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Polarized Light and Polarization Vision in Animal Sciences
Second Edition

This book covers advances made since the 2004 Springer volume "Polarized Light in Animal Vision" edited by Horváth and Varjú, but also provides reviews and synopses of some areas. Part I examines polarization sensitivity across many animal taxa including vertebrates and invertebrates and details both terrestrial and aquatic life. Part II is devoted to the description of polarized light in nature and explores how the physics of light must be taken into account when understanding how polarized light is detected by the visual system. This includes underwater polarization due to scattering, polarization patterns reflected from freshwater bodies; polarization characteristics of forest canopies; normal and anomalous polarization patterns of the skies; skylight polarization transmitted through Snell's window and both linearly and circularly polarized signals produced by terrestrial and aquatic animals. This Part also examines polarized "light pollution" induced by anthropogenic factors such as reflection off asphalt surfaces, glass panes, car bodies, and other man-made structures that are now known to form ecological traps for polarotactic insects. Part III surveys some of the practical applications of polarization vision including polarization-based traps for biting insects, ground-based polarimetric cloud detectors and an historical examination of the navigational abilities of Viking seafarers using the sky polarization compass. The deterrent qualities of ungulate pelage to polarization-sensitive biting insects is also examined in this section.

Horváth, Ed.

Springer Series in Vision Research

Gábor Horváth *Editor*



Polarized Light and Polarization
Vision in Animal Sciences

Polarized Light and Polarization Vision in Animal Sciences

Second Edition

Life Sciences



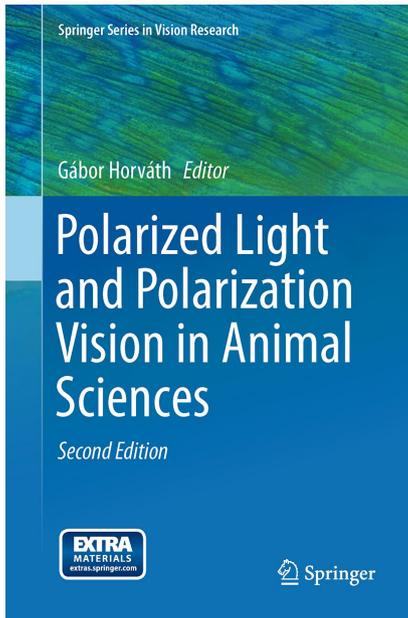
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G. Horváth (Ed.)

Polarized Light and Polarization Vision in Animal Sciences

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Polarized Light and Polarization Vision in Animal Sciences

Second Edition

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Preface to the Series

The Springer Series in Vision Research is a comprehensive update and overview of cutting-edge vision research exploring current breakthroughs at a conceptual level. It details the whole visual system from molecular processes to anatomy, physiology and behaviour and covers both invertebrate and vertebrate organisms from terrestrial to aquatic habitats. Each book in the series is aimed at all individuals with interests in vision including advanced graduate students, post-doctoral researchers, established vision scientists and clinical investigators. The series editors are N. Justin Marshall (Queensland Brain Institute, The University of Queensland, Australia) and Shaun P. Collin (Neuroecology Group within the School of Animal Biology and the Oceans Institute at The University of Western Australia).

This volume on polarisation vision is the second in the Springer Series in Vision Research and exemplifies the broad range and appeal we are aiming for in this series. It includes some aspects of review and collation of ideas but is largely concerned with recent advances in this field. Terrestrial and aquatic systems are considered, and both vertebrate and invertebrate visual systems are discussed. Invertebrate retinal design is, for reasons explained in some of the chapters, more conducive to polarisation vision, and as a result, most of the work contained in the volume is around our advancing knowledge in these taxa. Polarisation vision, or more strictly polarisation sensitivity, in animals is rapidly expanding to take up a level of importance alongside colour vision. We are learning that several species communicate with polarisation patterns for mate choice and that there may be an 'arms races' in the evolution of this visual modality, where predator and prey compete. Some animal groups, such as cephalopods and crustaceans may, in fact, glean more information from their environment using polarisation cues rather than colour cues. This is an exciting new world for us, as humans are largely insensitive to polarised light (but see Chaps. 14 and 25). We need filters, such as polarising

sunglasses, or polarisation-sensitive cameras to join the animals in their use of this property of light. Several of the chapters also touch on different technical engineering aspects, suggesting some of the ways that polarisation vision may be bio-inspirational for creating our own imaging systems.

Perth, Australia
Brisbane, Australia

Shaun P. Collin
N. Justin Marshall

Preface to the Volume

This book provides a much needed update on the Springer volume entitled *Polarized Light in Animal Vision—Polarization Patterns in Nature* (Horváth and Varjú 2004). Much has happened in this field in the last 10 years. The main goal of this volume is to summarise new results but also place these in the context of past work. Each of the chapters is written by relevant experts in each field and includes a thorough literature survey and explores future research directions. Literature prior to 2004 is also extensively cited here; however, we focus mainly on the results obtained in the last decade. Other useful reviews of the field that have appeared in this period include the special issue ‘New directions in biological research on polarized light’ in the *Philosophical Transactions of the Royal Society B* edited by Marshall et al. (2011) and the review by Wehner and Labhart (2006) on polarisation vision in the book entitled *Invertebrate Vision* edited by Warrant and Nilsson. The book of Können (1985) entitled *Polarized Light in Nature* and the booklet of Pye (2001) entitled *Polarised Light in Science and Nature* introduce the reader to the world of light polarisation and some of its applications.

This book is intended for anyone interested in animal vision, environmental optics, polarised light and polarisation sensitivity, including biologists, physiologists, ecologists and physicists. In particular, the recent advances in imaging polarimetry, which translate the parameters of polarisation into colour, allow the reader to understand the information within the polarisation patterns of the optical environment not directly accessible to the human visual system. Such instrumentation has also allowed polarisation research to advance rapidly, as we can now glimpse this previously hidden world.

Part I of the book deals with the polarisation vision in animals and humans. Chapter 1 gives an overview on the historical perspective of polarisation vision research. The subject of Chap. 2 is polarisation vision and orientation of ball-rolling dung beetles, which is governed partly by sky polarisation. Dung beetles, unlike most insect navigators, do not need to locate a stationary nest at the end of their foraging journey. Their main task is to roll their dung ball from the dung source as quickly and as far from potential competitors as possible. That is along a straight line to avoid the attack of other dung beetles that might steal the ready-made ball.

During their straight-line orientation, they rely on celestial compass cues to move along straight paths and can even achieve this at night using both moon and starlight. Chapter 3 summarises recent knowledge regarding polarisation vision in the most extensively studied groups such as ants, bees and wasps, using behavioural, anatomical and physiological approaches. Chapter 4 deals with polarisation-based behaviour, polarisation detectors and polarised-light processing in the brains of desert locusts, Monarch butterflies, crickets, houseflies and fruit flies. Polarisation sensitivity is also considered in the context of colour vision.

The topic of Chap. 5 is polarisation vision in aquatic insects. The recently discovered polarisation sundial of these insects explains why they fly at low and/or high sun elevations at different times of the day or evening. Polarisation-based water detection and positive polarotaxis (attraction to horizontally polarised light) in non-biting midges, dragonflies, mayflies and tabanid flies are surveyed. It is shown that the polarotaxis in egg-laying yellow fever mosquitoes is odour masked. Finally, it is demonstrated how negative polarotaxis in desert locusts can hinder flying over the sea.

Chapter 6 deals with the potential for circular polarisation vision of scarab beetles. The appearance of circular polarisation in the abiotic and biotic optical environment is surveyed, and the polarisation characteristics of circularly polarising scarab beetle cuticle, as measured by imaging polarimetry, are presented. Finally, behavioural evidence for the lack of circular polarisation sensitivity in four scarab species with a circularly polarising exocuticle—*Anomala dubia*, *A. vitis* (Coleoptera, Scarabaeidae, Rutelinae) and *Cetonia aurata*, *Protaetia cuprea* (Coleoptera, Scarabaeidae, Cetoniinae)—is presented. Previously suggested circular polarisation sensitivity in the scarab species *Chrysina gloriosa* is considered and criticised.

