

Polarized light pollution: a new kind of ecological photopollution

Gábor Horváth¹, György Kriska², Péter Malik¹, and Bruce Robertson^{3*}

The alteration of natural cycles of light and dark by artificial light sources has deleterious impacts on animals and ecosystems. Many animals can also exploit a unique characteristic of light – its direction of polarization – as a source of information. We introduce the term “polarized light pollution” (PLP) to focus attention on the ecological consequences of light that has been polarized through interaction with human-made objects. Unnatural polarized light sources can trigger maladaptive behaviors in polarization-sensitive taxa and alter ecological interactions. PLP is an increasingly common byproduct of human technology, and mitigating its effects through selective use of building materials is a realistic solution. Our understanding of how most species use polarization vision is limited, but the capacity of PLP to drastically increase mortality and reproductive failure in animal populations suggests that PLP should become a focus for conservation biologists and resource managers alike.

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The term “ecological light pollution” (ELP) has been coined to describe all kinds of photopollution that disrupt the natural patterns of light and dark experienced by organisms in ecosystems (Longcore and Rich 2004). ELP includes direct glare, chronically increased illumination, and temporary, unexpected fluctuations of light emitted from lighted structures (eg buildings, towers, bridges) and vehicles. Artificial lights can attract or repulse organisms, leading to increased predation, maladaptive migration behavior, selection of inferior nest sites or mates, collisions with artificial structures, altered competition for resources, reduced time available for foraging, and disrupted predator–prey relationships that can, in turn, alter community structure (reviewed in Longcore and Rich 2004). This positive or negative phototaxis is elicited by the intensity and/or color of artificial light, which has been considered

as the major visual phenomenon underlying ELP. Yet other characteristics of light are visible too, and are used as behavioral cues by animals.

In particular, it has become clear that many animals are capable of perceiving the polarization of light and use it as a rich source of information (eg von Frisch 1967; Lythgoe and Hemmings 1967; Schwind 1985, 1991, 1995; Danthararayana and Dashper 1986; Shashar *et al.* 1998; Wildermuth 1998; Marshall *et al.* 1999; Novales Flamarique and Browman 2001; Wehner 2001; Labhart and Meyer 2002; Dacke *et al.* 2003; Horváth and Varjú 2004; Waterman 2006; Wehner and Labhart 2006; Henze and Labhart 2007). In this work, we introduce the term “polarized light pollution” (PLP) as a new kind of ecological light pollution. PLP refers predominantly to highly and horizontally polarized light reflected from artificial surfaces, which alters the naturally occurring patterns of polarized light experienced by organisms in ecosystems. We first discuss known and potential sources of naturally occurring and artificially produced polarized light, and contrast the scale and timing of PLP with that of ELP. We then review our current understanding of the influence of PLP on the behavior of polarization-sensitive organisms and their ecological interactions and communities.

In a nutshell:

- Polarized light pollution includes light that has undergone linear polarization by reflecting off smooth, dark buildings, or other human-made objects, or by scattering in the atmosphere or hydrosphere at unnatural times or locations
- Artificial polarizers can serve as ecological traps that threaten populations of polarization-sensitive species
- Artificial polarized light can disrupt the predatory relationships between species maintained by naturally occurring patterns of polarized light, and has the potential to alter community structure, diversity, and dynamics

■ Natural and artificial sources of polarized light

Ordinary white light (eg sunlight, consisting of electromagnetic waves vibrating at all possible planes perpendicular to the direction of propagation) is unpolarized, but light is totally linearly polarized when its waves oscillate only in a single plane. Partially linearly polarized light with a given wavelength is commonly characterized by three parameters: the intensity I , the degree of linear polarization p , and the angle of polarization α , which

¹Biooptics Laboratory, Department of Biological Physics, Physical Institute, Eötvös University, Budapest, Hungary; ²Group for Methodology in Biology Teaching, Biological Institute, Eötvös University, Budapest, Hungary; ³WK Kellogg Biological Station, Michigan State University, Hickory Corners, MI *(roberbal@msu.edu)

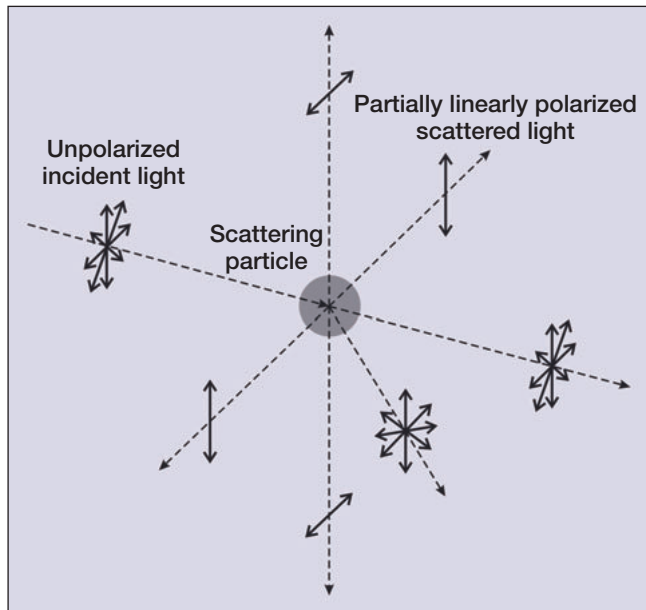


Figure 1. After scattering on a particle, unpolarized light – whose electric field vector (double-headed arrows) with the same length vibrates in all possible directions perpendicular to the direction of propagation (dashed arrows) – becomes partially linearly polarized. Its electric field vector is shorter in the plane of scattering than that perpendicular to this plane.

describes the alignment of the plane of oscillation of the electric field vector relative to a given reference (eg vertical) direction. I is proportional to the number of photons incident perpendicularly to a unit surface per a unit time interval; p is the percentage of photons vibrating in the plane of polarization. In the natural, optical environment, partially linearly polarized light is abundant; this arises from two primary sources: (1) the scattering of sunlight and moonlight within the atmosphere and hydrosphere (Figure 1), and (2) the reflection of light off the surface of water bodies and other non-metallic surfaces (eg rocks, soil, vegetation; Figure 2). We will focus en-

