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Horn Fly (Diptera: Muscidae)—Biology, Management, and Future Research Directions

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Abstract

The horn fly, *Haematobia irritans irritans* (L.), is one of the most important external parasites of cattle in North America and elsewhere. Horn fly adults have an intimate association with cattle, their primary host. With their often-high numbers and by feeding up to 38 times per day per fly, horn flies stress cattle. The resulting productivity loss is valued at more than 2.3 billion USD in the United States. Insecticides are commonly used to mitigate direct injury from feeding and indirect injury from disease transmission. This paper discusses horn fly biology, distribution, and management. Emphasis is on promising new approaches in novel insecticides, repellents, biological control, vaccines, animal genetics, and sterile insect technology that will lead to effective preventative tactics and the integration of smart technologies with horn fly management. We conclude with a discussion of research needs necessary to shift horn fly integrated pest management to an emphasis on preventative tactics and the precision use of reactive techniques.

Key words: *Haematobia irritans irritans*, pest profile, insecticide, resistance

The horn fly, *Haematobia irritans irritans* (L.), (Diptera: Muscidae), is in a family with more than 4,000 fly species worldwide. Two closely related subspecies of *Haematobia*, the horn fly, *H. irritans irritans* and the buffalo fly, *H. irritans exigua* DeMeijere, have morphological and genetic differences (Zumpt 1973, Low et al. 2014), and are pests of cattle in different regions of the world.

The horn fly was accidentally introduced into New Jersey, United States from Southern France prior to 1887 (Bruce 1964, Lancaster and Meisch 1986). It was identified in the West Indies, Central America, and South America presumably from flies originating in the United States (Zumpt 1973). Current worldwide distribution includes much of the temperate, subtropical, and tropical regions of Europe, Asia Minor, and North Africa as well as the Americas (Lancaster and Meisch 1986, Showler et al. 2014). The buffalo fly

is native to southeastern Asia and Indonesia and has been present in New Guinea and Australia before 1840 (Moon 2002). The horn fly is the most economically important fly pest of beef cattle in the United States (Kunz et al. 1991, Byford et al. 1992). These hematophagous flies feed many times a day (Lancaster and Meisch 1986), which results in annoyance causing animals to display fly combative behavior as well as disrupting grazing patterns of infested animals. Understanding the lifecycle of the horn fly is key to identifying new control options and better integrated pest management opportunities for producers. The objective of this manuscript is to review previous research on horn fly biology, distribution, and management; emphasize new approaches for management and provide a discussion of research necessity to shift management from reactive to preventative tactics and, when necessary, use of precision reactive techniques.

Life Stages and Life Cycle

Adult horn flies are 3–5 mm long (Fig. 1) and have a piercing/sucking proboscis. The maxillary palps are held appressed and are almost as long as the proboscis. Wing vein m1 is gently curved forward. The compound eyes of the adult male are set close together with a single row of bristles on each side of the midline between the eyes, while the female's eyes are more widely spaced. The thorax is black, and the abdomen has a median brownish stripe with dark-colored, posterior margins. Legs are dark brown to black and the wings have a dark tinge due to microscopic pubescence. Female coloration is similar to that of males except their legs are more yellow in color (McIntock and Depner 1954).

Horn flies are holometabolous, with active larval and adult stages and inactive egg and pupal stages. Mating occurs on the host for several days after adult emergence with oviposition occurring as early as 3 d after emergence (Lancaster and Meisch 1986). Female flies older than 5 d can oviposit daily (Krafsur et al. 1992). Oviposition occurs throughout the day with female flies leaving the host to lay eggs on fresh manure pats, with most oviposition occurring in the first 2 min, then immediately returning to the host (Sanders and Dobson 1969). Eggs are approximately 1 mm in length (Fig. 2) and are deposited on the under and lower portions of cattle feces in batches of approximately 20 eggs each. During her lifetime a female horn can lay up to 400 eggs.

Horn fly eggs can hatch in as little as 11 h with an optimal egg hatching temperature of 30–32°C (McIntock and Depner 1954). First-instar larvae are about 1.5 mm long and white in color with pointed heads. These larvae will immediately burrow into dung pats and molt through two additional instars within three to 5 d. The third and final instar is about 7 mm long (Fig. 3) and initiates pupariation inside of the dung pat or in the soil immediately beneath or around the dung pat (Lancaster and Meisch 1986). Prepupal (egg through third instar) development is optimal at temperatures of approximately 25–27°C, with rates ranging between 3.5 and 8.9 d at 34.5 and 20.1°C, respectively (Lysyk 1992). At high temperatures (44°C), moisture can be a limiting factor in larval survival following egg hatching (Lancaster and Meisch 1986). Optimal manure moisture content for larval development is between 84 and 90% (Kuramochi 2000). A laboratory study comparing horn fly development in standard larval diet with either horse (*Equus ferus* L. (Perissodactyla: Equidae)), sheep (*Ovis aries* L. (Artiodactyla: Bovidae)), bison (*Bison bison* L.), cow (*Bos taurus* L. (Artiodactyla: Bovidae)), or swine (*Sus scrofa* L. (Artiodactyla: Suidae)) feces indicated that only cattle feces supported horn fly larval development (Bruce 1964, Greer and Butler 1973).

