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Celestial based navigation in migrant birds with special attention to longitudinal east-west navigation

Jørgen Rabøl

(*Med et dansk resume: Øst-vest-navigation hos trækfugle baseret på Solen og stjernerne*)

Abstract Celestial-based east–west navigation is often dismissed as an unrealistic possibility, primarily because it is assumed to require biological clocks that are both highly accurate and stable over extended periods – ranging from several months to even longer. However, this clock-hypothesis may be too narrowly defined. In this paper, I demonstrate that celestial-based east-west navigation may be simpler than commonly assumed. Mastery of such navigation may require only that a bird:

1) keeps track of the date,

2) monitors the stellar clock in the northern sky,

3) determines the time of local noon relative to the Sun, and

4) maintains an awareness of the uncertainties associated with each of these steps.

Furthermore, where feasible, birds may supplement their biological clocks with information derived from magnetic declination.

Introduction

The prevailing view is that migratory birds use the starry sky solely for vector orientation (e.g. Holland 2014). The planetarium experiments conducted by Sauer (e.g. 1957), though initially influential, now appear flawed and somewhat unorthodox in retrospect. Emlen (e.g. 1967, 1975) found no evidence of stellar navigation, possible due to a) limited number of autumn experiments conducted on the species studied (Indigo Buntings *Passerina cyanea*), and b) the artificial sky in his experiments, which rotated abruptly by 3.75° every 15 minutes and then remained stationary for the next 15 minutes.

When entering the scene, I (Rabøl 1969) proposed not only stellar navigation but also goal-area navigation, i.e. navigation towards a target area that shifts along the migratory route over the course of the year, sometimes pausing for extended periods in the breeding grounds, wintering areas or stopover sites. This concept proved too radical for many scientists. Combined with Sauer's implausible results and Emlen's lack of supportive evidence, it led to widespread scepticism about stellar navigation – a scepticism that persists to this day.

I continued to explore goal-area navigation, while remaining open to alternative explanations of what appeared to be compensatory orientation following geographic displacements (e.g. fig. 1 in Rabøl 1994). Later, Thorup & Rabøl (2007) in a community-wide study, demonstrated significant compensatory orientation in juvenile migrants following real or simulated displacements – at least on starry autumn nights. Despite being published in a prestigious scientific journal, this important study is rarely cited, for reasons that remain unclear. There may be several reasons for this.

Stellar navigation is not the only hypothesis to have faced resistance. Olfactory navigation has also encountered scepticism. Wallraff (2013) demonstrated that pigeons rely on olfactory cues to navigate back to their home lofts after displacement. His evidence showed that olfactory deprived birds failed to orient homeward and almost never found their way home. Consequently, Wallraff concluded that the existence and importance of olfactory-based navigation could no longer be doubted. The remaining question, he argued, concerns how pigeons interpret olfactory signals within a navigational framework, and he proposed a model, acknowledging that it may not precisely reflect the birds' actual mechanisms. As he stated: "If it is possible to create virtual birds that orient their courses approximately towards home from various distant sites all-around by sole usage of real atmospheric trace gases, home-site winds and a compass (which they have anyway), why should it be impossible for living birds to achieve a similar output by sensing the same input?" The key phrase here is "why should it be impossible", a reminder of the limitations of our current understanding. That said, Wallraff's perspective is itself limited, as he recognises only olfactory navigation in birds, dismissing celestial and magnetic navigation as non-existent constructs.

Based on simulated displacements using planetary skies, Rabøl (1998) found significant evidence for both latitudinal and longitudinal stellar navigation. These findings were later supported by Thorup & Rabøl (2007). Following Wallraff's logic, the next step is to propose plausible models for how stellar-based navigation might function.

Stellar-based latitude navigation appears relatively straightforward: latitude is, by definition, the altitude of the celestial pole (near Polaris) above the horizon. It seems plausible that birds could estimate this altitude with sufficient precision for effective navigation.

In contrast, stellar-based longitude navigation is more challenging, as it requires the operation of biological clocks. Many researchers remain sceptical that such clocks could be accurate and stable enough over long periods to be practically useful.

Nevertheless, if we accept the evidence from Rabøl (1998) and Thorup & Rabøl (2007) supporting stellar navigation, we must also consider the likely involvement of biological clocks in celestial-based east-west navigation. But must we? Magnetic declination offers an alternative cue for east-west orientation, at least in regions, where the declination changes gradually along the east-west axis. Determining magnetic declination requires only a basic timekeeping mechanism to establish the time of year. Some evidence supports the use of magnetic declination (Chernetsov *et al.* 2017, appendix 1 in Rabøl 2023), although more recent findings by Chernetsov *et al*. (2020) did not corroborate this.

In this paper, I propose two models for stellar-based navigation, both of which may be viable in practice. These models should not be viewed as mutually exclusive; rather, they may operate in tandem.

Studies of celestial navigation

The term celestial refers to the sun, stars and moon and their respective movements. In principle, solar, stellar and lunar cues may be utilized for gradient/coordinate navigation.

The sun-arc navigation hypothesis was originally proposed by Matthews (1951a, 1951b, 1963, 1968) and later modified by Pennycuick (1960a, 1960b). Although this hypothesis was considered in the context of pigeon homing, it was never widely accepted and is notably absent from recent reviews such as Wallraff (2005) and Wiltschko & Wiltschko (2003). Nevertheless, sun-arc navigation remains a plausible mechanism in migratory birds, though likely not in homing pigeons. Indeed, researchers implicitly rely on a kind of solar navigation when employing geolocators to track migratory birds (e.g. Kristensen *et al.* 2013).

Stellar east-west navigation was claimed by Sauer (1957) and Sauer & Sauer (1960). However, the evidence was weakened and likely confounded by several factors: a) the very limited number of individuals (*Sylvia*-warblers), b) the lower half of the planetarium sky was obscured, c) the simulated stellar rotation was discontinuous – an abrupt 7.5° shift every 30 minutes and d) directional migratory activity was recorded visually by Sauer, who observed the birds from beneath as they fluttered within a circular cage. These methodological limitations make it difficult to extrapolate the findings to the behaviour of free-flying birds under natural starry skies.

