"Nonsense" orientation in Mallard; a resumé and an investigation of the mechanism of a sun-compass

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Introduction

A great deal of light has been thrown on the mysteries of bird navigation (reviewed in Matthews 1968, 1973; Schmidt-Koenig 1979; Baker 1984) by the simple technique of releasing birds one at a time and recording the bearings at which they vanished from sight. The fan of departure bearings which built up could then be statistically analysed to give evidence as to the accuracy of orientation and the extent to which it could be influenced by the prior or present conditions experienced by the bird. First used with homing pigeons *Columba livia* in 1948 (Matthews 1951) the technique has now been used in tens of thousands of observations by a multiplicity of workers.

In the late 1950s there was a massive over-population of Mallard *Anas platyrhynchos* on the Wildfowl Trust's refuge at Slimbridge, Gloucestershire, so an attempt was made to reduce numbers by catching birds and transporting them to pastures new in the hope that they would settle there. The opportunity was taken to obtain as much information as possible about their orientation behaviour on release. The research programme was completed in the late 1970s and most of the results have been published in a wide range of journals and books. The opportunity is now taken to summarise what is known about "non-sense" orientation in Mallard and other birds, and to set out in detail one facet of interest not fully published before.

The nature of "nonsense" orientation, particularly in the Mallard

The first indication that birds on release can show a marked orientation not related to the direction of home, migration or training was obtained by Griffin & Goldsmith (1955) with Common Terns *Sterna hirunda,* which had a south-easterly tendency in New England, USA. Bellrose (1958) showed that Mallard caught and released in Illinois, USA, had a strong tendency to fly NNW, but this could have been related to the axis of their north/south migration

A clear separation from any migratory or homeward direction was obtained with the Slimbridge Mallard, which did have a strong north-west tendency (Matthews 1961), yet these birds were either non-migratory or came from the east. A series of 27 sets of releases at 16 sites between 30 and 253 km from Slimbridge gave 714 vanishing bearings. Medians of the fans of the bearings fell between 294° and 337° and had no relation with the direction of home from the release points, which were situated right round the compass rose. The north-west orientation was found no matter what time of day the birds were released, regardless of the time of year (from the end of July through to the beginning of June), and irrespective of the sex or age of the birds. The north-west tendency became sharper in 439 birds released in groups of 2 to 7 instead of singly, as were 159 others (Matthews 1962). It therefore had not been evolved as a method of enabling individuals scattered (e.g. by a storm) to reassemble in a flock more surely than if they flew in all directions.

The orientation was immediate (clear within 15 seconds) but was short-lived, the subsequent recoveries of the ringed birds being not concentrated in the north-west but scattered all round the release points. By establishing relays of observers to the north-west of a release point, communicating by semaphore or radio (Matthews 1967), data on 493 birds showed that the flight became increasingly undirected and within 6 km had lost all connection with that in which the bird started. Most had indeed landed within 20 minutes of release. The proportion of recaptures at the original catching site indicated that a majority of birds returned there when released up to 50 km, but very few came back from over 100 km. To achieve the original object of the exercise, to displace surplus birds, was therefore rather expensive in terms of time and travel. It was the intrinsic fascination of the orientation that justified the continuation and elaboration of the tests.

The strength of the orientation is well

illustrated in Fig. 3. The original naming of this behavioural phenomenon as "nonsense" orientation, in that it made no sense to us, was a rather provocative title which irritated some. When it became evident that homing pigeons also had similar tendencies, which confused observation of their homeward orientation, Walraff (1978) suggested the neutral, indeed insipid, term "Preferred Compass Directions" or PCDs.

The "nonsense" became even more difficult to understand when it was found that Mallard caught in different areas had different directional tendencies (Matthews 1963a). Thus 188 male Mallard, caught and banished from St. James's Park, London, because of adverse public reaction to their rape activity, had, on release in the west of England, a predominantly southerly tendency. So did 307 Mallard caught at Nacton, Suffolk (Matthews & Revett 1982). Smaller numbers caught near Stockholm, Sweden, went predominantly south-east, others from Seeweisen, Bavaria, mainly south-west. In the case of Borough Fen Decoy, Peakirk, Cambridgeshire (formerly Northamptonshire), birds caught in the late summer and early autumn went north-west like those from Slimbridge, though rather more widely scattered. Birds caught in late autumn and through the winter gave almost a random scatter. This apparent seasonal breakdown of orientation was studied in detail by Matthews & Cook (1982), considering 5,109 vanishing bearings between the beginning of July and the end of March (by which time a north-west tendency had reappeared). The deterioration coincided with the main influx of foreign migrants to eastern England (Matthews 1963a; Ogilvie & Cook 1971) and it was postulated that the migrants were bringing with them their own, conflicting, directional tendencies, so that a sample caught when they were mixed with the local birds would give the impression of random scatter. A deterioration was not noticeable at Slimbridge because relatively few migrant Mallard penetrated to the west of England, while at Nacton the local population already had the southerly tendency apparently favoured by the immigrants. The acid test was to determine whether birds subsequently recovered abroad, in their breeding areas, had, when tested previously in England, shown more diverse orientations. Most recoveries are, of course, made during the shooting season, relatively few in summer. However, 138 of the latter had accumulated and showed clearly that the farther east they were subsequently found on the Continent, the more diverse had been their orientations.

