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Electrophysiologically Determined Spectral Responses in *Lobesia botrana* (Lepidoptera: Tortricidae)

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Abstract

Electrophysiological methods were used to test the visual sensitivity of European grapevine moth, *Lobesia botrana* (Lepidoptera: Tortricidae) to wavelengths ranging from 300 to 700 nm. For male and females tested, a main, peak response occurred in the 460–540 nm range (blue-green wavelengths) with females having a generally lower response to wavelengths in that range. A second smaller peak was observed for both sexes at the 340–420 nm range. A general linear model indicated that males, virgin females, and mated females did not react differently to changes in wavelength. No moths showed any obvious sensitivity to wavelengths between 580 and 700 nm. Based on our retinal recording data we suggest that UV light traps (≤480 nm) could be utilized alongside pheromone traps when monitoring *L. botrana* in high risk areas.

Key words: electroretinogram (ERG), spectral sensitivity, European grapevine moth

The European grapevine moth, *Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae) is an important pest of grapevines (Bovey 1966, Voigt 1972, Thiéry and Moreau 2005, Nadel et al. 2018). It has been reported to occur in Chile (2008), California (2009), and Argentina (2010) (Ioriatti et al. 2012). It was first discovered in the United States in Napa County California in 2009 and it subsequently spread to nine other counties in California (Gutierrez et al. 2012). A coordinated eradication program was set up and involved statewide trapping, vineyard inspections, regulating plant, and equipment movement from and within quarantine areas, mating disruption, along with precisely timed insecticide treatments (Simmons et al. 2018). It was declared eradicated from California in 2016 (NAPPO, 2016) but remains a potentially serious pest for most vine-growing areas.

Larvae feed on grapevines and numerous other plant species (Ioriatti et al. 2011). Adults have multiple broods (up to five generations) per year and a facultative diapause (Ioriatti et al. 2011). *L. botrana* larvae feed on flowers and berries of vines which make the fruit susceptible to the fungus *Botrytis cinerea* (Pers) (Helotiales: Sclerotiniaceae), leading to bunch rot (Ioriatti et al. 2011). Most economic loss is due to secondary infection from *B. cinerea* (Roehrich and Boller 1991). *L. botrana*-regulated products in California were valued at $5.7 billion in 2008 (USDA, 2010). In 2009, the United States was the third-largest producer and the second-largest exporter of grapes in the world (USDA, 2010). Eradication programs utilized insecticides in addition to pheromones for detection and mating disruption (Gutierrez et al. 2012) in an effort to combat the spread of this pest.

Electroretinogram (ERG) recordings can provide a method of determining spectral sensitivity curves of many insect species (Eguchi et al. 1982). The color vision system of most insects consists of three to four types of spectral receptors. These spectral receptors cover the wavelength regions between UV and 700 nm (Eguchi et al. 1982). ERG-determined peaks have been shown to correspond to specific spectral cell types (Autrum and von Zwehl 1964, Goldsmith and Fernandez 1968, Laughlin et al. 1980, Nosaki 1969). The shape of the ERG response (typically a rapid depolarization followed by a recovery to the baseline) can be affected by factors such as intensity and duration of illumination, the wavelength of light, microelectrode insertion depth, and the state of the visual adaptation (Byzov and Mazokhin-Porshnyakov 1963). These factors need to be carefully considered and replicated accurately when doing ERG based studies. Data from such recordings can help determine visual stimuli that might evoke a behavioral response (Brown and Cameron 1977). ERG data was shown to be particularly useful in the development of an effective, colored trap for the emerald ash borer, *Agrilus planipennis* (Fairmaire) (Coleoptera: Buprestidae) (Crook et al. 2009).

Effect of trap color can significantly improve trap performance (Crook et al. 2009) but has not been significantly studied with regards to *L. botrana*. Eguchi et al. (1982) tested the spectral responses of 35 Lepidoptera species which did not include *L. botrana*. Rayegan et al. (2016) performed a study based on interaction effects using various color traps. Information regarding spectral responses in *L. botrana* is very limited and previous ERG work has not been performed.

The aim of this research was to measure the spectral responsiveness of virgin males, virgin females, and mated females of *L. botrana* using electrophysiological methods (ERG) and compare the results with reported behavioral responses. Based on these findings it is hoped that recommendations for lighting systems and monitoring traps can be made.

