Acta Zoologica Academiae Scientiarum Hungaricae 56 (3), pp. 283–293, 2010

GLASS BUILDINGS AS BIRD FEEDERS: URBAN BIRDS EXPLOIT INSECTS TRAPPED BY POLARIZED LIGHT POLLUTION

ROBERTSON, B.[1], KRISKA, GY.[2], HORVÁTH, V.[3] and HORVÁTH, G.[3]

[1]*W. K. Kellogg Biological Station, Michigan State University*
3700 East Gull Lake Drive Hickory Corners, MI 49060, USA
[2]*Group for Methodology in Biology Teaching, Biological Institute, Eötvös University*
H-1117 Budapest, Pázmány sétány 1, Hungary, E-mail: kriska@ludens.elte.hu
[3]*Environmental Optics Laboratory, Department of Biological Physics, Physical Institute*
Eötvös University, H-1117 Budapest, Pázmány sétány 1, Hungary, E-mail: gh@arago.elte.hu

Glass buildings can highly and horizontally polarize reflected sunlight and skylight, fooling polarotactic aquatic insects into thinking they are exaggerated water surfaces and high quality breeding habitat. We find that several urban generalist bird species are exploiting a caddis fly population caught by reflected polarized light. Daily patterns of European Magpie foraging behaviour indicate birds regularly visit a highly polarizing glass building to feed on attracted polarotactic caddis flies near sunrise and sunset. Foraging behaviours used by terrestrial land birds to collect caddis flies were typical of those used in more natural environments. This is the first example of exploitation of a species that is victim of polarized light pollution. Results demonstrate the ability of polarized light pollution to create novel predator-prey interactions, a phenomenon that may be a common and widespread occurrence where polarizing structures are built near freshwater. Because birds are consuming prey that will eventually experience reproductive and adult mortality associated with the polarized light trap, this scenario appears to represent a clear case of compensatory mortality.

Key words: urban birds, visual deception, feeding, polarotaxis, polarized light pollution

INTRODUCTION

Rapidly changing environments have the potential to disrupt evolved behaviours because organisms using environmental cues to direct their behaviour may no longer experience the outcomes historically associated with responding to those cues (LEVINS 1968). Ecological traps are scenarios in which rapid environmental change leads organisms to actually prefer to settle in poor-quality habitats (DWERNYCHUK & BOAG 1972). They represent severe cases of behavioural maladaptation that have the potential to lead to population declines or extirpation (KOKKO & SUTHERLAND 2001). Despite rapidly growing awareness of ecological traps among ecologists and conservation biologists, evidence supports the existence of fewer than 10 well-documented cases (ROBERTSON & HUTTO 2006, 2007, HEDIN *et al.* 2008, CARRETE *et al.* 2009, RESATARITS & BINCKLEY 2009), many involving birds.

The most mechanistically well-understood cases of ecological traps are those in which strong artificial sources of horizontally polarized light (e.g. shiny dark asphalt) are supernormally attractive to polarotactic aquatic insects that have evolved the ability to locate lakes and rivers by the highly and horizontally polarized light they reflect (e.g. KRISKA *et al.* 1998). For example, KRISKA *et al.* (2008) and MALIK *et al.* (2008) have observed that caddis flies (*Hydropsyche pellucidula*) are lured to swarm *en masse* at dusk at vertical glass surfaces of buildings standing on the bank of the river Danube (Fig. 1A,B). Individuals land upon the glass panes where they mate and oviposit (Fig. 1C-E), actually preferring this artificial substrate to the nearby river. Eggs experience complete mortality (KRISKA *et al.* 2008) and most adults are unable to escape by overcoming their attraction to the polarized light signature of the building's glass surfaces and die of exhaustion, a phenomenon known as the 'polarization captivity effect' (HORVÁTH *et al*. 2009).

We report here on our observation that urban bird species are exploiting congregations of caddis flies trapped by a newly described form of ecological photopollution, the so-called "polarized light pollution" (HORVÁTH *et al*. 2009). This is the first example of exploitation of a species that is victim of polarized light pollution. Our goals are fourfold: to 1) characterize the distribution of caddis flies in relation to variation in artificial polarizing surfaces and other features on a riparian structure, 2) describe the bird species that are preying upon caddis flies caught by polarized reflected light, 3) describe the foraging behaviours birds are using to capture caddis flies, and 4) discuss the possible consequences of this novel ecological interaction for predators and polarotactic prey.