A final twist to the confusing Mallard story was given when it was found that 1,079 birds captured at Deeping Lake, a large water only 2 km away from Borough Fen Decoy, gave an entirely different orientation pattern. From August through to April, Deeping birds gave almost no indication of orientation. The lake did not appear to be used exclusively by foreigners, but there was a suggestion that Borough Fen in some way imposed an orientation whereas Deeping did not. An earlier attempt (Matthews 1963a) to disentangle learned and inherited effects by rearing Slimbridge and London Mallard side by side proved inconclusive because on release the birds did not fly far enough to give satisfactory vanishing bearings.

It has already been mentioned that "nonsense" orientations, varying from local population to population, were found in homing pigeons. Several species of wildfowl were found to be likewise equipped. Thus 234 European Green-winged Teal *Anas c. crecca* from Peakirk flew predominantly north-west (though the orientation was not strong), 88 from Piaam in the Netherlands went strongly WSW, 108 from Tour du Valat, S. France, went south-west (Matthews *et al.* 1963). In Illinois, Bellrose (1964) found that Canada Geese *Branta canadensis* went south-west, Blue-winged Teal *A. discors* north-west and Pintail *A. acuta* WNW (north-west, in Saskatchewan, Canada). Matthews & Revett (1982), however, found that 105 Pintail from Nacton went south-west, as did 82 Wigeon *A. penelope*.

Fixed orientations are therefore widespread and vary on a population, and indeed on a site, basis. They are carried with the birds on their migrations and are still demonstrated in situations radically different from those in which they were originally developed. We are still far from understanding their purpose, but, accepting their existence, we can use these well marked, rapid orientations to investigate the compass components of bird navigation to determine *how* the ducks determine the direction in which to fly, even if we do not know *why* they do so.

Landscape features may modify the initial orientation to some extent, but the birds were not deterred by, for example, a range of hills lying athwart their flight path. Water bodies, particularly familiar ones, may influence the direction of flight and its ending. However, Matthews & Cook (1977) were able to show by releases of 1,500 Mallard at short distances, 0.7–14.1 km from the capture point, that "nonsense" orientation could not be derived from landmarks alone, since it did not develop under heavy overcast and became apparent only in sunny conditions. In other words, the birds were not just heading north-west, but north-west by a sun-compass. A magnetic compass cannot be used by these birds, otherwise it should have been able to provide them with directional information in overcast conditions. Matthews & Revett (1982) further show that temporarily bird-borne magnets sufficient to disrupt the magnetic field in the head region had no effect on the orientation of 236 Mallard under sunny conditions

The existence of a sun compass had been inferred soon after the start of the series of tests (in 1960) when heavy lowering overcast scattered the birds all round the compass rose. In a 1961 release a break in the clouds in the north-west produced a false sunset there instead of in the south-west. Birds released at this time had their orientation twisted by approximately 90°, to the north-east. The final check was to shift the birds in time by keeping them in artificial light conditions six hours out of phase with external light. Of 72 birds, half served as controls, the others had their internal clocks shifted six hours early or six hours late. They appropriately flew south-west or north-east (Matthews 1963b). Thus the sun-compass is time-compensated, the birds allowing for the apparent passage of the sun across the southern sky at 15° per hour. It is the detailed working of this mechanism that is now to be considered.

Before that it may also be noted that Mallard flying at night show just as strong an orientation as they do by day. This was revealed by using temporarily bird-borne lights which enabled the paths of the Mallard to be followed with ease. Again orientation failed when there was heavy cloud but was shown well under a starlit sky, in observations of 249 bearings. There was no change in orientation or accuracy from September through to May. Clock-shifting treatment on 56 birds did not have any effect on their orientation. Together these findings indicate that orientation is not with regard to certain stars, correcting for their apparent movement with time round the night sky. Instead the birds would seem to be using the pattern of stars to determine the northern point about which they appear to rotate, marked by the Pole Star. Walraff (1972) was able to show that Mallard (and Teal) could learn the patterns of "stars" on a planetarium dome, even when the constellations were unnatural ones, and to recognise a direction therefrom.

In certain circumstances the cloud layer can be sufficiently thick to blot out the stars, but thin enough to allow the moon to shine through. Under these conditions "nonsense" orientation was shown clearly by 86 Mallard and remained constant despite the apparent travel of the moon round the southern sky. This strongly suggests that the moon-compass (like the sun-compass) is time-compensated, but tests with 67 clock-shifted Mallard have not been extensive enough to provide full confirmation (Matthews 1973).

