

Diel Periodicity in Males of the Navel Orangeworm (Lepidoptera: Pyralidae) as Revealed by Automated Camera Traps

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Abstract

Navel orangeworm, *Amyelois transitella* (Walker), is a key pest of walnuts, pistachio, and almonds in California. Pheromone mating disruption using timed aerosol dispensers is an increasingly common management technique. Dispenser efficiency may be increased by timing releases with the active mating period of navel orangeworm. Past work found that the peak time of sexual activity for navel orangeworm females is 2 h before sunrise when temperatures are above 18°C. Inference of male responsiveness from data collected in that study was limited by the necessity of using laboratory-reared females as a source of sex pheromone emission to attract males and the inherent limitations of human observers for nocturnal events. Here we used camera traps baited with artificial pheromone to observe male navel orangeworm mating response in the field over two field seasons. Male response to synthetic pheromone exhibited diel patterns broadly similar to females, i.e., they were active for a brief period of 2–3 h before dawn under summer conditions and began responding to pheromone earlier and over a longer period of time during spring and fall. But contrary to the previous findings with females, some males were captured at all hours of the day and night, and there was no evidence of short-term change of pheromone responsiveness in response to temperature. Environmental effects on the response of navel orangeworm males to an artificial pheromone source differ in important ways from the environmental effects on female release of sex pheromone.

Key words: camera trap, remote sensing, pheromone lure, protandrous response

Pheromones and other semiochemicals play an increasingly important role in insect pest management (Miller and Gut 2015, Evenden 2016, Abd El-Ghany 2019, Rizvi et al. 2021). Release of pheromones by insects, and response to them, are among the many aspects of arthropod biology that are controlled by circadian rhythm. Circadian rhythms are the natural biological and physiological responses insects go through in a 24-hour period, and diel periods are the observed rhythm resulting from a physiological circadian clock (Levi-Zada and Byers 2021). Mating is one of several important life processes that is controlled by a circadian clock; other examples include emergence, feeding, locomotion, and oviposition (Levi-Zada and Byers 2021). The timing of mating behaviors differs between species. For example, the codling moth *Cydia pomonella*, Linnaeus (Lepidoptera: Tortricidae) begins its mating period an hour

after dusk and stops before midnight while the tobacco hornworm *Manduca sexta*, Linnaeus (Lepidoptera: Sphingidae) starts at midnight and stops at the end of the scotophase (Groot 2014). In most moth species mating is mediated by a sex pheromone released by the female and used by the male to locate a mate (Allison and Carde 2016). There are, however, exceptions such as use of male-released pheromones and host volatiles in greater date moth *Aphomia sabella* Hampson (Lepidoptera:Pyralidae) (Levi-Zada et al. 2014) and acoustic signaling by male leks of the greater wax moth *Achroia grisella* Fabricius (Lepidoptera:Pyralidae) (Alem et al. 2015). In general, though, circadian control in moths can be viewed as sex-specific physiological processes controlling production and release of sex pheromone in the female, and perception and behavioral response in the male (Levi-Zada and Byers 2021). Diel periodicity

of moths is of practical significance due to ongoing technological advances in control and monitoring (Groot 2014, Levi-Zada and Byers 2021).

Diel periodicity is particularly relevant to pheromone-based mating disruption using aerosol dispensers (Benelli et al. 2019). These automated dispensers provide timed release of synthetic pheromone compounds from dispersed locations within a field or orchard. While aerosol dispensers have a higher cost per unit than passive dispensers, they can be deployed at a lower density in the field which lowers labor costs. Costs can be further reduced by limiting the time of emission to the period when the target pest is sexually active, which results in a lower amount of the active ingredient (pheromone) used. Improved understanding of the diel patterns of moths can therefore improve the efficiency of controlling the pests, without sacrificing efficacy.

Pest monitoring is an important part of integrated pest management, and remotely monitored traps are a growing part of this field (Lima et al. 2020, Preti et al. 2020). Several types of sensors have been developed, including camera traps (Preti et al. 2020), pseudoacoustic traps that detect wing beat frequency (Potamitis et al. 2017, 2018; Burks 2022), acoustic/seismic devices which detect vibrations in host plants (Lima et al. 2020), infrared detection of trapped insects falling through a passage (Goldshtein et al. 2017), near-infrared spectroscopy of cuticular lipids or host response to herbivory (Fuentes et al. 2021), and e-nose technology measuring insect associated volatile compounds (Fuentes et al. 2021). Of these technologies, camera traps are probably the most widely used commercially (Lima et al. 2020). For practical commercial use, camera traps typically take a photograph once per day of a sticky trap liner in a trap baited with a pheromone dispenser or other lure as an attractant. The photos are transmitted via cellular networks to a data server maintained by the provider, where these images are analyzed by machine learning algorithms to recognize and count newly trapped insects (Høye et al. 2021). Initially, to train these machine learning algorithms, a human observer must distinguish images of the target insect from nontarget images (other insects, debris, etc.). Counts for specific traps in specific fields or locations are sent back to the client via a user interface. Frequently, temperature data and possibly other climatological data such as relative humidity are collected to facilitate the use of the count data with degree-day models (Wu et al. 2014, Rebaudo and Rabhi 2018). While automated traps are generally used to guide commercial pest management decisions, they have also been used as a research tool to improve knowledge of diel cycles of pest species (Lucchi et al. 2018, Goldshtein et al. 2021). Researcher-built traps that automate data collection, but do not provide remote data access, have also been used for research of diel cycles (Hendricks 1985, Stevenson and Harris 2009).