MATERIALS AND METHODS

This study was conducted in April and May 2006 and 2007 at the northern building of the Faculty of Natural Sciences of the Eötvös University in Budapest, Hungary (47°29'N, 19°3'E). The building is situated 100 m from the bank of the river Danube. In natural environments, caddis flies (Trichoptera) emerge from bodies of water, where they swarm, copulate and lay only a single clutch of eggs on the water surface before dying (HOELL *et al.* 1998). Patterns of reproductive behaviour near the artificial polarizing surface of the building parallel this pattern. Caddis flies (*Hydropsyche pellucidula*) at this location swarm at dusk under calm and warm conditions peaking around 19 hours (= local summer time = UTC + 2 h), just prior to sunset (KRISKA *et al.* 2008, MALIK *et al.* 2008). Swarming ends at about 21 hours, at which time caddis flies that have not yet mated leave the glass buildings until the following day while a minority remain resting on the glass panes. Between two subsequent swarming periods at dusk, caddis flies rest in niches between bricks and on the glass panes of the shady regions of the building (KRISKA *et al.* 2008, MALIK *et al.* 2008).

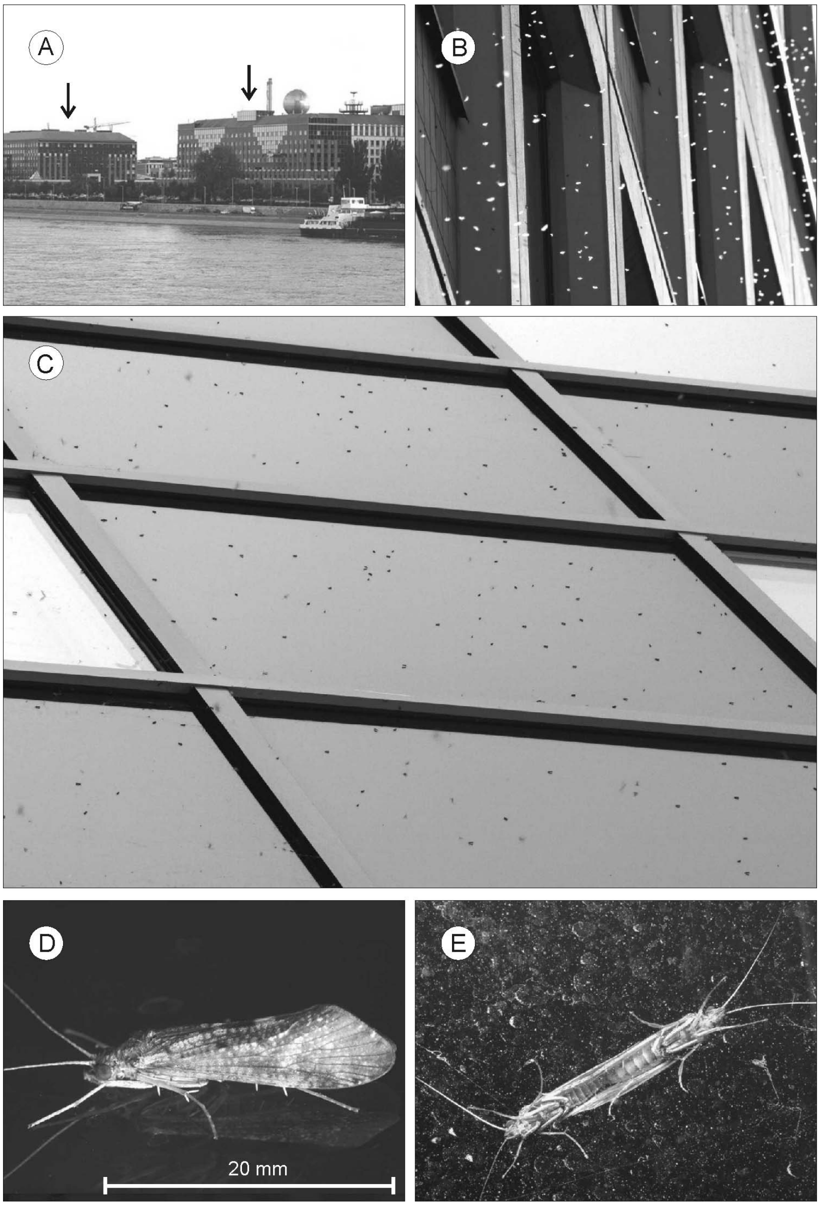

Fig. 1. (A) The southern (left arrow) and northern (right arrow) building of the Faculty of Natural Sciences of the Eötvös University in Budapest seen from the river Danube. (B) Mass-swarming caddis flies (*Hydropsyche pellucidula*, white dots) at the vertical glass surfaces of the northern building. (C) "Well-laid table" for urban birds: caddis fly imagoes (black dots) landed on white (untinted) and black (tinted) vertical glass surfaces. (D) An adult caddis fly landed on the outside surface of a window photographed from outside. (E) A copulating caddis fly pair on the outside surface of a window photographed from inside a room

Table 1. Numbers (mean ± standard deviation) of caddis flies (*Hydropsyche pellucidula*) landed on black (tinted) and white (untinted) vertical glass panes of the northern building of the Eötvös University in Budapest averaged for 50 black and 50 white quadratic (2 m × 2 m) glass surfaces. On a given day each counting for 50 black and 50 white glass surfaces was performed three times, at 17:30, 18:00 and 18:30 h (= local summer time = UTC + 2 h), and the counts made at each time interval within a day were averaged.

No.	date (2007)	vertical glass surface	
		black	white
1	19 April	6.6±3.5	2.2±1.0
2	20 April	10.1±4.2	3.0±1.3
3	22 April	17.2±5.3	5.3±2.2
4	1 May	28.5±11.3	5.1±2.1

