

Prologue

This contribution was intended for publication in FORUM, Journal of Avian Biology and submitted in Jan.2003. The comments from the scientific editor was positive but “Given the rather critical and non-enthusiastic comments on the present debate manuscript by the referees - - - “ it was rejected for publication.

In general, the three referees had problems understanding and accepting the overall message: **If we want to understand and describe properly the orientation / navigation system of migrant birds we have to sacrifice or at least reconsider some of the holy cows.**

The orientation/navigation-system of migrant birds – reflections inspired by “The concepts and terminology of bird navigation” (Able 2000)

***Jørgen Rabøl, Zoological Institute, University of Copenhagen, Universitetsparken
15, 2100 Copenhagen Ø, Denmark. E-mail: jrabol@zi.ku.dk www.jorgenrabol.dk***

First-time migrants make use of vector orientation. This is considered a law of nature, which, however, is not strongly supported by experimental results, and the one-sided focus it is subjected to blocks for any deeper understanding of the orientation system.

It is argued for that no qualitative/systemic differences exist between first-time/juvenile and adult migrants, and that compass orientation and gradient navigation are not two different processes but only different concepts/expressions of the same process namely gradient navigation. Furthermore, it is argued that Kramer’s two-step compass and map hypothesis leads to a distorted understanding of migratory navigation, and that in case of long-distance migrants, a one-step/one-and-a-half gradient navigation steering system is compatible with observations, which cannot be understood in terms of simple vector orientation.

Concepts and terminology

Recently, Able (2000) published a survey on “The concepts and terminology of bird navigation”. Together with Rosi and Wolfgang Wiltschko, Kenneth Able is probably the most influential person on the migrant bird “orientation mechanism” scene. Therefore, his survey deserves significant consideration.

I have rather few problems with and comments to the concepts and terminology of Able. However, the much used concept *clock-and-compass orientation* is not mentioned, and the synonym *vector navigation* is not an optimal term because “navigation” – at least in non-American English – signals goal-directed orientation, and Able classifies vector navigation as steered by compass orientation under the heading “Orientation behaviour not goal-oriented”. The prefix “vector” correctly refers to (compass) *direction* and *length* of the migratory route. If the term “clock-and-compass orientation” is discarded, *vector orientation* is a valid option. Able also refers to “gradient *map* navigation” where “gradient navigation” would suffice. No gradient “map” – in any human sense – is involved, and distorted associations arise by this designation. Birds have no gradient “maps”, they are actors directly on the gradient(s)/compass(es), exactly like the ancient Polynesian navigators (Wehner 1998).

The system and the mechanisms of migratory orientation/navigation

In order to understand a biological system such as bird orientation/navigation an exhaustive and appropriate array of terms, concepts, experiments, observations and hypotheses is necessary. It is important – and I am sure that Able will agree – that the concepts and terms accurately reflect the system and its components/processes. If the terms and frames are too simple, distorted or narrow we cannot describe the system and processes properly. Furthermore, to achieve unbiased insight it is important not to fall too much in love with a single explanation or solution but follow what Chamberlin in Platt (1964) designated the method of “multiple working hypotheses”. Wehner (1998) said the same using other words.

Why this warning? Because the survey of Able is not only about concepts and terminology but also much – implicitly and explicitly - about the system and mechanisms which Able seemingly pretend to know by sure. This is rather problematic because – at least in the mind of several “migration strategies” people – we still have much to learn and understand.

Clearly, Able – as the Wiltschkos – is fallen much in love with vector orientation (= vector navigation = clock-and-compass) as the one and only system behind the progress of first-time migrants (“ - - a first-time migrant is apparently not navigating towards a specific, defined goal area”, p.175). Able is also fallen much in love with the *two-step map and compass hypothesis of Kramer*, which is praised in extended passages.

Now, the perhaps provoking thesis of mine is that the strong emphasis of the leading “orientation mechanism” people on vector orientation and the two-step model of Kramer has distorted any proper understanding of the orientation/navigation system of migrant birds.

The field is in a (pre)state of change but most people apparently do not know or ignores the signals. Hedenström and Åkesson (2001) recognize the problems when concluding “The two traditions of migration research – migration strategies and orientation mechanisms – coexist without much interaction”. The *crucial question* – and the main obstacle for a happy marriage between the “migration strategies” and the

“orientation mechanism” people - is *whether first-winter migrants are able to make use of one or another kind of gradient navigation towards a location/area on Earth they never visited before*. According to the “conventional wisdom” of Able and the Wiltschkos this is not possible. Therefore the “orientation mechanisms” people play their repeated compass-game where migratory progress in first-time migrants is restricted and reduced to be a matter of the primacy, dominance, interaction and competition between various compasses only. The “orientation mechanisms” people locked themselves to the vector orientation hypothesis which is based solely in simple (clock-and-)compass orientation. Furthermore – and probably on the unconscious level - they also attain much significance to the two-step map and compass model of Kramer because it contains a significant and *independent compass* component detached from the map (“it is a two-component process dependent upon a position-fixing system and an independent compass capability” (Able 2000, p.180). The two-step map and compass model of Kramer was coupled to the obvious (but not necessarily true) interpretation of the Starling displacements of Perdeck (1958): adult (experienced) birds have a map (and a compass), whereas young (inexperienced) birds are endowed only with a compass. This interpretation lead to the generalization that first-time migrants of all species are endowed with a compass only, and their migratory progress is steered by a vector orientation system, alone.

However, *the simple vector orientation hypothesis is contradicted by much experimental evidence and though treated as a law of nature it is incompatible with several observations, experiments and simulations* (Rabøl 1985, 1994, 1998b, Thorup et al. 2000, Thorup and Rabøl 2001).

