

ORIENTATION AND MIGRATORY ACTIVITY
OF SONG THRUSHES (*Turdus philomelos*)
IN NORTHERN ITALY: CAGE AND RELEASE
EXPERIMENTS UNDER OVERCAST CONDITIONS

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ABSTRACT

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The autumn orientation and migratory activity of Song Thrushes at different periods around sunset were recorded in northern Italy using orientation cages and release experiments, mostly under overcast skies. The aim of the experiments was to examine the importance of timing and energetic condition for the orientation and relative migratory activity of Song Thrushes located close to the wintering area. The data demonstrate that the birds tested during sunset showed a mean orientation that coincided with the average sunset azimuth. The birds that were tested after sunset chose headings towards the south, significantly different from tests at sunset, showing oriented *Zugunruhe* in visually cueless situations. Lean migrants in funnel cages displayed relatively more activity than migrants with larger fat stores, but they also showed more scattered directional choices. A bird's energetic state did seem to affect the likelihood of undertaking night migration. Test birds with relatively small fat reserves at release were more likely to perform landing flights than birds with larger fat deposits. Although nocturnal passerine migrants generally show well-oriented responses only shortly after sunset, both cage and release experiments 1-2 h after sunset indicate that timing may not be critical for the initial orientation of Song Thrushes. However, cage tests performed before sunset resulted in more unclear responses by the test birds than tests performed after sunset.

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INTRODUCTION

Accurate estimates of migratory activity and orientation responses are important for the evaluation of models of migration strategies as well as for the interpretation of migratory experiments in the laboratory or field. While there is an extensive body of literature on sunset orientation data, few studies have reported actual

orientation or activity responses undertaken by birds at different test hours (Yong and Moore 1993, Åkesson and Sandberg 1994).

There are a number of papers with orientation experiments performed 1-2 h after sunset or even later, which have often shown a highly significant drop in activity or concentrated directional behaviour under overcast conditions compared to starry sky tests (Katz 1985, Prinz and Wiltschko 1992, Mouritsen 1998, Gudmundsson and Sandberg 2000, Rabøl *et al.* 2002). Although the results may indicate important differences in migratory motivation and directional behaviour between different test hours, they are not totally comparable due to differences in experimental procedures and must be treated with some caution.

The position of the setting sun may be an important orientation cue for nocturnal migrants to be able to evaluate different available cues before initiating a migratory flight (Cochran 1987, Åkesson and Sandberg 1994). In addition, the *e*-vector of polarized light can provide an axis of orientation for those animal species that can perceive it (Able 1980). These patterns can be seen as long as some blue sky is visible, which can provide information about the position of the sun. Furthermore, the *e*-vector is available during dawn and dusk when the sun is below the horizon.

Migratory birds deposit subcutaneous fat stores that are mobilized as the principal fuel for migratory flight, and hence, develop migratory activity, which manifests itself in increased locomotive activity or restlessness under captive conditions (Bairlein 1990, Gwinner 1990). Nocturnal restlessness in caged migrants corresponds to the daily and annual pattern of natural migratory activity, which provides an opportunity for controlled cage experiments. Moreover, by release experiments with free-flying migrants it is possible to study migratory behaviour in close to natural conditions (Able and Terrill 1987, Sandberg *et al.* 1991).

Many studies have shown that the amount of stored fat is an important predictor for birds' directional selections, especially when confronted with an ecological barrier (*e.g.* Sandberg *et al.* 1991, Sandberg and Moore 1996, Sandberg *et al.* 2002). It is expected from the energetic status hypothesis, that fat-free migrants display less migratory activity than migrants with undepleted fat stores (Yong and Moore 1993). However, birds from different populations during their autumn passage may produce different amounts of migratory activity, and more long-distance migrants produce more activity than short-distance migrants.

Song Thrushes are short- to medium-distance nocturnal migrants with a breeding range throughout the greater part of Europe and central Russia, as far north as about 70°N in Norway and south to northern Spain and Italy (Cramp 1988, Andreotti *et al.* 1999). The wintering range of the species covers W and SW Europe, Italy, the Balkans and further east, and northern Africa. In areas where breeding and wintering grounds overlap, it is a partial migrant. In general, there is a tendency for Song Thrushes to show "leap-frog" migration pattern (*i.e.* more northern birds migrating furthest south), however, this trend arises more in certain months than in others (Ashmole 1962). Migration of European populations of the Song Thrush was presented by Busse and Maksalon (1986).

Andreotti *et al.* (1999) claimed that three different routes towards Italy exist during autumn migration of Song Thrushes. These have been identified on the basis of ringing recoveries, namely: (1) a SW route from central-eastern Europe, (2) one from the Baltic countries to the Alps, and (3) a route from central Europe. Birds passing through some of the districts of Lombardia head mainly towards Mediterranean France, Spain, the Balearics and then Algeria, but a small fraction of the birds head south towards Toscana (Vigorita and Reguzzoni 1998).