Materials and Methods

Insects

Adult moths used in this study were obtained from an established colony of *L. botrana* at the Forest Pests Methods Laboratory, Buzzards Bay, MA, USA. Insects were reared according to the methods described by Nadel et al. (2018). Adults were maintained at 25 ± 2°C, 65 ± 3% relative humidity, and a photoperiod of 16:8 (L:D) h in an environmental chamber. Females usually mated after 48 hr. Mating was verified by dissection and presence of a spermatophore after heads were removed for electrophysiological tests.

ERG Recordings

The ERG system used in this study (previously described by Crook et al. (2014)) consisted of a 75-W Xenon short arc lamp that delivered light stimuli to a moth eye via a monochromator, liquid light guide cable, and focusing lens (Photon Technology International, Birmingham, NJ). The lamp housing unit (model A-1010-B) connected to a tunable high intensity illuminator (model L-201). This was powered by a power supply (model 220B) and igniter system (model LPS 221). Monochromatic light (ranging between 300 and 700 nm) was passed from the lamp through a monochromator (model 101) with 1,200 lines per millimeter and 300 nm grating. Light settings were set via a monochromator controller-shutter system (model MD-1000) connected to a desktop computer running MoCo (version 1.1, Windows 2000/XP, Photon Technology International, Birmingham, NJ). The monochromator bilateral slit was set to a 1.25 mm open setting (giving a 5 nm reciprocal dispersion). Selected wavelengths of light passed from the monochromator into a liquid light guide, terminating in a symmetric-convex lens (precision figured for 1:1 imaging). The lens focused a columnar 0.5-cm-wide beam directly onto the moth's eye preparation at a distance of 5 cm. Insect head preparation involved removing the head from the thorax. Antennae and palps were removed from the head along with any obstructing scales (under a lighted dissecting scope). An insect pin (size 000) was used to make a small hole on the dorsal surface of the head, directly between the compound eyes. The head was then attached to recording electrodes of an Electroantennogram (EAG) probe (Syntech, Hilversum, The Netherlands) using conductive gel (Spectra 360, Parker Laboratories, Fairfield, NJ). The recording probe tip was connected to the punctured opening so that the tip and gel were in contact with the inner edges of both the left and right eye, while the indifferent (ground) probe was attached firmly to the base of the cut head. Probe placement on moth head preparations was easily replicated and could be completed in less than a minute. Moth 'head probe' preparations were connected to an IDACC-232 serial data acquisition controller (Syntech). Signals and recordings were stored and analyzed on a desktop computer equipped with EAG software (Syntech 2004, version 2.6). Insect recordings were done between 9:00 a.m. and 12:00 p.m.

Before testing, insect ERG preparations were allowed to adapt to total darkness for ≥10 min. Insect head preparations remained in total darkness between stimulations. Stimulating light flashes lasted 1 s. The time interval between flash stimulations was 90 s. Two sets of flash stimulation runs were performed, each set including the whole range of selected wavelengths. Adult virgin males (n = 10), virgin females (n = 12), and mated females (n = 11) were stimulated using light wavelengths between 300 and 700 nm in 40 nm increments, presented randomly. At a setting of 500 nm the spotlight of the emitted beam was measured at 2.6 Lux (using a LX1330B Illuminance light meter, Dr Meter, Lewes, DE.). A 360-nm reference wavelength was flashed onto the moth head prep after four stimulations to maintain normalization assumptions. This allowed for the possible detection of any reduction or improvement of responses over the testing time period. Response was presented as a percentage of the reference response, which was designated 100%. For a higher-resolution responsivity to UV light, a second test was conducted where virgin males (n = 11), virgin females (n = 14), and mated females (n = 10) were randomly stimulated with light wavelengths between 320 and 450 nm in 10 nm increments. For data normalization of this second test, a 600-nm reference wavelength was flashed onto the moth eye prep after every four random stimulations.

Data Analysis

Responses between 300–500 nm and 320–450 nm were analyzed separately. We analyzed the spectral sensitivities by fitting general linear mixed models using the lme4 package (Bates et al. 2015) in R (R Core Team 2020). The normalized percentage responses were log-transformed and used as model outcomes, with sex, wavelength, and their two-way interaction included as categorical fixed effects. Insect subject was included as a random effect to account for multiple measurements across wavelengths taken on the same subjects. Predictors were assessed with likelihood ratio tests and mean responses were compared using z-tests from the emmeans (Lenth 2020) package with Tukey corrections for multiple comparisons.