Horn fly puparia are capsule-shaped and 3–5 mm in length (Fig. 4). Horn fly pupae require less moisture than prepupal stages with optimum emergence rates observed when developmental substrates maintain 7% moisture content (Lancaster and Meisch 1986). The pupal period ranges from 3 to 5 d and the total period from egg to adult has been reported as 9–12 d (Lancaster and Meisch 1986) and 7–11 d (Melo et al. 2020).

The horn fly mouthparts are adapted for skin piercing and blood sucking with both males and females being obligate blood feeders. Soon after adult emergence, horn flies search for a host to begin blood-feeding. Male and female flies tend to cluster on the back, sides, and withers except during the hottest times of the day when they tend to migrate to the belly of the host (McIntock and Depner 1954). Blood meal acquisition is necessary for general survival, sexual maturation, and egg production.

Horn flies feed as many as 20–38 times per day (Lancaster and Meisch 1986) with each fly feeding for 96 and 163 min per day for males and females, respectively (Harris et al. 1974a). Blood meal size per feeding activity of colony horn flies of known age and sex ranged from 1.4 to 1.7 mg (Harris and Frazier 1970). Kuramochi and Nishijima (1980) tested field collected horn flies of mixed age and sex, and determined bloodmeal size was approximately 1.5 mg on average. Mullens et al. (2018a), using field collected male and female horn flies, observed bloodmeal size averaged 0.5–1.0 mg for males and 2.0–2.7 mg for females. Kuramochi (1985) found males averaged 0.6–1.0 mg of blood, while females consumed 1.7–2.7 mg and required 33 mg of blood to complete the development of the first batch of eggs.

The number of horn fly generations per year varies broadly with climate. Six to nine generations per year are typical of cool temperate regions while warm, subtropical zones can expect 12–14 generations per year (Showler et al. 2014). In northeastern Brazil, 30 generations were documented in a single year due to a life cycle of 7–11 d (Melo et al. 2020); thus, in these regions horn flies consistently infest cattle year around (Showler et al. 2014).

In temperate areas such as northwest Arkansas and northern Texas, horn fly populations are seasonally bimodal with an initial peak in late spring/early summer and a second peak in late summer/early fall (Lancaster and Meisch 1986). At this latitude, populations tend to decline during the hot, dry months of summer then resurge following late summer/early fall rains and improved forage conditions (Kunz 1980).

Horn fly overwintering, while extensively documented, remains poorly understood and may not be true diapause, although frequently described as diapause in the literature (Showler et al. 2014 and citations



Fig. 1. The adult horn fly is 3–5 mm long and has a piercing/sucking proboscis. The maxillary palps are held appressed to the haustellum and are almost as long as the haustellum. The compound eyes of the male (left) have a narrow vertex with a single row of bristles on each side of the midline between the eyes. The female (right) has a wider vertex between the compound eyes. Both sexes have a curved M1 wing vein (arrows), characteristic of *Musca* spp. (Photograph by Matt Bertone, North Carolina State University).

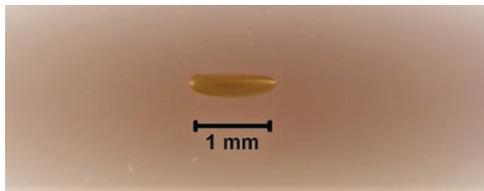


Fig. 2. Horn fly eggs are 1.0 mm. (Photograph by Dan Fitzpatrick, University of Florida).



Fig. 3. Third instar horn fly larva (7 mm). (Photograph by Dan Fitzpatrick, University of Florida).

therein). In lower latitude areas such as the lower southeastern United States, horn flies overwinter as active adults though with reduced abundance, whereas, in higher latitude areas with colder winters, a portion of the horn fly population overwinters in a dormant state as pharate adults, a post-pupal stage inside the puparia (Thomas 1985, Showler et al. 2014). Overwintering pupae are found under the manure pats or in the soil below manure pats (Hoelscher et al. 1967). Early research suggested that horn fly overwintering is an interaction between shortening photoperiod and reduced temperatures (Wright 1970). A later report suggests that overwintering (diapause) does not appear related to photoperiod but rather, to the prolonged development time associated with lower temperatures (Lysyk and Moon 1994). The ability of horn flies to survive and overwinter at diverse latitudes and temperature conditions is a key survival trait associated with the horn fly as a global pest (Showler et al. 2014).

Effects on Host Animals

The horn fly is primarily a pest of cattle but populations are occasionally found on other domestic animals such as sheep, goats, horses, mules, and dogs, and in some situations are considered pests. For instance, horses pastured with or near cattle can be infested with horn flies and problematic populations require control (Jones et al. 1988, Loftin and Corder 2010); fortunately, horses carry fewer flies than cattle kept in the same pasture (Greer and Butler 1973). Horn flies are key pests for cattle in production systems where cattle graze in pastures (Byford et al. 1992).

