

## OLFACTORY CUES PERCEIVED AT THE HOME LOFT ARE NOT ESSENTIAL FOR THE FORMATION OF A NAVIGATIONAL MAP IN PIGEONS

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### Summary

Deflector lofts consist of a 'pinwheel' arrangement of four stationary deflector panels attached to the sides of a cube-shaped cage. These panels are made of wood and Plexiglas and rotate incoming winds in either a clockwise or counterclockwise direction. When released at a distant site, homing pigeons (*Columba livia*) raised in deflector lofts exhibit a shift in orientation relative to controls which corresponds to the clockwise or counterclockwise rotation of winds in their loft, suggesting the involvement of wind-borne olfactory cues in pigeon navigation. As part of a long-term study designed to test whether orientation cues other than odors might also be involved in creating the deflector-loft effect, we carried out experiments in upstate New York, USA, in which deflector lofts were modified to reverse the direction of light reflected from the Plexiglas panels while leaving the rotation of winds unchanged. The results indicate that the orientation of pigeons raised as *permanent* residents of these altered deflector lofts is not influenced by reflected light cues; i.e. they exhibit the same orientation bias as birds raised in the lofts with normal panels. This is in direct contrast to our previous findings that *non-resident* pigeons kept in the altered lofts for short periods exhibit a reversal of initial orientation compared to birds from the lofts with normal panels. However, when permanent-resident birds are prevented from having a direct view of the horizon sky by the addition of 'anti-cheating' slats (which prevent the birds from seeing beyond the end of each panel), the deflections are either greatly reduced or eliminated entirely, contrary to the predictions of olfactory navigation models. This disappearance of the deflector-loft effect in the presence of anti-cheating slats suggests that the positions of the deflector panels in the two experimental lofts must be differentially influencing important visual orientation cues reaching the birds housed inside. We believe that these cues are probably derived from polarized skylight emanating from the horizon, and that the obstruction of specific regions of horizon skylight by the deflector panels in the two experimental lofts is

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responsible for a miscalibration of the pigeon's sun compass. This miscalibration, in turn, generates the orientation bias observed for deflector-loft birds. Our findings force us to conclude that, at least for pigeons raised in New York (and perhaps those from other geographical locations as well), olfactory cues perceived at the home loft do not contribute to the formation of the navigational map.

### Introduction

Homing pigeons (*Columba livia*) are thought to employ a two-step navigational process when orienting from a distant release site (Kramer, 1952). The first step involves the use of a 'map', which allows the bird to determine its geographical position relative to the home loft, while the second requires a 'compass' to aid in choosing an appropriate flight direction once the home bearing has been determined. A variety of potential map cues have been proposed over the past 30 years (reviewed by Able, 1980), but olfaction has received the most attention recently. A wide variety of experiments have yielded results that are apparently consistent with the occurrence of odor navigation in pigeons (reviewed by Papi, 1976, 1982, 1986), but the interpretation of these results remains a matter of continuing debate (see discussions by Papi, 1986; Schmidt-Koenig, 1987; Waldvogel, 1987, 1989). Nevertheless, supporters of the olfactory model feel that the evidence is compelling. Indeed, they have suggested that odors represent both a necessary and a sufficient element in the formation of the pigeon's map (Wallraff, 1981, 1983; Papi, 1982, 1986), thus calling into question the concept of a navigational system that employs multiple, and perhaps even redundant, orientation cues (Keeton, 1974). Among the experiments often cited as support for the essential role of odors in pigeon homing are those in which olfactory cues perceived at the home loft have been systematically manipulated. One such experimental design is the deflector loft (Baldaccini *et al.* 1975).

Deflector lofts are cube-shaped cages with a pinwheel arrangement of deflector panels attached to the four corners of each cage (Fig. 1). One loft rotates incoming winds in a clockwise direction, while the other rotates winds in a counterclockwise direction. According to the olfactory model, pigeons raised in deflector lofts are presumed to acquire an olfactory map that has been rotated either clockwise or counterclockwise relative to a map learned by control birds, which are raised in a loft lacking deflector panels. When released from a distant site, the model predicts that the experimental birds should manifest their 'rotated' maps as a bias of initial orientation relative to controls; i.e. pigeons from the clockwise (CW) loft should orient clockwise of control birds, while pigeons from the counterclockwise (CCW) loft should orient counterclockwise of controls. A large number of experiments using so-called 'permanent-resident' deflector-loft birds (i.e. homing pigeons raised in deflector lofts from the time of fledging) have tended to support the predictions of the olfactory model (Baldaccini *et al.* 1975, 1978; Kiepenheuer, 1978, 1979; Waldvogel *et al.* 1978; Waldvogel and Phillips, 1982). An orientation bias persists in deflector-loft birds even after repeated releases under sunny skies

at the same site (Baldaccini *et al.* 1978) as well as from year to year (Waldvogel and Phillips, 1982). In addition, if the direction of wind rotation within the two experimental lofts is reversed by realigning the deflector panels (i.e. clockwise is switched to counterclockwise and *vice versa*), the birds living in the lofts will, after several weeks, reverse their orientation bias accordingly (Baldaccini *et al.* 1978). Finally, Foà *et al.* (1986) report that deflector-loft pigeons that have been subjected to sectioning of the anterior commissure can exhibit more than one type of deflection when alternately housed in the CW and CCW lofts with either the left or right nostril plugged. Thus, for example, a bird might have its left nostril plugged while housed in the CW loft and its right nostril occluded while residing in the CCW loft. When tested subsequently with one or the other nostril plugged, the bird exhibits a deflection appropriate for the loft type in which the unoccluded nostril had access to olfactory information. Since the anterior commissure is a region of the avian forebrain that mediates interhemispheric transfer of olfactory neural information, these findings suggest that pigeons might actually create two separate olfactory navigational maps under some circumstances.

