Chapter 16
Time-Compensated Celestial Navigation

James Frederick Cheeseman

Abstract Animals and in particular insects, despite their diminutive size, have a remarkable ability to use the environmental information around them to perform complex navigational tasks to forage for food and to return home. Some of the most prominent of these environmental cues are those observed in the sky, first among which is the sun. The purpose of this chapter is to describe the time-compensated celestial navigation in insects which relies on an accurate continually consulted circadian clock. It draws heavily on the research on two species, the honey bee *Apis mellifera* and the monarch butterfly *Danaus plexippus*, which have been used extensively to study complementary aspects of navigation behavior.

Keywords Circadian · Migration · Orientation · Sun compass

16.1 Introduction

For an animal to show true navigation, it needs not only to know in which direction to move but also to have a concept of where it is in its geographic environment even in unfamiliar territory. For the purposes of this chapter, this definition of navigation is broadened to include orientation more generally. Many insects achieve way-finding through visual cues including using landmarks either in isolation or through panorama matching. These are relatively simple way-finding mechanisms which are robust while the animal is in visual range of them.

The strongest celestial cue which provides direction is light from the sun either directly during the day or reflected by the moon at night. It provides an instantaneous compass direction and allows the animal to calculate a bearing.

Even when the sun is occluded from view by cloud, a partial view of the sky is enough to see and orient by the polarized pattern of light known as the e-vector

---

J. F. Cheeseman (✉)
Department of Anaesthesiology, School of Medicine, The University of Auckland, Auckland, New Zealand
e-mail: j.cheeseman@auckland.ac.nz

H. Numata, K. Tomioka (eds.), *Insect Chronobiology*, Entomology Monographs,
https://doi.org/10.1007/978-981-99-0726-7_16

(Rossel et al. 1978), and knowledge of this e-vector is sufficient to obtain compass information by several insect models including the honey bee *Apis mellifera* (Evangelista et al. 2014), the fruit fly *Drosophila melanogaster* (Warren et al. 2019), and the monarch butterfly *Danaus plexippus* (Reppert et al. 2004).

The challenge is that celestial cues, viewed by those on earth, move across the sky. During the day the sun rises in the east and tracks across the southern part of the sky (in the northern hemisphere) before setting in the west. In the southern hemisphere, the sun's path tracks to the north. The night sky is of course quite different. The moon is the most prominent cue but is not always visible and even when full provides a fraction of the daytime light from the sun. At night at least in the northern hemisphere, the sky appears to rotate around the northern pole star. Mammals and birds can use stars for orientation, but there is little evidence that insects can decipher individual stars and might rather use the generalized pattern of the Milky Way such as in the example of the dung beetle *Scarabaeus satyrus* (Dacke et al. 2013).

For short-distance homing in many insects, the movement of the celestial cues may not be a problem because the timeframe of the excursions is so short. However, for insects which fly and forage over several kilometers over several hours, this poses a significant challenge as the sun or moon will have moved in the sky over time.

The travel of the sun across the sky every day means that in order to use it as a compass, animals require an accurate circadian clock to interpret the directional information. This ability to consult a continuously updated biological clock gives rise to the concept of time-compensated sun-compass orientation first described in insects by von Frisch (1954) in honey bees.

16.2 Honey Bee Flight Using the Sun as a Compass

16.2.1 Navigating with a Clock

Karl von Frisch (1954) explained how the flights of honey bees are made with reference to the sun's position and that they communicate this information through the famous waggle. Bees can be trained to and from a sugar water feeder simulating a flower's nectar with relative ease. Depending on the quality of the "nectar," recruits are quickly added from the hive. The number of recruits can be titrated by increasing or decreasing the concentration of sugar water. Trained foragers fly quickly and directly between the hive and the feeder in a "vector flight" (Menzel et al. 1998) and once satiated return to the hive reversing this vector. The direction of this vector is made with specific reference to the sun. This ingrained behavior provides a system that can be manipulated experimentally in a number of ways to test the role of the sun and other navigational cues and has been the fundamental research tool in the study of honey bee behavior for several decades.