Direct Effects

The economic impacts of horn fly infestations on cattle are manifested through effects on animal production. In general, decreased weight gain, feed efficiency, and milk production are the hallmarks of high horn fly populations causing animal distress that results in economic losses for cattle producers. In fact, yearling steers and heifers on which flies were controlled gained up to as much as 17.7% (Haufe 1982, Kunz et al. 1984) and 14% (DeRouen et al. 2003) more weight, respectively, when compared with animals without horn fly control. Control of horn flies resulted in a 4.45-kg



Fig. 4. Horn fly puparium. (Photograph by Dan Fitzpatrick, University of Florida).

weight gain advantage for steers (Kinzer et al. 1984) and a 15.44-kg weight gain for mature cows (Smythe et al. 2019). The overall economic impact of horn flies on cattle productivity in the United States has been estimated at more than \$2.3 billion USD (Kunz et al. 1991, Byford et al. 1992).

Indirect Effects

Horn fly effects on mature cows are often indirectly assessed through offspring performance. Calves paired with insecticide-treated cows had an increase in average daily weight gain up to 0.06 kg/d (Huston et al. 1979, Kunz et al. 1984, Quisenberry and Strohbehn 1984a), and an increase in weaning weight of 5.86–16.28 kg (Campbell 1976, Cocke et al. 1989, Smythe et al. 2019).

Mastitis is an inflammation of the mammary gland or udder caused by environmental bacteria found in the farm environment. Poor udder health or mastitis is a leading cause of reduced milk quality resulting in annual losses estimated to be \geq \$200 per cow (Keown and Kononoff 2007). The connection of horn flies and incidence of intramammary infection was established when a survey showed farms using some form of fly control displayed lower rates of *Staphylococcus aureus* Rosenbach (Bacillales: Staphylococcaceae) mastitis in heifers compared with herds using no fly control (Nickerson et al. 1995). Additionally, animals from herds not using any fly control method had more scabs and lesions on their teats, which were associated with *S. aureus* colonization (Nickerson et al. 1995). Owens et al. (1998) used DNA fingerprinting to identify an isolate of *S. aureus* colonizing horn flies. The isolate was identical to isolates from the teat ends and mammary secretions of heifers exposed to these same flies (Gillespie et al. 1999). Ryman et al. (2013) confirmed horn flies are important in the development of *S. aureus* mastitis among dairy heifers and suggested flies should be included in a mastitis management plan. Antibiotics can be used to control mastitis, while insecticides can significantly reduce the spread of

S. aureus among cattle by controlling the horn flies (Nickerson et al. 1995, Oliver et al. 2005).

Economic Injury Levels

Insect economic injury levels are used to make informed decisions whether an insect management intervention is justified to protect commodity quality or to prevent economic losses and expenses (Southwood and Norton 1973). Campbell (1976) was one of the first to demonstrate the economic importance of horn fly control in cow-calf operations. Later, simple (nominal or static) thresholds of about 200 horn flies per animal were suggested (Gordon et al. 1984, Kunz et al. 1984, Schreiber et al. 1987). However, static thresholds are limited in use since they only consider a single pest species and do not change regardless of production practices or other variables.

As early as 1974, Haufe listed criteria needed to develop dynamic thresholds for horn flies. In addition to pest and host interaction parameters, dynamic thresholds consider economic production variables and input costs of pest management to reflect current and local conditions (Haufe 1974). Parameters such as the population dynamics of multiple pests, abiotic stressors, nontarget impacts, and distributed environmental costs can be included to achieve a comprehensive threshold that considers a broader system perspective (Pedigo and Rice 2009). Unfortunately, we still lack dynamic and comprehensive economic thresholds for horn flies and this topic remains a research priority, especially considering that the beef industry has undergone dramatic changes in practice such that animals are genetically different, the environment is changing with climatic shifts, consumers are indicating a preference for insecticide-free animals raised on pasture, and producers are facing limited choices for fly control.

Production Systems

Horn flies can affect grazing beef animals and dairy animals with these being examples of extensive and intensive systems, respectively. Other production systems included organic and mixed.

Intensive

Production systems with high numbers of animals per unit area of land or barn space are considered intensive animal systems (Gerry 2019, Talley and Machtinger 2020). Adult horn fly populations on cattle tend to be low in intensive production systems such as feedlots and confined dairy operations because crowding and routine movement of cattle for feeding and drinking disturbs cattle dung, making dung pats unsuitable or at least subpar, for horn fly development (Gerry 2019). Frequent cattle dung management and removal can play a role in disrupting immature development as well. However, horn fly abundance can be elevated in confined intensive systems when the operation is close or adjacent to pastured cattle.

Dairy farms are unique intensive systems with most production animals housed in small, confined spaces that may be paired with pastured areas for the dairy cows and heifers to graze. Where present, these grazing areas offer increased opportunity for horn fly population development in undisturbed cattle dung (Sjostrom et al. 2016). Increasingly, dairies are moving toward a more intensive model with increased animal density and limited access of animals to pasture, or toward a less intensive model with increased grazing space. The latter of these two trends is particularly common for organic dairy production and the increased pasture at these dairies is conducive to increased abundance of the horn fly.