Furthermore, *the interpretation of the two-step Kramer map and compass model is significantly distorted* (Rabøl 2001), and a simple one-step/one-and-a-half gradient navigation system seems more appropriate for the understanding of the progress of migrant birds (both adults and first-time migrants). In such a system the compass reference is directed into the axis of the (principal) navigatory gradient and any clear distinction or separation between compass orientation and gradient navigation is diluted.

Vector orientation, cross-axis orientation and gradient navigation

In principle, migratory progress may be steered by the following systems:

Vector orientation (= vector navigation) defined by Able (2000) as “Compass orientation in directions dictated by heritable endogenous information about the direction of the first migration; some correlate of distance may also be encoded”. This “direction of the first migration” equals the *standard direction* (Fig.1A) and a central (implicit) expectation of Able (2000) is that the funnel/cage orientation of a first-time migrant (or a sample of first-time migrants) should be unimodal and not deviate significantly from the standard direction. Furthermore, a first-time bird migrating over a uniform landscape under calm conditions should always proceed in the standard direction. Many deviations from these expectations may be explained or explained away in one way or another. Anyway, at least the funnel/cage orientation of a) captive breed first-time migrants, or b) first-time migrants trapped in the post-fledging area before the start of the migratory season should not deviate significantly from the

standard direction and a unimodal distribution. However, they often do, e.g. Gwinner and Wiltschko 1978, Beck and Wiltschko 1982, Bingman 1984, and Weindler 1994. Rabøl 1998b gives several more examples. As emphasized by Rabøl (1994) it is illegal to transform bi- or tri-modal patterns into grand mean vectors in order to “adapt” to any operational system of vector orientation (e.g. Gwinner and Wiltschko 1978, Weindler et al. 1998, the NAT birds in Fig.1).

Cross-axis orientation is a concept/system introduced and developed by Rabøl (1983, 1985, 1993, 1994, and 1998b). Just recently this system (not considered by Able 2000) has received some attention (Nievergelt et al. 1999). The cross-axis system consists of four vectorial components: one in the standard direction, a reverse vector and two at right angles to the standard/reverse axis (Fig.1B). Which vector is in operation depends on the kind and level of motivation, and this is influenced by both intrinsic and extrinsic signals and states. In contrast to a simple vector orientation system, bi- or tri-modal patterns or a unimodal orientation deviating significantly from the standard direction are valid – and normal – outcomes of a cross-axis system in action.

Gradient navigation is described by e.g. Wallraff (1974), Rabøl (1985, 1988, 2001) and Able (2000). Normally, two or more gradient axes are considered. One or more of these axes may coincide with and be used as a compass reference in the system.

In a simple variant (Fig.1C) the single gradient and the (leading) compass reference are identical/coinciding as e.g. the point of stellar rotation. On the northern hemisphere it is close to Polaris. The altitude of Polaris signals latitude and constitutes a (potential) N/S gradient. Polaris may also be used as the compass reference geographical N. The magnetic field of the Earth offers another example; in many regions a close coincidence exists between the compass direction of magnetic N and the gradients of magnetic inclination and magnetic intensity.

The one-gradient system of Fig.1C may be extended into a two-gradient system (Fig.1D). As an example a second E/W gradient may be based on *time* (Rabøl 1980). Such a gradient presupposes a rigid biological clock not entrained/calibrated by the external day/night cycle. Also the *declination* (the angular difference between magnetic N and geographical N) might be used as an approx. E/W navigation gradient.

The systems of Fig.1C through 1D are considered as and designated a *one-step, one-and-a-half gradient* system. In 1C there is no second gradient, only a right angle E/W axis established in relation to the single gradient/compass reference. This E/W-axis might be a gradient with a zone-of-uncertainty (e.g. Rabøl 1985, 2001) approaching infinity. In case of the two-gradient system (1D) the zone-of-uncertainty around the second gradient is considered to be wider than that of the first/principal gradient. Rabøl (1998a) demonstrated compensations for both N/S and E/W “displacements” in a star planetarium indicating the existence of an operational E/W gradient based on time (at least for longitudinal displacements more than 1-2 hours) and a N/S gradient based in the Polaris altitude.

As strongly emphasized by Able (2000) gradient navigation is normally considered a two-step process (however, Able considers the sun-arc navigation system of Matthews (e.g.1968) as a one-step process). As discussed in the next section, this two-step consideration probably rely on a misinterpretation.

Kramer's two-step map and compass model.

This model developed in order to describe and understand homing in (clock-shifted) pigeons.

According to Kramer (1961, cited in Able 2000, p.180) “The first (step) would consist of establishing the geographic position of the release site relative to the home site, including the ‘theoretical’ homing direction. The latter is an immediate deduction from the first: both, therefore are considered as one step and are called the ‘map’ constituent. The second step would consist of ascertaining the deduced homing direction in the field. This in the analogous human performance, is usually done by means of a compass; it is therefore called the ‘compass’ step”.

Kramer (1959) explained the orientation of clock-shifted pigeons as follows: “Let us remember that the deviation as produced by shifting (the biological clock) can be explained only – and sufficiently – in terms of compass orientation, although the birds are faced with a problem of goal finding, not one of direction finding. From this it must be concluded that direction finding (by the sun) is only a constituent in a complex. The other constituents must have done their work before, because direction finding can enter in action only on the basis of data specifying the position of the new place in relation to home. When this is done, the bird is in a condition comparable to that of a scout who has done his map work, including determination of the required direction. The rest of the job consists in materializing the “deduced” direction in the field, and here the shifted clock must be fatal if ever compass directions are determined by the sun”.