Results

300–700 nm Responses

All insect groups had higher mean percentage responses at wavelengths between 460 and 540 nm (blue-green region), with mated females having a generally lower response at those wavelengths than males and virgin females (Fig. 1). A smaller peak in sensitivity for both sexes was observed between 340 and 420 nm. The estimated model indicated that the effect of wavelength did not depend on whether the insect was male, virgin female, or mated female (χ^2 = 25.27, df = 20, p = 0.19), so the interaction term was dropped. The reduced model indicated differences in mean percentage responses to different wavelengths (χ^2 = 451.70, df = 10, p < 0.001) (Fig. 2) and marginal differences in mean percentage response between males, mated females, and virgin females (χ^2 = 5.42, df = 2, p = 0.07).

320–450 nm Responses

Mean percentage responses of moths were generally highest at wavelengths 340–380 nm and ≥440 nm, with male responses generally lower than virgin or mated females (Fig. 3). The estimated model

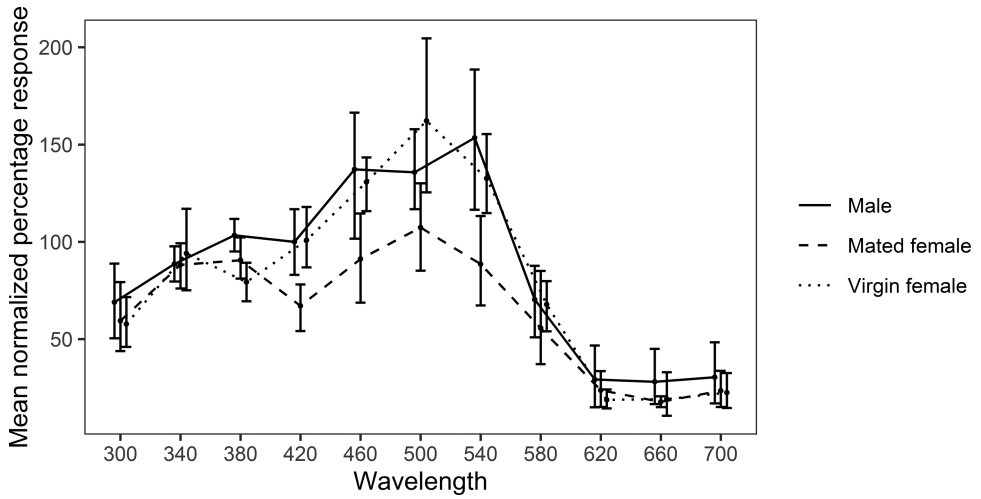

Fig. 1. Visual response of *Lobesia botrana* as measured by ERG to wavelengths of light between 300 nm and 700 nm. Response is given in percentage (%) based on the reference response calculated to be 100% at 360 nm.

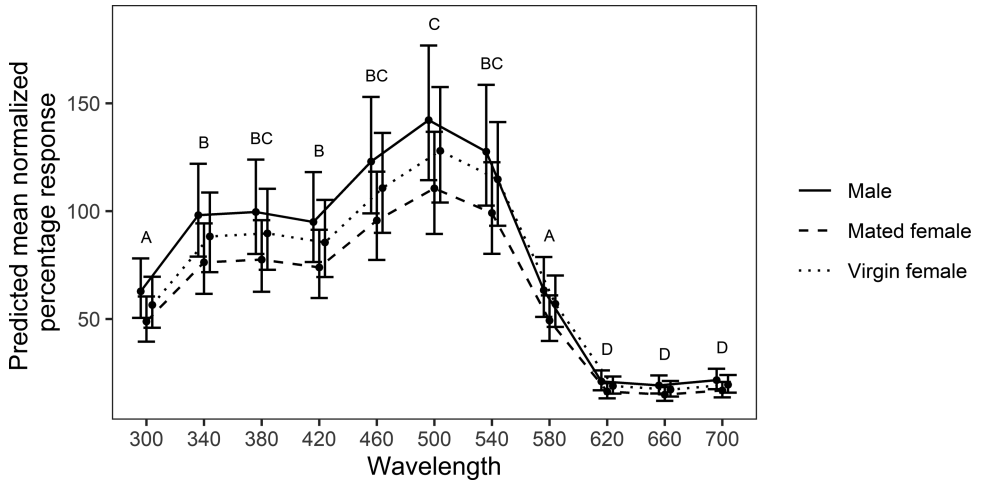

Fig. 2. Reduced model showing differences in mean percentage visual responses to different wavelengths for male, mated female, and virgin female *Lobesia botrana*.