On five days between 19 April and 5 May 2007 we counted the numbers of *H. pellucidula* on 100 vertical panes of glass (each 2 m × 2 m) of the building (Fig. 1, Table 1). Using binoculars, we counted caddis fly numbers on each pane every day at 17:30, 18:00 and 18:30 hours (UTC + 2 h) under clear sky, in calm and warm weather. Each counting period took approximately 5 minutes. The brightness and colour of artificial polarizing surfaces is known to affect the degree of polarization of reflected light (darker surfaces reflect more highly polarized light, reviewed in HORVÁTH & VARJÚ 2004). Because glass panes on the structure are either darkly tinted or untinted, we divided our observations between 50 tinted and 50 untinted vertical panes that were randomly selected daily. We tested for differences in caddis fly abundances between tinted and untinted panes using repeated-measures ANOVA, with caddis fly abundance each day as the repeated measure and tinted/untinted as the between-subject factor (Table 1).

Bird identifications were made between 17 and 23 May 2007. To document the occurrence of birds attracted by the caddis flies swarming at and landing on the building's glass surfaces, a common web camera was placed in a room at the third floor, in the south-west corner of the building. The camera was positioned so that it could simultaneously monitor any bird behaviour at each of two windows (both tinted) aligned perpendicularly to each other in one of the corners of the room. This location was chosen because small ledge runs along the edge of the building outside and below both windows, where anecdotal observations showed birds commonly appeared and foraged. The web camera recorded the scenery continuously for 24 hours every day. Video data was stored on a personal computer, then evaluated visually at a later date. During this same period, we supplemented video observations with observations made through binoculars of birds feeding on caddis flies that had landed upon the building or were swarming in close proximity. In order to enable the observation of more species, these binocular observations were specifically directed to other spots of the building. From the data obtained with the use of the webcam we determined whether daily patterns of avian foraging behaviour on the building was distributed randomly throughout the day using Rao's U-test (ZAR 1999). Times of detections were converted to decimal hours for analysis and reconverted to a 24 hour clock for presentation (Fig. 3). For statistical analyses we used Statistica 6.0.

RESULTS

A repeated measures ANOVA of the data in Table 1 revealed caddis flies (average body length = 20 mm, average body mass = 0.4 gram) were more abundant upon black (tinted: mean = 25.5, standard deviation = 15.6) than white (untinted: mean = 4.9, SD = 1.19) glass panes (see also Fig. 1C) ($F_{4,388} = 239.1$, $P < 0.0001$), and their number increased throughout the five day sample period ($F_{4,388} = 372.7$, $P < 0.0001$). The assumption of sphericity was met ($\chi_1 = 3.0$, $P = 0.08$).