The navel orangeworm *Amyelois transitella* (Walker) is the primary insect pest of California's economically important tree nut industry (Wilson et al. 2020). Mating disruption is an established management technique for this pest (Higbee et al. 2017, Burks and Thomson 2019, 2020; Haviland et al. 2021, Higbee and Burks 2021). Aerosol technology is used in three of the four commercial formulations for which efficacy has been demonstrated (Haviland et al. 2021). The three available aerosol dispensers each have slightly different approaches to the frequency, timing, and amount of pheromone released (Burks and Thomson 2019). A recent study showed that releasing pheromone before the start of the mating period did not increase control, suggesting that cost-effectiveness is optimized by releasing closer to the actual mating period (Burks and Thomson 2019, 2020).

The most thorough characterization of the diel patterns of sexual activity of navel orangeworm females was performed by Landolt and Curtis (1982). The timing of female calling behavior, in which the female distends the abdomen to expose the pheromone gland and release pheromone, was observed in laboratory-reared females placed in mesh cages in a sticky trap in the field. Male response was measured as the time of capture of males. Additionally, calling time of laboratory-reared females was also observed in a walk-in environmental chamber at 13, 18, and 27°C. The data indicated that the onset of female calling and male orientation to the pheromone source occurred in the last two hours of darkness at temperatures >18°C. However, sexual activity began earlier in the night as a linear function of temperature between 11 and 18°C (Landolt and Curtis 1982). Modification of diel patterns of female calling in response to temperature has been observed in several moth species (Levi-Zada and Byers 2021).

This previous study (Landolt and Curtis 1982) collected mating timing data for both sexes, but this work was inherently centered on female diel patterns. Synthetic sex pheromone lures were not available until recently (Higbee et al. 2014), so the researchers had to use caged female moths as the source of sex pheromone. Consequently, the male responses observed were dependent on female calling behavior (Landolt and Curtis 1982). This is an important distinction as studies of other moth species have found that males often become responsive to synthetic sex pheromone prior to the female calling period, and may remain responsive after it has concluded (Kawasaki et al. 1983, Hendricks 1985, Kaster et al. 1989, Stevenson and Harris 2009).

Several companies have provided remote monitoring of navel orangeworm on either an experimental or a commercial basis (Supp Table 1 [online only]). This enhanced monitoring capability provides the opportunity for a more direct study of diel response of male navel orangeworm to sex pheromone. This understanding may in turn improve the ability to interpret data from such traps. Likewise, understanding male diel response is important for optimization of aerosol mating disruption systems for navel orangeworm (Burks and Thomson 2019) and for understanding the mechanisms involved in mating disruption for this species (Burks and Thomson 2020). In objective of the present study is to elucidate the diel period of navel orangeworm over the course of the almond growing season, and the relative influence of temperature on this period. To this end, a commercial camera trap baited with synthetic sex pheromone was modified to provide an image every 30 min. Time of capture of males arriving in these traps was compared to temperature data collected by the camera traps. Data from these traps was used to relate time of male captures with photoperiod and temperature, and the patterns observed were compared with the model developed earlier for females (Landolt and Curtis 1982).

Materials and Methods

Camera Traps

During the 2019 and 2020 growing seasons five camera traps (Trapview, Hruševje Slovenia) (Fig. 1A and Supp Table 1 [online only]) were used in an observational study examining the time of male capture using sex pheromone monitoring lures. These traps consisted of a housing unit that holds the camera above with a platform below that contains a horizontal roll of sticky film on the floor of the trap where insects were captured. The sticky film refreshes itself once per week. The trap also contained a weather sensor that collected temperature and relative humidity (r.h.). The unit was powered by a separate battery housing unit that included a solar

panel. Data were sent from the camera every 30 min, and the temperature sensor summaries were sent every hour to Trapview servers via a cellular connection provided by a SIM card in the device. Data from these traps were recorded in datetime format for the location of the trap ('America/Los Angeles' in the Olson name convention, UTC - 7 under daylight saving time).

The trap assembly was mounted on two U-posts, one to support the camera trap unit and the other to support the battery, solar panel, temperature/r.h. sensors, and an antenna to boost cellular connectivity. The traps were placed on the edge of each orchard row to allow the sun to reach the solar panel. Proprietary manufacturer software identified each image of a navel orangeworm adult that was new since the previous picture. Each of the putative navel orangeworm images was verified by the researchers via a web interface (Fig. 1B and C). Count data based on the verified images and temperature/r.h. data were downloaded via the web interface. The traps were equipped with a self-cleaning mechanism that allows the sticky roll to be remotely moved over the platform within the housing unit to ensure that the sticky trap surface was not oversaturated with moths. Traps were cleaned and the sticky rolls were replaced as needed, and any malfunction that prevented the traps from collecting useful images was fixed in the field as soon as possible.