Able (2000, p.180) agrees: 1) “In the first step, a displaced pigeon estimates its position in space relative to home; this yields the homeward direction as a compass bearing, e.g., something like “I am south of home”. In the second step, a compass is employed to identify the actual direction of the homeward bearing, e.g., something like “That way is south””. 2) “It is clear from the clock-shift experiments that the map component of homing navigation is not disturbed: *the pigeons know in what direction home lies* (my underling); their sun compass simply identifies an incorrect, but predictable, direction as the homeward bearing. This experimental manipulation provides the strongest evidence that map-based homing navigation does in fact involve a position finding component and an independent compass component”. Wiltschko and Wiltschko (1998, 1999) explain the two-step Kramer using almost the same words.

However, *these explanations of the process of homeward navigation are not rewarding – at least not when gradient navigation is involved*. If the sun compass is the dominant compass reference and the biological clock of the pigeons is shifted e.g. 6 hours backwards, then the gradients (the “map”) is rotated 90° clockwise and the departure direction correspondingly rotated. The question is whether this is a one-or two-step process because the clock-shifted pigeon does not (firstly) determine/know the right direction towards home, and then (secondly) it makes an error in the final compass step. There is no final compass step. The phase-shifted pigeon *believes* it knows the right direction home but this it is (predictably) wrong because *the “map” including the solar compass reference is rotated in response to the phase-shift*.

However, in the present context it is not so important whether pigeons use a one- or two-step process. The problem is that the two-step map and compass model in pigeons is expanded to migrant birds where it lends support to *one of the central scenarios: compass orientation in the standard direction is a process – genetically fixed – which is totally separate from gradient navigation which always is based in experience*, i.e. per definition a migrant bird is not able to navigate towards a goal, where it has never been before. Therefore, according to “conventional wisdom” first-time migrants can perform vector orientation, only. *If so* the many compass-cue conflict experiments – including some rather remote non-rotating “16-star-sky” experiments - make sense and are highly relevant and respectable science. However, if the real world system cannot be reduced to and conceived as simple compass reactions then such experiments sometimes appear rather meaningless.

In conclusion, *Kramer’s two-step model is based on a distorted interpretation of the mechanism behind the departure orientation of clock-shifted pigeons*, and the appraisal of the model by Able (2000, p.181) cannot be maintained. Anyhow, it seems critical to expand a model of the homing system in resident pigeons to a model of the orientation/navigation system in long-distance migrants.

First-timers and experienced/adult migrants

Displacements

As already mentioned the results – and interpretations – of the Starling displacements of Perdeck (1958) are almost always generalized: first-time migrants make use of a simple vector orientation system, whereas the adult/experienced birds goal-navigate towards sites/areas where they previously have spent breeding, resting or wintering times at least once. Somehow the adult birds were imprinted on and stored some gradient values or extended mosaic patterns which later were recalled from one season to the next. This may be a short-range homing system much like the one in pigeons that is based on olfactory gradients and/or landscape patterns recognized by vision (Wallraff 1996, Rabøl 2001). Furthermore (long-range), the system may include navigation based on celestial and/or magnetic gradients (e.g. Rabøl 1978, Alerstam and Åkesson 1998).

However, the results and interpretations of Perdeck (1958) are not compatible with Rüppell (1944) who found that after lateral displacement in spring, neither adult nor first-year Hooded Crows were generally recovered on the straight line towards the normal breeding area; i.e. apparently a significant part of the birds were not imprinted on any gradient-values of previous breeding or post-fledging areas (in fact the recovery pattern was highly suggestive of a simple vector orientation system). The same holds true of the juvenile Starlings displaced from Holland to Barcelona (Perdeck 1967). The recoveries next spring and summer were mostly *displaced in parallel* to the south of the normal migratory route and breeding range. This pattern was noticed by Perdeck (1967), but normally not by other people when the Perdeck (1958) results were used for generalization. Neither, the funnel orientation of Robins displaced from Denmark to Canary Islands (Rabøl 1981), nor Pied Flycatchers, Garden Warblers and Lesser Whitethroats displaced from Denmark to Kenya (Rabøl 1993) could be understood in terms of the generalizations of the Perdeck results; the

first-time Robins compensated *more* than the adults, and in case of the Pied Flycatchers no clear difference could be found between the age groups.

In general, first-time nocturnal migrants tested in funnels compensate for geographical displacements and for simulated displacements under a planetarium sky (Rabøl 1994, 1998a, Rabøl and Thorup 2001, see however Mouritsen 1999). This means that the orientation system of first-time migrants cannot be considered as based on simple vector orientation, only. Furthermore, even when adult migrants compensated, the act of compensatory orientation *per se* may have arisen in another system than gradient based navigation towards a goal ahead on the migratory route. As an example, the adult Starlings of Perdeck (1958) may have been making use of a system based in 1) compass orientation alone (a hybrid between a vector in the standard direction and a route reversal vector), 2) a hybrid between a vector in the standard direction and gradient navigation back towards Holland, or 3) cross-axis orientation (Fig.1 in Rabøl 1994).

The recovery distributions of ringed migrants

Thorup et al. (2000), and Thorup and Rabøl (2001, in prep.) demonstrated, by means of simulations of recovery distributions of ringed first-time passerine migrants and calculations of within- and between individual variation of the orientation of caged migrants tested in funnels, that a simple vector orientation system seems not to work properly, i.e. there is a poor match between expectations and actual findings. Mouritsen (1998) argued for a simple vector orientation system, whereas Mouritsen (2000) and Mouritsen & Mouritsen (2001) challenged the results and conclusions of Thorup et al. (2000) though on the basis of several misunderstandings.

If the recoveries of first-time migrants ringed in e.g. Sweden have progressed following a simple vector orientation system, then the shape of the distribution will be a *parabola* (Mouritsen & Mouritsen 2001). Migrants following a gradient navigation system towards a moving goal area in principle will lead to recoveries within a *band* of a certain width. Migrants that are gradient navigating towards a distant site, in principle will show an *ellipsoid* recovery distribution. The same will be true for migrants starting in a simple vector orientation system and ending using gradient navigation towards a final goal. In particular, the recovery distributions of Spotted Flycatchers and Marsh Warblers were indicative of a system based on some kind of gradient navigation (Thorup & Rabøl 2001).