A remaining problem: the functioning of the angle-correcting mechanism of the sun-compass

If a bird is to fly in a certain direction with reference to the sun's position in the sky (or, more likely, its downward projection to the horizon, the azimuth) the angle the bird sets must change during the day to take account of the apparent movement of the sun round the southern sky at 15° per hour. Since orientation is very rapid, even when the bird has not observed the sun for quite a while, the birds must have a good appreciation of time. The existence of biological clocks was an astonishing concept only 40 years ago. It is now fully established and orientation work with birds and other animals has helped greatly to gather the facts. Follett & Follett (1981) provide a group of papers summarising the current thinking. Widespread in animals are circadian clocks, so called because their intrinsic free-running period is not exactly 24 hours, but about that length *(circa dies)*. They are kept geared to the seasonally changing length of day by certain time cues (Zeitgeber) of which the light changes at sunrise and sunset are the most important. If these time cues can be shifted artificially the clock can likewise be shifted to run early or late. This technique has been used, as described above, to demonstrate the existence of a time-compensated sun-compass, using six-hour shifts which twist orientation through 90°.

Now a bird seeking to fly north-west has to set a smaller and smaller angle to the sun azimuth as the day proceeds (Fig. 1). How does the angle-correcting mechanism function through the hours of darkness to change the small angle appropriate to sunset back to the large one appropriate to sunrise? Logically there would seem to be two possibilities. The angle correction could continue in the same sense, as if correcting for an (unseen) sun moving on round through the north during the night. Alternatively the angle-correction could be reversed, as if correcting for an (unseen) sun moving back through the south during the night (Fig. 1). Workers with invertebrates, fishes and reptiles have demonstrated both "winding-on" and "unwinding" angle-correction mechanisms in different species and sometimes in the same species (summarised in Matthews 1968). In birds, Hoffmann (1959) direction-trained 3 Starlings *Sturnus vulgaris* in cages at 53°N and found they could be retrained at 68°N to allow for the clockwise movement of the midnight sun they were able to observe. Schmidt-Koenig (1961) time-shifted 2 homing pigeons and testing them in their physiological night. The results suggested an unwinding process. However, when 3 pigeons were direction-trained at 36°N and tested against the actual night-time sun at 71°N they sometimes allowed for its observed clockwise movement and sometimes reacted as if it should be moving anti-clockwise (Schmidt-Koenig 1963).

In view of the limited and conflicting data, it was desirable to carry out further tests with birds, preferably without the restraints that cage-training imposed on them. Since the interest was what happened during the night when the sun is not visible, there was little point in undertaking the expensive task of flying birds for release north of the arctic circle to view the unexpected sight of the sun at midnight. Instead it was cheaper and more convenient to make the sun appear in the middle of a bird's physiological night by reversing its biological clock through 12 hours. Predictions can then be made as to the orientation to be expected (Fig. 1). Birds which normally flew north-west should, if

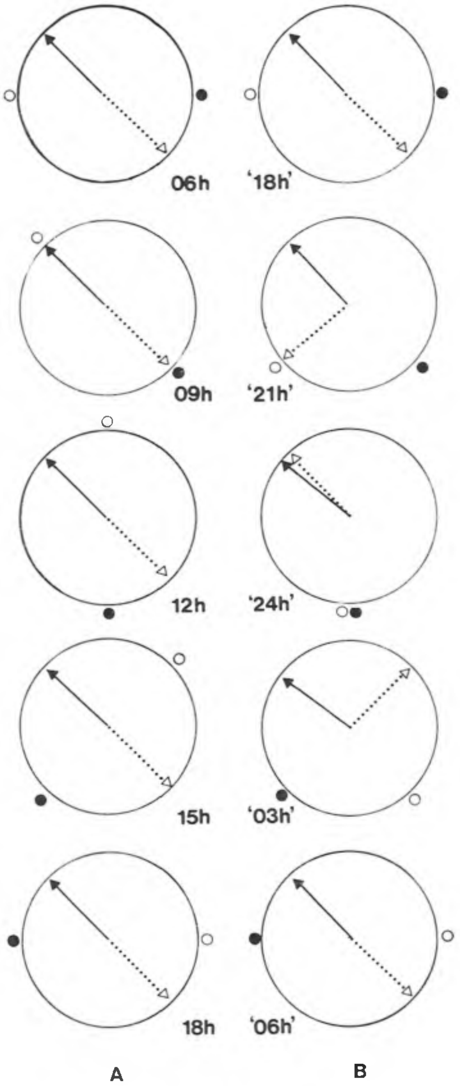

Figure 1. Angle-correction in a sun-compass. The sun during the day (•) moves from east to west via south. By night (o) it could be visualised (A) as moving on through the north or (B) back through the south. Untreated control birds (solid arrows) fly north-west at an angle to the sun which decreases through the day. Birds time-shifted through 12 hours (dotted arrows) and released by day (but in their physiological night) could be expected to fly south-east if (A) applies or in different directions according to time of day if (B) applies. Time according to controls (e.g. 06 h) and time-shifted birds (e.g. '18 h') shown for each pair.

