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Schweizerische Vogelwarte, Sempach, Zoologisches Institut, Universität Zürich und Fachbereich Biologie, Zoologie, Universität Frankfurt a.M.

The Orientation Behaviour of Chaffinches, *Fringilla coelebs*, Caught during Active Migratory Flight, in Relation to the Sun

Rachel Muheim, Lukas Jenni & Peter Weindler

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Abstract

The few orientation studies that have been carried out with day-migrating birds show that they are able to use solar and magnetic orientation cues for orientation. Previous orientation experiments in Emlen funnels have been carried out either with hand-raised birds or with birds caught during resting periods at stop-over sites. The aim of our study was to test whether birds caught during active flight show a higher concentration of migratory activity in the seasonally appropriate migratory direction in the funnels than birds that had not experienced migration just before the funnel experiments. The topography at the alpine pass Col de Bretolet at the border of Switzerland and France allowed us to capture birds during active migratory flight. These birds were in full migration disposition. Orientation experiments with chaffinches suggested an influence of the sun because chaffinches did not orient in the seasonally expected direction, but probably showed positive phototaxis towards the light of the sun at the opposite side of the funnel. Chaffinches tested under overcast conditions oriented to the north-west which probably was a 'nonsense' orientation and not a reverse migration or compensatory behaviour. We conclude that freshly caught birds are too stressed to show appropriate orientation when tested immediately after catching.

Corresponding author: R. Muheim, Department of Animal Ecology, Lund University, Ecology Building, S–223 62 Lund, Sweden. E-mail: rachel@zool.unizh.ch

Introduction

In contrast to the orientation of night-migrating birds (Baker 1978; Alerstam 1990), only a few studies have examined the cues and behaviour of orientation of birds migrating during the day. Two main directional cues have been found. As first suggested by mirror experiments with starlings *Sturnus vulgaris* (Kramer 1951), diurnal migrants use the sun as a directional cue for orientation. The sun compass is based on the relation between sun azimuth, time of day and geographic direction and is independent of the sun's elevation or whether the sun is ascending or descending (Wiltschko & Wiltschko 1988; Schmidt-Koenig 1990). However, day migration of passerines takes place even under completely overcast conditions when the sun is not visible (pers. obs.; De Crousaz 1973; Hilgerloh 1981) and certain day-migrants also regularly migrate during the night (Alerstam 1990).

Orientation experiments with starlings and meadow pipits *Anthus pratensis* showed that birds also oriented under overcast conditions as when the sun was visible above the horizon (W. Wiltschko 1980; Orth & Wiltschko 1981). A magnetic compass has been described as a second orientational cue for yellow-faced honeyeaters *Lichenostomus chrysops* (Munro & W. Wiltschko 1993), goldcrests *Regulus regulus* (Weindler 1994), chaffinches (Bäckman et al. 1997), common redpolls *Carduelis flammea* (Bäckman 1995) and is suggested for meadow pipits (Orth & Wiltschko 1981; Helbig et al. 1987) and starlings (Wiltschko 1981).

Our main interest in this study was to compare the orientation behaviour of day-migrating chaffinches in funnels tested under clear sky with birds tested under overcast condition, in order to examine the influence of the sun. Orientation experiments in funnels, generally using hand-raised birds or migrant birds caught during resting periods at stop-over sites, usually show much greater variation in direction than recoveries of ringed birds. Therefore, we tried to use birds in full migratory disposition. In the Swiss Alps, at Col de Bretolet, the topography allows birds to be caught during active migratory flight, so that they can be tested immediately after capture in their natural migration environment. We therefore expected better orientation of these birds compared with other orientation experiments and a good agreement of orientation directions in the funnels with the species-specific recovery directions of ringed birds.