Emlen (1967, 1975) conducted experiments using numerous individual Indigo Buntings. However, (a) the planetarium's simulated stellar rotation was suboptimal, consisting of abrupt 3.75° shifts every 15 minutes, and (b) nearly all experiments were conducted during spring, which may be a confounding seasonal factor. Unlike Sauer's birds, Emlen's buntings did not exhibit compensatory orientation in response to simulated displacements of 3, 6, or 12 hours east or west. This absence of compensatory orientation suggests vector orientation rather than a gradient based navigation system. In a Royal Institute of Navigation Forum discussion in 2011, R. Wiltschko referred to Emlen's findings as definitive evidence against stellar navigation in birds. This stance likely reflects a longstanding tendency by R. & W. Wiltschko to dismiss or overlook the potential role of stellar navigation in avian orientation.

In my early displacement experiments (Rabøl 1969, 1970, 1972), I found indications consistent with stellar-based goal-area navigation. While caution is warranted, the results as presented were at least compatible with such a mechanism.

Two long-distance displacement experiments: 1) from Denmark to the Canary Islands (Rabøl 1981) and 2) from Denmark to Kenya (Rabøl 1993), yielded some evidence of compensatory behaviour. Further support for stellar navigation emerged from Rabøl (1998), who conducted three series of planetarium experiments with juvenile European Pied Flycatchers *Ficedula hypoleuca* and Common Redstarts *Phoenicurus phoenicurus* during autumn. For unclear reasons: a) possibly due to the author JR, b) the low-ranking journal Dansk Orn. Foren. Tidsskr. or c) general inconvenience, these significant findings have been largely ignored or misrepresented by major reviewers such as Wallraff, Kishkinev *et al.* (2010), and R. & W. Wiltschko.

Thorup & Rabøl (2007) compiled all cage/funnel-experiments involving real and simulated displacements of juvenile migratory passerines. Rabøl (2023 appendix 6) added further experiments conducted since 2007 or previously unpublished. The majority of these experiments were conducted at night, during autumn and under stellar or simulated stellar conditions. On average, the birds significantly compensated for displacements, indicating the operation of a stellar navigation mechanism.

General considerations: the stellar sky and biological clocks

Most observers will have noticed that the appearance of the stellar sky at a given location on Earth, changes with the seasons: Polaris remains fixed in both direction and altitude, always located due geographical north. In contrast, constellations such the Big Dipper vary in elevation throughout the year, appearing low in the northern sky during autumn and high during spring.

In the Northern hemisphere, the stars appear to rotate counterclockwise around Polaris completing one full revolution in approximately 23 hours and 56 minutes. Since the solar day and night is 24 hour, this means that over the course of a year, the stars effectively “gain” one full revolution on the sun.

When observing the northern circumpolar region, the line connecting the two posterior stars of the Big Dipper points almost directly towards Polaris. This alignment can function as a pointer in a conceptual “stellar clock”. At the same solar time on the following night, this stellar pointer will have shifted approximately 0.986° counter-clockwise (i.e. 360° divided by 365.242 days). Over a span of 70 solar days, this amounts to a cumulative shift of roughly 68.995° counter-clockwise.

It remains unknown whether birds perceive the two posterior stars of the Big Dipper as a functional pointer in such a clock. However, experimental evidence from Sauer (1957), Wallraff (1972), Emlen (1967) and Rabøl (1998) suggests that nocturnal migratory birds possess a remarkable ability to imprint and utilise the stellar sky for orientation and navigation.

Both models I and II (see below) are considered within the framework of goal-area navigation as defined by Rabøl (1969, 1978, 1985). In this context, the migratory bird is assumed to navigate towards a goal area, that gradually shifts along the migratory route over the course of the season. In autumn this goal area ultimately coincides with the wintering grounds (for simplicity, we consider a single wintering area; see Tøttrup *et al.* (2012) for a broader discussion). In such a navigational system, errors do not accumulate *en route* but are confined to the final destination.

In principle, navigation using the stellar sky is straightforward. The altitude of Polaris (effectively the centre of stellar rotation), indicates latitude. It is conceivable that birds possess a genetically encoded program instructing them to migrate from one imprinted Polaris altitude to another – for example, descending 50° in altitude over a period of 70 nights.

Longitudinal (east-west) navigation based on highly accurate biological clocks (model I) is theoretically simple, but likely more challenging to implement in practice (see below). However, strict biological clocks may not be essential; model II assumes a less rigid mechanism.

Model I: Stellar navigation via intrinsic clock synchronisation

The foundational principles of Model I were first proposed by Rabøl (1980, Fig. 1).

In this model, a juvenile bird remains in or near its fledging area for a period of independence, before initiating autumn migration on night 0. Prior to departure, the bird observes the stellar sky, imprinting both the altitude of Polaris and the rotational phase of the stars. Through this imprinting-like process, the bird synchronises its intrinsic, highly stable and precise clock with external stellar time.

The potential for longitudinal east-west navigation lies in the interplay between the stellar time observed at the bird's current location and the time maintained by its intrinsic clock (Fig. 1). If the migratory route is due south, the period of the intrinsic east-west navigational clock all autumn is 23 hours and 56 minutes, the time on its intrinsic clock is just the same as the time on the stellar watch in the northern stellar sky. However, if the route includes an east or west component, the bird can detect this deviation by comparing the time on its intrinsic clock with the stellar time. For instance, if the intrinsic clock has a period of 23 hours and 54 minutes, it will run ahead of stellar time, signalling to the bird that it must adjust its course eastward to compensate.

Consider the following example: The start position is 60° N, 20° E, and the final goal position of the wintering area is 10° N, 0° E. Furthermore, the migratory progress is intended to take 80 days and nights.[1]

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[1] Reading Ouwehand *et al.* (2016), I learned that the migration in Dutch European Pied Flycatchers was a much shorter affair, about two weeks in spring and three in autumn. Perhaps, this is a precondition for use of celestial navigation and biological clocks where (short) time matters much on accuracy.