released after such a time shift, fly south-east (12 x 15° = 180°) if their angle-correction mechanisms "wound on" through the night. This would hold whatever the time of day. On the other hand, if their angle-correction mechanism "wound back" a variety of orientations could be expected according to the time at which they were released, i.e. according to the extent to which the mechanism had unwound. Thus at true sunrise the bird would put in the sunset value, its night having not begun; at sunset the unwinding would be complete and the bird would be expecting sunrise. In both cases the maximum error of 180° would be expected. At true noon the bird would be at its personal midnight and the angle-correction half unwound, giving a value that would coincide with that appropriate to noon, so producing nil error. In between there would be a decreasing error from 180° to nil in the morning and an increasing error from nil to 180° in the afternoon. Thus a 12-hour shifted bird seeking to go north-west at the equinoxes would go successively south-east at 0600, south-west at 0900, north-west at 1200, north-east at 1500 and south-east at 1800. To decide between these two hypotheses, a series of tests was undertaken.

Material and methods

Mallard were caught in the Duck Decoy at Slimbridge (51°44'N, 02°24'W). Prior to release, each batch of test birds was maintained under a 12-hour phase shift lasting for at least 7 days, with control birds maintained under normal light schedules. Details of lighting, housing and so forth used for time-shifting are given in Matthews (1963a). This was sufficient to reverse the clocks of the birds so that when they were released by day they were mostly in their physiological night. To avoid marginal statistics, which have vitiated much work on bird navigation (Matthews 1974), 300 birds were treated and released, together with 300 untreated control birds. Fifteen sets of releases were undertaken, each with 20 test and 20 control birds, grouped equally in five time-bands, after sunrise, in mid-morning, around noon, in mid-afternoon and before sunset. For each time-band, 20 + 20 birds were released at each of three sites, whose bearing to and distance from Slimbridge were:

Shrewton:	330°	72 km
Madley:	137°	45 km
Coln St. Dennis	254°	38 km

The possibility that unknown factors pertaining to any one place, direction, day or year were affecting the issue was thus eliminated. Releases were as near the autumn or spring equinoxes as possible so that days and nights were not very different in length. Only birds lost to sight in powerful binoculars while in full flight were used in calculating orientation patterns. All releases were in good weather, the sun being visible at the very least as a disc through veiling cloud. Winds were less than Beaufort Force 3, since stronger winds had earlier been shown to impart some biases on orientation flights. Birds were tossed up singly, the next one not being released until its predecessor had been lost to sight. The bearing of the flying bird was noted every 30 seconds and the time taken to reach vanishing point recorded.

The scatters of vanishing points were examined by using vector analysis to calculate their mean direction and the length (r) of that vector. The value of r gives a measure of the scatter's difference from random distribution, the significance of which is determined by the Rayleigh test (Batschelet 1982).

Results

Initial flight behaviour

Of the 300 test birds, 273 were lost to sight in full flight, as against 264 of the control birds. The time-shifting treatment was thus not any disadvantage in this respect. However, it was obvious that the time-shifted birds were somewhat confused; initially some adopted unusual modes of flight or shook their heads repeatedly. Like Tweedledee they doubtless found it somewhat odd to see the sun shining in the middle of their night. More objective measures of initial uncertainty are provided by the length of time the birds were in sight and the deviation of the final bearing from that at 30 seconds (Table 1). The test birds clearly were less direct in their flight, consistently remaining longer in sight, and with their final bearing deviating more widely from the direction they first took.

Orientation behaviour

The results are set out in Table 2 for individual sets of releases and shown grouped by time-bands in Fig. 2 (12-hour shifted birds), and in Fig. 3 (controls).

The untreated controls gave the usual result of a strong north-westerly orientation. Every one of the 15 sets of releases was very highly significantly non-random ($P \leq 0.01$) and the orientation did not change in any consistent way with time of day or of season. The releases at Shrewton were a trifle more southerly than those at Coln St. Dennis and Madley, a minor bias probably related to the particular landscape. The median of the controls in each set is taken as the reference direction when considering below various hypotheses to explain the behaviour of the time-shifted birds.

These latter, in line with their more uncertain flight behaviour, gave much less clear-cut orientations. Indeed, in 5 out of the 15 sets of releases the scatters could not be discriminated from random at the $p = 0.05$ level. However, when combined within the five time-bands, the resultant orientations are all non-random ($p < 0.01$). Moreover, using the Watson & Williams

Table 1. Decisiveness of flight after release of time-shifted (T) and control (C) Mallard.

Time-band	No. final bearings		Mean time in sight (min)		Mean deviation 30 sec v. final bearings	
	T	C	T	C	T	C
Sunrise	52	50	3.9	3.2	57°	46°
Morning	55	51	4.3	3.5	68°	53°
Noon	56	54	4.2	2.7	56°	33°
Afternoon	54	53	3.8	3.3	64°	50°
Sunset	56	56	3.9	3.5	69°	52°
All	273	264	4.0	3.3	62°	47°

Table 2. Orientation of Mallard released at various times and dates after being time-shifted by 12 hours or as untreated controls.