While these experiments tend to support the olfactory explanation of the deflector-loft effect, others raise questions about the role of olfaction in this phenomenon. For example, Kiepenheuer (1979) demonstrated that temporary chemical anosmia has no significant effect on the magnitude or direction of the permanent-resident birds' deflections. In addition, Kiepenheuer (1982) modified his deflector lofts by substituting a meshwork netting for the vertical slats which made up the cage walls in previous experiments, thus eliminating the laminar flow of air and creating a 'whirlwind' pattern of airflow inside the cage. The resultant blending of winds from all four directions into an ambiguous clockwise or counterclockwise circulation effectively eliminates any possibility of the birds

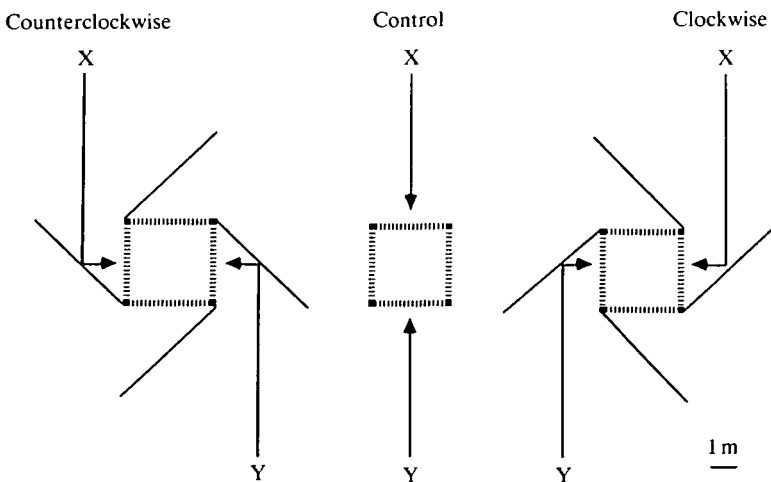


Fig. 1. Schematic overhead view of the counterclockwise, control and clockwise deflector lofts, showing the rotation of wind-borne odors (X and Y) induced by each loft type.

associating odors with particular directions. When raised in this directionless olfactory environment, Kiepenheuer's pigeons continued to show normal deflections, indicating that a clear perception of odor direction is not essential for generating biased orientation.

In previous experiments we have demonstrated that permanent-resident deflector-loft birds raised in upstate New York require the sun in order to exhibit a deflection (Waldvogel and Phillips, 1982). We tested birds at the same release site in successive experiments under conditions of sun, overcast and then sun again, and found that the deflection was greatly reduced or even eliminated entirely when the sun was not visible. Control tests involving successive releases in sunlight from the same site showed no decrease in the magnitude of the deflection, indicating (1) that the sun's presence is required for normal expression of the deflector-loft effect, and (2) that the reduction in deflection was not due to repeated flights at the same release site (in agreement with Baldaccini *et al.* 1978). These results, as well as others from experiments involving short-term residents of the deflector lofts, which implicate light cues in generating the deflector-loft effect (Phillips and Waldvogel, 1982; Waldvogel *et al.* 1988), have led us to propose that the deflector lofts rotate the apparent position of a compass calibration reference system derived from skylight polarization patterns. This rotation causes a miscalibration of the pigeon's sun compass which, in turn, leads to biased orientation (Phillips and Waldvogel, 1988). We therefore hypothesize that the deflector-loft effect in short-term residents is a result of the bird's use of a faulty sun compass mechanism, rather than a biased olfactory map. The present paper describes the results of experiments designed to investigate further the idea that celestial light cues, in particular skylight polarization patterns visible near the horizon, might also be responsible for generating the *permanent-resident* deflector-loft effect. Our experiments also bear directly on the question of whether olfaction contributes in any significant way to generating the deflector-loft effect.

## Materials and methods

### *Loft construction*

Details regarding the design and construction of our deflector lofts are available elsewhere (Waldvogel *et al.* 1978; Waldvogel and Phillips, 1982). Two major loft modifications were made for the experiments described in this paper. The first involved manipulating reflected light patterns visible within the lofts, and the second masking unreflected light patterns visible beyond the end of each panel.

The upper half of each normal deflector panel is made of 0.6 cm thick transparent Plexiglas sheets. In some of our experiments these panels were replaced by 'altered' panels, which are complex arrangements of alternating clear plate glass and opaque fiberboard (see Phillips and Waldvogel, 1982, for details). The altered panels cause reflected light patterns to be rotated in the reverse direction relative to a loft with normal panels, while patterns of wind rotation remain the same. For example, winds are rotated counterclockwise in both the

normal and altered CCW lofts, while reflected light patterns are rotated counterclockwise in the loft with normal panels and clockwise in the altered-panel loft (Fig. 2A). The situation is reversed when considering the normal- and altered-panel CW lofts.