The experimental proof of time-compensated sun-compass orientation in bees has been described by Lindauer (1961) and others since in several elegant stages. First

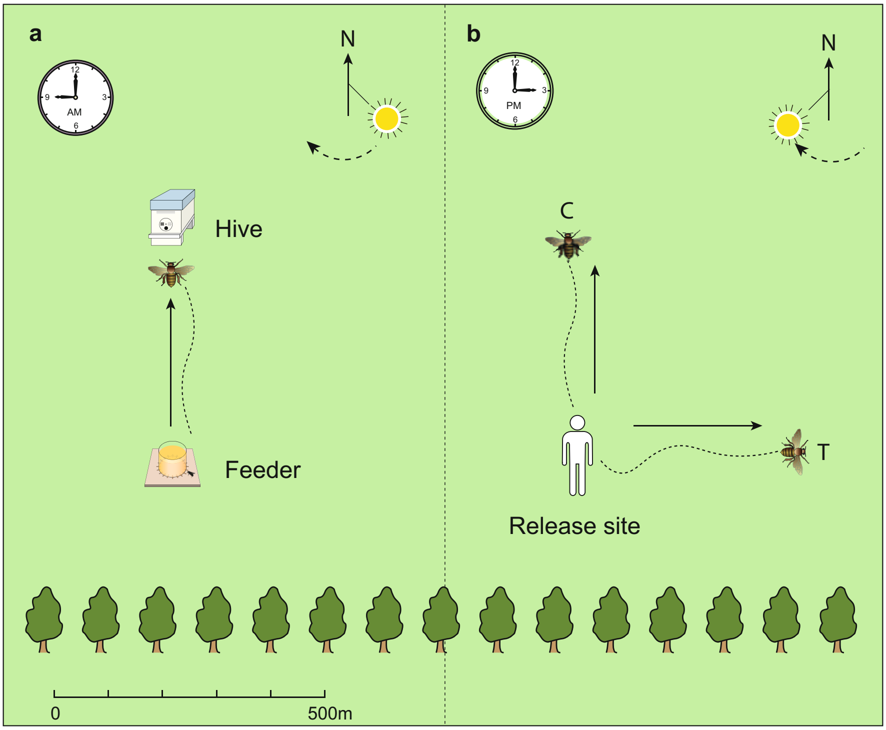

Fig. 16.1 Diagrammatic representation of sun-compass orientation in honey bee flights. (**a**) and (**b**) are contiguous in space but separated in time by 6 h in time. In (**a**) the bees are trained to a feeder and return to the hive by a vector flight north with reference to the sun. In (**b**) two examples are shown. Control bees (C) that have been caught at the feeder and displaced by several hundred meters are released 6 h later and, with functional clocks, compensate for the movement of the sun in the sky and fly their vector flight north to where the hive should be. Anesthetized bees (T) in which the clock has been phase shifted make an error in their vector flight direction proportional to the phase shift of the clock

when bees are trained to a feeder, for example, to the south of the hive, and that feeder and bees are displaced several hundred meters to the east from its original position, the bees still fly north when released on their homeward flight (Fig. 16.1). In this instance the bees have made an error by heading in the northerly direction that will not return them home. It is typically not until they reach the end of the return vector flight that they perform search patterns and rely on a hierarchy of other navigational information such as landmarks to find their hive (Menzel et al. 1998). However it is not just the case that the bees fly “blindly” with respect to sun compass and if prominent landmarks are sufficiently strong, the bees will override the incorrect sun-compass information navigating instead with regard to familiar or generalized landmarks (Cheeseman et al. 2014).

