



Essay

The sun compass revisited

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Many animals, and birds in particular, are thought to use directional information from the sun in the form of a time-compensated sun compass, with predictably deviated orientation under clock shift being regarded as the litmus test of this. We suggest that this paradigm obscures a number of other ways in which solar-derived information could be important in animal orientation. We distinguish between the known use of the sun's azimuth to provide absolute geographical direction (compass mechanism) and its possible use to detect changes in heading (heading indicator mechanism). Just as in an aircraft, these two kinds of information may be provided by separate mechanisms and used for different functions, for example for navigation versus steering. We also argue that although a solar compass must be time-referenced to account for the sun's apparent diurnal movement, this need not entail full time compensation. This is because animals might also use time-dependent solar information in an associatively acquired, and hence time-limited, way. Furthermore, we show that a solar heading indicator, when used on a sufficiently short timescale, need not require time compensation at all. Finally, we suggest that solar-derived cues, such as shadows, could also be involved in navigation in ways that depend explicitly upon position, and are therefore not strictly compass-related. This could include giving directionality to landmarks, or acting as time-dependent landmarks involved in place recognition. We conclude that clock shift experiments alone are neither necessary nor sufficient to identify the occurrence of all conceivable uses of solar information in animal orientation, so that a predictable response to clock shift should not be regarded as an acid test of the use of solar information in navigation.

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The finding that birds use a time-compensated sun compass for orientation is one of the great enduring discoveries of animal navigation research (Kramer, 1950, 1952; Schmidt-Koenig, 1958). Although not the only compass that birds use, the sun compass appears to be dominant in diurnal species. As a very distant but highly visible object, the sun can provide reliable compass guidance because its geographical direction effectively does not change as the animal's position changes. However, the Earth's spin produces an arc of apparent movement of the sun across the sky through the day, and this means that the sun's geographical direction does change slowly through time. The same holds true for its attendant directional cues such as polarization patterns or shadows (Chappell & Guilford, 1995). Insects have long been known to use sky polarization patterns in orientation (Reppert, Gegear, & Merlin, 2010; Wehner, 1998), and there is growing evidence that birds, and other vertebrates apart from mammals, may do so too (Muheim, 2011). Remarkably, birds appear capable of

learning enough about the pattern of the sun's directional movement through the day to compensate for it, and hence to use the sun as a compass.

The time-compensated sun compass enjoys an unchallenged position at the centre of our understanding of bird navigation, where, in combination with large-scale map factors, it is thought to control navigation from unfamiliar places in a two-step map-and-compass process (Baker, 1978, 1984; Kramer, 1961; Wallraff, 2005; Wiltschko & Wiltschko, 2009). It is also thought to be important in homing from familiar sites (Fuller, Kowalski, & Wiltschko, 1983; Luschi & Dall'Antonia, 1993), and even in fine-scale orientation tasks such as food storing (Sherry & Duff, 1996; Wiltschko & Balda, 1989; Wiltschko, Balda, Jähnel, & Wiltschko, 1999) and laboratory maze learning (Budzynski, Dyer, & Bingman, 2000; Chappell & Guilford, 1995; Zimmerman, Nicol, & Guilford, 2009). Central to inferring the operation of a time-compensated sun compass is the clock shift (or phase shift) procedure, in which animals that have had their endogenous diurnal clock phase-shifted predictably misinterpret the geographical direction of the sun and orient in a direction appropriate to their own shifted subjective time (Wallraff, 2005; Wiltschko & Wiltschko, 2009).

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Evidence for the use of time-dependent solar cues in orientation has been found in many other taxa, including frogs (Landreth & Ferguson, 1968), turtles (DeRosa & Taylor, 1978; Graham, Gergoes, & McElhinney, 1996), lizards (Adler & Philips, 1985), rodents (Fluharty, Taylor, & Barrett, 1976; Haigh, 1979), sandhoppers (Pardi & Grassi, 1955; Ugolini, Melis, Innocenti, Tiribilli, & Castellini, 1999) and insects (Lepidoptera: Perez, Taylor, & Jander, 1997; Reppert et al., 2010; Hymenoptera: Wehner & Müller, 1993). Although we frame our argument here in relation to birds, the ideas that we develop are sufficiently general that they should also apply to other taxa. Fundamentally, this is an ideas paper in which we revisit the sun compass concept and suggest that while birds almost certainly do use a time-compensated sun compass in the classical sense, this does not exclude the possibility that they use solar cues in other ways for orientation.

Some other uses of solar cues have been proposed previously. For example, it was once conjectured that the sun might provide birds, and other long-distance migrants and navigators, with positional information on a global scale, and not just with directional information. Mathews' sun arc hypothesis (Baker, 1978) recognized that latitudinal information from the sun's arc, and longitudinal information from the time of dawn, dusk or zenith, when compared with the time of these events at home, could provide an animal with an approximate position on the Earth's surface, a fact long exploited by mariners in possession of ephemeris data, a sextant and a chronometer. But the experimental data largely did not fit Mathews' hypothesis, and students of animal navigation have come to accept that solar information is used to provide direction and not position (Baker, 1978). For this reason, we do not consider Mathews' hypothesis further here. Instead, we put forward a number of different ways in which solar cues may provide directional information on a more local scale, and articulate a number of problems with current acceptance of the mainstream hypothesis. In particular, we distinguish between varying degrees of time compensation, suggesting that the sun can be a useful compass even if it is not fully time-compensated but instead is used in more restricted, time-limited ways. We also argue that solar cues may be used for certain functions in orientation without the need for time compensation at all, such as in maintaining a course that has already been set. Finally, we argue that solar cues may provide guidance by modifying the appearance of the landscape, whether by giving direction to landmarks through shadowing, or by adding distinctive components to the visual appearance of a place that become salient during learning and recognition.