A second loft modification prevented the birds from having direct access to unmanipulated light cues. In addition to the region of sky that is visible as light transmitted through or reflected from the panels, the original deflector loft design allows the birds direct visual access to four small segments of unaltered horizon sky visible beyond the end of each deflector panel (Fig. 2B). To prevent this, the altered lofts were fitted with 'anti-cheating' slats. These thin, opaque wooden slats were installed across the first meter of each of the four cage walls, starting at the end farthest away from the corner where the deflector panel makes its attachment to the wall (Fig. 2B inset). When in position, the anti-cheating slats prevent the birds from seeing skylight that is not either transmitted through or reflected from the deflector panels. The rationale for using the altered-panel lofts in these anti-cheating slat experiments (instead of the normal-panel lofts) was to force the birds into relying solely on reflected light cues. We thus expected them to show a deflection opposite to that normally exhibited by permanent residents of the lofts with normal panels (as has been repeatedly observed for short-term deflector-loft pigeons housed in the altered-panel lofts; Phillips and Waldvogel, 1982;

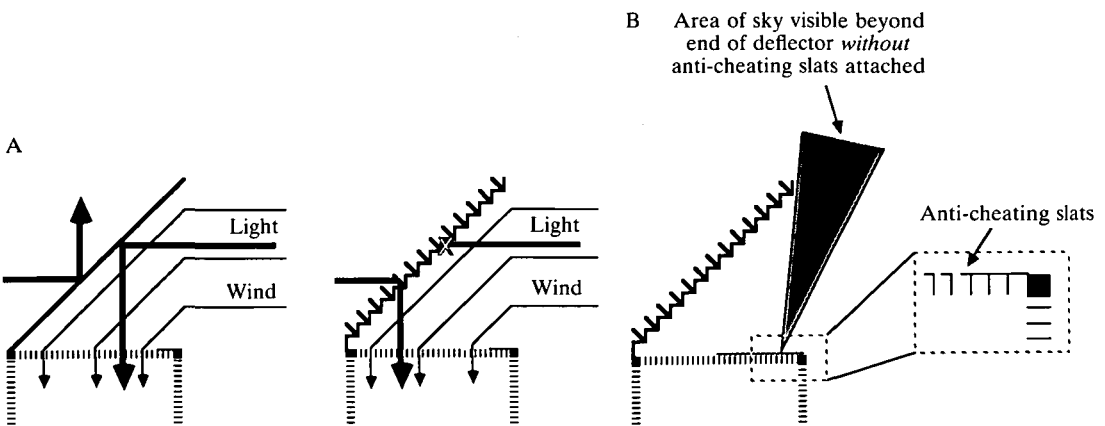


Fig. 2. (A) The effect of normal (left) and altered (right) deflector panels on wind-borne and light cues in a counterclockwise (CCW) deflector loft. Only a single panel is shown in relation to a portion of the cage walls (dashed line). The upper half of the normal panel is made of clear Plexiglas, which rotates winds and reflects light cues in the same direction. The altered panel reverses the rotation of reflected light relative to the normal panel but leaves the pattern of wind deflection unchanged. (B) Altered CCW loft with anti-cheating slats, showing the approximate region of horizon sky (shaded area) that the birds are able to see *before* the slats are attached to the loft. Inset shows the manner in which the anti-cheating slats are connected to the vertical slats that make up the cage wall.

Waldvogel *et al.* 1988). In other words, if permanent-resident birds resort to reflected light cues once a direct view of natural skylight is eliminated, they should reverse their deflection relative to that of birds raised in lofts without anti-cheating slats attached.

### *Training and testing of birds*

The pigeons used in our experiments were bred at the main loft facility of the Cornell University Pigeon Project, located 4.1 km south-southeast of the deflector lofts near Ithaca, New York, USA. During the early summer months (May and June) of 1977–1983, groups of 30–50 young homing pigeons were weaned into each of our deflector lofts 5–7 weeks after hatching. They were held captive in their lofts for 6–10 weeks, at which time they were given occasional free flights around midday in the immediate vicinity of the loft. Initially, our birds received very little flight experience beyond sight of the lofts unless they voluntarily strayed away during exercise flights (Waldvogel *et al.* 1978). Over the years, however, we found that allowing our birds brief flights of 15–30 min in the immediate loft area shortly after their arrival, and again after short training flights of less than 5 km at a later date, significantly reduced losses and improved vanishing times in experimental releases.

Many of our pigeons were kept as residents of the deflector lofts for several consecutive years. Unfortunately, New York winters do not permit the housing of birds in the deflector lofts from early November until late March. During this time our permanent-resident birds lived at the main loft facility where, to prevent their relearning the correct olfactory and visual world, they resided in one of four enclosed clockshift rooms with the light cycle synchronized to ambient conditions. This over-wintering technique did not appear to affect the birds' orientation bias, since normal deflections were observed when the birds were returned to the deflector lofts each spring.

In all, we used seven different release sites in our permanent-resident deflector-loft tests. The distance of these sites from the lofts ranged between 9.2 and 34.4 km. Two of the sites were located east of home (home directions=272° and 296°), two more to the south (home directions=347° and 8°), two others to the north (home directions=158° and 164°) and one to the west (home direction=98°). Testing consisted first of transporting the birds to a release site inside cloth-covered baskets while riding in the back of an open truck. These baskets eliminated a direct view of landmarks and celestial cues, but permitted the birds to smell natural odors. Once at the test site, the pigeons were released individually from the hand under sunny skies. The release of birds from different experimental groups was alternated, and each bird was observed with 10×50 binoculars until it vanished from view. Departure bearings were recorded to the nearest degree using a hand-held compass. Release times and vanishing intervals were also noted, and observers located at the deflector lofts recorded the arrival times of birds for use in determining homing speed and homing success.