Extensive

Animal systems that encompass large land areas with low densities are considered extensive systems (Gerry 2019, Talley and Machtinger 2020), i.e., pastured cattle. Extensive beef cattle systems are in three main sectors: 1) cow-calf; 2) stockers; and 3) seed-stock producers. Each of these sectors of the beef industry rely upon pasture or native range areas as their main production site. Cow-calf production systems, designed to sustainably produce calves every year, are impacted by both direct and indirect horn fly stress (Talley and Machtinger 2020). The beef stocker sector, also known as backgrounding, pastures weaned calves in forage-based areas for 75–300 d. Operators attempt to reduce any stress, including that caused by horn flies that can affect weight gain efficiency before the calves are sent to a beef feedlot (Talley and Machtinger 2020).

Another extensive production operation is the seed-stock system focused on improving the genetic background of animals to improve the larger cow-calf sector. This sector is a leader in promoting technologies to improve beef production including tactics and approaches to limit stress from external parasites such as horn flies. One priority for this sector is to develop genotypes of beef animals with increased tolerance or resistance to horn fly infestations (McKay et al. 2019).

Organic

Organic livestock production systems promote an integration of cultural, biological, and mechanical practices that foster a cycling of resources, promote an ecological balance, and conserve biological diversity. Within this system all ruminant livestock, for example cattle, are required to have access to pastures daily (Rinehart and Baier 2011). In addition, pastures must be maintained to provide sufficient quality and quantity of forage during the grazing season.

A survey conducted by Roberts et al. (2007) reported the most common production challenges in organic livestock production were in controlling disease (such as mastitis) and parasites (such as horn flies).

In certified organic operations (dairy or livestock production) some synthesized and natural fly control products are allowed for use and are listed in the USDA Organic Regulations (7-CFR-205 document). Organic systems can use essential oils and botanicals such as natural pyrethrins applied as sprays, oiler/rubs, or wipes. Diatomaceous earth can be applied using dust bags in forced or free-choice arrangements. The protection of competitor species such as dung beetles is important to manage larval fly stages in dung pats. Larval management can appear ineffective if adult horn flies migrating to pastures from other locations sustain high on-animal horn fly numbers. Reports of horn fly dispersals of up to 1.3 km (Eddy et al. 1962, Tugwell et al. 1966) and 11.7 km (Kinzer and Reeves 1974) are based on the most distant sampling location from release points of each study.

Mixed

Mixed livestock management systems use a combination of pasture and dry lot venues (Talley and Machtinger 2020). Cattle grazing pastures adjacent to a semi-confined dry lot will deposit enough manure to produce horn flies through the fly season. The flies developing from manure in the pastures will provide a source population infesting cattle while they are grazing or in the dry lot. Dairy cattle in this setting could be subject to intramammary infection.

Horn Fly Management

Management strategies for horn flies include nonchemical control methods such as biological control, pasture management, and

trapping. However, conventional insecticides remain the mainstay of horn fly control and various registered chemistries and application methods are discussed. Biorational insecticides and their application to fly control are of increasing interest and are similarly covered. Because of advances in research methods the potential of tactics such as breeding for horn fly resistance, vaccines, and sterile insect techniques are considered.

Monitoring

Monitoring horn fly numbers on cattle is an essential component of much applied research and in making treatment decisions. Visual observations have been used extensively to assess on-animal horn fly populations (Morgan 1964, Tugwell et al. 1969, Williams and Westby 1980, Skoda et al. 1987) and Lysyk (2000) discussed the variety of visual observation techniques used. More recently, digital techniques have been used to overcome shortcomings of visual estimates of horn fly populations (Lima et al. 2002, Castro et al. 2005, Mullens et al. 2016). However, digital images require time-consuming manual annotation, and animal color and image quality can reduce accuracy (Smythe et al. 2017). Smythe et al. (2020) contrasted visual and digital techniques to assess horn fly populations and discussed the potential of computer aided processing to facilitate accurate assessments. A neural network to automate the determination of horn fly population levels on cattle from digital images is discussed by Psota et al. (2021).

Pasture Management

Pasture design and grazing systems that promote diversity and richness of dung beetles are more likely to reduce populations of developing horn flies than pastures with low dung beetle diversity (Nichols et al. 2008). Silvopastoral systems with an integration of trees, forage, and grazing increased parasitoid biodiversity (Oliveira et al. 2017, Gusmão et al. 2020) and abundance of dung beetles (Oliveira et al. 2017). Specifically, a silvopastoral system study found 1.4 times more dung removed per beetle and horn fly numbers were 40% lower on cattle compared to an open pasture system (Broom et al. 2013). However, not all silvopastoral environments have shown the same benefits (Alonso et al. 2020, Lopes et al. 2020) suggesting more research is needed to understand the underlying complexity.

In a study comparing cattle breeds, rotational and continuous grazing systems, and insecticide treatments Steelman et al. (2003) found cattle in the rotational grazing system had lower (but not statistically different) numbers of horn flies than cattle in the continuous grazing system. Their study suggests that rotational grazing, being adapted to improve grassland productivity and stocking rates (Zhou et al. 2019), to increase soil quality (Galindo et al. 2020), and to improve diversity of high forage value (Vecchio et al. 2019) may also affect horn fly larval survival.