Chapter 7 is about the polarisation vision of crustaceans. It surveys the polarised light sources for crustaceans, the structural basis and neural processing of polarisation sensitivity and polarisation-based behaviours in crustaceans. Chapter 8 details polarisation sensitivity and its functions in cephalopods. Chapter 9 summarises the recent results about the structural and neural mechanisms of polarisation sensitivity in fishes, the functions of which are object recognition, navigation and camouflage. Chapter 10 is devoted to polarisation sensitivity in amphibians. It describes amphibian photoreception, the pineal complex, the use of polarisation sensitivity in orientation and the possible connection between polarisation sensitivity and magnetoreception. Chapter 11 surveys the photoreceptors and mechanisms underlying polarisation sensitivity in crocodiles, lizards and snakes. It also considers the possible use of polarisation sensitivity for orientation in reptilian migration. Chapter 12 examines polarisation vision in birds. It deals with avian celestial orientation and migration, the importance of skylight polarisation in avian compass calibration and the behavioural evidence for polarisation sensitivity in birds.

Chapter 13 examines some of the possible interactions between colour vision and polarisation vision. It is shown how polarisational false colours could help

visual discrimination between smooth (shiny) and rough (matte) leaf surfaces but cannot unambiguously code surface orientation. This chapter also demonstrates how uniformly polarisation-sensitive retinas can perceive polarisation-induced false colours. Chapter 14 reviews the available knowledge of human polarisation sensitivity. It deals with Haidinger's and Boehm's brushes and the potential mechanisms underlying these visual phenomena. Some applications of human polarisation sensitivity are also considered.

Part II of the book concerns mainly descriptions of the physics of polarised light in nature but with specific reference to animal polarisation vision. Chapter 15 is about underwater polarisation induced by scattering hydrosols. It considers the sources of polarised light in the ocean, the transmission (refraction) of polarised light at the air–water interface, the attenuation of polarisation by scattering and absorption, the effect of water turbidity on polarisation, measurements and modelling of polarisation in clear and turbid waters and the polarisation-based response of animals living in turbid waters.

Chapter 16 presents polarisation patterns of freshwater bodies and their likely role in guiding water detection in aquatic insects. Polarisation visibility of water surfaces is also measured and calculated as a function of the solar elevation angle, which explains why water-seeking polarotactic aquatic insects might fly at low and/or high sun elevations.

Chapter 17 presents the polarisation characteristics of forest canopies and shows how the azimuth of the foliage-occluded sun can be determined from the pattern of the direction of polarisation of sunlit foliage canopies. Why dusk-active cockchafers sense downwelling polarisation in the green part of the spectrum is also explored.

Chapter 18 demonstrates the robustness of the celestial E-vector pattern, which is the basis of orientation of many polarisation-sensitive animals and the basis for hypothetical sky-polarimetric Viking navigation. It is shown how well the Rayleigh model describes the pattern of the angle of polarisation of clear and cloudy skies. The polarisation characteristics of foggy, partly cloudy, overcast, twilight and eclipsed skies are also revealed including fogbows and the 'water-skies' above arctic open waters. The anomalous sky polarisation due to forest fire smoke is also presented as a way of explaining why some polarisation-sensitive insects disorient under smoky skies. Similarly, the changed sky polarisation during total solar eclipses is discussed with respect to its influence on the orientation of honeybees. Finally, it is shown how skylight polarisation is transmitted through Snell's window on flat water surfaces.

Chapter 19 surveys the linearly and circularly polarised signals from terrestrial and aquatic animals, such as butterflies, beetles, flies, dragonflies, spiders, fiddler crabs, birds, stomatopods, cephalopods and fishes.

Chapter 20 is devoted to anthropogenic polarisation and polarised light pollution (PLP), which induces polarised ecological traps for polarotactic insects, such as water beetles, aquatic bugs, dragonflies, mayflies, caddisflies and stoneflies. It is shown that the maladaptive attractiveness of solar panels to polarotactic insects can

be reduced by surface fragmentation due to white grid patterns. The PLP of asphalt surfaces, black horizontal agricultural plastic sheets, glass surfaces, shiny black gravestones and dark car bodies is considered in detail. The insectivorous animals (birds, spiders and bats) lured by the polarotactic insects attracted to polarised-light-polluting artificial surfaces are also surveyed. The questions of why vertical glass panes attract polarotactic insects and why these insects remain on such glass surfaces after landing are answered. It is shown how the vertically polarised mirror image of bridges on the water surface can deceive flying mayflies and what are the ecological consequences. Finally, it is explained why strongly polarising black and burnt stubble fields do not attract polarotactic aquatic insects.

Part III of the book summarises several practical applications of polarisation vision and patterns. Chapter 21 surveys existing knowledge about polarisation as a guiding cue for oviposition in non-biting midges (chironomids) and mosquitoes. Chapter 22 presents recent research about linearly polarised light and its use as a guiding cue for water detection and host finding in tabanid flies. It is shown that bright animal coats are only weakly attractive to polarotactic tabanids. A new explanation of the evolutionary advantage of zebra stripes and spotty fur patterns is also presented. We show that stripes and spots make ungulates unattractive to host-seeking female tabanid flies, and stripes disrupt the odour attractiveness of host animals to tabanids.

Chapter 23 surveys novel polarisation-based insect traps. Polarisation chironomid traps are initially considered, followed by three different polarisation tabanid traps, which are presented as a new technique of horsefly control to capture host- and water-seeking tabanids.

Chapter 24 is devoted to polarisation cloud detection with imaging polarimetry. It reviews the full-sky photometric imagers and photometric cloud detection algorithms and examines the airborne PARASOL and POLDER polarisation cloud detectors. The applications of polarisation cloud detection for the determination of cloud distribution, cloud-base height, solar forecasting, aerosol characterisation, Viking navigation and the study of animal orientation are also presented.

Chapter 25 examines the possibility and the atmospheric prerequisites of hypothetical sky-polarimetric Viking navigation. Modern sky-polarimetric navigation, the medieval Norse sailing routes, the climatic conditions in the Viking era and the presumed nature of the enigmatic Viking sunstone are initially considered. Then, the possibility of sky-polarimetric Viking navigation under various weather conditions is discussed. The hypothesised Viking solar navigation instruments (horizon board, Viking sun compass, twilight board, medieval twilight navigation toolkit, sun-shadow board with a sundial and millennium-old carved schedule) are all surveyed. Some atmospheric-optical phenomena providing alternative navigation cues are also summarised.

Additional photographs, polarisation patterns, tables, graphs and video films are provided electronically.

We dedicate this book to the late Professors Talbot H. Waterman and Dezso Varju and to Professor Rudiger Wehner on the occasion of his 75th birthday.

The oeuvre of Waterman was appreciated recently by Cronin, Marshall and Wehling (2011). Dezső Varjú, the mentor of the editor of this volume, Gábor Horváth, and one of the authors of the book *Polarized Light in Animal Vision—Polarization Patterns in Nature*, unfortunately died in August 2013. Finally, we greet Professor Rudiger Wehner on the occasion of his 75th birthday.

Budapest, Hungary
Perth, Australia
Brisbane, Australia
January 2014

Gábor Horváth
Shaun Collin
Justin Marshall

References

- Cronin TW, Marshall J, Wehling MF (2011) Dedication: Talbot H. Waterman. *Philos Trans R Soc B* 366: 617–618
- Horváth G, Varjú D (2004) Polarized light in animal vision—polarization patterns in nature. Springer, Heidelberg, p 447
- Können GP (1985) Polarized light in nature. Cambridge University Press, Cambridge
- Marshall J, Cronin T, Wehling MF (2011) New directions in the detection of polarized light. *Philos Trans R Soc B* 366:615–616
- Pye JD (2001) Polarised light in science and nature. Institute of Physics Publishing, London
- Wehner R, Labhart T (2006) Polarization vision. In: EJ Warrant, DE Nilsson (eds) *Invertebrate vision*. Cambridge University Press, Cambridge, pp 291–348

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Budapest, Hungary

Gábor Horváth

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Part I
Polarization Vision in Animals
and Humans

Chapter 1

Polarization Vision: A Discovery Story

Rüdiger Wehner

Abstract During the last half a century, polarization vision has become a flourishing field of multidisciplinary research in neuroethology and sensory ecology spanning the full methodological range from membrane biophysics and photo-receptor optics to behavioural analyses in the laboratory as well as in the field. It comprises a multitude of behavioural tasks accomplished by various groups of animals in both terrestrial and aquatic environments. The fact that this richness of behaviours mediated by naturally occurring polarized light has come to the fore only rather recently is certainly due to our own inability to perceive these polarized light phenomena without the aid of special optical devices. While in the present book the chapters are arranged according to animal taxa, so that questions are posed and arguments are presented within the branching pattern of the phylogenetic tree, this introductory chapter retraces the time arrow of discovery. For example, immediately after Karl von Frisch had demonstrated that bees can perceive the polarization of skylight, the 1950s were dominated by the search for the polarization analyser in arthropod eyes. The 1970s and early 1980s became high noon for the behavioural experimental analysis of the bee's and ant's skylight compass, followed in the 1990s by the advent of forceful neurobiological investigations of the polarization vision network residing in the insect (especially locust) brain. At about the same time polarized reflections from water surfaces were recognized as cues used by flying aquatic insects on dispersal. In the late 1980s vertebrates, mainly fish and birds, appeared on the polarization vision scene as well. Since the turn of the millennium long-standing studies of various aspects of underwater polarization vision have received an enormous boost, especially by including small-field, close-range polarization signalling, and now advance at an ever increasing pace. Most recently, with new technologies at hand, the interest in the basic mechanisms of polarization sensitivity comes full circle when now a closer and

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more sophisticated look can be taken at the molecular mechanisms of how dichroism is generated within the photoreceptor membrane.