*Statistical analysis*

Statistical testing of the data was performed using methods described by Batschelet (1981). Mean vanishing bearings (MVBs) were calculated for individual experiments using vector analysis and then tested against the null hypothesis of a uniform distribution using the Rayleigh test. The Watson  $U^2$ -test was used to compare distributions from different treatments directly. In most cases, the difference in mean vanishing bearing between experimental treatments ( $\Delta$ MVB) is the measure of interest in deflector-loft tests. When mean vectors for a specific treatment type (e.g. lofts without anti-cheating slats), which had been obtained at different release sites or in multiple years were pooled, second-order MVBs and 95 % confidence ellipses were determined for the distribution using Hotelling's one-sample test. Homing times and vanishing intervals were analyzed using the Mann-Whitney  $U$ -test, and homing success was compared with Fischer's exact test.

**Results**

Over the 7 years of our permanent-resident deflector-loft experiments, virtually all deflections obtained in releases under sunny conditions were in the direction predicted by the olfactory model (37 of 39 tests), regardless of whether the lofts were equipped with normal or altered panels. Although individual tests sometimes showed statistically significant differences among treatments with regard to vanishing intervals, homing times or homing success, at no time were we able to discern any consistent or repeatable overall patterns among these variables.

Fig. 3 shows the results of our permanent-resident deflector-loft tests plotted as a function of loft type. Since these data are from tests conducted at different release sites in different years, they have been normalized by setting the mean vanishing bearing of the CCW-expected group to zero (i.e. the top of each circular diagram) for every test and then plotting the relative orientation of the mean vector of the CW-expected group for that test. Vectors to the right of zero signify a clockwise deflection, while those to the left indicate a counterclockwise deflection. The 21 tests of birds housed in the deflector lofts with normal panels (Fig. 3A) exhibit a highly significant clockwise deflection in accordance with the expectations of the olfactory model (mean  $\Delta$ MVB=60°,  $r=0.6$ ). This result demonstrates the robust nature of the deflector-loft effect both within and between years.

Results from experiments involving altered-panel permanent residents are shown in Fig. 3B,C. The nine groups housed in altered lofts without anti-cheating slats attached (Fig. 3B) show a significant deflection in the olfactory predicted direction (mean  $\Delta$ MVB=80°,  $r=0.53$ ). This distribution does not differ significantly from the normal-panel condition (Fig. 3A), as indicated by the complete overlap of confidence ellipses for the two treatments. Thus, unlike short-term residents, which reverse the direction of their deflection when housed in altered-panel lofts (Phillips and Waldvogel, 1982, 1988), permanent residents do not

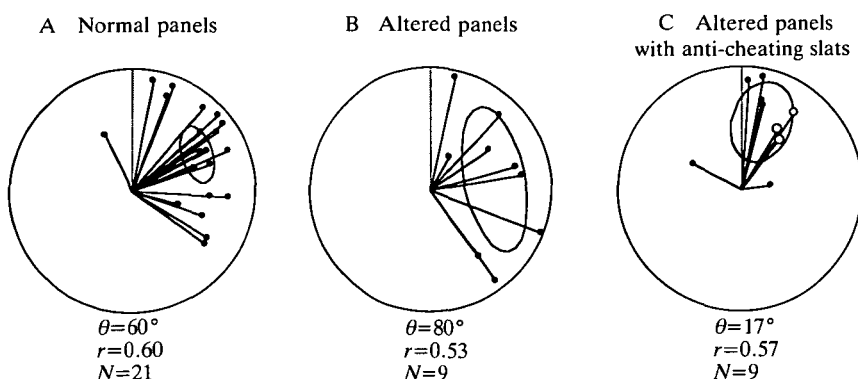


Fig. 3. Summary of results from permanent residents in deflector lofts obtained under sun between 1977 and 1983 using (A) normal-panel lofts, (B) altered-panel lofts and (C) altered-panel lofts with anti-cheating slats attached. Since the data are from seven different release sites, all three diagrams were created by setting the mean bearing of the CCW-expected group in each test to  $0^\circ$  (dashed line) and then plotting the change in mean vanishing bearings ( $\Delta\text{MVB}$ ) for that test as a single vector whose length corresponds to the degree of scatter for the CW-expected group from that particular test. Clockwise deviations from zero thus represent deflections in the olfactory-predicted direction. Ellipses indicate 95 % confidence limits based on Hotelling's one-sample test. If the ellipse excludes the origin of the diagram, the distribution is statistically non-randomly oriented. If the ellipse includes  $0^\circ$  (dashed line) then the distribution does not exhibit a significant deflection.  $\theta$ , mean angle for the sample (i.e. the central tendency of the confidence ellipse);  $r$ , vector length of  $\theta$  (a measure of scatter in the pooled distribution); and  $N$ , sample size. Open symbols in C represent three special releases referred to in the text.

appear to respond to reflected light cues. However, when the portion of the sky visible beyond the ends of the deflector panels is eliminated from view by adding anti-cheating slats to the altered lofts, the permanent-resident deflector-loft birds exhibit a much reduced deflection of initial orientation that does not differ significantly from zero (mean  $\Delta\text{MVB}=17^\circ$ ,  $r=0.57$ ; Fig. 3C). The residual (albeit statistically insignificant) deflection that remains when anti-cheating slats are present appears to result mainly from the three tests indicated by open symbols in Fig. 3C (bearings= $31^\circ$ ,  $35^\circ$  and  $37^\circ$ ) which used older birds that had had previous experience with the deflector lofts prior to the addition of anti-cheating slats. These birds may have retained a portion of their former deflection by means of loft-specific directional cues that were not eliminated by the presence of anti-cheating slats.