Field Sites –Year 1

Five camera traps were deployed from 24 April 2019 to 4 November 2019. The traps were positioned in almond and pistachio fields in Fresno County, California (Table 1). The traps were placed on the edge of orchard row to provide full access to the sun for the solar panel powering the trap. The sites A and B were approximately 2

km apart in western Fresno County. Sites C and D were small experimental almond and pistachio plots, respectively, near Parlier and approximately 2 km apart. Site E was in an almond orchard about 50 miles to the north of Sites A and B, also in western Fresno County. Sites C and D were 100 km east of site E, and 70 km northwest of sites A and B. Traps were baited with a pheromone lure (NOW BioLure, Suterra LLC, Bend, OR). The lures have a field life of 6–8 wk and were changed within a 6–7-week period throughout the duration of the experiment.

Field Sites –Year 2

Based on the high navel orangeworm counts observed at site A in year 1, four traps were placed there in the spring of 2020. Traps were deployed from 12 March 2020 to 22 September 2020. The year 2 observation period was curtailed by an earlier harvest than compared to year 1, and a grower request to remove the traps for harvest. As in year 1, the traps were placed on the southern edge of the field to maximize energy production by the solar panels. Traps were placed at 60 m intervals. On 15 June two of the traps (A1 and A3) had the housing unit changed to better resemble wing traps which previous research had shown more effective for capturing navel orangeworm with pheromone lures (Burks and Higbee 2015). Two more traps (A2 and A4) were converted to the new housing unit on 2 July, and the fifth trap was placed in the field 7 July after a delayed start due to mechanical/electrical problems. In year 2 the traps were baited with a different commercial pheromone lure (Pherocon NOW L2-L, Trece, Adair OK) because the lures used in year 1 were not commercially available in year 2. The lures have a field life of 4–6 wk and were changed within a 4–5-week period throughout the duration of the experiment.

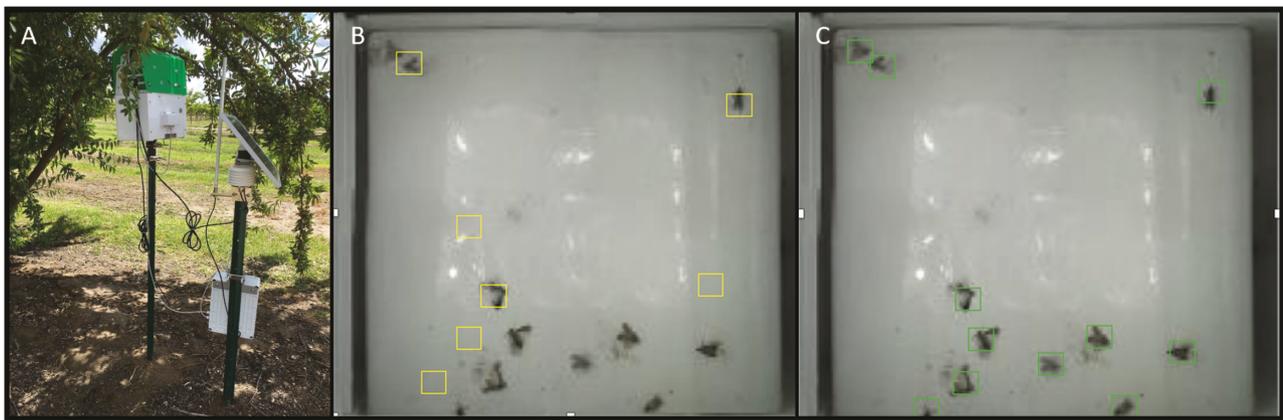


Fig. 1. (A) Trapview camera trap setup in the field. Including Trapview camera, sticky trap, and cleaning unit in the green and white unit, and solar panel with battery box and weather station. (B) and (C) demonstrate training of machine learning algorithm. (B) Photo of the sticky card in the trap where yellow boxes indicate provisional positive results as determined by the manufacturer's propriety machine learning software. (C) The green boxes indicated confirmed of the target pests; as confirmed or entered by the user.

Table 1. Locations of camera traps for the 2019 and 2020 field season

Year	Site	Trap location	Coordinates	Crop
2019	A	Huron, CA	36.1086 N, 120.1452 W	Pistachio
	B	Huron, CA	36.1086 N, 120.1311 W	Pistachio
	C	Parlier, CA	36.5969 N, 119.5155 W	Almond
	D	Parlier, CA	36.5975 N, 119.5077 W	Pistachio
	E	Firebaugh, CA	36.7083 N, 120.6413 W	Almond
2020	A1–A5	Huron, CA	36.1086 N, 120.1452 W	Pistachio