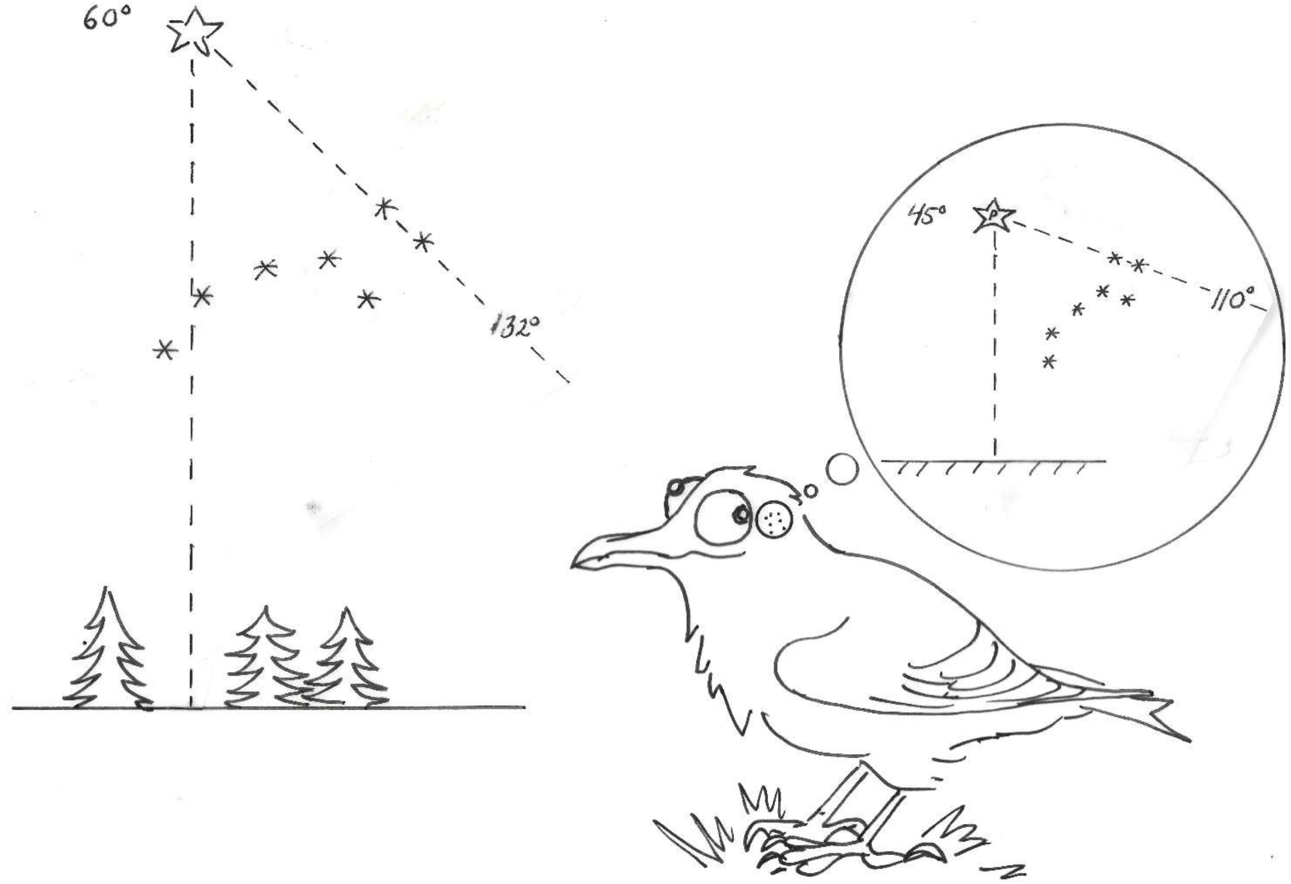

Fig. 1. Stellar navigation, Model I. In essence, the juvenile bird possesses a mental perception that enables it to compare the current northern the starry sky with the expected configuration in its goal area. Once migration begins, this internal movie unfolds according to a fixed program, and it is not possible to change the parameters. Shifts in the LD-cycle has no influence on the fixed biological clock that governs this process. The bird simply needs to observe the starry sky to determine its position relative to the goal area. In the illustrated example, the bird determines its current latitude to be 60° (based on the altitude of Polaris), and the rotational phase of the stellar sky to be 132°. According to its intrinsic program, at this same moment the expected altitude of Polaris should be 45° and the rotational phase 110°. The bird performs a straightforward calculation: "I am north and west of my actual goal area; therefore, I must move approximately southeast."
Stjerne-navigation følgende Model I. I sin hjerne har fuglen – hele tiden - et billede af stjernehimlen; hvordan den ser ud i målområdet efter, at den blev kickstartet, da efterårstrækket gik i gang. Fuglen ser, at Nordstjernen står højere det sted, hvor den befinder sig (i forhold til hvad billedet i dens hjerne siger). Den kan også se, at stjernehimlen i sin rotations-fase er bagud (132° contra 110°) i forhold til, hvad den er i målområdet her og nu. Simpel hovedregning fortæller fuglen, at den skal syd på og øst på = SØ for at trække mod målområdet.

This implies an average westward movement of 20°/80 = 0.25° per night, equivalent to a 1-minute delay per night. Thus, the birds' intrinsic clock should be programmed with a period of 23 hours and 57 minutes, implying that it lags behind stellar time. If the bird remains stationary for 8 days, stellar time will finally be eight minutes ahead of its intrinsic clock: a clear signal to the bird to adjust westwards, to balance the time of the two clocks. Simultaneously, the bird must also be programmed to move from 60° N to 10° N, i.e. 50° towards S over 80 nights, equating to 0.625° per night or approximately 69.444 km (0.625 × 111.111 km).