Perhaps the initial autumn system in *both* first-time and adult migrants is similar to simple vector orientation, whereas the system changes towards gradient navigation when the bird approaches important stop-over sites such as the wintering ground and the post-fledging/breeding area.

Imprinting on a distant goal

The possibility may be acceptable that a first-time/juvenile migrant such as a Lesser Whitethroat after arriving to Sudan will after some time imprint on the local gradient values/coordinates of the Polar star 10° above the horizon and a declination of -2° .

But the very same accept will probably not extend to an identical first-time migrant gradient-navigating from somewhere in Europe towards a position in Sudan with a Polaris altitude of 10° and a declination of -2° . However, such an “inherited” program may begin in the pre-migratory period, in the initial migratory phase, and/or later in autumn when the first-time migrants learned about the factors that constitute the gradient(s) of the orientation system. In the initial migratory phase, the first-time migrant departs in the standard direction – or any (“nonsense”) direction – which for the sake of simplicity could be perceived as being established as a compass course. In course of the migratory progress the first-time migrant experiences shifting values/coordinates of the navigatory gradient(s) and somehow armed with these observations the bird eventually fixes on the goal/target values of e.g. a polar star altitude of 10° and a declination of -2° . Clearly, again somehow (an expectation on) these values were stored in the genes.

On the programming and uncertainties of systems based on vector orientation and gradient navigation

The perception of a vector orientation system in first-time migrants is not rooted only in the generalization of Perdeck (1958). Vector orientation is also considered a much simpler and therefore a much more likely system/process than is gradient navigation.

However, it is difficult to understand why an inherited *direction* in combination with an inherited *distance* should take up less gene space and/or should be transferred from the genes into practical life with more ease than should the combination of *two* inherited *gradient values*. Furthermore, it is easy to understand that the *degree of uncertainty is much higher in a system based on vector orientation than in a system based on gradient navigation*.

First, as pointed out by Rabøl (1978) and Mouritsen (1998, 2001) this uncertainty expressed as the directional concentration within and between the individuals is a *potential* problem for the vector orientation system. As claimed by Thorup et al. (2000) and Thorup & Rabøl (2001) it also seems to be a problem for the vector orientation system in *real life*; the spread of the recoveries of at least some populations of long-distance migrants is seemingly too small for a steering system based on only vector orientation. Now, in the simulations above, only the variance/uncertainty on the compass direction was considered. If the variation on the step-length had been added certainly the fits would have been even lower of the simulated recovery distributions.

Secondly, also the outcome of a system based in gradient navigation will be burdened with uncertainty but *whereas the uncertainty in a vector orientation system is the sum of the products of establishment and maintenance variation in every step, only the establishment variation in the few “final” steps is present in a gradient navigation system*. The latter system is a closed, negatively feed-backed system, whereas vector orientation is an open system without negative feed-back for errors and wind-drift.

In a vector orientation system it is very important (in order to reduce the variance) that already from the very start and in all steps the migrants compensate for the wind-drift (by means of instantaneous shifts of the heading into the wind and/or reverse

path integration in the following step). In a gradient based navigation system any wind-drift will be a negligible problem (except if the length/cost of the migratory progress is significantly increased or in cases of drift across extended waters or deserts).

Clearly, a navigatory progress, building only on the extension of some gradient values experienced in the breeding/post-fledging area will in the long run be burdened excessively with uncertainty and probably be no better than a simple vector orientation system. However, such a past goal may be important for compensations for displacements in the near future (Rabøl 1994, Fig.1). In order, to be efficient the few “end” goals should originate as sketched in the section “Imprinting on a distant goal”.

Towards a integration of compass orientation and gradient navigation

It is important to realize that the models of vector orientation, cross-axis and gradient navigation are not mutually exclusive; they only are so in the mind of competitive scientists. I am convinced that if we have to understand migratory orientation in birds we have to perceive compass orientation and gradient navigation as different stages or expressions in the same one-step system (Fig.1): there is no gradient navigation without compass(es), and there is no compass orientation detached from gradient(s) – at least not in the ontogenetic past. The principal N/S gradient constitutes the compass-reference. On the intentional level but not in a clear operational way Rabøl (1985) was an attempt of an integration of the two concepts (see also Rabøl 1983, 1994).

The cross-axis system could (also) be considered as a transitory model on the psychological level preparing the way for an integration of vector orientation and gradient navigation. The cross-axis system may be replaced by a one-step, one-and-a-half gradient system such as Fig.1C/D, i.e. the standard, reverse and right angle directions are not established in the way depicted at Fig.1B but as a resultant between a gradient-vector towards N or S and a vector towards E or W. For prolonged periods the polarity and strength of the N/S- and E/W vectors in a Pied Flycatcher in autumn may be locked in a resultant vector in the standard direction (SSW-SW). In other cases/circumstances or in shorter periods the resultant vector will be in the reverse direction (NNE-NE), or in a right angle direction (ESE-SE or WNW-NW), i.e. the system is just as open (not truly negatively feed-backed) as the cross-axis system. However, the system may sometimes change towards a true, negatively feed-backed navigatory system under influence of compensatory gradient values (or “mosaic” patterns) based on inherited processes or imprinting, or both. For a free-flying migrant the wind may be included as a third “gradient”; heading into the wind serves the very important purpose to compensate drift (e.g. Rabøl 1967).