1.1 Introduction

The story of polarization vision started with an observation that appeared mysterious at the time. In 1914 Felix Santschi showed that ants were able to maintain their straight homeward courses even if they could see only a patch of unobscured sky offered to them via an open-topped cardboard cylinder. While this cylinder was carried along with the moving ant, it continuously screened off the sun. Even though Santschi tested only a few specimens of ants belonging to some *Messor*, *Monomorium*, *Cataglyphis* and *Camponotus* species, the results were clear-cut: The sun-free sky had presented the ants with sufficient compass information. Unaware of the phenomenon of polarized light, Santschi hypothesized that light intensity gradients perceived by the ants within the circular skylight window might have provided the decisive cues, or that the ants endowed with heavily shielded small-field light detectors (ommatidia) in their compound eyes might have been able to see the stars in the daytime sky, ‘just as Aristotle had surmised that a person sitting at the bottom of a deep well could perceive the stars in the blue diurnal sky’. Even though Santschi did not draw the right conclusion from his startling discovery, which he published only many years later (Santschi 1923), he was the first to show that insects could derive compass information not only from the direct light of the sun but also from the scattered light in the sky (for a biographical account on Felix Santschi published on the occasion of the 50th anniversary of his death, see Wehner 1990).

Several decades later, in 1947, Karl von Frisch not knowing of Santschi’s early account did an experiment in bees that was almost identical to the one Santschi had performed in ants, with the only difference that he studied the bees while they were performing their recruitment dances in the hive rather than their foraging journeys in the field. When he provided the dancing bees with a small patch of cloudless sky, he got the same result and asked the same question which Santschi had pondered on, but in contrast to Santschi—and advised by the physicist Hans Benndorf—he checked for polarized light. Next summer he did the crucial experiment. He placed one of the polaroid sheets which had just become commercially available above a bee dancing on a horizontal comb. As he rotated the polarizer, the bee changed the direction of its dance accordingly (von Frisch 1949). On the one hand, this discovery stimulated quite a number of scientists to place polarizing sheets above walking insects and other arthropods and to demonstrate that the animals changed their courses when the polarizer was rotated (e.g. ants: Vowles 1950; Carthy 1951; Jander 1957; flies: Wellington 1953; beetles: Papi 1955a; amphipod crustaceans: Pardi and Papi 1952; spiders: Papi 1955b; Görner 1958). On the other hand,

Chapter 2

Polarized Light Orientation in Ball-Rolling Dung Beetles

Marie Dacke

Abstract Many dung beetles, unlike most insect navigators, do not need to locate a stationary nest at the end of their foraging journey. This makes the nature of their orientation task fundamentally different, and in the case of straight-line orientation, the beetles appear to rely single-handedly on celestial compass cues to move along straight paths. With a focus on the sky, diurnal dung beetles rely on the sun and the skylight cues that span the entire sky. These cues include the linear polarization pattern of skylight. As day turns to night, crepuscular and nocturnal dung beetles start to fly at around sunset. At this time, the full sky is polarized in one single direction, and the ball-rolling beetles can be observed to turn sharply when rolling under a linear polarizer placed with its E-vector oriented 90° to that of skylight. When the moon has risen, the beetles continue to orient along straight paths well after sunset, guided by the celestial polarization pattern created by the scattered moonlight. The intensity of this relatively dim polarization pattern will gradually decline as the moon wanes. Remarkably, even the extremely dim celestial polarization pattern formed around a crescent moon is sufficient to guide the nocturnal beetles along straight paths. Moreover, straight-line orientation on these dark nights is performed with the same precision and speed as in dung beetles orienting under the much brighter polarization pattern of the sun or full moon. So strong is their desire to roll their balls of dung that nocturnal beetles can be made to roll at day and diurnal beetles can be compelled to roll in the middle of the night. This incredible flexibility opens up the possibility to perform a new set of experiments directed towards an understanding of how celestial compasses have been adapted to the visual environment in which the insect is normally active.

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Chapter 3

Polarisation Vision in Ants, Bees and Wasps

Jochen Zeil, Willi A. Ribi, and Ajay Narendra

Abstract We review here what is known from behavioural, anatomical and physiological studies about polarisation sensitivity in the hymenopteran insect groups of ants, wasps and bees. We briefly summarise the behavioural evidence for the use of polarised skylight in orientation and navigation, including some lesser known or less accessible older work, and then review our state of knowledge of the polarisation sensitivity and the arrangement of photoreceptors in compound eyes and in ocelli. We note in particular how little we know about the role of ocelli in polarisation vision.

3.1 Introduction

As central place foragers, hymenopteran insects, such as ants, bees and wasps, routinely return home to their nest, hive or burrow at the end of each foraging trip. To achieve this, they employ two distinct navigational mechanisms: landmark guidance and path integration. The degree to which insects rely on landmark guidance or path integration depends on the navigational information content of their specific habitat (e.g. Cheung et al. 2012). In landmark-poor, featureless environments, such as salt pans, the desert ants of the genus *Cataglyphis* have to rely exclusively on path integration (Wehner and Wehner 1986). During path integration, insects monitor two components of their foraging path in order to

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Chapter 4

Polarized-Light Processing in Insect Brains: Recent Insights from the Desert Locust, the Monarch Butterfly, the Cricket, and the Fruit Fly

Stanley Heinze

Abstract The pattern of linearly polarized light in the sky can be used for orientation behavior by many insects. Although such behavioral responses have been well described in bees and ants over several decades, until recently it remained largely elusive how polarized-light information is processed in the insect brain. However, over the last decade, substantial advances in understanding polarized-light processing have been made, based on behavioral, electrophysiological, and anatomical data. Particularly, progress was made in the desert locust, but based on comparative work in the field cricket, the monarch butterfly, and the fruit fly broader conclusions about how polarized-light information is encoded in the insect brain in general begin to emerge. After polarized light is detected by photoreceptors of specialized parts of the compound eye, this information passes through the optic lobe, the anterior optic tubercle, and the central complex. In these brain regions, detailed neural responses to polarized light have been characterized in a large set of anatomically defined neurons that together comprise the polarization vision network. This work has begun to unravel how polarized light is integrated with unpolarized light, and how response characteristics of involved neurons are modulated in context-dependent ways. Eventually, all skylight cues appear to be combined to generate a neural representation of azimuthal space around the animal in the central complex of the brain, which could be used as a basis for directed behavior. Polarized-light information is likely contributing to such a representation in many insects and thus this modality could be crucial for illuminating how the insect brain in general encodes the position of the animal in space, a task that all animal brains have to master.

