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Visual System

Reaction of Imagos of the Adzuki Bean Borer *Ostrinia Scapulalis* to Light Stimuli in a Wind Tunnel

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The attraction of nocturnal insects by light is a known phenomenon with unknown physiological mechanisms. Butterflies of the superfamily Pyraloidea mount the strongest reactions to light, though the spectral preferences of these insects have not been studied. The moth *Ostrinia scapulalis*, which lives on dicotyledonous plants and is a pest of hemp and hops, is the ancestral form of the Asian and European corn borers, widespread pests of corn. Studies using a wind tunnel modified to include a light source were run to test the responses of males and females to light stimuli with emission maxima of 532, 440, and 365 nm at an illumination of 2 lx created at the point at which the insects were released; the light used was able to stimulate the photoreceptors of both compound eyes (sensitivity peaks at 352, 413, 480, and 530 nm) and simple eyes, i.e., ocelli (main sensitivity peak in the ultraviolet region of the spectrum, with an additional peak in the green region (360 and 520 nm)). Ultraviolet light was found to be the most attractive stimulus. A small percentage of insects responded to green light and displayed freezing responses close to the light source. The least attractive was blue light, which also induced freezing. Thus, flight of *O. scapulalis* was induced by short-wavelength light. This response is more consistent with the sensitivity of ocelli than that of compound eyes. Blue or green radiation led to masking reactions.

Keywords: brush-footed moth, *Ostrinia scapulalis*, reaction to light, ultraviolet, photoreception.

Introduction. The brush-footed moth *Ostrinia scapulalis* (Wlk.) is a nocturnal insect of the grass moth family (Crambidae), whose closest relatives are widespread pests of agricultural crops such as the European *O. nubilalis* (Hbn.) and the Asian *O. furnacalis* (Gn.) stem corn moths [Mutuura and Munroe, 1970]. Thus, *O. nubilalis* is a major pest of maize in Europe, North Africa, and North America, *O. furnacalis* damages maize in Asia and Australasia, while *O. scapulalis* feeds on various species of dicotyledonous host plants in Europe and Asia, damaging cultivated legume crops: *Vigna* spp., hops *Humulus lupulus* L., and hemp *Cannabis sativa* L., as well as a number of wild and weed species, such as wormwood *Artemisia vulgaris* L., cocklebur *Xanthium strumarium* L., giant sumpweed *Cyclachaena xanthiifolia* (Nutt.) Fresen, ragweed *Ambrosia artemisiifolia* L., and many others [Mutuura and Munroe, 1970; Frolov, 1984; Ishikawa et al., 1999; Frolov et al., 2007]. Feeding on dicotyledonous species of fodder plants is an ancestral trait in the genus *Ostrinia* [Yang et al., 2021]. Results from behavioral and electrophysiological experiments have provided grounds for suggesting the existence of sensory preadaptations to feeding on cereal host plants in *O. scapulalis*, which has retained ancestral trophic relationships with dicotyledonous host plants [Schenikova et al., 2020]. Although *O. nubilalis* and *O. scapulalis* are characterized by identical polymorphism of the pheromone signal in females [Huang et al., 2002; Takanashi et al., 2005], the two species retain their identities in conditions of sympatry, despite the fact that interspecies hybrids are fully viable and capable of producing fertile offspring in labora-

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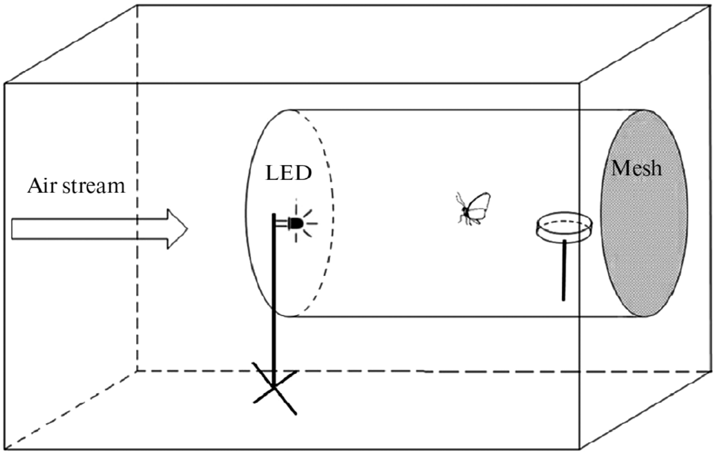