On the basis of our observations with the use of binoculars, we identified four bird species predating caddis flies from the surface of the building or in its immediate airspace: white wagtails (*Motacilla alba*), house sparrows (*Passer domesticus*), great tits (*Parus major*) and European magpies (*Pica pica*). Although it is imaginable that our webcamera have repeatedly observed the same individuals, e.g. a single pair of magpies, from the visual (binocular) observations we established that

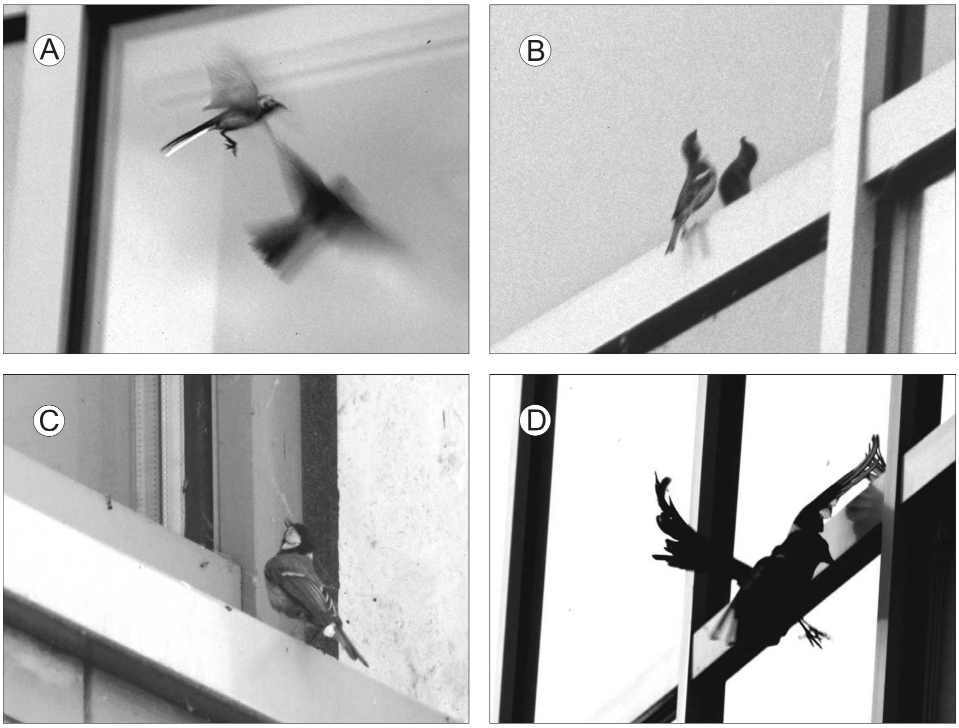

Fig. 2. (A) Hovering white wagtail (*Motacilla alba*) catching caddis flies from a window. (B) House sparrow (*Passer domesticus*) capturing caddis flies from a vertical glass surface. (C) Great tit (*Parus major*) standing on a window's edge and catching caddis flies. (D) European magpie (*Pica pica*) on wing capturing landed caddis flies from a window

about 5–6 individuals of each bird species mentioned occurred continuously around the building. White wagtails typically perched on the building's ledges, or high on the roof edge from which they flew up to hover-glean caddis flies from window surfaces (Fig. 2A). Individuals appeared to move systematically to a new pane of glass after exhausting the supply of prey upon their closest pane. Wagtail individuals remained at a single location for several minutes before flying up to glean a caddis fly from the glass. House sparrows (Fig. 2B) and great tits (Fig. 2C) exhibited similar foraging techniques for capturing caddis flies. Individuals stood on the narrow metal window-frames surrounding each glass pane while closely focusing their attention on caddis flies upon the glass above them (Fig. 2B,C). Unlike wagtails, great tits and house sparrows were never observed to catch flying caddis flies.