Wallraff (1980, 1986) has raised the possibility that good orientation in deflector-loft pigeons subjected to chemical anosmia or other treatments (such as anti-cheating slats) could be the result of a switch from true homing orientation to a preferred compass direction (PCD) response. If so, then pooled bearings from releases conducted symmetrically around the home loft should be randomly oriented with respect to the home direction, but significantly oriented in a PCD



when plotted geographically. To determine whether a PCD was involved in the orientation of our deflector-loft birds, we pooled data from six 1982 releases carried out at sites located symmetrically around the deflector lofts (two North, two South, one each from the East and West) using birds raised in deflector lofts equipped with anti-cheating slats. These particular tests were selected for analysis because they represented a geographically balanced set of releases that were all conducted during the same field season using birds of approximately equivalent flight experience. Table 1 presents the standard orientation statistics for each individual release. Fig. 4 shows the pooled mean bearings for each treatment plotted with respect to both home direction and geographic north. All treatments are significantly oriented with respect to home, and for none of the three treatments do the second-order MVBs differ significantly from the home direction (CCW-expected MVB=14°,  $r=0.49$ ; control MVB=1°,  $r=0.44$ ; CW-expected MVB=14°,  $r=0.5$ ). The same data plotted with respect to geographic north

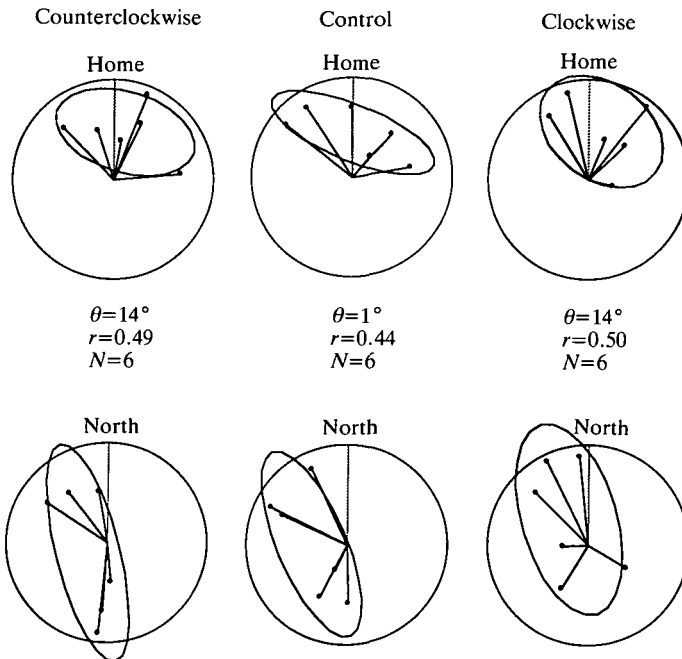


Fig. 4. Pooled results for six releases conducted symmetrically around the deflector lofts in 1982. These tests involved only permanent residents of the CW and CCW altered-panel lofts with anti-cheating slats attached, as well as their controls. In the top row the six mean vectors for each treatment group have been plotted with respect to the home direction and in the bottom row with respect to geographic north (represented by the dashed line in both cases). 95 % confidence ellipses as calculated by the Hotelling one-sample test are provided for each distribution. All other symbols and conventions are as in Fig. 3. The pooled distributions for all three treatment groups are well oriented in the homeward direction, but randomly oriented when plotted relative to geographical coordinates.

Table 1. *Test statistics for 1982 symmetrical releases of birds housed in lofts with anti-cheating slats attached*

	Counterclockwise-expected				Control				Clockwise-expected			
	<i>N</i>	$\theta$	<i>r</i>	<i>P</i>	<i>N</i>	$\theta$	<i>r</i>	<i>P</i>	<i>N</i>	$\theta$	<i>r</i>	<i>P</i>
South test no. 1 (home=347°)	13	303	0.71	<0.001	13	296	0.83	<0.001	14	315	0.74	<0.001
South test no. 2 (home=8°)	9	350	0.52	0.087	10	335	0.82	<0.001	10	354	0.88	<0.001
East test (home=296°)	11	322	0.62	0.01	10	295	0.70	<0.005	11	334	0.92	<0.001
West test (home=98°)	10	183	0.68	0.007	10	178	0.58	<0.03	10	120	0.44	0.15
North test no. 1 (home=164°)	10	174	0.39	0.22	10	204	0.28	0.48	10	211	0.50	0.08
North test no. 2 (home=164°)	9	185	0.91	<0.001	11	206	0.58	0.02	12	267	0.25	0.49

*N*, sample size;  $\theta$ , mean angle; *r*, mean angle vector length; *P*, Rayleigh probability.

produce highly scattered distributions which, although tending to the west, are not statistically different from random. In fact, of the three treatment groups it is the *controls* whose orientation most closely approaches a statistically significant westward tendency, rather than either of the experimental groups. Thus the anti-cheating slat effect does not appear to represent a simple switch to PCD orientation, but is instead a genuine elimination of the deflector-loft effect manifested in the form of relatively accurate homeward orientation on the part of all three treatment groups.