Forage type may affect larval survival. Some of the alkaloids occurring in endophyte-infested tall fescue reduced larval and adult survival (Dougherty et al. 1998; Parra et al. 2013, 2016). Parra et al. (2013) found approximately 30% more larval mortality in manure pats and decreased adult horn fly abundance on cattle that grazed endophyte-infested tall fescue when compared to cattle grazing on endophyte-free fescue. Fly abundance decreased according to the increase in the percentage of endophyte present in the pastures. Brown et al. (1993) studied cattle genotype (Angus, Brahman, and F1 crossbred heifer) impact on horn fly abundance in bermudagrass versus endophyte-infested tall fescue. Their findings suggest that cattle genotype can interact with endophyte-infested tall fescue to further decrease horn fly abundance. In some situations, pasture

burning can be used to reduce horn fly development. Pyric-herbivory, defined as fire-driven grazing, is a pasture management system that mimics evolutionary grazing patterns (Fuhlendorf and Engle 2001). In tests of patch-burn systems, a type of pyric-herbivory, horn fly populations in Oklahoma were reduced by 41% at peak horn fly periods without the use of insecticides (Scasta et al. 2012). Scasta et al. (2015) concluded that the combination of burning with live-stock preference to graze previously burned patches disrupts the horn fly life cycle, effectively reducing the size of subsequent generations. Patch-burning studies have been conducted on units as small as 40.5 ha up to areas greater than 8,000 ha (Weir et al. 2013). Patch-burning management is a pre-emptive approach that when coupled with strategic applications of insecticides may be useful in some locations.

Mechanical Controls

Mechanical control of horn flies such as physical traps and pasture dragging help reduce the need for application of insecticides and thus supports an integrated pest management approach to fly control. The original Bruce trap (Bruce 1938) required cattle to walk through a darkened, building-like structure where brushes disturb flies off the animal. The dislodged flies are attracted to a light source and are passively captured. In Texas, Bruce (1938) observed a 50% reduction in horn fly numbers on cattle using this trap. Hall and Doisy (1989) observed horn fly reductions of 54 and 73% during a 2-yr study in Missouri. Tozer and Sutherst (1996) tested a variation of the Bruce trap for use in dairy systems that gave a 90% or greater reduction in horn fly numbers. Miraballes et al. (2017) reported that a walk-through horn fly trap in dairy is an efficient tactic to manage horn flies; reducing numbers between 82 and 88% without the use of insecticides.

A recent alternative design is the commercially available Cow Vac (Spalding Laboratories, Reno, NV), which is a walk-through device that actively captures flies dislodged from cattle using a vacuum system. This vacuum system reduced flies by 72% over 17 wk of use compared to untreated cattle (Denning et al. 2014). Kienitz et al. (2018) also tested the fly vacuum system and were able to reduce horn fly numbers by 44%. However, at present the Cow Vac requires access to electrical power and it is expensive which limits its utility.

Another mechanical method, suitable only for small pastures, is to drag pastures or otherwise physically break the cow pat apart to reduce larval development (Bruce 1940). Breaking manure pats remains a recommended technique for limited situations; however, this method can also damage a pasture (Wise and Waldron 2020).

Biological Control

Dung beetles (Coleoptera: Scarabaeidae) are generally considered biological control organisms for larval horn flies and compete with horn flies for nutritional resources. However, their modification of dung ecology, especially speeding dung drying, can reduce the effectiveness of some generalist predators that prey on horn fly eggs and larvae (Legner and Warkentin 1991, Nichols et al. 2008). The dung beetle, *Digitonthophagus gazella* F., was introduced into Australia and the Americas from Asia to hasten dung breakdown and to help control cattle parasites developing in dung (see references in Oyarzún et al. 2008). Controlled studies have reported that *D. gazella* decrease the emergence of *H. irritans* and *H. i. exigua* from buried dung (Bornemissza 1970, Blume et al. 1973). However, despite *D. gazella* populations of 40–70 adult beetles per dung pat and an increase in larval horn fly mortality from 38 to 56%, horn fly levels on cattle remained at harmful levels. A contributing factor

is that when *D. gazella* densities were greater than 40 adult beetles per dung pat Staphylinidae beetle populations were reduced (Legner and Warkentin 1991). Besides Staphylinidae, Histeridae, and Hydrophilidae beetles interact with dung beetles and prey on immature horn flies in dung achieving mortality rates of about 93% (Thomas and Morgan 1972). Other important predators are Macrochelid mites that are phoretic with dung beetles and disperse within dung pats where they prey on fly eggs and larvae (Krantz 1983, Azevedo et al. 2015).

Parasitoids in the genus *Spalangia* (Hymenoptera: Pteromalidae) have been associated with horn flies in Hawaii (Marlatt 1910), Denmark (Hammer 1941), the United States (Peck 1974), Canada (Depner 1968), and southeastern Brazil (Mendes and Linhares 1999). In a field trial, Watts and Combs (1977) recovered species of *Spalangia* and *Pseudeucoila* Weld (Hymenoptera: Cynipidae) from dung pats with *S. nigroaenea* (Curtis) and *S. cameroni* Perkins being the most abundant. In a lab study, *Muscidufurax raptor* Girault and Sanders (Hymenoptera: Pteromalidae), *S. cameroni*, and *Spalangia endius* (Walker) readily attacked horn flies (Geden et al. 2006). Although parasitoids are widely distributed and associated with horn flies their use as an integrated pest management option needs further field study to be adapted.