European magpies were detected by a web camera every day during the sampling period (range 2–11 detections/day). Magpies settled on the horizontal surface of the building edge and picked up the caddis flies from the surface of the horizontal ledge, but were also observed to glean prey from the vertical glass panes while in flight (Fig. 2D). After repeated successful captures, magpies were often observed to move to the next adjacent window pain before resuming foraging. The web camera primarily captured European magpie activity (47/48 detections), so we confined analysis of daily foraging patterns to this species. According to Fig. 3, the timing of

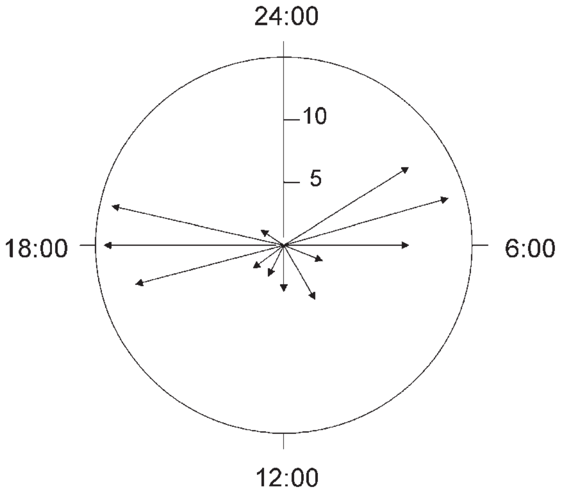

Fig. 3. Timing of foraging visits of European magpie (*Pica pica*) to the northern building of the Eötvös University as detected by a web camera from 17:00 h on 16 May to 20:00 h on 23 May in 2007. Arrow lengths represent the proportion of all visits made during a particular hour over the course of the 8-day observation time (scale = 0–15%)

magpie visits to camera-visible ledges was non-random (Rao's U = 156, P = 0.01, n = 47) and exhibited a bimodal pattern of visits peaking around dawn and sunset. These results obtained with the web camera were corroborated by those gathered during our visual observations around the buildings with the use of binoculars.

DISCUSSION

We found that several common urban-breeding bird species (Fig. 2) are able to supplement their diet by taking advantage of an atypical prey species caught by polarized light pollution (Fig. 1). It is known that predators can act as the agent of selection reducing the fitness of other organisms in their preferred habitats, and so trigger the creation of ecological trap (REMEŠ 2003, WELDON & HADDAD 2005, ROBERTSON & HUTTO 2007), but this is the first example of exploitation of a species that has already become trapped by polarized light pollution.

Under natural conditions, caddis flies may become accessible prey to terrestrial land birds when they perch on riparian vegetation, but their tendency to remain on, above or under the water surface when in their adult form (HOELL *et al.* 1998) makes them generally inaccessible to avian predators such as wagtails, great tits and magpies, for example. Foraging tactics used by birds observed to capture caddis flies on the buildings in this study (Fig. 2) were typical of their techniques in more natural settings (MADGE & BURN 1994, HARRAP & QUINN 1996, BADYAEV 2003, ANDERSON 2006). Moreover, daily patterns of magpie occurrence (Fig. 3) illustrate that at least a few individuals exploit caddis flies attracted to the horizontally polarized light reflected off the glass building as a food source (Fig. 1).

It remains unclear whether or not any individual caddis flies are able to escape this polarized ecological trap once attracted to the building, but the link between caddis fly abundance on glass panes and the darkness (tinting) of glass panes on this building demonstrate that some portions of the structure are less attractive to caddis flies (Fig. 1C, Table 1) and, so may also be to birds. The single most important habitat selection cue for polarotactic aquatic insects including caddis flies (*Hydropsyche pellucidula*) is the presence of horizontally polarized light, because it is the most reliable visual signal indicating the presence of water under variable illumination conditions (HORVÁTH & VARJÚ 2004). Strong reliance on this cue and the supernormal degree of polarization associated with artificial polarizers like glass buildings (~100%) relative to natural water bodies (typically < 70%, HORVÁTH & VARJÚ 2004), suggests severe and persistent ecological traps will occur for these insects wherever artificial polarizing structures are built in close proximity to natural water bodies. Consequently, birds exploiting trapped populations of polarotactic aquatic insects as prey may be a geographically widespread phenomenon.