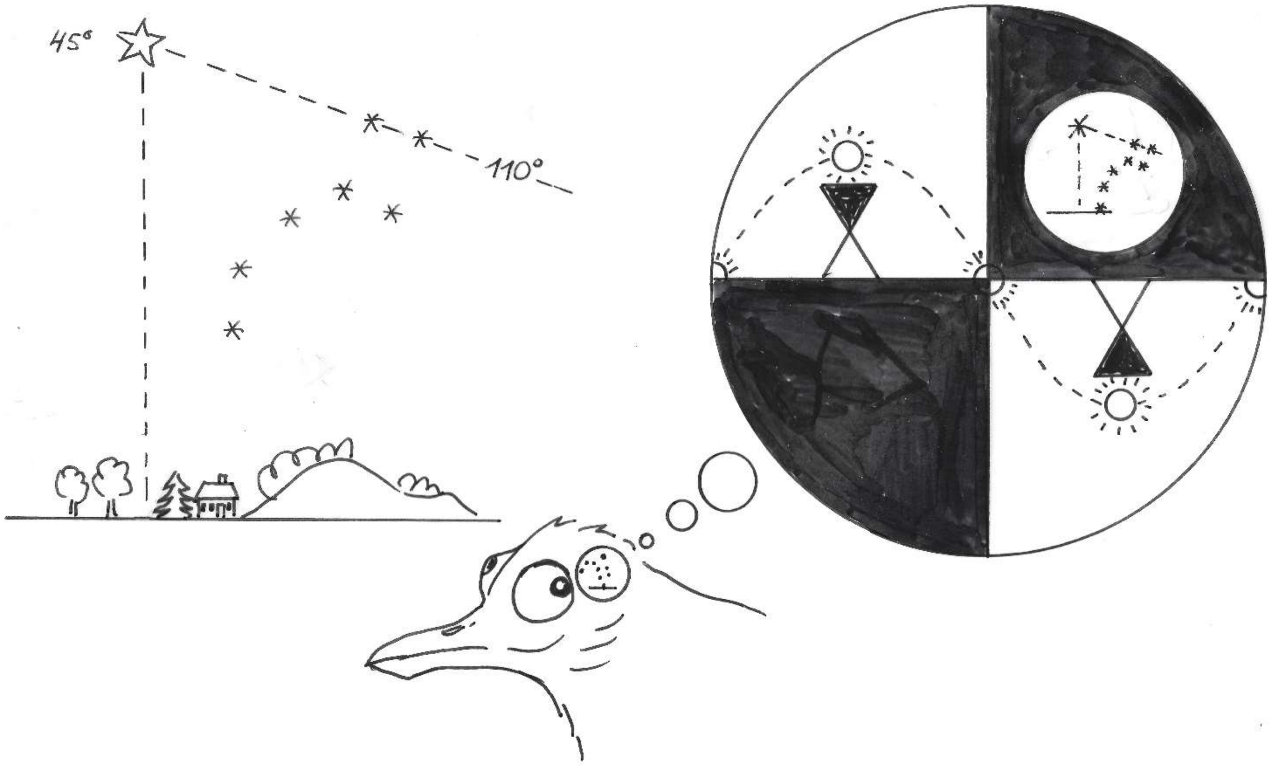

Fig. 2. Stellar navigation, Model II. This relies on the integration of several cognitive skills and processes, as outlined in the text. The picture in the brain of the bird signals, that the bird measures and establishes the time of local noon. Using an internal mechanism akin to an hourglass, it projects this time forward by 12 hours to estimate local midnight. At local midnight the bird compares time and angle on the intrinsic stellar watch with time and angle on the actual stellar watch. In the example shown, local time is about the same as on the intrinsic stellar watch. This means that the bird is on the right longitude. Furthermore, it appears that the Polaris altitude in the intrinsic program is lower than in the actual position, so the combined reaction of the bird should be to move about due south.

Stjerne-navigation følgende Model II. Model II er meget mindre determineret og mindre automatisk end Model I. Som forklaret i teksten kommer reaktionen ud som følge af et integreret samspil af fire processer. Her er især symboliseret, hvordan fastlæggelsen af kl.12 midt på dagen gennem en timeglasagtig proces forlænges 12 timer frem til lokal midnat. På dette tidspunkt kikker fuglen op på stjernehimlen og noterer sig tiden på himmeluret, og da den har regnet datoen ud, kan den sammenligne med hvordan tiden er i dens hjerne på himmeluret i målområdet på samme dato. Som man kan se, befinder den sig på ca. samme længdegrad som i målområdet. Derimod er der forskel på Nordstjernens højde; den står højere på det sted, hvor fuglen befinder sig. Den trækker derfor mod stik S for at komme 'hjem'.

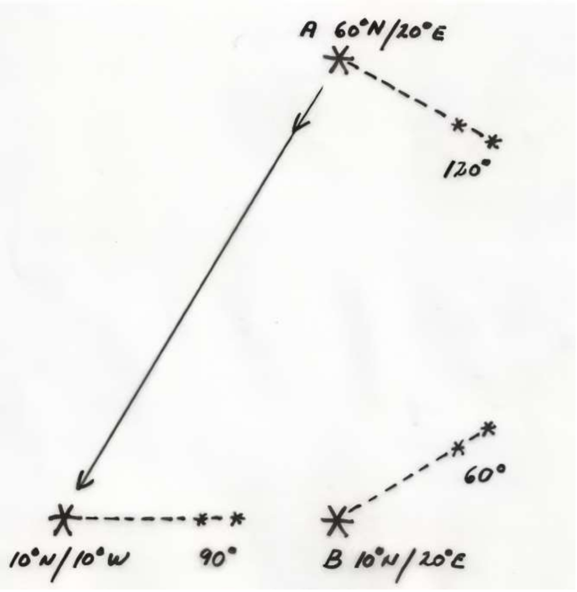

Fig. 3. Constructed example of stellar navigation following model II. In this illustrative example, a juvenile bird begins its autumn migration from point A (60° N/20° E) on 10 Aug. at midnight and is genetically programmed to reach its wintering area at 10° N/10° W after 60 days and nights. At the starting point (A), the bird observes the stellar sky: the two posterior stars of the Big Dipper form a pointer (hatched line) directed 120 clockwise relative to Polaris. Sixty days later, at local midnight on the same longitude but at latitude 10° N (point B), the pointer will have shifted to 60° clockwise. However, the bird is programmed to end its migration at 10° W where the angle at midnight will be 90° clockwise. Summing up, the bird is programmed to move 50° towards south, and 30° towards west, and this can be achieved if the bird is capable of counting the number of days and nights since departure, estimate the time of local noon, and read time on the stellar watch. The loxodromic direction from A to 10° N/10° W is 204.64° and the distance is 6112.09 km. To perform goal-area migration, the bird would need to break down its journey into daily increments of 0.5° longitude (equivalent of 2 minutes of stellar time) and 0.8333° latitude per day/night. Whether the bird possess the capacity to execute such fine-grained navigation remains open to discussion. However, such a program is easily implemented in machine-language, and – regardless of navigation system – one may argue that no alternative (e.g. a m agnetic system) is conceptually simpler. This model could also be expanded to accommodate more complex, dog-legged migratory routes, such as those observed in Dutch Pied Flycatchers (Ouwehand *et al.* 2016), Appendix 2.

Konstrueret eksempel på stjerne-navigation følgende model II. Fuglen starter i 60°N/20°Ø (øverst til højre) og er programmeret til at bevæge sig 50° mod S og 30° mod W, så den ender i vinterkvarteret i 10° N/10° W 60 dage efter starten (nederst til venstre). For at kunne gøre det, må minimumskravene være, at fuglen kan tælle døgn, bestemme tidspunktet for Solens kulminationshøjde på himlen (= middag), samt aflæse tiden på 'himmeluret' (viserne på 'himmeluret' er vist med forbindelseslinjen mellem de to stjerner i Karlsvognens 'bagsmæk'). For at kunne målområde-navigere skal den også kunne gå ind mellem de to yderpunkter og operere/intrapolere på en daglig basis. Det er ikke nemt, men magnetisk navigation – alternativet, som så mange tror på – er efter min mening endnu sværere at udføre.