Materials and Methods

Study Site and Bird Catching

Chaffinches were caught with mist nets in the morning hours during their migratory flights at the ringing station Col de Bretolet (46°09′N, 06°47′E) 1923 m above sea level at the border between Switzerland and France (Fig. 1). Most day-migrants reach Col de Bretolet by following the mountain ridges of the northern border of the Alps that form a leading edge and compress the migration between the Jura Mountains and the Alps (Bruderer & Winkler 1976; Bruderer & Jenni 1990; Bruderer 1996; Liechti et al. 1996). Only a few birds drift into the valley of the Rhone when reaching Lake Geneva on westerly winds, and thus follow the Val d'Illiez to compensate for this deviation from their migratory direction (Bruderer & Winkler 1976; B. Bruderer, pers. comm.).

Time and Set-up of Experiments

All experiments were carried out between 1 and 23 Oct. 1995 in modified Emlen funnels (Emlen & Emlen 1966), the interior of which was covered with typewriter correction paper (Tipp-ex) as described by Beck & Wiltschko (1981). The funnels had a top diameter of 350 mm, a bottom diameter of 100 mm, a height of 155 mm and were covered with a dark-coloured mosquito net (Beck & Wiltschko 1983; Helbig 1991). They were made from aluminium so as not to influence the bird's magnetic compass. To avoid any possible influence on the orientation direction because of attraction to the seam of the Tipp-ex paper we randomized its

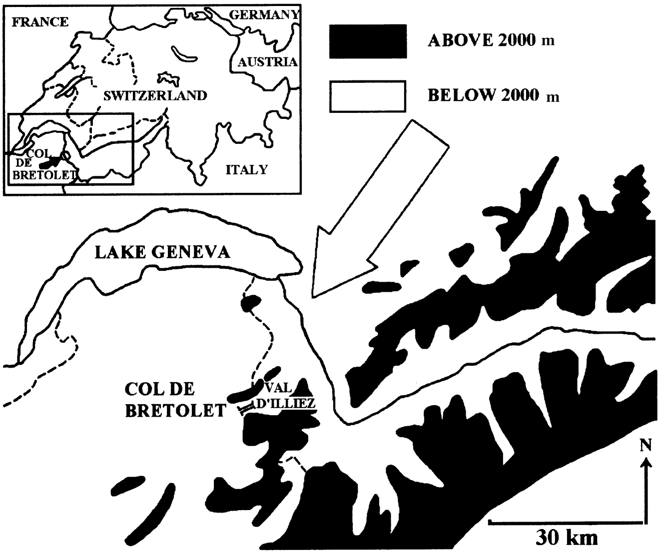

Fig. 1: Simplified relief of the study site Col de Bretolet, Switzerland, and its surrounding area. The large unshaded arrow indicates the primary direction of autumn migrants. Based on Vuilleumier (1963)

position within the funnel. The surrounding mountains were shielded off by a screen $\approx$100 mm high, allowing the birds to view $\approx$120° of the natural sky when standing in the centre of the funnel. Birds that jumped up to the mosquito net saw the sun when it was at a minimum elevation of 19° above the horizon.

The chaffinches were ringed, measured, and tested between 0900 h and 1230 h, within 4 h after catching. Experiments lasted 1 h. The same individual was tested only once. For every bird tested under clear sky (cloud cover 0/8–3/8) the position of the sun (azimuth and elevation above the horizon) in the middle of the experiment was calculated using the program EME PLANNER.

Data Analysis

Each Tipp-ex paper was subdivided into 24 sectors, and the number of scratches within each 15° sector was counted over a light table (Helbig 1991). When single scratches were not visible owing to too much activity, we estimated their number by comparing the scratch density with countable parts of the Tipp-ex paper. Therefore, the activity in highly scratched sectors is possibly underestimated. Experiments were included in the analysis if a minimum number of 35 scratches was counted. We defined two measures from the distribution of the scratches for every active bird. 1. The mean orientation direction of individual birds was calculated by vector addition (Batschelet 1981; Fisher 1993). We applied the method of doubling the angles to test for axiality. An individual was considered axial when the mean vector length of the scratch distribution with doubled angles was larger than the one without doubled angles (Batschelet 1981). When the individual showed an axial distribution the part of the mean vector closer to the one of the unimodal distribution of the same individual was included in further analyses. In all experiments the distribution was significantly directed according to the Rayleigh test. This does not, however, provide accurate probability estimates because the single scratches on the Tipp-ex paper are not independent from each other (Batschelet 1981; Sandberg et al. 1988). 2. We also measured the individual concentration, calculated from the distribution of the scratches around the circle. Because the individual mean vector length of equally spread samples decreases with increasing number of scratches (Batschelet 1981), it cannot be used as a direct measure of individual concentration. Therefore, we used the residuals from the regression line of mean vector length on the logarithm of the number of scratches ($y = 0.78 - 0.11x$, $n = 174$, $r = 0.63$, $p < 0.001$).

