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Source: International Journal of Insect Science, 6(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/IJIS.S15246

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International Journal of Insect Science

Horn Fly, *Haematobia irritans irritans* (L.), Overwintering

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ABSTRACT: The horn fly, *Haematobia irritans irritans* (L.), is an ectoparasitic blood feeder mainly on cattle. Its cosmopolitan distribution extends from boreal and grassland regions in northern and southern latitudes to the tropics. Stress and blood loss from horn flies can reduce cattle weight gain and milk production. Horn flies show substantial plasticity in their response to winter. Populations in warmer, lower latitudes have been reported to overwinter in a state of dormancy, but most overwinter as active adults in normal or reduced numbers. As latitudes increase, winters are generally colder, and correspondingly, larger percentages of horn fly populations become dormant as pharate adults (a post-pupal, pre-emergent stage) or die. Reports on the effect of elevation on horn fly dormancy at high elevations were contradictory. When it occurs, dormancy takes place beneath cattle dung pats and in the underlying soil. The horn fly's mode of dormancy is commonly called diapause, but the collective research on horn fly diapause (behavioral and biochemical) is not conclusive. Understanding the horn fly's overwintering behaviors can lead to development of pre-dormancy insecticide spray strategies in colder latitudes while other strategies must be determined for warmer regions.

KEYWORDS: diapause, dormancy, horn fly, photoperiod, quiescence, season, temperature

CITATION: Showler et al. Horn Fly, *Haematobia irritans irritans* (L.), Overwintering. *International Journal of Insect Science* 2014:6 43–47 doi:10.4137/IJIS.S15246.

RECEIVED: March 5, 2014. **RESUBMITTED:** April 2, 2014. **ACCEPTED FOR PUBLICATION:** April 3, 2014.

ACADEMIC EDITOR: Helen Hull–Sanders, Editor in Chief

TYPE: Short Review

FUNDING: Authors disclose no funding sources.

COMPETING INTERESTS: Authors disclose no potential conflicts of interest.

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Introduction

The horn fly, *Haematobia irritans irritans* (L.) in the dipteran family Muscidae, is an ectoparasitic pest of livestock that was originally described from southern France. The insect's current distribution encompasses much of the tropical, subtropical, and temperate regions of the Northern Hemisphere,[1] including Europe, North Africa, and Asia Minor. In the Americas, the fly occurs from southern Canada to temperate areas of Argentina and Uruguay.[2–5] An obligate blood feeder,[6] the horn fly is hosted primarily by cattle, but it has also been reported parasitizing horses, water buffalo, sheep, goats, and some nondomesticated mammals.[1,5,7,8]

Horn fly adults are problematic because their habit of repeated daily feeding causes stress to livestock, often resulting in anemia related to blood loss and reduced weight gain in beef cattle.[9,10] During particularly intense infestations (1,000–4,000 flies can settle on individual cows),[1] cows may shed nearly 0.25 kg each day.[1] In addition, milk production by dairy cows is sometimes diminished by 10–20%.[10,11] Infestations in North America alone are thought to inflict economic losses of as much as US $1 billion annually, including US $60 million spent on insecticides and their application.[5–7,12] In general, horn flies are generally not considered to be important vectors of livestock diseases, but they are the intermediate host for a filarial nematode, *Stephanofilaria stilesi* Chitwood, which causes skin lesions on cattle.[5]

About 4 mm long, the adult horn fly is brown-gray with a greenish-yellow sheen and four dorsal longitudinal thoracic stripes, the outermost two of which are broken. The abdomen is blotchy or checkered.[1] Adults pierce the host animal with their mouthparts, rarely leaving the host, mostly settling on the back, sides, neck, and sometimes the head.[5,7] Individuals typically feed 20–38 times per day,[5–7] and feeding is required for mating and egg production.[5] Females deposit their eggs in dung so fresh that one of the only times they leave the host involves moving toward the tail to deposit their eggs on and under feces, sometimes before the cow completes voiding, returning to the host within one minute.[5,13] A single female can produce as many as 400 eggs in its lifetime, deposited in clusters of 20–25 eggs.[7]

The eggs hatch within 20–24 hours, and the larvae, living within dung pats, undergo two molts to the third instar followed by pupation[5,7] inside the dung or in the soil just beneath it.[14] Development from egg to pupa generally requires 4–8 days, dependent upon temperature.[15] In cool temperate areas, six to nine generations can occur per year, and 12–14 generations are completed in warmer temperate and subtropical regions.[7]

