to equip the pigeon with a radio-controlled instrument allowing the experimenter to manipulate stimuli postulated to be used in selecting the homeward direction. Walcott and Green [13] reported that artificial magnetic fields around a pigeon's head caused deterioration in homing under overcast skies. Replication of this experiment with remote control of the artificial field might open up an important new approach to the challenging problem of bird navigation.

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The sun compass

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Summary. The sun compass was discovered by G. Kramer in caged birds showing migratory restlessness. Subsequent experiments with caged birds employing directional training and clock shifts, carried out by Hoffmann and by Schmidt-Koenig, showed that sun azimuth is used and sun altitude ignored. McDonald found the accuracy to be $\pm 3° - \pm 5°$. According to Hoffmann and to Schmidt-Koenig, caged birds trained at medium northern latitudes were able to allow for the sun's apparent movement north of the arctic circle but not in equatorial and trans-equatorial latitudes.
In homing experiments, and employing clock shifts, Schmidt-Koenig demonstrated that the sun compass is used by homing pigeons during initial orientation. This finding supports the existence of a map and compass navigational system. Pigeons living in equatorial latitudes utilize the sun compass even under the extreme solar conditions of equinox (Ranvaud, Schmidt-Koenig, Ganzhorn et al.). The use of the sun compass during zenith passage of the sun is being investigated.
Key words. Sun azimuth compass; clock shift; initial orientation; directional training; homing pigeon.

Experiments with caged birds

Discovery of the sun compass

In the late forties, Gustav Kramer [8] discovered that migratory restlessness of caged migrants was directed rather than random. In a series of pioneering studies with starlings (*Sturnus vulgaris*) Kramer [9] was able to show that the sun is the directional cue used by the birds during daytime. Following Santschi's mirror experiment [18], mirrors attached to the testing cage shifted the bird's directionality as predicted (fig. 1). These initial investigations were dependent upon the bird's migratory restlessness, which is highly seasonal and restricted to certain hours of the day. In order to overcome these restrictions Kramer and St. Paul [11] and Kramer [9] succeeded in training starlings in a circular cage to look for food in a certain compass direction. This technique made experimenting independent of migratory season and time of day.
With only sky and sun visible to the birds in the training apparatus, the birds maintained their training direction in the course of the day. This result strongly supported the conclusion of the preceding mirror experiment:

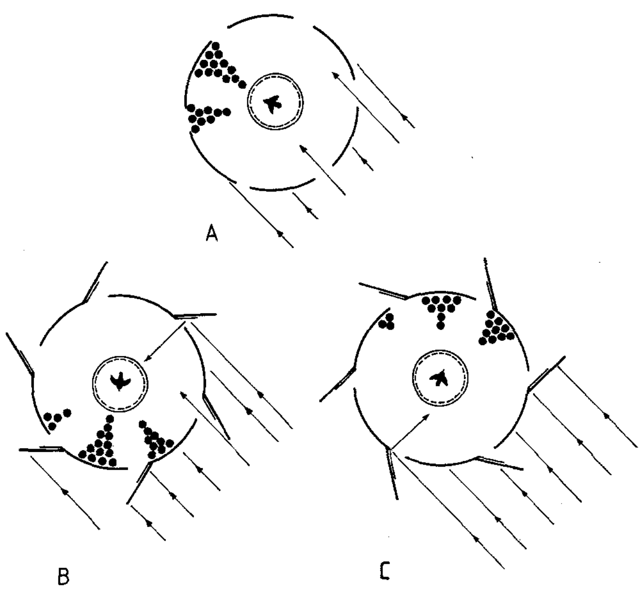


Figure 1. Gustav Kramer's[9] mirror experiment with a migratorily restless starling in a circular arena with 6 windows. Each dot inside the arena symbolizes one average direction observed in a 10-s interval. *A* Control condition, *B* with mirrors attached clockwise and *C* attached counterclockwise. Arrows indicate the direction of incoming sunlight.

Kramer had discovered the sun compass in birds. The starlings allowed for the sun's apparent movement. For this task the bird needs to keep track of the time of day, i.e., it must possess a chronometer, also known as an internal or biological clock, and it must have knowledge of the sun's apparent movement.