Once it has been established that the bees use the sun to calculate their vector flights, a second experiment can be performed to test whether they can compensate for the movement of the sun. In this instance bees trained to the original feeder are caught as they take off full of nectar for the flight home. These bees are kept in the dark, without reference to the sun, for several hours before being released and observed to fly directly and quickly home on their correctly attuned homeward vector flight direction (north in the above example). Importantly the bees fly in this northerly direction regardless of whether the release site has been displaced indicating they have compensated for the movement of the sun (Lindauer 1961).

A third experiment can be performed in which the same system of hive and feeder can be employed with the catch and release method. Once trained to feeder, the entire hive can be moved overnight to a completely novel site outside the experience of the bees. In this way one might discount the possible influence of landmarks or other cues that might influence the behavior. Multiple feeders, this time without sugar or scent, can be arranged around the hive, and the number of bee visits is observed at each feeder. Invariably the feeder in the compass direction relative to the hive in its original site is the one most visited by the foragers and also at the right time.

Together these experiments indicate that bees have an innate time sense (named Zeitgedächtnis) which is driven by a circadian clock. “Flower constancy” is a strong driver of this behavior as individual species of flower show maximum secretion of nectar over limited periods each day with bees visiting each species at the appropriate time such as illustrated in Linnaeus’ “Horologium florae (Flower clock)” (Linnaeus 1751). So accurate is the bees’ time sense that it is possible to train foragers to between at least five (von Frisch 1954) and as many as nine (Bloch 2010) separate periods during a single day. The resolution of the clock is such that it is accurate to within minutes.

The remarkable ability for the forager bees to communicate the position of food (distance and direction) with respect to the sun through the waggle dance is further evidence of the time-compensated behavior. Even in poor weather when bees are confined to the hive by rain, foragers will continue to dance adjusting their angle on the comb relative to the sun’s position. If the quality of the food source has been sufficiently good, dancing may continue in the so-called marathon dances which go into the night indicating the position of the food relative to the sun on the other side of the world where the bees have never seen it.

The circadian clock of the honey bee has been very well described and is based on the familiar positive and negative feedback loops of the known clock genes which regulate their own transcription. Interestingly the bee clock seems to be more similar in its mechanism to the mammalian clock in some respects than to other insect models such as *Drosophila* (Rubin et al. 2006; Yuan et al. 2007; Bloch 2010). *cryptochrome* (*cry*) and *period* (*per*) mRNA levels in the brain undergo strong oscillations, and *cycle* protein oscillates in antiphase to *per* (Bloch 2010) in diurnal light cycles as well in the constant conditions of the hive.

It is relatively straightforward to phase shift individuals (Ludin et al. 2012) and whole colonies of bees (Moore and Rankin 1993) in the laboratory with light cycles and temperature cycles, and these experiments can reliably phase shift times of food anticipatory behavior. Similar experiments have been conducted in the hoverfly

(Massy et al. 2021). A phase response curve derived from the response of locomotor activity to 1-h light pulses administered to individual bees indicates phase delays in the evening (between CT9[1] and CT18) (Ludin et al. 2012). Smaller phase advances were observed late in the subjective night and into the early morning (between CT18 and CT3).

16.2.2 *Shifting the Circadian Clock with Anesthesia and Its Effect on the Time Compensation of the Sun Compass*

It transpires that the circadian clock can be phase shifted with anesthesia. Exposing honey bees to the general anesthetic isoflurane during the day causes a phase delay in their foraging behavior. This has been demonstrated in several experiments (Cheeseman et al. 2012) and provides a useful tool to interrogate the bees' navigation systems.