Fig. 1. Apparatus. The arrow shows the direction of air flow. LED – light-emitting diode, Mesh – mesh air outlet.

tory conditions [Frolov, 1984]. Morphologically, these species are very similar, and they are still confused [Frolov et al., 2007], so it is not surprising that although *O. scapulalis* is a very dangerous pest, the behavior and sensory systems of this insect still remain virtually unstudied.

Attraction of insects with crepuscular/nocturnal lifestyles to light is widely used to collect them, though the mechanisms of this behavior have received little study [Zhukovskaya et al., 2022; Frolov, 2022], largely because of the difficulty of creating light sources with the required characteristics.

Moths have two types of eyes – a pair of large, faceted, compound eyes and a pair of simple eyes, i.e., ocelli [Belušič et al., 2017]. Compound eyes in *Ostrinia* are of the superposition type, which is typical of many nocturnal insects, and are capable of increasing sensitivity by reducing the resolving power of the eye through the migration of screening pigment along the axis of the ommatidia. Each ommatidium of the compound eye consists of 12 photoreceptor cells, which belong to four spectral classes with sensitivity maxima of 352, 413, 480, and 530 nm, while two cells in the lower tier have the characteristics of polarization detectors [Belušič et al., 2017; Chen et al., 2019]. The overall sensitivity of the eye, measured by electroretinography, is maximal in the green part of the spectrum [Belušič et al., 2017]. Paired ocelli located on the crown, near the dorsal edge of the compound eyes, have a main sensitivity peak in the ultraviolet region of the spectrum and a small peak in the green region [Belušič et al., 2017]. This photoreceptor organ structure indicates that light of different wavelengths has a significant role in the behavior of these insects, though data accumulated to date have only identified the attraction of adults by UV light [Grushevaya et al., 2019; Frolov et al., 2021]. It is likely that the diversity of visual pigments and photoreceptors was inherited from ancestral forms, as the superfamily Pyraloidea, which includes brushfoot moths and contains species with diurnal activity [Kawahara et al., 2018]; moreover, some species of the genus *Ostrinia*, namely *O. marginalis* (Wlk.) and *O. peregrinalis* (Ev.), found at high latitudes, as well as *O. orientalis* (Mutuura et Munroe) from Japan, display mating behavior during the daytime [Ishikawa et al., 1999]. It is possible that nocturnal moths are able to use color vision both in twilight and at night, as has been previously demonstrated for the hawkmoths *Deilephila elpenor* L., *Hyles galii* (Rott.), and *H. lineata* (F.), as well as the carpenter bee *Xylocopa tranquebarica* (F.), not only for seeking nectar-bearing flowers, but also for orientation during migration [Kelber et al., 2002, 2003; Somanathan et al., 2008; Warrant and Somanathan, 2022]. Brushfoot borers, like corn borers, are primarily nocturnal [Huang et al., 1997], though observations made on the Amami Islands, located south of Kyushu, indicate that moths of this species mate during the day [Ishikawa et al., 1999]. Lepidopteran imagoes seeking host plants suitable for the development of their offspring are guided both by odor stimuli and by visual signals [Jakobsson et al., 2017].

The aim of the present work was to study the behavioral responses of brushfoot moth *O. scapulalis* imagoes to light signals of different spectral ranges in laboratory experiments.

Materials and Methods. Overwintered *O. scapulalis* pronymphs (inactive last-instar caterpillars) were collected in the spring of 2022 in wormwood plant residues in the vicinity of Zarya (formerly Zharyn) village, Smolensk region. The collected living specimens were placed in 0.5-liter glass vessels containing corrugated sheets of writing paper. Post-diapause reactivation of pronymphs was induced by thoroughly wetting the paper inserts in the vessels containing the insects with distilled water followed by transfer to an MLR-352 climate chamber (Sanyo, Panasonic), where the temperature was maintained at 25 ± 2°C with a 18:6 h light regime with the lights turned on daily at 18:00. Virgin males and females aged 3–5 days were used in the experiments. One hour before the experiment started, moths were placed individually in standard-sized Petri dishes and kept in complete darkness until the experiments were carried out.