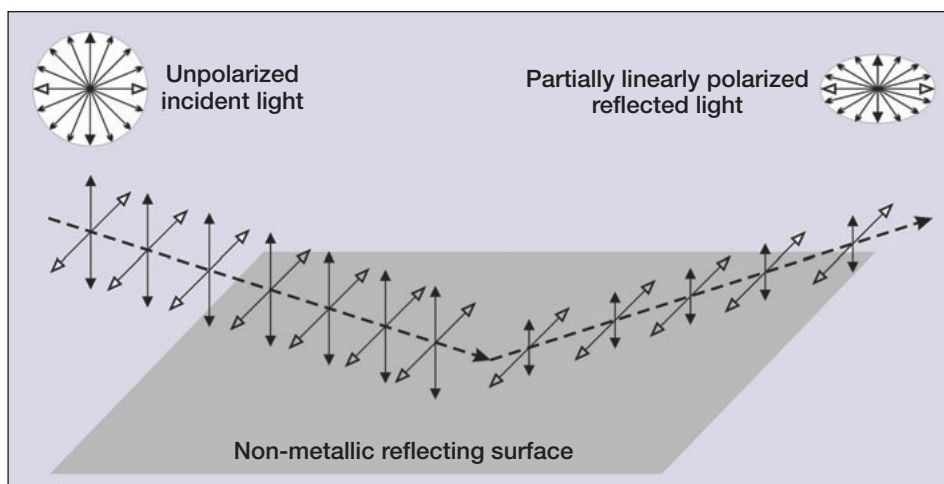


Figure 2. After reflection from a non-metallic surface, unpolarized light becomes partially linearly polarized. The electric field vector is shorter in the plane of reflection (double-headed arrows with black heads) than in the perpendicular plane (double-headed arrows with open heads).

tirely on partially linearly polarized light, the most common naturally occurring form of light polarization on Earth.

Solar radiation is unpolarized before entering Earth's atmosphere, but is partially linearly polarized through interactions with atmospheric gases, aerosols, water droplets, and ice crystals (Coulson 1988; Figure 1). The result is a characteristic celestial polarization pattern with skylight usually polarized perpendicular to the plane of scattering (defined by the observer, the celestial point observed, and the position of the Sun or Moon), and maximum p is generally found at 90° from the Sun or Moon (Können 1985). Patterns of polarized light in the sky provide reliable information about the location of these celestial bodies that animals can use to orient themselves and direct their movements. Aquatic and marine organisms can rely on a similar polarization pattern, produced by the scattering of light in the hydrosphere (Lythgoe and Hemmings 1967; Shashar *et al.* 1998; Marshall *et al.* 1999; Novales Flamarique and Browman 2001; Waterman 2006).

Unpolarized light can also undergo strong polarization by reflection (Figure 2). Water is the primary natural source of horizontal polarization by reflection (Figure 3a), and its depth, turbidity, transparency, surface roughness, substratum composition, and illumination strongly influence the reflection–polarization characteristics of its surface (Horváth and Varjú 2004). In general, the extent to which an object polarizes light depends on the angle of reflection and on the material from which its surface is made, with darker and smoother (shinier) surfaces producing higher p (Umow 1905).

Diffuse reflection from rough surfaces in all possible directions results in depolarization (reducing p), because the reflected electromagnetic waves vibrate in many planes. The net p of light returned by an object is determined by the relative intensities of (1) light reflected from the object's surface and (2) light scattered back from the object's material and refracted at its surface. The first and second components are polarized parallel and perpendicular to the reflecting surface, respectively, and therefore have a mutual, depolarizing effect on one another. If, in a given part of the spectrum, the first component is more/less intense than the second one, the net plane of polarization of returned light is parallel/perpendicular to the reflecting surface. If both components are equally intense, the returned light is unpolarized. When the returned light is polarized parallel to the surface, the more intense the second component, the lower the net p . On the other hand, the more/less intense the second component, the