WHAT A COMPASS IS

We recognize that in introducing mechanistic distinctions that may previously have been overlooked, there is an inherent danger of semantic confusion. We have therefore used the term 'compass' to refer to any mechanism that provides absolute geographical direction independent of position, and have avoided use of the term where this is not the case. This distinction is not as obvious as it sounds. For example, in the cockpit of most aircraft there is, in addition to a magnetic compass, another instrument called a heading indicator. This looks very much like a compass, being marked with the cardinal directions and a 360° scale. However, the heading indicator is just a gyroscope that holds its direction in an inertial frame of reference, which for practical purposes means holding direction with respect to the stars. A heading indicator can therefore only provide absolute geographical direction with respect to the Earth's surface if its direction is calibrated against some external reference such as a magnetic compass or the known direction of a runway. Even then, it needs to be recalibrated periodically to compensate for the steady drift that results from the

Earth's spin. Nevertheless, the heading indicator serves a crucial purpose in allowing the pilot to steer a course while making turns whose acceleration would cause a magnetic compass needle to deviate from north. As we discuss below, the sun and its attendant cues could serve as a heading indicator in birds, with no requirement for time compensation when used to steer over sufficiently short periods of time, or when calibrated against some external reference. The distinction between a solar compass and a solar heading indicator is an important one, therefore, which the animal navigation literature has previously ignored.

THE SUN AS A COMPASS

A compass is a mechanism that indicates absolute direction with respect to the Earth's surface, wherever it is placed. A direction may be said to be absolute if it is known relative to some geographically fixed direction, such as 'north'. For example, a magnetic compass indicates absolute direction relative to the local magnetic field line running north to south between the Earth's magnetic poles. A solar compass, on the other hand, indicates absolute direction relative to the local meridian running north to south between the poles of the Earth's spin. To inform an animal of this direction, however, a solar compass must somehow be compensated for the apparent movement of the sun across the sky as the Earth spins. Because this movement is regular and predictable, such compensation can of course be achieved by reference to an accurate internal clock. This is not the only possible compensation method, however, especially if solar information is being used in a time-limited way. North of the Tropic of Cancer, for example, the sun always lies south when it reaches its zenith, so on any given day of the year, the shortest shadow that an object casts always points north. Likewise, at latitudes close to the equator, a line drawn between the tips of the shadows cast a few minutes apart by the same object always points approximately to the west. We do not necessarily mean to say that birds make use of these heuristics, or of the many others that can be derived from them; rather we mean to show that full time compensation is not the only way to derive true compass information from the sun.

Degrees of Time Compensation

Classically, because the sun's azimuth changes through the day, the sun compass has been regarded as requiring time compensation. Deviation under clock shift has therefore been considered an acid test of the use of solar information for orientation (Baker, 1978; Wiltschko & Wiltschko, 2009), and demonstrated in a large number of species and studies (see e.g. Wallraff, Chappell, & Guilford, 1999). However, this leaves open the question of the accuracy or degree to which time compensation occurs. In principle, time compensation can enable use of the sun compass accurately throughout the day (we call this 'full time compensation'), but more limited compensation for particular times of day, or with limited temporal resolution, could also provide simple compass guidance without the need for full time compensation. This is because the sun's azimuth at a set time of day provides a reliable directional cue that can be used to guide orientation, or indeed to calibrate other compass systems (see e.g. Papi, 1992). As obvious examples, the azimuth of the rising and setting sun indicates east and west year-round at the equator reasonably reliably, while at higher latitudes, the sun's midday azimuth reliably indicates north or south in the southern and northern hemispheres, respectively (Pennycuik, 2008).

A simple associative account of the sun compass would suggest that animals might learn to use solar cues because they have proved informative on previous occasions. So, if return home from a particular direction always occurred at roughly the same time in

the evening, say, then the sun might be used to provide just a single direction, limiting its effectiveness to that particular time of day. A more varied experience of return directions might allow the animal to learn that the evening sun's direction could be used as a more general reference, still in a time-limited way, but with different homing tasks requiring different flight angles to the sun. Full time compensation would provide a more general compass still, but an additional degree of informational complexity is needed to achieve this generality: not only is the appropriate flight angle to the sun dependent on where the animal is homing from, it now also needs to be adjusted in relation to the time of day.