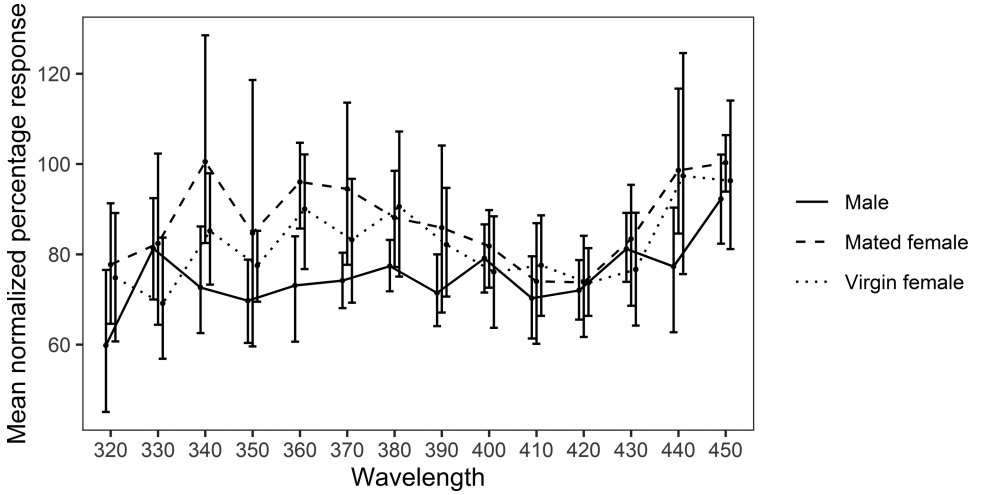

Fig. 3. Visual response of *Lobesia botrana* as measured by ERG to wavelengths of light between 320 nm and 450 nm. Response is given in percentage (%) based on the reference response calculated to be 100% at 600 nm.

indicated that males, virgin females, and mated females did not react differently to effect of wavelength (χ^2 = 24.37, df = 26, p = 0.56), so the interaction term was dropped. The reduced model indicated differences in mean percentage responses to different wavelengths (χ^2 = 45.63, df = 13, p < 0.001) (Fig. 4) and no differences in mean percentage response among males, mated females, and virgin females (χ^2 = 4.29, df = 2, p = 0.12).

Discussion

Our current and detailed understanding of *L. botrana* life history and its management can be mainly attributed to the research response that led to *L. botrana* being successfully eradicated from California in 2016 (Schartel et al. 2019). Thanks to the extensive collaboration between regulatory agencies (both state and federal), university researchers (both domestic and abroad), local grape/wine producers, and the general public, there are now highly effective pest strategies to deal with future invasions of *L. botrana* (APHIS 2016). Grape growing regions do, still remain at risk from *L. botrana*. Introduction risks include larvae or pupae on infested 'Old World' propagation material and imported 'consumer' grapes along with movement of un-sanitized machinery. Larvae are reported to feed on over 40 species of plants in 27 different families (Gilligan et al. 2011, Ioriatti et al. 2011) which offers other potential avenues of reintroduction. Researchers are continuing efforts to improve and refine current strategies that would be used to predict and manage future biological invasions of *L. botrana*. For example, Schartel et al. (2019) recently reconstructed and examined the recent *L. botrana* invasion trapping data in California using geospatial data and habitat suitability modeling. After reconstructing the spatiotemporal dynamics of the moth it was found that infested areas were clustered in 'hotspots'. Infestations appeared to be linked to transportation corridors indicating that human-aided transport played a key role in the spread of *L. botrana*. That study stressed the importance of early detection and rapid response to any future invasions. At the peak of the cooperative *L. botrana* eradication program in California over 60,000 pheromone baited delta traps were monitored in approximately 325,000 ha of vineyards (Schartel et al. 2019). *L. botrana* pheromone is primarily used as a control method (mating disruption [MD]) due to its low environmental impact and good effectiveness when compared to conventional insecticides (Arn et al. 1997, Lucchi et al. 2018b). The success of MD for *L. botrana* is directly linked to the pest's population density. Insecticide use may therefore be required at high population levels (Gutierrez et al. 2012). For *L. botrana*, the effectiveness of MD is drastically reduced above densities of 4,000 pairs of moths/ha (Feldhege et al. 1995). Estimating efficacy of MD in vineyards can be done by examining infested grape clusters for preimaginal stages or trapping with tethered females, field cages, and food traps; but, these methods are impractical and labor-intensive (Ioriatti et al. 2011). As they do not catch males in vineyards that already contain high pheromone concentrations, pheromone traps tend to be inefficient for estimating MD efficacy.

Recent research efforts have attempted to identify other types of volatiles that may attract both male and female *L. botrana*. For example, Larsson et al. (2020) tested microbial breakdown products (from grapes) that would more likely stand out against host volatile related background odors. They found that a two-component blend of 2-phenylethanol (2-PET) and acetic acid (AA) caught significant numbers of male and female *L. botrana* although the authors reported that some lure loadings resulted in a high amount of bycatch.