Bees fitted with radiofrequency identification tags can be time-trained to a feeder over several days, and these foragers continue to return to that feeder at the same time of day for several days after the feeder is emptied of food. Anesthesia of the whole colony for 6 h during the day delays the flights of foragers on subsequent days by at least 3 h (Cheeseman et al. 2012). Importantly this delay continues for several days despite the colony's being kept in the open with exposure to the sun. Only after the third day do the flights of the foragers return to their preanesthesia schedule. This suggests strongly that time perception has been altered by anesthesia and therefore could affect time compensation of the sun compass. To test this the catch and release experimental paradigm can once again be employed to investigate the effect of the anesthesia on the bee's navigation. The advancement of technology to track individual bees in flight with harmonic radar (Riley et al. 1996; Menzel et al. 2005) has greatly increased the ability to investigate flight tracks. To return to the method in the earlier example (Fig. 16.1a), bees can be trained from a hive to a feeder to the south. As they alight the feeder full of nectar, they perform the fast vector flight north toward home. This behavior can be exploited to test the effect of anesthesia on time compensation too. If they are caught just as they take off from the feeder and anaesthetized in the dark, we can test the hypothesis that the anesthesia does in fact alter time perception. One might reasonably predict if anesthesia stops the perception of the passage of time the bees may make an error in their time compensation, equal to the time anaesthetized, and miscalculate the correction to make in the time the sun has moved. Given the sun moves on average 15° per hour, a 6-h anesthetic would therefore result in a 90° error in flight direction (Fig. 16.1b (T)). The bees do indeed make an error consistent with a period of time being lost; however it is not an error of the magnitude equal to that under anesthesia. After

---

[1] Circadian time. CT0 and CT12 correspond to onset and offset of activity, respectively.

6 h the average error of bees returning home was approximately 60°, the implication being that anesthesia has phase shifted rather than stopped the clock.

The comprehensive proof that anesthesia is acting on the clock itself comes from analysis of the expression of the clock genes themselves. In a further series of experiments, whole colonies of bees were kept in constant dim light in the laboratory and the activity rhythms of the colony measured for at least a week. The whole colonies were anaesthetized for 6 h during the day or at night and activity monitored for a further week. During this behavioral experiment, individually marked foragers of known age were collected and assayed for mRNA levels of *per*, *cry*, and *Clock* every 6 h over a time course of 72 h (approximately 36 h before and 36 h after anesthesia). Anesthesia during the day strongly phase delayed the expression patterns of *per* and *cry* and did not change the expression of *Clock*. This was entirely consistent with a delay in the colony's overall activity of the same magnitude. However when the experiment was repeated in a control experiment at night, no such phase delay occurred in either activity behavior or clock gene expression. This is not just a diurnal effect but a circadian one, and the subtlety of the effects of anesthesia on the bee clock has since been further described in an anesthesia phase response curve (Ludin et al. 2016) in which both advances and delays are observed on activity rhythms over the circadian cycle.

The importance of these findings is that the mechanism of navigation (time-compensated sun-compass orientation) is, perhaps unsurprisingly, inextricably linked to the circadian clock. However exactly how they are connected and where this occurs in the brain in the bee is not yet known. To investigate this further, we turn to another insect model the monarch butterfly.

16.3 Long-Distance Migration Using a Time-Compensated Sun Compass in the Monarch Butterfly

16.3.1 The Remarkable Journey

Perhaps the most impressive performance of insect navigation described is the migration of the monarch butterfly in which millions make their way from North America to their overwintering grounds in Mexico (Reppert and de Roode 2018). There are several reasons for this migration: to escape the freezing temperatures and the lack of their primary food source, milkweed plants, and also to escape from a protozoan parasite *Ophryocystis elektroscirrha* (Reppert and de Roode 2018).

The migration is unique because it typically takes between three and five generations of butterflies to complete the approximately 4500-km round journey (Miller et al. 2012; Tyler Flockhart et al. 2013, 2017). Furthermore the familial descendants return to the same location (Reppert and de Roode 2018). A significant change in physiology occurs between generations. In the late summer, the generation about to set out on the southern migration enters reproductive diapause to survive the journey and winter before becoming reproductively active again in the spring. Several generations are then required to populate the northern range over the spring and summer (Reppert and de Roode 2018).