### Discussion

If reflected polarized light is the orientation cue responsible for generating the deflector-loft effect in permanent-resident birds, as has already been demonstrated for short-term residents (Phillips and Waldvogel, 1982, 1988), one would predict that raising pigeons in lofts with altered panels should reverse the direction of their deflection relative to that of birds raised in lofts with normal panels. Our data do not support this prediction (Fig. 3A). Not only are the deflections of altered-panel permanent residents biased in the olfactory-predicted direction, they are on average larger than those of normal-panel deflector-loft pigeons (Fig. 3B). However, when the anti-cheating slats are added to the altered lofts, thus eliminating a direct view of the horizon sky beyond the end of the deflector panels, the permanent-resident deflection becomes negligible despite the fact that odor cues remain essentially unchanged (Fig. 3C). We believe that the residual deflection which remains in the presence of anti-cheating slats (approximately  $17^\circ$ ) is probably not the result of olfactory influences, however, since the three groups that were well oriented and exhibited modest deflections in the olfactory-predicted direction under these conditions were all experienced birds that had been housed in the same lofts during the previous field season (or earlier in the same season) *before* the anti-cheating slats were attached. It is therefore likely that the residual deflection present in these groups is due to prior experience in the lofts before the anti-cheating slats were installed. We conclude that, instead of using olfaction or *reflected* light as their primary orientation cue, permanent-resident deflector-loft birds are being influenced by unreflected light cues which emanate from the regions of horizon sky visible beyond the ends of each deflector panel. [Interestingly, the one anomalous deflection from the olfactory-predicted direction in Fig. 3C was also obtained from a group of birds with prior deflector-loft experience before anti-cheating slats were installed. While this point represents an obvious exception to the generalization just described, it should be remembered that this particular test is the *only* one out of 18 experiments conducted over five consecutive field seasons in which altered-panel birds exhibited non-olfactory-predicted deflections (see Fig. 3B,C)].

We believe that the orientational influence of the anti-cheating slats is unlikely to stem from a disruption in the pattern of airflow within the lofts. As cited earlier, removal of the vertical slats which make up the sides of the deflector cages

produces a whirlwind pattern of air currents within the loft but does not eliminate the orientation bias (Kiepenheuer, 1982). Our anti-cheating slats create less of a disturbance in airflow than does the complete removal of the slatted cage walls, which means that any change in the birds' orientation must be due to factors other than modified airflow. Moreover, the olfactory model predicts that, if the birds are unable to discern a regular pattern of wind direction, they should not be able to learn an olfactory map and should either exhibit random orientation or orient along a PCD, rather than in the home direction (Wallraff, 1980). When raised in the altered-panel deflector lofts with anti-cheating slats attached, our pigeons clearly show good homeward orientation in the absence of a deflection and exhibit little or no evidence of a PCD (Fig. 4). Kiepenheuer (1979, 1982) reached a similar conclusion regarding elimination of the deflector-loft effect in permanent-resident birds that had been subjected to topical anesthesia of the olfactory mucosa.

To explain the response of short-term residents to reflected light cues, we have previously suggested (Phillips and Waldvogel, 1982, 1988) that pigeons use a near-ultraviolet-sensitive visual mechanism (Chen *et al.* 1984) to detect the vertically aligned band of maximum polarization (BMP; Brines, 1980) which is present at sunrise and sunset. Since the sunrise and sunset azimuth positions of the BMP are symmetrical with respect to geographical coordinates (Fig. 5), they can be averaged to determine the direction of geographic north and can thus provide a

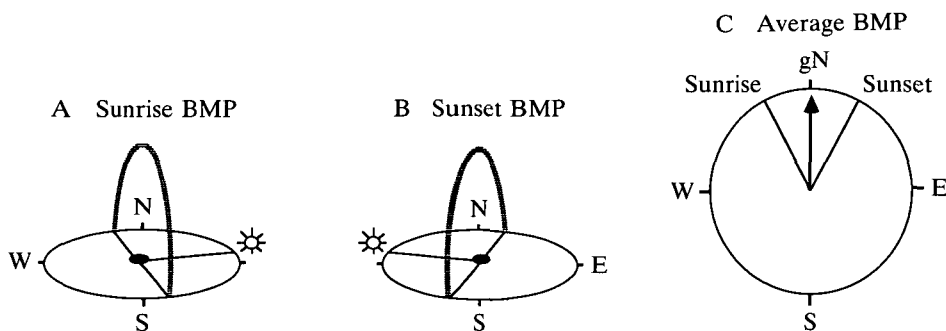


Fig. 5. Position of the band of maximum polarization BMP at (A) sunrise and (B) sunset during early summer in New York state (latitude  $42^{\circ}$  N). Large circles represent the visual horizon and the solid spot at the center indicates the location of the home loft. The hatched line denotes the BMP, which passes through the zenith at sunrise and sunset. Note that the BMP is actually a broad region of sky rather than the narrow band depicted in the figure, and that the azimuth positions of the BMP at sunrise and sunset are symmetrical around geographic north and south. (C) Diagram showing how pigeons might obtain a measure of geographic north (gN, arrow) by averaging the sunrise and sunset azimuth positions of the BMP. The birds would have to distinguish between the north and south ends of the BMP and then average the azimuth positions of the BMP at one end or the other of this axis (see Phillips and Waldvogel, 1982, 1988). The 'polarity' of the BMP axis can be determined using properties inherent in the polarization pattern (e.g. BMP rotation direction; Brines, 1980) or by using an independent source of information (e.g. the BMP relationship to sunrise, sunset or the earth's magnetic field).