The interaction between chronometry and the sun's apparent movement was particularly illuminated in experiments subsequently carried out by Hoffmann[5], who demonstrated that the starling's biological clock could be reset experimentally. The number of hours of resetting – 6 h counterclockwise in Hoffmann's original experiment – resulted in a predictable shift of the bird's directional orientation in the training apparatus. The prediction is roughly 15° of directional shift for every h of time or clock shift. The sun's rate of change of azimuth is on the average 15°/h.

The bird's clock is easily reset if the bird is confined in a light-proof room with artificial light regimes, e.g. shifted 6 h clockwise or counterclockwise with respect to the local photoperiod. In training experiments with homing pigeons, Schmidt-Koenig[19–21] tested the effect of clock shifts of 6 h clockwise (CW), 6 h counterclockwise (CCW) and 12 h (to a reversed photoperiod). The results agreed with the prediction, and confirmed and extended Hoffmann's results with starlings; a time shift of 6 h CW resulted in a directional shift of approximately 90° CCW, a time shift of 6 h CCW resulted in a directional shift of approximately 90° CW, a time shift of 12 h produced directional reversal by approximately 180°. Schmidt-Koenig[19,21] also demonstrated that shifts of 6 h CW or CCW take 4 days and that 12-h shifts take 6 days to attain full effect. There was no indication that the birds paid attention to sun altitude even if expected sun altitude (e.g. near the horizon at 06.00 h) was grossly different from that actually seen (e.g. culminating at 12.00 h), or if the sun was ascending rather than descending and vice versa. Only sun azimuth seemed to be used by the birds. This compass was therefore called a sun azimuth compass.

After the sun compass had been firmly established, experiments were extended to answer a number of relevant questions: a) how accurate is the sun compass? b) how do birds cope with the latitudinal variability of the sun, i.e., in high northern latitudes and under equatorial and transequatorial conditions? c) do birds use their sun compass out of doors, e.g., for short range orientation or long distance navigation and homing? d) how is the sun compass established ontogenetically in the individual bird?

Accuracy of the sun compass

The 'Kramer cages' used through the late sixties were technically considerably improved compared with the original model, but investigations were still plagued with a rather large scatter of the results. This methodological drawback essentially prevented the assessment of the accuracy of the sun compass. McDonald[14] introduced an operant conditioning technique which overcame this methodological problem. With this technique the bird trains itself automatically with much less scatter. The pigeon's performance turned out to be quite disappointing. Though the bird was fixed and sitting, and not exposed to the additional shaking of flying in turbulent air, the pigeons' sun compass accuracy was found to be between $\pm 3.4°$ and $\pm 5.1°$. A sun compass accuracy of $\pm 3.4° - \pm 5.1°$ is not as good as one would expect. However, computer simulations of homing flights suggested that a sun compass accuracy similar to that demonstrated in these training experiments would be sufficient for homing success and would achieve the speeds actually recorded in homing experiments if the birds correct en route with sufficient frequency.

More experiments on the accuracy of the sun compass have been carried out in homing experiments with pigeons under the special conditions of equatorial zenith culmination[3] and will be discussed below in the section on homing experiments.

Latitudinal variability

The sun's apparent path, or its azimuth component, varies with season but most drastically with geographical latitude. Migrants migrating within one hemisphere, even more so migrants migrating to equatorial latitudes, and particularly transequatorial migrants, have to cope with this variability when using a sun compass. There is as yet insufficient experimental evidence to answer the questions raised by this.

Starlings[6] and homing pigeons[23], after sun compass directional training at medium northern latitudes, have been tested in their training cages after displacement north of the Arctic Circle (starlings from Wilhelmshaven, Germany, to Abisco, Sweden; pigeons from Durham, N.C., USA, to Barrow, Alaska). Both allowed, by and large, for the local sun during that part of the day that was also day in their home latitude. The starlings were also well oriented under the midnight sun. The pigeons' sun compass orientation 'at night' was somewhat less clearcut.

