orientation cannot be totally excluded (Fig. 2 in I). When some of the test birds were deprived of access to most visual cues, by placing diffusing Plexiglas on top of the cages, the birds oriented either randomly or along the approximate axis of the e-vector polarization (Fig. 3 in I). This suggests that polarization cues may override magnetic cues in the case of a cue-conflict situation.

The results for the test birds exposed to inclination angles they do not normally encounter, i.e., to a field inclination found well within the southern hemisphere of the Earth, demonstrate that redwings can distinguish between fields with different inclination angles. There is a plenty of evidence confirming that birds use the inclination of the geomagnetic field for their orientation (see Wiltschko & Wiltschko 1996). It has been demonstrated with hand-raised

birds that orientation capability develops in the absence of any experience of the natural sky, on the basis of magnetic directions (Able & Able 1990a), while other experiments indicate development of the visual orientation mechanism independent of any influence from the magnetic field (Able & Able 1997). Weindler et al. (1996) have indicated the significance of magnetic information for the development of migratory directions with respect to stellar orientation. Experiments with pied flycatchers (*Ficedula hypoleuca*) seem to indicate an interaction between magnetic field and sunset point that might take place as an imprinting-like process by the end of the nestling period (Alerstam & Högstedt 1983) and that seems to be important for the birds' orientation during migratory period (Åkesson & Bäckman 1999).

The results of this study indicate that thrushes are also dependent on visual cues for their orientation. The increase in scatter observed in redwing test groups under overcast skies indicates a certain lack of clarity caused by insufficient directional information from celestial cues. Thus, the ability or the motivation to orient properly under overcast sky conditions seems to be strongly reduced, as has been observed in several other studies (Katz 1985, Åkesson 1993, 1994, Åkesson & Bäckman 1999, Åkesson et al. 2001). If the findings in this study apply to thrushes, the larger dispersion around the mean under overcast skies could be mainly attributable to a weaker ability or motivation for orientation. However, before questioning the orientation capabilities of thrushes, it has to be remembered that their migration occurs regularly under overcast skies (Graber & Cochran 1960, Cochran et al. 1967, Alerstam 1976, Cochran & Kjos 1985, Cochran 1987; Huttunen, *personal observations*). Several radio-telemetric studies (see references above) have

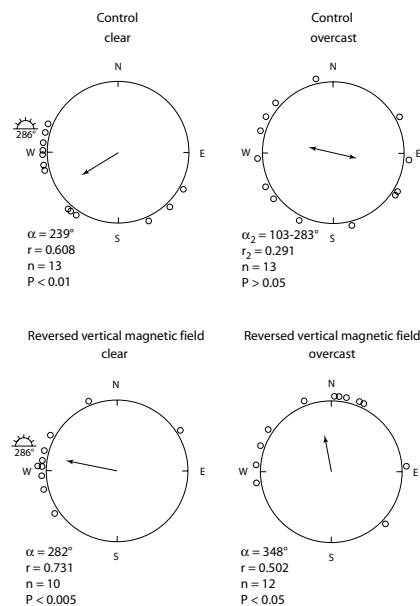


Figure 3 Directional choices of redwings in control and vertical magnetic tests under autumn clear and overcast skies. Each small circle in the circular diagram represents the direction of one individual. The arrows are sample mean vectors (α) or axes (α_2), and their length is proportional to the unit radius of the circle ($= 1$). The mean position of the setting sun 40 min after sunset (i.e. in the middle of the test period) is indicated outside the circular diagrams of the clear sky tests. For further details of test conditions, see I.

shown that the thrushes are not disoriented during overcast or even rainy conditions, but that they probably require at least partly clear skies during the day or evening before departure.

In many cage tests, birds displayed activity towards the direction of sunset (I, II). Why they did this is unclear, but usually it indicates escape behaviour towards the brightest part of the autumn sky. One might argue that in some cases, e.g. phototaxis, birds' behaviour may have nothing to do with orientation. It is worth noting that these individuals are not disoriented in any way, given the vector lengths yielded in cage tests, i.e. individual variability in response in such a heterogeneous group of test birds must be taken into consideration. The possibility that sunset factors provide directional information for nocturnal migrants was first suggested by Vleugel (1953). The birds' ability to use sun-related cues for twilight orientation was later confirmed by many other authors (Moore 1985, 1986, Moore & Phillips 1988, Able & Able 1990b, Helbig 1991, Åkesson & Bäckman 1999; but see also Katz 1985, Sandberg 1988, Sandberg et al. 1988b). As the sun sets in the west, the band of maximal polarization and the e-vector of linearly polarized light are oriented north to south, which may well play an important role in birds' orientation.

