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RESEARCH

Differences in Diel Timing of Flight May Reduce Hybridization Between Native and Introduced Geometrid Moth Congeners

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Abstract Hybridization between exotic and native species can lead to negative ecological and economic consequences. The invasive winter moth (WM), *Operophtera brumata*, uses the same sex-attractant pheromone and mates and produces fertile offspring with a native congener the Bruce spanworm (BSW), *O. bruceata*, and a stable hybrid zone has formed where their ranges overlap in the northeastern United States. However, the fact that the two species have not merged, despite seasonal overlap of flight, suggests that one or more pre- or post-mating barriers to hybridization might therefore exist. Here, we evaluate the hypothesis that interspecies differences in diel timing of flight might provide pre-mating isolation and explore whether these two species change their diel timing of flight differently in response to changes in temperature. Our results indicate that the flight timing of WM and BSW broadly overlap during the nighttime hours, although WM males fly almost exclusively at dawn, dusk, and night whereas BSW males fly during both daytime and nighttime hours. Flight activity also differed between the two species in response to nighttime temperatures < 0 °C, wherein WM flight largely stopped while BSW flight continued and the proportion of males flying during the daytime increased. This partial partitioning may help explain why the native BSW has not been completely outcompeted by the invasive WM.

Keywords Allochronic speciation · Bruce spanworm · Hybrid zone · Invasive species · Winter moth

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Introduction

Interspecific hybridization between native species commonly occurs in nature with at least 25% of plants and 10% of animals involved in hybridization with at least one other species (Mallet 2005). While hybridization between native species can be adaptive in that it may introduce genetic variation into a population (Mallet 2005), hybridization between native and introduced species can have negative ecological consequences such as the extinction of the native species (Allendorf et al. 2001). With globalization and the associated accidental introductions of alien species (Seebens et al. 2017) comes an increase in opportunities for hybridization between species that would have never met without human mediation, termed "anthropogenic hybridization" (Allendorf et al. 2001; McFarlane and Pemberton 2019). Anthropogenic

hybridization can result in the introgression of maladaptive genes into native species and the increase in establishment and spread of introduced species via introgression of locally adapted gene complexes from native species (McFarlane and Pemberton 2019). Hybrids may also possess a combination of parental phenotypes that allows them to outcompete both parent species, allowing more rapid invasion, which has the potential to result in the creation of a hybrid swarm, a population consisting of hybrids of two parental taxa whose genotypes are no longer present (Allendorf et al. 2001; Hegarty 2012).

In contrast to the clinal hybrid zones typical of native species, characterized by a relatively narrow geographic spatial gradient of admixture from one parent species to the other, hybrid zones between native and introduced species are more often mosaic (Harrison and Rand 1989). Examples of mosaic hybrid zones between native and introduced species have been observed in multiple systems (Harrison and Larson 2016), and likely form as a result of the heterogenous geographic nature of invasive species establishment across the landscape. The hybridization of invasive winter moth (WM), *Operophtera brumata* (Lepidoptera: Geometridae), and the native congener Bruce spanworm (BSW), *O. bruceata* in the northeastern United States (U.S.; i.e., New England and New York) presents a rare example of a stable clinal hybridization zone between a native and introduced species (Andersen et al. 2019, 2022). Males of both species are attracted to the same pheromone compound used by WM and BSW females to attract mates (Roelofs et al. 1982) and where the ranges of WM and BSW overlap in the northeastern U.S., the two species are capable of mating and producing viable offspring (Andersen et al. 2019, 2022). However, hybridization of WM and BSW is asymmetric, resulting in low occurrence of BSW backcrosses compared to WM backcrosses, which may be an indicator of low hybrid fitness (Havill et al. 2017; Andersen et al. 2019, 2022).

Despite the ability of BSW and WM to produce fertile hybrids, a hybrid swarm has not formed in this region, and the occurrence of hybrids across the hybrid zone appears stable at around 10% of the population on average each year (Havill et al. 2017; Andersen et al. 2019, 2022). Since there are no known sexual or postzygotic barriers to hybridization (Havill et al. 2017; Andersen et al. 2019, 2022), we hypothesized that one or more temporal premating barriers to hybridization are responsible for maintenance of the stable clinal hybrid zone between BSW and WM in New England. In combination with selection on seasonal timing of flight (Peterson and Nilssen 1998; Andersen et al. 2023), natural selection on diel timing of flight may maintain reproductive isolation through reinforcement (Servedio and Noor 2003), preventing a hybrid swarm from being generated.