TABLE 1. Numbers of *Ostrinia Scapulalis* Males and Females Responding and not Responding to Light in the Wind Tunnel

Light	Reactions of insects	Number	
		Females	Males
Green	Take-off	4	8
	Flight to source	4	8
	Landing by source	3	4
	Flight from source	0	0
	No reaction	16	22
	Total imagoes in experiment	20	30
Blue	Take-off	1	2
	Flight to source	1	1
	Landing by source	0	0
	Flight from source	0	1
	No reaction	11	10
	Total imagoes in experiment	12	12
UV	Take-off	20	19
	Flight to source	20	18
	Landing by source	13	14
	Flight from source	0	1
	No reaction	12	17
	Total imagoes in experiment	32	36
Control	Take-off	1	1
	Flight to source	1	1
	Landing by source	0	0
	Flight from source	0	0
	No reaction	9	11
	Total imagoes in experiment	10	12

The responses of males and females did not differ in terms of any of the parameters (χ^2 test, $p > 0.05$).

Experiments were run using single insects. Males were tested first and females second, with the aim of preventing the possible influence of female sex pheromones on males.

An air flow with a speed of 0.2–0.3 m/sec was generated in a wind tunnel made of plexiglass (150 × 70 × 70 cm) (Fig. 1) [Royer and McNeil, 1993].

Laminar air flow was ensured by placing a transparent pipe 1.00 m long and 0.40 m in diameter in the tunnel. The light source was placed at the beginning of the pipe and the Petri dish containing the insect was placed at the end of the pipe, at a height of 0.1 m from the floor of the pipe. Illumination of the initial location of insects in the tunnel was provided by LED lamps with emission peaks at 532, 440, and 365 nm at a level of 2.0 lx (illuminance was monitored using a Yu16 lux meter with an F102 photocell). Control experiments were run without turning these LED lamps on. Experiments were carried out during the dark phase of the daily cycle – the time at which the activity of these insects is maximal. After an adaptation period (3 min), the top cover of the dish containing the insect was carefully removed and the light stimulus was turned on. Observations were carried out under red (650 nm) illumination of 0.7 lux at an air temperature of 25 ± 2°C for 10 min. Take-off time, the direction of movement towards or away from the light source, and landings near the light source were recorded. Each insect was used only once in the experiment.

Experimental data were processed statistically using parametric (Student's test) and non-parametric (Fisher's ex-

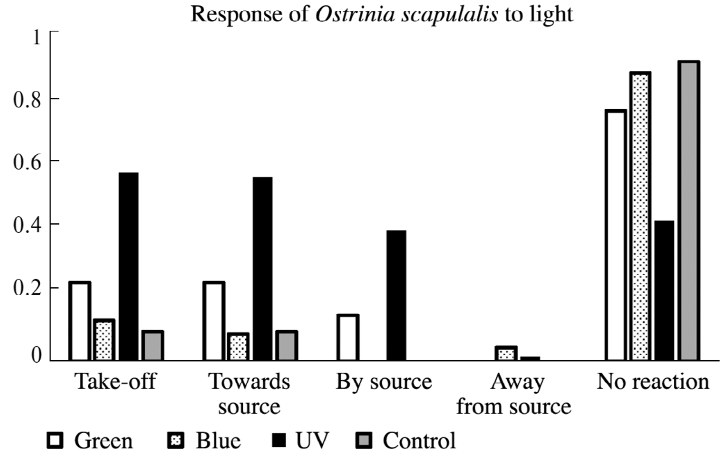

Fig. 2. Proportions of adults reacting to light with different spectral characteristics. Statistically significant differences (Fisher's exact test, $p < 0.001$) were found between reactions to UV vs. green and UV vs. blue light.

act test, Mann–Whitney test, χ^2 test) methods in MS Excel and the online calculator at http://vassarstats.net/.