Model II: Stellar navigation without a fixed intrinsic clock

Model II explores whether a navigation system can be simulated with more flexible assumptions – ones that sceptics might find plausible. Inspired by Wallraff's virtual pigeons, this model was developed in collaboration with Henning Noer, and preliminary simulations (Appendix 2) yielded promising results.

Unlike Model I, Model II does not rely on a long-term, highly accurate internal clock. Instead, the bird must possess the following capabilities (translated into human terms; Figs 2 and 3):

1) Temporal awareness. The bird should track of the number of days and nights since the migration began, for example recognising that it is 43 days (and nights) into its journey.

2) Understanding stellar drift. The bird must be aware that, at a fixed location, stellar time advances approximately 4 minutes per day relative to solar time. Thus, the stellar pointer (e.g. the line from Polaris to the posterior stars of the Big Dipper) shifts roughly 1° counterclockwise each night (see above).

3) Estimating local midnight. This can be achieved by extrapolating from the previous local noon (maximum solar altitude). While local midnight is a convenient reference, it may not be optimal. A more biologically relevant baseline could be one hour after sunset, when nocturnal migration typically begins. However, sunset time varies with latitude and season, making a fixed offset impractical. Evolution has likely addressed this complexity, so for simplicity, the midnight scenario is retained.

4) Estimating local noon. The bird should be able to determine the time of solar noon, which aids in estimating midnight.

5) Reading the stellar pointer. At the chosen reference time (e.g. midnight), the bird should assess the angle of the stellar pointer – such as the line from Polaris to the two posterior stars of the Big Dipper.

6) Integration of inputs. The bird must integrate all the above elements – elapsed time, stellar drift, solar cues and stellar orientation – to guide its navigation.

Accuracy in stellar navigation

The previous section outlines the necessary skills a migratory bird must possess to navigate using stellar cues. This section addresses accuracy with which a bird may perform the required measurements and estimations.

Longitude estimation. We begin with point 5: estimating the angle or "time" of the stellar pointer. It is reasonable to assume that, following millions of years of natural selection, migratory birds are significantly more adept at this task than the unaided human eye. Based on personal experience working with angular estimation, I conducted tests using three dots arranged at various angles on a white wall to mimic the configuration of Polaris and the two posterior stars of the Big Dipper. Only a few estimations deviated by more than 3°, and the average error across a large sample was approximately 1° or 2°, with smaller errors when the angle was close to vertical or horizontal. Given this, it is plausible that a migratory bird estimates the angle of the stellar pointer with a binomial distribution: -1° (0.25), 0° (0.50), +1° (0.25).

Greater uncertainty likely arises in estimating the time of local midnight (points 3 and 4). As illustrated in Fig. 2, point 3 could be conceptualized as an hourglass emptied over 12 hours, turned at local midday when the sun culminates in the southern sky. Perhaps also sunset and sunrise times – and their estimated/calculated mean time = midnight – is involved in one or another way. Muheim *et al.* (2006) hypothesized that this average might serve as primary compass reference in birds.

The standard deviation in estimating local time of noon and midnight is likely around 4 minutes which corresponds to an expanded binomial distribution: -2° (0.0625), -1° (0.25), 0° (0.375), +1° (0.25), +2° (0.0625). In Model I, this uncertainty translates to a cumulative error of 4 minutes over 80 nights – equivalent to 3 seconds per night. While a timepiece gaining or losing 3 seconds per day is not considered highly accurate, such precision may exceed the capabilities of a biological clock. Nevertheless, it is likely sufficient for avian navigation.

To account for combined uncertainties in longitude estimation – including angle measurement, time estimation and day-counting – we may expand the binomial distribution further. For example:

> -3° (0.015625), -2° (0.09375), -1° (0.234375), 0° (0.3125), +1° (0.234375), +2° (0.09375), +3° (0.015625), or
>
> -4° (0.00390625), -3° (0.03125), -2° (0.109375), -1° (0.21875), 0° (0.2734375), +1° (0.21875), +2° (0.109375), +3° (0.03125), +4° (0.00390625)

In the latter expansion, we included uncertainty on (1) counting number of days following the start: -1° (0.0), 0° (0.50), +1° (0.25). Instead of considering binomial distributions these may be changed to normal distributions for greater realism.

Latitude estimation.: Latitude estimation is based on the altitude of Polaris above the horizon. From personal testing, I found altitude estimation in degrees to be more difficult than angular estimation of the stellar pointer. Whether birds experience similar difficulty is unknown, but it may be prudent to assume a slightly broader distribution of uncertainty. Rather than the simple binomial: -1° (0.25), 0° (0.50), +1° (0.25), a more realistic distribution might be: -2° (0.0625), -1° (0.25), 0° (0.375), +1° (0.25), +2° (0.0625).

Further considerations

The complexity of the navigational system

Regardless of the type – solar, stellar, magnetic, olfactory, or otherwise – avian navigational systems are inherently complex. Yet birds do navigate successfully. Therefore, the existence of at least one functional system is undeniable. It is not a valid argument to dismiss a system simply because it appears too complex; complexity does not preclude biological feasibility.

Biological clocks

Dmitry Kishkinev (*in litt.*) kindly brought my attention to recent works in biological clocks. Kishkinev *et al.* (2010) note: "… recent neurophysiological and molecular evidence suggest that at least some animals possess multiple biological oscillators that synchronize at different speeds".

In correspondence, I wrote: "When I many years ago started thinking in terms of a fixed clock (or rather a fixed clock with a period which may shift) as the base of east-west navigation, we knew much less about biological clocks than today and as I understand you, the possibility of a fixed clock is considered (even) lower today than formerly. But has there been (recent) experiments trying to demonstrate such a clock and/or falsify its possible existence? (for a superficial survey there was nothing in the references you sent). Maybe it is like conditioning experiments and magnetic sensing; the best approach for demonstrating magnetic sensing is not a traditional conditioning procedure but an approach directly into a biological meaningful context, e.g. an orientation experiment shifting magnetic North x° to the right and then record the response under conditions with no other directing compasses available. If the response – in repeated experiments – turns out to be a shift about x° to the right, then the presence of a magnetic sense is inferred. In a similar way, if you want to demonstrate the presence of a fixed clock used for W-E-navigation then go into a star-planetarium and test – for example – a sample of Swedish/Finnish juvenile Pied Flycatchers trapped on Christiansø. Sometimes you should not be too intimidated of former results and theoretical considerations but just do the job. By the way, if most recent clock investigations are carried out with rats you should be cautious using the rat as a model for what is going on in long-distance bird migrants. Sedentary laboratory-rats possibly have no use/need of a fixed clock mechanism. The ellipsoid recovery patterns of e.g. juvenile Spotted Flycatcher *Muscicapa striata* and Eleonora' Falcon *Falco eleonorae* indicates that at least often there is a sort of 'final' goal area also in juveniles, and the question then is what constitutes the gradient values determining such a goal. Reasonable guesses are a) stellar latitude (height of the rotational point above the horizontal and b) star longitude steered by a fixed clock. Another possibility is of course a navigational grid based on c) total magnetic intensity and d) magnetic inclination, which – in case of the wintering ground of the falcon – crosses each other on rather right angles in northern part of Madagascar (in combination with a simple vector orientation system and 0° inclination (magnetic equator) as a signpost for a directional shift to ESE). Most people would love such a magnetic system. The only hurdle is to accept the final step as gradient-navigation in the so called inexperienced juvenile birds."