The diel timing of flight may differ between WM and BSW due to physiological differences in how the two species are adapted to winter flight. Heinrich (1987) demonstrated that many moth species that fly in late fall or winter vibrate their wing muscles to elevate their thoracic temperature prior to taking flight. Interestingly, BSW was the one species in Heinrich's study able to function and fly at or below freezing that did not vibrate wing muscles, and thoracic temperatures remained equivalent to ambient temperature (Heinrich 1987). Studies of male WM have noted that flight ceases as temperatures fall towards freezing (Roelofs et al. 1982; O'Donnell and Groden 2017), likely as a result of physiological difficulties of flight at cold temperatures (Heinrich 1987), and because response to female pheromone does not occur below 4 °C (Roelofs et al. 1982). Perhaps for similar reasons, Heinrich anecdotally observed that BSW flight shifted to include more daylight hours as the season progressed into winter, possibly as a strategy to take advantage of warmer daylight hours as temperatures decreased (Heinrich 1987). Whether this is true for WM as well is unknown; however, in Europe, the seasonal timing of WM flight is thought to be optimized to avoid predation from birds (Peterson and Nilssen 1998), and thus it is also possible that an avoidance of daytime flight evolved to further reinforce predator avoidance. By conducting pheromone trapping of BSW in a region where WM is absent and trapping WM where it is at such high densities that traps reliably capture exclusively WM (i.e., we trapped on either side of the stable hybrid zone) and logging the daily timing of flight, we investigated whether WM and BSW diel periods of flight overlap and tested whether BSW shifts toward daytime flight as temperatures decrease. Differences in these two species' evolutionary adaptations to flight during cold temperatures may influence the prevalence of their hybrids and future population demographics in the introduced range of WM.

Methods

Diel Timing of Flight

To compare hourly flight of Bruce spanworm to that of winter moth, we used Universal Green Bucket Traps (Great Lakes IPM, Vestaburg, MI) baited with winter moth pheromone (Alpha Scents, Inc., Canby, OR and Great Lakes IPM, Vestaburg, MI; Underhill et al. 1987) and fitted with infrared beam event recorders (Onset Computer Co., Bourne MA) to record time of capture of adult moth males (Tobin et al. 2009). The pheromone lures used in this study equally attract BSW and WM adult males (Roelofs et al. 1982). Traps that logged times of captures were deployed during November and/or December 2009, 2010, 2012, 2013, and 2016 in eastern and western Massachusetts (MA). To confirm that hourly capture event records were representative of actual captures, we conducted additional trapping in 2022 in both eastern and western MA, checking traps at 9:00 and 15:00 h daily to record numbers of moths captured during daylight compared to dawn, dusk, and night hours (hereafter referred to as nighttime). Eastern MA sites captured exclusively winter moth and western MA sites captured exclusively Bruce spanworm, except in three instances that were excluded from analyses (see Table 1 for detailed trap information, including GPS coordinates and number of trap nights). Moths trapped in 2009–2016 were identified to species via restriction enzyme digestion analyses of a portion of the single-copy nuclear locus glucose-6-phosphate dehydrogenase (G6PD) for at least 10 individuals from each trap (when available) using the protocols presented in Elkinton et al. (2010). Species identifications for 2022 moths were confirmed with quantitative PCR (qPCR) using species-specific fluorescent probes that bind to a portion of mitochondrial locus cytochrome oxidase 1 (COI) (Artemis Roehrig, Personal Communication).