Results. There were no statistically significant differences in the responses of male and female brushfoot moths to light (χ^2 test, $p > 0.05$ for all cases, Table 1), so further analysis of data did not take individuals' sex into account.

The responses of moths to UV radiation were found to be significantly greater than their responses to both green and blue light (Fig. 2): 57% of all individuals tested responded to UV light by taking off, which was significantly more than the proportions taking off in response to green and blue light (in both cases $p < 0.001$, Fisher's exact test).

The proportions of individuals reacting to blue and green light did not differ from each other ($p > 0.05$, Fisher's exact test). Most of the flying insects headed towards the light source. When presented with blue or green light, individuals landing on illuminated surfaces often demonstrated complete immobility; in response to ultraviolet light, insects stopped briefly at the source and took off repeatedly, circling above the source. Response latencies also differed between UV and visible light. Thus, the take-off time for green light was significantly longer than that for UV light ($p < 0.05$, Mann–Whitney test) (Fig. 3). As only three moths responded to the blue light, statistical comparison of this series with the others was not possible.

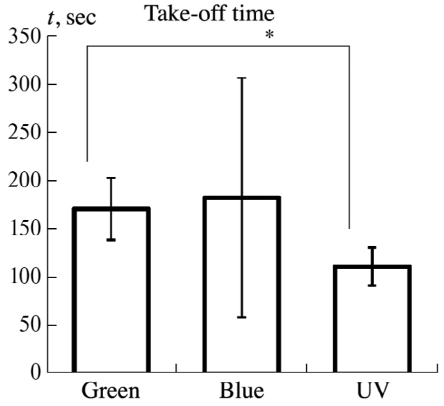

Fig. 3. Latent periods of reactions to light of different parts of the spectrum (sec) in *O. scapulalis* moths. *Significant differences ($p < 0.05$, Mann–Whitney test).

Discussion. Light is known to attract many insects belonging to different taxonomic groups [Pachkin et al., 2022]. However, the expansion of the species composition of the group of species studied here has led to the accumulation of data demonstrating significant diversity in the spectral characteristics of light that attracts insects. Thus, the oriental armyworm moth, *Mythimna separata* (Wlk.), prefers green light (520 nm) [Kim et al., 2018]. The rice yellow stem borer moth *Scirpophaga incertulas* (Wlk.) flies best under UV light (365 nm), while the rice leafroller moth *Cnaphalocrocis medinalis* (Gn.) prefers more violet light, at 400 nm [Chiranjeevi and Velmathi, 2021]. The rice green leafhopper *Nephotettix cincticeps* (Uhler) exhibits positive phototaxis over a wide range of wavelengths, from 480 to 740 nm, which appears to be mediated by a green-sensitive visual pigment with an absorption maximum at about 520 nm [Wakakuwa et al., 2014].

Wind tunnels have long been used to study the behavioral responses of insects to olfactory stimuli [Miller and Roelofs, 1978; Carde and Hagaman, 1979; Baker and Linn, 1984; Colvin et al., 1989; Charlton et al., 1993]. The directed air flow in our experiments clearly facilitates flight initiation due to stimulation of wind-sensitive receptors [Svidersky, 1980; Mohl, 1989] and allows near-natural conditions to be simulated in the laboratory. The attractiveness of visual stimuli is most frequently studied in laboratory conditions without air flow [Wakakuwa et al., 2014; Kim et al., 2018; Chiranjeevi and Velmathi, 2021], though wind has been shown to facilitate responses to green light in the whitefly *Bemisia tabaci* (Gennadius) [Isaacs et al., 1999].