Ringing Recoveries

Recoveries of ringed birds (ringing recovery data base at the Swiss Ornithological Institute, Sempach) were used to determine the migration directions of chaffinches. To prevent the inclusion of recoveries of birds that made directional changes along their migration route, we selected only those birds that were ringed and found in the same migration season within 120 d. Two migration directions were defined. 1. The direction of origin is the direction along which the birds came from the north on their way to Switzerland and was calculated from ringing recoveries made in Switzerland. 2. The migratory direction, the direction the birds took when migrating from Switzerland to their wintering grounds, was determined by including all recoveries of chaffinches ringed at Col de Bretolet. Since 83.3% of all short-distance recoveries (3–89 km) were made at the ringing station at Col de la Golèze, France, 3 km SSW (200°) of Col de Bretolet, and in the nearby village Champéry (7 km, 60°) we only included recoveries of birds made at a distance of > 10 km in the analysis.

Circular Statistics

We used the Rayleigh test statistic to determine whether groups of birds (e.g. those that were exposed to the sun and those that were not, or those in funnel experiments and ringing recoveries) showed significantly different orientation directions (Batschelet 1981). To analyse whether a group orientation was axial or unimodal we applied the method of doubling the angles as described in the section data analysis.

To perform multisample comparisons we used the one-way classification test (Mardia 1972; Watson–Williams F-test in Batschelet 1981).

Differences in the mean orientation direction and in scatter between two groups were analysed using randomization methods (Manly 1991; Fisher 1993). We used a modification of the TURBO-PASCAL program written by Cabrera et al. (1991), which pools the samples (individual birds) and randomly assigns them to two groups. This procedure was repeated 5000 times, as recommended by Adams

& Anthony (1996). Comparisons of the sample directions were performed by using the absolute difference between the medians of the two random samples and comparing it with the median difference of the original sample (median-comparison). Differences in scatter were detected accordingly, by comparing the absolute differences between the 50% interquartile ranges (iqr-comparison). The p-values (two-tailed probability) are the proportions of times the randomly generated differences exceeded the observed ones. Spot-check comparisons between this method and circular nonparametric tests (Watson–Williams F-test and Mardia–Watson–Wheeler test, in Batschelet 1981) using test samples showed good agreement. Median-comparisons were conducted only when both groups had a significant mean direction according to the Rayleigh test ($p < 0.05$).

Results

Comparison between Funnel and Recovery Directions

The chaffinches showed a well-directed distribution to the north-west in the funnel experiments. This direction does not correspond to the observed SSW orientation of free-flying birds (unpubl. data), nor to the SSW directions of short- or long-distance recoveries of ringed birds (Fig. 2a–c, Table 1).

Since the orientation of birds tested with a view of the sun was influenced by its position, as shown below, one would expect that birds that did not see the sun to orient in the seasonally expected direction; however, this was not the case. The group without view of the sun (cloud cover 7/8–8/8) was well directed, but also to the north-west, which differed significantly from the expected migratory direction of ringing recoveries (Fig. 2b,d, Table 1). The individuals showed much more scattered directions in the funnel experiments compared with the ringing recoveries. There was no significant directional difference between adult and young individuals (median comparison, $p > 0.05$) or between tests carried out at three different periods of time of day (one-way classification test, $F_{2,39} = 1.50$, $p > 0.05$).

Individual scatter of birds was found to have an influence on the mean group scatter, but not on individual activity. Those individuals that spread more were less well concentrated as a group than the individuals with a good concentration (Fig. 3a, Table 2).