Some test birds had two 'mean' directions in the funnel paper (I). One possible explanation might be that the birds first chose a direction towards the west/sunset point, and later changed to magnetic orientation when sunset cues were no longer useful. Because both lean and fat birds were used in the orientation experiments, there was no guarantee that the test birds would be motivated to continue migration in a seasonally appropriate direction. On the other hand, in inland areas, all birds do not carry high levels of fat loads before

departure (Höytiäinen bird observatory, *unpublished ringing data*).

Is there a population-level bias toward choosing routes to wintering areas? It is possible that the birds caught in different years may have included individuals from different migratory populations with distinct breeding areas (especially redwings), which could explain the high variation in their intended directions to different wintering areas and a rather large scatter during the tests.

Bimodal orientation has been observed for different species of nocturnal bird migrants in orientation cage experiments (e.g. Sandberg et al. 1988b, Able & Able 1990a, 1993, Sandberg 1994). The reason for this axial or bimodal orientation is suggested to be an innate mechanism (Sandberg et al. 1988b, Sandberg 1994). Further, recent studies have suggested that there might be a link between photoreception and magnetoreception in the animal sensory system, since birds have been observed to respond to magnetic cues that depend on the wavelength of light (Ritz et al. 2002, Wiltschko et al. 2002, for review see Wiltschko & Wiltschko 2002). Tests with robins imply that magnetoreception for compass orientation is strongly lateralized, with dominance of the right eye/left brain hemisphere (birds tested in orientation cages oriented well when using their right eye only; Wiltschko et al. 2002). For future investigations, one possible outcome might be to repeat the polarization detection tests by Kreithen & Keeton (1974; see also Coemans et al. 1990, Horváth & Varjú 2004), for redwings and/or song thrushes.

The test birds were caught either during the first hours in the morning or in the evening, but their status – whether they were ready for take off or still preparing – was not clear. The other problem around experimentation was that the origin of the birds caught during

migration was unknown – whether they were local breeders (some of them certainly were) or migrants from more distant eastern or north-eastern areas (e.g. Russia). Interestingly, according to some studies, birds may need to move away from their breeding ground at least some hundreds of kilometres before they can respond appropriately in most of the cue conflict experiments (R. Wiltschko, *in litt.*).

Basically, there is a notable difference between the cage and release conditions at twilight. During the cage experiments, the only visual cues available are sunset and polarized light cues. During the release tests, these cues vanish from the birds' sight and there are only some stars available at that moment. This situation may cause some of the discrepancy between the directions observed in cage and release experiments. Supposing that the autumn orientation of nocturnal migrants would be either 1) relative to the sunset (start and keep flying when the sunlight is on the right), or 2) relative to the e-vector of polarized light (keep flying parallel to the axis of polarization, with the sunlight on the right), these cues would only enable birds to select their migratory direction and initiate migratory flight, but would not help them to maintain it later in the night.

The term 'calibration' generally describes the process by which directional information is transferred from one cue system to another, for example from magnetic to celestial cues. If the test birds calibrated their compasses after sunset, they would consider the magnetic field manipulation experienced during the test hour, and select their initial orientation on the basis of the visual/celestial cues available at release. As this was the case, when I released the thrushes during the magnetic test conditions, they vanished in a direction that indicated that their celestial compass

had been recalibrated on the basis of the magnetic field they had just experienced in the cages during the sunset hour (Fig. 4). It would be interesting to find out what (celestial) compass mechanism birds can use for orientation under total overcast conditions once the migratory direction has been determined during twilight. Cochran et al. (2004) showed that *Catharus* thrushes exposed to the altered magnetic field flew in the wrong direction according to their recalibrated magnetic compass, but on subsequent nights, they headed in the right direction. This suggests that thrushes orient with a magnetic compass calibrated, perhaps on a daily basis, from twilight cues.

It has been demonstrated that celestial rotation alone, either by rotating stars at night or by the polarized light pattern during the day, may provide a

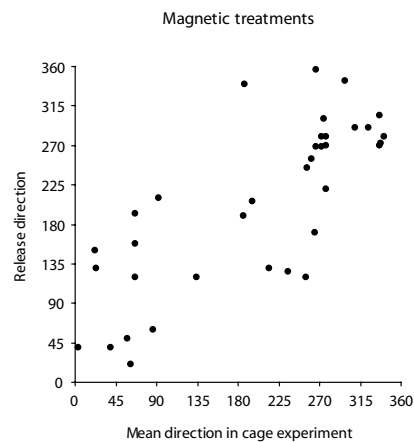


Figure 4 Comparison of directions for test birds that were active in both cage and release experiments: release direction in relation to mean direction in cage tests (in degrees) for redwings ($n = 28$), song thrushes ($n = 4$), fieldfares ($n = 2$) and blackbirds ($n = 2$) tested in two magnetic experimental conditions ($r = 0.775$, $P < 0.003$, $n = 36$).