Table 1 Locality information for pheromone traps, years surveyed, and dataset use

Dataset	Year(s) trapped	Coordinates	Trap name	Trap days	Species trapped[1]
Hourly	2009	(42.061301, −70.843882)	Hanson	8	WM
	2009	(41.657553, −70.556412)	Otis	5	WM
	2010, 2012, 2013	(42.362660, −72.438897)	Pelham	25	BSW
	2010, 2013	(42.604416, −72.733158)	Shelburne	14	BSW
	2012, 2013, 2016	(42.322018, −72.501563)	Amherst	10	BSW
	2012	(41.654980, −70.233038)	W. Yarmouth	18	WM
	2013	(42.626990, −72.879665)	Charlemont	7	BSW
Day/Night	2022	(42.419125, −72.493754)	N. Amherst	17	BSW
	2022	(42.322018, −72.501563)	S. Amherst	11	BSW
	2022	(42.317283, −72.468310)	SE. Amherst 1	18	BSW
	2022	(42.318049, −72.469722)	SE. Amherst 2	18	BSW
	2022	(42.485196, −71.434780)	Acton	15	WM
	2022	(42.407538, −71.292241)	E. Lincoln	12	WM
	2022	(42.403428, −71.322086)	W. Lincoln	14	WM

[1]BSW = Bruce spanworm, *Operophtera bruceata*; WM = winter moth, *O. brumata*

Weather Data

Using the package CHILLR (Luedeling 2023) in the statistical program R version 3.6.2 (R Core Team 2022), we acquired temperature data from National Oceanic and Atmospheric Administration (NOAA) weather stations for each trap location. To examine hourly temperature differences, we converted minimum and maximum daily temperature records to hourly temperatures using the function 'make_hourly_temps' in CHILLR which fits a sine curve for increasing daytime temperatures, and a logarithmic decay function for nighttime cooling and accounts for differences in daylength based on geographic location-specific sunrise and sunset times (Luedeling 2023).

Analyses

To summarize the hour of flight detection, we first grouped 2009–2016 individual detections by hour of the day (0:00 h – 23:00 h) to calculate the total number of capture detections per trap hour. We then calculated mean and standard error of hour of capture for each species using circular statistics in the R package CIRCULAR (Agostinelli and Lund 2022). Grouping flight data by hour allowed us to analyze the relationship between temperature and flight for each species by regressing number of hourly capture detections against hourly temperature for 2009–2016 trap data. For 2022 trap data we regressed daily captures, after logarithmic transformation to achieve normality, against minimum daily temperature.

To further analyze the effect of temperature and time of day on time of capture, we calculated the proportion of hourly detections for each hour of trapping per site. We focused these analyses on BSW and not WM because the latter species had almost no flight during daylight hours. This calculation mathematically corrects for multiple detections that may have resulted from a single individual (i.e., total daily detections may not always equal total moths trapped) by compiling detection events into total hourly detections and dividing by total daily detections per hour per day per trap. We modeled the hourly proportion of BSW flight with a generalized linear mixed model with a binomial distribution and logit link in R. The model included hourly proportion of flight as the response variable and minimum daily temperature and hours from noon as fixed effects. We used the number of hours from noon (i.e., the absolute value of 12 subtracted from hour of the day) instead of sequential hour (i.e., 0–23) since we were interested in whether flight was taking place during day vs. night and did not need to differentiate between before and after noon. We conducted post-hoc Tukey's pairwise comparisons using the R package EMMEANS (Lenth 2020). In order to visualize and further examine the effect of the interaction of time and minimum temperature on proportion of BSW flight (Fig. 4), we plotted proportion of flight against number of hours from noon for three minimum temperatures: the mean minimum temperature, mean minimum temperature + 1 SD, and mean minimum temperature – 1 SD (Aiken and West 1991).

Results

Analyses of hourly moth captures in pheromone traps indicated that WM flight is almost completely nocturnal, while BSW flies throughout the day and night (Fig. 1), and that these patterns were consistent across study sites (Fig. 2). The mean (±SE) hourly time of WM flight was 19.69 h ± 0.02 h and 13.05 h ± 0.06 h for BSW flight (i.e., approximately 7:41 pm for WM and 1:03 PM for BSW). Day vs. night pheromone trapping in 2022 indicated that significantly more BSW than WM were captured during the day (35.70% of BSW captures vs. 3.36% of WM captures; $X^2 = 170.82$, $P < 0.001$). Results from both pheromone trapping data sets showed that minimum temperature did not predict BSW flight (2009–2016: $\beta = -0.0029 \pm 0.0045$, $t = -0.63$, df = 164, $P = 0.53$; 2022: $\beta = -1.18 \pm 0.61$, $t = -1.92$, df = 57, $P = 0.06$), but hourly 2009–2016 WM flight was predicted by hourly temperature ($\beta = 0.046 \pm 0.0096$, $t = 4.79$, df = 262, $P < 0.001$), and minimum daily temperature also predicted 2022 daily WM captures ($\beta = 2.43 \pm 0.55$, $t = 4.44$, df = 32, $P < 0.001$) (Fig. 3).