Sun compass orientation after equatorial and transequatorial displacement has been investigated in the same species by the same authors[22]. Unfortunately, the starling is not an equatorial or transequatorial migrant, and the pigeon does not migrate at all. Both responded alike; they referred to the sun of the southern hemisphere – rising in the east, culminating in the north and setting in the west – as if it were the sun at home. This means the birds were incorrectly oriented. Attempts by Schmidt-Koenig (unpublished data) to repeat the experiment with a passerine transequatorial migrant, the bobolink (*Dolichonyx oryzivorus*) failed because birds trained in North Carolina either escaped or died before they had been displaced and tested in South America. Thus, basic questions as to the sun compass function in equatorial and transequatorial migrants remained unanswered. However, the use of the sun compass under equatorial sun conditions was tested, or is being tested, in homing experiments with pigeons living in and homing to lofts at the equator. These experiments will be discussed below.

The use of the sun compass in short range orientation

The use of the sun compass in short range orientation has been investigated in scrub jays (*Aphelocoma coerulescens*)[32]. In their natural environment they harvest seeds of the pinyon pine and cache them underground. Captive birds were tested in octagonal outdoor aviaries. Cups filled with sand, inserted in the floor, were arranged in four 90°-sectors. In each experiment one sector only was offered for caching. During critical tests all sectors were available to the birds for searching. In control tests, the birds preferentially probed the cups in the sector in which they had cached the seeds. Upon a time shift of 6 h CCW, the birds preferentially probed the sector to the right (CW) of the sector in which seeds had been cached. This result conforms to the prediction. The jays seemed to use their sun compass to directionally retrace their caches despite the fact that ample familiar visual landmarks were available to them. This evidence parallels the findings in homing pigeons (to be discussed below); it underlines that sun compass orientation is very prevalent in spatial orientation in everyday tasks, and not just in long distance migration and homing.