In this study, an orientation data set comprising 63 cage tests and 66 release tests in Song Thrushes was used to evaluate migratory activity and orientation in relation to: (1) the timing of migratory movements and (2) the energetic condition (fat content). Based on ringing recoveries (Vigorita and Reguzzoni 1998, Andreotti *et al.* 1999), the test birds were expected to orientate south-west or south, except for those birds tested during the sunset which may alternatively head towards the sunset or the brightest part of the sky. Sandberg (1991) claimed orientation towards the sunset direction was an escape or phototactic response because of an overly restricted availability of visual cues close to the horizon. It has also been predicted that in full overcast conditions during the night both activity and directionality will drop dramatically (Busse 1995; see also Sandberg *et al.* 1991).

METHODS

Experimental birds and study area

Song Thrushes were captured with mist-nets at the Arosio Bird Observatory, Lombardia (EURING area IA04; Fig. 1) in northern Italy (45°43'N, 9°12'E) during their peak autumn migration period (Micali and Massa 1983) from 13 to 19 October 2000. They were measured, aged and ringed for individual identification. All measurements and the fat scores quantified in a six-point scale (F0-F5) were made according to Busse (1970). Only birds with fat classes from F1 to F3 were available in this study. The adult-young ratio of the test birds was approx. 1 : 4. All test birds were caught during the morning hours and were kept indoors in individual cages (35×25×20 cm) before the same evening's tests. The birds were fed *ad libitum* with pigeon berries (*Phytolacca spp.*) and water.

Experimental equipment and test procedure

Orientation cage experiments

Cage and release experiments were executed at the roof of the observatory main building, on the top of a low hill facing the Po valley. The total magnetic field at the test arena was not specifically measured but the horizontal component of the field was carefully checked with a compass for every individual cage test. The tests were performed outdoors without any magnetic or celestial manipulation, using plastic Emlen-type funnels with net cover and typewriter correction paper (Tipp-Ex®) as

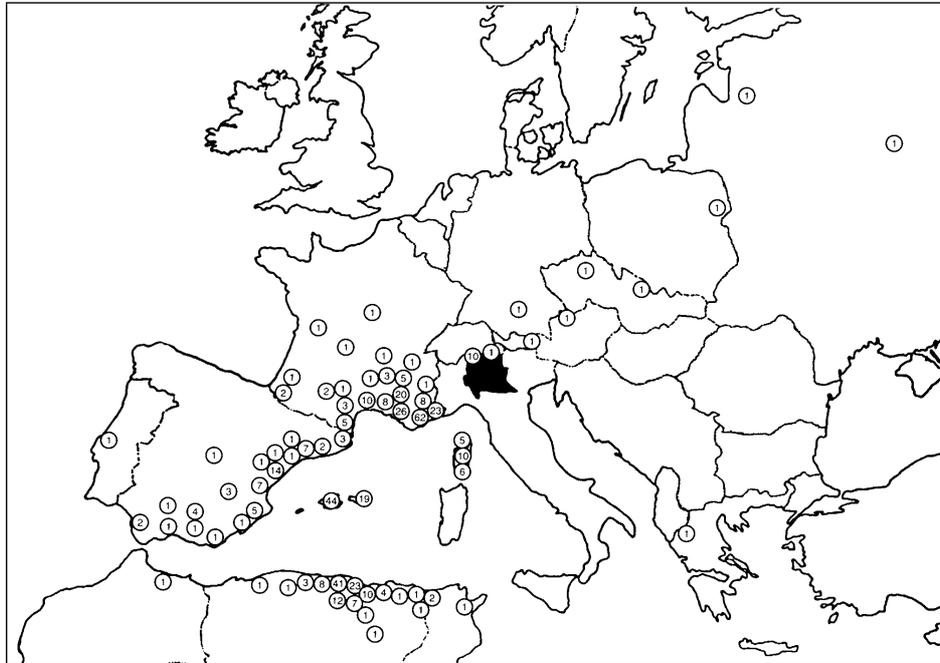


Fig. 1. The foreign recoveries of Song Thrushes ringed in Lombardia from 1977 to 31 January 1998. The total number of 80 531 individuals were ringed at the Lombardia Ringing Stations in this period, of which 439 were recovered in Italy and 458 abroad. A black area indicates the study site location – Arosio Bird Observatory (after Vigorita and Reguzzoni 1998, modified).

the recording medium (top diameter of the funnel – 50 cm). Each test lasted one hour. No restricting screens were used, thus there was a view of the clear horizon or sunset sky when available.

For the cage and release experiments, the tests were divided into three groups: (1) birds tested approx. one hour before the time of sunset and ending at sunset (*pre-sunset tests*), (2) birds tested at the time of sunset and ending one hour after sunset (*sunset tests*), and (3) birds tested approx. one hour after the time of sunset and ending two hours after sunset – *i.e.* in complete darkness (*post-sunset tests*). The mean sunset azimuth 30 minutes after sunset (in the middle of the sunset test hour) was 264°.