Although there was not a significant linear relationship between minimum temperature and BSW flight, the interaction of minimum daily temperature and number of hours from noon (0–12 with 0 representing midday and 12 representing midnight) significantly influenced the hourly proportion of BSW flight ($X^2 = 51.10$, df = 1, $P < 0.001$; Fig. 4). In the same model, the main effect for minimum temperature was significant ($X^2 = 88.33$, df = 1, $P < 0.001$) but the

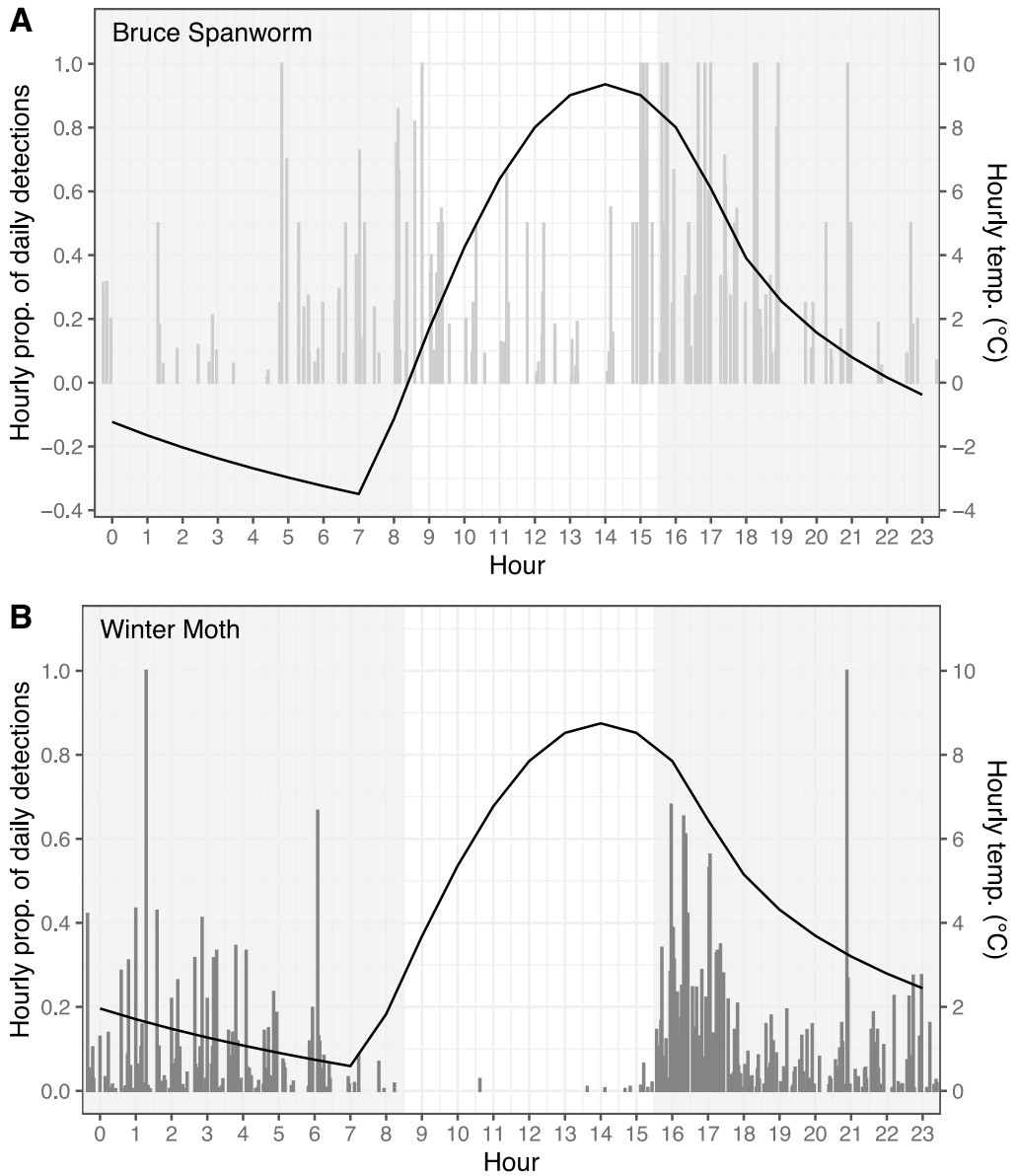

Fig. 1 Histograms of the hourly proportion of daily moth capture detections (i.e., the proportion of the total daily detections that occurred during each hour of the day) of (**A**) Bruce spanworm (BSW, *Operophtera bruceata*) and (**B**) Winter moth (WM, *Operophtera brumata*). The black line on each panel represents the average hourly temperatures during moth detections

main effect of hours from noon was not ($X^2 = 0.168$, df = 1, $P = 0.682$). *Post-hoc* pairwise comparisons indicated that at six hours from noon there was no significant difference between minimum temperatures that were