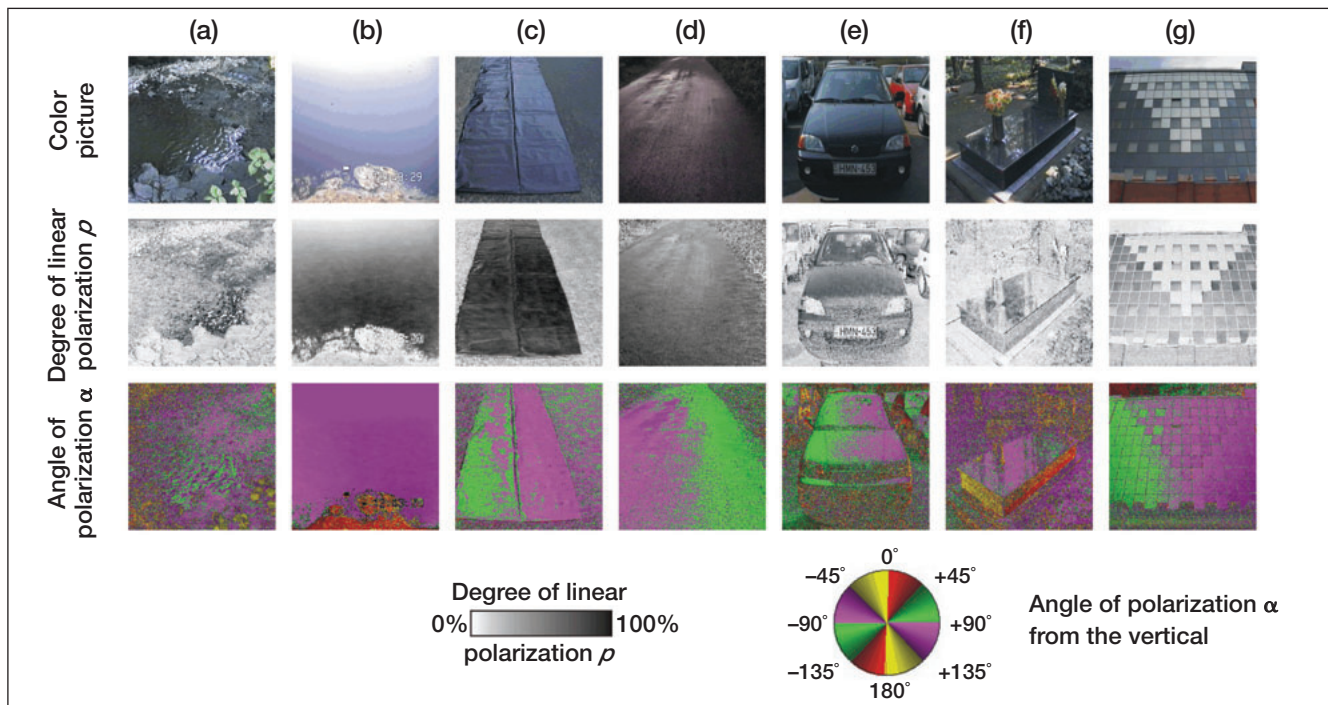


Figure 3. Color photos, patterns of the degree of linear polarization p , and the angle of polarization α of a water surface (a) and different artificial surfaces (b–g) causing PLP. (a) Dark water body. (b) Crude oil lake in the desert of Kuwait. (c) Black plastic sheet on an asphalt road. (d) Dry asphalt road. (e) Black car. (f) Polished black gravestone. (g) Windows with gray/black glass ornamentation. p is the percentage of photons vibrating in the plane of polarization. Darker gray tones encode higher p (white: $p = 0\%$, black: $p = 100\%$). α is the alignment of the plane of polarization measured clockwise from the vertical. Different α values are encoded by different colors and hues (red: $0^\circ \leq \alpha < +45^\circ$, green: $+45^\circ \leq \alpha < +90^\circ$, violet: $+90^\circ \leq \alpha < +135^\circ$, yellow: $+135^\circ \leq \alpha < +180^\circ$). At a given color, the hue encodes different angles α with a step of $\Delta\alpha = 1^\circ$.

brighter/darker the object. Thus, in a given part of the spectrum, brighter/darker surfaces reflect light with lower/higher p . This phenomenon is called the Umow effect (Können 1985).

One of the consequences of this phenomenon is that, in a given spectral range, smooth darker surfaces are more effective at producing PLP than are brighter ones. Hence, there is an inverse correlation between the brightness of a smooth surface and the amount of PLP produced by it. Thus, if a smooth object is bright/dark in the ultraviolet (UV) spectral range, it reflects UV light with low/high p . Consequently, brighter UV reflectors are less effective at producing PLP. This is important in light of the widespread UV sensitivity of birds and insects (Schwind 1991, 1995; Tovée 1995). Many aquatic insects that are attracted to horizontally polarized light sources are also attracted to unpolarized UV blacklight (Nowinszky 2003). Therefore, one can decide only with appropriately designed multiple-choice experiments whether it is the UV spectrum or the polarization of light that serves as the attractant signal (eg Schwind 1985, 1991, 1995; Danthanarayana and Dashper 1986; Horváth *et al.* 1998, 2007, 2008; Kriska *et al.* 1998, 2006a, 2007, 2008a; Bernáth *et al.* 2001b; Dacke *et al.* 2003; Horváth and Varjú 2004).

Modern human development has resulted in the introduction of different sources of polarized light pollution to natural habitats, primarily as a byproduct of the human

architectural, building, industrial, and agricultural technologies. Many human products – including black plastic sheets (used in agriculture), asphalt roads, oil spills and open-air waste oil reservoirs, dark-colored paintwork (eg of automobiles), black gravestones, and glass panes (Figure 3b–g) – share important physical characteristics of the most common natural polarizer, the surface of dark waters (Figure 3a), and polarize light strongly.

The phenomenon of PLP is global and has increased rapidly over the past several decades, following the rapid spread of urban development, road systems, and industrial agriculture. Although the magnitude and prevalence of PLP have greatly increased with human activity, PLP can also occur naturally (eg ancient asphalt pits). Because ELP results from the incidence of visible light at times and places where it does not occur naturally, ELP is predominantly a night-time phenomenon, affecting nocturnal and crepuscular species. In contrast, PLP can occur during both light and dark cycles in terrestrial environments, and in other permanently dark habitats, as long as both artificial light sources and polarizing substances are present.

■ Ecological effects of polarized light pollution

Many animals, including birds, reptiles, amphibians, fish, insects, crustaceans (eg crabs and shrimp), and even echinoderms, have amazingly well-tuned polarization

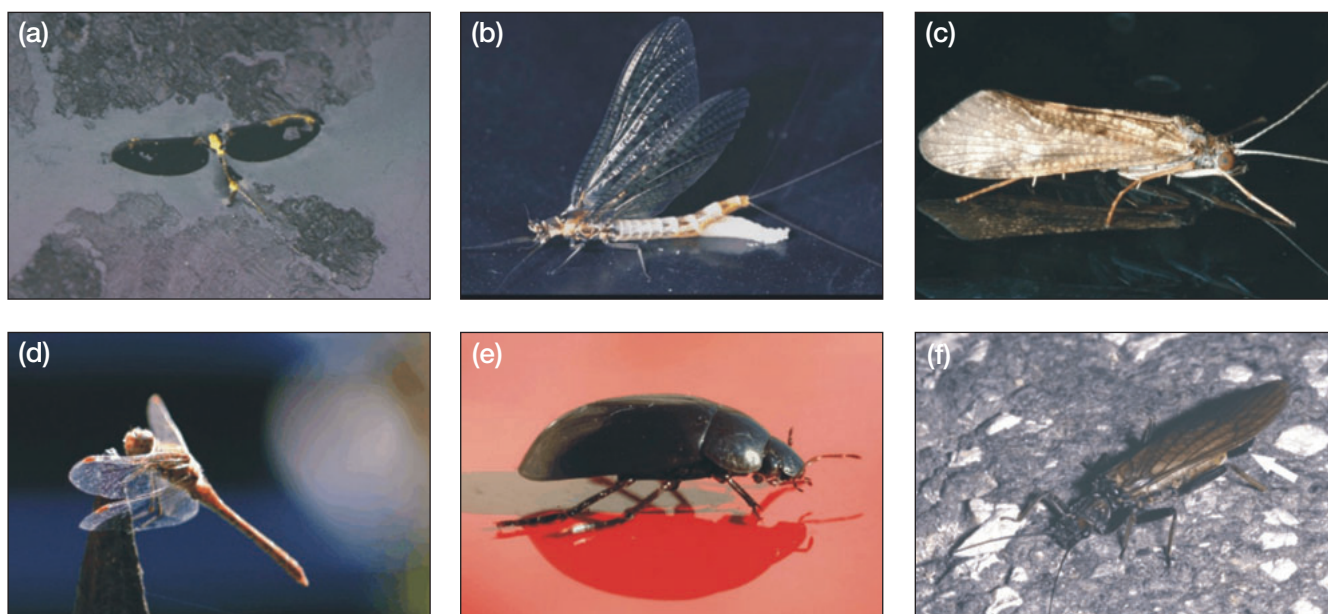


Figure 4. Polarotactic, water-loving insects attracted to different PLP sources. (a) Mayfly trapped in a waste oil lake in Budapest, Hungary; (b) mayfly laying eggs on a horizontal black plastic sheet; (c) caddisfly on a vertical glass pane (the picture is rotated by 90°); (d) male dragonfly perching above a polished horizontal black tombstone; (e) water beetle on a red car roof; (f) ovipositing stonefly (white arrow: eggs) on a dry asphalt road.

vision (reviewed in Danthanarayana and Dashper 1986; Schwind 1995; Wehner 2001; Labhart and Meyer 2002; Horváth and Varjú 2004; Waterman 2006; Wehner and Labhart 2006). In this section, we review cases in which anthropogenic sources of polarized light affect the behavior and fitness of polarization-sensitive animals, directly or indirectly, and discuss the potential for PLP to influence ecological interactions with other species.