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Chapter 5

Polarization Vision of Aquatic Insects

Gábor Horváth and Zoltán Csabai

Abstract In this chapter we show that primary aquatic insects fly predominantly in mid-morning, and/or around noon and/or at nightfall. We describe the different types of their diurnal flight activity rhythm characterised by peaks at low and/or high solar elevations. We present here experimental evidence that the polarization visibility $Q(\theta)$ of water surfaces is always maximal at the lowest (dawn and dusk) and highest (noon) angles of solar elevation θ for dark waters, while $Q(\theta)$ is maximal at dawn and dusk (low solar elevations) for bright waters both under clear and partly cloudy skies. The θ -dependent reflection-polarization patterns, combined with an appropriate air temperature, clearly explain why polarotactic aquatic insects disperse to new habitats in mid-morning, and/or around noon and/or at dusk. This phenomenon is called the “polarization sundial” of dispersing aquatic insects. We also show that non-biting midges (Chironomidae, Diptera) are positively polarotactic and like many other aquatic insects, their females are attracted to horizontally polarized light. We present here measured thresholds (i.e., the minimum degrees of linear polarization of reflected light that can elicit positive polarotaxis) of the ventral polarization sensitivity in mayflies, dragonflies and tabanid flies. The mayflies *Palingenia longicauda* swarm exclusively over the river surface; thus, they need not search for water. It could be assumed that this species is not polarotactic. We show here that also *P. longicauda* has positive

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polarotaxis, which, however, can be observed only when the animals are displaced from the water and then released above artificial test surfaces. *P. longicauda* is the first species in which polarotactic water detection was demonstrated albeit it never leaves the water surface, and thus, a polarotactic water detection seems unnecessary for it. The yellow fever mosquito, *Aedes aegypti*, has been thought to locate its breeding habitats exclusively by chemical cues. We demonstrate here that horizontally polarized light can also attract ovipositing *Ae. aegypti* females when they are deprived of chemical cues. *Aedes aegypti* is the first known water-associated species in which polarotaxis exists, but does not play a dominant role in locating water bodies and can be constrained in the presence of chemical cues. Finally, we deal with the negative polarotaxis in the desert locust, *Schistocerca gregaria*, the ventral eye region of which detects the horizontally polarized water-reflected light, and thus can navigate towards or away from large water surfaces.

5.1 The Polarization Sundial of Aquatic Insects: Why Do Water Insects Fly at Low and/or High Sun Elevations?

The seasonal and diel flight activity of aquatic insects (Fernando 1958; Popham 1964; Zalom et al. 1990; Behr 1993) and the influence of environmental variables on their dispersal flight (Landin 1968; Nilsson and Svensson 1992; Weigelhofer et al. 1992) have been studied by light trapping at night, when insect phototaxis dominates (Nowinszky 2003). However, daily changes in the flight activity of aquatic insects cannot be assessed by 24-h light trapping, because the attraction of light traps to insects is considerably reduced by day due to the higher ambient light intensity. While suction traps may be of use for monitoring small, weakly flying insects, assessment of the diel pattern of a wide range of aquatic insects needs a method that is similarly efficient by day and night.

Both primary (where both adults and larvae are aquatic) and secondary (where only the larvae live in water) aquatic insects recognise their habitat by means of the horizontal polarization of light reflected from the water surface (Schwind 1991, 1995; Horváth and Varjú 2004). The higher the degree of linear polarization of reflected light, the more attractive is a reflecting surface to aquatic insects. Thus, a horizontal shiny black plastic sheet is an ideal trap for aquatic insects, because it always polarizes the reflected light strongly and horizontally (Horváth and Varjú 2004). Csabai et al. (2006) observed in the field that in mid-morning, near noon and at dusk the rattling noise caused by thousands of primary aquatic insects crashing into such shiny black plastic sheets created the impression of an intense “rain” of aquatic insects.

Csabai et al. (2006) explored the diel flight activity patterns of primary aquatic insects and assessed the most important factors governing their daily activity rhythm. Using aspirators and nets, they captured aquatic insects landing on shiny black plastic sheets (9 m × 3 m) laid on the ground in a Hungarian wetland from

Chapter 6

Circular Polarization Vision of Scarab Beetles

Gábor Horváth, Miklós Blahó, Ádám Egri, Ramón Hegedüs,
and Győző Szél

Abstract In this chapter the occurrence of circularly polarized (CP) light in nature (both in the abiotic and biotic optical environment) is surveyed. We deal with the reason and the possible adaptive significance of CP light reflected from the exocuticle of many beetle species belonging to the Scarabaeoidea. This unique feature of the insect exocuticle seems to have evolved only in scarabaeoids. The imaging polarimetry of circularly polarizing scarab beetles and its results are reviewed. The alleged CP sensitivity in *Chrysina gloriosa* scarabs is briefly discussed. Finally, the experimental evidence for the lack of CP vision in the scarab species *Anomala dubia*, *A. vitis* (Coleoptera, Scarabaeidae, Rutelinae), *Cetonia aurata*, and *Protaetia cuprea* (Coleoptera, Scarabaeidae, Cetoniinae) with circularly polarizing exocuticle is presented.

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Chapter 7

Polarisation Vision of Crustaceans

Justin Marshall and Thomas Cronin

Abstract The photoreceptor design of crustaceans, often containing regular arrays of intrinsically polarisation-sensitive microvilli, has had a profound influence on the visual biology of this subphylum. The land-based arthropods (insects and arachnids) also construct photoreceptors from ordered microvilli; however while in many species polarisation sensitivity results, a general overview of these groups suggests a major difference. With notable exceptions discussed in this chapter, many crustaceans seem to have “invested” in polarisation vision more than colour vision. This may be the result of the relatively limited spectral environment found in much of the aquatic world or due to the information content in polarisation being as useful as colour. The terrestrial arthropods are generally trichromatic with specialised visual areas for polarisation-specific tasks. Crustaceans are mostly di- or monochromats and most of their visual field displays polarisation sensitivity. This chapter examines the anatomical, neurophysiological and behavioural evidence for polarisation vision in a few of the many crustacean groups. Common themes are emerging such as the possession of vertical and horizontal E-vector sensitivity. This two-channel orthogonality is carried through the neural processing of information and reflected in behavioural capability. A few groups such as the stomatopods possess both complex colour and polarisation sensitivity, and particularly in this group, the evolutionary pressures responsible are centred on unique

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polarisation signalling structures used in social interaction. Other functions of polarisation sensitivity in crustaceans include navigation, phototaxis and potentially increasing visual range through de-hazing in a turbid world.

7.1 Introduction

Crustaceans are numerous, with more than 67,000 known species exhibiting a great variety of body plans from metre long lobsters and crabs to tiny, sub-millimetre planktonic organisms. They inhabit all of the available aquatic niches from lakes, rivers and coastlines to ocean depths beyond 7,000 m. A few, like the oniscid isopods, woodlice or pill-bugs, for example, have truly ventured onto land, while littoral species, such as mud-flat dwelling fiddler crabs or beach-bound ghost crabs, are best thought of as conducting vision mostly in air rather than water. The physical and optical challenges of living in and around water have driven the evolution of a great variety of eye designs, as Mike Land (1984) notes: “*Although one usually thinks of the Crustacea as linked to the insects by the presence of an exoskeleton and compound eyes, there is actually a much greater diversity of eye types in the Crustacea than the insects or any other invertebrate group.*”

Paired, lateral apposition or superposition compound eyes are found in most crustacean groups, being stalked and mobile in the decapods, euphausiids and mysids, and sessile or essentially embedded in the heads of amphipods and isopods. The copepods possess single element “simple eyes” with a variety of, in fact rather complex, lens arrangements and others like the ostracod *Gigantocypris* have even branched out into reflective optics (Land 1984; Land and Nilsson 2012). This diversity is largely centred around modifications in optical design and it is perhaps surprising to find that beneath the dioptrics the construction of crustacean photoreceptors and their optic neuropils is relatively conservative (Land 1984; Strausfeld and Nässel 1981; Marshall et al. 1999a). Within each ommatidium, most possess a central fused rhabdom constructed from eight cells, very often arranged with a distal cell named “R8” in a tier above the remaining seven “R1–R7” cells (Fig. 7.1). The smaller members of the subphylum, particularly the copepod and related lineages, may diverge from this typical photoreceptor arrangement and, in truth, there are many crustacean eyes that we know little about.

In common with many arthropods, crustacean rhabdoms are constructed from microvilli and are therefore inherently sensitive to the direction of the electric vector (E-vector henceforward) of linearly polarised light, which is maximally absorbed if the E-vector is parallel to the long axis of the membrane tubules (Fig. 7.1 and Chap. 4; Snyder 1973). With a few exceptions, the crustaceans investigated so far are less interested in colour than their aquatic neighbours, the fish. Many possess one or at most two visual pigments, and, paralleling the also largely colour-blind cephalopods, crustaceans have developed polarisation vision more than colour sense (Marshall and Messenger 1996; Marshall et al. 1999a, b).