reference direction away from its centre, i.e., southwards (Wiltschko et al. 1998, see also Muheim et al. 2006). Celestial rotation provides possibly independent, stable information about geographical directions that is common to both the day and the night sky. However, the finally selected directions towards specific wintering areas can be regulated only with respect to the magnetic field. In this study, short-term calibration seemed to occur between compass systems among redwings. While there are few data for other thrush species, this does not suggest any interspecific differences in the calibration process (Fig. 4).

3.2 Influence of timing, weather and body condition on the orientation and migratory activity of thrushes (*Turdus* spp.)

There were major differences in orientation and migratory activity between the song thrushes tested at different time periods during the evening and early night (Fig. 5; II). In pre-sunset tests, unmanipulated song thrushes were reluctant to orient themselves, showing a random distribution in cage experiments. They showed significant orientation in an appropriate migration direction only in sunset and post-sunset tests, as was expected. As the tests mostly took place in overcast situations, the brightest part of the sky overhead or the polarization patterns probably indicated the sunset direction to the sunset test birds. Later, during the post-sunset tests, i.e., 1–2 h after sunset, in visually cueless situations, thrushes perhaps followed their innate magnetic compass. The speculative use of the distant landmark cues during the cage experiments were not supported by the release headings, which were oriented in the seasonally correct migratory directions (II). The reason for the differences in direc-

tion between cage experiments and the following releases remains unsolved.

The appearance of a clear starry sky may increase the activation level of test birds in orientation cages, as observed in the test arena (I). The next moment, when the sky turns cloudy again, their activity will drop suddenly. This behaviour may be witnessed even with birds carrying relatively large fat stores. A

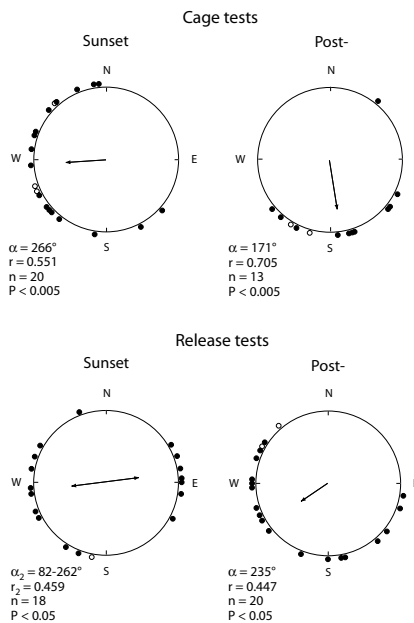


Figure 5 The orientation of unmanipulated song thrushes, captured at Arosio, in cage and release experiments tested during the sunset and post-sunset periods. Mean vectors are drawn relative to the radius or diameter of the circle = 1. Mean directions (α and α_2), lengths of vectors (r and r_2), and probability levels (P , based on number of individuals) according to the Rayleigh test were calculated using standard procedures given in Batschelet (1981). Filled dots denote overcast sky tests and open dots represent clear sky tests. For further details of test conditions, see II.

similar increase in activity was observed at the beginning of vertical magnetic tests (I), possibly due to the birds' lack of experience and the strange geomagnetic field.

In papers I and II it was possible to investigate how the amount of stored fat influences the orientation and activity of test birds. The orientation of the test birds carrying small fat reserves were compared to those birds with larger fat stores. The results showed no consistent differences between the fat categories. In contrast to many other studies, birds that had relatively small fat reserves displayed either more activity in orientation cages (II; Fig. 6) or more accuracy in orientation (Table 1 in I) than those birds with larger fat stores. However,

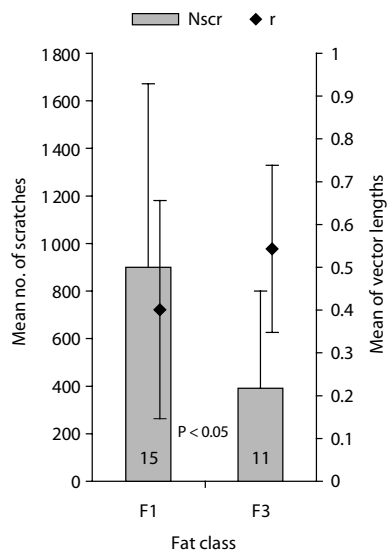


Figure 6 The mean number of scratches (Nscr – grey bars) and the mean of vector lengths (r – black diamonds) in two fat classes. The numbers in bars show the sample sizes. The p-value refers to the significance of the difference between the mean number of scratches in the fat classes. For further details, see II.