The time-compensated sun compass is once again critical to this behavior of the monarch butterfly and relies on a functional circadian clock for successful navigation (Froy et al. 2003). The study of the mechanisms at the behavioral, physiological, neural, and genetic levels has been championed by Steven Reppert and his laboratory, some highlights of which are summarized here.

16.3.2 Sensing the Position of the Sun

The monarch's compound eye retina is attuned to sensing the sun's azimuth, and the dorsal rim of the eye is sensitive to the angle of polarization (the e-vector) (Reppert et al. 2004; Labhart et al. 2009). This dorsal rim area is a specialized detector of linearly polarized light and is common to *Drosophila* (Warren et al. 2019), desert locust *Schistocerca gregaria* (Homberg 2004), the honey bee, ants (Lebhardt and Ronacher 2014), and others (Labhart et al. 2009). Both signals, the sun's azimuth and e-vector information, are sent from the eye to the butterfly's central complex in the brain which is believed to integrate them to determine the sun's position. It is this central complex which is most likely the core structure of sun-compass orientation in the monarch (Reppert and de Roode 2018), and this is consistent with findings in other insects including *Drosophila* (Strauss 2002), the dung beetles *Scarabaeus lamarcki* and *S. satyrus* (el Jundi et al. 2018), and the desert locust (Homberg 2004) in which the central complex is implicated in integration of information from celestial cues for movement and navigation.

16.3.3 Testing the Time Compensation of the Sun Compass

The strength of the autumn migratory behavior can be exploited experimentally by flying harnessed monarchs in a flight simulator. This has provided a powerful paradigm to test the sun-compass mechanism. In the simulator individuals with a view of the sun orient southwest and happily fly for many days. Clock shifting experiments using artificial light cycles reliably change the subsequent flight direction of the phase-shifted individuals so that a phase shift of 6 h results in a 90° change in direction (Merlin et al. 2009).

16.3.4 Location of the Mechanism for Time-Compensated Sun-Compass Orientation

Using the same flight simulator, protocol allowed the discovery that the clock mechanism for the monarch's sun-compass system is located in the antennae. Each antenna has a circadian clock which is directly photosensitive and can be entrained by light. Stopping the light signal by painting black or removing both antennae from an individual means it cannot perform time-compensated sun-compass orientation. Removing the paint from antennae rescues this ability (Guerra et al. 2012). Only one antenna is required for correct orientation behavior. If one is damaged or removed, the other is sufficient for correct orientation. However conflicting information from each intact antenna disorients the individual if either antenna is covered in paint blocking the light (Guerra et al. 2012).

These peripheral, antennal clocks are able to operate independently or at least are not strongly coupled together. Furthermore the clocks in the antennae appear to act somewhat independently of the central clock in the brain. The blocking of the light to the antennae results in free-running of the antennal clocks, but the central brain clocks remain entrained.

Examination of the expression of key core clock genes *per* and *timeless* (*tim*) in the antennae shows strong oscillations in light-dark cycles. In the example above when an antenna is painted black stopping light transmission, both *per* and *tim* expressions are highly dampened (Guerra et al. 2012). This is consistent with the general observation that peripheral clocks are not as strongly persistent in the absence of entrainment (Hardin 1994; Yildirim et al. 2022).

In contrast the central brain clock, generally predicted to be in the paired pars lateralis in Lepidoptera (Brady et al. 2021), is strongly endogenous. The implication is that it is not the central clock, in the monarch at least, that is important for providing the timing mechanism to synchronize the sun-compass information but rather the peripheral antennal clocks. What is fascinating is that there seem to be several systems working requiring clock input. The central clock in the brain determines the circadian phase of the animal and presumably the diurnal cycle, but the antennal clocks provide the key to time-compensate the sun-compass information.