The value of full time compensation is that birds are able to generalize across instances of directional guidance informed by the sun's position at different times of day, and to use this generalization to extrapolate to unusual (that is, not yet experienced) times of day. It is therefore a distinctly cognitive concept, allowing flexible compass orientation throughout the day, and across directional tasks. Again, an associative account might posit that the animal could use a range of goalward orienting experiences at different times of day, registered by its endogenous diurnal clock, as contexts for response to the sun's azimuthal direction (see [Petruso, Fuchs, & Bingman, 2007](#), for a discussion of time–space learning). With sufficient generality across experiences of time, we might even say that the animal had developed full time compensation. However, the extents to which animals have a dedicated template for linking endogenous time with the sun's direction, form truly cognitive constructs of time compensation or, more simply, generalize to their closest temporal experiences are unanswered questions. Indeed, simple associative processes might even lead to relatively appropriate responses along a temporal stimulus dimension well beyond the range of experience (a kind of natural extension of the peak shift phenomenon: [Weary, Guilford, & Wiseman, 1993](#)). Evidence is equivocal. On the one hand, some experiments with homing pigeons show that they are only capable of learning to use the sun effectively at times of day that they have experienced ([Wiltschko, Nohr, & Wiltschko, 1981](#); [Wiltschko & Wiltschko, 2009](#)), at least when combined with having to use their navigational map to home from an unfamiliar site. On the other, [Budzynski et al. \(2000\)](#) showed that pigeons can learn to use the sun's direction to locate a food goal in an arena at least approximately at an unfamiliar time of day (in the morning) whether they have experienced the sun's movement during the entire day (controls) or only during the afternoon (experimental birds). These results accord with findings for insects and fish too (reviewed in [Budzynski et al., 2000](#)). Furthermore, birds do seem to be able to learn that the sun's azimuth does not move evenly around the horizon through the day, which would indicate that fairly subtle information can be acquired (summarized in [Wallraff, 2005](#)). There is even some evidence that migratory birds using postsunset cues for orientation will respond to clock shift in a way that produces orientation appropriate to a shifted time during the night at which the sun's cues are not even available ([Able & Cherry, 1986](#)). Nevertheless, at least one pigeon in [Budzynski et al.'s \(2000\)](#) experiment apparently learnt to use the sun as a fixed directional reference rather than in a time-compensated manner, emphasizing that birds may respond to their associative experience of the sun in different ways (and that there is much still to understand about the associative processes underlying sun orientation).

How could different degrees of time compensation be distinguished? [Schmidt-Koenig \(1958\)](#) was the first to show that re-entraining the pigeon's internal clock to a shifted day–night cycle leads to predictable deviation in initial orientation in homing releases. The idea is that since the bird chooses a flight angle to the sun appropriate for its subjective time of day, misreading the actual time of day leads it to choose the wrong angle. The result is very

general, but pigeons in particular reliably show full clock shift effects when displaced to release sites that can confidently be regarded as unfamiliar ([Wallraff et al., 1999](#)), suggesting full dependence on a time-compensated sun compass (at least until they have somehow determined that it is faulty). However, an effect of clock shift does not necessarily distinguish full time compensation from a simpler, more limited use of time compensation. An animal using more limited time compensation might also respond to clock shift with deviated orientation if released at an unusual, and biased, time of the natural day as a consequence of the experimental procedure. So, strictly, demonstration of full time compensation requires demonstration that deviation in orientation under clock shift is not dependent on the time of day at which the birds are trained and released.

To elaborate, if an animal always experiences the sun's position to be in approximately the same direction following a repeated experimental or natural displacement, then it could learn that this direction can be used to provide guidance on the return journey. Subsequently, displacement at a time of day when the sun in fact had a different azimuth might then lead to shifted orientation, precisely because the bird was not employing time compensation for the sun's movement. Following experimental clock shift, the available release window in which both actual and subjective daytime coincides is shortened, towards the end of the natural day for slow shifts or the start of the natural day for fast shifts, potentially inducing deviation biases in the same directions as those predicted by time compensation if experimentally shifted birds are consistently released later (slow) or earlier (fast) during testing than during training. One test for this limited form of time-compensated compass would be to investigate the orientation of unshifted birds at the same biased time of day, for they too should be similarly affected. This should of course happen normally in well-conducted experiments in which experimental releases are temporally interleaved with controls. Our point here is not that full time compensation is unimportant, unreal or undemonstrated, but rather that birds may also make use of the sun in a simpler, more limited manner that could influence the outcome of orientation experiments in a confusing way.

The point we wish to make then is that a true sun compass need not be fully time-compensated to be useful, and that deviation under clock shift is not necessarily sufficient to demonstrate that the underlying mechanism is fully time-compensated. This is because time compensation could take many forms, some potentially very restricted in their use, and it could emerge simply, but idiosyncratically, as a result of the animal's particular prior experiences. This idiosyncrasy might even explain some of the high variability that emerges in the results of clock shift experiments (see e.g. [Chappell, 1997](#)), although of course other accounts are possible, for example to do with the poorly understood processes of rephasing the internal clock.

THE SUN AS A HEADING INDICATOR

Having set a heading by whatever means, animals, like aviators, must make continued use of directional information in order to maintain that heading. Although it is possible in principle to use a compass for this task, the directional information that is required to maintain a heading need not involve any absolute geographical reference at all. The value of this simpler kind of directional information will be familiar to anyone who has strayed from a footpath in dense forest, flown through cloud or dived in murky waters. In such circumstances, it may not matter that you know which way is north or south, but it matters greatly that you can monitor your heading so as to maintain a straight course in a given direction, and reverse it accurately if required. Surface-bound animals may use

idiothetic cues associated with walking on a substrate to achieve this, but such cues are absent when moving through the air. On the other hand, the sun and its attendant cues, such as the polarization axis of the sky, provide a reliable celestial heading reference, analogous to the inertial heading reference provided by the gyroscope in an aircraft's heading indicator (see above).