Free-flight release experiments

To study the orientation performance under natural conditions, release experiments with a technique similar to the method described by Ottosson *et al.* (1990) and Sandberg *et al.* (1991) was used. A small chemiluminescent plastic lightstick (Cyalume® Lightstick, 2.9×24 mm, 0.15 g, yellow 95281-56) was attached to the two outer rectrices with transparent adhesive tape on one side of the bird's tail. Before fastening, the lightstick was bent in order to break a small enclosed glass container, thus allowing two chemical components to mix. This simple activation pro-

duces a clearly visible yellow light, which can be tracked to distances of up to 1000 m. When the adhesive tape gets wet the lightstick will fall off the bird's tail.

For flying animals weighing less than 70 g, tags should not exceed 5% of the animal's mass to minimize effects on their behaviour (Aldridge and Brigham 1988). The miniature lightsticks used in this study, weighed approx. 0.15 g, and so by the 5% rule they could be used to mark animals as small as 3 g. The risks are reduced to a minimum, because birds cannot easily puncture or damage these lightsticks.

The experimental birds were tossed into the air and then followed using 8×42 binoculars until they had vanished from sight. Upon release, initial bearings were observed with a compass and vanishing times were recorded with a stop watch. It is often easy to assess whether the test birds are motivated to migrate or not because they are likely either to ascend while circling and subsequently take off on a direct course, or land almost immediately. All releases were made directly after the cage tests in a given period. Five birds were experimentally released under clear skies (cloud cover: $cc = 0/8-1/8$) and 61 birds under near or total overcast skies ($cc = 7/8-8/8$).

Data analysis and statistical evaluation

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 the activity. For evaluation, the funnel paper was divided into 24 equal 15° sectors and the number of scratches in them was counted for each bird. The number of scratches is proportional to the number of hops. Beck and Wiltschko (1983) have computed a mean number of 5.7 scratches per hop. Eight Song Thrushes that left less than 50 scratches were considered "inactive" in the funnel, whereas the remaining 55 birds showed moderate to high activity leaving an average of 655 scratches during the test periods (see Table 1 and 2). Three test birds showed bimodal directionality while hopping against funnel walls, thus yielding seemingly "inappropriate" headings.

Table 1

Numbers of Song Thrushes captured at Arosio Bird Observatory and tested in orientation cage and release experiments during different test periods. Three more birds were released than were tested in cages due to occasional rain that impeded some of the cage tests.

	Active	Inactive	Unclearly oriented	Landed	Total (<i>n</i>)
Cage tests					
Pre-	10	0	4	–	14
Sunset	20	0	7	–	27
Post-	13	8	1	–	22
Release tests					
Pre-	9	–	–	5	14
Sunset	18	–	–	9	27
Post-	20	–	–	5	25

Table 2

Means and standard deviations of the number of scratches and vector lengths for Song Thrushes tested in orientation cages during the test periods and the results of ANOVA testing for differences among the test groups: $Nscr_{act}$ – number of scratches of active birds, $Nscr_{all}$ – number of scratches of all test birds, r_{act} – vector length of active birds, r_{all} – vector length of all test birds; active birds are test birds with $Nscr \geq 50$ and $r \geq 0.245$.

	All tests	Pre-	Sunset	Post-	ANOVA	
	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	F	p
$Nscr_{all}$	608 \pm 557	489 \pm 309	811 \pm 516	202 \pm 500	$F_{2,60} = 12.79$	<0.001
$Nscr_{act}$	655 \pm 636	736 \pm 580	982 \pm 553	380 \pm 674	$F_{2,33} = 2.41$	0.105
r_{act}	0.534 \pm 0.163	0.404 \pm 0.137	0.592 \pm 0.131	0.541 \pm 0.181	$F_{2,33} = 4.32$	0.021
r_{all}	0.427 \pm 0.228	0.289 \pm 0.176	0.440 \pm 0.229	0.538 \pm 0.213	$F_{2,52} = 4.88$	0.011
n	63	14	27	22		

A minimum of 50 scratches and a vector length $r \geq 0.245$ was set as the limit for the inclusion of a particular test bird in the data set – cf. $nr^2 < 3.0$ in Ottosson *et al.* (1990). The limit, set to $p > 0.05$, according to the Rayleigh test (cf. Batschelet 1981), was used simply as a criterion to exclude not clearly oriented and unreliable results from the analysis. 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). Mean vectors are relative to the radius (r) or diameter (r_2) of the circle = 1. The Rayleigh test was used to show whether the orientation results differed significantly from a random circular distribution (Batschelet 1981). As the active birds' mean angle of orientation under clear ($\alpha = 240^\circ$, $r = 0.754$, $n = 5$, $p < 0.05$) and overcast ($\alpha = 215^\circ$, $r = 0.331$, $n = 38$, $p < 0.01$) conditions were not different ($F_{1,41} = 0.4$, *ns*) the data were pooled in this respect.