Chapter 8

Polarization Vision in Cephalopods

Nadav Shashar

Abstract Polarization sensitivity, namely sensitivity to linearly polarized light, has been known in cephalopods for over 50 years. So far our neurological understanding of this polarization sensitivity has remained at the level of the retina, and our knowledge of how polarization information is processed is lacking. However, when examining function, a range of tasks in which polarization vision plays a role have been identified. These include, but are not limited to, detailed examination of the environment, target (including both prey and predator) detection and recognition, short range navigation, image stabilization and most likely communication. Neurological examination of the processing of polarization information and its integration with other sensory inputs on the one hand, along with a physical understanding of the propagation of the polarization signals under various conditions, are needed for a better understanding of the function of polarization vision in the lives of cephalopods.

8.1 Introduction

Polarization sensitivity, or sensitivity to the E-vector orientation of linearly polarized light, was first discovered in cephalopods half a century ago by Moody and Parriss (1960, 1961), who were able to train octopuses to prefer light of a given E-vector orientation over another. This finding was reached just 12 years after von Frisch (1949) reported the existence and use of polarization sensitivity in honeybees. However, over time the direction, in which the study and our understanding of

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Chapter 9

Polarisation Vision of Fishes

Nicholas William Roberts

Abstract Since the first edition of this book, our understanding of vertebrate polarisation vision has increased significantly. Much of this work has concentrated on a number of species of fish, and the aim of this updated chapter is to highlight some of the new discoveries and new directions this area of animal polarisation vision has seen. Three distinctive research directions stand out and form the main sections of this chapter update: (1) mechanisms of polarisation sensitivity, (2) neural processing of polarisation information and (3) behavioural evidence of polarisation vision and associated visual ecology. The new additions to this chapter bring together work on molecular mechanisms of dichroism in cone photoreceptors and new evidence that questions the original measures of the levels of diffusion of the visual pigment in outer segment membranes. Advances in our understanding of how intra-retinal feedback influences the neural coding of polarisation information are also considered. Finally, several studies into the ability of fish to react to dynamic polarisation-based stimuli are also presented in conjunction with evidence that some fish also manipulate the degree of polarisation in the light that they reflect. However, it is still clear that this area of research lacks depth in much of the evidence, leaving many questions still wide open for future studies.

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Chapter 10

Polarization Sensitivity in Amphibians

Victor Benno Meyer-Rochow

Abstract Polarization sensitivity (PS) in amphibians has been examined in some species of anurans and urodelans. Gymnophiones, on account of their tiny eyes and fossorial or aquatic lifestyles, are considered unlikely candidates for PS. Some anura and urodela have been shown to detect the direction of polarization with photoreceptors of the pineal organ rather than their lateral eyes. An ordered array of light-absorbing visual molecules is paramount for PS, but an ordered array of radical pairs generated through photo-induced electron transfer is also essential for magnetoreception, which suggests that there is some interaction between the two senses. An anatomical requirement for PS is a constant and characteristic orientation of the photoreceptor's disc membranes. A closer look at ultrastructural modifications in different retinal regions of species deemed polarization sensitive seems warranted. Polarization sensitivity may help to relocate breeding sites in philotropic species and to improve visibility of prey in predatory larval and adult urodeles plus those few anurans that hunt under water. Furthermore, it could possibly be of assistance in separating overlapping shadows and play a role during courtship in species with distinct sexually dimorphic colouration.

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Chapter 11

Polarization Sensitivity in Reptiles

Victor Benno Meyer-Rochow

Abstract Somewhat questionable evidence in support of reptilian polarization sensitivity (PS) has come from field and laboratory observations on the behaviour of a few species of marine and freshwater turtles. More convincing are conclusions based on PS-aided orientation in the lizards *Uma notata*, *Tiliqua rugosa* and *Podarcis sicula*. It is suggested that submersed hunters like, for instance, sea snakes ought to be included in examinations for PS since contrast enhancement by PS under water could bestow some benefits to them during food procurement. Courtship displays in certain species of lizards could also contain signals for which the presence of PS would be advantageous, but as yet polarization signals have not been demonstrated in any species. Results based on electrophysiological recordings to demonstrate PS in photoreceptors of the lateral eyes or pineal organs are scant and a connection between PS and magnetoreception is regarded as likely.

11.1 Introduction

Reptiles represent a class of amniotic vertebrates. Most taxonomists distinguish four reptilian orders, namely the Crocodylia, the Sphenodontia, the Squamata (which include the worm-like amphisbaenids, the lizards and the snakes) and the Testudines (turtles and tortoises). Being ectothermic, reptiles generally cannot tolerate cold climates or, in case we deal with aquatic species, cold water and are therefore poorly represented in regions of high latitude or altitude. The few species that do manage to

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Chapter 12

The Ecology of Polarisation Vision in Birds

Susanne Åkesson

Abstract Birds have evolved a mobile lifestyle in which vision is of major importance when controlling movements, avoiding predators, finding food and selecting mates. Birds have extraordinary colour vision and have been suggested to perceive the linear polarisation of light. Behavioural experiments support this idea, but still the exact physiological mechanism involved is not known. The twilight period, when the sun is near the horizon at sunrise and sunset, is of crucial importance for migrating birds. At this time millions of songbirds initiate migration when the degree of skylight polarisation is the highest and all compass cues are visible in a short range of time. The biological compasses are based on information from the stars, the sun and the related pattern of skylight polarisation, as well as the geomagnetic field, and may be recalibrated relative to each other. The celestial polarisation pattern near the horizon has been shown to be used in the recalibration of the magnetic compass, but conflicting results have been obtained in experiments with different bird species. For the future we should understand the physiological mechanisms of avian polarisation vision and investigate the interrelationship and calibrations between the different compasses, including the one based on the pattern of skylight polarisation. A conditioning paradigm may be fruitful, but the risk of introducing optical artefacts needs to be minimised in behavioural experiments, as well as in cage experiments with migratory birds.

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Chapter 13

Polarization-Induced False Colours

Gábor Horváth and Ramón Hegedüs

Abstract If the photoreceptors of a colour vision system are polarization sensitive, the system detects polarization-induced false colours. It has been hypothesized that egg-laying *Papilio* butterflies could use these polarizational colours as a cue to detect leaf orientation and to discriminate between shiny and matte leaves. In this chapter, we show that a shiny green surface with any orientation can possess almost any polarizational false colour under any illumination condition (for different solar elevations and directions of view with respect to the solar azimuth as well as for sunlit and shady circumstances under clear skies). Consequently, polarizational colours cannot unambiguously code surface orientation. Polarization sensitivity is even disadvantageous for the detection of surface orientation by means of colours. On the other hand, the colour changes due to retinal rotation can be significantly larger for shiny surfaces than for matte ones. Thus, polarizational colours could help polarization-dependent colour vision systems to discriminate between shiny and matte surfaces. Earlier it has been believed that a uniformly polarization-sensitive retina (UPSR)—in which receptors of all spectral types have the same polarization sensitivity ratio and microvilli direction—cannot detect polarization-induced false colours. Here we show that, contrary to this belief, a colour vision

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based on a UPSR is subject to polarization-related artefacts, because both the degree and the angle of polarization of light reflected from natural surfaces depend on wavelength. These findings are of general importance for polarization-dependent colour vision systems.

13.1 Polarizational False Colours and Visual Discrimination Between Smooth (Shiny) and Rough (Matte) Leaf Surfaces

According to Wehner and Bernard (1993), the interference of colour vision and polarization vision has to be avoided; otherwise polarizational (i.e. polarization-induced) false colours are induced if both visual qualities are mixed. They showed that the function of the photoreceptor twist in the eyes of honeybees (*Apis mellifera*) is to avoid the polarizational false colours of leaves and flower petals reflecting partially linearly polarized light. The degree and direction of polarization of plant-reflected light depend strongly on the roughness and orientation of the plant surface (Horváth et al. 2002). For flower visitors these reflection-polarization characteristics could cause serious problems, because the photopigments underlying colour vision are in photoreceptors with different microvilli orientations. Thus, each receptor gives a signal that depends not only on the intensity and the wavelength but also on the direction and the degree of polarization of plant-reflected light. If the receptors of a colour vision system are polarization sensitive, the system generates false colours that may obscure the real colours determined by the spectral characteristics of flowers and leaves and perceived by polarization-insensitive (-blind) colour vision systems.