high (i.e. one SD above the mean; 1.22 °C), average (i.e., mean; − 3.43 °C), and low (i.e. one SD below the mean; − 8.08 °C) in the proportion of hourly flight that occurred (mean vs. high: odds ratio = 1.00 ± 0.052, $Z = 0.076$, $P = 1.00$; mean vs. low: odds ratio = 1.00 ± 0.052, $Z = 0.076$, $P = 1.00$; high vs. low: odds ratio = 1.00 ± 0.104, $Z = 0.076$, $P = 1.00$). However, at noon the proportion of flight was significantly higher at low temperatures compared to high temperatures (odds ratio = 0.24 ± 0.039,

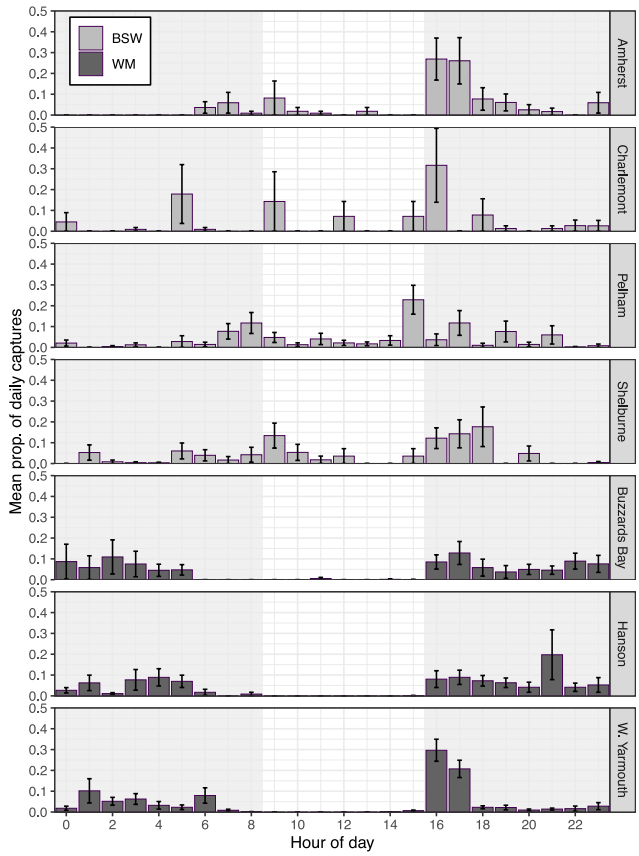

Fig. 2 Average (mean ± SE) hourly proportion of moth capture detections (i.e., the proportion of the total daily detections that occurred during each hour of the day) for Bruce spanworm (BSW, *Operophtera bruceata*; light bars in top 4 panels) and Winter moth (WM, *Operophtera brumata*; dark bars in bottom 3 panels) by trapping location

$Z = -8.927$, $P < 0.001$), and conversely, at midnight the proportion of flight was lower at low temperatures compared to high temperatures (odds ratio = 4.19 ± 1.18, $Z = 5.062$, $P < 0.001$; Fig. 4).