Indeed, before the advent of GPS, pilots flying transpolar routes used the polarization pattern of the sky to check their heading (Pedersen, 1958). Likewise, sun compasses were routinely used by the British Army to set and maintain heading in the featureless deserts of North Africa and the Middle East during the Second World War and First Gulf War. As a rule of thumb, the sun compasses used in these conflicts were supposed to be readjusted once every 15 min to account for the azimuthal movement of the sun, but could still be used to maintain heading between adjustments (Howard MKII Sun Compass Manual). This is because heading at a constant angle to the sun produces only a slight curvature in trajectory, and the deviation from a straight path is scarcely noticeable on so short a timescale. To be specific, if the sun's azimuth were to change at its average rate of $\pi/12$ radians (i.e. 15°) per hour, then the resulting trajectory would trace a circular arc of radius $12/\pi$ times (i.e. approximately four times) the distance travelled in an hour. To put this in perspective, at a cruising speed of 60 km/h, and in the absence of any wind, a homing pigeon maintaining a constant heading with respect to the sun would fly a circular arc of radius 229 km. Clearly, the curvature of so wide an arc would be indiscernible over a few minutes of flight, and over a 15 min period, the bird would make 15 km progress on its initial heading, while straying less than 0.5 km from it. Furthermore, any such drift could be eliminated by continuously adjusting the heading angle with respect to the sun at a constant rate of $\pi/12$ radians/h (i.e. 15° /h). This offset correction would compensate for drift away from the initial heading, but would not amount to true time compensation in the sense required for the sun to be used as a compass (see above). In particular, because the offset correction would be made on the basis of time elapsed, rather than time of day, it would not be susceptible to perturbation under clock shift.

In reality, the rate of change in solar azimuth can vary markedly through the day about its mean rate of $\pi/12$ radians/h. Fig. 1a–c takes account of this variation, plotting the trajectory that a bird released from the Royal Observatory, Greenwich, would follow at various times of year, if it always flew at a constant speed and on a constant heading with respect to the sun. Once again, the curvature of these trajectories is indiscernible over a few minutes of flight (see inset to Fig. 1b). Eliminating this curvature completely would require perfect knowledge of the ephemeris function and perfect knowledge of the time of day, but it is interesting to note how much straighter the trajectory becomes if the heading angle with respect to the sun is simply adjusted at a constant rate of $\pi/12$ radians/h. The resulting trajectories are plotted in Fig. 1d–f, and demonstrate that it is possible in principle to maintain an almost straight heading for several hours simply by applying a constant offset correction. Once again, because the offset correction would be made on the basis of time elapsed, rather than time of day, it would not be susceptible to perturbation under clock shift.

It is important to emphasize that neither the uncorrected solar heading indicator mechanism (Fig. 1a–c) nor the offset-corrected solar heading indicator mechanism (Fig. 1d–f) meets our definition of a compass, because neither mechanism provides a measurement of absolute geographical direction. Rather, each hypothesized mechanism simply allows an arbitrary heading to be maintained with a reasonable degree of accuracy on timescales of a few minutes to a few hours, dependent upon whether or not an offset correction is applied. Nevertheless, the simpler kind of directional information that this mechanism provides could still be

of immense value to an animal in maintaining, and indeed reversing, a course. We discuss these possible functions of a solar heading indicator further below.

POTENTIAL FUNCTIONS OF DIRECTIONAL SOLAR INFORMATION

A Compass for Navigation

The first function of a compass that we consider is that central to Kramer's original map-and-compass navigation concept: the compass, not necessarily the sun, provides a mechanism for traversing terrain in the direction of a goal, following identification of the appropriate direction from a navigational map. The map-and-compass model (originally Kramer, 1950) has been described as a two-step process involving a 'map step' determining the home direction and a 'compass step' locating the home direction (Wiltschko & Wiltschko, 2009). It has long been recognized that the sun can provide the necessary compass information in this second step. But to these two steps we should perhaps add a third, in which directional information is used to maintain a heading that has been set, without updating that course on the basis of some updated estimate of position relative to home. This third step is important, because it allows the animal to make progress towards a goal without having to reassess its position constantly. Indeed, it might also allow the traversing of areas in which navigational information is for some reason unavailable or highly confused, freeing the bird from potential navigational traps.

Adding or distinguishing this third step may seem an unnecessary complication, but is important in making clear our key point that different solar information might, in principle, be used for different aspects of map-and-compass navigation. This could have important consequences for our interpretation of the results of clock shift experiments. For example, the finding that a clock-shifted bird tends to fly in the wrong direction on its first release from a site, but in the correct direction on subsequent re-releases, is usually taken to indicate either that its sun compass was recalibrated or that it was ignoring solar cues when setting a course in favour of direct guidance by landmarks or resort to a magnetic compass (Gagliardo, Odetti, & Ioalè, 2005a, 2005b; Wiltschko, Stapput, & Siegmund, 2005). Neither interpretation excludes the possibility that a bird still makes use of the sun as a heading indicator to assist in holding course once an initial heading has been set.