C = Coln St. Dennis, M = Madley, S = Shrewton – release points. n = number of final bearings, m = mean vector (in brackets if not statistically significant), r = length of that vector.

Release point	Day Month	GMT range	Time-shifted			Untreated		
			n	m	r	n		r
C	5.9	0525–0730	19	(065°)	0.259	17	326°	0.833
M	30.4	0503–0631	16	128°	0.725	16	321°	0.751
S	14.5	0430–0724	17	109°	0.432	17	321°	0.593
		Sunrise	52	110°	0.421	50	323°	0.724
C	29.9	0810–0958	20	(258°)	0.256	18	327°	0.792
S	3.4	0814–0956	18	207°	0.720	17	293°	0.516
M	2.5	0840–1013	17	(221°)	0.233	16	323°	0.792
		Morning	55	221°	0.376	51	317°	0.680
C	18.10	1105–1257	18	(334°)	0.330	18	338°	0.825
M	21.10	1022–1319	18	330°	0.472	17	331°	0.914
S	2.11	1047–1243	20	337°	0.465	19	316°	0.804
		Noon	56	334°	0.424	54	328°	0.836
C	8.10	1336–1522	20	360°	0.486	19	318°	0.908
S	12.3	1412–1542	18	0.76°	0.547	19	304°	0.721
M	24.4	1333–1545	16	036°	0.476	15	324°	0.792
		Afternoon	54	038°	0.425	53	310°	0.803
C	13.9	1616–1814	20	150°	0.535	20	330°	0.691
S	12.4	1653–1820	17	126°	0.786	18	290°	0.688
M	14.4	1552–1815	19	(166°)	0.379	18	320°	0.772
		Sunset	56	144°	0.537	56	311°	0.688