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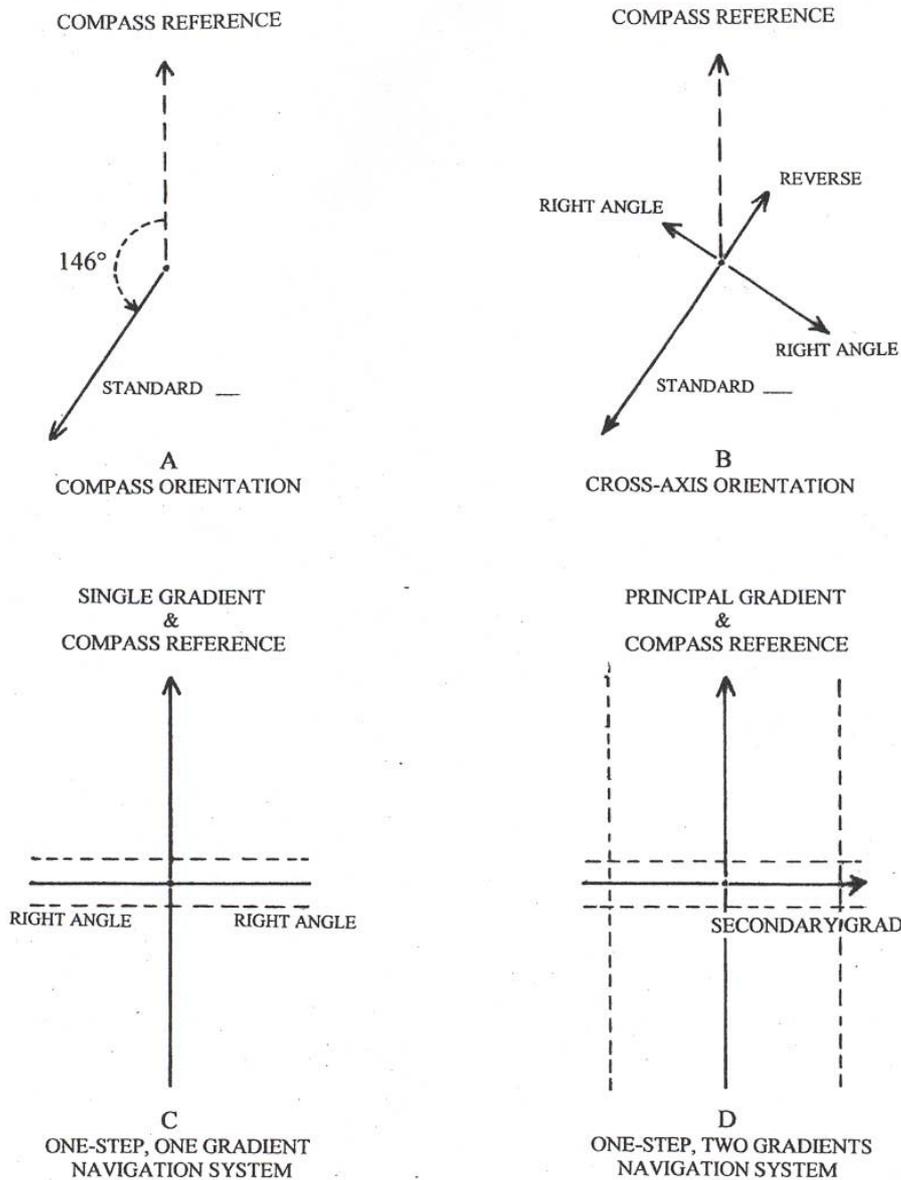
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Fig. 1: Three different orientation/navigation systems. To the left (A) is depicted compass orientation in a simple vector orientation system. The orientation in the standard direction (SSW-SW) is established and maintained in relation to a compass reference which could be stellar rotation or magnetic N. B depicts a cross-axis system with the same standard direction as in case of the simple vector orientation system (A). The (relative) lengths of the four vectors (9, 3, 4 and 6) are considered proportional to the overall probabilities for a compass response in the four directions considered. The two right figures (C and D) depict the “confidence limits” of a one-step, one-and-a-half gradient navigation system where the principal (D) or only (C) N/S-gradient and the compass reference are coinciding. The hatched lines in C and D depict zones-of-uncertainties.



Commentaries

The following comments from the Rev.1 should be quoted:

“The main concern of Rabøl is not terminology but his enduring fight against “vector orientation” of juvenile migrant birds as opposed to his ideas of “gradient navigation”. A referee comment is not the place to go into an extended material discussion of these concepts. Also, it would be difficult to do so, because the author argues quite long-winded and circumstantial rather than clear-cut. For instance, it is neither obvious in what way Kramer’s “map-and-compass concept” is connected with first-autumn migration nor is it obvious why the author disputes it in general. His final conclusion of a lengthy discussion is a sentence (p.8, lines 190-192) with which everybody (including Kramer) would agree. So what? We could even speak of four steps or components: The shifted light-dark cycle results in a shifted clock results in a shifted compass results in a shifted map. But the fact that the map is shiftable as a whole (at any site N, E., S or W of home) by just that angle that corresponds to the angular difference between expected and observed sun azimuth, makes clear that the internal structure of the map remains unaffected and that the sun acts only as a directional reference and not as a component (gradient?) of the map. The boy scout whose compass needle is deflected by 90° towards W instead of N, turns its map with the topside towards W. Where is the problem?”*

It is difficult to understand the assumed relationship between the constructs shown in the figure (cross-axis, right angle, one-and-a-half gradient navigation) and observations that can be made in the real world. The crucial question behind the constructions is quite simple: Do first-autumn migrants perform pure fixed-direction compass orientation (with the intended direction possibly changing over time) or goal-oriented “true” navigation (with the intended goal possibly changing over time)? This question cannot be answered by reflections but only by means of empirical data. Several related experiments and evaluations have been conducted, but there is disagreement among different researchers (recently most distinctly between Mouritsen and Rabøl) on the conclusiveness of the various data sets and on the conclusions which can be drawn from them. Rabøl realizes correctly that the majority opinion is against him. He can hardly change this condition, however, by treating his readers with extended theoretical considerations. If at all, he can change the situation only if he can convincingly explain why the empirical data supporting his view are more trustworthy than those staying against his view (e.g. Mouritsen & Larsen 1998). Only on condition that he should be successful in this respect, he may find an audience that is interested in hypotheses on “gradient navigation” towards a non-experienced geographical goal”.