A navigational map aids homing from unfamiliar places, but once birds are familiar with an area, they are thought then to resort more readily to a map consisting of familiar landmarks (Guilford & Biro, 2014). One hypothesis for how such a map provides guidance is via goalward compass instructions associated with memorized local position cues (e.g. a configuration of landmarks) at each known place in a mosaic of familiarity: the mosaic map (Wiltschko & Wiltschko, 2009). Like the map-and-compass model, the mosaic map also uses compass information to inform a traverse between known focal places, with the advantage that the animal does not need to know where it is all of the time, allowing a more efficient, more sparsely represented, familiar area map. Hence, just as in map-and-compass navigation, solar information could usefully serve as a heading indicator on the short timescales involved in traversing between focal places when using a mosaic map.

In summary, although the map-and-compass and mosaic map concepts both definitively require compass information to set an initial course, there is no necessary reason why compass information must also be used to steer that course. The simpler directional information provided by a heading indicator is sufficient for steering, and as navigation operates on a much longer timescale

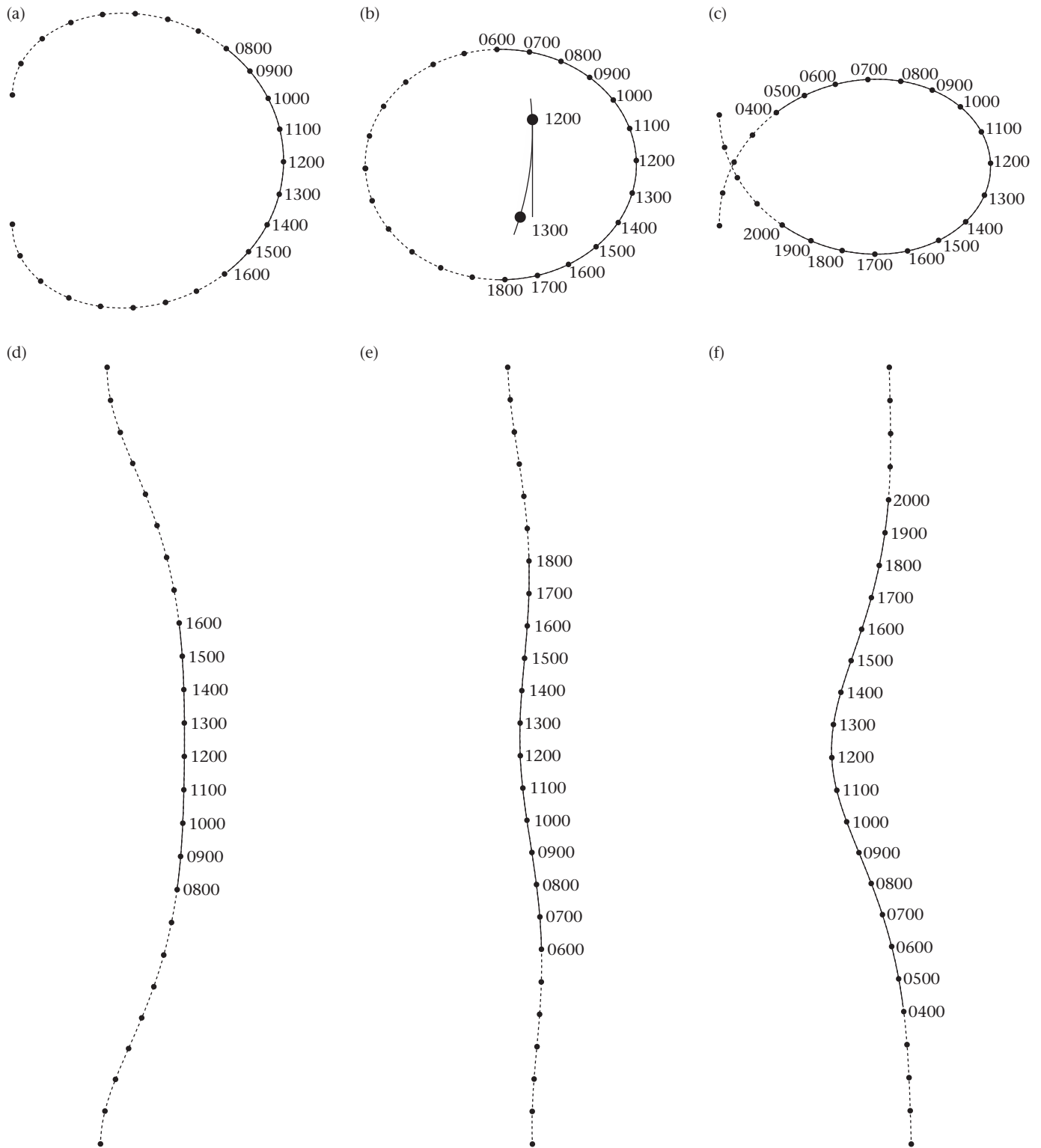


Figure 1. Illustration of the principle of a solar heading indicator, showing the trajectories that would be followed by (a, b, c) a bird that always flew at a constant heading angle with respect to the sun, and (d, e) a bird that flew at a heading angle corrected for drift at a constant rate of $\pi/12$ radians/h. The trajectories are drawn using ephemeris data for the Royal Observatory Greenwich, at (a, d) the winter solstice, (b, e) the spring equinox and (c, f) the summer solstice. Each trajectory covers an entire 24 h period for the insight that this yields; that period during which the sun would not be visible is shown by a dashed line; the filled circles mark hourly intervals. To read the graphs, simply pick a release time (in GMT) and follow the trajectory forward in time from this point. Note that there is little curvature apparent in any of the graphs on a timescale of much less than an hour, and that an almost straight trajectory can result on a timescale of much longer than an hour if drift is corrected at a constant rate of $\pi/12$ radians/h (i.e. $15^\circ/\text{h}$). The inset to (b) shows an enlarged view of the trajectory between 1200 and 1300 hours, to provide a better indication of the extent of the deviation from straight flight in this simple case in which the bird follows an elliptical trajectory. Ephemeris data were obtained using the NASA Jet Propulsion Laboratory's HORIZONS software (Giorgini et al., 1996).

than steering, there is no reason to assume that they must necessarily make use of the same directional cues. It follows that both time-referenced and nontime-referenced solar information could in principle be involved in both kinds of homing process.