In colder temperate regions such as southern Alberta, Canada, adult horn fly populations tend to peak in midsummer, but in warmer temperate regions, such as Missouri and Texas, two population peaks occur, one in early summer and the other in late summer or early fall.[1,7,16,17] The two peaks in warmer climates result from unfavorably high heat in midsummer that also depresses adult numbers.[7,18,19] In some temperate areas, however, the peak population is limited to a single interval in late summer and early fall.[20]

Horn flies were first believed to survive cold winters on host animals, or hidden in barn trash and hay lofts, but later studies indicated that overwintering commonly occurs as pupae beneath cattle dung pats and in the underlying soil (depth is influenced by soil type).[21] The scientific literature includes examples of horn flies surviving winters in different ways. The purpose of this review is to show what is currently known about how the horn fly responds to winter.

Warm Winter Latitudes

In temperate regions that remain relatively warm during winter, and in subtropical and tropical areas, adult horn flies have been reported to feed on livestock throughout the winter, albeit sometimes to lesser extents than are encountered during the population peaks of spring, summer, and early fall. In the Southern Hemisphere tropics of Brazil (eg, São Paulo in east-central, and Santa Catarina in southern coastal regions), for example, adult horn fly populations continually infest cattle regardless of seasonal changes,[16,17,22] and in the Pantanal (west-central region), ≥64% of the cattle host horn flies throughout the year.[23] Mendes and Linhares[14] reported that only 7.7–9.9% of horn flies in tropical Brazil underwent winter diapause, but they were unable to find any winter pupae. In the subtropics of central Argentina, winter populations of adult horn flies on cattle were reported in each of nine consecutive years (1992–2000).[24] Another study in the same region showed that up to 55% of the peak adult horn fly population was detected during winters.[25] Adult horn flies were also observed on cattle year-round in the subtropical Tacuaremó Department of Uruguay.[20] Northern Hemisphere tropical horn flies in the humid lowlands of Veracruz State, Mexico, are also found on cattle year-round.[26,27] Under subtropical conditions of the Northern Hemisphere, Almazán et al[28] reported that winter adult horn fly populations in Tamaulipas State, Mexico, were 45.4% as great as those of warmer seasons. In the same region of Mexico, Soberanes et al[29] recorded three population peaks during the year, one of which occurred during January. Adult winter populations in relatively warm subtropical areas of the southern United States such as south Florida and Texas (below latitude 29°) have been reported,[30] even during periods of low temperatures.[31,32] Thomas et al[33] found that, in temperate Missouri, the highest incidence of diapause reached 80% and that adults persisted during winter.

Cold Winter Latitudes

In relatively cold regions where adult horn fly populations undergo substantial winter declines, populations are replenished during the following spring from eggs laid the previous fall that develop and enter winter as pupae.[21,34] As latitudes increase into temperate regions where winters are colder, horn flies tend to overwinter in a dormant state that is widely accepted as being diapause.[18,35,36] Thomas[37] suggested that if horn flies diapaused, it occurred at the adult pharate stage (a stage that is post-pupal but within the pupal case, and before adults emerge and become free living). The timing of horn fly diapause induction generally appears to change as latitude increases.[38] In regions close to the equator, such as Brazil, diapause starts in early winter (ie, June).[14] Farther north, diapause begins in southern Arkansas in late September and in the northern part of the state in mid-September. Most horn flies in Arkansas, however, entered diapause in October.[36] Near the horn fly's northernmost distribution limit, in Canada, diapause has been reported to commence in August.[34]

Winter diapause is an adaptation to preserve sufficient numbers of individuals through cold winters to permit the species to exist from year to year. In cold temperate areas like Alberta, horn fly overwinter survival ranged from 0 to 85%, and low temperatures, especially <10°C, resulted in the fewest survivors.[34] Diapause is a neurologically governed mode of dormancy[39] involving low metabolic activity, reduced morphogenesis, increased resistance to environmental extremes, and altered or diminished behavioral activity that can occur during any stage of insect development, generally triggered by changes in environmental parameters that precede unfavorable conditions.[40–42] Arrested development has been reported to occur in different embryonic stages, larval instars, pupae, pharate adults, and adults, but diapause usually occurs at only one stage of a given species.[43] Diapause induction requires processes that monitor environmental changes and the ability to maintain that information until the insect reaches its appropriate developmental stage.[43] Once diapause has begun, metabolic arrest is maintained even when unfavorable conditions become favorable, ensuring that the life cycle of the insect remains in phase with changing seasons.[40,41] Although diapause is frequently assumed to be "programmed" through up- and down-regulation of genes at certain times, the precise roles of those events are not well understood.[43–45]