To calculate a mean axis of orientation for bimodal data, vector analysis was performed after first applying the doubling-of-angles procedure recommended by Batschelet (1981). A mean axis of orientation was used in the sunset release tests, as the mean vector length calculated from double angles (r_2) is greater than the mean unimodal vector (r). However, this was not used in the pre-sunset release tests though it gave a better fit for the data ($r_2 = 0.576$, $p < 0.05$ vs $r = 0.479$, *ns*), because this would have yielded only two individuals on the other side of the axis.

The 95% confidence interval was used to analyse whether the birds' mean orientation differed from the direction towards the mean position of the setting sun (Batschelet 1981). Tests for differences in the mean angles of orientation were made by using a "one-way classification test" (F) according to Mardia (1972). Differences in scatter between groups were examined with a "test for homogeneity of concentration parameters" (t) according to Mardia (1972). If one or both of the samples were randomly distributed or bimodal, Watson's U^2 -test was used (Batschelet 1981).

Since the activity data and concentrations were normally distributed (one-sample Kolmogorov-Smirnov test) a one-way ANOVA was used to analyse difference in activity among the test periods. Variances among the test groups were not statistically different (F -test, $p > 0.05$).

The basic assumptions of the procedure used were questioned by Busse and Trocińska (1999), but because the goal of the paper is a comparison between conditions of experiments, the elaboration procedures are of secondary importance and they will not be discussed here.

RESULTS

Orientation cage and release experiments

Orientation cage tests with three test groups resulted in different mean directions between west and south (Fig. 2). Birds tested before the sunset oriented slightly towards the south-southwest ($\alpha = 200^\circ$) while later tests showed different orientation responses towards the west and south, respectively, with birds tested during the sunset ($\alpha = 266^\circ$) and after the sunset ($\alpha = 171^\circ$).

In the subsequent release tests, the birds headed differently in all three test groups, as they did when compared to previous cage tests (Fig. 2). In the pre-sunset tests, the birds selected a north-western mean direction ($\alpha = 323^\circ$). In the sunset tests, the birds showed a more bimodal orientation response and headed along the east-west axis ($\alpha_2 = 82^\circ$ - 262°). Post-sunset birds headed towards the south-west ($\alpha = 235^\circ$).

The mean orientation of the sunset test birds was virtually the same as the sunset direction (264°), even under overcast skies (Fig. 2). The difference between the mean orientation of the cage test birds and the direction towards sunset was $\alpha = +2^\circ$ (95% conf. int. = $\pm 33^\circ$, $r = 0.551$, $n = 20$). The post-sunset cage test birds, on the other hand, showed a seasonally appropriate mean orientation, which was significantly different from the sunset direction ($\alpha = -93^\circ$, 95% ci = $\pm 26^\circ$, $r = 0.705$, $n = 13$).

The mean orientation in the first cage test hour (pre-sunset tests) was not significantly different from the mean orientation in the second test hour (sunset tests; $U^2 = 0.122$, $p > 0.05$). The mean orientation of the post-sunset birds differed significantly from that of the sunset birds ($F_{1,31} = 15.4$, $p < 0.001$), whereas no difference in the mean angles of orientation was found between the first and third cage test hours ($U^2 = 0.128$, $p > 0.05$).

In addition to the differences in mean orientation between the test groups, they could also be compared with respect to the scatter around the mean angles. When this was done, however, there were no significant differences in the distribution of scatter between any of the test groups (t between 0.1 and 1.9, $p > 0.05$ in all cases).

For those individual birds that were active (see *Methods*) during both cage and release tests the orientation behaviour could be compared by subtracting the re-