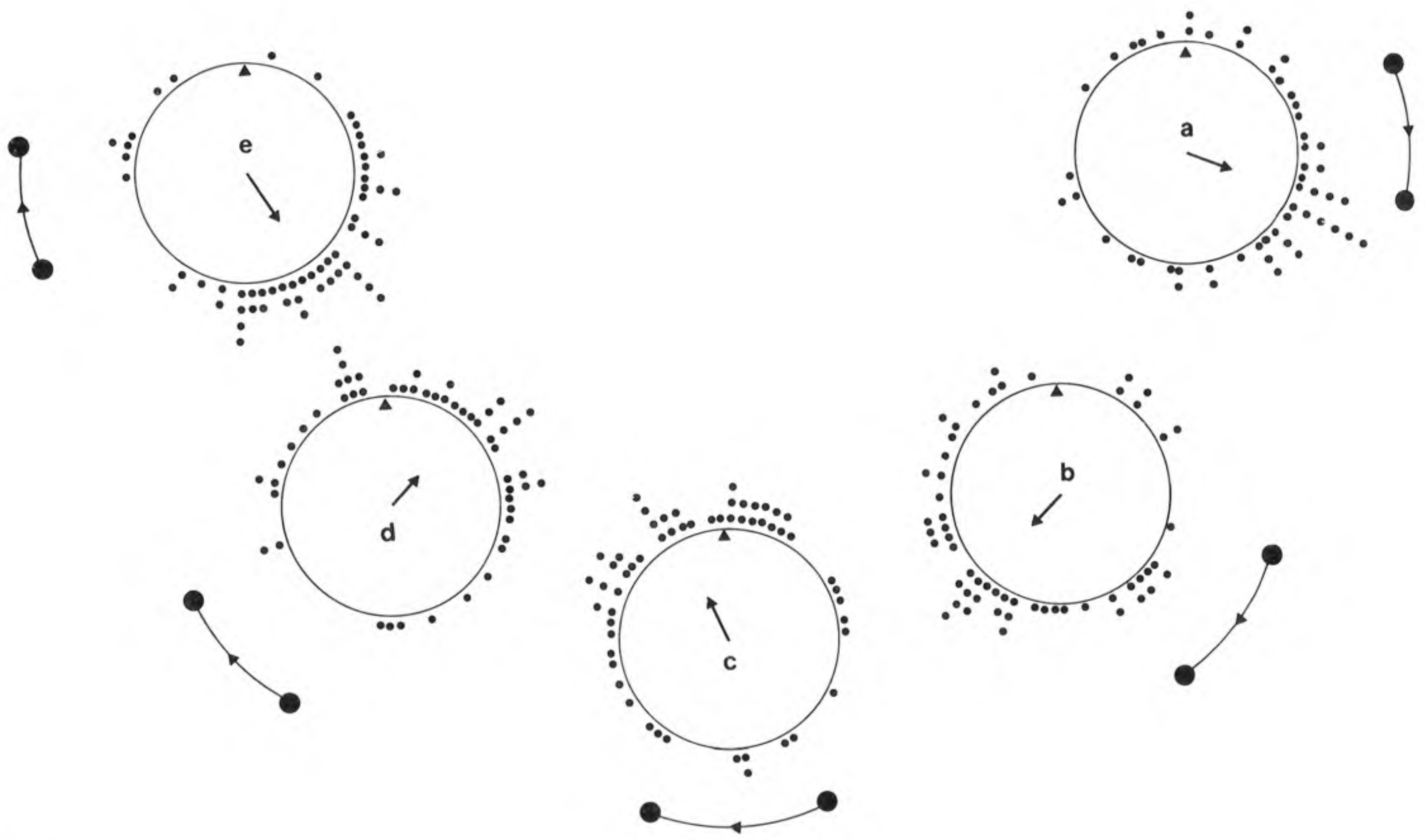

Figure 2. Orientation of 12-hour time-shifted Mallard released in their physiological night at various times of day. a) sunrise b) morning c) noon d) afternoon e) sunset. Outer linked circles indicate range of sun azimuths during releases. Each dot represents one bird lost to sight on that bearing. Other conventions as Fig. 3.

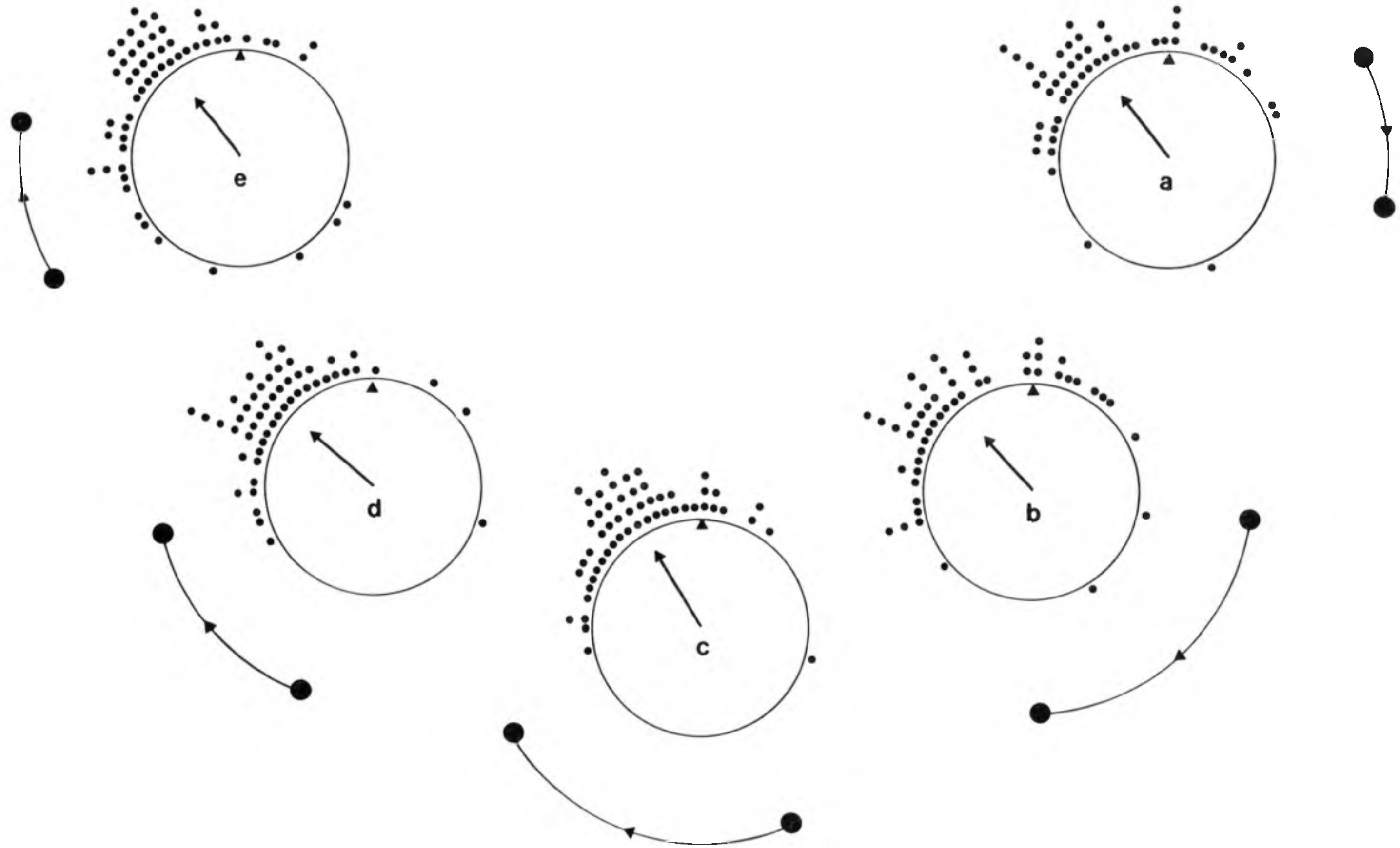

Figure 3. Orientation of untreated Mallard released at various times of day. Centripetal arrows indicate mean direction of bearings, the longer the arrow the less their scatter about the mean (r & m in Table 2). North is represented by shaftless arrowheads. Other conventions as Fig. 2.