*There is no final compass step. The phase-shifted pigeon believes it knows the right direction home but this is (predictably) wrong because the “map” including the solar compass reference is rotated in response to the phase-shift.

The important points raised by the referees are 1) **the map-and-compass system**, and 2) **the systems presented in Fig.1**. These two points are highly interconnected.

The map-and-compass system

The remarks of mine in the JAB manuscript on the Kramer model is not outstanding:

Rabøl (2001, p.9) writes: "*Wallcott acknowledges "Kramer's idea that pigeon homing is a two-step process: A 'map' to determine the directions towards home and a compass to guide the birds in that direction (Kramer 1953)". However, this dissociation of the "map" and the compass may be misleading, which becomes obvious when Wallcott observes that "clock-shift experiments - - - introduced an error into the sun compass system, but since the pigeon flies off at an angle with respect to the home direction, the birds still obviously knows the direction towards home". In my opinion it is not so; the "map" or the navigatory axes are tightly locked to one or several compasses, and following a clock-shift the whole system turns temporarily because of the dominant sun compass. Consequently, for example, a 6 hour fast clock makes departing pigeons believe that that home is 90° to the left of the true home direction"*".

Hans Wallraff knows this paper as he commented on a draft of the paper, and Wallraff (2004) says much the same, and also in his example used a 6 hour fast clock-shift which because of reference to latitude 50°N on 24 May and 20 July and sun at 0800 hours and 1400 hours were not changing theoretical 90° but true natural 130°.

Wallraff (2004) writes: "*Over 50 years, Kramer's 'map-and-compass concept' remained an accepted constant, probably profiting from the fact that it articulates only a general principle and does not claim to be a functional model with defined inputs, connections and outputs. Although the concept is formulated as an anthropomorphic metaphor, it has often been taken quite literally (step 1: determine on your map that home is to the south; step 2: ask your compass where is south; e.g. Figure 2 in Wiltschko & Wiltschko 2003a). In its consequence, however, the concept does not only say that the birds have two independent devices, a map and a compass. The 'and' in between is the core of the system which implies an appropriate linkage of its components (cf. Wallraff 1974, 1991). In a simplified schema, shown in Fig. 1a, it is assumed that the values of the two fictitious variables, x and y , increase monotonically in particular directions. Thus, x and y can be used as spatial coordinates to determine a bird's current position P in relation to the position of its home site H . If a bird knew the steepness of the gradients of x and y and could directly measure their directions, the system would operate by itself and would not need a signal from the outside such as the sun. However, pigeons do use the sun and thus apparently need it as a directional reference. A pigeon with its clock going 6 h fast interprets the real 0800 hours sun as a 1400 hours sun (Fig. 1b). The bird knows that under the recorded Δx and Δy condition it has to fly away from the sun at that time. By flying away from the real 0800 hours sun, the pigeon departs towards west-nordwest, thus deviating by 130° to the left from the correct homeward course. For human observer, the birds departs in a false direction (open-headed arrow in Fig. 1a), but for the bird everything appears all right, as he does not realize that his whole system has rotated by 130° (Fig. 1b)"*.

Obviously, Rev.1 in his somewhat irritated and annoyed way says/means much the same as Rabøl (2001) and Wallraff (2004). Furthermore, he asked the question "*Where is the problem?*" At least concerning the pigeons I have no practical problems with the Kramer model. It is just distorted and results in misleading

associations. The real problem first arises – on a psychological level - when generalizing/extending from the traditional perception of the Kramer-system of pigeons to the orientation/navigation system of (long-distance) migrants: The question here is whether there is an independent compass responsible for a vector orientation system in juvenile migrants. If you believe in an independent compass in pigeons then you – too easily – buy an independent compass in the navigation system of migrant birds and the vector orientation model too.

Wallraff (2004) refers to Wiltschko & Wiltschko (2003). In this paper the Wiltschkos split up the two steps in the map-and-compass even more than usual.

The Wiltschkos also explicitly connects the two-step system of homing pigeons and migratory birds:

“The model of a two-step process originally described for homing can be applied to navigation tasks within the home range and migration as well (Fig.9)”.

And later on:

“Another common characteristic of homing and migratory orientation is the change in strategy with increasing experience, which mainly concerns the mechanisms providing the compass course (e.g. Perdeck 1958, Wiltschko and Wiltschko 1985a). Navigation by young, inexperienced birds must be based on innate mechanisms, because other mechanisms are not yet available. In homing, very young, inexperienced birds use path integration with the magnetic compass as an external reference (e.g. R. Wiltschko & Wiltschko 1978, 2000); in migration, the first-time migrants are guided by the inherited migration program (e.g. Berthold 1988), using the geomagnetic field and celestial rotation as reference (e.g. W. Wiltschko et al. 1998).”

Now, the message from me is that (at least concerning celestial and magnetic gradients) the map and the compass in a gradient-navigation system are locked so tightly together that the traditional dichotomy in 1) a compass and 2) two or more gradients obscures for a proper understanding of the orientation/navigation system in migrant birds because we are forced to select the side: Is this observed pattern the result of simple compass orientation or gradient navigation.