Habitat selection and oviposition

Polarized light pollution caused by artificial planar surfaces has clear and deleterious impacts on the ability of animals to judge safe and suitable habitats and oviposition sites. In particular, PLP presents severe problems for organisms associated with water bodies. Orientation to horizontally polarized light sources is the primary guidance mechanism used by at least 300 species of dragonflies, mayflies, caddisflies, tabanid flies, diving beetles, water bugs, and other aquatic insects. This is used to search for suitable water bodies to act as feeding/breeding, habitat, and oviposition sites (Schwind 1991; Horváth and Kriska 2008). Because of their strong horizontal polarization signature, artificial polarizing surfaces (eg asphalt, gravestones, cars, plastic sheeting, pools of oil, glass windows) are commonly mistaken for bodies of water (Horváth and Zeil 1996; Kriska *et al.* 1998, 2006a, 2007, 2008a; Horváth *et al.* 2007, 2008). Because the p of light reflected by these surfaces is often higher than that of light reflected by water, artificial polarizers can be even more attractive to positively polarotactic (ie lured to horizontally polarized light) aquatic insects than a water body (Horváth and Zeil 1996; Horváth *et al.* 1998; Kriska

et al. 1998). They appear as exaggerated water surfaces, and act as supernormal optical stimuli.

The ecological consequences of attraction to these PLP sources vary. Attraction to oil spills and pools typically results in mortality for organisms that touch or land on the surface of the oil and cannot escape. Large numbers of dragonflies, mayflies, caddisflies, water bugs, and water beetles are trapped by waste oil pools and oil spills in spring, summer, and autumn, during their annual swarming and migration (Horváth and Zeil 1996; Bernáth *et al.* 2001a; Figure 4a). Some insect species are attracted to plastic sheeting, which causes them to swarm, land, crawl, copulate, and lay eggs (Figure 4b), while many others (eg aquatic bugs – Heteroptera, and water beetles – Coleoptera) dry out and perish within hours (Bernáth *et al.* 2001b; Kriska *et al.* 2007). Emerging caddisflies (*Hydropsyche pellucidula*) are attracted to the vertical glass surfaces of buildings on river banks (Figure 4c) as a result of their strong, horizontal polarization signature (Kriska *et al.* 2008a; Malik *et al.* 2008; Figure 3g), an effect that is strengthened by building lights after dark. Because they copulate and remain attracted to the glass panes for hours, many individuals become trapped by partly open tilttable windows and perish.

Many aquatic insects experience complete reproductive failure when they lay eggs on artificial polarizers. Dragonflies (Wildermuth 1998; Figure 4d) and mayflies (Figure 4a, b) carry out sexual behaviors and lay eggs on unsuitable surfaces (eg shiny cement floors, black benches, glass panes, black plastic sheets, and horizontal black gravestones) that, like water, reflect horizontally polarized light. Strong polarization patterns also make black or red cars (Figure 3e) attractive to a host of species

(Kriska *et al.* 2006a; Figure 4e). Male dragonflies often perch on car antennas and establish territories on automobile hoods, while females frequently land and lay their eggs on horizontal car surfaces, where they fail to hatch (Wildermuth and Horváth 2005). Polarotactic mayflies and other insects (Figure 4f) commonly swarm above, land/copulate on, and oviposit onto dry asphalt surfaces that reflect horizontally polarized light (Kriska *et al.* 1998; Figure 3d). Attraction to PLP sources is often so great that individuals appear incapable of leaving, a behavior we call the “polarization captivity effect” *sensu* Eisenbeis (2006), which culminates in the death of the insects as a result of dehydration and exhaustion.

It is not surprising that water-seeking insects use horizontally polarized light to locate water bodies – among the available visual cues, polarization is the most reliable under variable lighting conditions (Schwind 1985; Horváth and Varjú 2004). Certain waterbirds are attracted to pools of oil, in which they drown, and they also try to forage on plastic sheeting laid on the ground, which appears to them as a small body of water (Bernáth *et al.* 2001a). Foraging on this type of inappropriate, artificial habitat wastes time and energy, but landing on artificial reflectors can be lethal for other species.

Obligate waterbirds, such as the ruddy duck (*Oxyura jamaicensis*), common loon (*Gavia immer*), dovekie (*Alle alle*), and brown pelican (*Pelecanus occidentalis*), are occasionally found dead or injured and stranded (unable to take off) in large asphalt parking lots (McIntyre and Barr 1997; Montevecchi and Stenhouse 2002), or on asphalt roads in the desert (Kriska *et al.* 2008b). Strandings commonly take place at night, when bright, downward-facing streetlights are reflected upwards by asphalt surfaces, creating a strong optical signature during a time of day when few cues for locating water bodies are available. Studying the possible role of polarization vision of these waterbirds in water detection is the task of future research.

Foraging ecology

Polarization sensitivity can be used by certain predators to help detect suitable prey. Underwater, both the degree and the direction of polarization created by scattering depend on the position of the Sun or Moon. But when scattered light passes through the transparent body of small aquatic prey animals (eg jellyfish, ctenophores), its polarization signature is altered, increasing the visual contrast of the prey species relative to the background (Lythgoe and Hemmings 1967; Shashar *et al.* 1998): transparent bodies repolarize transmitted, reflected, or refracted light and stand out against a background polarized in a different plane and at a different magnitude. Plankton feeders are adept at detecting zooplankton in the water column that would otherwise be transparent (Novales Flamarque and Browman 2001). In this way, cephalopods, trout, and other aquatic predators can detect the polarization signature of camouflaged and/or

distant prey (Shashar *et al.* 1998; Marshall *et al.* 1999; Novales Flamarque and Browman 2001). Longfin squid (*Loligo pealei*) also use polarized light as a hunting cue and will eat clear, polarizing beads in preference to non-polarizing ones (Shashar *et al.* 1998).