Homing experiments with pigeons

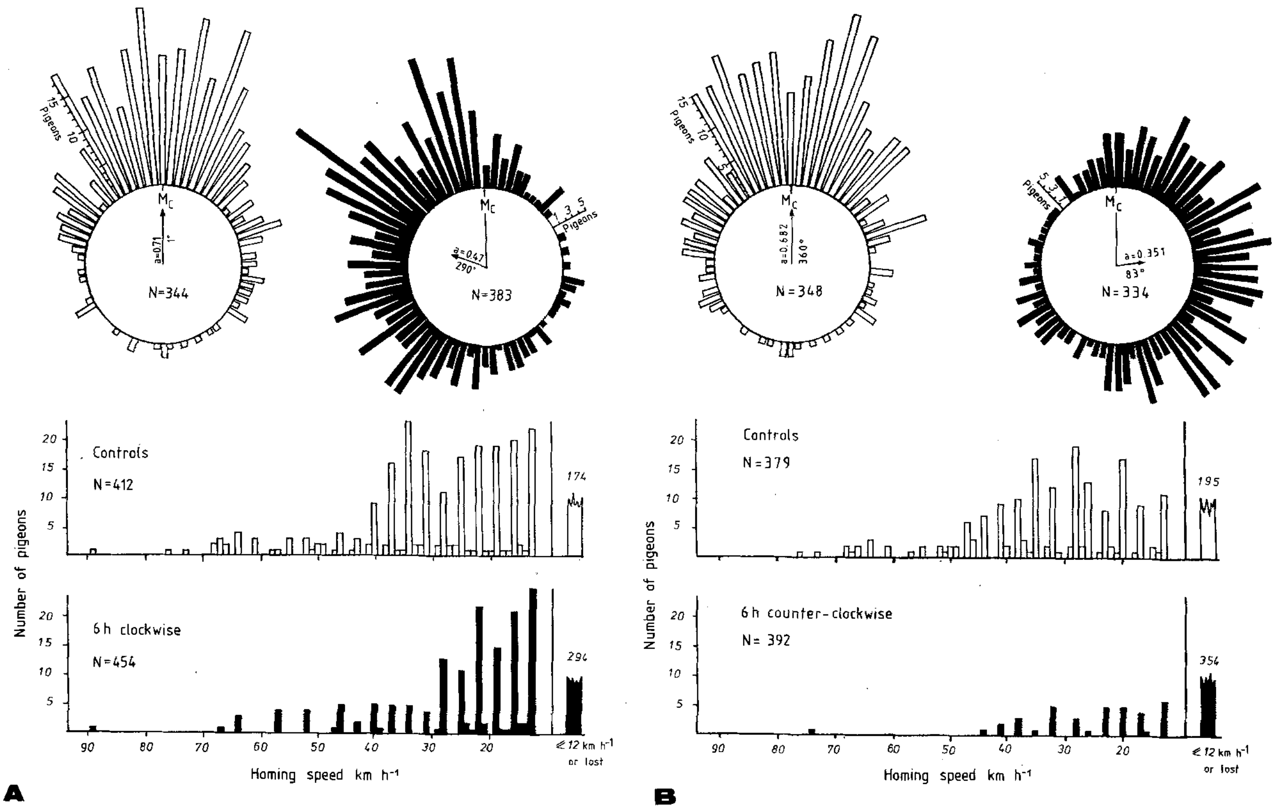
The sun compass in initial orientation

The sun compass was discovered in laboratory experiments with caged migratorily restless passerine birds. Details of its functional principles have been studied mostly in laboratory experiments with nonmigratory homing pigeons. Even the most convincing results obtained in the laboratory do not provide evidence that the demonstrated capacities are also used in migration or homing. The laboratory provides an experimental environment which purposefully and considerably reduces sensory stimulation and input. A partial orientation task in the laboratory, such as sun compass training, is accomplished out of the context of a navigational process. Experiments involving actual navigation, such as homing in pigeons, are crucial.

In contrast to the situation in migrating birds, in the case of homing pigeons it was easy to apply clock shifts and test whether or not the sun compass is, in fact, used in homing. As in the laboratory experiments with single birds, groups of pigeons were time-shifted 6 h CW, 6 h CCW, or 12 h. Control birds were held in rooms for the same time without shifted light regimes. After at least 4 days in the shifting rooms in the case of 6 h shift, and at least 6 days in the case of 12 h shift, the birds were taken to release sites and released. Figure 2A–C summarizes initial orientation and homing performance in a large series of homing experiments from many release sites, carried out by Schmidt-Koenig[21, 24, 26]. It is obvious, and statistical treatment of the data confirms, that the shift of initial orientation accomplished by time-shifting the clock and compass, respectively, correspond to the prediction; the sun compass is used during initial orientation. As a consequence of the misled initial orientation, homing performance was clearly reduced (fig. 2, A–C, rectangular diagrams). In additional homing experiments, smaller degrees of clock shift produced smaller deflections of initial orientation[25]. The effect of clock shifts on initial orientation and homing speeds has been confirmed everywhere and many times[2, 7, 15, 29–31, 33] always confirming predictions with clearcut results and interpretations.

Clock shift is to date the only experimental interaction with pigeon homing to produce reliable, predictable and unequivocally interpretable results. Clock shifts have been widely used as experimental tools and they turned out to deflect birds at distances of several hundred kilometers, as well as within less than 2 km from the loft[1, 4, 27]. Even when the loft building was plainly visible to the human observer from the release site, at least some clock-shifted birds flew according to their shifted compass, and some were even reported far away. These findings are important inasmuch as they demonstrate that pigeons try to navigate even when close to the loft, and that they pay little if any attention to familiar landmarks, either visible or possibly of other kinds.

The evidence that the sun compass is in fact used supported Kramer's[10] original concept of a navigation system of 'map and compass'. In the first, the navigation step, the displaced animal establishes its position in relation to the goal; in the second step it uses its compass to