Our data indicate the high attractiveness of UV light for *O. scapulalis* adults as compared with the longer-wavelength light perceived by their photoreceptors. Blue and green light did not induce significant positive phototaxis despite the fact that these insects have photoreceptors able to perceive this radiation [Belušič et al., 2017]. Blue and green light stimuli, although causing a small proportion of the moths to fly to the light source, produced radically different behavior in the animals: they sat on the illuminated surface and remained motionless. This behavior points to a masking reaction, i.e., a manifestation of behavior typical of the daytime phase of the cycle in nocturnal illumination [Mrosovsky, 1999; Novikova and Zhukovskaya, 2017] which may be associated with biological clock mechanisms. Unfortunately, the literature contains no data on the spectral characteristics of the light synchronizing circadian rhythms in moths of the genus *Ostrinia*, though in at least some Lepidoptera the circadian photoreceptor is known to be the cryptochrome pigment in brain cells [Brady et al., 2021], which is activated by blue light.

The fact that ultraviolet light was found to be the most attractive stimulus suggests that ocelli play a significant role in the flight of moths to light in nocturnal conditions – summation of the signal from a large number of photoreceptors allows initiation of a response to low-intensity light, such as moonlight under the canopy of vegetation or starlight [Mizunami, 1995]. Experiments in which ocelli were occluded or ablated showed that these organs provide an assessment of the threshold illumination for the onset of flight activity in adult *Trichoplusia ni* (Hbn.) moths [Eaton et al., 1983]. In addition, processing of signals from ocellar neurons and transmission of information to the thoracic ganglia, which is faster than from the photoreceptors of compound eyes, allows the insect to align its body position in flight in low light [Van Kleef et al., 2008].

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REFERENCES

Baker, T. C., and Linn, C. E., Jr., “Wind tunnels in pheromone research,” in: *Techniques in Pheromone Research*, Hummel, H. E. and Miller, T. A. (eds.), Springer, New York (1984), Chapter 3, pp. 75–110, https://doi.org/10.1007/978-1-4612-5220-7_3.

Belušič, G., Šporar, K., and Meglič, A., “Extreme polarisation sensitivity in the retina of the corn borer moth *Ostrinia*,” *J. Exp. Biol.*, **220**, No. 11, 2047–2056 (2017), https://doi.org/10.1242/jeb.153718.

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

Cardé, R. T. and Hagaman, T. E., “Behavioral responses of the gypsy moth in a wind tunnel to air-borne enantiomers of disparlure,” *Environ. Entomol.*, **8**, No. 3, 475–484 (1979), https://doi.org/10.1093/ee/8.3.475.

Charlton, R. E., Kanno, H., Collins, R. D., and Cardé, R. T., “Influence of pheromone concentration and ambient temperature on flight of the gypsy moth, *Lymantria dispar* (L), in a sustained-flight wind tunnel,” *Physiol. Entomol*, **18**, No. 4, 349–362 (1993), https://doi.org/10. 1111/j.1365-3032.1993.tb00608.x.

Chen, Q. X., Chen, Y. W, and Li, W.-L., “Ultrastructural comparison of the compound eyes of the Asian corn borer *Ostrinia furnacalis* (Lepidoptera: Crambidae) under light/dark adaptation,” *Arthropod Struct. Dev.*, **53**, 100901 (2019), https://doi.org/10.1016/j.asd.2019.100901.

Chiranjeevi, M. and Velmathi, G., “Phototactic behavior of yellow stemborer and rice leaf folder moths to surface mount device-light emitting diodes of various wavelengths,” *Int. J. Appl. Sci*, **19**, No. 1, 1–9 (2021), https://doi.org/10.6703/IJASE.202203_19(1).005.

Colvin, J., Brady, J., and Gibson, G., “Visually-guided, upwind turning behaviour of free-flying tsetse flies in odour-laden wind: a wind-tunnel study,” *Physiol. Entomol*, **14**, No. 1, 31–39 (1989), https://doi.org/10.1111/j.1365-3032.1989.tb00934.x.

Eaton, J. L., Tignor, K. R., and Holtzman, G. I., “Role of moth ocelli in timing flight initiation at dusk,” *Physiol. Entomol*, **8**, No. 4, 371–375 (1983), https://doi.org/10.1111/j.1365-3032.1983.tb00370.x.

Frolov, A. N., “Biotaxonomic analysis of pest species of the genus *Ostrinia* Hbn,” *Etol. Nasekom.*, **6**, 4–100 (1984).