lean test birds were more likely to show large variation in their directions, and at release, to perform landing flights. The rather small number of test birds in different fat groups did not allow for comparison of directional choices. The only reported differences were with song thrushes tested during the sunset period, between the fat classes F1, F2 and F3 (II). In general, birds that showed fair activity in the expected migratory direction could not be traced or categorised on the basis of fat class. High activity displayed by lean birds may not reflect migratory restlessness at all and is more likely to be associated with foraging activity or escape behaviour (Bäckman 2002).

In article II song thrushes in northern Italy were only in the lower fat classes, which seem to be linked to the remaining migratory distance for the autumn (Table 2). On the other hand, in this stopover area, birds still have many refuelling opportunities before continuing their migration to the south-west. Since the species is totally migratory in the capture area, it was suggested that the birds were heading further to common wintering grounds.

Results of orientation cage and release experiments often show a large variation between individual test birds. It has to be remembered that the birds' choice of direction might be influenced

Table 2 Mean weight (\pm s.d.) of active cage test birds ($n = 43$) between the fat classes F1, F2 and F3. The fat classes quantified on a six-point scale (F0–F5) were according to Busse (1970).

Fat class	Mean \pm s.d. (g)	n
F1	63.8 \pm 3.6	11
F2	67.2 \pm 3.5	24
F3	69.1 \pm 4.4	8

by fat reserves, age and experience, as well as major geographical factors (e.g. Sandberg & Moore 1996). In addition, each experimental study may have its own disadvantages in that more data would probably lead to significant or otherwise acceptable distributions. It is also supposed that the birds exposed to cages are prone to relatively high stress, which restricts the repeated use of individual birds within or between different test conditions.

One important though inconsistent finding was related to the birds' jumping activity in the funnel cages. A significant negative correlation between migratory activity (expressed as number of scratches) and orientation (mean vector length) was observed for song thrushes in all the cage tests (Fig. 5 in II). Again, testing for this relationship within each of the test groups showed non-significant results, but all suggested the same negative trend. Generally, the more active the birds were, the more unclear their orientation would be (II; see Marchetti & Baldaccini 2003). Compared to song thrush tests in Italy, all the other tests performed with thrushes in eastern Finland showed a positive correlation between migratory activity and orientation accuracy, but only very slightly (I). Considering the observed inconsistency between directional selections, activity level and fuel loads in thrushes, thorough studies are needed to clarify these factors.

3.3 Why do thrushes (*Turdus* spp.) head WNW during the autumn migration?

Diurnally migrating thrushes showed no correlation between the wind direction and the orientation of birds (III). Instead, they seemed to migrate most often towards the WNW–NW sector, irrespective of wind direction – only

one of the many surprises produced by the project (Fig. 7). Again, the only species in which the visible migration records seemed to correspond well with ringing recoveries was the mistle thrush. In article III, several potential explanations for the observed patterns of thrush migration were put forward, including 'nonsense orientation', 'topographical orientation', and the 'different populations' hypothesis. Besides thrushes, WNW–NW orientations are frequently observed among some other passerine species in eastern Finland, which might be related to 'topographical orientation' (for explanation, see III). There have so far been few ringing recoveries from the NW sector, perhaps due to the small human population in northern parts of Scandinavia (Table 3).

The large movements by juvenile thrushes in their first migration could perhaps explain part of this 'nonsense' orientation towards WNW–NW (cf. Matthews 1968). From the orientation point of view, there is no difference between migrating 3,000 or 6,000 km, i.e., whether the individual bird is a medium-distance or a long-distance migrant, as long as the migrant birds are able to correct e.g. for possible wind drifts. However, from the survival point of view, if we think, for example, of the ca. 6,000 km route of long-distance migrants, the birds making a random choice of direction with a precision corresponding to a 2° angular deviation (a.d.), they will reach their destination safely with a probability of 0.99 (survival rate = 99%), but a 10° a.d. will result in a success probability of 0.64 and a 20° a.d. of only 0.43 (Baker 1978). This means that directional selections will have to be made within a smaller interval ranging from 5 to 10° (survival rate: 86–65%) since orientation errors constitute only part of the possible mortality risks that birds encounter during their annual life cycle. Moreover, there