Orientation in Relation to the Sun

When analysing chaffinches tested under clear skies (cloud cover 0/8–3/8), we subdivided the mean directions into 10 groups based on date and time of testing. Within each group, the birds were exposed to the same environmental conditions and equal sun positions. A multisample comparison of the different group directions gave significant differences between the 10 samples (one-way classification test, $F_{9,122} = 12.49$, $p = 0.001$; Fig. 4). Their mean direction was related to the azimuth position of the sun. In most groups, the birds tended to prefer the opposite direction of the sun, which was north-west, except for groups 9 and 10, or showed

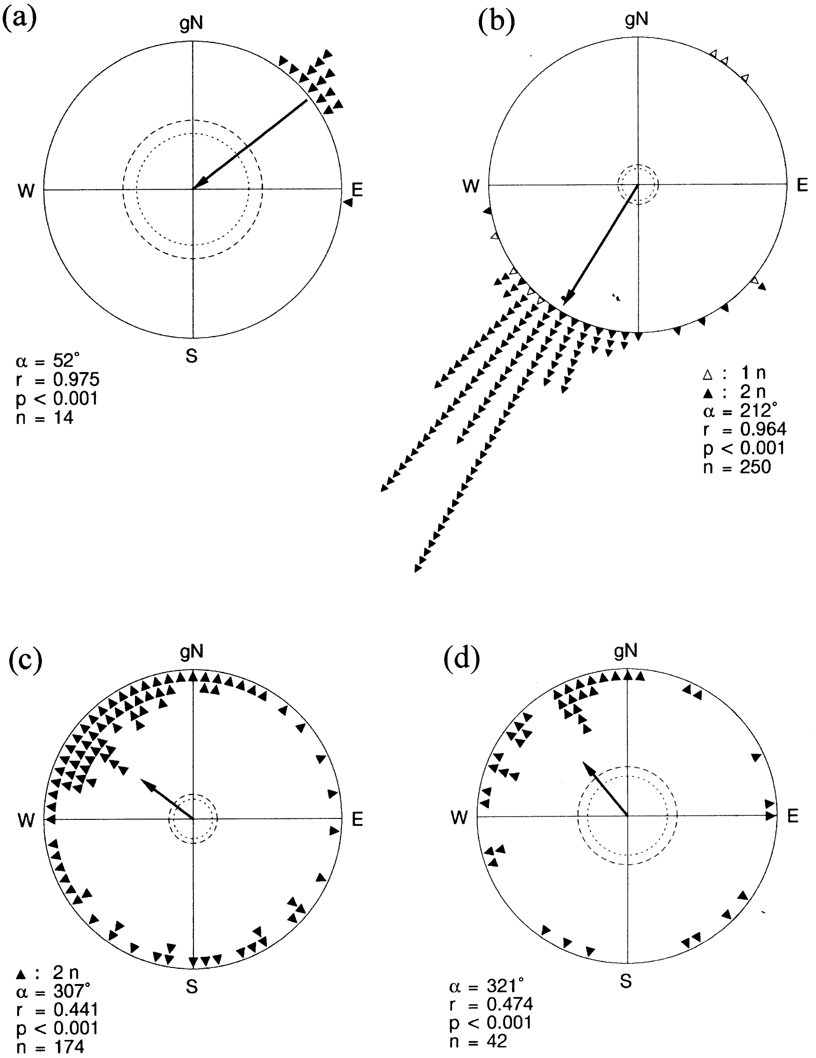

Fig. 2: Mean orientation directions of chaffinches at Col de Bretolet according to: a. recoveries of birds coming from the north (direction of origin); b. recoveries of birds flying to the south (migration direction; white triangle = one short-distance recovery, 10–98 km; black triangle = two long-distance recoveries, > 100 km); c. funnel experiments of all birds tested; d. funnel experiments of birds tested without view of the sun. Each small triangle represents the mean heading of one or two individuals. The arrow gives the mean direction (α) of the sample and is drawn according to the mean vector length (r) relative to the radius of the circle = 1. The inner dotted circle indicates the 5%, the outer broken circle the 1% significance level. gN = geographic north. See Table 1 for statistical comparisons