Discussion

In Europe, the seasonal timing of winter moth (WM) flight is highly variable based on latitudinal and elevational differences across the continent, with higher elevation/latitude populations flying, in general, earlier in the season than lower elevation/latitude populations. These differences are thought to have evolved and to be locally optimized so that peak flight corresponds with the period of time after avian predators have migrated from the region, but before the onset of snow and < 0 °C temperatures (Peterson and Nilssen 1998). In contrast to WM, little is known about regional differences in the timing of the North American Bruce spanworm (BSW) flight and much remains to be learned about factors that influence the seasonal timing of BSW flight. Though a recent study suggested that similar elevation/latitude differences in the timing of flight might exist in New England (Andersen et al. 2023), Heinrich (1987) observed that BSW males shift from nighttime to daytime flight when temperatures fell below 0 °C. This behavior is markedly different from what studies in both Europe and North America have found for WM, where flight exclusively occurs during nighttime hours, with a peak generally 2 h after sunset (e.g., Graf et al. 1995; O'Donnell and Groden 2017). Here, we confirm the observations of Heinrich, as we found a clear change in the proportions of BSW males flying during the daytime as a response to decreasing nighttime temperatures (Fig. 4) and provide further evidence for the near complete avoidance of daytime flight by winter moth (Fig. 1b).

It is curious that two species as closely related as BSW and WM would have such different behavioral