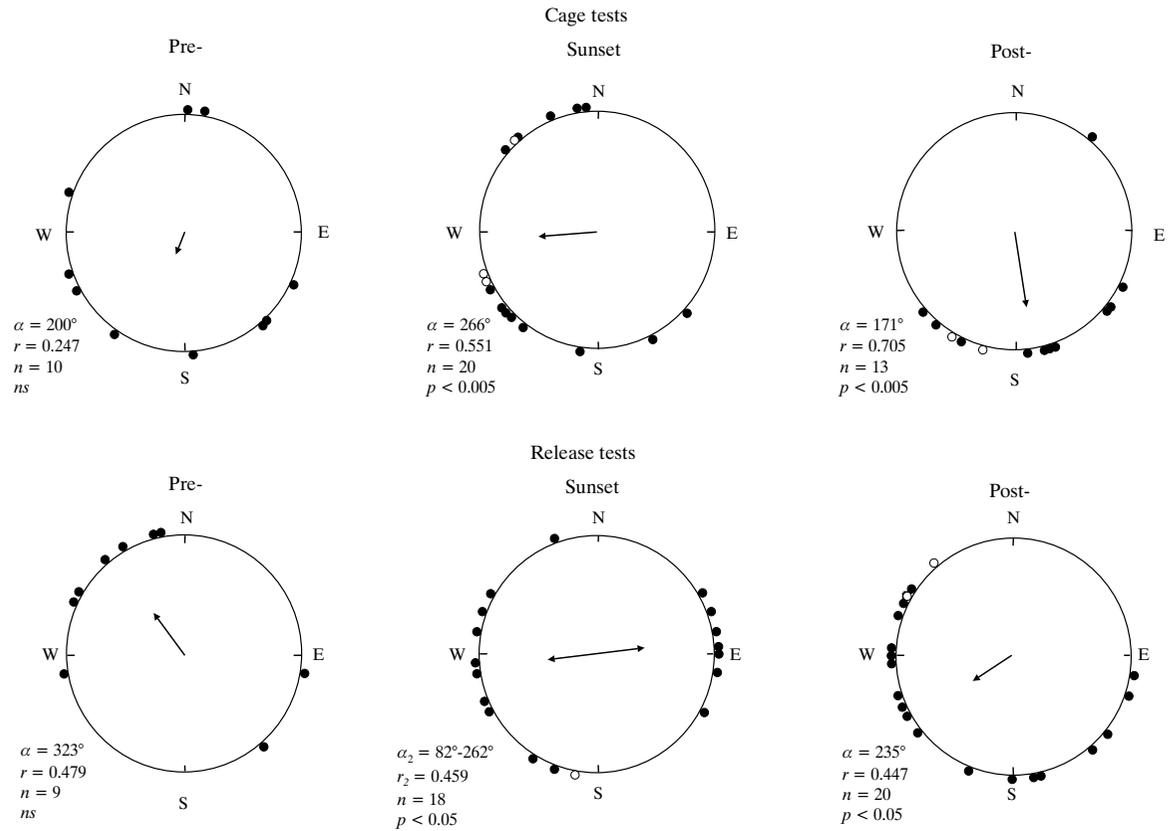


Fig. 2. The orientation of Song Thrushes captured at Arosio in cage and release experiments, tested before, during, and after the sunset period. Mean vectors are drawn relative to the radius or diameter of the circle equal 1. Mean directions (α and α_2), lengths of vectors (r) and axis (r_2), and probability levels (p) based on the number of individuals (n), according to the Rayleigh test were calculated by using standard procedures given in Batschelet (1981). Filled dots denote overcast sky tests and open dots represent clear sky tests.

corded cage direction from the release heading, thus giving a mean of differences (α_{diff}) – see Sandberg *et al.* (2000). From this, the correspondence between the results of these two techniques could be checked. Under the pre-sunset conditions the test birds showed a significant mean of differences ($\alpha_{diff} = 125^\circ$, $r = 0.627$, $n = 8$, $p < 0.05$, $95\% ci = \pm 52^\circ$) and revealed significantly different orientation results when cage and release tests are compared (α_{diff} fell outside the $95\% ci$). This was also the case with sunset birds ($\alpha_{diff} = 95^\circ$, $r = 0.605$, $n = 16$, $p < 0.005$, $95\% ci = \pm 37^\circ$) and post-sunset birds ($\alpha_{diff} = 49^\circ$, $r = 0.844$, $n = 12$, $p < 0.001$, $95\% ci = \pm 20^\circ$). The duration of individual vanishing intervals ranged from 16 to 69 s (mean = 28.3 ± 9.5 s, $n = 47$).

Migratory activity in Song Thrushes

There were significant differences in migratory activity between the test groups (Table 2). Sunset birds showed highest activity, and together with post-sunset birds they also tended to show less scattered orientation.

Fatter birds were, on average, less active in cage experiments, but were more clearly oriented than lean birds (F1 vs F3, all test birds: $t_{1,24} = 1.98$, $p < 0.05$; Fig. 3). There was a tendency for lean birds to show more inactivity or unclear orientation than expected by chance as compared to fatter birds (Fig. 4). This is also evident

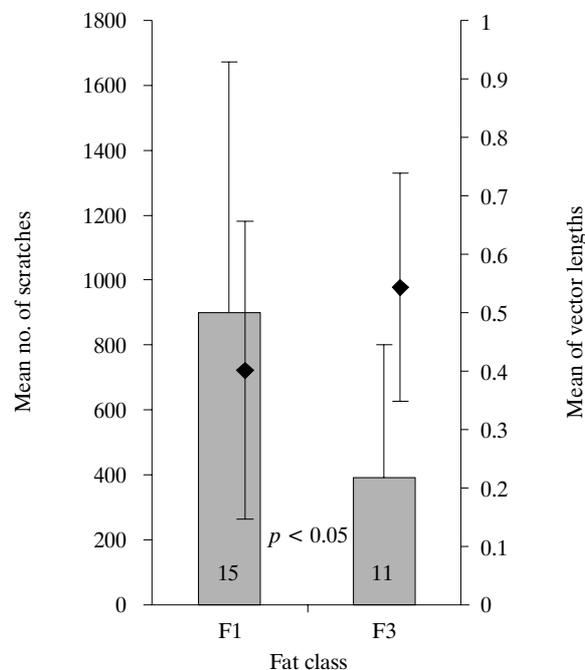


Fig. 3. The mean number of scratches (N_{scr} – grey bars) and the mean of vector lengths (r – black diamonds) in two fat classes; variation is shown. The numbers in bars show the sample sizes. The p value refers to the significance of the difference between the mean number of scratches in the fat classes (t -test).