Table 1: Mean orientation direction of chaffinches in the funnel experiments (all birds and birds tested only under overcast conditions), compared with the migratory direction (migr. dir.; recoveries of >10 km only) and the direction of origin (origin) of free-flying birds according to ringing recoveries. The table shows significance levels of the median- and iqr-comparisons between the experimental direction and the expected direction as well as the direction of origin

Ringing recoveries			All chaffinches tested (n = 174)		Chaffinches tested under overcast (n = 42)	
			Median 304.0°	iqr 89.0°	Median 331.0°	iqr 61.0°
	Median	iqr	Median-comp.	iqr-comp.	Median-comp.	iqr-comp.
Migr. dir. (n = 258)	213.5°	12.0°	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Origin (n = 14)	48.5°	10.0°	$p = 0.007$	$p = 0.026$	$p = 0.039$	$p = 0.044$

Median = median direction; iqr = 50% interquartile range.

bimodal mean directions (Fig. 4, Table 3). The elevation of the sun had no noticeable influence.

Individual chaffinches that showed a low individual concentration oriented in a direction of 139° relative to the sun. This is significantly different from the direction of 170° that more concentrated birds chose relative to the sun (Fig. 3b, Table 2). The individual concentrations of the birds also had an influence on the spread of the data groups. Individuals with a low concentration oriented in more different directions, which resulted in a very scattered group. In contrast, birds that were highly concentrated as individuals oriented in more similar directions (Fig. 3b, Table 2).

Discussion

Chaffinches tested at the alpine pass Col de Bretolet did not orient in the seasonally expected direction known from ringing recoveries even under clear sky. Instead, our data suggest an influence of the sun when it was visible. The birds showed phototactic reactions, usually towards the lightest part of the funnel in the opposite direction of the light source in the north-west. When the sun was obscured by clouds the chaffinches showed a north-west orientation that also did not correspond to the expected migratory direction.

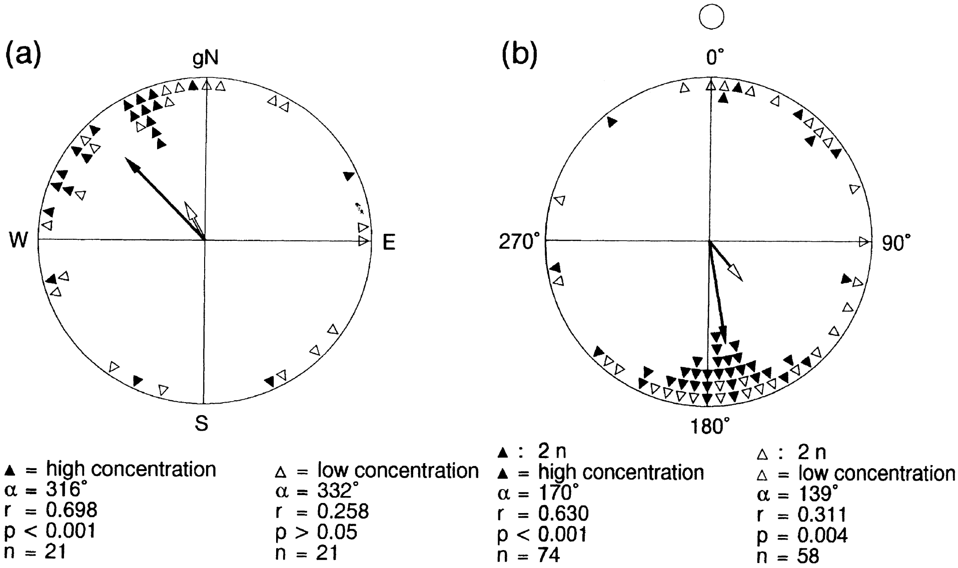

Fig. 3: Mean orientation direction of highly and poorly concentrated chaffinches: a. under overcast conditions (7/8–8/8), without view of the sun; b. in relation to the sun (0°) = circle. Each white triangle indicates the mean direction of an individual bird that was badly concentrated, each black triangle the mean direction of a bird with a good individual concentration. In b, each triangle represents two individuals. The mean directions and scatter of the two groups are indicated by white and black arrowheads, respectively. The arrows are drawn according to the mean vector lengths (r) of the groups relative to the radius of the circle = 1. For further explanations see Fig. 2. See Table 2 for statistical comparisons