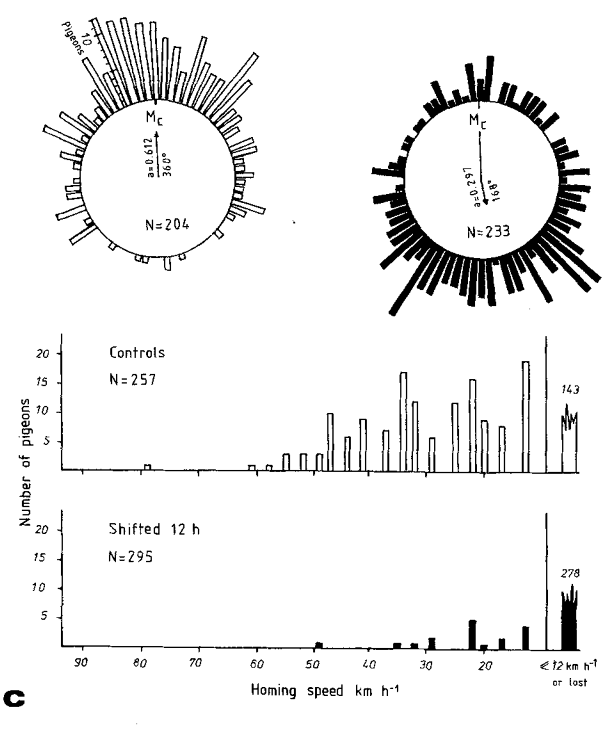


Figure 2A–C. Summary of initial orientation (circular diagrams) and homing performance (rectangular diagrams) in the clock-shifting experiments of Schmidt-Koenig[21,24,26]. Experimental birds are given in solid bars, controls in open bars according to scale. The time shift involved in series A, B, C is indicated in the lower rectangular diagram of each series. The length of bars are proportional to the number of birds according to the scale given. Initial orientation of control birds is plotted with means coinciding up. Initial orientation of experimental birds is plotted with reference to the mean of controls (M_c). Total sample sizes (N) as well as mean vectors as centrifugal arrows with length (a) and direction (°).

steer home. It turned out that the sun is used for compass purposes and not for navigation as suggested by Matthews[12,13]. Sun azimuth was used by the birds, and sun altitude was ignored. After this basic question had been answered, additional details remained to be clarified.

Accuracy and seasonal variability

One of the additional questions that remained was that of the accuracy of the sun compass under natural conditions of homing. The angular shift of initial orientation actually observed in clock-shifted birds did not always exactly agree with the prediction, particularly if seasonal

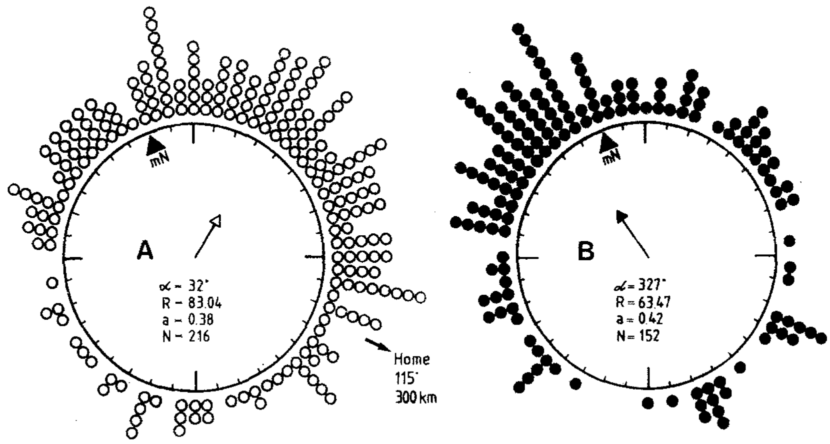


Figure 3. Summary of initial orientation of homing pigeons released at the equator in NE Brazil, *A* at about 30° sun zenith distance in the forenoon and afternoon, *B* within ± 6° sun zenith distance around zenith passage of the sun. Symbols as in fig. 2, however, plotted with reference to geographic north (up). Magnetic north (mN, 20° left of geographic north) is given. From Schmidt-Koenig, Ganzhorn and Buschold[28].

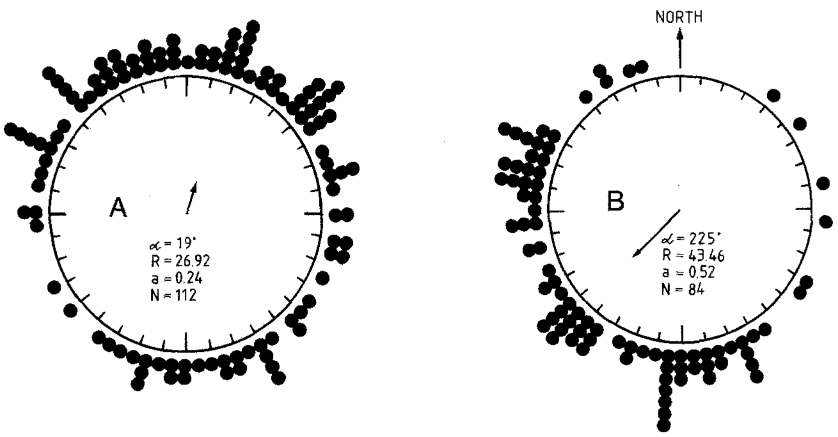


Figure 4. Summary of initial orientation at the equator of pigeons clock-shifted 4 h CCW vanishing at solar zenith distance of 30°–22.5°. *A* summarizes releases performed before noon, *B* summarizes releases performed after noon. Geographic north is up, magnetic north is 20° west of geographic north. From Ganzhorn et al.[3].