Kishkinev *et al.* (2010) proposed a "double clock or jetlag mechanism" for detection of east-west displacements: "… two coupled, re-synchronizable clocks. The first clock is slowly synchronized to a local light-dark (LD) regime, whereas the second clock, the fast-entraining one, is the well-known biological oscillator that becomes quickly synchronized to a local LD cycle. The time difference between the two clocks would enable birds to determine their east-west position after displacement on the basis of time zone or “jet lag effects”. They further note “one of these clocks, the slow-synchronizing one, is not synchronized (or is synchronized slowly) with the local light-dark (LD) regime.”

This conception raises questions. In my view, the slow-synchronising clock should ideally not synchronise at all—it should function as a fixed clock, akin to Greenwich Mean Time used by human navigators (i.e. Model I). Probably also, as a minimum, the birds should be confronted with the outdoor sky and celestial, and in particular, solar cues. Without such a fixed reference, errors accumulate in the system, and the spread of the progressing population becomes parabolic rather than ellipsoid. In contrast, true navigation systems concentrate uncertainty around the final goal.

Matthews (1968), citing DeCourtsey (1962), reported that “A flying squirrel kept in constant dark conditions for 26 days. A circadian rhythm of 23 hours 58 minutes (± 4 minutes) was maintained and drifted very slowly out of phase with the external time.” Now this period of 23 hours 58 min. was observed under “constant dark” conditions. Had the light intensity been different – e.g. constant twilight – the period might have differed. While it is commonly believed that activity rhythms are entrained by the offered LD cycle, this does not preclude the existence of a clock with a constant period that remains un-entrained. A bird could, metaphorically speaking, "close its eyes" to disconnect from the external LD cycle.

Clock-shifts versus rotational phase of the celestial sky

When investigating whether migratory birds compensate for east-west displacements, one may initially consider two seemingly interchangeable experimental approaches: (a) Shifting the rotational phase of the celestial sky (e.g. in a planetarium), or (b) shifting the light-dark (LD) cycle forward or backward (i.e. clock-shifting).

While these methods may appear equivalent in principle, they are not necessarily interchangeable in practice. For a migrating bird, the connection between stellar rotation and the LD cycle may be tenuous or non-existent.

Clock-shifts during daytime and sunny conditions

Emlen (1975) proposed that clock-shifts could help distinguish between solar compass orientation and sun-arc navigation. It is well established that LD shifts of ±6 hours result in directional shifts of approximately ± 90° in the vanishing bearings of homing pigeons. These shifts are consistently observed, but they do not produce concentrated east- or westward orientation, as would be expected if pigeons used the sun for true navigational compensation.

Able & Cherry (1986) showed that a 3-hour LD-shift in White-throated Sparrows *Zonotrichia albicollis* produced a predictable ~45° shift in orientation based on the sunset-compass.

Matthews (1963) displaced Mallards *Anas platyrhynchos* under daylight and sunny conditions. Control birds departed north-northwest, i.e. displayed `nonsense` orientation, not directed towards home. Clock-shifted birds showed the expected deviations: approximately 15° per hour, counterclockwise for advanced shifts and clockwise for delayed shifts.

Clock-shifts during starry nights

Rabøl (1970) applied an 8-hour backward LD shift to simulate a geographical displacement of 120° eastward (e.g. to Chabarowsk in Russia's far east). The experiment aimed to test whether birds would compensate using rhumb-line or great-circle navigation towards a goal area in western Europe. The birds maintained a southerly orientation, similar to controls, indicating no compensation.

Matthews (1963) also displaced Mallards during night-time and starry conditions. The birds departed north-northwest, i.e. displayed 'nonsense' orientation not directed towards home. Contrary to the day experiments (see above) clock-shifted birds showed no significant deviations from north-northwest.

Moore (1980) clock-shifted five Savannah Sparrows *Passerculus sandwichensis* by six hours in spring. The birds were placed in funnels during sunset and later on tested during night. First night with no stars on the sky and subsequent nights with stars. The orientation of not clock-shifted control birds was very concentrated about north-northwest. Under the two test-conditions the birds were more scattered. Nonetheless 2 + 3 birds showed unimodal orientation around north-northwest to north, while (3 + 2 other birds exhibited bimodal north-northwest or south-southwest-orientation. Apparently, the clock-shift had no influence on the orientation; at least the expected ~ 90° shift was not observed.

This result contrasts with Able & Cherry (1986), despite the species being closely related and supposed to react in a similar way. The key difference may lie in timing: the Able & Cherry birds were tested during sunset, whereas the birds of Moore were tested during night, and in fact reacted as the Mallards of Matthews. Perhaps, it was also influential that Moore used a six hour slow and Able & Cherry a three-hour fast clock-shift. Perhaps Moore's birds were not adequately prepared for the sunset cue.

Displacement experiments and LD shifts

Chernetsov *et al.* (2008) displaced Common Reed Warblers *Acrocephalus scirpaceus* from Rybashy to the Moscow region (~1000 km east). Birds orientated – in funnels – northeast at Rybashy and at north-northwest at Moscow, suggesting compensation towards breeding grounds in the Finnish Bay/Ladoga area.

Kishkinev *et al.* (2010) repeated the experiment, exposing Rybachy-trapped warblers to an LD regime advanced by one hour (simulating Moscow conditions). These birds oriented about north-northeast to northeast, i.e. not significantly different from the warblers of Chernetsov *et al.*

Apparently, the birds were not considering this treatment as a geographical displacement towards east, as the orientation was north-northeast, not statistically different from north-northeast to northeast as shown by the control birds. This indicates that east-west compensatory orientation cannot be induced and steered alone by shifts in the LD regime.