Fungi in the order and families of Entomophthorales: Entomophthoraceae (*Entomophthora muscae* (Cohn) Fresen. and *Furia americana* (Thaxt.) Humber) (Steenberg et al. 2001), Hypocreales: Cordycipitaceae (*Verticillium lecanii* (now *Lecanicillium lecanii* (Zimm.) Zare & W.Gams), *Isaria farinose* (Holmsk.) Fr. and *I. fumosorosea* Wize) (Steenberg et al. 2001, Zimmerman 2008), and Hypocreales: Clavicipitaceae (*Metarhizium anisopliae* (Metsch.) Sor., *Beauveria bassiana* (Bals.) Vuill. and *Paecilomyces fumosoroseus* (Wize) (Steenberg et al. 2001, Angel-Sahagún et al. 2005, Lohmeyer and Miller 2006, Mochi et al. 2010a, Bawer et al. 2014, and Holderman et al. 2017) have been found naturally occurring or tested for efficacy against horn flies.

Adult infections with *B. bassiana* and *M. anisopliae* had promising results although most applications were at relatively high concentrations (Angel-Sahagun et al. 2005, Lohmeyer and Miller 2006, Holderman et al. 2017). However, *B. bassiana* isolate selection is also important as specific strains are more efficacious against horn flies closely related to the original host population (Holderman et al. 2017). Specificity may be result from differential germination or penetration factors or growth parameters (Heale et al. 1989).

In a lab study, artificial cowhide was dusted with conidia and blastospores of *B. bassiana*, *M. anisopliae*, and *P. fumosoroseus*. Horn flies were allowed to walk on the hide for 2 h, and then transferred to cages. Seven days post-treatment mortality was 100% with *B. bassiana*, 73% with *M. anisopliae* and 33% with *P. fumosoroseus* (Lohmeyer and Miller 2006). In another lab study, Mochi et al. (2010b) assessed the entomopathogenic capacity of three fungi to horn fly eggs and larvae and found that infestations of *M. anisopliae* and *I. farinose* caused lethal egg, larval, and pupal infections. However, *B. bassiana* was ineffective. Applications of fungi as a feed-through to kill eggs and developing larvae or pupae in manure pats have occurred and showed a reduction in adult fly eclosion from treated animals (Mochi et al. 2009). On-animal spray applications of strains of *M. anisopliae* and *I. fumosorosea* were done in the dry tropics, and both fungal strains reduced horn fly infestations 94–100% by day 13 post-treatment (Galindo-Velasco et al. 2015). It was concluded that on-animal applications of both *M. anisopliae*

and *I. fumosorosea* can provide effective biological control of the horn fly (Galindo-Velasco et al. 2015).

Bacillus thuringiensis Berliner, (Bacillales: Bacillaceae) (BT) is arguably the most widely used biopesticide in agriculture and much of the success comes from the various BT products that are available to provide targeted pest control with limited adverse effects (Bravo et al. 2011). BT specificity is due to a large range of Cry proteins with narrow binding affinity with host proteins (Bravo and Soberón 2008, Bravo et al. 2011).

Lysyk et al. (2010) screened *B. thuringiensis* var. *israelensis* Barjac isolates for activity against immature horn flies and identified five with high toxicity. Gough et al. (2002) tested 96 *B. thuringiensis* isolates for activity against the closely related Buffalo fly (*H. i. exigua*) and found 45 isolates that caused more than 90% larval mortality. They also tested whether the toxicity was caused by β -exotoxins by heat denaturing the labile proteinaceous δ -endotoxins because some locations will not register BT isolates producing non-specific β -exotoxins (Glare and O'Callaghan 2000). Today, BT applications for fly control are usually applied as sprays or dusts, but Gingrich (1965) tested commercial BT products as feed-throughs and achieved effective control of horn fly and stable fly larvae in dung and manure-associated development sites. Based on work conducted by (Lysyk et al. 2010), feed-through or bolus delivery of BT isolates should be reassessed.

Another approach to bacterial control of the horn fly is to induce infection of flies with *Wolbachia* Hertig (Rickettsiales: Ehrlichiaeae), a maternally transmitted endosymbiotic bacteria that can cause reproductive distortions and reduced overall fitness of infected flies (Madhav et al. 2020). A horn fly cell line (HIE-18) has been successfully established and transfected with three *Wolbachia* strains demonstrating the potential of *Wolbachia* as a novel biological control organism for horn fly management (Madhav et al. 2020).

Currently, little is known about horn fly viruses, but potential and reduced cost of next generation DNA sequencing and metagenomic studies will likely increase our capacity for viral discovery. Ribeiro et al. (2019) identified evidence of a Nora virus and a novel densovirus in the horn fly midgut transcriptome. The identified viruses may not be pathogenic but because they replicate in horn fly cell lines they may be useful to transform pathogenic dipteran viruses to infect and replicate in the horn fly.