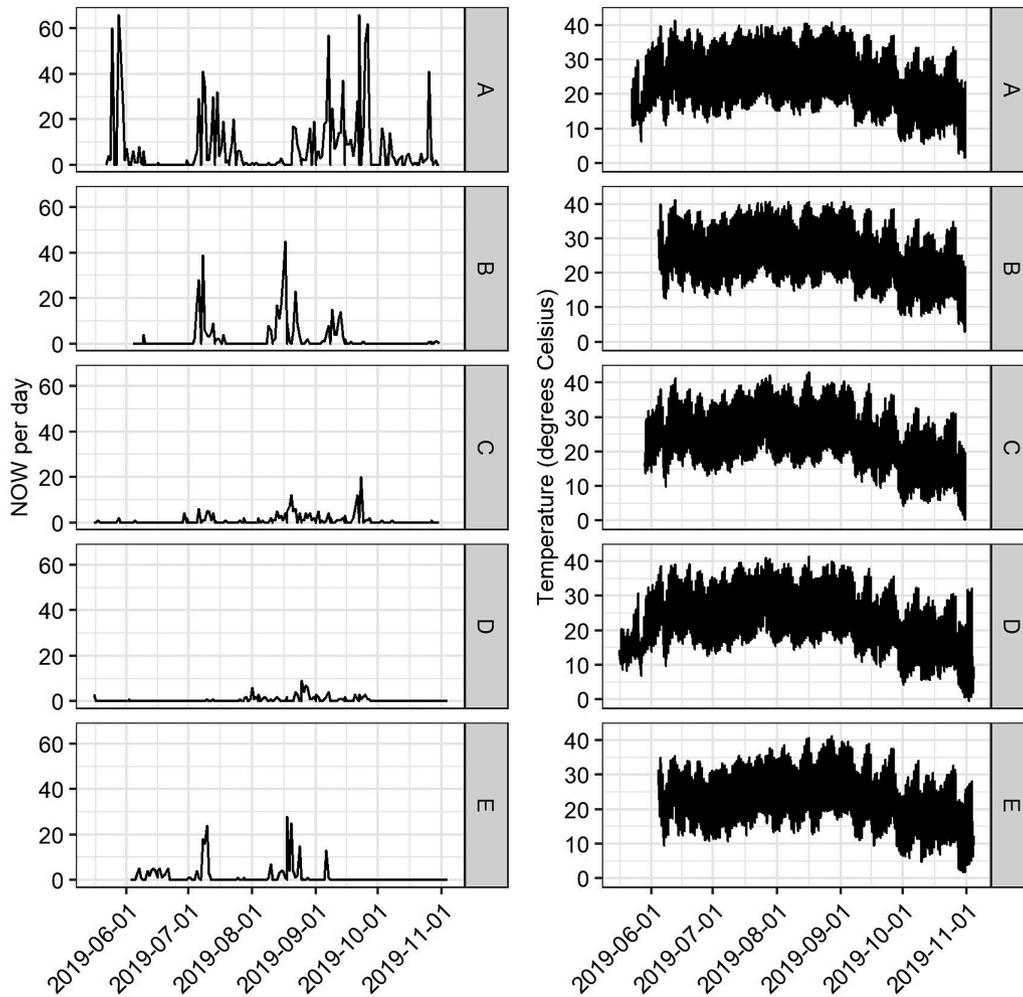


Fig. 2. Daily total capture (left) of navel orangeworm and hourly temperature (right) at five research locations in 2019.

Data Analysis

Stored data were downloaded from Trapview LLC servers (<https://trapview.com/>) and R 4.2.1 (R Core Team 2022) was used to remove low quality and erroneous data points and summarize findings. Scripts used for this purpose can be found at <https://github.com/ChuckBV/ms22-now-male-diel-response>. The proportion of males captured during daylight hours was compared between year 1 and year 2 using a chi-square 2×2 contingency table. The central tendency of time of male capture was compared between months using the Kruskal–Wallis nonparametric one-way analysis of variance (Zar 1999). In cases of significant differences, the Dunn Test was used with a Bonferroni adjustment (Dunn 1964, Dinno 2017) for multiple comparisons to find which months differed significantly, with an overall alpha of 0.05. Correlation analysis was performed in base R to examine the association of the time of the median capture with the temperature at that time. Spearman nonparametric rank correlation was used to minimize the probability of spurious findings of association due to outliers.

Results

Seasonal Abundance and Phenology

A robust sample of adults was obtained in the traps from April to September in both years of the study (Figs. 2 and 3; Table 2). In year 1 abundance varied between the five locations and was greatest at

site A (Fig. 2). All five traps were therefore deployed at site A in year 2. Trapping was initiated earlier in year 2 than in year 1, but was also terminated earlier due to a grower request to remove the traps. Equipment failures in year 2 are documented by the temperature plots (Fig. 3), but this did not occur synchronously so at least one trap was active at site A in year 2 throughout the period of deployment. Temperature data documents a mean daily temperature swing of approximately 20°C through much of the field season, with lows between 15 and 21°C and highs from 35 to 41°C .