One of the problems with biochemical determination of diapause status is that there seem to be few, if any, definitive conditions characterizing horn fly diapause.[42,43] Most studies, including one on biochemical diapause markers,[46] that assume the occurrence of horn fly diapause offer vague or no criteria.[2,18,21,30,35,36,47–49] The extent to which populations enter diapause can be misperceived because all horn flies in natural populations might not diapause, but instead, cold temperatures kill nondiapausing individuals, implying that 100% of the remaining (living) individuals are diapausing.[33] Sometimes the term "diapause" is viewed broadly and used interchangeably with the term "dormant" and at other times it is defined by specific criteria that would make it one of several modes of dormancy.[50] In an applied context, what might be most important is that in some regions horn flies overwinter in a dormant state regardless of the specific underlying mechanism. Attempts to identify biochemical characteristics of horn fly diapause have relied on the assumption that any winter-collected pupa is diapausing, hence, molecules found in abundant or reduced quantities in these individuals are taken to reflect diapause status. Respiration and moisture content decreased and amounts of protein changed during horn fly dormancy,[35,51,52] common responses among insects exposed to cold.[53] Differences in lipid concentrations were not detected in diapausing horn flies,[35] which does not agree with diapause criteria (including fat body hypertrophy) indicated for horn fly diapause.[54] Glycerol, recognized as a cryoprotectant,[42,55] was only found in small amounts in diapausing horn flies.[35]

An investigation of genetically controlled protein regulation during horn fly diapause was inconclusive.[46] Upregulated genes in individuals undergoing diapause were identified but the genes and their products were found to be involved in many aspects of insect physiology including metamorphosis, melanization, sclerotization of the puparium, and cellular defense that are not necessarily linked with diapause.[46]

Diapause induction cues are most often cited as being seasonal changes in temperature and photoperiod, and sometimes diet.[43,50,56] Short daylengths of late summer can signal the arrival of winter to insects in temperate regions, hence, cold winter temperatures are anticipated.[43] The time during which such insects prepare themselves for diapause is often relatively short and the developmental stage preceding the diapause stage is usually prolonged in order to permit diapause-destined insects the opportunity to accumulate metabolic reserves and locate hibernacula.[43] Depner[2] suggested that the effect of photoperiod on adult parent horn flies, or on the developing, unlaid egg, predisposed the offspring to diapause. More pupae were reported to enter diapause after parent adults were subjected to a 12-hour photoperiod than to a 16-hour photoperiod, and more diapaused after adult parents were subjected to 16-hour photoperiod than to 20 hours. Also, bovine blood contains an ultraviolet factor that might induce diapause in the horn fly's progeny.[2,47] Researchers have suggested that diapause in horn flies was controlled by a combination of diminishing photoperiod and temperature.[33,36,54] Laboratory experiments indicated that the horn fly's "diapause factor" probably involves adult parent exposure to diminishing photoperiod, but adults that held without light at 21°C did not necessarily produce progeny predisposed to diapause even when the progeny were held at a low-temperature regimen.[54] Adults on cattle during late fall were identified as the parents of the following spring's population in areas where diapause is assumed to occur,[54] although that might be true of any form of overwintering dormancy.

One study concluded that diapause was unrelated to daylength or numbers of light-dark cycles, but diapause induction increased with declining temperature.[38,57] At low daily temperatures (ie, 21°C) for 1–12 hours (remaining hours were held to 27°C), 12.2–45.6% of tested horn flies entered diapause, but some flies diapaused when temperatures were a constant 27°C.[54] Alternatively, horn fly diapause in Missouri was characterized by another researcher as any individual that required >34 days or 440 degree-days to develop.[33]