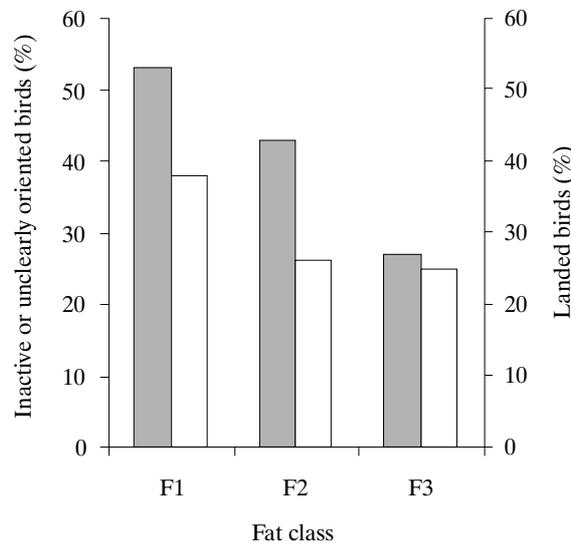


Fig. 4. The percentage of inactive or unclearly oriented birds (cage tests – grey bars) and landed birds (release tests – white bars) in three fat classes.

when mean directions in different fat classes are considered: lean birds (F1: $\alpha = 255^\circ$, $r = 0.425$, $n = 9$, $p < 0.2$) were unclearly oriented in comparison to fatter birds (F2: $\alpha = 195^\circ$, $r = 0.395$, $n = 26$, $p < 0.02$) but different sample sizes must be noted. In addition, after release experiments 38% of the F1 birds landed, whereas the numbers for F2 and F3 birds were 26 and 25%, respectively (Fig. 4). However, if only active birds are considered, there was no difference between the fat classes in migratory activity ($Nscr_{act}$: $F_{2,33} = 0.15$, ns) or in orientation responses (r_{act} : $F_{2,33} = 1.26$, ns).

Testing for differences in mean directions among birds with different fat loads within each test group showed significant results only during sunset (F1: $\alpha = 290^\circ$, $r = 0.748$, $n = 6$, $p < 0.04$; F2: $\alpha_2 = 338^\circ-158^\circ$, $r_2 = 0.639$, $n = 10$, $p < 0.003$; F3: $\alpha = 243^\circ$, $r = 0.936$, $n = 4$, $p < 0.03$) and post-sunset tests (F2: $\alpha = 180^\circ$, $r = 0.835$, $n = 11$, $p < 0.001$).

A significant negative correlation between migratory activity (expressed as number of scratches) and orientation (mean vector length) was observed for all cage test birds (Pearson's correlation: $r = -0.33$, $n = 53$, $p < 0.05$; Fig. 5). Again, testing for this relationship within each of the test groups showed non-significant results ($p = 0.07$, 0.05 and 0.46 , respectively), but all suggested the same negative trend. Generally, the more active birds were the more unclear their headings would be. Thus, the greater dispersion around the mean in pre-sunset tests (Fig. 2, Table 2) might be attributed to less directed activity for the initiation of migratory flight.

There were no significant differences between the age categories in the migratory activity (mean no. of scratches: young = 665, adults = 606), concentration (mean vector length: young = 0.420, adults = 0.448) or orientation responses (mean direction: young = 193° , adults = 210°); in all cases $p > 0.05$.

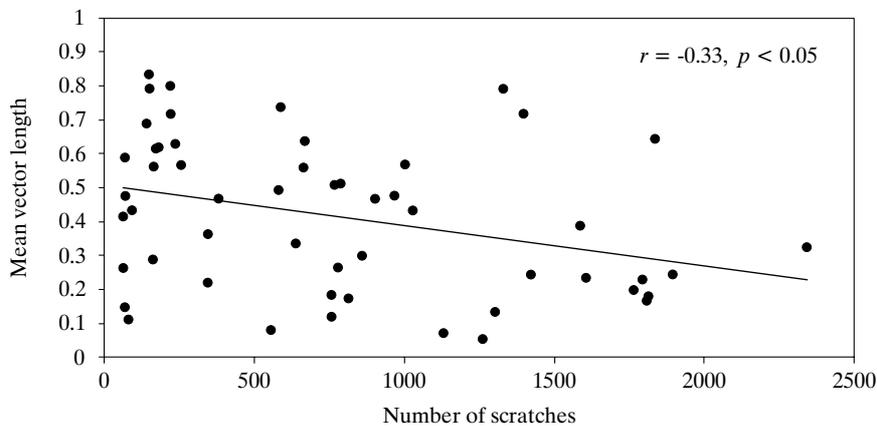


Fig. 5. The mean vector length of test birds in relation to activity as indicated by the number of scratches. r – Pearson's correlation coefficient, $N = 53$.