Kelber (1999) and Kelber et al. (2001) demonstrated that *Papilio* butterflies perceive polarization-induced false colours if their photoreceptors are stimulated by artificially strongly polarized and unnaturally quasi-monochromatic light under laboratory conditions, because their colour-sensitive receptors are weakly polarization sensitive. However, polarizational false colours have been believed to be disadvantageous, and are usually eliminated in insect eyes by a proper photoreceptor twist (Wehner et al. 1975), or by random microvilli orientations, or by colour blindness (monochromacy) of the polarization-sensitive receptors (Wehner and Bernard 1993). Thus, there may be some selective advantages to *Papilio* butterflies that have retained the polarization sensitivity of their colour vision (Kelber 1999; Kelber et al. 2001). Female *Papilio* butterflies lay eggs on the shiny, smooth leaves of plants in the Rutaceae or *Citrus* family. Kelber and her collaborators suggested that the polarizational false colours perceived by these butterflies may be relevant during oviposition.

Kelber (1999) hypothesized that horizontal leaves could be more attractive than vertical or tilted leaves to an ovipositing butterfly, because the former could provide a better landing for the butterfly and offer more protection for the eggs and young larvae. The reflection-polarization characteristics of plant surfaces depend strongly

Chapter 14

Human Polarization Sensitivity

Juliette McGregor, Shelby Temple, and Gábor Horváth

Abstract Humans can detect the E-vector of incident polarized light using a subtle, transient visual phenomenon known as Haidinger's brush. The effect is a result of the human macula having the properties of a radial analyser with peak absorption at 460 nm. A number of mechanisms, each capable of generating radial diattenuation, have been proposed: (1) oblique light incident on cone outer segments, (2) form dichroism in the Henle fibre layer (the photoreceptor axons) and (3) a perpendicular arrangement of dichroic carotenoid pigments with respect to the radially oriented Henle fibres. A close correlation between the dichroic ratio of the macula and the optical density spectrum of liposome-bound lutein and zeaxanthin provides strong evidence that macular pigment plays a key role. Corneal birefringence can affect the contrast and perceived angle of the brush, together with the appearance of the phenomenon in circularly polarized light. When the retina is photographed between crossed polarizers, a brush-like pattern is observed; this is a result of the birefringence of the Henle fibre layer and cornea and is distinct from the radial diattenuation that generates Haidinger's brush. A secondary entoptic phenomenon that allows humans to detect the orientation of polarized light was described by Gundo von Boehm. Boehm's brush is only visible when a polarized

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light source rotates in the peripheral visual field against a dark background and results from light scattering off axis into the photoreceptors. Both phenomena allow for the detection of polarized light by the unaided human eye; however, there is no evidence to suggest that such capabilities are adaptive.

14.1 Introduction

In 1844, Wilhelm Karl von Haidinger (1795–1871), an Austrian physicist, geologist and mineralogist, discovered that the human eye is able to perceive the linear polarization of light due to an entoptic phenomenon that was later given his name. This discovery of Haidinger's brush preceded, by 100 years, Karl von Frisch's (1949) discovery that honeybees (*Apis mellifera*) are sensitive to the linear polarization of skylight and use it for orientation and navigation. The ability to detect the orientation of the electric field vector (E-vector) of polarized light is surprising as human photoreceptors, like those of all vertebrates, are generally thought to be insensitive to the E-vector orientation of axially incident light (exceptions to this are detailed in Chap. 9). Human polarization sensitivity appears to be a by-product of the dichroic properties of the retinal layers; specifically the macula. To date, there has been no biological function assigned to the human ability to detect the E-vector orientation of polarized light. In 1940, Gundo von Boehm described another entoptic phenomenon that enables the human eye to perceive polarized light. 'Boehm's brush' is most visible when a small polarized light source is viewed against a dark background in the peripheral visual field and is only perceived if the E-vector of the light source is rotating. The literature on human polarization sensitivity has also been reviewed by Lester (1970), Zhevandrov (1995), Fairbairn (2001), Horváth and Varjú (2004, pp. 355–361).

14.2 Haidinger's Brush

If one gazes at a homogenous polarized white light field, a faint pattern can be seen consisting of a small yellowish bowtie or 'brush' with bluish intervening areas (Fig. 14.1). This faint entoptic image referred to as Haidinger's brush subtends approximately 5° and rotates about the fixation point as the E-vector of the incident light is rotated. If the polarized light field remains unchanged, neural adaptation causes the effect to fade within a couple of seconds.

Usually, a little practice is needed to see Haidinger's brush, but the effect can be enhanced and maintained by changing the E-vector's angle of the polarized light. Looking at a white polarized light field in which the E-vector alternates between two perpendicular E-vector orientations (e.g. horizontal and then vertical) can make the effect more visible, as the afterimage of one orientation of the brush reinforces the

Part II
Polarized Light in Nature with Implications
to Animal Polarization Vision

Chapter 15

Underwater Polarization by Scattering Hydrosols

Amit Lerner

Abstract During more than six decades of underwater polarization research, polarization by hydrosols has got little attention. It was somewhat neglected by both optical oceanographers and marine biologists, because Rayleigh (molecular, sub-micronic) scattering was generally assumed as the main process determining the polarization field in water, similarly to the one in the atmosphere. Recent measurements and modeling have shown that the Rayleigh assumption is inaccurate, and instead Mie scattering (i.e. scattering by particles suspended in water, such as plankton and minerals of microns in size) should be considered as the dominating process, even in clear waters. This chapter focuses on the physical processes that determine the polarization in water, and presents the theoretical basis of scattering and radiative transfer which is needed to investigate and solve the effect of scattering particles of varied sizes and shapes on polarization, and the methods in use to measure it in situ. The chapter also reviews past studies on underwater polarization modeling and measurements, emphasizes the missing knowledge in the topic, and thus encourages future research.

15.1 Introduction

Polarization in water has got little attention in Horváth and Varjú (2004), who mainly concentrated on aquatic animals that perceive it, although the research in the water has been performed by optical oceanographers in parallel to the one in air along the last six decades since the pioneering polarization research of Karl von Frisch (1949, 1950, 1967) on honeybees. However, ocean optics did not always

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Chapter 16

Polarization Patterns of Freshwater Bodies with Biological Implications

Gábor Horváth

Abstract In this chapter we show that the polarization visibility of water surfaces is an important factor in the colonization of aquatic habitats by flying water beetles using horizontal polarization of water-reflected light to seek potential locations. After mowing of cattail (*Typha* sp.), for example, in freshwater marshes, aquatic beetles become more abundant due to the higher water temperature and the enhanced polarization visibility of the water surface. Here we also show that it is worth flying at dusk for aquatic insects, because the polarotactic water detection is easiest at low solar elevations. Polarotactic water insects interpret a surface as water if the degree of linear polarization of reflected light is higher than a threshold and the deviation of the direction of polarization from the horizontal is lower than a threshold. At sunrise and sunset the polarization visibility of water surfaces is maximal. Thus, the risk that a polarotactic insect will be unable to recognize the surface of a dark or bright water body is minimal at low solar elevations. The daily change in the reflection-polarization pattern of water surfaces is an important visual ecological factor that contributes to the preference of the twilight period for habitat searching by polarotactic water insects. Air temperature at sunrise is generally low, so dusk is one of the optimal periods for polarotactic aquatic insects to seek new habitats.

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Chapter 17

Polarization Characteristics of Forest Canopies with Biological Implications

Gábor Horváth and Ramón Hegedüs

Abstract In this chapter we show that the pattern of the direction of polarization of sunlit grasslands and sunlit tree canopies is qualitatively the same as that of the clear sky. Since the mirror symmetry axis of this pattern is the solar–antisolar meridian, the azimuth direction of the sun, occluded by vegetation, can be assessed in forests from this polarization pattern. This robust polarization feature of the optical environment in forests can be important for forest-inhabiting animals that make use of linearly polarized light for orientation. Here we also present an atmospheric optical and receptor-physiological explanation of why longer wavelengths are advantageous for the perception of polarization of downwelling light under canopies illuminated by the setting sun. This explains why the upward-pointing ommatidia of the dusk-active cockchafer, *Melolontha melolontha*, detect the polarization of downwelling light in the green part of the spectrum. We show that the polarization vision in *Melolontha melolontha* is tuned to the high polarized intensity of downwelling light under canopies during sunset. This is an optimal compromise between simultaneous maximization of the quantum catch and the quantum catch difference.