Table 2: Median- and iqr-comparisons between data groups of chaffinches (see Fig. 3)

	Individual concentration	Median	iqr	Median-comp.	iqr-comp.
Chaffinches without view of the sun	Low (−0.301–−0.062)	343.0° ns	117.5°	—[1]	p = 0.021
	High (−0.041–0.581)	329.0°	46.0°		
Chaffinches with view of the sun	Low (−0.443–−0.056)	145.0°	141.0°	p = 0.001	p = 0.001
	High (−0.032–−0.415)	171.5°	331.0°		

ns, p > 0.05.

[1] No median-comparison because of undirected sample.

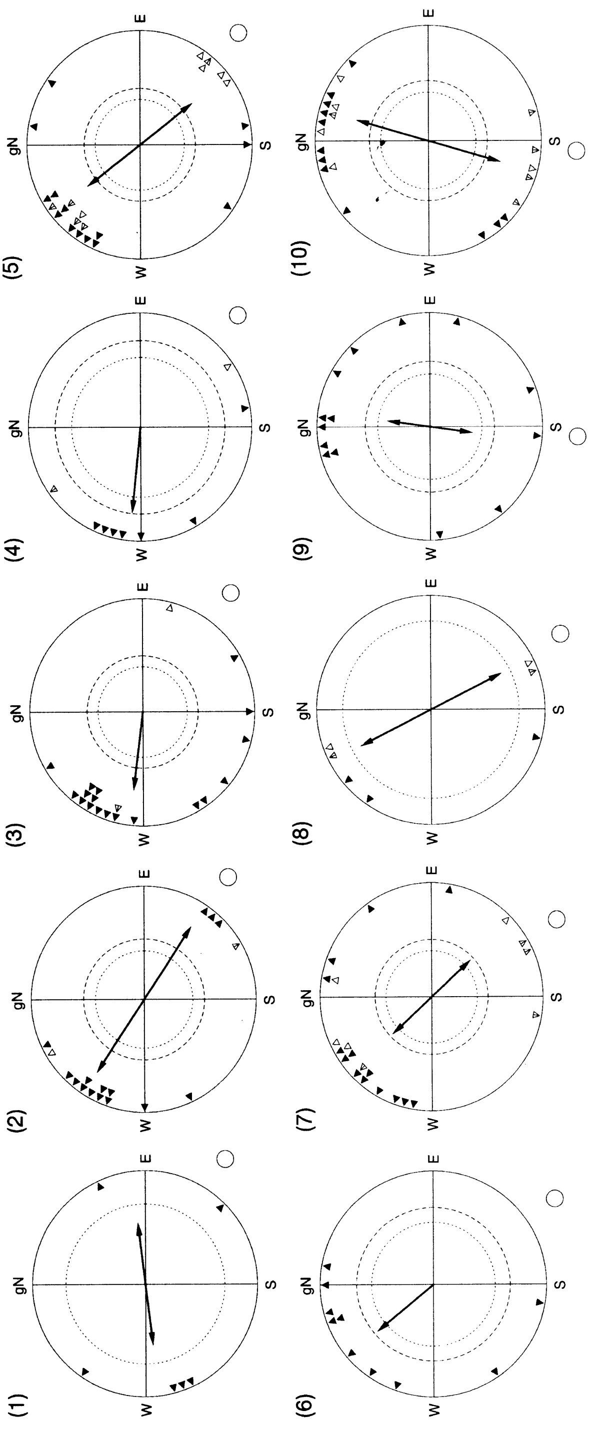

Fig. 4: Mean orientation directions of 10 groups of chaffinches tested under the same position of the sun. Axial individuals are marked with two white triangles 180° apart. The direction closer to the unimodal direction and thus included in the statistical analysis is marked with a line. Circle = sun. For further explanations see Fig. 2. See Table 3 for statistical comparisons