To conclude this chapter: shifts in the LD-cycle cannot substitute and simulate geographical east-west displacements. They cannot be used as a way to disprove the existence of sun-arc or stellar navigation, nor the existence of a fixed-time biological clock. For such a clock to be useful in navigation, it must be fixed and immune to natural or induced LD-shifts.

East-west navigation in spring

Emlen's (1967, 1975) planetarium experiments simulating stellar 'displacements' were conducted in spring. No compensatory orientation was observed in these trials.

Rabøl (1997) also failed to demonstrate compensatory orientation in a spring planetarium experiment. A sample of Pied Flycatchers and Redstarts were trapped during stopover on Christiansø (55° N, 15° E) between 3 and 7 May 1994. On 6 May, 19 birds were tested in orientation funnels during late sunset and early night. The sky was clear and the sunset was prominent in about northwest. The mean orientation of the sample was northwest to north-northwest, likely influenced phototaxically by the sunset. Most birds, when released at night, were positioned on the inner slope of the funnel facing north-northeast.

On 8 May, 16 birds were transported to Copenhagen and following day to Aarhus (56° N, 10° E), where experiments were conducted in the Steno Planetarium over the following five nights. The birds were tested under a simulated stellar sky rotating with normal direction and speed. The 'stellar sky' presented to the birds were: 55° N, 10° E (9 May), 70° N, 10° E (10 and 11 May), 70° N, 60° E (12 May), and 55° N, 60° E (13 May). As the presumed breeding area is about 58-65° N, 15-25° E. the expected mean orientations – if the birds navigated by means of the stars – would be approximately: northeast, southeast, west-southwest and west-northwest, respectively.

However, these expectations were only partly met. On 9 May, eight birds out of 12 were oriented and the sample mean vector was significant, 29° ($r = 0.917$, $P < 0.001$) The sample patterns on 10 and 11 May resembled each other in being bimodal with a major peak in east-southeast (between 90° and 145°), and a slightly smaller peak in north (between 330° and 15°). The orientation of a single birds felt between the two peaks (55°), and four birds were, as individuals, bimodally oriented. Compared to 9 May more bimodal patterns were observed in the individual birds, and most orientation and all cases of clear unimodal orientation were towards east-northeast (25° through 105°).

The sample mean vectors on 12 and 13 May were 63° – 0.766, N = 9, P < 0.01, and 77° – 0.740, N = 10, P < 0.01, respectively.

These results suggest that the stellar sky may not be used for navigation during the light nights of May, when other cues – such as olfaction or magnetic declination – could be more influential. It is notable that Polaris altitude, which could serve as a north–south coordinate, was apparently not used – though it may have played a partial role at 70° N/10° E. The absence of a clear stellar east-west component may reflect its unreliability/uncertainty as a coordinate, especially if it was imprinted the previous autumn. As magnetic north in the Steno Planetarium is 12° W of geographic north, the easterly orientations on 12 and 13 May on 60° E (and perhaps also 10 and 11 May on 70°/10° E) may be taken as compensation in reference to the magnetic declination. If so, this could be interpreted as form of magnetically referenced navigation.

Free-flying contra funnel testing

There seems to be a pattern in displacement studies that free-flying juveniles are not compensating – or compensate less effectively – than adults. This has been observed in Starlings (Perdeck 1958, 1967), Common Cuckoos *Cuculus canorus* (K. Thorup pers. com.) and *Zonotrichia* sparrows (Thorup *et al.* 2007). In contrast, juveniles tested in funnels – autumn, starry nights (Thorup & Rabøl 2007) – normally show compensatory behaviour, even more pronounced than in adults. This discrepancy warns against the generalization of Perdeck's (1958) results that young birds rely solely on a clock-and-compass system. It is plausible that, if left un-displaced, their natural migratory progress would involve navigation towards a moving goal area.

Indirect indication on celestial east-west navigation in vagrants

The consistent movements towards west by Asian vagrants in autumn, are perhaps an indication of an east-west coordinate system, governed by a biological clock, where a time-error is accelerating in course of the autumn, resulting in progressive displacement.

Thorup (1998) found bimodal west-southwest/east-southeast headings of Yellow-browed Warblers *Phylloscopus inornatus* and Pallas's Leaf Warblers *Phylloscopus proregulus* tested in autumn in funnels on Christiansø in the Baltic Sea (Appendix 3).

Further, Thorup (2004) reported that vagrants in northwestern Europe showed stronger evidence of mirror-image migration towards the west than towards the north. This raises an intriguing question: why is westward mirror-image migration more common than northward? It seems more plausible that a bird might make a short reverse error from southern Europe than a prolonged reverse error from Asia – supporting the hypothesis of a time-based east-west coordinate system.

Resumé

Øst/vest-navigation hos trækfugle baseret på Solen og stjernerne

Man har i mange år diskuteret, hvordan Brevduer finder hjem efter en flytning fra fx Nyborg til Sundsvall (N for Stockholm) eller Antwerpen (i Belgien). Det var hvad min far i Nyborg i halvtredserne udsatte sine duer for. Jeg skrev en artikel om det i DOFT (Rabøl 2001), hvoraf det fremgik, at slaget især stod mellem brug af Jordens magnetfelt eller duft-gradienter. Efter min og de flestes mening var der mest, der tydede på sidstnævnte som basis for det hjemfindende navigations-system, men 'magnetisterne' har ikke givet op endnu, og måske er der regionale forskelle og flere navigations-systemer vævet ind i hinanden. Måske lugter duerne i en eller anden forstand magnetismen. Der er nok af muligheder, (bort)forklaringer, fortsat spin og 'fake news'.

Men nu har H. G. Wallraff (2013) skåret igennem ved at slippe det han kalder virtuelle duer løs. Wallraff starter med at konstatere, 1) at duer uden lugtesans ikke kan finde hjem efter en forflytning. Dufte betyder altså noget afgørende. Brevduer berøvet muligheden for magnetisk navigation finder derimod hjem efter en forflytning normalt uden forsinkelser af nogen art. Spørgsmålet er så, om Wallraff kan påvise tilstedeværelsen af 2) et rimeligt fungerende duft-navigations-system. Det kan han. Wallraff fokuserede på forskellige dufte og koncentrationen af disse i luftrummet over Tyskland, hvor han har lavet sine forsøg med symmetriske flytninger af brevduer (symmetriske slip indebærer slip i et kors, fx i retningerne N, Ø, S og V i forhold til dueslaget, og gerne også i forskellige afstande, fx 50 km, 100 km og 200 km i de fire forskellige retninger fra 12 slipsteder).