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Chapter 18

Polarization of the Sky

Gábor Horváth, András Barta, and Ramón Hegedüs

Abstract Based on full-sky imaging polarimetric measurements, in this chapter we demonstrate that the celestial distribution of the angle of polarization (or E-vector direction) of skylight is a very robust pattern being qualitatively always the same under all possible sky conditions. Practically the only qualitative difference among clear, partly cloudy, overcast, foggy, smoky and tree-canopied skies occurs in the degree of linear polarization d : The higher the optical thickness of the non-clear atmosphere, the lower the d of skylight. We review here how well the Rayleigh model describes the E-vector pattern of clear and cloudy skies. We deal with the polarization patterns of foggy, partly cloudy, overcast, twilight, smoky and total-solar-eclipsed skies. We describe the possible influences of the changed polarization pattern of smoky and eclipsed skies on insect orientation. We consider the polarization of ‘water-skies’ above Arctic open waters and the polarization characteristics of fogbows. Finally, we deal with the change of skylight polarization due to the transmission through Snell’s window of the flat water surface.

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Chapter 19

Polarisation Signals

Justin Marshall, Nicholas Roberts, and Thomas Cronin

Abstract Humans are fascinated by the colour vision, colour signals and ‘dress codes’ of other animals as we can see colour. This property of light may be useful for increasing the contrast of objects during foraging, defence, camouflage and sexual communication. New research, largely from the last decade, now suggests that polarisation is a quality of light also used in signalling and may contain information at least as rich as colour. As many of the chapters in this book detail, polarisation in animals is often associated with navigation, habitat choice and other tasks that require large-field processing. That is, a wide area of the light field, such as the celestial hemisphere, is sampled from. Polarisation vision that recognises and extracts information from objects is most likely confined to processing through small numbers of receptors. This chapter examines the latest evidence on polarised signals from animals and their environments, including both linear and circular polarisations. Both aquatic and terrestrial examples are detailed, but with emphasis on life underwater as it is here that many recent discoveries have been made. Behaviour relative to signals is described where known, and suggestions are given as to how these signals are received and processed by the visual system. Camouflage as well as signalling in this light domain is also considered, with the inevitable conclusion for this new field that we need to know more before solid conclusions can be drawn.

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Chapter 20

Anthropogenic Polarization and Polarized Light Pollution Inducing Polarized Ecological Traps

Gábor Horváth, György Kriska, and Bruce Robertson

Abstract In the last decade it has been recognized that the artificial polarization of light can have uniquely disruptive effects on animals capable of seeing it and has led to the identification of polarized light pollution (PLP) as a new kind of ecological photopollution. In this chapter we review some typical examples for PLP and the resulting polarized ecological traps. All such polarized-light-polluting artificial surfaces are characterized by strongly and horizontally polarized reflected light attracting positively polarotactic aquatic insects, the larvae of which develop in water or mud, such as aquatic beetles (Coleoptera), water bugs (Heteroptera), dragonflies (Odonata), mayflies (Ephemeroptera), caddisflies (Trichoptera), stoneflies (Plecoptera) and tabanid flies (Tabanidae), for example. We survey here the PLP of asphalt surfaces, solar panels, agricultural black plastic sheets, glass surfaces, black gravestones and the paintwork of black-, red- and dark-coloured cars. We show how

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the maladaptive attractiveness (PLP) of certain artificial surfaces to polarotactic insects can be reduced or eliminated. We consider how birds, spiders and bats exploit polarotactic insects trapped by different sources of PLP. We deal with the phenomenon that the vertically polarized mirror image of bridges seen at the river surface can deceive swarming polarotactic mayflies, which is an atypical kind of PLP. We explain why strongly polarizing black burnt-up stubble fields do not attract aquatic insects, which is an example for a horizontal, black polarizing surface that does not induce PLP and thus is an exception proving the rule. Finally, we show that phototaxis and polarotaxis together have a more harmful effect on the dispersal flight of night-active aquatic insects than they would have separately. This provides experimental evidence for the synergistic interaction of phototaxis and polarotaxis in these insects.

20.1 Polarized Light Pollution and Polarized Ecological Traps

Illumination of the night sky by electric lights, as in urban areas, that interferes with astronomical observation is known as ‘astronomical light pollution’ (Riegel 1973; Upgren 1996; Wilson 1998; Cinzano et al. 2001). This and other artificial light that has the effect of disrupting biological systems is known as ‘ecological light pollution’ (ELP) (Verheijen 1958, 1985; Longcore and Rich 2004, 2006; Rich and Longcore 2006). By appearing at atypical locations or times, artificial light can disorient, attract or repulse animals, disrupting critical behaviours and negatively impacting their survival or reproductive success (Rich and Longcore 2006, p. 3). ELP includes sky glow, direct glare, chronically increased illumination and temporary, unexpected fluctuations in lighting associated with lighted structures (e.g. bridges, buildings and towers), street and security lights and vehicle lights (Rich and Longcore 2006, pp. 3–4). The documented and the possible ecological consequences of all these artificial night lighting were comprehensively summarized in the monograph edited by Rich and Longcore (2006).

Attraction (positive phototaxis) or repulsion (negative phototaxis) of animals by the spatiotemporally enhanced intensity of light relative to the dark environment defines a major axis of animal responses to ELP, and researchers have historically focused on understanding animal movement in relation to the intensity and/or colour of artificial light. More recently, however, it has been recognized that the artificial polarization of light can have uniquely disruptive effects on animals capable of seeing it and has led to the identification of ‘polarized light pollution’ (PLP) as a new kind of ecological photopollution (Horváth et al. 2009). Two typical examples are shown in Fig. 20.1. PLP is characterized by strongly (i.e. with high degrees of linear polarization) and horizontally polarized light reflected from smooth (shiny) artificial surfaces (Figs. 20.2 and 20.3) having negative fitness on polarotactic aquatic insects which generally include all insect taxa whose larval stages require water bodies to mature into adults: aquatic beetles (Coleoptera), water bugs (Heteroptera), dragonflies (Odonata), mayflies (Ephemeroptera), caddisflies (Trichoptera), stoneflies (Plecoptera) and tabanid flies (Tabanidae), for example (Fig. 20.4).

Part III
Practical Applications of Polarization
Vision and Polarization Patterns

Chapter 21

Polarization as a Guiding Cue for Oviposition in Non-biting Midges and Mosquitoes

Amit Lerner

Abstract Recently, a new utilization for light polarization has been demonstrated: the use of reflection polarizations from water surface to assess habitat quality and choose oviposition sites for water-living insects. While contradicting results were shown in the laboratory and at the natural habitat of long-living mosquitoes, their short-living, non-biting relatives, the chironomids (Chironomidae, midges, which serve as the host of the *Cholera* pathogen among many other species of bacteria), have shown clear response both under confined and unconfined conditions. The understanding of the advantage of following reflection polarizations to detect suitable reservoirs for oviposition opens a new research field of controlling pest insects using reflection-polarization traps, which has not been addressed to date.

21.1 Introduction: Purposes for Polarotaxis in Dipterans

Sensitivity to light polarization is very common among two-winged flies (Diptera) as apparent from behavioural studies showing polarotaxis [see reviews in Horváth and Varjú (2004) and in Part I]. Species in this order contain photoreceptive retinula cells with orthogonal microvilli, and in some species even cells with a third orientation of 45° exist, which allows for a full and most accurate detection of the two polarization components: the partial linear polarization and the orientation (E-vector) of polarization. Nonetheless, the purpose for detecting light polarization by dipteran insects was somewhat vague. As the dorsal rim area (DRA) of their compound eyes was found to be more polarization sensitive than other eye regions in some species (Labhart 1980; Nilsson et al. 1987; Labhart et al. 1992, 2009;

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Chapter 22

Linearly Polarized Light as a Guiding Cue for Water Detection and Host Finding in Tabanid Flies

Gábor Horváth, Ádám Egri, and Miklós Blahó

Abstract In this chapter we show that tabanid flies are attracted to horizontally polarized light stimulating their ventral eye region. Female and male tabanids use this polarotaxis governed by the horizontal E-vector to find water, while another type of polarotaxis based on the degree of polarization serves host finding by female tabanids. We show that female tabanids are less attracted to bright than dark hosts, the reason for which is partly that dark hosts reflect light with higher degrees of polarization than bright hosts. We also demonstrate that the use of a striped fur pattern has the advantage that such coat patterns attract far fewer tabanids than either homogeneous black, brown, grey or white equivalents. The attractiveness of striped patterns to tabanids is also reduced if only polarization modulations (parallel stripes with alternating orthogonal directions of polarization) occur in homogeneous grey surfaces. The attractiveness to tabanids decreases with decreasing stripe width, and stripes below a certain width threshold are unattractive at all to tabanids. Further, the stripe widths of zebra coats fall in a range where the striped pattern is most unattractive to tabanids. Tabanids are strongly attracted by CO₂ and ammonia emitted by their hosts. We show here that the poor visual attractivity of stripes to tabanids is not overcome by olfactory attractiveness. Finally, we show that dark spots on a bright coat surface also disrupt the visual attractiveness to tabanids. The smaller and the more numerous the spots, the less attractive the host is to tabanids. The attractiveness of spotty patterns to tabanids is also reduced if the target exhibits spottiness only in the angle of polarization pattern, while being homogeneous grey with a constant high degree of polarization. This could be one of the possible

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evolutionary benefits that explains why spotty coat patterns are so widespread in mammals, especially in ungulates, many species of which are tabanid hosts.