A Compass for Racing

A compass may also be used to home over long distances in a simpler way than envisaged by either true navigation or the mosaic map. With repeated training from just a single direction, birds have the opportunity to learn that their goal can always be reached by attending to compass information alone. Indeed, it is common practice in the sport of pigeon racing to train birds to fly only from release sites with a common direction to home (see [Griffin, 1952](#)). Individual birds may be designated 'north road' or 'south road' birds depending on which kind of training they have had, and therefore which kind of race they are destined to compete in. An associative account might be that a single compass bearing always provides reliable guidance for homing, so that racing birds learn to ignore other navigational cues, at least until they are near home, thereby enhancing their performance, especially in very long races. A solar compass used for this purpose would need to be well time-compensated to be effective, but it would not need to involve any context of position, and certainly no map, because the goalward direction is invariant.

It is not obvious that a racing compass would have much natural use, for it would rely on resources always being located in the same direction, but it seems analogous, at least, to the innate compass orientation of first-time migrant birds (e.g. [Newton, 2008](#)) or the time-compensated sun compass control of migrant monarch butterflies ([Mouritsen et al., 2013](#); [Reppert et al., 2010](#)). However, it does indicate the potentially important influence of simple associative processes on avian orientation, and might well emerge from specific training regimens (e.g. [Dell'Arciccia, Dell'Omo, & Lipp, 2009](#)). We should therefore be wary of it in scientific homing experiments aiming to determine the role of compass guidance. Some experiments demonstrating an effect of clock shift after extended training from a single familiar site may, in fact, have stumbled upon this kind of compass use. [Fuller et al. \(1983\)](#) showed a large deviation under clock shift in pigeons following at least 55 releases from the same site >40 km from home. Although this experiment is often cited in discussions of mosaic map type navigation in the familiar area ([Holland, 2003](#); [Wiltschko & Wiltschko, 2009](#)), it is possible that the result, in fact, indicates use of a racing compass, induced by extensive directional training prior to the critical release (see also [Wallraff, 2001](#)). Entrained directional orientation can dominate initial orientation after rather few releases (as few as three in [Michener and Walcott's \(1967\)](#) studies), so we must be cautious of generalizing about compass function from such situations.

Directional Information for Steering

Time compensation is only strictly necessary if the sun is to be used to locate a particular geographical direction at an arbitrary time of day. If direction is required only for steering a straight course, or for measuring drift away from it, then the sun's azimuth could be used without true time compensation. In this case, we would regard the sun as a heading indicator. Of course, there is no reason why time-compensated solar information should not be used for steering also, and in this case we would regard the sun as a compass. The distinction that we are drawing here is not merely a semantic one, because the directional information that a solar heading indicator provides is expected to be invariant under clock shift, in contrast to the directional information provided by a time-compensated sun compass (see above).

We suggest three related scenarios in which birds might use directional solar information for steering. First, a flying animal might use the sun to maintain a constant heading towards a target with which it is not in sensory contact. We have mentioned this already in relation to the use of the sun as a heading indicator in the map-and-compass and mosaic map models of navigation. However, the same mechanism might also fare in exploration, where there is no specific target but where the return journey will be simpler if the outbound track can be kept straight. Second, a flying animal might use the sun for steering when it needs to measure changes in heading angle made in the course of exploration, or in avoiding obstacles. Thus, time-independent use of the sun as a heading indicator could be a common mechanism in the path integration systems used by many animals to compute and update their current direction to home when their outbound track is not straight. Third, a flying animal might use the sun for steering even when it is in direct sensory contact with the visual landmarks that it is using for guidance. This point requires a little further explanation, but as we now show, the most obvious benefit arises when there is a significant crosswind.

If a bird heads directly for a distant, visible landmark, then a crosswind will lengthen its geographical path and produce a curved geographical trajectory. Without compensation the bird will 'kite' windward, turning all the while, until either the target is reached or its heading becomes aligned with the wind. The same phenomenon occurs on, or in, moving water. Windward drift can be avoided by adjusting heading into the wind, which is precisely what an aircraft's pilot does when making a crabbed landing on a runway with a strong crosswind, but it requires recognition of the drift away from a straight track. Although it is possible to detect wind drift by attending to the relative motion of the underlying landscape, a more reliable method is simply to adjust the heading so that the target remains on a constant bearing. Adjusting the heading so that the angle between the target and the sun is kept constant will produce a geographically straight trajectory to the target over periods of time short enough that the sun's own geographical direction does not change significantly.