Koncentrationen af en bestemt duft tiltager generelt mest i en bestemt retning (og aftager mest i den modsatte retning). Man taler om en duft-gradient, der måske løber mod ØNØ. En anden duft tiltager mest mod SSV, en tredje mod NV, osv. Nu er det sådan, at koncentrationen af de enkelte duftstoffer for et givet dueslag er temmelig foranderlig i tid og sted og meget vindafhængig. Hvis man derimod betragter koncentrationen af duft A i forhold til koncentrationerne af duftene B, C og D, så danner en sådan ratio meget mere stabile gradienter, der kan bruges som basis for et duft-navigations-system. Wallraff opstillede nu nogle simple regler for, hvordan hans virtuelle duer skulle reagere på forskellene i ratio-værdierne i hjemmet og på slipstedet. Når de virtuelle duer så blev 'sluppet fri' kom der 'bortflyvningsmønstre' frem, der til forveksling lignede bortflyvningsmønstre af rigtige brevduer sluppet fri fra symmetrisk beliggende slipsteder omkring dueslaget. Det tog Wallraff som en klar indikation på, at duft-navigation kan lade sig gøre i naturen ud fra de givne duft-forhold. Om duerne så gør det helt efter Wallraffs' model, er ikke sikkert, men man kan ikke (mere) hævde, at duft-navigation ikke kan lade sig gøre på grund af for stor kompleksitet og dermed yderst lav sandsynlighed.

Jeg har nu overtaget essensen af denne tankegang og måde at argumentere på med hensyn til trækfugle og stjerne-navigation. De forskere, som studerer fugle anvendelse af magnetisme til orientering, mener generelt ikke, at stjerne-navigation finder sted eller kan lade sig gøre. En af dem – R. Wiltschko – gik så vidt som at påstå, at Steve Emlen med sine Indigofinke-forsøg havde bevist at stjerne-navigation ikke eksisterer. Men man kan ikke generalisere ud fra nogle udvalgte og

specielle forsøg, og andre forsøg (Rabøl 1998 og Thorup & Rabøl 2007) har vist, at trækfugle (i hvert fald arterne Broget Fluesnapper og Rødstjert) bruger 'stjernehimlen' i et planetarium til at kompensere for reelle eller simulerede forflytninger. Kompensationer – og specielt sådanne i planetarier, hvor der ikke ændres på andre omverdensfaktorer end 'stjernehimlens' rotations-fase og omdrejningspunktets højde – kan kun fortolkes på den måde, at der ligger en eller anden form for stjerne-navigation bag.

Spørgsmålet er så, om det kan det lade sig gøre at opstille et realistisk stjerne-navigations-system, der ligger bag sådanne kompensationer? Det mener de fleste (også) er umuligt, og det system, som de forkaster, er det (eller en variant deraf), der nedenfor bliver benævnt model I.

Jeg opstiller nu to stjerne-navigations-systemer, model I og model II, der er forskellige med hensyn til, hvordan længdegraden (Ø/V-koordinaten) fastlægges, men som er ens med hensyn til fastlæggelsen af breddegraden (N/S-koordinaten). Som det måtte være de fleste bekendt, indtager Nordstjernen en (næsten) fast position på nordhimlen, og alle de andre stjerner drejer modurs omkring den med en omdrejning i døgnet minus 4 minutter. Nordstjernens højde over horisonten er lig breddegraden, og kender fuglen Nordstjernens højde i målet vil en sammenligning med dens aktuelle højde afgøre, om den er N eller S for målet.

Model I blev foreslået af Rabøl (1978, 1980) og svarer i princippet til den traditionelle menneske-måde at gøre det på, hvor man inkluderer medvirken af et ur, der kører på Greenwich-tid svarende til medianen/længdegraden gennem London (0° Ø). Ud fra Solens kulminationshøjde bestemmer man tidspunktet for kl.1200 stedlig tid på det sted, hvor man er. Hvis tiden/klokken på det medbragte ur samtidigt viser fx 1400, er man 2 timer V for London svarende til længdegraden 30° V. I sin helt simple – men dog samtidigt avancerede – form behøver fuglen ikke bestemme tidspunktet for Solens kulminationshøjde, men den kikker 'bare' op på N-stjernehimlen det sted, hvor den er, og sammenligner omdrejningsfasen her med omdrejningsfasen på sit indre ur. Er sidstnævnte forud (mere modurs) orienterer den sig mod Ø; er det bagud mod V. Fuglen kan i praksis reagere i forhold til, hvad den ser i forhold til stjernehimlen. Skal den bevæge sig Ø eller V for at synkronisere sin position. Nu har dyr ikke et (ydre/ledsagende) ur at gøre godt med, men de er udstyret med det, som man kalder et indre ur. Det viser sig ved, at de under konstante lysforhold stadigvæk opretholder de samme ca. 24 timers rytmer så som temperatur, søvn osv., ligesom de stadig har en god fornemmelse af, hvad klokken er. Men det er vanskeligt at forestille sig et indre ur, der angiver tiden meget præcist, hvorfor trækfugle-forskere i al almindelighed afviser tanken om Ø/V-navigation ved hjælp af et indre ur.

Model II. Som reaktion på ovennævnte reservationer, har jeg udviklet et mere simpelt Ø/V-navigations-system kaldet model II. Her skal trækfuglen godt nok kunne nogle flere ting, men disse er hver for sig at betragte som lettere at udføre. 1) Fuglen skal kunne holde rede på, hvor mange døgn den er henne i trækforløbet. 2) Den skal kunne bedømme tidspunktet for stedlig midnat, og den simpleste måde at gøre det på er 3) ud fra tidspunktet for Solens kulminations-højde den forudgående dag (svarende til hvad den gør – eller måske gør – i model I). Denne tid skal den så kunne forlænge 12 timer fremad så den rammer tiden for lokal midnat (på Fig. 2 er det illustreret med en timeglasagtig proces). 4) Den skal kunne aflæse tiden på det, jeg kalder himmeluret (Fig. 1) svarende til omdrejnings-fasen og vide at denne pr. døgn forskyder sig 1° modurs. 1) kan måske ske uden fejl, medens både 2), 3) og 4) er fejlbehæftede. Der er usikkerhed på at kunne bestemme tidspunktet for Solens kulminationshøjde. Der er også usikkerhed på tids-forlængelsen 12 timer frem til lokal midnat. Desuden på bedømmelsen af omdrejnings-fasen. Det sidste kan jeg gøre – efter lang tids øvelse – med en usikkerhed på 1° til 2°, medens en trækfugl – efter mange tusind års selektion – er sikkert noget bedre til det.

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