16.4 Time-Compensated Moon Compass

So far the examples of time-compensated celestial navigation discussed have all been with reference to the sun compass. The hypothesis of a time-compensated moon compass has been discussed, if only rarely since 1960 (Papi 1960). One can imagine a similar time-compensated system using a lunar clock of period close to 24.8 h that could function a similar way as the sun compass. However there are several additional challenges an animal faces in being able to use this. The moon does not always rise at the same time, and the intensity changes with the lunar cycle and also when covered by cloud. Nevertheless behavioral experiments in at least one species of amphipod sand hopper, *Talitrus saltator*, have been performed which indicate clock shifting the lunar clock results in change in orientation (Ugolini et al. 1999). However, at this point at least, there does not appear to be an example of an insect which uses time compensation to translate positional information from the moon to correct its course. Furthermore, unlike the circadian clock system which is very well described, we know very little of the circalunar clock in terms of mechanism, so there is much to learn in this field.

The moon is not the only nighttime celestial cue. Both the dung beetle (Dacke et al. 2013) and the large yellow underwing moth, *Noctua pronuba* (Sotthibandhu and Baker 1979), for example, can orient by the stars as well. Analysis of the tethered flight behavior of the moth showed no evidence that the night sky cues were time-compensated (Sotthibandhu and Baker 1979; Dreyer et al. 2018a). A final example of an insect which undergoes long-distance migration similar to the monarch but entirely at night is the bogong moth, *Agrotis infusa*, of Australia. This example would be ideal if it were shown to use a moon- or star-compensated compass and this has been investigated. However, the recent evidence suggests that it employs a terrestrial-based compass in the form of magnetic sense to make the 1000-m migration rather than nighttime celestial cues (Dreyer et al. 2018b).

16.5 Conclusions

Time-compensated celestial navigation has been observed in many insects. It is complex system with many components. Not only does the animal need a circadian, or perhaps circa-lunar, clock but also some way integrating the spatial and clock-based information to determine orientation and/or position. Several aspects of circadian clock-based information are used including but not exclusively (1) a clock to tell absolute time, (2) a clock to tell the organism when to feed, and (3) a clock to interpret the sun-compass information.

Much of what we know about the system so far comes from the work on two remarkable insects, the honey bee and the monarch butterfly. There are clear similarities and differences in these model insects. How insects perceive light directly from the sun and polarized light through the dorsal rim of the compound eye is well conserved across several insect orders. However, the antennal clocks of the monarch have not yet been described in other species like the bee.

The immediate future direction for study into the time compensation of the celestial compass is through the comparative anatomy of the brain and sensory systems in insects. This has begun and there is a lot to learn.

At this point in time, there does not appear to be evidence of the ability of insects to compensate for the movement of the celestial components of the night sky. It is, however, tempting to think there could be species such as moths which do fly large distances at night that might employ orientation behavior based on the night sky in a time-compensated way.

References

Bloch G (2010) The social clock of the honeybee. J Biol Rhythm 25:307–317. https://doi.org/10.1177/0748730410380149

Brady D, Saviane A, Cappellozza S, Sandrelli F (2021) The circadian clock in Lepidoptera. Front Physiol 12:776826. https://doi.org/10.3389/fphys.2021.776826

Cheeseman JF, Winnebeck EC, Millar CD, Kirkland LS, Sleigh J, Goodwin M et al (2012) General anesthesia alters time perception by phase shifting the circadian clock. Proc Natl Acad Sci USA 109:7061–7066. https://doi.org/10.1073/pnas.1201734109

Cheeseman JF, Millar CD, Greggers U, Lehmann K, Pawley MDM, Gallistel CR et al (2014) Way-finding in displaced clock-shifted bees proves bees use a cognitive map. Proc Natl Acad Sci USA 111:8949–8954. https://doi.org/10.1073/pnas.1408039111

Dacke M, Baird E, Byrne M, Scholtz CH, Warrant EJ (2013) Dung beetles use the milky way for orientation. Curr Biol 23:298–300. https://doi.org/10.1016/J.CUB.2012.12.034