We did not quantify the abundance or predation efficiency of avian predators in order to estimate their potential impact on the caddis fly population, but we expect it to be negligible. This situation appears to represent a clear and extreme example of a "doomed surplus" in which predation from a particular predator is a surplus, or compensatory source of mortality, rather than an additive one (ERRINGTON 1946). Even in the absence of predation by birds, caddis flies attracted to artificial polarizing structures will experience reproductive failure followed by mortality associated with the effects of the ecological trap (exhaustion) and the species semelparous natural history (KRISKA *et al.* 2008, HORVÁTH *et al.* 2009). Even if predators were to become hyper-abundant, they should have no effect upon caddis fly population growth unless a significant fraction of caddis flies are both capable of escaping the trap prior to oviposition and are predated before this can happen. In contrast, equivalent levels of avian predation of polarotactic insect species with iteroparous life-history strategies (e.g. diving beetles, KRISKA *et al.* 2006) caught in traps would be predicted to have measurable population-scale effects because these individuals would otherwise have the opportunity to reproduce again.

We frequently observed white wagtails, house sparrows and great tits with their bill full of captured caddis flies, indicating prey were being collected to provision young. Food availability is an important factor influencing current and future reproductive success in birds (HANSSEN *et al.* 2005, HEANEY & MONAGHAN 1996) and so we expect the availability of a highly visible and abundant prey source to have a generally positive impact on species able to capture them. The period of feeding young is regarded as the most energetically demanding periods in the annual cycle of birds (WEATHERS & SULLIVAN 1993) and caddis fly concentrations are likely to increase foraging efficiency of parents, freeing up time and energy for investment in other activities.

Our finding represents a case of animal innovation, although the birds did not use novel behavioural techniques, they exploited a novel resource both in terms of prey species and foraging site. If this is really a geographically widespread phenomenon, as we suggest, it might be a significant factor affecting urban bird ecology and even conservation. For example, increasing densities of nest predators (e.g. magpies) could have detrimental effects on the reproductive success of other urban nesting birds. Alternatively, higher densities of non-native cavity nesting birds (e.g. House Sparrow) could increase competition for nest sites with native birds.

This work demonstrates for the first time the ability of polarized light pollution to create novel predator-prey interactions which are qualitatively similar to the hunting of insects attracted to streetlamps at night by anuran amphibians (BUCHA-

NAN 2006), reptiles (PERRY & FISHER 2006), birds (EISENBEIS 2006), bats (RYDELL 2006) and spiders (FRANK 2006), a well-known secondary effect of the conventional (non-polarized) ecological light pollution.

*

Acknowledgements – GÁBOR HORVÁTH is grateful for the equipment donation of the German Alexander von Humboldt Foundation. This work was supported by the grant OTKA K-6846 of the Hungarian Sciencific Research Fund.

REFERENCES

ANDERSON, T. R. (2006) *Biology of the ubiquitous House Sparrow: from genes to populations*. Oxford University Press, Oxford, UK.

BADYAEV, A. V. (2003) Family Motacillidae. *In:* PERRINS, C. (ed.): *Encyclopedia of birds*. Edward Grey Institute of Field Ornithology and Andromeda Oxford Limited, Oxford, UK.

BUCHANAN, B. W. (2006) Observed and potential effects of artificial night lighting on anuran amphibians. Pp. 192–220. *In:* RICH, C. & LONGCORE, T. (eds): *Ecological consequences of artificial night lighting*. Island Press, Washington – Covelo – London.

CARRETE, M., SERRANO, D., ILLERA, J. C., GUILLERMO, L. P., VÖGELLI, M., DELGADO, A. & TELLA, J. L. (2009) Goats, birds, and emergent diseases: apparent and hidden effects of exotic species in an island environment. *Ecological Applications* **19**: 840–853.

DWERNYCHUK, L. W. & BOAG, D. A. (1972) Ducks nesting in association with gulls – an ecological trap? *Canadian Journal of Zoology* **50**: 559–563.

EISENBEIS, G. (2006) Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. Pp. 281–304. *In:* RICH, C. & LONGCORE, T. (eds): *Ecological consequences of artificial night lighting*. Island Press, Washington – Covelo – London.

ERRINGTON, P. L. (1946) Predation and vertebrate populations. *Quarterly Review of Biology* **21**: 144–177.

FRANK, K. D. (2006) Effects of artificial night lighting on moths. Pp. 305–344. *In:* RICH, C. & LONGCORE, T. (eds): *Ecological consequences of artificial night lighting*. Island Press, Washington – Covelo – London.