Underwater plastic garbage is another source of PLP, and may prompt aquatic organisms into consuming inappropriate and dangerous items. Transparent plastic is an abundant pollutant in marine environments throughout the world (reviewed in Derraik 2002); it alters the polarization of light passing through it, in the same way as small transparent organisms, because its index of refraction is different from that of water. The polarization signature of plastic refuse may also be problematic for sea turtles, since they may also be sensitive to polarized light (C Mora *pers comm*). Turtles commonly ingest plastic, particularly transparent plastic bags (Gramentz 1988; Bugoni *et al.* 2001), which have a polarization signature similar to that of prey items they commonly target (eg jellyfish, ctenophores). In addition to direct mortality (Duguy *et al.* 1998), sea turtles may experience reduced growth rates, which increases their vulnerability to large predators, and reduced energy reserves and migratory ability, as a consequence of plastic ingestion (McCauley and Bjorndal 1999). Plastic bags may attract sea turtles solely on the basis of their transparency and similarity in shape to jellyfish, yet the role of polarization signals in the interaction between plastic garbage, sea turtles, and other aquatic organisms deserves further study. Polarization vision in piscivorous predators should enhance detection of silvery-colored fish, by breaking their spectral camouflage (Marshall *et al.* 1999). The polarized light signatures of plastic refuse should therefore enhance its attractiveness to a number of polarization-sensitive predators (eg fish, cephalopods, birds; reviewed in Wehner 2001; Horváth and Varjú 2004; Waterman 2006; Wehner and Labhart 2006), making the potential scope of the problem both taxonomically and geographically widespread.

Navigation and orientation

Many taxa (eg birds, reptiles, fish, insects, crustaceans, and echinoderms) use polarized light patterns in the sky or hydrosphere as an orientation cue (reviewed in Danthanarayana and Dashper 1986; Schwind 1995; Wehner 2001; Labhart and Meyer 2002; Horváth and Varjú 2004; Waterman 2006; Wehner and Labhart 2006). Artificial polarized light (eg reflected from glass buildings or scattered in water around fishing boats and undersea research vessels) could therefore disrupt evolved polarization-based navigation and orientation behaviors. Certain bees, crickets, desert ants, and beetles, for instance, use the skylight polarization patterns as a cue for orientation during their dispersal and migration (eg von Frisch 1967; Labhart and Meyer 2002; Dacke *et al.* 2003), yet a wide range of nocturnal insects are attracted to, and “trapped” by, artificial point sources of polarized light (Kovarov and

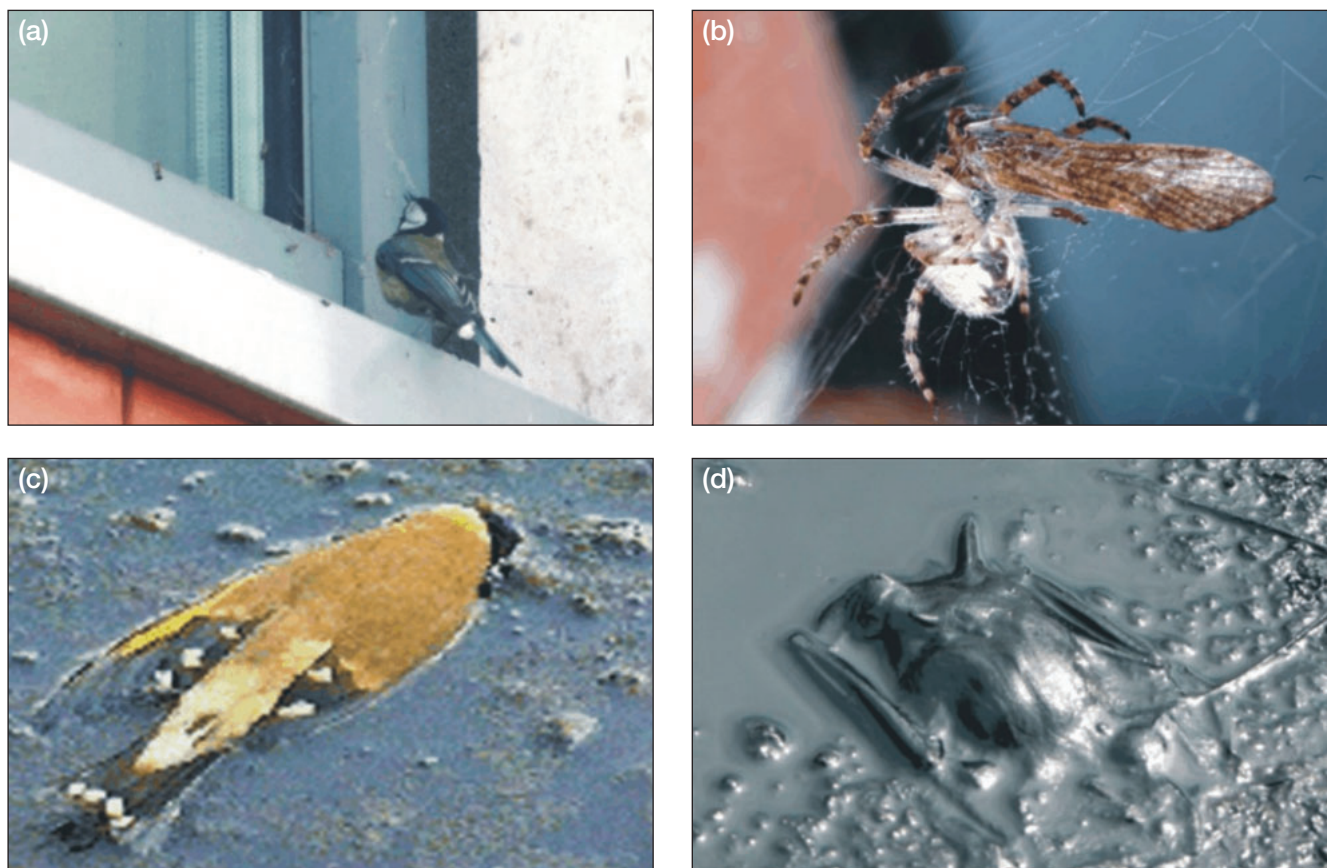


Figure 5. Predators feeding on polarotactic insects attracted to two PLP sources. (a) A great tit and (b) an orb-weaver spider feeding on caddisflies attracted to vertical glass surfaces; (c) carcasses of a European goldfinch and (d) a bat trapped by a waste oil lake in Budapest, Hungary.

Monchadskiy 1963; Danthanarayana and Dashper 1986). The maximum p of skylight is highly variable, ranging from 15–75% (Coulson 1988), so highly polarizing artificial surfaces (Horváth and Pomozi 1997) that reflect light downwards may easily become supernormal polarization signals to which different species are attracted. Field crickets (*Gryllus campestris*), for example, can orient to degrees of polarization of only 5–7% (Henze and Labhart 2007), while artificial polarizing surfaces may produce a signal as high as 80–95% (Horváth and Varjú 2004). Artificial surface reflections may therefore be confused with natural polarized light produced by scattering in the atmosphere.