Time of Capture

Time of capture is plotted in Fig. 4 versus hours after 18:00 local time (Pacific Daylight time), so 12 on this scale is 06:00 local time (Supp Table 2 [online only]). Sunset on this scale is at 1.6, 2.3, and 0.4 on 15 April, 15 June, and 15 October respectively. Sunrise is at 12.4, 11.7, and 13.4 on these respective dates. There were significant differences between months in both capture time distribution (Kruskal–Wallis, chi squared = 275.17, $df = 6$, $P < 0.0001$) and median capture time (Dunn test with Bonferroni adjustment for multiple comparisons, $P < 0.05$). From April to September half of captures (25th to 75th percentile, Fig. 4) occurred within the hours immediately preceding dawn, approximately 8 h after sunset to 11 h after sunset. The interquartile interval was narrower from June to August, extending from around 10–11 (Fig. 4). The capture timing window was most narrow during the summer months of

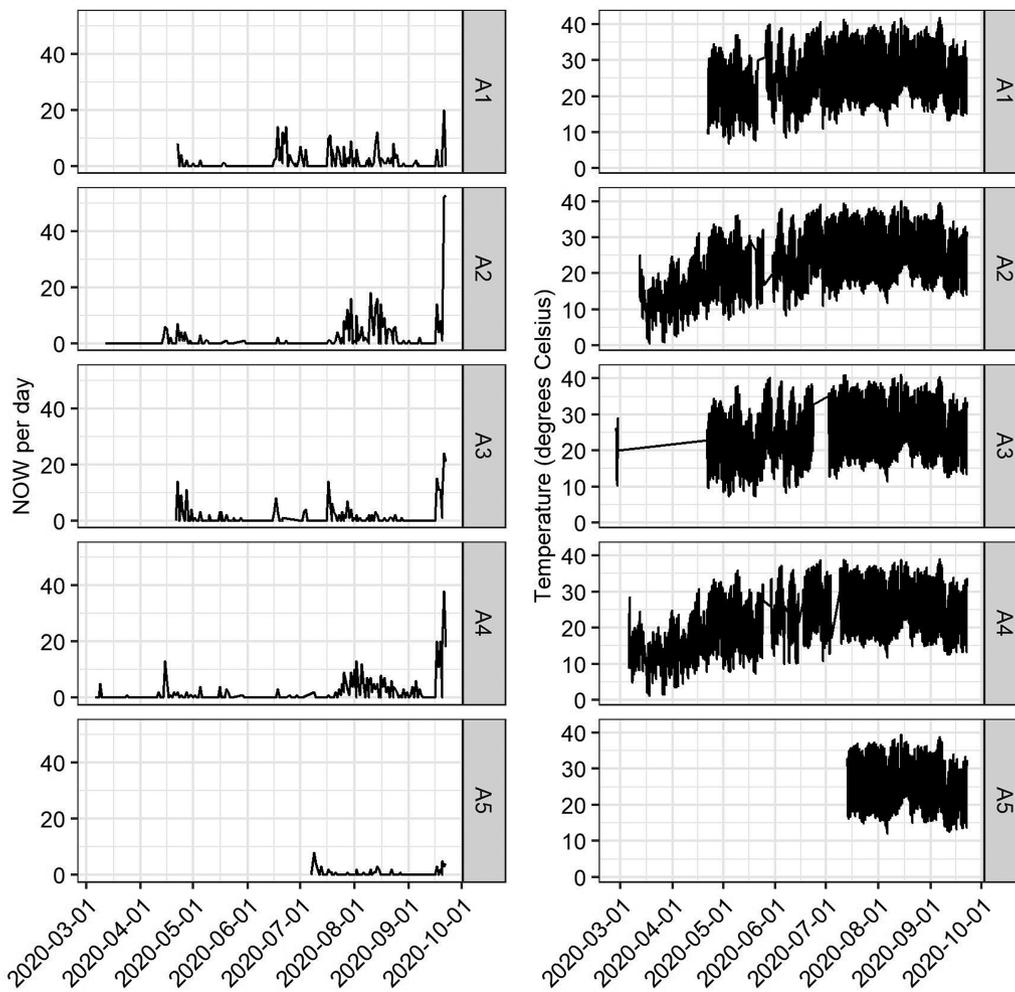


Fig. 3. Daily total capture (left) of navel orangeworm and hourly temperature (right) at five research location in 2020.

Table 2. Total *Amyelois transitella* captured in all trap locations by year and month

Year	Mar.	April	May	June	July	Aug.	Sept.	Oct.
2019	0	29	249	94	507	528	709	143
2020	6	123	44	96	377	377	424	0

June through August, where the 25th to 75th percentile observation occurred between 10 h after sunset and 11 h after sunset. In October the median time of capture was midnight local time (hour 6 in Fig. 4) and the interquartile range extended from 2 to 10 h after sunset.

While captures were concentrated around the early sunrise period for most of the season, trap data revealed that male navel orangeworm moths could be captured at all hours of the day. These daytime moths represented a minority of samples, as for both years and all sites (data not shown) around 8% of captures occurred in daylight hours between 07:00 and 18:00 (\geq hour 13 in Fig. 4). The proportion of males captured during the day did not differ significantly between year 1 and year 2 ($\chi^2 = 0.066$, $P = 0.797$).