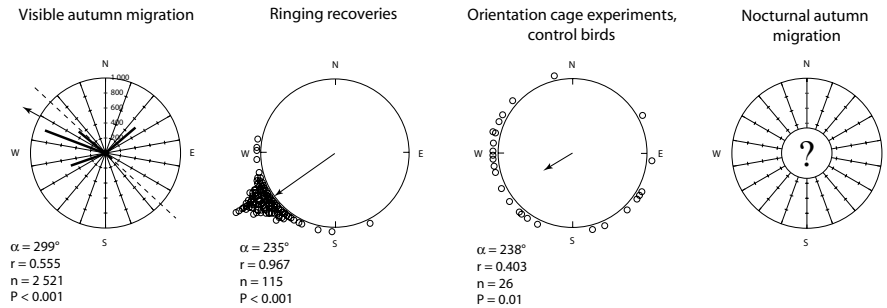


Figure 7 Diurnal migrations of the redwing *T. iliacus* over eastern Finland are oriented towards WNW (III), whereas both ringing recoveries (III) and cage experiments (I) have shown orientation directions towards SW. However, since there is a large scatter in the orientation of control birds, these may also include birds whose preferred compass direction is towards WNW, i.e. the same as that of the majority of birds during visible migration. Nocturnal migratory directions are unknown. For further details of other species, see I and III.

is no specific mechanism by which errors in the directional choices may be corrected; therefore, the effect of such mistakes will accumulate over the course of the journey.

An individual's daily maximum migration distance covered may exceed 100 or even 200 km in song thrushes and redwings, but it is much lower for blackbirds (Hildén & Saurola 1982, Ellegren 1993). Given the hypothetical 3,150 km route from eastern Finland via central Norway to southern France, this would take a bird only a month or two, depending on the daily average speed of migration (100 km or 50 km, respectively), and thus it would be no problem for birds to first follow a W/NW direction and then later shift to a SW migratory route. According to theoretical calculations, the potential migratory distance (one-way journey) for redwing is 6,500 km (Hedenström & Alerstam 1998).

Another explanation for the W/NW oriented movements is provided by the migration routes of Finnish populations of Arctic terns (*Sterna paradisaea*). According to Lemmetyinen (1968) only populations from the Gulf of Finland

migrate to the SW, whereas Arctic terns that breed round the Gulf of Bothnia and in the SW archipelago migrate NW across Scandinavia to the Norwegian coast before turning S. These latter breeding populations probably originated on the coast of Norway some time towards the end of the 19th century. The reason for this phenomenon could have been an extension of the familiar area

Table 3 The number of north-western recoveries (direction $\geq 270^\circ$, distance > 100 km, elapsed time < 180 days from ringing) of five thrush species *Turdus* spp. ringed in Finland between 1913–2001.

Species	No. of NW recoveries		Per cent of NW-birds ringed as nestlings
	Foreign	Finnish	
Redwing	7	1	50
Fieldfare	8	14	82
Song Thrush	–	1	100
Blackbird	4	3	14
Mistle Thrush	–	–	–

by exploratory migrants. It is suggested, that this route has persisted because, for the first year of their lives, young Arctic terns mainly rely on social communication in establishing their familiar area.

The general tendency is for all thrushes of the Fennoscandian populations to move in the sector SW to SSW for winter (e.g. Ashmole 1962). Ringing recoveries suggest that the main autumn direction of movement from eastern Finland is SW for redwings, fieldfares and song thrushes, WSW for blackbirds and S for mistle thrushes (III). Sometimes thrushes may be subjected to lateral wind-drift, which alters their course towards SSE or SE (Alerstam 1975).

Quite a number of ringing recoveries have been made in the SE sector, i.e., along the other part of the migration axis considered (Table 4; III). This is also interesting from an ecological or even evolutionary point of view. The seasonal migrations of redwings and fieldfares are rather irregular as regards their timing and direction. For example, both NW and NE movements are regularly observed during autumn redwing migration over eastern Finland. Further, there is considerable variation within some redwings and fieldfares between subsequent winters in totally different areas of SW and SE sectors. However, within the song thrush migration, for example, the angular distribution of ringing recoveries, visible migration directions and individual or within-brood variation in wintering grounds is much narrower (III).

Optimal migratory behaviour therefore does not necessarily imply that birds should follow the shortest route, but appears to be an adjustable compromise between food availability, risk avoidance and straight flight, depending on endogenous and environmental conditions. When such a situation is encountered it suggests that the gradi-

ents of selective pressures acting on the migration pattern are species-specific.

Basically, the comparison of visible migration and ringing recoveries reveals the fact that a bird does not follow anything like a straight path between ringing and recovery places or between breeding and wintering areas. May this even suggest totally different migratory strategies between groups of birds or populations during diurnal and nocturnal migration? The reality of the visible migrations that are apparent for different thrush species as well as many other species seems to be accepted, at least provisionally, by the majority of birdwatchers in the area. However, until there is corroborative evidence from ringing recoveries or from ceilometer/radar analysis during nocturnal autumn migration, it cannot be accepted without reservation that these figures represent the true migration patterns of the species concerned.