Predation

Although the direct effects of PLP on polarotactic organisms are commonly negative, PLP can indirectly benefit species that feed on, or compete with, polarotactic organisms. Anuran amphibians, reptiles, birds, bats, and spiders hunt insects attracted to streetlamps at night (reviewed in Rich and Longcore 2006); this is a well-known, secondary effect of conventional (non-polarized) ecological photopollution. Similarly, wagtails (*Motacilla alba* and *M. flava*) readily hunt polarotactic insects attracted to dry asphalt roads and highly polarizing black plastic sheets

laid on the ground, which function like a huge bird feeder (Kriska *et al.* 1998; Bernáth *et al.* 2008). Caddisflies attracted to vertical glass surfaces lure diverse predators, including birds, such as European magpies (*Pica pica*), white wagtails (*M. alba*), house sparrows (*Passer domesticus*), and great tits (*Parus major*; Horváth and Kriska unpublished data), which systematically hunt and catch the caddisflies that have landed on glass panes or are swarming near windows (Figure 5a). Spiders are also attracted in large numbers to feed on these caddisflies (Figure 5b).

Cascading effects may result if predators, initially benefiting from the abundance of caddisflies attracted to the glass surfaces, become prey themselves. For example, magpies gathering near caddisfly congregations could represent an enhanced predatory risk for the chicks of other bird species that nest in the immediate vicinity of glass buildings, because magpies are nest predators of other, smaller birds (Parker 1984). In this way, the ecological trap for caddisflies could actually trigger a secondary ecological trap for several bird species that prey upon the caddisflies. Spiders attracted to prey upon caddisflies also become prey animals in this altered food web (Figure 5b; Horváth and Kriska unpublished data).

A similar, but more complex food web has been observed by Bernáth *et al.* (2001a) at an open-air waste

oil reservoir in Budapest, Hungary. The strongly, horizontally polarizing black surface of the oil (Figure 3b) attracts large numbers of polarotactic aquatic insect species. These insects lure various insectivorous birds and bats, which are then trapped by the sticky oil (Figure 5c, d). The carcasses of these birds and bats in turn attract other carnivorous birds (eg owls, kestrels, hawks), which may also become trapped in the oil. Ancient natural asphalt seeps have acted as massive animal traps, the most famous example of which are the Rancho La Brea tar pits in Los Angeles, California (Akersten *et al.* 1983). It is generally thought that animals were initially caught when they accidentally stumbled into these tar pools, which may have been camouflaged by dust or leaves (Akersten *et al.* 1983). Alternatively, these asphalt seeps may sometimes have been covered by rainwater, thus strengthening their polarization signature and attracting polarotactic insects and birds, and initiating a cascading trap for predators attracted to the trapped prey species.

Population ecology

The attraction of aquatic insects to PLP sources is one of the most compelling and well-documented instances of ecological traps to date (Robertson and Hutto 2006). Ecological traps occur when rapid environmental change leads organisms to prefer to settle in poor-quality habitats (Gates and Gysel 1978); behavioral cues are no longer correlated with their expected fitness outcomes. Because PLP sources can polarize light more highly than water, aquatic insects prefer to settle and lay eggs upon artificial, horizontally polarizing surfaces, even when there are suitable water bodies nearby (Horváth *et al.* 1998, 2007; Kriska *et al.* 2008a). Ecological traps that result in mortality or reproductive failure are predicted to have severe fitness consequences, leading to rapid population declines and, in some cases, complete extirpation (Kokko and Sutherland 2001). Because the most common response to PLP is attraction, and since highly and horizontally polarized light is more attractive than less polarized light (Horváth and Varjú 2004), supernormal polarization signatures may be a common mechanism for triggering ecological traps among polarization-sensitive taxa.

Because population-scale studies of the effects of PLP are just beginning, its ability to cause population declines or alter the structure, diversity, or dynamics of ecological communities is still speculative. For example, populations of certain aquatic insect groups (eg mayflies and dragonflies) are declining in countries with highly dense human populations, but this could result solely from habitat alteration and destruction. Experimental approaches would address the importance of PLP by using large, temporary, polarization traps near aquatic habitats that are otherwise unaffected by PLP. Subsequent changes in the local population size of polarization-sensitive species, their biotic interactions with other organisms (eg competition, predation), and alterations in community struc-

ture or diversity could then be attributed to the effects of PLP. Observational studies could indirectly assess the effects of PLP by comparing populations of polarotactic taxa and their aquatic communities in wetland or riparian landscapes surrounded by varying acreages of artificial polarizers (eg asphalt roads and glass buildings).

Conclusions

The surprising ubiquity of anthropogenic polarizing surfaces combined with the occurrence of sensitivity to polarized light in so many animal taxa suggest that caution in the placement and use of artificial polarizers is warranted from a conservation perspective. Great potential exists for the mitigation and elimination of the ecological consequences of PLP, through the use of alternative materials that reduce the polarization signature of human activity. Because rough surfaces reflect light with lower p values at a given angle of reflection (Kriska *et al.* 2006b), one solution is to use building materials that are as rough as possible (eg avoiding shiny bricks and glass in favor of matte surfaces). Where shiny materials cannot be avoided, lighter-colored building materials should be used in place of shiny dark (black, dark gray, or dark-colored) ones. Night lighting in parking lots and near buildings should be minimized and/or directed away from buildings, asphalt, and cars. It is particularly important for these guidelines to be implemented in proximity to rivers, lakes, and other water bodies. Because polarotactic organisms can also use cues other than polarized light in selecting habitats, even relatively moderate reductions in the polarized light signature associated with human structures (eg with a degree of polarization more typical of natural habitats) may allow organisms to make adaptive decisions.

Although it is clear that the extent of PLP in natural environments is likely to increase proportionally to the enhanced use of artificial polarizers in human endeavors, the magnitude of the ecological consequences associated with increases in PLP is still difficult to predict with certainty. Future research needs regarding PLP can be grouped into two major categories: (1) monitoring and measuring the sources of PLP with imaging polarimetry, and (2) probing the organismal and ecological consequences of PLP. Surveying the human-made optical environment to establish further possible sources of PLP is essential. For example, photovoltaic solar panels are a possible source of PLP (Figure 6a), and production of these is predicted to increase in response to rising energy prices.