Temperature and Male Capture in Pheromone Traps

There was no significant association of the time of median capture with the temperature for any month but August (Fig. 5; Table 3), and association of median time of capture and temperature was low at that point as well. However, general patterns appeared

to differ between the months. In April, May, and October, there was a tendency toward a constant temperature (ca. 13°C) at time of median capture, while the time of median capture itself was more variable. In June through August the data suggest a converse trend, with the time of median capture most often at 10 or 11 h after sunset and the temperature at that time varying between 13 and 25°C. In May through September median capture occasionally occurred at higher temperatures later in the day or very early in the night.

Discussion

The camera trap in this study was not used in a way that is typical of commercial applications, where photos are usually taken a single time per day. Instead, it was used to record hourly data on moth activity in order to elucidate diel activity. This same commercial camera trap was modified for a similar study of diel patterns of sexual activity of the European grapevine berry moth, *Lobesia botrana* (Denis

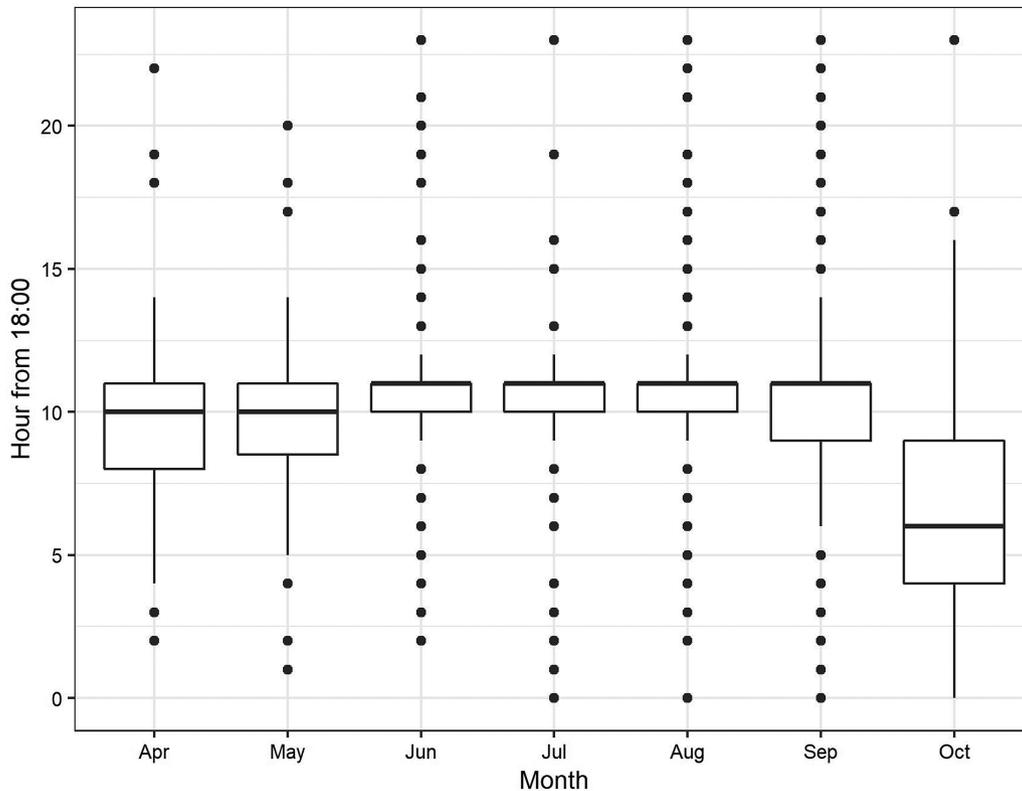


Fig. 4. Box plot showing hourly capture (0 = 18:00) by month for all navel orangeworm captured in five camera traps in 2019 and 2020. The distribution of capture times was significantly different between the months (Kruskal–Wallis, experiment-wise $P < 0.05$). Mean capture times were significantly different for month with different letters (Dunn test, $P < 0.05$, with Bonferonni adjustment for multiple comparisons).

and Schiffermüller) (Lucchi et al. 2018). Other studies have used different methods to achieve similar measurements, including infrared beam detectors for noctuid moths (Hendricks 1985) or a modified funnel trap that dropped moths onto a disk-shaped sticky liner mounted on a clock movement for a study of the pecan casebearer, *Acrobasis nuxvorella* (Neunzig) (Stevenson and Harris 2009). Here, the camera traps used in this study had the advantage of unambiguously identifying the target species when it was first captured, and was likely the best design for this type of study since, for instance, navel orangeworm is not efficiently captured with pheromone in funnel traps (Burks and Higbee 2015). Alternatively, in comparison to the other purpose-made traps, these camera traps have the disadvantage of high expense (variable subscription cost, approximately \$25 per acre per year) and requiring the use of a proprietary server to offload the data. However, the expense may be reduced, and server resources may become less limiting if this type of trap is widely adopted commercially. Another approach that might be more common in the future is field videography with multi-purpose single-board computers such as the Raspberry Pi (Milosavljević et al. 2020).