test (Batschelet 1982), it can be shown that the orientation of the scatter for each time band differs in a highly significant way from its predecessor. The critical value (p = 0.01) of the statistic F for two samples totalling 100 is 6.90, whereas the successive pairs of time-bands gave for sunset/morning 29.7, for morning/noon 57.5, for noon/afternoon 32.2, and for afternoon/sunset 77.5. We can therefore dismiss the hypothesis that the angle-correcting mechanism "winds on" during the night as if it were correcting for a sun moving on through the north. If that were the case, the 12-hour shifted birds would have shown no variation in orientation with time of day; they would all have gone to the south-east.

The results are much more in accord with the alternative hypothesis that the angle-correcting mechanism "winds back" during the night as if for a sun moving back through the south. With successive means through the day to the ESE, SW, NNW, NE and SE it seems certain that an oscillatory mechanism of this sort is indeed involved.

Exactly how the return of the "sunset angle" to the "sunrise angle" is achieved is more difficult to ascertain. We can exclude the possibility that the return is in the nature of an instantaneous flick-back triggered either by sunset or sunrise. If the former, then the sunrise angle would be set to the sun position whatever stage of the physiological night had been achieved. This would orientate the time-shifted birds successively NW, N, NE, E and SE in each of the five time-bands. If the latter, the appearance of the sun would be taken as sunrise and the successive mean orientations would be the same. This is contrary to the findings and it therefore follows that the unwinding process must continue through the night.

The next question is whether the unwinding is at a steady rate or varies through the night. The latter would, on the face of it, seem to be the more likely. Although the sun's movement round its southerly arc is nearly constant at 15°/hour, its downward project to the horizon (azimuth) changes slowly in the morning (while the sun is climbing) and more rapidly in the middle of the day (while the sun is moving more horizontally). Thus during the day a varying rate of angle change to the sun's azimuth position must be input; therefore an oscillation back might well mirror the variable rate of angle closure by day. This should work well at the spring and autumn equinoxes when the sun is visible for 12 hours and invisible for 12 hours. At other times of the year day and night are unequal in length, the extremes being reached at the solstices. Unfortunately practical considerations make the necessary tests then difficult to carry out; around the summer solstice the birds are in the moult and, indeed, for a time flightless; around the winter solstice the days are short and the frequency of inclement weather high. Although the present set of tests was set around the equinoxes for these reasons, several were sufficiently removed to give quite large day/night ratios, the extremes being 890/550 minutes (2 May) and 520/920 minutes (2 November). The unwinding at night could then well be at fixed rates (for the above two extremes, 2.6 and 7.1 minutes per degree), rather than a varying rate as if the sun at night in summer traced a path equivalent to that which it would trace by day in winter.

An attempt was made to distinguish between the various possibilities by calculating the direction a bird ought to go if it were using the method in question. This was done taking into account the variation from Greenwich Mean Time and the Equation of Time (deviation from the Mean Time) applicable to the date, i.e. the actual sun time (and position) was used. The declination of the sun from the celestial equator, changing with the seasons, north in summer and south in winter, was built into the calculations. Only those birds released in their physiological night were used, those in the overlap between true and time-shifted days being discarded. This reduced the sample size to 205. First were calculated the bearings expected if there were a rapid "flick-back" after sunset (or at sunrise) to the sun-angle appropriate for sunrise, with the first view of the sun (on release) being taken as sunrise. The deviation of the observed from the expected bearings gave an average of ±81°. Since totally random deviations would give ±90°, we are justified in concluding that the "flick-back" method is not used, confirming the conclusion already reached more empirically above. Similarly we can dismiss the hypothesis that any fixed angle to the sun position is maintained through the night and set to the sun azimuth whenever it appears. The average deviation in this case is ±99°. The constant rate unwind method gave a much smaller average deviation of ±62°, but so did the more sophisticated varying rate unwind method. In neither case were there any indications of increasing "errors" with increasing length of unwind period through the night. Thus although an unwind method is confirmed as being the plausible mechanism, the present results do not enable any further discrimination of method. It must be remembered that the observed scatters about the means of the time-shifted birds are themselves wide (Table 2); expressed in the average deviations used above the figure is ±57° (as against ±32° for the controls).

It is therefore unlikely that field tests of this nature will resolve the details of the sun-angle correcting mechanism. Classical or operant conditioning tests with restrained birds such as those of Walraff (1972) and Whiten (1978) may need to be used. In view of the demonstration of time-compensated moon-orientation in Mallard (Matthews 1973) it might just be possible that birds presented with a sun in the middle of their physiological night might lock on to it as if it were the moon. This is unlikely in that the moon would not have been up at the relevant time of night in five sets of releases (those on 29.9, 8.10, 2.11, 14.4 and 2.5). However, the expected moon position was calculated for the releases when the moon would be expected above the horizon at the relevant (shifted) time. This concerned 116 bearings and the observed deviated from the expected on average by ±82°, i.e. showed little evidence of any relation to moon position.