Research continues to add to the surprisingly long list of animals that have evolved the ability to detect polarization as well as to describe fascinating new uses for it. Yet our knowledge of the functional nature and the importance of polarization sensitivity in animals remains relatively limited. Because some organisms (eg polarotactic insects) are attracted not only by linearly polarized light, but also by artificial night lights, we need to investigate the synergistic interactions between polarotaxis

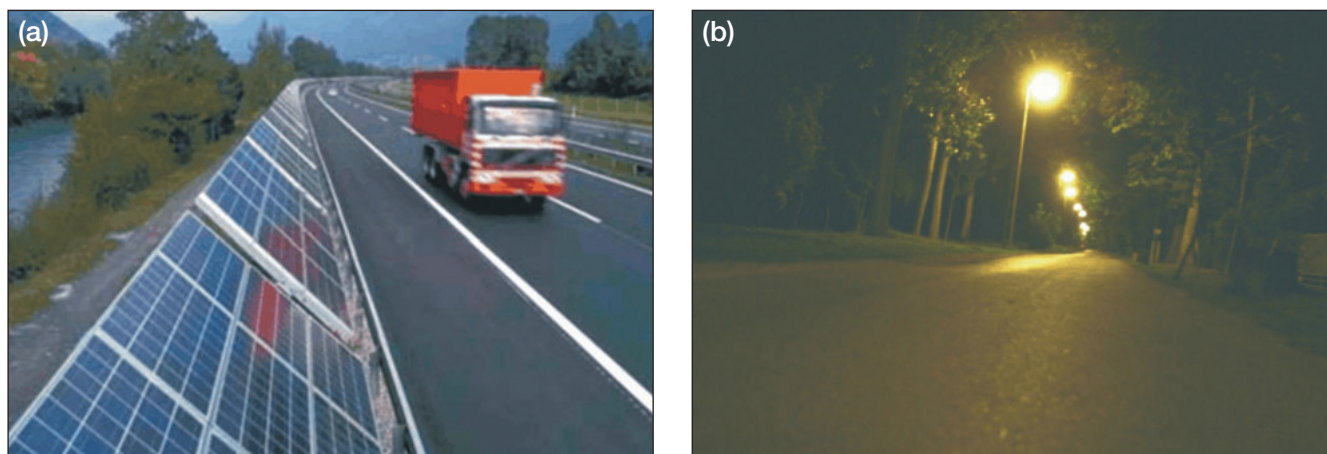


Figure 6. PLP sources to be studied. (a) The PLP induced by the shiny, black surface of photovoltaic solar panels at the edge of an asphalt road running alongside a river bank is synergetically strengthened by the PLP caused by the asphalt surface. (b) The PLP of asphalt roads illuminated by streetlamps at night is synergetically supported by the photopollution of the lamps. Night-flying polarotactic insects may be lured by phototaxis to the streetlamps, and are then attracted to the horizontally polarizing asphalt.

and phototaxis in the behavioral ecology of these species (Figure 6b). In addition to their diurnal effects, artificial lights illuminate a vast array of marine and freshwater habitats at night, in both urban and rural areas. Night lighting is a major source of ELP, but can also produce PLP via (1) reflection from buildings and other structures (Figures 2 and 3) and (2) the creation of underwater polarization signatures through scattering in the hydrosphere, which may affect ecological interactions among aquatic organisms.

Because the advantages of sensitivity to polarized light in some taxa are still unclear, forecasting the importance of PLP to the survival of populations and the integrity and function of ecosystems remains largely speculative. Even so, the ever-increasing levels of PLP and its ability to negatively affect behaviors and to alter interspecific interactions constitute an important conservation problem, which requires increased attention from conservation professionals and researchers alike.

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■ References

- Akersten WA, Shaw CA, and Jefferson GT. 1983. Rancho La Brea: status and future. *Paleobiol* **9**: 211–17.
- Bernáth B, Szedenics G, Molnár G, *et al.* 2001a. Visual ecological impact of a peculiar waste oil lake on the avifauna: dual-choice field experiments with water-seeking birds using huge shiny black and white plastic sheets. *Arch Nature Conserv Landsc Res* **40**: 1–28.
- Bernáth B, Szedenics G, Molnár G, *et al.* 2001b. Visual ecological impact of “shiny black anthropogenic products” on aquatic insects: oil reservoirs and plastic sheets as polarized traps for insects associated with water. *Arch Nature Conserv Landsc Res* **40**: 89–109.
- Bernáth B, Kriska G, Suhai B, and Horváth G. 2008. Wagtails (Aves: Motacillidae) as insect indicators on plastic sheets attracting polarotactic aquatic insects. *Acta Zool Acad Sci H* **54**: 145–55.
- Bugoni L, Krause L, and Petry MV. 2001. Marine debris and human impacts on sea turtles in southern Brazil. *Marine Pollut Bull* **42**: 1330–34.
- Coulson KL. 1988. Polarization and intensity of light in the atmosphere. Hampton, VA: A Deepak Publishing.
- Dacke M, Nilsson ED, Scholtz CH, *et al.* 2003. Insect orientation to polarized moonlight. *Nature* **424**: 33.
- Danthanarayana W and Dashper S. 1986. Response of some night-flying insects to polarized light. In: Danthanarayana W (Ed). *Insect flight: dispersal and migration*. Berlin, Germany: Springer-Verlag.
- Derraik J. 2002. The pollution of the marine environment by plastic debris: a review. *Marine Poll Bull* **44**: 842–52.
- Duguay R, Moriniere P, and Lemilinaire C. 1998. Factors of mortality of marine turtles in the Bay of Biscay. *Oceanol Acta* **21**: 383–88.
- Eisenbeis G. 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: Rich C and Longcore T (Eds). *Ecological consequences of artificial night lighting*. Washington, DC: Island Press.
- Gates JE and Gysel LW. 1978. Avian nest dispersion and fledging success in field–forest ecotones. *Ecology* **59**: 871–83.
- Gramentz D. 1988. Involvement of loggerhead turtle with the plastic, metal and hydrocarbon pollution in the central Mediterranean. *Marine Pollut Bull* **19**: 11–13.
- Henze MJ and Labhart T. 2007. Haze, clouds and limited sky visibility: polarotactic orientation of crickets under difficult stimulus conditions. *J Exp Biol* **210**: 3266–76.
- Horváth G and Zeil J. 1996. Kuwait oil lakes as insect traps. *Nature* **379**: 303–04.
- Horváth G, Bernáth B, and Molnár G. 1998. Dragonflies find crude oil visually more attractive than water: multiple-choice experiments on dragonfly polarotaxis. *Naturwissenschaften* **85**: 292–97.
- Horváth G and Varjú D. 2004. *Polarized light in animal vision–polarization patterns in nature*. Berlin, Germany: Springer-Verlag.
- Horváth G, Malik P, Kriska G, and Wildermuth H. 2007.