However, very probably the sun (and magnetic) compass in the map-and-compass system of Homing Pigeons is something different from an integral compass in the navigation system of medium- and long-distance migratory birds (however, see below).

Homing Pigeons and their olfactory gradients are probably very different from migratory birds and their regional - or even world-wide navigation systems (but not – necessarily so – from local navigation systems in migratory birds). But the Wiltschkos (2003) explicitly make the comparison between pigeons and migratory birds and other people do so implicitly on the unconscious level. In essence, I do not consider the system of first-time migrants all the way down to the wintering as only the outcome of (an inherited) vector orientation system. Already before actual start in the post-fledging area gradient navigation comes in/develops (as sketched in the manuscript).

In 2005 Hans Wallraff released his book **Avian navigation: Pigeon homing as a paradigm.**

It is a very well written and lucid book – though very little about other birds than pigeons, and obviously Wallraff is not very interested in bird migration and homing of migratory birds.

Wallraff (2005) has changed a lot since Wallraff (1974). Formerly, the navigation system of pigeons - as other organisms - was considered in general terms as two gradients with zero axes and zones-of-uncertainty. Rabøl (1985, 1988, 2001) elaborated this system and the PCD was considered an inevitable outcome of the such a system. Wallraff (2005) barely mentions zero axes and zones-of-uncertainties which could not be found in the index. The navigation system of pigeons is now purely based on olfaction and an array of olfactory gradients based on different ratios/mixtures of airborne compounds. In fact, there are no real gradients but different olfactory compositions/"landscapes" are connected with different directions (in reference to the sun- and a magnetic compass). On p.145 Wallraff writes " - a bird merely needs to correlate, at home, varying olfactory sensations with varying wind directions and to fly, at a distant site, in that compass direction towards which the wind usually blew while the sensation was most similar to the current one. In doing so, the pigeon need not to have a map-like representation in its brain and need not to know anything about gradients". There is no navigational map, and Kramer's map-and-compass concept is abandoned (p. 145 "The animals behave as if they had a map"). Or, p.146 "If we concede them a map at all, it would be a sort of 'radial map' (Gould 1998) approximately indicating the radius along which an animal is displaced, but not including a reliable measure of distance". There is still a PCD - also in anosmic pigeons - but the PCD is considered as a loft-specific constant disconnected from the "navigation" system, and poorly understood.

Now Wallraff never refers to my papers - such as Rabøl (1985, 2001) - as he sometimes should do for the sake of broadness. Anyway, he is legally excused for not referring to my book (Rabøl 1988) *The Migration and Orientation of Birds*, because of the Danish language. In this book I focused on the departure and recovery directions of the control and anosmic pigeons of Wallraff around Würzburg applying his own system based on zero axes, zones of uncertainties and polarized orientations within the zones of uncertainties, I obtained a good degree of description/explanation if hypothesizing on an about N/S-running olfactory gradient with a narrow zone of uncertainty (and polarized N-orientation within this zone). The other gradient axis was about E/W with a much broader zone of uncertainty (and polarized W-orientation within this zone). In the anosmic pigeons the narrow zone of uncertainty at right angles to the olfactory gradient in the controls now changes to a very broad zone, i.e. only N-orientation comes out in connection with W-(most release sites) or E-orientation from the other gradient, and as a general rule the PCD of the anosmic pigeons shifts clockwise and becomes more significant compared with the PCD of control birds.

As far as I can see (Wallraff will highly dislike such an interpretation) the olfactory gradient of "mine" could be perceived as a resultant gradient of several/many/all olfactory gradients in the universe of Wallraff - most of which probably are polarized from about N to S (stronger intensity). The other about E/W-directed gradient of "mine" could also be rooted in odours, or involves the sense of time/a circadian clock which presumably - at least in principle - should be much more workable in short-term displacements of pigeons than during the whole season of a migratory bird.

Finally, in the book of Wallraff (2005) long-distance migrants are considered (reduced to) a kind of pigeons with two "home-areas", one for breeding and one for wintering connected with a vector orientation system. Each "home-area" consists of a small core based in vision, and a much larger surrounding area based in olfaction. A migrant hitting this outer area will be able to "navigate" its way to the core (Fig.10.8).

Wallraff is not considering compensatory orientation as part of this system but this may well be incorporated.

Wallraff may be right. This could be the system in long-distance migrants. If so, many people including the Wiltschkos and myself to a large extent had lived and worked a whole life in vain. Congratulations! But of course, this should not be the only reason to reject Wallraff. We have to come up with better arguments.

The system presented in Fig.1:

Rev.1 says that only experiments and not talking can decide whether first-autumn birds make use of pure fixed-direction compass orientation or goal-oriented “true” navigation. Then he says people – such as Mouritsen and me - do not agree about the interpretation of the empirical data. However, he overlooks that Mouritsen (1999) bases his conclusions on an array of selected displacement experiments not considered in concert, but makes his overall conclusion on the basis **whether** or not the majority of single cases show significant compensation for the displacement. On the other hand, Rabøl & Thorup (2001) – referred to in the JAB manuscript but seemingly not considered by any of the referees – is based on a meta-analysis including not a selection but all published cage/funnel displacement experiments. This meta-analysis – now also presented in a different design by Thorup & Rabøl (2007) - concludes that there is a significant overall tendency for compensatory orientation following a real or simulated geographical displacement. In the simple universe of Rev.1 such compensatory orientation is indicative of goal-oriented “true” navigation. Unfortunately, it is not that simple as realized by Rabøl (1994, Fig.1). It is **only a strong indication that simple compass orientation is not sufficient**, but as seen in Fig.1 of the JAB manuscript there are two stages (B and C) in between simple compass orientation (A) and true bi/multi-coordinate/gradient navigation (D).