and latitudinal variability of the sun's rate of change of azimuth was taken into account. In order to test this aspect of accuracy, Ranvaud, Schmidt-Koenig and Ganzhorn et al.[3,17,18] carried out homing experiments with pigeons under the special solar condition of zenith passage of the sun at the equator in NE Brazil. During the equinox, the sun rises in the east and azimuth is due east all morning. The sun culminates in the zenith and azimuth stays due west till sunset.

In an extended series of homing experiments pigeons were time-shifted 4 h CCW. The experimental birds should expect transit from east to west azimuth 4 h after local noon when the sun is and remains due west; they would actually experience transit of sun azimuth from east to west 2 h after their subjective sunrise when they expect the sun due east. Corresponding shifts of initial orientation of 180° would be expected with a period of time of possible disorientation around zenith passage of the sun when the sun azimuth compass cannot work. To date only the latter condition has been tested experimentally with pigeons from local stocks.

As summarized in figure 3 A and B, untreated birds departed on the average NE when released during forenoon and afternoon at sun zenith distance of around 30°. The finding of a 'local bias' in untreated birds of roughly 90° to the left of home is not uncommon. When released around zenith passage of the sun (fig. 3 B), birds were not disorientated but departed towards NNW. As can be seen in figure 4 A and B, pigeons clock-shifted 4 h CCW and released in the morning at a sun zenith distance of 30°–22.5° showed a mean vanishing direction of 19°. Releasing pigeons clock-shifted 4 h CCW at 22.5°–30° solar zenith distance in the afternoon yielded the expected reversal of mean vanishing direction by about 180°. This clearcut result demonstrates that pigeons use the sun as a reference for directional orientation even under equatorial conditions.

Figure 5 A–C shows that pigeons clock-shifted 4 h CCW, released shortly before noon (12.00 h), when the sun's zenith distance was between 6° and 3° a.m., showed a mean vanishing direction of 345° (fig. 5 A). This distribution of vanishing bearings is not different from that of the

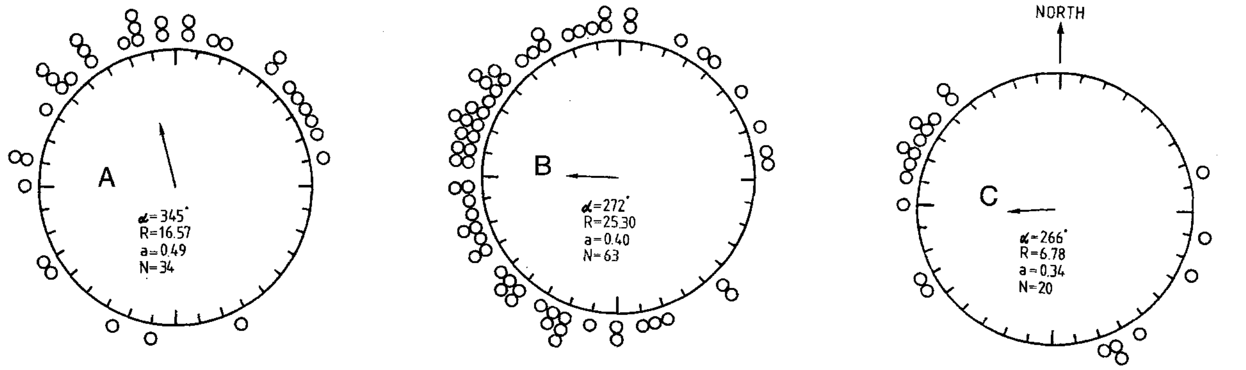


Figure 5. Summary of initial orientation at the equator of pigeons clock-shifted 4 h CCW vanishing at solar zenith distance of 6° a.m. to 7° p.m. *A* sun zenith distance between 6° a.m. and 3° a.m., *B* sun zenith distance between 2.9° a.m. and 2.9° p.m., *C* sun zenith distance between 3° p.m. and 7° p.m., symbols as in figs 2 and 4, respectively. From Ganzhorn et al.[3].