OTHER POTENTIAL USES OF SOLAR INFORMATION

We have focused so far upon categories of directional solar information that use the sun either as a compass or as a heading indicator. However, the potential roles of solar cues in navigation and orientation may be richer and more complex still. First, we consider how the time-dependent effects of the sun can change the visual appearance of landmarks, and suggest that in extreme cases this could lead to a failure to recognize a place when viewed at an unfamiliar or incorrectly interpreted time. Second, we consider how the time-dependent effects of the sun can visually superimpose directionality on landmarks in the visual scene.

Time-compensated Landmarks

We are used to thinking of the sun as providing compass information because its geographical direction remains essentially fixed over short timescales despite changes in the viewer's position. However, when viewed in conjunction with the landscape, the sun itself can be a distinctive landmark, albeit one whose relative position varies with the time of day ([Fig. 2a](#); [Bingman & Ioalè, 1989](#)). The sun's influence upon the visual landscape becomes even clearer when we consider how profoundly it affects patterns of light, shade and colour in any visual scene ([Fig. 2b](#)). The problem with all of this visual information is that it is time of day, and weather, dependent. Compare the two representations of the same visual scene painted at different times of day in [Fig. 2b](#) and [c](#). For

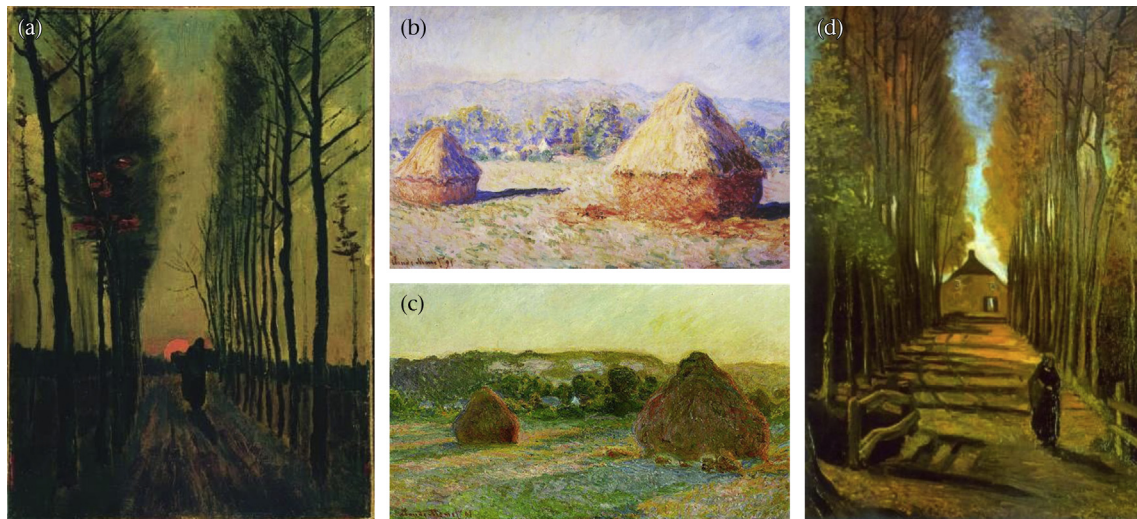


Figure 2. (a) The sun itself can serve as a time-dependent landmark in conjunction with the landscape, as in this painting of an avenue of poplars at sunset by Van Gogh (Nuenen, October sunset, 1884), in which we assume that the woman is walking towards the viewer. Had the woman in the painting walked to and from work along this road, she would have known to head away from the sun at the end of the day. (b) The sun can change the appearance of landmarks in a time-dependent fashion, and can even superimpose directionality on an otherwise undirected landmark, as in this painting of a radially symmetric haystack by Monet (Giverny, grainstacks in the sunlight, morning effect, 1890). (c) A second painting by Monet, of haystacks this time in the evening, shows how visually different solar-derived cues can make the appearance of a scene (Giverny, wheatstacks end of summer, evening, 1890–1891). (d) Shadows can confer directional sense to linear features of the landscape, as in this painting of an avenue of poplars by Van Gogh (Nuenen, autumn 1884). Had her house not been visible at the end of the avenue, the woman could have found her way back home by walking the road with the shadows on her left.

visual cues to be used to recognize a place as a single familiar location at any time of day, this time-dependent information must somehow be parsed out of the common representation of the place.

It is possible, of course, that animals only memorize those features of the visual landscape, such as the relief of the horizon, that do not vary with the sun's position. This would happen automatically under the simplest associative account of visual scene recognition, provided that the scene were viewed at different times of day during learning. This is because the features of the scene that the animal learns to associate will be those that are the most reliable across occasions. But if the animal is always trained to learn the same scene at the same time of day, then its learned representation of the scene will be intrinsically time-limited. In this case, it is possible that a trained bird might fail to recognize a familiar place if released at a different time of the natural day, such as during a clock shift experiment, simply because the sun's effect upon the visual landscape has drastically changed.

A more sophisticated mechanism for solving the same problem could be to acquire multiple time-limited representations of the visual scene, so that the sun and its diurnally varying effects, such as shadows, become time-dependent landmarks. With sufficient experience, a fully time-compensated representation of the visual landscape might emerge. We could think, for example, of a particular geographical location being represented as a file of different place memories, each corresponding to a different time of day. The sense in which this file is understood to have a common file name, a higher order identifier as a single discrete location, is of course open to question. Nevertheless, the idea serves to emphasize that the recognition of a location free of its time-dependent visual cues is not necessarily a simple process. A critical consequence of this is that clock shift might cause failure to recognize a familiar place because the time-coded aspects of the landscape apparently do not fit with the bird's subjective time.