Improved light traps may offer an alternative monitoring tool in fields under MD and behavioral responses of *L. botrana* to specific wavelengths of light should be examined further. Light-emitting diodes (LEDs) have been used successfully to test the phototactic behavioral responses of the Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) to specific wavelengths of light (Park and Lee 2016) and could be utilized for studying *L. botrana*.

Field video observations (Lucchi et al. 2018a) have shown that male *L. botrana* flight occurs mostly between 21:00 and 23:00 h (GMT+1, daylight saving time) when female calling is optimal (Harari et al. 2011, 2015; Muller et al. 2016, Navarro-Roldán and Gemeno 2017). Flight activity of females (based on circadian activity in the laboratory) has been shown to be concentrated in the 6 h around onset of scotophase (Hurtrel and Thiéry 1999). Our results show that male and female *L. botrana* have a maximum visual response between 460 and 540 nm (blue-green region of visible spectrum). A second smaller peak in sensitivity was observed for both sexes between 340 and 420 nm which is the region of the spectrum considered behaviorally maximal in night flying insects (Mikkola 1972, Crook et al. 2014). Möller (2002) suggested that a chromatic interaction between a UV-sensitive receptor and a long-wavelength receptor allows for a reliable discrimination between sky and earth.

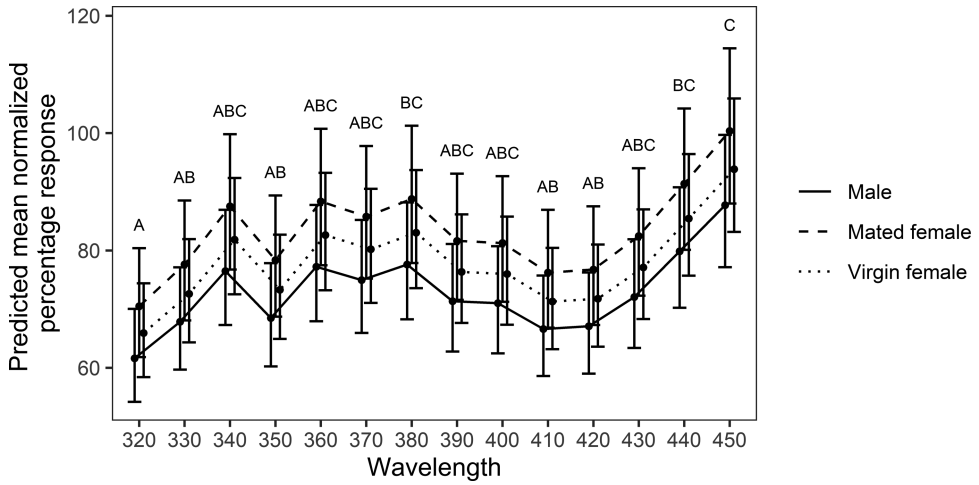

Fig. 4. Reduced model showing differences in mean percentage visual responses to different wavelengths (between 320 nm and 450 nm) for male, mated female, and virgin female *Lobesia botrana*.

It is feasible that *L. botrana* utilizes its UV and blue-green sensitive receptors as a compass cue in a similar way to honey bees and ants (Wehner 1989).

The response curves we observed for *L. botrana* are similar to studies done on *Lymantria dispar* (Linnaeus) (Lepidotera: Erebidae, Noctuidea) (Brown & Cameron, 1977 and Crook et al. 2014), which is known for being highly attracted to UV light sources emitting ≤480 nm (Wallner et al. 1995). Our results therefore suggest that UV-based light traps could potentially be used to enhance current monitoring efforts both in areas under MD and as a detection tool in suspected 'hot-spot' regions that may be suitable for establishment of *L. botrana*. Light traps (125 W mercury-vapor) were often used to monitor the activity of night flying fruit tortricids until pheromone traps became more widely used (Wardlow et al. 1978). In a recent study, mercury vapor light traps were used to survey over 30 species of tortricid moth in several localities of Kashmir, India (Ganai and Khan 2017). Light traps also have the benefit of catching both male and female adults. With a value of over (USDA 2010) $4B in California alone, the grape industry needs to maintain a robust and sensitive monitoring program for *L. botrana* and other invasive grape pests. For post eradication surveillance trapping in high risk areas or previously infested areas (such as Napa-Sonoma) we suggest pheromone traps be utilized along with UV light traps.

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