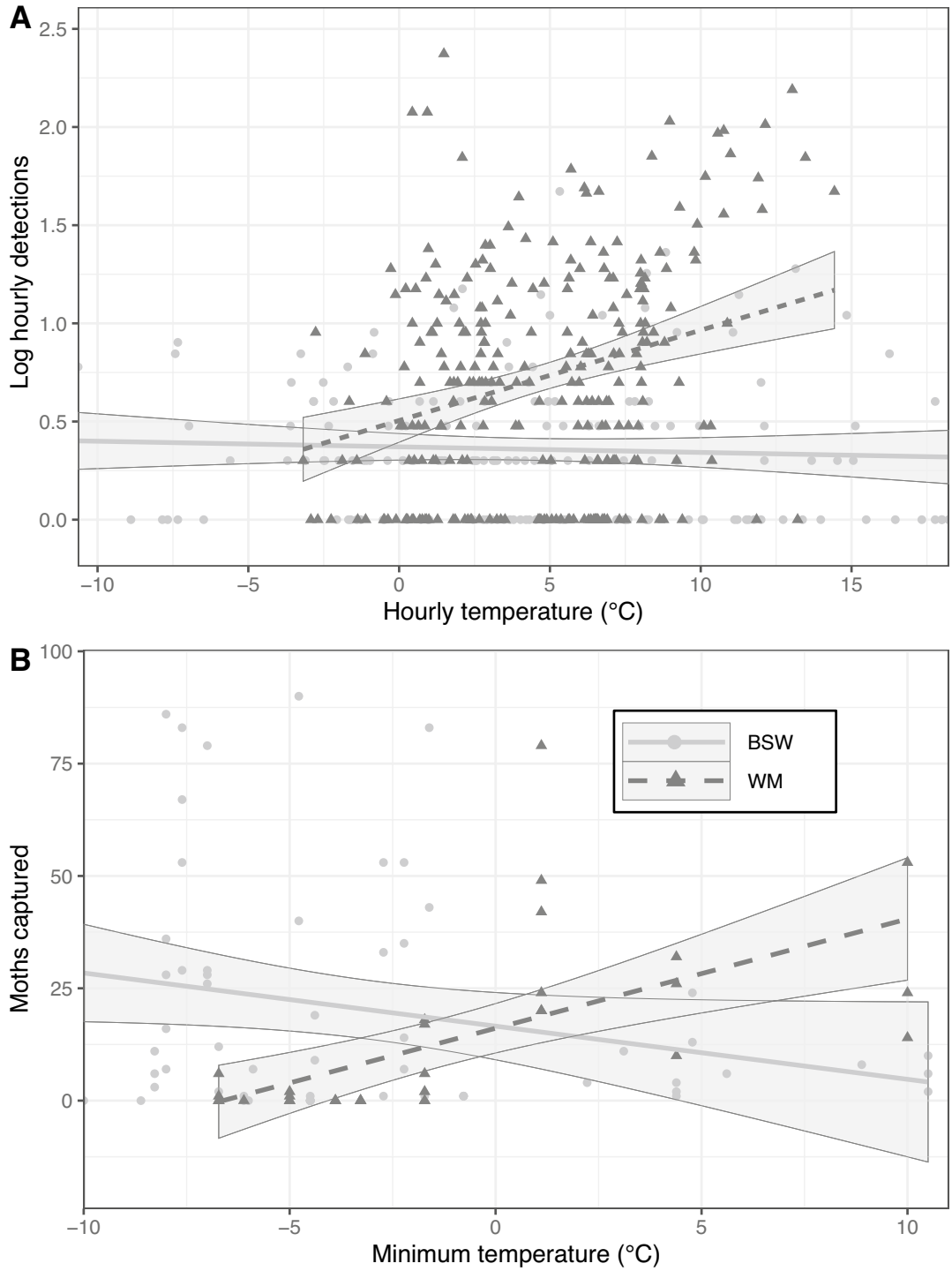

Fig. 3 The linear relationship between (**A**) capture detections and hourly temperature from 2009–2016 and (**B**) 2022 males captured and daily minimum temperature for winter moth (WM; *Operophtera brumata*) and Bruce spanworm (BSW, *Operophtera bruceata*)

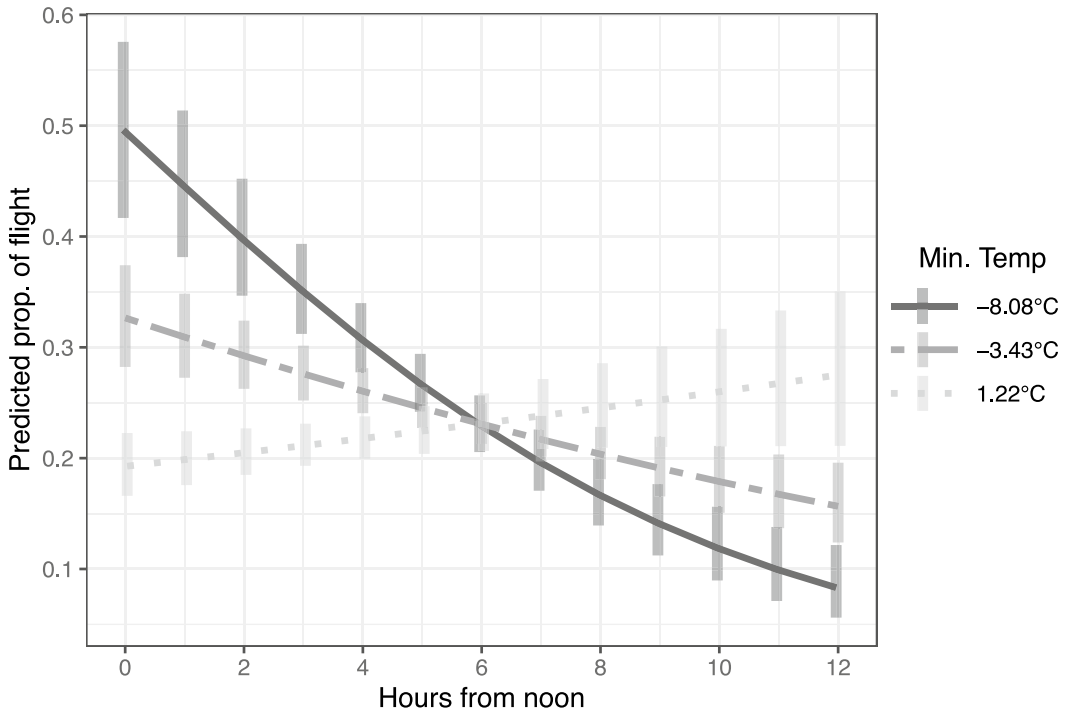

Fig. 4 Proportion of hourly Bruce spanworm (BSW, *Operophtera bruceata*) flight detections as a function of time of day (hours from noon) and minimum temperature (mean -1 SD: −8.08 °C, mean: −3.43 °C, mean + 1 SD: 1.22 °C) as predicted by a binomial generalized linear model. The x axis, represents number of hours from noon (e.g. 0 is equivalent to noon and 10 represents both 2 am and 10 pm)