Frolov, A. N., “Controlling the behavior of pest insects: light, chemical signals, and their joint action,” *Entomol. Obozr.*, 101, No. 3, 453–502 (2022), https://doi.org/10.31857/S0367144522030017.

Frolov, A. N., Bourguet, D., and Ponsard, S., “Reconsidering the taxonomy of several *Ostrinia* species in the light of reproductive isolation: a tale for Ernst Mayr,” *Biol. J. Linn. Soc.*, **91**, No. 1, 49–72 (2007), https://doi.org/10.1111/j.1095-8312.2007.00779.x.

Frolov, A. N., Grushevaya, I. V., and Kononchuk, A. G., *Modern Types of Traps for Monitoring Lepidoptera Using the Corn Borer as an Example. A Monograph*, Naukoemkie Tekhnologii, St. Petersburg (2021).

Grushevaya, I. V., Kononchuk, A. G., Malysh, S. M., et al., “An LED trap for monitoring the corn borer *Ostrinia nubilalis*: test results in the Krasnodar region,” *Vestn. Zash. Rasten.*, 102, No. 4, 49–54 (2019), https://doi.org/10.31993/2308-6459-2019-4-102-49-54.

Huang, Y., Takanashi, T., Hoshizaki, S., et al., “Female sex pheromone polymorphism in adzuki bean borer, *Ostrinia scapulalis*, is similar to that in European corn borer, *O. nubilalis*,” *J. Chem. Ecol.*, **28**, No. 3, 533–539 (2002), https://doi.org/10.1023/A:1014540011854.

Huang, Y., Tatsuki, S., Kim, C. G., et al., “Identification of sex pheromone of adzuki bean borer, *Ostrinia scapulalis*,” *J. Chem. Ecol.*, **23**, No. 12, 2791–2802 (1997), https://doi.org/10.1023/A:1022567111508.

Isaacs, R., Willis, M. A., and Byrne, D. N., “Modulation of whitefly take-off and flight orientation by wind speed and visual cues,” *Physiol. Entomol*, **24**, No. 4, 311–318 (1999), https://doi.org/10.1046/j.1365-3032.00144.x.

Ishikawa, Y., Takanashi, T., Kim, C. G., et al., “*Ostrinia* spp. in Japan: their host plants and sex pheromones,” *Entomol. Exp. Appl.*, **91**, 237–244 (1999), https://doi.org/10.1007/978-94-017-1890-5_30.

Jakobsson, J., Henze, M. J., et al., “Visual cues of oviposition sites and spectral sensitivity of *Cydia strobilella* L,” *J. Insect Physiol.*, **101**, 161–168 (2017), https://doi.org/10.1016/j.jinsphys.2017.06.006.

Kawahara, A. Y., Plotkin, D., Hamilton, C. A., et al., “Diel behavior in moths and butterflies: a synthesis of data illuminates the evolution of temporal activity,” *Org. Divers. Evol.*, **18**, No. 1, 13–27 (2018), https://doi.org/10.1007/s13127-017-0350-6.

Kelber, A., Balkenius, A., and Warrant, E. J., “Colour vision in diurnal and nocturnal hawkmoths,” *Integr. Comp. Biol*, **43**, 571–579 (2003), https://doi.org/10.1093/icb/43.4.571.

Kelber, A., Balkenius, A., and Warrant, E. J., “Scotopic colour vision in nocturnal hawkmoths,” *Nature*, **419**, 922–925 (2002), https://doi.org/10.1038/nature01065.

Kim, K. N., Song, H. S., Li, C. S., et al., “Effect of several factors on the phototactic response of the oriental armyworm, *Mythimna separata* (Lepidoptera: Noctuidae),” *J. Asia Pac. Entomol.*, **21**, 952–957 (2018), https://doi.org/10.1016/j.aspen.2018.07.010.

Miller, J. R. and Roelofs, W. L., “Sustained-flight tunnel for measuring insect responses to wind-borne sex pheromones,” *J. Chem. Ecol.*, **4**, No. 2, 187–198 (1978), https://doi.org/10.1007/BF00988054.