The findings in the current study had both similarities and important differences from the previous study based on observation and use of calling females (Landolt and Curtis 1982). This previous study, like the current one, found a general seasonal pattern of male activity occurring at the end of the night under summer conditions, and beginning earlier and extending longer in the spring and fall. However, that previous study did not observe occasional activity of males outside of nighttime hours. Additionally, Landolt and Curtis (1982) found a strong linear relationship between the initiation of male activity and temperature, suggesting that the hour of onset of activity

was strongly influenced by short-term changes in temperature. That finding was strengthened by an observation of earlier activity on an unusually cool June morning and by laboratory observations of the time of female calling at three different temperatures. In contrast, in the current study few males were captured in pheromone traps at times much earlier or later than the majority. This suggests that while female calling behavior may be influenced by temperature, as seen in Landolt and Curtis (1982), male receptivity to calling may not be. Moreover, while the relationship between the time of male captures and temperature differed between months, there was little evidence that temperature influenced that relationship within a given month. This was particularly true during summer months.

In the present study only pheromone baited camera traps were used. In the absence other information, the sex of the NOW adults captured and their reason for entering the camera trap might be open to interpretation. Previous studies, however, indicate that passive captures in unbaited traps occur very rarely, e.g., around 0.1 adults per trap every two weeks, or around 0.1% the rate of a pheromone trap (Burks et al. 2009, 2016), and the rate of female captures in traps baited with pheromone is vanishingly small (Higbee et al. 2014). Taking these previous studies into account, the simplest explanation for capture of a few males in the pheromone baited camera traps at seemingly random hours is that they responded to the pheromone lure at that time.

Biological differences in diel activity between male and female moths have been documented in several previous studies. For instance, responsiveness of males to pheromones prior to female calling was demonstrated in the smaller tea tortrix moth, *Adoxophyes honmai* (Yasuda) (Kawasaki et al. 1983). In that study, when traps baited with unmated females and synthetic sex