sample of vanishing bearings of pigeons clock-shifted 4 h CCW released earlier during the day at sun zenith distance of 30°–22.5° (fig. 4A), i.e., when the sun compass is clearly available to them. This suggests that both groups of pigeons were using the same mechanism to find their direction. During zenith passage, when sun zenith distance was between 2.9° a.m. and 2.9° p.m., pigeons vanished on the average at 272° (fig. 5B). This distribution is significantly different from that obtained with pigeons released shortly before noon (fig. 5A) when sun zenith distance was between 6° and 3° a.m. When the sun's zenith distance had increased to 3° and 7° p.m., i.e. after the sun's passage through the zenith, the pigeons' vanishing bearings appeared to show a bimodal distribution (fig. 5C). This is the preliminary result of an as yet unfinished series. Doubling the angles yielded $\alpha_2 = 233°$, $a_2 = 0{,}60$, $N = 20$. After doubling the angles of all samples this distribution is significantly different from any sample considered in this analysis.

According to the data presented here, homing pigeons use different cues for direction-finding when sun zenith distance is less than $\pm 3°$ than at larger values of sun zenith distance. Pigeons released just before noon at solar zenith distance of 6°–3° (fig. 5A) behave similarly to pigeons released earlier in the morning (fig. 4A), indicating that their sun compass is still operating. During zenith passage of the sun, pigeons still showed a pronounced directional preference but their mean vanishing direction was rotated CCW with respect to the sample recorded just before noon. After zenith passage of the sun and after it had descended from zenith distance 3° p.m. to 7° p.m., the vanishing bearings appeared to be distributed bimodally (fig. 5C). These changes are not consistent with the predictions. First, when the sun was within 2.9° of the zenith, the vanishing bearings were not distributed randomly. Rather, pigeons flew towards the west (fig. 5B). For the time being there is no explanation for this phenomenon. Secondly, the 180° reversal of direction expected after zenith passage of the sun did not occur immediately, though the bimodality of the last group of pigeons (fig. 2C) could be considered as the beginning of a reversal.

Though the interpretations of this experiment are speculative, the results indicate that homing pigeons obtain cues from the sun for compass orientation even in the extreme solar conditions of the equator and even when the sun is very close to the zenith.

Ontogenetic development of the sun compass

Another question was that of the ontogenetic development of the sun compass in the individual bird. Experimental results published by Wiltschko et al.[34] and Wiltschko and Wiltschko[33] indicate that the sun compass is learned, rather than innate as previously assumed. The authors reared pigeons under conditions of permanent clock shift of 6 h CCW. The birds were given free flight and short-distance training flights during the afternoon, i.e., during the common light period of the 6 h CCW and the natural day. When released, experimental birds and control birds were oriented towards home. After resynchronization of the 6 h CCW shift to natural conditions, the experimental birds performed like birds after a shift 6 h CW. Their initial orientation was shifted CCW from that of control birds. In later releases the sun compass turned out to be readjusted to natural conditions and the birds could now orient correctly. Hence, the birds' association of time, sun azimuth, and geographic direction appears to be established in a learning process. The sun compass may be recalibrated and it does not seem to be innate. There is some evidence that the sun compass is calibrated on the basis of the magnetic compass[34]. An alternative model by Phillips and Waldvogel[16] suggests that the pigeon's sun compass may be calibrated with respect to celestial polarization patterns.

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Magnetic orientation and celestial cues in migratory orientation

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Summary. Young birds on their first migration possess innate information on the direction of their migration route. It is present in two forms, using celestial rotation and the geomagnetic field as references. These two systems, together with information provided by factors associated with sunset, interact in a complex way to establish the migratory direction. During ontogeny, celestial rotation appears to be dominant; during migration, however, celestial cues appear to be controlled by the magnetic field. The factors associated with sunset – the view of the setting sun, the characteristic pattern of polarized light – are important secondary cues which seem to derive their directional significance from the magnetic field. Their role appears to be more variable, with possible species-specific differences. During spring migration and later autumn migrations, flying in the migratory direction is complemented by navigational processes which enable the birds to return to a specific home site known from previous stays.
Key words. Migration; magnetic compass; star compass; celestial rotation; polarized light; navigation.