The "required day number" hypothesis on diapause induction necessitates two components: an internal "clock" for measuring photoperiod and a photoperiodic "counter" that sums the number of days during a particular window of time, or "sensitive period".[58] Lysyk and Moon[38] suggested that diapause sensitivity in the horn fly was between two age values on a physiological age scale of immature development, and that 50% of a horn fly population entered diapause in 19.1 days of the sensitive period. Lysyk and Moon[34] explained that the variability relating to diapause in Canada is influenced by temperatures during a "sensitive period" of only two weeks when diapause is induced, and that spring populations likely arise from eggs laid during a three to six week interval in the preceding August and early September. Diapause was not induced when temperatures during the sensitive period exceeded 23°C, and larvae produced during cold periods were likely physiologically incapable of overwintering.[34] Studies on horn fly diapause from the tropics to the insect's northern most temperate limit have speculated that horn fly diapause is facultative.[14,30,34–36,38] Although facultative diapause likely depends on exposure to environmental cues, particularly temperature and photoperiod, such overarching parameters do not necessarily influence entire horn fly populations in an area or a region. Lysyk and Moon[34] found that although all horn flies diapaused by August in Alberta, Canada, temporal patterns in the proportions of diapausing horn fly populations varied substantially between cohorts and years. Such differences suggest that seasonal changes alone, independent of specific climatic factors, might not fully govern the incidence and extent of diapause. In central Texas, for example, some horn flies failed to diapause and emerge from pupae held under winter conditions four to five days after pupation began,[30] and in Missouri, only 20–22% of horn flies entered winter diapause from eggs that were laid in September.[33]

Termination of horn fly diapause, determined by the emergence of free living adults, was reported to occur at different times when pupae were kept at different temperatures. Under field conditions, termination of overwinter dormancy has been observed to begin in late February in central Texas,[48] mid- to late March in Arkansas and Mississippi,[35,36] and mid-February to mid-April in Missouri.[18] Adult emergence was reported to cease when temperatures dropped below 15.6°C.[35]

Elevation

Increasing altitude can parallel increasing latitude in terms of temperature, but evidence concerning its influence on horn fly diapause is inconsistent. In tropical regions of central Mexico, adult horn flies were not found on dairy cattle grazing 3,000 m above sea level for up to 60 winter days,[59,60] but another study in Mexico indicated that, at about the same altitude, diapause among horn flies was "faint" and "incomplete".[49]

Conclusions

Winter dormancy in horn flies has been of interest primarily from an applied standpoint with the aim of enhancing control strategies. The goal is to apply insecticides during the fall to reduce horn fly populations whose progeny will become dormant, thereby reducing spring adults.[36,61,62] This tactic has not been demonstrated, but it might work much in the same way as so-called "diapause spraying" of boll weevils, *Anthonomus grandis grandis* Boheman, in temperate regions with sufficiently cold winters.[50,63] The rationale behind the late-season sprays is to reduce populations before they are further reduced by lethally cold temperatures. Late-season sprays against adult boll weevils in temperate regions appear to be effective even if diapause might not be the technically correct term for the pest's mode of overwintering.[50,63] In warm climates, such as in the subtropical Lower Rio Grande Valley of Texas, late-season sprays have not been effective against boll weevils because the extent of overwinter mortality is low relative in temperate regions.[63] Although cattle feed-through insecticides might be useful against late-season horn fly larvae in dung, it is likely that the most vulnerable life stage for control measures would be the adults, which congregate on livestock making concentrated targets that, unlike the immature stages, are not hidden within their food substrate.

This review shows that, notwithstanding some confusion about whether or not diapause is the mode of overwintering dormancy in temperate regions, there is a range of responses to the onset of winter that appear to be linked with temperature and associated with latitude, and possibly elevation. Responses of populations include year-round adult activity, reduced adult activity, and dormancy accompanied by varying levels of mortality. The plasticity of approaches to overwintering has permitted the horn fly to disperse and become established in a relatively wide range of latitudes and elevations such that it has largely become a cosmopolitan pest of livestock.

Author Contributions

Conceived and designed the experiments: AS. Analyzed the data: AS. Wrote the first draft of the manuscript: AS. Contributed to the writing of the manuscript: AS. Agree with manuscript results and conclusions: AS, WO. Jointly developed the structure and arguments for the paper: AS, WO, KL. Made critical revisions and approved final version: AS. All authors reviewed and approved of the final manuscript.

DISCLOSURES AND ETHICS

This paper was subject to independent, expert peer review by a minimum of two blind peer reviewers. All editorial decisions were made by the independent academic editor. All authors have provided signed confirmation of their compliance with ethical and legal obligations including (but not limited to) use of any copyrighted material, compliance with ICMJE authorship and competing interests disclosure guidelines and, where applicable, compliance with legal and ethical guidelines on human and animal research participants.

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