Sun-angle correction and mythology

There is now good evidence that birds *learn* the parameters of the sun's apparent movement across the sky (e.g Wiltschko *et al.* 1976) even though the specialist ability for such learning must be innate. It could, however, be argued that the way in which an animal adjusts its angle-correction mechanism during the night must be innate, for it does not see the sun then. Schwassmann (1960) suggested that the two methods of angle-correcting mechanism might reflect the evolutionary origins of the animals concerned. Thus those with a "wind-on" mechanism could have originated in high latitudes where the sun may be seen for much or all (above the Arctic Circle) of the night. Then those animals with a "wind-back" mechanism, such as has been demonstrated in the Mallard, would, according to this hypothesis, have originated in low latitudes where the sun is not to be seen for much of the 24 hours. Too much should not, perhaps, be made of this, but it is interesting that Murton & Kear (1976) concluded for quite different reasons (connected with the timing of breeding seasons) that *Anas* species were of a tropical origin and had spread from there to the latitudes in which they are mostly now to be found. Moreover the Ancient Egyptians would have subscribed to a "wind-back" mechanism of sun-angle correction. To see why, it is necessary to digress somewhat and consider the way in which they accounted for the alternation of day and night. The story is illustrated on the funereal papyrus of the 18th Dynasty (c. 1500 BC) shown at Fig. 4.

The god of the air, Shu, had twins: Geb, the earth god, and Nut, the sky-goddess. The twins became lovers and this displeased Shu who wrenched them apart and thereafter held Nut aloft with only her toes and fingers touching the earth. Geb remained

Figure 4. The sky-goddess Nut spanning the earth while her twin, the earth-god Geb, lies propped on his elbow below. From Egyptian funereal papyrus of 18th Dynasty (c. 1500 BC).

where he had been thrown, supported on one elbow with one knee bent, symbolising the undulations of the earth's crust. His emblem, interestingly enough in the present context, was a gander, the Great Cackler, whose female, according to some sources, laid the cosmic egg containing the sun. Be that as it may, the sun in the guise of a human-headed falcon, Ra, was born each morning in the east from the womb of Nut. The rosy colour of the sky at dawn represented the birth-blood being shed. Ra then floated under Nut's belly in a solar barque, hiding with his brilliance the stars with which she was spangled. When the sun arrived in the west, Nut swallowed him (sunset) and the stars were revealed. During the night the sun floated back unseen through Nut's body until he was born again in the east next morning.

Epilogue

The series of investigations into the "nonsense" orientation of Mallard reviewed and supplemented in this paper was based on the observations of a great many flight vanishing points of ducks released after having been caught in the duck decoys of Slimbridge, Borough Fen and Nacton. It is unlikely that opportunities for work on such a massive scale will present themselves again. In the late 1970s the catches at the decoys began to fall away, although there was no decline in duck populations either nationally or in the regions of the decoys. The lease on Nacton Decoy was given up in 1982 because it had become uneconomic to operate with a professional decoyman, when taking only 500 duck of all species per annum; it had been catching 5,000 in the 1950s and 1960s. Borough Fen is still leased and maintained as an Ancient Monument (it was in operation in 1640) but barely catches 100 duck, whereas in its heyday in the 1960s it was topping 3,000. Slimbridge has also declined but by rather less, from 2,000 to several hundreds.

What appears to have happened is that the very success of the conservation movement, in which the Wildfowl Trust has played no small part, has resulted in a plethora of "safe" waters to which duck can retire without being shot at or otherwise disturbed. They no longer have to seek out the secluded pools of the decoys, deep in sheltering woods, from which they could be enticed by food or dog into the netted-over pipes curving from their corners. While substantial numbers of duck are caught by feed-in cages, as at Abberton Reservoir, Essex, the individual catches there tend to be smaller, involve more handling, and holding facilities are lacking. Gone it would seem, are the days of substantial decoy catches, pulled (more or less) at will from the roosting throng. We have, indeed, been "hoist with our own petard".

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Summary

The state of knowledge on fixed direction "nonsense" orientations is reviewed, with particular emphasis on those shown by the Mallard *Anas platyrhynchos*. A detailed report is given of 12-hour time-shifting tests whereby Mallard were released by day in their physiological night, to determine how the angle-correcting mechanism of a sun-compass operates between sunset and sunrise. The results support the hypothesis that the angle-correction, having been closed up during the day to take account of the sun's apparent movement across the southern sky, is opened out again through the night, as if the sun ran back through the south rather than on through the north. A parallel with Ancient Egyptian mythology is mentioned.

Tests on the scale reviewed are unlikely to be possible hereafter because of the decline in catching ability of duck decoys. Ironically this is due to the success of conservation measures.

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