In order to test the different assumptions presented in III properly, more detailed knowledge is needed about thrush migration over eastern Finland and other areas as well. Whether this migration can be considered to be a widespread phenomenon remains to be

Table 4 The number of all south-eastern foreign recoveries of five thrush species *Turdus* spp. ringed in Finland between 1913–2001.

Species	No. of SE -recov.	Percent of all recov.	Percent of SE-birds ringed as nestlings
Redwing	56	3.1	38
Fieldfare	21	1.9	29
Song Thrush	7	0.6	0
Blackbird	7	1.7	14
Mistle Thrush	6	42.9	50

evaluated. At present one can only speculate, but further ringing and constant observations will probably provide the answers.

3.4 Homing behaviour of displaced redwings (*Turdus iliacus*) and fieldfares (*T. pilaris*): implications for navigational abilities

Birds are likely to return to the region of the previous year's breeding with the most suitable habitats (Greenwood & Harvey 1982, Ketterson & Nolan 1990). Both male and female redwings make a relatively large investment in the breeding home range relative to variable wintering patterns and they also have a very high degree of return compared to fieldfares (Huttunen, *unpublished data*). In this study, familiarity with the release site was excluded by displacing thrushes

outside their normal range to unfamiliar habitats, where they were released. During transportation to the release site, I tried to prevent the thrushes from perceiving any information about the environment by enclosing them in cloth bags, and driving them by car using circuitous routes. Their homing ability from unfamiliar sites was likely to be impaired by these methods in terms both of initial orientation and homing success.

In these displacement experiments, two thirds of the redwings and half of the fieldfares were observed to return to their home territories, most of the cases in less than 24 hours. The mean directions in cage and release experiments by individual birds showed a significant preference for the home direction (Fig. 8; IV). In addition, there was seemingly no difference between birds' orientations under clear or overcast skies.

In the homing experiments, three

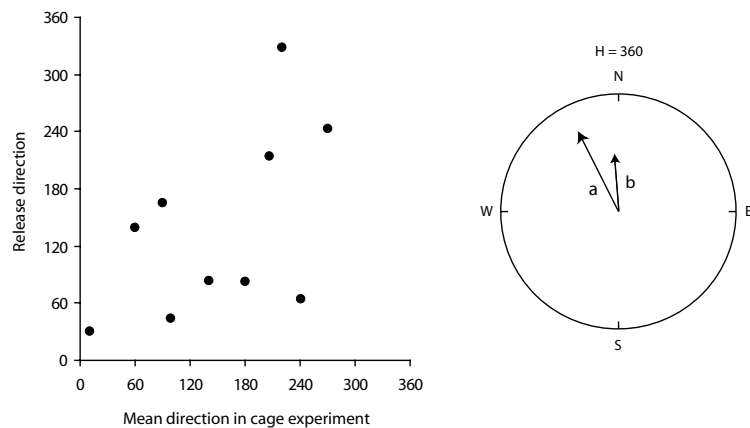


Figure 8 On the left, release direction in relation to mean direction in cage tests (in degrees) for the displaced birds that showed activity in both the experimental conditions ($r = 0.544$, $P < 0.1$, $n = 10$). In the right-hand graph, arrows (a) show mean direction in all cage tests ($\alpha = 333^\circ$, $r = 0.707$), and (b) mean direction in all release tests ($\alpha = 356^\circ$, $r = 0.447$). The home direction for a test group is given by the azimuth standardized to 360° outside the circular diagram. The arrows are sample mean vectors (α) and their length is proportional to the unit radius of the circle ($= 1$).

important parameters in homing behaviour were obtained: (1) vanishing direction (whether the initial orientation is randomly determined or oriented towards 'home'), (2) homing speed (return time, days after release), and (3) homing success (the ratio of birds that reach home). However, almost nothing was known about the birds' behaviour between their vanishing from sight and their arrival at the home site. In general, the range of observation can be enlarged, e.g. by radio-tracking from the ground, expensively by aeroplane or helicopter, or with a path reconstruction device carried by birds in flight (Papi et al. 1991).