Insecticides

Present-day control of horn flies is reliant on insecticides with different modes of action (Table 1), see also the VetPestX insecticide database (Gerry 2020). Insecticides are typically applied to cattle using air-projected capsules, dusts, feed-throughs, injections, insecticide impregnated ear tags, pour-ons, and sprays. Dust bags and oilers/rubs can be placed in gate areas separating water stations or mineral stations and forcing animals to self-treat as they pass through the gate. Animal sprays can be applied using low pressure or mist blower sprayers. Spray applications need to be re-applied on a regular basis throughout the fly season to achieve adequate fly control. Pour-ons and air-projected capsules provide about 3 wk of horn fly control before reapplication is needed. Insecticide impregnated ear tags work by continuously applying a small amount of insecticide to the cattle hair coat as an animal moves its head. Typically, two insecticide-treated tags are applied to adult animals, but some formulations are effective when only a single tag is applied. To enhance ear tag performance, application should be delayed until horn fly numbers are near the economic injury level of 200 flies per animal. Depending on the tag, and if one or two tags are applied, control has been reported

Table 1. Insecticides and modes of action currently labeled for adult and larval horn fly control, in historical order of appearance in the literature^a

Insecticide and IRAC Group No. (www.ircac-online.org)	Primary site of action	Target life stage	Delivery methods	References
Organophosphates (1B)	Acetylcholinesterase inhibitors	Adult, larva	Dusts, ear tags, oil/rub, feed-through	Casida (1956), Kearns (1956), O'Brien (1963), O'Brien (1966), Thompson (1999)
Natural pyrethrum (3A)	Sodium channel modulator	Adult	Sprays	Sun and Johnson (1960), Cox (2002), Arnason et al. (2012), Singh (2014)
Benzoylureas (15)	Inhibitors of chitin biosynthesis, type 0	Larva	Feed-through	Miura et al. (1976), Grosscurt (1977, 1978), Grosscurt and Jongsma (1987)
Synthetic pyrethroids (3A)	Sodium channel modulator	Adult	Dusts, ear tags, pour-ons, sprays, oilers/rubs, air-projected capsule	Elliott and Janes (1978), Vijverberg et al. (1982), Casida et al. (1983), Coats (1990)
Methoprene (7A)	Juvenile hormone analogue	Larva	Feed-through	Sla'ma and Williams (1965, 1966), Bowers et al. (1969), Manville (1975, 1976), Manville and Kritz (1977)
Avermectins (6)	Chloride channel activator	Adult	Ear tag, pour-on, air-projected capsule	Campbell (1981), Bloomquist (1996), Martin (1997)
Pyrazoles (21A)	Mitochondrial electron transport inhibitor	Adult	Ear tag	Fukami (1985), Hollingworth and Ahammadshib (1995), Hackler et al. (1998), Lümme (1998)
Fatty acids (not classified)	Acetylcholinesterase and octopaminergic receptors	Adult	Spray	Don-Pedro (1990), Perumalsamy et al. (2015)
Essential oils ^b (not classified)	Neurotoxic, neuromodulator octopamine, GABA-gated chloride channels	Adult	Sprays	Isman et al. (2007), Cloyd et al. (2009), Khater (2012)

^aSee Nauen et al. (2019) and VetPestX insecticide database (www.veterinaryentomology.org) for a list of labeled fly control products.

^bMinimum risk pesticides exempt from Environmental Protection Agency registration under Section 25b of the Federal Insecticide Fungicide Rodenticide Act.

to remain effective for up to 16 wk (Swiger and Payne 2017); however, tag removal and reapplication may be required in locations with longer fly seasons.

Feed additives and feed-throughs containing insect growth regulator insecticides reduce development of horn fly larvae in manure pats of treated animals. However, immigration of horn flies from untreated neighboring herds from distances of up to 11.7 km (Kinzer and Reeves 1974) can provide adults that maintain high fly populations on treated cattle.

Conventional Insecticides

Avermectins/milbemycins (macrocyclic lactones) are closely related compounds produced through fermentation by soil-dwelling *Streptomyces* Waksman and Henrici (Streptomycetales: Streptomycetaceae). Commonly used macrocyclic lactones in veterinary medicine include abamectin, ivermectin, eprinomectin, doramectin, selamectin, and milbemycin oxime. Macrocyclic lactones can be applied to livestock for horn fly control as a pour-on, as insecticide impregnated ear tags, or as air-projected capsules. Ivermectin applied as a pour-on reduced horn fly numbers for 6 wk with efficacy exceeding 80% for 26 d (Marley et al. 1993). Similarly, a single application of doramectin as a pour-on provided 80% control of horn flies during the first 2 wk after treatment, with horn fly abundance reduced to <50 flies per cow for up to 8 wk and horn fly emergence from dung pats suppressed for 35 d (Andress et al. 2000). Delivery of ivermectin via microspheres (Miller et al. 1998) provided up to 10 wk of 98% control of horn fly larvae in manure after a single injection. Moxidectin given in daily doses to cattle gradually increases in the serum over time, at least up to 21 d and caused reductions in fly survival and egg production (Miller et al. 1994).

Abamectin ear tags were introduced in the early 2000s and provided an alternative to organophosphate and synthetic pyrethroid insecticide ear tags. Field studies conducted by Swiger and Payne (2017) found herds treated with macrocyclic lactone products had higher percent reduction in horn fly numbers compared to herds utilizing organophosphate or synthetic pyrethroid ear tags.