DISCUSSION

Orientation of Song Thrushes in northern Italy

Throughout Europe there is a south-westerly trend in the autumn migration of Song Thrushes (Ashmole 1962, Busse and Maksalon 1986). In comparison with some other *Turdus* species, there is very little evidence that Song Thrushes move great distances during a single winter or spend successive winters in widely different areas. Since Song Thrushes may winter in northern Italy, it can be assumed that only a proportion of the test birds would proceed further in their migration. However, the species is totally migratory in the capture area, from where the birds are heading to common winter quarters (Micali and Massa 1983; see also Fig. 1). Recoveries of birds ringed in Italy indicate that autumn migrants flying along the westernmost part of the pre-Alps (e.g. Lombardia) head mainly towards the western Mediterranean (Andreotti *et al.* 1999).

The objective of this study was to examine orientation behaviour close to the wintering area at different periods around the sunset in relation to visual orientation cues. In view of the expectations presented in *Introduction*, neither overcast conditions nor proximity to the wintering grounds seemed to have any major influence on orientation results. Although a majority of birds chose directions in the western and southern quadrant, quite many individuals in sunset release tests preferred easterly courses (see Fig. 2). The observed differences in concentration of mean directions of test birds in three test periods can be explained by assuming the passage of birds of different geographical origins across Lombardia (Andreotti *et al.* 1999). The fact that no birds are heading west during post-sunset cage tests argues against the “different populations” hypothesis. However, since there is no evidence that the test birds were derived from the same population, the possibility that varia-

tion in the population composition of the samples may have influenced the results cannot be excluded.

The observed variability in the compass orientation in a population may always be a composite function of variation within and among individuals, even in species like the Song Thrush, which among the *Turdus* species shows relatively narrow angular deviation in migratory directions based on ringing recoveries (e.g. Alerstam 1991). For example, Busse (1995) observed different types of local vector patterns, including bimodality, when testing directional preferences of Song Thrushes with a new cage technique.

In pre-sunset test arrangement the birds seemed to be unable to orient themselves, showing a random distribution in cage experiments, however, they showed less scattered directional choices toward the north-west in release tests, which were performed nearer to the time of initiation of migration (Fig. 2). The birds are likely to use the sun's twilight azimuth, when available, to select the direction of their migration. The brightest part of the sky overhead, or the polarization pattern, probably indicated the sunset direction to the sunset test birds. Unfortunately, the number of clear sky tests is too small to permit a more detailed comparison of orientation performance between the test groups.

The mean southerly direction among post-sunset birds results from cage tests under overcast sky without hardly any cues available. Perhaps most post-sunset birds follow their innate magnetic compass, rather than orienting towards some exogenous reference point, but this is speculative. The use of a magnetic compass mechanism was proposed for the headings flown by a migrating Swainson's Thrush (*Catharus ustulatus*) when solar and stellar cues were not visible (Cochran 1987). Moreover, radiotelemetric studies of migrating *Hylocichla* and *Catharus* thrushes in North America have shown that individual birds, regardless of the speed and direction of the wind, cloud cover or landscape maintained a constant heading and speed during the flights (Cochran and Kjos 1985, Cochran 1987), by selecting flight altitudes with the most favourable winds.

Release experiments with Song Thrushes tested for directional preferences under free-flying circumstances show that they were able to select seasonally correct migratory directions even when released under overcast skies, though the scatter around the mean vector was notable. The large scatter of release bearings could be attributed to the fact that under overcast conditions, many birds could still be selecting the appropriate flight direction when 1 km away from the observer (detection range). Normally, migrants seem to have difficulties in selecting seasonally appropriate directions under solid overcast (Cochran *et al.* 1967, Able 1978, Emlen and Demong 1978). Why there is such a difference or change in direction between cage experiments and the following free-flight release tests remains to be resolved. Throughout the study, the distant landmark cues of a large city (approx. 35 km to the SSE) appeared to be used minimally, if not at all, by the migrating thrushes.

Migratory activity in Song Thrushes

Several potential sources of error must be considered when using the cage technique for recording migratory orientation in captive birds. Besides the common tendency for caged birds to respond to horizon glow, moonlight, artificial lights *etc.*, or simply to show escaping attempts, the orientation of test birds might be influenced by the cage system itself, such as the position of the paper overlap in the funnel, the grid pattern of the mesh screen top or the placement of all the features. These should be varied in a random manner between tests. Sandberg (1991) found that tests in which the lower part of the sunset sky was screened from the Robins' (*Erithacus rubecula*) view resulted in totally different behaviour from that in tests with a full view of the sky.