HANSSEN, S. A., HASSELQUIST, D., FOLSTAD, I. & ERIKSTAD, K. E. (2005) Cost of reproduction in a long-lived bird: Incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society of London, Series B* **272**: 1039–1046.

HARRAP S. & QUINN, D (1996) *Tits, Nuthatches and Treecreepers*. Princeton University Press, Princeton, New Jersey, USA.

HEANEY, V. & MONAGHAN, P. (1996) Optimal allocation of effort between reproductive phases: The trade-off between incubation costs and subsequent brood rearing capacity. *Proceedings of the Royal Society of London, Series B* **263**: 1719–1724.

HEDIN, J., ISACSSON, G., JONSELL, M. & KOMONEN, A. (2008) Forest fuel piles as ecological traps for saproxylic beetles in oak. *Scandinavian Journal of Forest Research* **23**: 348–357.

HOELL, H. V., DOYEN, J. T. & PURCELL, A. H. (1998) *Introduction to insect biology and diversity.* 2nd ed., Oxford University Press, Oxford, UK. 320 pp.

HORVÁTH, G. & VARJÚ, D. (2004) *Polarized light in animal vision – polarization patterns in nature*. Springer Verlag, Heidelberg – Berlin – New York, 447 pp.

HORVÁTH, G., KRISKA, G., MALIK, P. & ROBERTSON, B. (2009) Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment* **7**: 317–325.

KOKKO, H. & SUTHERLAND, W. J. (2001) Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research* **3**: 537–551.

KRISKA, G., HORVÁTH, G. & ANDRIKOVICS, S. (1998) Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *Journal of Experimental Biology* **201**: 2273–2286.

KRISKA, G., MALIK, P., SZIVÁK, I. & HORVÁTH, G. (2008) Glass buildings on river banks as “polarized light traps” for mass-swarming polarotactic caddis flies. *Naturwissenschaften* **95**: 461–467.

KRISKA, G., CSABAI, Z., BODA, P. & MALIK, P. G. (2006) Why do red and dark-coloured cars lure aquatic insects? The attraction of water insects to car paintwork explained by reflection–polarization signals. *Proceedings of the Royal Society of London B* **273**: 1667–1671.

LEVINS, R. (1968) *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, USA, 120 pp.

MADGE, S. & BURN, H. (1994) *Crows and Jays: A Guide to the Crows, Jays and Magpies of the World*. A. & C. Black, London, UK, 191 pp.

MALIK, P., HEGEDÜS, R., KRISKA, G. & HORVÁTH, G. (2008) Imaging polarimetry of glass buildings: Why do vertical glass surfaces attract polarotactic insects? *Applied Optics* **47**: 4361–4374.

PERRY, G. & FISHER, R. N. (2006) Night lights and reptiles: observed and potential effects. Pp. 169–191. *In:* RICH, C. & LONGCORE, T. (eds): *Ecological consequences of artificial night lighting*. Island Press, Washington – Covelo – London.

REMEŠ, V. (2003) Effects of exotic habitat on nesting success, territory density and settlement patterns in the Blackcap (Sylvia atricapilla). *Conservation Biology* **17**: 1127–1133.

RESETARITS, W. JR. & BINCKLEY, C. A. (2009) Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. *Ecology* **90**: 869–876.

ROBERTSON, B. A. & HUTTO R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* **87**: 1075–1085.

ROBERTSON, B. A. & HUTTO, R. L. (2007) Is selectively harvested forest an ecological trap for Olive-sided Flycatchers? *Condor* **109**: 109–121.

RYDELL, J. (2006) Bats and their insect prey at streetlights. Pp. 43–60. *In:* RICH, C. & LONGCORE, T. (eds): *Ecological consequences of artificial night lighting*. Island Press, Washington – Covelo – London.

WEATHERS, W. W. & SULLIVAN, K. A. (1993) Seasonal patterns of time and energy allocation by birds. *Physiological Zoology* **66**: 511–536.

WELDON, A. J. & HADDAD, N. M. (2005) The effects of patch shape on Indigo Buntings: evidence for an ecological trap. *Ecology* **86**: 1422–1431.

ZAR, J. H. (1999) *Biostatistical analysis*. 4th ed., Prentice Hall, Upper Saddle River, New Jersey, USA, 929 pp.

Revised version received November 21, 2009, accepted April 19, 2010, published August 27, 2010