Table 3: Groups of chaffinches tested simultaneously and under the same environmental conditions, listed for increasing sun azimuth. The table shows the date and time of testing, the number of individuals per group (n), the mean group direction (α), the mean vector length (r), and the significance of the distribution of each group according to the Rayleigh test (p). Also given is the position of the sun in the middle of the experiment, indicated by the axis of the azimuth and elevation

	Funnel experiments						Sun	
	Date (1995)	Time (h)	n	α	r	p	Azimuth + axis	Elevation
1	2 Oct.	0900	6	83° + 263°	0.546	ns	123° + 303°	23°
2	10 Oct.	0900	16	123° + 303°	0.774	0.0001	125° + 305°	21°
3	16 Oct.	0900	19	277°	0.694	0.0001	127° + 307°	19°
4	8 Oct.	0930	8	276°	0.755	0.0105	132° + 312°	26°
5	11 Oct.	0930	19	142° + 322°	0.592	0.0013	132° + 312°	25°
6	2 Oct.	1030	10	320°	0.649	0.0148	145° + 325°	34°
7	19 Oct.	1030	18	137° + 317°	0.479	0.0161	149° + 329°	29°
8	23 Oct.	1030	5	153° + 333°	0.695	ns	150° + 330°	28°
9	23 Oct.	1230	14	8° + 188°	0.384	ns	184° + 4°	32°
10	21 Oct.	1230	17	16° + 196°	0.662	0.0006	184° + 4°	33°

ns, $p > 0.05$.

Orientation under Sunny Conditions

Although the use of a time-compensated sun compass in diurnal bird orientation has been widely accepted (Wiltschko 1981; Schmidt-Koenig 1990), it probably plays only a secondary role in the orientation cue system of day migrants. Experiments with starlings and Australian yellow-faced honeyeaters suggest that the magnetic field of the earth is the prominent orientation cue when establishing the orientation direction (W. Wiltschko 1980; Munro & R. Wiltschko 1993). The sun can be used by day-migrating birds as a landmark that serves as a temporary target toward which to orient (R. Wiltschko 1980).

At Col de Bretolet, the groups of chaffinches tested under sunny conditions also had access to the natural geomagnetic field. The chaffinches primarily showed phototactic behaviour towards the best lit parts of the funnel. Groups 9 and 10 (Fig. 4) suggest that it is not a simple north-west orientation, as in the birds tested without view of the sun, although mirror experiments would be required to test these conclusions. Similar results were found during spring migration on a Danish island (Petersen & Rabøl 1972). Bramblings *Fringilla montifringilla* and chaffinches tested during the morning hours also showed an antisun-taxis and did not orient in the seasonally appropriate NNE direction under overcast condition but to the south-west and south-east, respectively (Petersen & Rabøl 1972). However, chaffinches tested in Sweden in autumn oriented in the seasonally expected migratory direction or showed an axial distribution. Their orientation behaviour was not influenced by the sun and there were no differences between clear sky and overcast conditions (Bäckman et al. 1997).

The individual chaffinches tested at Col de Bretolet that were well concentrated in the funnels were more sun-dependent. Birds with only a poor individual concentration chose directions independent of the sun. Their individual activity, however, did not differ from the group with a good individual concentration (unpubl. data). This indicates that when the sun was visible, it prominently influenced the orientation behaviour of the chaffinches, but not their activity in the funnels. This orientation towards a point of light is most likely an escape reaction from the orientation cage rather than a sun compass orientation.

Orientation under Overcast Conditions

The chaffinches without a view of the sun chose directions to the north-west. Individual birds with a high concentration of scratches in the funnel oriented more clearly in this direction than did birds with a low individual concentration. This indicates that birds that had made a clear directional decision chose a north-west direction. The reasons for this north-west orientation of chaffinches that could not see the sun could be reverse migration, a compensatory behaviour to return to the initial migration route, or nonsense orientation or default behaviour.