There are several other indications that simple compass orientation alone is insufficient, e.g. Thorup and Rabøl (2001): For example, a) the narrow belt of autumn migration within E-Africa of the Marsh Warbler (*Acrocephalus palustris*), and the ellipsoid recovery pattern with lack of recoveries from E-Africa in Nordic Spotted Flycatchers (*Muscicapa striata*). Furthermore, in a recent publication Thorup et al. (2007) demonstrate general tendencies for a significant directional variation **among individuals** in various funnel-tested samples. This observation is **not compatible** with a migratory system based on simple compass/vector orientation alone.

Rev.2 has problems understanding why I call it “*one-and-a-half gradient system*”. I do so because I think that the bird is most/all of its time aware of the major (N/S-) gradient, whereas the other E/W-component is sometimes just a right angle compass response and sometimes “truly” navigatory, i.e. resting on a process where the bird on basis of environmental stimuli and an intrinsic “feeling” decide whether it is to the left or right of its intended goal.

Wallraff (2004) says that Kramer’s model worked so good for so long time because it was general and not too precise. The same is intended with the Fig.1 of mine. **The important point in the model of mine is that refers to celestial (or magnetic) orientation/navigation-system(s) where the major navigatory gradient also constitutes the major compass reference**, and the standard direction is considered a resultant vector between a vector in the major gradient direction (i.e. S in autumn) and

another vector directed W or E. One may also consider the standard direction vector as the mean output it as a crooked-legged cross(-axis system) in the four cardinal directions – sometimes capable of true navigatory compensations and sometimes/most of the time just compensatory on the background of open “feelings”. **Because the compass reference originates in the same system as the navigatory gradients it will often be difficult to be precise about whether a certain response is (the outcome of) compass orientation or gradient navigation.** In this connection, Bonadonna et al. (2003) remind us that evolution is about tinkering not engineering: Birds make use of “elementary gradient-based orientation mechanisms (“getting there” solution) rather than bicoordinate map (“knowing where” solution)”.

Rev.3 writes that “*He is right in that the clock-and-compass model describing the endogenous components of migration should not be taken in the very mechanistic it was originally propagated e.g. by Berthold years ago. But today, most authors are aware that it represents just the innate component of a program that is highly flexible, being modified by a number of external factors e.g. ecological barriers, magnetic conditions en route, habitat preference, local food supply etc*”. I fully agree with Rev.3 but the problem is – as already emphasized by Rabøl (1985, 1994) – that included in these additions to simple clock-and-compass/vector orientation are various kinds of compensations, including navigatory responses. Therefore, the line of division for “most authors” is not between 1) simple vector orientation and 2) gradient navigation, but between 1) vector orientation + simple navigation and 2) more elaborated gradient navigation.

Outlook

A positive feeling of mine, and a negative feeling of others

For many years I had a strong feeling – finally ending up in clear indications (Rabøl 1985, Rabøl 1998, Thorup & Rabøl 2007) – that first-time juvenile birds were able to perform more than just simple vector orientation: It was difficult to understand their compensatory orientation without involving some “soft” kind of gradient navigation.

However almost all other people do not believe in gradient navigation in first-time juvenile migrants. Gradient navigation towards a certain point or area was something that developed by experience, and that kind of extrapolated experience that I suggested in the JAB manuscript for the Lesser Whitethroat wintering in Sudan was not considered as a serious possibility – perhaps because it never occurred to people.

A negative feeling of mine and a positive feeling of others

Up to now I mostly had negative feelings about magnetic gradient navigation. At the time when Wiltschko & Wiltschko (1995) made their big survey on magnetic orientation in animals there were no clear indications of magnetic gradient navigation – though clearly enough this possibility was seriously considered a possibility by some pigeon-people such as the Wiltschkos, Walker and others. Able (1996) told the Wiltschkos that from now on the burden of the proof was on the side of people believing in magnetic navigation. When I wrote my survey on pigeon navigation I was also totally on the olfactory side of Able (1996), Wallraff (1996) and Wallcott

(1996) – and against magnetic navigation as consistently suggested by R. Wiltschko (1996).

However, things have changed somewhat: In recent years magnetic gradient navigation or “alike” is increasingly suggested or even claimed – and not only by the traditional people but also by Phillips, Lohman and many others (e.g. Freake et al. 2006) including formerly dis-believers such as Luschi et al. (2007). Even Wallraff and Wallcott seem to be dragging their feet.

Also in the discussion between Wallraff (2000) and Wiltschko & Wiltschko (2000) on the significance of reverse path integration in a system based on magnetic compass orientation in very young pigeons - the proposal and interpretation of the Wiltschkos - it is difficult not to accept their hypothesis.

This directly leads to the observation of Papi’s (2001) remark on “a confusion between *natural* situations and *experimental* situations”. The explicit message from Papi is that if pigeons are displaced passively over long distances and more or less en route deprived of environmental stimuli the only system which appears important for successful homing is olfactory navigation. Magnetic navigation plays no role/could not be traced. Now, the implicit message is, that under natural conditions magnetic orientation/navigation may well play a role.

So obviously, I have to reconsider my negative feelings about (the reality of) magnetic gradient navigation – or at least be conscious and constructive about the (apparent) paradox between my positive attitude of celestial and olfactory (gradient) navigation and my negative attitude in magnetic navigation – and to overcome my irritation about the field of animal orientation/navigation dominated by people believing in magnetic navigation – or perhaps more correctly by people realizing that it is rewarding to publish papers claiming magnetic navigation. These people repeatedly report that something happens (a right angle response, flights in parallel to the isoclines of the magnetic intensity and so) when a treatment or the circumstances change the magnetic field and then always make the interpretation that magnetic gradient-navigation is involved. However, this is a long discussion which I will take up another time.

These references relates to my commentaries only:

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