The question then arises, what mechanism does a bird resort to in the absence of access to a coherent familiar landscape map (because it has been clock-shifted)? One logical suggestion is that it might resort to its system for navigating in unfamiliar places: a system using position cues that are independent of time (such as an

olfactory map) but that may then rely on a time-compensated compass to locate the homeward direction. Thus, clock shift might cause deviation at familiar sites simply because it triggers resort to the navigational map, and not because onward guidance is normally compass-controlled at familiar sites. In [Bingman and Ioalè's \(1989\)](#) experiments, clock-shifted birds familiar with their release site only showed deviation if they had their olfactory sense intact, and hence by implication were able to access an alternative navigational map (for further discussion of the effects of clock shift in olfactorily impaired birds, and the role of hippocampal brain structures, see [Gagliardo, Ioalè, & Bingman, 1999](#); [Gagliardo et al., 2005a](#)). Thus, the proposition that birds might revert to a navigational map-and-compass even at familiar sites where familiar landmark recognition has been disrupted by clock shift seems reasonable. Far from being the acid test of a mosaic map model of familiar area navigation, clock shift experiments are ambiguous.

There is continued debate over whether familiar landmarks provide direct guidance for animals orienting in a familiar area (i.e. in pilotage), or whether guidance is provided by memorized compass instructions tied to familiar places in a mosaic map ([Holland, 2003](#)). Since an effect of clock shift is usually taken to confirm the use of a sun compass ([Biro, Freeman, Meade, Roberts, & Guilford, 2007](#); [Wiltschko & Wiltschko, 2009](#)), the possibility that birds might use time-dependent landmark cues is fundamentally problematic for the interpretation of clock shift experiments. This problem almost certainly applies to fine-scale orientation tasks too, because a long-overlooked study by [McDonald \(1972\)](#) shows that pigeons that were trained to peck at a different key for food, according to the position of a light source, learned to do so using the pattern of shadows present in the visual scene. In addition, [Armstrong et al. \(2013\)](#) showed that pigeons continue to deviate under clock shift even when their final goal, the loft, is both close and directly visible.

The idea that birds might use time-limited or time-compensated visual landmarks could therefore have important consequences for navigation and orientation research. In common with a true sun compass, time-dependent landmarks would be expected to provide deviated guidance under clock shift, but they

would presumably be compromised by guidance information coming from the time-invariant features of the landscape. Moreover, in contrast to a sun compass, they would not be expected to provide guidance at all beyond direct visual contact with the memorized scene.

Directed Landmarks

Most visual landmarks look different when viewed from different angles, but they are unlikely to provide sufficiently fine-grained directional information to be very useful alone, and it is therefore only in combination that landmarks are usually thought to be useful in pilotage. Nevertheless, it is possible that the movement of the sun through the day could modify the appearance of such landmarks sufficiently to superimpose directionality upon the landmarks themselves. A tall, upright landmark such as an isolated tree could serve, in effect, as the gnomon of a sundial, casting a shadow that could be used in a time-dependent way to indicate direction (Fig. 2d; McDonald, 1972). A directed landmark of this sort could integrate information on position with information on direction in a single, local, time-dependent visual cue.

The sun can confer directional sense upon linear landscape features much more generally. Pigeons follow linear landscape features such as roads when homing from familiar sites (Biro et al., 2007), but the simple instruction 'follow the road until you reach your destination' would be as likely to lead away from home as it would be to lead towards it, unless combined with knowledge of which way to fly along the road in question. The linear features that birds follow tend to be associated with vertical relief, such as a hedgerow or tree line, and so the shadows that this relief casts could in principle be used as a simple, binary indicator of directional sense (Fig. 2d). As a simple example, in higher northern latitudes, a bird that regularly flies east along a road running east to west will find itself flying along a linear feature in which the shadows fall from the right at most times of day. For a bird that regularly flies north along a road running north to south, the shadows will fall from the right in the morning and from the left in the afternoon. A directed linear landmark of this sort would integrate information on direction and route in a single, time-dependent visual cue.

Where landmark familiarity is sufficiently well entrained, such as when following individually distinctive homing routes across the landscape, our directed landmark hypothesis might provide a mechanism to account for continued attention to time-compensated solar information throughout a journey as has been found in precision tracking experiments with clock-shifted pigeons (Biro et al., 2007). However, the general message of this section is that without careful analysis of the effects of clock shift on orientation, and perhaps also of the past experiences that led to these effects, it may be very difficult to distinguish effects that are due to a sun compass from effects that are due to the influence of the sun on the visual landscape and the landmarks within it.

CONCLUSION

Since its discovery in the 1950s, the sun compass has been central to our understanding of avian navigation, with the concept of time compensation at its heart, and a response to clock shift its axiomatic test. We have developed theoretical arguments to show that solar information may have much more varied roles in avian orientation, and that these roles, and how they interact, remain little understood. We suggest that the sun's direction could be useful even without full time compensation, and especially for short timescale orientation tasks as a heading indicator, and we suggest that time-dependent solar information might also be used

in a manner that does not conform to the characteristics of either a compass or a heading indicator. Although we frame our ideas with reference to birds, many should apply equally to other highly mobile taxa, particularly those that move through fluid media.

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