visual reference for calibrating the bird's sun compass. The reliance on a short-wavelength-sensitive mechanism to carry out polarized light discrimination may explain why the orientation of permanent-resident pigeons raised in the lofts with altered panels without anti-cheating slats is biased in the same direction as the orientation of normal-panel birds. All light that enters the altered lofts *via* the deflector panels is transmitted through at least one pane of glass (Fig. 2A). Because plate glass attenuates wavelengths below 380 nm, the intensity of near-ultraviolet light which the birds can see in the altered-panel lofts is greatest from the regions of sky visible beyond the ends of the deflector panels. Thus, when the anti-cheating slats are attached to the altered-panel lofts, the intensity of near-ultraviolet light reaching the birds is greatly reduced and may not provide the necessary amount of polarized light that a *naive* bird needs to establish its compass reference system. In this situation, the pigeons raised in lofts with altered panels with anti-cheating slats attached presumably switch to some non-visual compass system that is not influenced by the deflector panels (e.g. magnetism) and, as a result, show no appreciable deflection. The dependence of the permanent resident deflector-loft effect on light cues visible beyond the ends of the deflector panels also explains why permanently covering the Plexiglas portion of normal deflector panels with translucent plastic (Kiepenheuer, 1982) or temporarily covering them with opaque sheets of plywood at sunrise and sunset (F. Papi, personal communication) does not eliminate the deflection in permanent-resident birds.

If permanent residents are attending to the distribution of polarized light in the regions of the sky visible beyond the ends of the deflector panels, it would appear that the sunset azimuth position of the BMP alone must be sufficient to obtain a measure of geographic north. At the time of year when permanent-resident birds are put into the deflector lofts as fledglings (May–June), the apparent position of the BMP at sunset is located near the counterclockwise edge of the east (and west) deflectors in the CW loft, and near the clockwise edge of the north (and south) deflectors in the CCW loft (Fig. 6). Because the birds' vision is restricted to  $\pm 20^\circ$  to  $\pm 30^\circ$  from the cardinal compass directions by the wooden slats that make up the cage walls, the BMP should be perceived as occurring at  $70\text{--}80^\circ$  (also  $250\text{--}260^\circ$ ) magnetic in the CW loft and  $10\text{--}20^\circ$  (also  $190\text{--}200^\circ$ ) magnetic in the CCW loft, resulting in a  $\Delta\text{MVB}$  of about  $60^\circ$ . [This value corresponds very well with the mean  $\Delta\text{MVB}$  obtained from the pool of our 21 normal-panel loft tests without anti-cheating slats (Fig. 3A)]. In contrast, at sunrise the intensity of polarization in the CCW loft is approximately equal in all four regions of sky visible beyond the end of the panels, and therefore does not provide useful reference information. It thus seems that the polarized light cues visible at sunset must be sufficient to provide the primary source of reference information for permanent residents of the deflector lofts (Phillips and Waldvogel, 1988).

If access to ultraviolet light is a requirement for deriving a compass reference system from celestial polarized skylight, why do short-term residents in the altered-panel lofts without anti-cheating slats reverse their bias when permanent residents of the same lofts do not? Perhaps this is because permanent-resident and

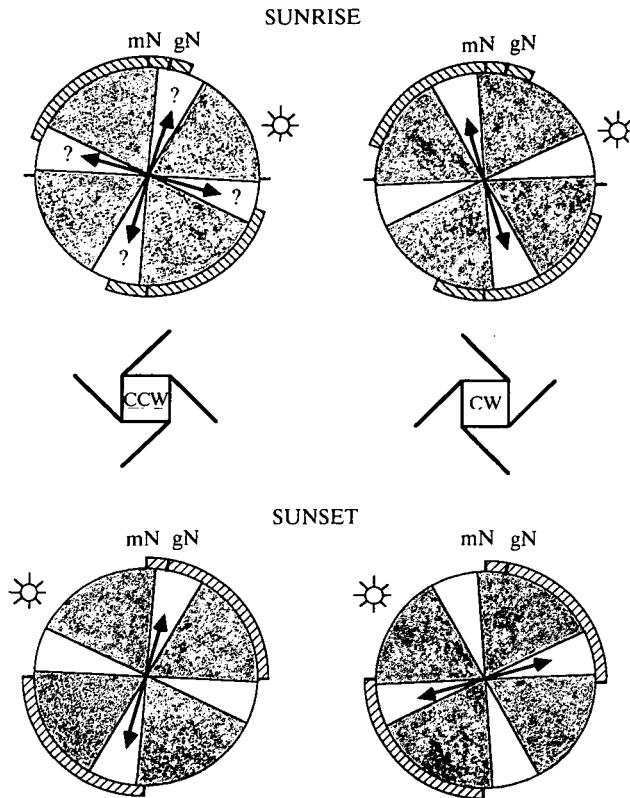


Fig. 6. Schematic overhead view of the relationship between the sunrise (upper diagrams) and sunset (lower diagrams) azimuth positions of the band of maximum polarization (BMP) during early summer as visible to pigeons housed in the clockwise (CW) and counterclockwise (CCW) deflector lofts. Circles represent the visual horizon with the azimuth positions of sunrise and sunset indicated at the circle's periphery. Hatched areas at the circle's edge represent the sky quadrant where maximum polarization is found at sunrise or sunset. The unshaded wedges in each circle indicate the area of sky visible to the birds when the anti-cheating slats are *not* present on the lofts (refer to Fig. 2B). Shaded wedges represent the areas where near-ultraviolet light vision is blocked by the deflector panels. Magnetic north (mN) and geographic north (gN) (which differ by  $11^\circ$  around our lofts) are indicated at the top of each diagram. Note that the principal axes of the deflector lofts are aligned on magnetic coordinates, while the sunrise and sunset positions of the BMP are symmetrical with respect to geographical coordinates. The double-headed arrows represent the BMP axis that is perceived by the birds in the lofts owing to their restricted vision. In most instances a single BMP axis is clearly discernible to the birds, but at sunrise in the CCW loft the intensity of polarization is approximately equal along two perpendicular axes. Further explanation is provided in the text.