Reverse migration

Reverse migration is an exploration back along the migration route for suitable stop-over sites (Baker 1978). Migrants with small fat reserves reverse their flight direction when encountering an ecological barrier such as a coast (Alerstam 1978). In chaffinches and bramblings, the proportion of lean and young birds was larger in birds showing reverse migration than in those proceeding in the normal direction (Lindström & Alerstam 1986). Reversing the orientation direction in front of an ecological barrier, such as a coast, may be advantageous for small landbirds because the availability of food is usually greater at sites further away from the barriers and competitors, and predators may be less numerous than at the coast (Alerstam 1978). However, chaffinches showing north-westerly orientation directions at Col de Bretolet were not in the situation of being in front of an ecological barrier but had just surmounted the Alps. Directional comparisons revealed no differences between lean and fat or between young and old birds. Furthermore, since no migration of free-flying chaffinches was visible to the north-west, this phenomenon cannot be explained as reverse migration.

Compensatory behaviour

Birds that are blown from their original migration route by wind or that have to make detours because of topographic barriers, may compensate for this deviation in different ways (Alerstam 1979, 1990). Most of the birds caught at Col de Bretolet do not have to make directional changes to reach the pass, except for the few day-migrants from the direction of Lake Geneva. Therefore, we do not think that the chaffinches were compensating. All the visible chaffinch migration at Col de Bretolet is directed to the south-west and no migration is obvious in the direction to the north-west, although there is a valley leading towards the latter. Why should the birds in the funnel display compensatory behaviour while the free-flying birds were not?

Nonsense orientation or default behaviour

Nonsense orientation has been described in birds which oriented towards the north-west (Matthews 1961; Sandberg et al. 1988, 1991a; Åkesson et al. 1995) even in release experiments (Sandberg et al. 1991b). Sandberg et al. (1991a) proposed that this meaningless north-westerly orientation could result from either an inability to perceive the geomagnetic field or a simple default behaviour. They argue that birds that could not see the lower parts of the sky and the horizon were unable to measure the inclination angle of the geomagnetic field relative to it. We suspect that birds calibrate their inclination compass to the true vertical (i.e. to gravity) since, in mountainous regions, vertical horizons are rare. However, a default behaviour seems reasonable to us. Birds placed in a situation where they cannot assess enough orientation cues resort to a default response. However, why this default direction is north-west in many cases (Matthews 1961; Sandberg et al. 1988, 1991a,b; Åkesson et al. 1995; this study) is still unclear and requires further investigation.

Conclusions

Why were the chaffinches in this study unable or unwilling to orient in the seasonally appropriate migratory direction, and what caused the phototactic behaviour? Magnetic anomalies in the area of Col de Bretolet can be excluded (Fischer et al. 1979). The main difference between our experiments and most other studies is that we tested the chaffinches immediately after catching. The procedure of catching, ringing and testing must have confounded the birds' ability to choose the appropriate direction. Handling stress and perhaps unknown physiological factors may explain the inability to orient properly, thereby leading to default behaviour. The birds are perhaps very motivated to continue their migration but are too stressed to orient properly. This could also explain why the chaffinches studied by Bäckman et al. (1997) oriented in the seasonally expected migratory direction and were not influenced by the sun. In their study the chaffinches were held in captivity for up to 14 d prior to the experiments. Since our chaffinches were captured during migratory flight they already had selected their migratory direction before they started their flight in the early morning. Possibly, this compass course cannot be changed during migratory flight, but only maintained. How birds maintain their chosen migratory direction or how and whether they choose new directions during flight has not yet been examined.

The following conclusions can be drawn from the experiments of this study: Funnel experiments are a good method to study orientation behaviour provided that the birds are not stressed too much. In contrast to hand-raised birds or birds kept for some time in captivity, freshly caught birds appear to be less suitable for such experiments. They may have problems recalibrating their orientation cues or just be too stressed to show any orientation behaviour at all. Our expectation, that birds caught during active migration can use orientation information collected on their incoming flight in the funnel experiments after handling, was not confirmed.

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