It can be stated that neither a view of the sun at the release nor visual information during the displacement are necessary for the birds to orient correctly towards home. The ability to navigate over unfamiliar terrain requires both a compass sense (knowing in what direction to move) and a map sense (knowing the location of home or some other goal). Although humans are handicapped when it comes to navigating across unfamiliar terrain without a map and compass, many other animals show no such disability (see e.g. Kirschvink et al. 1985). Why do birds not use the sun azimuth compass for homing under clear sky conditions? Perhaps the changes in the sun's movement are too small for time compensation during these relatively short displacements. However, there is some evidence that sun compass orientation is used in spatial orientation in everyday tasks, and not only in long-distance migration and homing (Wiltschko & Balda 1989).

It is most likely that birds build up their map sense by learning landmarks. Birds have an advantage in that, while flying, they have a wide view of the landscape below. If we think about the theoretical range of vision of birds (see Alerstam et al. 2006), a redwing flying at an altitude of 100 m will probably see

a low-level landmark at an altitude of 10 m from a distance of 47 km. If the flying altitude is 50 m, the range of vision decreases to 36.5 km, and at an altitude of 25 m it decreases to 29 km. However, birds do not normally fly that high during the breeding season. The possibility that birds could use landmarks to head home from unfamiliar areas cannot, however, be totally excluded.

Generally, it is suggested that homing success decreases with increasing distance from the home site, but with the exception of short (1 km) to medium (10–100 km) distances, experimental displacements would be needed over longer distances (100–1 000 km or more) as well. Some proposals have been put forward as to how thrushes determine the home direction. These include Type I–III orientation by Griffin (1955) and inertial navigation by Barlow (1964), but none of them could be verified experimentally. As a result, it has been suggested that, by using their magnetic compass or in some unknown way, the thrushes apparently monitored the direction of displacement during passive transport, and then used this information to estimate a direct return course with a magnetic compass or some other map and compass concept (see Wiltschko & Wiltschko 2003). Able et al. (1984) proposed the involvement of magnetic cues in the homing process by thrushes, and this was later confirmed in migration studies by Sandberg et al. (2002) and Cochran et al. (2004). By the use of radio-tracking, Able and his co-workers also excluded the possibility of homing by random search.

Ringed recoveries have shown that the precise destination of redwings performing a given circuit in autumn may vary considerably from year to year, but they still seem to be capable of accurate homing to places where they have bred – or been born, in some cases. Given

(1) the variable wintering patterns, (2) the high fidelity to the previous year's breeding areas, and (3) annual variations in wind conditions *en route* and food supply, these findings would really suggest good orientation and navigation abilities. An attempt to interpret the overall orientation capacity of birds or other animals, is a challenge for future investigations.

4 CONCLUSIONS

Presently, orientation experiments performed with different species of Nearctic and Palaearctic thrushes have shown that they may use information from the sun and its associated polarized light patterns and the earth's magnetic field to adjust their migratory directions for a given season (Table 5). For European thrushes of the genus *Turdus*, it seems that the uniform direction of SW in autumn is dominant on the basis of orientation experiments and ringing recoveries, but their directional tendencies are more sophisticated as regards the

overall view of the migration period.

My conclusion is that both magnetic and visual cues seem to be important for the early orientation of thrushes in migration. The results demonstrate that thrushes use a magnetic compass during the autumn migratory period, and that their magnetic compass may function as an inclination compass. The importance of visual cues often results in a compromise orientation between the position of the setting sun and the expected magnetic direction. During clear sky tests, dominance of sunset cues over magnetic information was found in case of cue-conflict situations. However, under cloudy skies, when sunset information was not available, the magnetic cues turned out to be the dominant factor. These findings support the data of many other passerine species tested and that thrushes seem not to behave much differently. However, since the results and their interpretation are from a few selected investigations, especially concerning the use of polarization cues, they may have been generalized too far and will need to be investigated further.

One important finding was a high

Table 5 The use of different orientation cues by thrush species studied on the basis of information from the sun and its associated polarized light patterns, and the earth's magnetic field. Generally, a magnetic compass is calibrated with respect to sunset related cues in the twilight period. This means that birds select the direction e.g. relative to the sun's azimuth and later adjust their headings according to the magnetic compass. The question marks refer to proposed indications only.

Species	Orientation cue	Compass use	Reference
<i>Catharus ustulatus</i> <i>C. minimus</i>	} Sun's twilight azimuth Magnetic	Magnetic	Cochran 1987, Sandberg et al. 2002, Cochran et al. 2004
<i>Hylocichla mustelina</i>	Visual/magnetic ?	Magnetic ?	Able et al. 1984
<i>Turdus iliacus</i> <i>T. philomelos</i> <i>T. pilaris</i>	} Sun's twilight azimuth Magnetic Polarization ?	Magnetic Visual ?	Huttunen, this study

correlation between orientations in the funnel cage and after release. The cue-conflict situation at twilight obviously led to a recalibration of the celestial cues, which allowed the experimental redwings, at release, to continue in the altered direction without need of further information from the magnetic field. Under overcast conditions, when there was hardly any directional information available from the celestial cues, birds had to maintain their course by some visual compass system yet unknown, calibrated from magnetic cues.