Mizunami, M., “Functional diversity of neural organization in insect ocellar systems,” *Vision Res.*, **35**, No. 4, 443–452 (1995), https://doi.org/10.1016/0042-6989(94)00192-O.

Möhl, B., "Sense organs and the control of flight," in: *Insect Flight*, Goldsworthy, G. J. (ed.), CRC Press, London, New York (1989), pp. 75–97.

Mrosovsky, N., "Masking: history, definitions, and measurement," *Chronobiol. Int.*, **16**, No. 4, 415–429 (1999), https://doi.org/10.3109/07420529908998717.

Mutuura, A. and Munroe, E., "Taxonomy and distribution of the European corn borer and allied species: genus *Ostrinia* (Lepidoptera: Pyralidae)," *Mem. Ent. Soc. Can.*, **102**, S71, 1–112 (1970), https://doi.org/10.4039/entm10271fv.

Novikova, E. S. and Zhukovskaya, M. I., "Freezing response to bright light in the American cockroach *Periplaneta americana*," *Sens. Sistemy*, 31, No. 1, 44–50 (2017).

Pachkin, A., Kremneva, O., Leptyagin, D., et al., "Light traps to study insect species diversity in soybean crops," *Agronomy*, **12**, No. 10 (2022), https://doi.org/10.3390/agronomy12102337.

Royer. L. and McNeil, J. N., "Effect of relative humidity conditions on responsiveness of European corn borer (*Ostrinia nubilalis*) males to female sex pheromone in a wind tunnel," *J. Chem. Ecol.*, **19**, 61–69 (1993).

Schenikova, A. V., Zhukovskaya, M. I., Selitskaya, O. G., et al., "Sensitivity of the olfactory system in sibling species of the genus *Ostrinia*: pre-adaptation to the development of a new host plant?" *Zh. Evol. Biokhim. Fiziol.*, **56**, No. 7, 723–729 (2020), https://doi.org/10.31857/S004445292007253x.

Somanathan, H., Borges, R. M., Warrant, E. J., and Kelber, A., "Nocturnal bees learn landmark colours in starlight," *Curr. Biol.*, **18**, No. 21 (2008), https://doi.org/10.1016/j.cub.2008.08.023.

Sviderskii, V. L., *Insect Flight*, Nauka, Moscow (1980).

Takanashi, T., Huang, Y., Takahasi, K. R., et al., "Genetic analysis and population survey of sex pheromone variation in the adzuki bean borer moth, *Ostrinia scapulalis*," *Biol. J. Linn. Soc.*, **84**, No. 1, 143–160 (2005), https://doi.org/10.1111/j.1095-8312.2005.00421.x.

Van Kleef, J., Berry, R., and Stange, G., "Directional selectivity in the simple eye of an insect," *J. Neurosci.*, **28**, No. 11, 2845–2855 (2008), https://doi.org/10.1523/JNEUROSCI.5556-07.2008.

Wakakuwa, M., Stewart, F., Matsumoto, Y., et al., "Physiological basis of phototaxis to near-infrared light in *Nephotettix cincticeps*," *J. Comp. Physiol. A*, **200**, 527–536 (2014), https://doi.org/10.1007/s00359-014-0892-4.

Warrant, E. and Somanathan, H., "Colour vision in nocturnal insects," *Philos. Trans. Roy. Soc. Lond. B, Biol. Sci*, **377**, No. 1862 (2022), https://doi.org/10.1098/rstb.2021.0285.

Yang, Z., Plotkin, D., Landry, J. F., et al., "Revisiting the evolution of *Ostrinia* moths with phylogenomics (Pyraloidea: Crambidae: Pyraustinae)," *Syst. Entomol*, **46**, No. 4, 827–838 (2021), https://doi.org/10.1111/syen.12491.

Zhukovskaya, M. I., Severina, I. Yu., and Novikova, E. S., "Anthropogenic light pollution: effects on insects," *Biosfera*, 14, No. 2, 126–136 (2022), https://doi.org/10.24855/biosfera.v14i2.669.