22.1 Polarotaxis in Tabanid Flies

22.1.1 *Ventral Polarization Vision in Tabanids: Attraction to Horizontal Polarization*

The tabanid flies (Diptera: Tabanidae, including horseflies of the genus *Tabanus* and deerflies of the genus *Chrysops*, as the economically two most important tabanid genus) are distributed worldwide (Baldacchino et al. 2014). Adult tabanids feed on nectar and pollen, and the females usually feed also on (mainly mammalian) blood which aids the development of their eggs (Hayakawa 1980; Hall et al. 1998; Lehane 2005; Krcmar and Maric 2006). Tabanid females usually lay their eggs on marsh plants next to freshwater bodies, because after egg hatching the larvae must drop down into water or onto mud, where they develop (Tashiro and Schwardt 1953). The haematophagous female tabanids can find their host animals by odours, heat and visual cues (Thorsteinson et al. 1965; Allan et al. 1987; Krcmar 2005a, b, 2013; Krcmar et al. 2005; Lehane 2005). With multiple-choice experiments in the field, Horváth et al. (2008) showed the attraction to horizontally polarized light stimulating the ventral eye region in both males and females of 27 tabanid species. This behaviour is called positive polarotaxis.

The positive polarotaxis in water-seeking tabanids was discovered in a Hungarian cemetery (in the town of Kiskunhalas) where tabanids were abundant, because there was a horse school in the immediate vicinity. In this cemetery the reasons for attraction of *Sympetrum* dragonflies to polished black gravestones were studied (Horváth et al. 2007). During these experiments it was observed that tabanid flies are also lured to the strongly and horizontally polarizing shiny smooth surfaces of black tombstones (Fig. 22.1). This accidental observation inspired the subsequent systematic field experiments (Horváth et al. 2008). Hansruedi Wildermuth (Rüti, Switzerland; personal communication, 2008) observed similar reactions of *Tabanus* species to horizontal black plastic and dark brown perspex sheets during field experiments designed for the examination of dragonfly responses to shiny surfaces (Wildermuth 1998).

Horváth et al. (2008) experienced that among white, black and aluminium (colourless) horizontal, smooth or matte test surfaces laid on the ground, both female and male tabanids preferred only the strongly and horizontally polarizing smooth (shiny) black surfaces against weakly and not horizontally polarizing surfaces (positive or negative phototaxis; furthermore, colour, temperature and odour preferences were excluded). The female-to-male ratio of the attracted tabanids was about 1.7, but this ratio differed slightly from site to site and was also species specific. The attracted tabanids touched the black surface 2–50 times. They landed on the surface directly, or prior to landing, they performed a typical

Chapter 23

Applying Polarization-Based Traps to Insect Control

Gábor Horváth, Miklós Blahó, Ádám Egri, and Amit Lerner

Abstract Following the new findings described in Chap. 21 regarding the use of polarization cues by chironomids to detect water bodies suitable for oviposition, an effort was initiated to apply reflection-polarization traps to divert chironomid females from laying their eggs in the natural reservoir and by this to control the chironomid population. In this chapter we first review this effort and its outcome and suggest insights into the future development of chironomid reflection-polarization oviposition traps and population control. Then we present three different types of polarization-based tabanid trap: a liquid trap, a sticky horseflypaper and a photovoltaic trap. All three trap types share the common feature that they lure positively polarotactic tabanid flies with strongly and linearly polarized light reflected from special shiny black visual targets. Due to their horizontally polarizing bait surface, the liquid and the photovoltaic traps as well as the horizontally aligned horseflypaper capture water-seeking male and female tabanids attracted to the horizontal polarization of bait-reflected light. If the surface of the horseflypaper is vertical, it catches host-seeking female tabanids lured to the strongly polarized trap-reflected light. The tabanid-capturing efficacy of all three trap types has been proven in field experiments. The scientific basis of these traps

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is the two kinds of positive polarotaxis in tabanid flies. The advantages and disadvantages of these different tabanid traps are also discussed here; furthermore, it is described how these traps could be improved in the future, and how they can be combined with the traditional canopy trap, for instance. These studies demonstrate well how basic scientific knowledge, i.e. the positive polarotaxis in chironomids and tabanids, can be applied in the design of new insect traps.

23.1 Polarization Chironomid Traps

Amit Lerner

23.1.1 *Field Experiment to Divert Ovipositing Chironomid Females to Artificial Sites (Egg Traps)*

As described earlier in Chap. 21, chironomid females are strongly directed by reflection polarization during oviposition and choose to lay eggs in highly and horizontally polarizing wet surfaces. This is raising the opportunity to use such traps to lure the females from egg laying in their natural sites and collect their eggs in a trap to control the population. Such an attempt was conducted, where highly polarizing traps were placed on the ground nearby the chironomids' natural pond (Lerner et al. 2012). The traps were 40 litre black tubs filled with very turbid pond water, which were shown to be effective in a previous experiment (see details in Chap. 21). The tubs were placed along the bank of the chironomid natural pond. In the first two weeks, the oviposition rates in the pond (on floating Styrofoam rafts) and in the tubs were monitored. Then the bank was covered with a white plastic sheet to reduce natural oviposition sites and direct the females to oviposit in the tubs. The eggs were counted and removed each day. Once the number of natural egg-laying sites (the pond bank in this case) was reduced, the traps' effectiveness increased, as increasing numbers of egg batches of chironomids were found. Such a response suggests that egg traps reflecting highly and horizontally polarized light should effectively lure the females to oviposit in them and therefore may be useful to control the pest population. However, polarization egg trapping is still in its infant stage to date.

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Chapter 24

Polarization Cloud Detection with Imaging Polarimetry

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Abstract In this chapter we show some practical applications of 180° field-of-view (full-sky) imaging polarimetry. The concept and structure of some full-sky imagers (Total Sky Imager, Whole Sky Imager, All Sky Imager) widely used in environmental optics are presented. Some algorithms dealing with photometric cloud detection, a hot topic in meteorology, are described. A brief summary of the satellite-borne PARASOL/POLDER imaging polarimeter is given. Two versions of full-sky imaging polarimetry are described. Both use the measured extra polarization information of skylight. Their advantageous features are (1) enhancement of accuracy and reliability of cloud detection, (2) estimation of the relative cloud-base distance distribution in the sky and (3) applicability in solar forecasting, a very special current topic.

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Chapter 25

Sky-Polarimetric Viking Navigation

Gábor Horváth, Alexandra Farkas, and Balázs Bernáth

Abstract It is a widely discussed and regularly cited theory that Viking navigators might have been able to locate the position of the sun occluded by clouds or below the horizon with a mysterious birefringent or dichroic crystal, the sunstone, on the basis of the pattern of skylight polarisation. In this chapter we describe the steps and the experimentally tested efficiency of this sky-polarimetric navigation method, and we show modern navigation instruments that operate in a similar principle. We investigate the atmospheric optical prerequisites of sky-polarimetric Viking navigation, looking for the ideal weather conditions, under which sunstones could be used for this navigational task. We also discuss other hypothesised Viking navigation instruments, like the horizon board and the sun compass or twilight board. Finally, we consider the Medieval Norse sailing routes and some alternative atmospheric optical navigation cues, which also could help during the long-time marine voyage of Viking seafarers.

25.1 Introduction

It is a frequently cited theory that Vikings—seafaring Norse people flourishing from the eighth to the twelfth century—might have been able to navigate by means of the polarisation pattern of the sky. The theory was first outlined by Ramskou (1969) as an analogy of a modern polarimetric navigational instrument (the Kollsman’s polarised

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