According to my results, there were differences in orientation and migratory activity between the thrushes tested at different time periods during the evening. They showed significant orientation in an appropriate migration direction during sunset and post-sunset tests, but not before sunset. The difference was expected, since the night migrants generally start their migration shortly after sunset. An inconsistent result was the high migratory activity, which correlated negatively with orientation accuracy in tests with song thrushes. This means that the more active birds were in cages, the more unclear their orientations would be. In addition, fatter birds were less active in cage experiments, but were more clearly oriented than lean birds. However, compared to the song thrush tests carried out in Italy, all the other tests performed with thrushes in eastern Finland showed a slight positive correlation between migratory activity and orientation accuracy. Moreover, for some reason, lean birds seemed to be more properly oriented than fat birds in the control and horizontal cage experiments, but not so in the vertical cage experiments. Therefore, it can be concluded that the amount of stored fat does not seem to be an important predictor for the directional selections of migratory thrushes in inland test sites. Probably, tests conducted in coastal areas would

give different results.

The total overview of thrush migration over eastern Finland seems rather variable, and is largely unknown in the case of nocturnal migration. For most of the species, visible migration records did not correspond at all to ringing recoveries. There are at least two reasons for this: a kind of 'nonsense' orientation when birds head WNW-NW along the shorelines of the main lake districts further on, and when they do this without any substantial influence from weather or winds on their orientation. One may agree that the observations and assumptions put forth are interesting and worth investigating further. At the same time, it can be concluded that some alternative explanations may not be equally compatible with the data, even if these explanations involve only daytime migrants/migration behaviour. In the future, there is a need for extensive observations of diurnal and nocturnal thrush migration from inland sites, as well as more ringing recovery data from the unknown migration sectors of NW and SE.

On a global scale, redwing orientation seems to be inaccurate and unpredictable, depending, at least partly, on wind conditions and/or availability of food. Nevertheless, most of them winter in SW Europe in large numbers. Orientation is more precise on a local scale, however, as regards homing experiments and return records to the same breeding sites year after year. The behaviour of displaced wild birds has shown a significant preference for the home direction after various cage and release experiments. Both male and female adult redwings also show strong fidelity to their breeding territory within a breeding season and from one year to the next. These records obviously point to the fact that they are able to navigate to near and distant goals.

ACKNOWLEDGEMENTS

I am much indebted to my supervisors, Prof Jorma Tahvanainen, Dr Jorma Sorjonen and Prof Heikki Roininen, for their help with both practical and formal matters during the studies. I should like to thank the technical staff at Joensuu University for their helpful cooperation, especially Matti Savinainen for his help with the magnetic coil construction. I am most grateful to Prof Heikki Hyvärinen, former Head of the Department of Biology, for encouraging these studies and for permission to use the Department roof for orientation tests.

Thanks are due to all the field ornithologists and ringers who have worked at the ringing station in Höytiäinen bird observatory, especially Ari Latja, Juha Miettinen and Jouko Tiussa for their experience and enthusiasm. I had the opportunity to visit Lund University in southern Sweden three times, in a very enjoyable environment. It has also been a pleasure to do research at Arosio, in northern Italy. I would particularly like to thank Johan Bäckman, Giuseppe Micali and Roland Sandberg for advice and sometimes far-reaching discussions on migration and orientation. Björn Holmquist (Department of Statistics, Lund University) offered valuable help with the statistical analysis.

Many thanks to Ville Kuittinen who helped in many ways with the computer work during the various phases connected with this thesis. I also wish to thank Rosemary Mackenzie and Dr Greg Watson for their advice regarding the English language of the summary text and the three articles presented in this thesis, respectively.

I acknowledge the financial support received for my research from the Department of Biology, University of Joensuu; the Faculty of Biosciences, University of Joensuu; the Centre for International Mobility (CIMO), Finland; the Ministry of Foreign Affairs, Rome, Italy; A.N.U.U. – Associazione Migratoristi Italiani; the Kordelin Foundation; Nordisk Forskerutdanningsakademi (NorFA); the Finnish-Swedish Cultural Fund; the Wihuri Foundation; and the Nordic Ecological Society Oikos.

Not least, thanks to all the Prog and Jazz masters for make life much more sound!

Last and most important, I owe my family, Jaana and Tommi, for love and patience. Mary, our Birman cat and I share a never-ending interest in the same subject: our feathered friends.

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