- Ecological traps for dragonflies in a cemetery: the attraction of *Sympetrum* species (Odonata: Libellulidae) by horizontally polarizing black gravestones. *Freshwater Biol* **52**: 1700–09.
- Horváth G and Kriska G. 2008. Polarization vision in aquatic insects and ecological traps for polarotactic insects. In: Lancaster J and Briers RA (Eds). *Aquatic insects: challenges to populations*. Wallingford, UK: CAB International Publishing.
- Horváth G and Pomozi I. 1997. How celestial polarization changes due to reflection from the deflector panels used in deflector loft and mirror experiments studying avian navigation. *J Theor Biol* **184**: 291–300.
- Horváth G, Majer J, Horváth L, *et al.* 2008. Ventral polarization vision in tabanids: horseflies and deerflies (Diptera: Tabanidae) are attracted to horizontally polarized light. *Naturwissenschaften* **95**: 1093–1100.
- Kokko H and Sutherland WJ. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evol Ecol Res* **3**: 537–51.
- Kovarov BG and Monchadskiy AS. 1963. About the application of polarized light in light-traps to catch insects. *Entomologicheskoy Obozrenie* **42**: 49–55.
- Können GP. 1985. *Polarized light in nature*. Cambridge, UK: Cambridge University Press.
- Kriska G, Horváth G, and Andrikovics S. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *J Exp Biol* **201**: 2273–86.
- Kriska G, Csabai Z, Boda P, *et al.* 2006a. Why do red and dark-coloured cars lure aquatic insects? The attraction of water insects to car paintwork explained by reflection–polarisation signals. *P Roy Soc B* **273**: 1667–71.
- Kriska G, Malik P, Csabai Z, and Horváth G. 2006b. Why do highly polarizing black burnt-up stubble-fields not attract aquatic insects? An exception proving the rule. *Vision Res* **46**: 4382–86.
- Kriska G, Bernáth B, and Horváth G. 2007. Positive polarotaxis in a mayfly that never leaves the water surface: polarotactic water detection in *Palingenia longicauda* (Ephemeroptera). *Naturwissenschaften* **94**: 148–54.
- Kriska G, Malik P, Szivák I, and Horváth G. 2008a. Glass buildings on river banks as “polarized light traps” for mass-swarming polarotactic caddis flies. *Naturwissenschaften* **95**: 461–67.
- Kriska G, Barta A, Suhai B, *et al.* 2008b. Do brown pelicans mistake asphalt roads for water in deserts? *Acta Zool Acad Sci H* **54**: 157–65.
- Labhart T and Meyer EP. 2002. Neural mechanisms in insect navigation: polarization compass and odometer. *Curr Opin Neurobiol* **12**: 707–14.
- Longcore T and Rich C. 2004. Ecological light pollution. *Front Ecol Environ* **2**: 191–98.
- Lythgoe JN and Hemmings CC. 1967. Polarized light and underwater vision. *Nature* **213**: 893–94.
- Malik P, Hegedüs R, Kriska G, and Horváth G. 2008. Imaging polarimetry of glass buildings: why do vertical glass surfaces attract polarotactic insects? *Appl Optics* **47**: 4361–74.
- Marshall J, Cronin TW, Shashar N, and Land M. 1999. Behavioural evidence for polarisation vision in stomatopods reveals a potential channel for communication. *Curr Biol* **9**: 755–58.
- McCauley SJ and Bjørndal KA. 1999. Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatchling loggerhead sea turtles. *Conserv Biol* **13**: 925–29.
- McIntyre JW and Barr JF. 1997. Common loon (*Gavia immer*). In: Poole A (Ed). *The birds of North America online*. Ithaca, NY: Cornell Lab of Ornithology.
- Montevicchi WA and Stenhouse IJ. 2002. Dovekie (*Alle alle*). In: Poole A (Ed). *The birds of North America online*. Ithaca, NY: Cornell Lab of Ornithology.
- Novales Flamarique I and Brownman HI. 2001. Foraging and prey-search behaviour of small juvenile rainbow trout (*Oncorhynchus mykiss*) under polarized light. *J Exp Biol* **204**: 2415–22.
- Nowinszky L. 2003. *The handbook of light trapping*. Szombathely, Hungary: Savaria University Press.
- Parker H. 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. *J Wildl Manage* **48**: 1197–1205.
- Rich C and Longcore T. 2006. *Ecological consequences of artificial night lighting*. Washington, DC: Island Press.
- Robertson BA and Hutto RL. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* **87**: 1075–85.
- Schwind R. 1985. Sehen unter und über Wasser, sehen von Wasser. *Naturwissenschaften* **72**: 343–52.
- Schwind R. 1991. Polarization vision in water insects and insects living on a moist substrate. *J Comp Physiol A* **169**: 531–40.
- Schwind R. 1995. Spectral regions in which aquatic insects see reflected polarized light. *J Comp Physiol* **177**: 439–48.
- Shashar N, Hanlon RT, and Petz AM. 1998. Polarization vision helps detect transparent prey. *Nature* **393**: 222–23.
- Tovée MJ. 1995. Ultra-violet photoreceptors in the animal kingdom: their distribution and function. *Trends Ecol Evol* **10**: 455–60.
- Umow N. 1905. Chromatische depolarisation durch Lichtstreuung. *Phys Z* **6**: 674–76.
- von Frisch K. 1967. *The dance language and orientation of bees*. Cambridge, MA: Belknap Press/Harvard University Press.
- Waterman TH. 2006. Reviving a neglected celestial underwater polarization compass for aquatic animals. *Biol Rev* **81**: 111–15.
- Wehner R. 2001. Polarization vision – a uniform sensory capacity? *J Exp Biol* **204**: 2589–96.
- Wehner R and Labhart T. 2006. Polarization vision. In: Warrant EJ and Nilsson DE (Eds). *Invertebrate vision*. Cambridge, UK: Cambridge University Press.
- Wildermuth H. 1998. Dragonflies recognize the water of rendezvous and oviposition sites by horizontally polarized light: a behavioural field test. *Naturwissenschaften* **85**: 297–302.
- Wildermuth H and Horváth G. 2005. Visual deception of a male *Libellula depressa* by the shiny surface of a parked car (Odonata: Libellulidae). *Int J Odonatol* **8**: 97–105.