Dreyer D, el Jundi B, Kishkinev D, Suchentrunk C, Campostrini L, Frost BJ et al (2018a) Evidence for a southward autumn migration of nocturnal noctuid moths in central Europe. J Exp Biol 221 (24):jeb179218. https://doi.org/10.1242/JEB.179218

Dreyer D, Frost B, Mouritsen H, Günther A, Green K, Whitehouse M et al (2018b) The earth's magnetic field and visual landmarks steer migratory flight behavior in the nocturnal Australian bogong moth. Curr Biol 28:2160–2166.e5. https://doi.org/10.1016/j.cub.2018.05.030

el Jundi B, Warrant EJ, Pfeiffer K, Dacke M (2018) Neuroarchitecture of the dung beetle central complex. J Comp Neurol 526:2612–2630. https://doi.org/10.1002/CNE.24520

Evangelista C, Kraft P, Dacke M, Labhart T, Srinivasan MV (2014) Honeybee navigation: critically examining the role of the polarization compass. Philos Trans R Soc B Biol Sci 369:20130037. https://doi.org/10.1098/rstb.2013.0037

Froy O, Gotter AL, Casselman AL, Reppert SM (2003) Illuminating the circadian clock in monarch butterfly migration. Science 300:1303–1305. https://doi.org/10.1126/science.1084874

Guerra PA, Merlin C, Gegear RJ, Reppert SM (2012) Discordant timing between antennae disrupts sun compass orientation in migratory monarch butterflies. Nat Commun 3:958. https://doi.org/10.1038/ncomms1965

Hardin PE (1994) Analysis of period mRNA cycling in *Drosophila* head and body tissues indicates that body oscillators behave differently from head oscillators. Mol Cell Biol 14:7211–7218. https://doi.org/10.1128/MCB.14.11.7211-7218.1994

Homberg U (2004) In search of the sky compass in the insect brain. Naturwissenschaften 91:199–208. https://doi.org/10.1007/s00114-004-0525-9

Labhart T, Baumann F, Bernard GD (2009) Specialized ommatidia of the polarization-sensitive dorsal rim area in the eye of monarch butterflies have non-functional reflecting tapeta. Cell Tissue Res 338:391–400. https://doi.org/10.1007/s00441-009-0886-7

Lebhardt F, Ronacher B (2014) Interactions of the polarization and the sun compass in path integration of desert ants. J Comp Physiol A 200:711–720. https://doi.org/10.1007/s00359-013-0871-1

Lindauer M (1961) Time-compensated sun orientation in bees. Cold Springs Harb Symp Quant Biol 25:371–377. https://doi.org/10.1101/SQB.1960.025.01.039

Linnaeus C (1751) Philosophia botanica. apud Godofr. Kiesewetter, Stockholm

Ludin NM, Rescan M, Cheeseman JF, Millar CD, Warman GR (2012) A honey bee (*Apis mellifera*) light phase response curve. Chronobiol Int 29:523–526. https://doi.org/10.3109/07420528.2012.667468

Ludin NM, Cheeseman JF, Merry AF, Millar CD, Warman GR (2016) The effects of the general anaesthetic isoflurane on the honey bee (*Apis mellifera*) circadian clock. Chronobiol Int 33:128–133. https://doi.org/10.3109/07420528.2015.1113987

Massy R, Hawkes WLS, Doyle T, Troscianko J, Menz MHM, Roberts NW et al (2021) Hoverflies use a time-compensated sun compass to orientate during autumn migration. Proc R Soc B 288: 20211805. https://doi.org/10.1098/rspb.2021.1805

Menzel R, Geiger K, Joerges J, Müller U, Chittka L (1998) Bees travel novel homeward routes by integrating separately acquired vector memories. Anim Behav 55:139–152. https://doi.org/10.1006/anbe.1997.0574

Menzel R, Greggers U, Smith A, Berger S, Brandt R, Brunke S et al (2005) Honey bees navigate according to a map-like spatial memory. Proc Natl Acad Sci USA 102:3040–3045. https://doi.org/10.1073/pnas.0408550102