responses to the onset of sub-zero winter temperatures. The delayed seasonal timing of flight by WM compared to BSW may reduce the fitness of WM males by preventing them from having enough thermal energy for flight and for mate-finding and might be partially responsible for the maritime distribution of this species in its invaded regions (Andersen et al. 2023). In contrast to this environmentally restricted distribution, BSW (including its subspecies) has a trans-continental distribution in North America (Troubridge and Fitzpatrick 1993). While our study design does not address the contribution of the timing of female pheromone production to diel patterns of mating, this behavioral adaptation may help mitigate the difficulties associated with sensing female pheromones at below-optimal temperatures (Batiste et al. 1973; Jackson and Resh 1991; Levi-Zada and Byers 2021). Why WM does not shift to daytime flight as well is puzzling, and while we can only speculate, we assume that this strong avoidance of daytime flight has evolved to reduce exposure to predators that may still be active in Europe but are absent or in lower abundances in North America.

The partial diel partitioning of flight timing by WM and BSW in North America might also provide a possible explanation for the presence and persistence of a stable hybrid zone in the northeastern U.S., as observed in Andersen et al. (2022). The evolution of reproductive isolation between two insect species is commonly maintained through differences in diel timing (Batiste et al. 1973; Jackson and Resh 1991; Devries et al. 2008; Levi-Zada and Byers 2021), and recent simulation work suggests that when two species with little to no niche differentiation overlap and interbreed, one or both species are driven to extinction under most scenarios (Irwin and Schluter 2022) through a process known as hybridization to extinction (Todesco et al. 2016). However, as ecological differentiation increases, more scenarios occur where both species can co-exist without extinction occurring or the creation of a hybrid swarm (Irwin and Schluter 2022). For WM and BSW, partial diel partitioning of flight might provide such a scenario where the less

abundant BSW has opportunities to mate without outcrossing, resulting in sufficiently pure BSW persisting in the population to maintain species boundaries and stabilize the hybrid zone. Under this logic, it is also conceivable that in locations where the successful biological control of WM has occurred, and WM densities are maintained at levels at or below those of BSW (e.g., Elkinton et al. 2021), diel partitioning might further reinforce the species boundaries in this system and could, through time, drive WM populations to localized extinction as they repeatedly outcross with BSW (which would always be active during the same hours that WM mating occurs) while BSW populations would remain relatively stable as mating would occur both during periods of the time when WM is active but also during daylight hours when BSW is active.

Studying the interactions of invasive populations of WM and populations of the native BSW provides fascinating opportunities to unravel the many ecological and evolutionary factors that influence reproductive isolation, such as the observed differences in diel timing described here, and seasonal timing, described in Andersen et al. (2023). Further study of hybrid fitness in this system is needed, particularly to observe whether the proportion of BSW individuals flying during the day increases due to reinforcement in regions where WM and BSW overlap – a shift that could provide genetic separation between native BSW populations – and/or if introgression of BSW alleles in WM populations might drive a shift towards daytime flight in this species as well. Further studies are also needed to understand the importance of predators for optimizing the timing of flight in this system, and how these predatory pressures differ between Europe, North America, and across the invaded regions that WM occupies.

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Author Contributions Jennifer Chandler: conceptualization (supporting), investigation (equal), data curation (lead), formal analysis and visualization (lead), writing – original draft (lead), writing – review and editing (equal). Joseph Elkinton: Conceptualization (lead), writing – review and editing (equal), investigation (equal), funding acquisition (equal). George Boettner: conceptualization (supporting), investigation (equal), writing – review and editing (equal). Jeremy Andersen: conceptualization (supporting), investigation (equal), writing – review and editing (equal), funding acquisition (equal).

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Data Availability Data available upon request to corresponding author.

Declarations

Competing Interests The authors declare no competing interests.

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