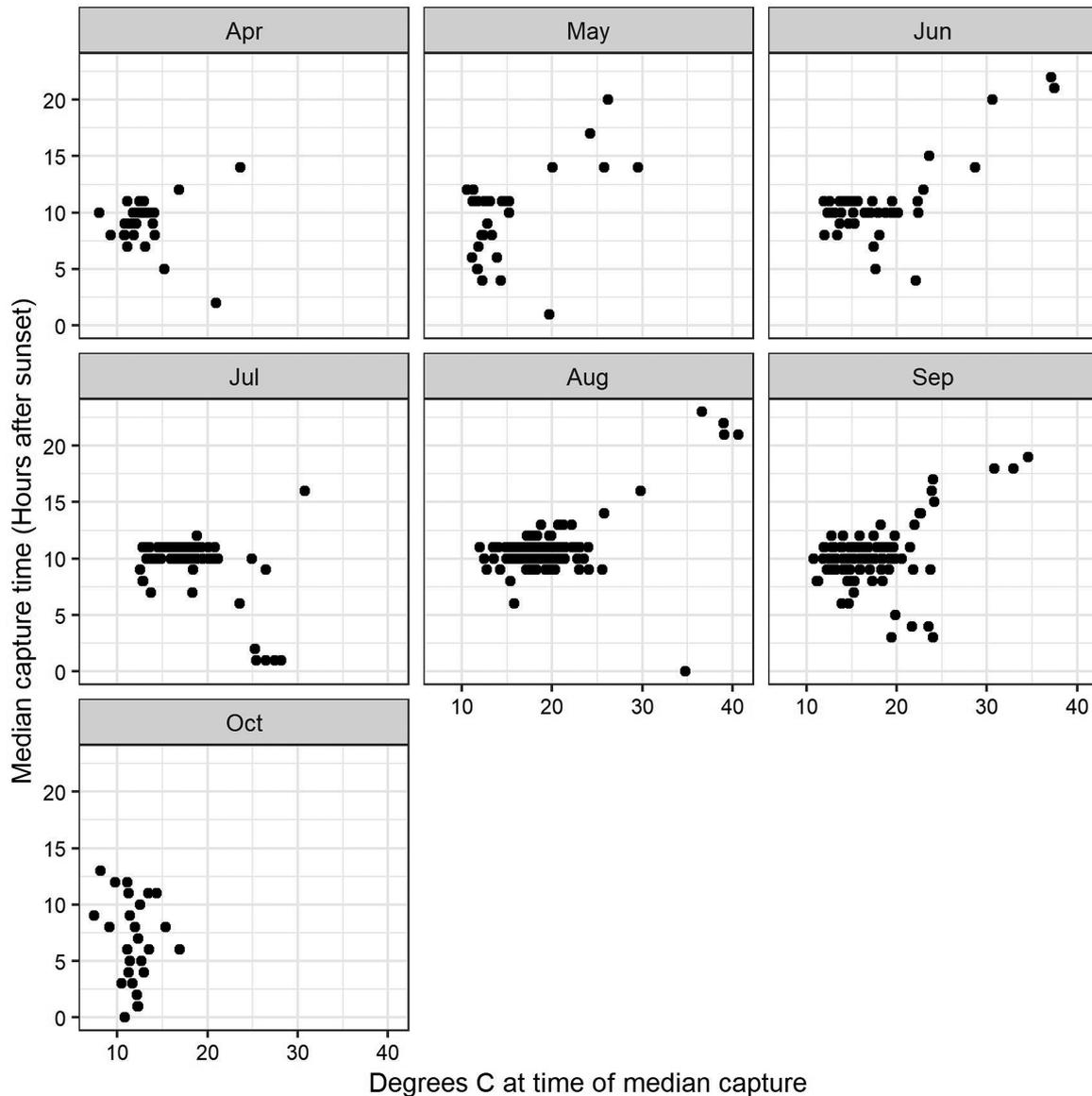


Fig. 5. Hour of median daily capture by month for all navel orangeworm captured in five camera traps in 2019 and 2020. There low association between temperature at the time of median capture and the time of day of the median capture for all months (Spearman's $\rho \leq 0.35$).

Table 3. Nonparametric Spearman rank correlation coefficient of for association of the hour of the daily median capture with temperature at the time of capture

Month	N	rho	P
April	30	0.18	0.34
May	30	0.35	0.06
June	50	0.23	0.11
July	122	-0.13	0.16
Aug.	184	0.01	0.85
Sept.	113	0.21	0.03
Oct.	27	-0.12	0.55

pheromone lures were checked hourly throughout the night, males were clearly captured in the traps with synthetic sex pheromone an hour earlier than traps baited with unmated females. Similarly, a study of the black cutworm *Agrotis ipsilon* (Hufnagel), a migratory moth, examined the effect of age of unmated females and time

of year on males in female-baited traps (Kaster et al. 1989). While protandrous response was not the focus of that study, male moths were captured in traps baited with synthetic sex pheromone one to two hours earlier than traps baited with virgin females, suggesting that protandrous response also occurs within this species. Finally, a study of *A. muxvorella* is perhaps the most similar to the work described here (Stevenson and Harris 2009), in which an automated funnel trap baited with synthetic sex pheromone used a sticky disk mounted on a clock movement to determine time of capture. That study found that males were captured earlier and later than the 01:00 to 03:00 h window of activity previously identified for female calling. As with the present study, male capture also continued into the day. The findings for male navel orangeworm response to pheromone traps presented here differ from those of a previous study of navel orangeworm females, which concluded that the initial time of calling began earlier at cooler temperatures (Landolt and Curtis 1982). Previous studies documented a shift to earlier calling time in response to decreased temperature in various moths (Cardé et al.

1975, and citations therein). In some species, the influence of temperature on circadian rhythm was evident in both sexes, as was seen in the Oriental fruit moth *Grapholita molesta* (Busck) (Baker and Cardé 1979). However, similar to the present study, temperature was found to alter female calling and not male responsiveness in codling moth *Cydia pomonella* (L.) (Castroville and Cardé 1979). In this current study, to determine the influence of temperature on male navel orangeworm responsiveness to sex pheromone, median capture time was plotted against temperature at time of capture. If there was a general trend toward earlier capture times at lower temperatures, that should have been evident with an earlier median. Instead, the patterns were generally similar when these data were plotted using the 25th percentile rather than the median (data not shown).

The data from the present study indicate that, for navel orangeworm males in the field, changes in the circadian timing with respect to trap capture are affected by longer term environmental influences and not just immediate temperature. In June through August there was a 25°C swing between the daytime high (median 39°C, typically in late afternoon) and the nightly low (median 14°C, typically at sunup). In March the median high and low temperatures were respectively 19.5°C and 6°C, and in October these temperatures were respectively 30°C and 6°C. Figure 5 indicates that temperatures that led to earlier captures in April, May, and October were less likely to do so in June, July, and August. It is possible that the occasional males captured in the day or outside the hours of more frequent capture are older. It is also possible that the regulation of calling of navel orangeworm females under field conditions is more complex than a simple response to the immediate temperature. Further research would be required to test these hypotheses.

The most relevant application of these data is in understanding and informing timing of application of aerosol mating disruption dispensers (Benelli et al. 2019; Burks and Thomson 2019, 2020). In previous studies that evaluated the timing of mating disruption treatments for navel orangeworm, the extent to which synthetic pheromone emission before midnight was necessary for male suppression was dependent on whether or not the temperature had fallen from 21–32°C to 10–21°C by midnight (see Figs. 2 and 3 in Burks and Thomson 2020). It should also be noted that the data from that study of mating disruption for NOW indicated substantial suppression and significant reduction of damage to almonds (Burks and Thomson 2020).

In summary, the present data indicate that the response of navel orangeworm males to a consistent sex pheromone source appears to begin before and extend beyond the typical period of female calling. Furthermore, under field conditions, some males seem to have little or no diel pattern at all in their response to a consistent pheromone source.

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Author Contribution

CSB: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, methodology, Project administration, Resources, Software, Supervision, Visualization, Writing – reviewing and editing. FSH: Data curation, Formal analysis, Investigation, Visualization, Writing – original draft. HW: Conceptualization, Funding acquisition, Resources, Writing – reviewing and editing. JAW: Project administration, Formal analysis, Supervision, Writing – original draft, Writing – reviewing and editing.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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