Merlin C, Gegear RJ, Reppert SM (2009) Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies. Science 325:1700–1704. https://doi.org/10.1126/science.1176221

Miller NG, Wassenaar LI, Hobson KA, Norris D (2012) Migratory connectivity of the monarch butterfly (*Danaus plexippus*): patterns of spring re-colonization in eastern North America. PLoS One 7:e31891. https://doi.org/10.1371/JOURNAL.PONE.0031891

Moore D, Rankin MA (1993) Light and temperature entrainment of a locomotor rhythm in honeybees. Physiol Entomol 18:271–278. https://doi.org/10.1111/j.1365-3032.1993.tb00599.x

Papi F (1960) Orientation by night: the moon. Cold Spring Harb Symp Quant Biol 25:475–480. https://doi.org/10.1101/SQB.1960.025.01.049

Reppert SM, de Roode JC (2018) Demystifying monarch butterfly migration. Curr Biol 28:R1009–R1022. https://doi.org/10.1016/j.cub.2018.02.067

Reppert SM, Zhu H, White RH (2004) Polarized light helps monarch butterflies navigate. Curr Biol 14:155–158. https://doi.org/10.1016/J.CUB.2003.12.034

Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL, Williams IH et al (1996) Tracking bees with harmonic radar. Nature 379:29–30. https://doi.org/10.1038/379029b0

Rossel S, Wehner R, Lindauer M (1978) E-vector orientation in bees. J Comp Physiol 125:1–12. https://doi.org/10.1007/BF00656826

Rubin EB, Shemesh Y, Cohen M, Elgavish S, Robertson HM, Bloch G (2006) Molecular and phylogenetic analyses reveal mammalian-like clockwork in the honey bee (*Apis mellifera*) and shed new light on the molecular evolution of the circadian clock. Genome Res 16:1352–1365. http://www.genome.org/cgi/doi/10.1101/gr.5094806

Sotthibandhu S, Baker RR (1979) Celestial orientation by the large yellow underwing moth, *Noctua pronuba* L. Anim Behav 27:786–800. https://doi.org/10.1016/0003-3472(79)90015-0

Strauss R (2002) The central complex and the genetic dissection of locomotor behaviour. Curr Opin Neurobiol 12:633–638. https://doi.org/10.1016/S0959-4388(02)00385-9

Tyler Flockhart DT, Wassenaar LI, Martin TG, Hobson KA, Wunder MB, Norris DR (2013) Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. Proc R Soc B 280:20131087. https://doi.org/10.1098/RSPB.2013.1087

Tyler Flockhart DT, Fitz-gerald B, Brower LP, Derbyshire R, Altizer S et al (2017) Migration distance as a selective episode for wing morphology in a migratory insect. Mov Ecol 5:7. https://doi.org/10.1186/S40462-017-0098-9

Ugolini A, Melis C, Innocenti R, Tiribilli B, Castellini C (1999) Moon and sun compasses in sandhoppers rely on two separate chronometric mechanisms. Proc R Soc B 266:749–752. https://doi.org/10.1098/rspb.1999.0700

von Frisch K (1954) The dancing bees: an account of the life and senses of the honey bee. Methuen, London

Warren TL, Giraldo YM, Dickinson MH (2019) Celestial navigation in *Drosophila*. J Exp Biol 222 (Suppl. 1):jeb186148. https://doi.org/10.1242/jeb.186148

Yildirim E, Curtis R, Hwangbo D-S (2022) Roles of peripheral clocks: lessons from the fly. FEBS Lett 596:263–293. https://doi.org/10.1002/1873-3468.14251

Yuan Q, Metterville D, Briscoe AD, Reppert SM (2007) Insect cryptochromes: gene duplication and loss define diverse ways to construct insect circadian clocks. Mol Biol Evol 24:948–955. https://doi.org/10.1093/molbev/msm011