The cage experiments are open to some criticism mainly because the birds are stressed by the unusual situation and would like simply to escape rather than to migrate. It may well be that when each wild-caught bird is tested only once, the escape response after the recent stress of being caught may override migratory orientation. Under clear skies, the escape direction would most likely be directed toward the light, *i.e.* the setting sun, thus suggesting (in late autumn north temperate latitudes) a westerly directional preference. The test birds in this study were accustomed to being caged normally for up to 12 hours. Even if there are suggestions that the bird in a particularly stressful situation can change its directional behaviour (Busse 1992), cage experiments are generally a reasonably good method for studying orientation behaviour in the field.

In this study, lean birds showed considerable hopping activity, which was not well-directed but rather may have resulted from escape responses (see Fig. 3). Individuals with smaller average fat deposits, however, also showed inactivity or landing flights more often than birds with relatively larger fat reserves (Fig. 4). There is ample evidence that in many bird species lean birds are less migratory active or more likely to be inactive than fat birds. Yong and Moore (1993) and Sandberg and Moore (1996) found that the autumn night activity was directly related to the amount of available fat in *Hylocichla* and *Catharus* thrushes, and Red-eyed Vireos (*Vireo olivaceus*), respectively. On the other hand, some other studies show no clear correlation between migratory activity and fat load. The amount of visually estimated fat had no discernible effect on the quantity of migratory activity in a number of species of North American warblers in the study of Able (1977), but the proportion of individuals that showed oriented migratory restlessness increased significantly with larger fat deposits. Sandberg (1994) found no significant differences in activity (mean hops/h) of Robins between different fat classes, although *e.g.* F2 birds showed slightly more activity than F5 birds both in clear and overcast sky tests.

Does body condition affect the migratory route chosen by Song Thrushes or the condition is a result of different flight history? May this be also somehow related to inactive or unclearly oriented movements found among lean test birds? Nocturnal migrants may choose a direction only once per night, prior to darkness. If there is

unclear orientation when put into a funnel cage after dark, this may just reflect a lack of motivation to orient, because the appropriate time of evening for a directional choice has been missed. In Sweden, Song Thrushes departed mainly during civil and nautical twilight (sun elevations less than 12° below the horizon) periods (Åkesson *et al.* 1996). On the other hand, Cochran *et al.* (1967) followed 10 *Hylocichla* thrushes on their spring migration and found that half of the birds migrated for just about an hour or less (though in some cases the flights were interrupted due to bad weather), whereas the rest of the birds had flights that lasted for 4 to 8 hours. Although orientation tests with nocturnal passerine migrants often show well-directed responses only during sunset tests, both cage and release experiments 1-2 h after sunset indicate that timing may not be that critical for the initial orientation of Song Thrushes.

There were no indications of age-related differences in the migratory activity or orientation of experimental categories. It may not necessarily be so that first autumn migratory restlessness in a migrant bird differs from that of more experienced one, especially as it is considered to be an endogenously preprogrammed system. However, release experiments by Sandberg *et al.* (1991) suggest that adult birds orient with higher accuracy due to experience (see also Rabøl 1978, Moore 1984). At least for some long-distance migrants, the pattern of autumn *Zugunruhe* appears to be related to the pattern of actual migration in freeliving conspecifics (Gwinner and Czeschlik 1978, Gwinner 1990). Not all nocturnal restlessness in migratory species can be considered as migratory, but careful comparative studies may distinguish true migratory restlessness from other types of nocturnal unrest.

CONCLUSIONS

This study confirms the fact that there are major differences in orientation and migratory activity between the bird groups tested at different time periods during the evening and early night. Some general conclusions can be drawn from the results.

Song Thrushes showed significant orientation in an appropriate migration direction only in sunset and post-sunset tests. The difference was quite expected, as the night migrants generally start their migration shortly after sunset (see references in Åkesson *et al.* 1996). However, both the unimodal distribution and westerly orientation of sunset cage birds suggest that the birds were responding to the brightest part of the overcast sky during this treatment. It is suggested that in later tests the birds could only orient in respect to the earth's magnetic field because there were hardly any visual cues available at that moment.

Another general conclusion is that the high migratory activity correlated negatively with the accuracy of orientation. All the highest activities were recorded for lean birds but they were also likely to show most unclear orientation. Factors that could have influenced the contradictory result for the activity of the test birds are

(1) near or total overcast conditions for most of the time, *i.e.* absence of most orientation cues available in given time, (2) handling effects and (3) body condition.

One would agree that bird ringing still represents the best way of describing migratory movements of birds whose native grounds are known. The interpretation of results obtained through orientation cage and release experiments may be complicated by the distribution of the passage of birds from widely different areas. At any one time, different individuals may have different preferred compass directions and wind speed and direction may contribute to the individual's composite migration threshold. There are also certain biases in the distribution of ringing activities and of recoveries of thrushes, which must be borne in mind. Birds ringed at observatories may not properly represent the population from which they originate.

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