short-term resident birds differ in the conditions under which they initially experience polarized light information; only the permanent residents are exposed to the abnormal conditions prevailing in the deflector lofts during the sensitive

phase for learning sun compass orientation (Wiltschko, 1983). If naive birds initially apply a strict set of 'rules' concerning spectral composition to identify natural skylight, as do honeybees (Wehner and Rossel, 1985), the early experience of permanent-resident birds in the deflector lofts may cause them to attend only to the directly viewed component of skylight visible beyond the ends of the deflector panels. In contrast, short-term resident birds have their initial experience with the compass reference system while residing in the unaltered visual environment of their home loft. If subsequent developmental factors or experience enable older birds to detect the band of maximum polarization over a broader range of conditions, then short-term residents that are placed in the deflector lofts as yearlings or old birds (i.e. with considerable prior flight experience) may be influenced to a greater extent by light originating from the deflector panels than are the naive young permanent residents. Although the degree of polarization in near-ultraviolet light originating from certain deflector panels is higher than that of light that is visible beyond the ends of the deflector panels (J. B. Phillips and J. A. Waldvogel, 1988), the *overall* intensity of near-ultraviolet light emanating from the panels is lower (J. B. Phillips and J. A. Waldvogel, unpublished data). Unfortunately, relatively little is currently known about polarization sensitivity in homing pigeons (see discussions by Kreithen and Keeton, 1974; Delius *et al.* 1976; Martin, 1985), and so these suggestions must remain speculative until additional physiological experiments are carried out to determine how polarized light sensitivity in pigeons depends on such parameters as intensity, spectral composition and percentage polarization.

Returning to the role of olfaction in pigeon homing, four separate lines of evidence now indicate that the deflection of permanent-resident deflector-loft birds is not due to olfactory cues: (1) pigeons continue to home and show a normal deflection even when deprived of olfactory information by anesthesia of the olfactory mucosa (Kiepenheuer, 1979); (2) transformation of the normal pattern of airflow in the deflector lofts to create a whirlwind pattern with no discernible relationship to the actual wind direction does not eliminate the deflection (Kiepenheuer, 1982); (3) the deflection is absent under overcast conditions, although overcast should not preclude the use of olfactory cues (Waldvogel and Phillips, 1982); and (4) the deflection is eliminated, although homing is unaffected, if pigeons are prevented from viewing the region of sky visible beyond the ends of the deflector panels (this paper). We believe that the significance of these findings goes beyond simply understanding the results of one particular experimental approach. If wind-borne odors perceived at the home loft are involved in the production of an olfactory map, then the deflector lofts *must* produce a deflection of initial orientation and the deflection *must* be influenced by olfactory cues. Since this does not appear to be the case (at least for birds in New York and Germany), olfactory cues perceived at the home loft cannot be claimed as universally *essential* for the development of a functional map sense in pigeons.

In view of our evidence that the deflector-loft effect is a consequence of light cues, rather than olfactory ones, the deflector-loft experiments conducted by Foà

*et al.* (1986) using Italian birds subjected to sectioning of the anterior commissure are especially interesting. The results of these experiments indicate that different olfactory information reaching the two brain hemispheres results in two differently calibrated navigational systems. Proponents of olfactory models of homing interpret these results as evidence that the birds are learning two distinct olfactory maps. However, as we and others have proposed (Phillips and Waldvogel, 1982, 1988; Wiltschko *et al.* 1987a), it is also possible that the primary influence of olfactory cues is a non-orientational effect which activates the appropriate *non-olfactory* orientation mechanisms. Thus, an alternative explanation for the results of deflector-loft experiments using anterior-commissure-sectioned birds is that each hemisphere acquires a differently calibrated sun compass, and that both the learning and the expression of this miscalibrated compass system are triggered by olfactory inputs. While it may prove true that olfaction represents an important element in the navigational system of Italian homing pigeons, it nevertheless remains the case that our alternative explanation for the results of these anterior commissure experiments has neither been adequately tested nor eliminated as a possibility, despite claims to the contrary (Foà *et al.* 1986). Perhaps the easiest way to distinguish between these competing interpretations would be to test the birds' orientation under total overcast. We predict that the deflected orientation exhibited by surgically treated birds would be eliminated at times when they are unable to rely on their sun compass (i.e. when flown under total overcast), or if they were raised in the altered-panel deflector lofts with anti-cheating slats attached, a condition that would prevent them from having access to a light-based reference system.

Finally, it is important to note that a host of other modified loft designs have been used to test the olfactory model of homing (reviewed by Papi, 1986; Schmidt-Koenig, 1987), and that a large number of these experiments have also yielded results consistent with olfactory expectations. These results may truly indicate an important role of olfactory information in homing, perhaps with some degree of geographical specificity in the use of odors, as suggested by Wiltschko *et al.* (1987b) and Waldvogel (1987, 1989). It is worth pointing out, however, that in most cases adequate controls have not been carried out for these experiments so as to exclude unequivocally the possibility that presumed olfactory effects on orientation and homing might actually be due to non-olfactory cues or to an influence of olfactory cues that may be unrelated directly to the navigational map. We believe that these additional strict controls are critical, especially in view of the results from deflector-loft experiments which now argue convincingly against the involvement of directional olfactory information in the development of the homing pigeon's navigational map.

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