Insect growth regulators accelerate or inhibit a physiological regulatory process essential to the normal development of the insect or its progeny (Siddall 1976). S-Methoprene (Altosid) is a juvenile hormone mimic that interferes with normal hormone levels at critical development periods (Sla'ma 1971). Methoprene in mineral blocks containing (0.94, 0.12, or 0.01%) or sustained released bolus (1%) inhibited horn fly development in manure of treated animals in the field by 87% and 10–12 wk on average, respectively (Harris et al. 1974b, Miller et al. 1977). Diflubenzuron (Dimilin) is a chitin synthesis inhibitor which interferes with normal synthesis of insect exoskeletons during molting or at egg hatch. Diflubenzuron suppressed horn fly numbers by 75 and 83% in manure from cows provided mineral blocks with 0.05 and 0.1%, respectively (Barker and Jones 1976).

Feed additives and feed-throughs containing insect growth regulator insecticides reduce development of horn fly larvae in manure pats of treated animals. However, immigration of horn flies from untreated neighboring herds from distances of up to 11.7 km (Kinzer and Reeves 1974) can provide adults that maintain high fly populations on treated cattle.

Organophosphates are applied as dusts, feed-throughs, insecticide impregnated ear tags, oilers/rubs, and sprays. Self-treatment devices such as dust bags and oilers/rubs are still commonly used by livestock producers and are often positioned near water stations or mineral feeders and used by cattle on a 'free-choice' or 'forced-use

basis'. Currently, there are four emulsifiable concentrate products coumaphos (Co-Ral), dichlorvos (Vapona), prolate (Prolate/Lintox-HD), and tetrachlorvinphos + dichlorvos (Ravap) available. All four products carry age application restrictions. Vapona and Ravap are also restricted use pesticides.

Presently, there is one organophosphate (Rabon) used as a feed additive, which is typically incorporated into mineral blocks or added to mineral or feed. This product kills developing fly larvae in manure of treated cattle. Organophosphate ear tags have been available to livestock producers for many years. Campbell et al. (2006) observed a 77% reduction in horn fly numbers with experimental formulations of diazinon and a combination ear tag containing diazinon and coumaphos compared to untreated cattle. Swiger and Payne (2017) found herds treated with organophosphate ear tags had 82% fewer horn flies throughout the study compared to untreated control herds. Maciel et al. (2015) showed that treatment of calves with a single diazinon ear tag was efficacious in reducing fly numbers relative to flies on untreated calves and in increasing weight gain.

Synthetic pyrethroids are formulated as dusts, pour-ons, sprays, insecticide impregnated ear tags and air-projected capsules. Pyrethroid insecticides have been used by livestock producers beginning in the early 1980s (EPA 2006). Early generation pyrethroid ear tags provided season long horn fly control. In response to horn fly resistance, industry began to combine classes of insecticides and to develop newer generations of synthetic pyrethroids for ear tag use. Campbell et al. (2006) demonstrated an 86% reduction in horn fly numbers on cattle with pyrethroid ear tags compared to untreated cattle. In a 2-yr study, Swiger and Payne (2017) showed a 74–83% reduction in horn fly numbers on cattle with pyrethroid tags. A multi-year insecticide ear tag study by Boxler et al. (2018) indicated pyrethroid tags reduced horn fly numbers on average by 73%.

The **pyrazole insecticide class** are mitochondrial complex I electron transport inhibitors (IRAC 2020) providing a new mode of action to manage insecticide resistance in horn fly populations. Tolfenpyrad is an example of a pyrazole insecticide and recently became available for horn fly control in an insecticide impregnated ear tag. Boxler et al. (2018) evaluated tolfenpyrad ear tags against horn flies on Nebraska cattle and found an 88% reduction in horn fly numbers. In addition, horn fly abundance on the tolfenpyrad treated herd remained below the economic injury level for 11 wk.

Biorational Insecticides

A major group of biorationals are derived from plant essential oils. They are complex mixtures of volatile organic compounds produced as secondary metabolites in plants; included are hydrocarbons (terpenes and sesquiterpenes) and oxygenated compounds (alcohols, esters, ethers, aldehydes, ketones, lactones, phenols, and phenol ethers; Maia and Moore 2011).

Carapa oil is obtained from Andiroba, *Carapa guianensis* Aublet (Sapindales: Meliaceae), a tree common in the Amazon rainforest (Oliveira et al. 2018). In vitro studies testing the toxicity of andiroba oil at 1 and 5% concentrations applied as a contact spray against horn flies had 100% mortality at 4 h post-treatment (Klauck et al. 2014). A companion, in vivo study using 5% andiroba oil applied at 30 ml per cow reduced horn fly numbers on dairy cattle by more than 50% for up to 24 h post-treatment compared to the untreated group, but by 48 h post-treatment there were no differences in fly numbers between groups (Klauck et al. 2014).

Catnip oil is obtained from *Nepeta cataria* L. (Lamiales: Lamiaceae). Catnip oil reduced horn fly feeding and exhibited

residual activity for up to 3 d in a laboratory study (Zhu et al. 2015) and on-animal applications reduced horn fly numbers for 24 h. A 2% concentration of catnip applied to cows provided significant suppression of horn fly numbers from 1 to 3 d (Mullens et al. 2017).

Eucalyptus oil is from plants in the genus *Eucalyptus* L' Herit (Myrtales: Myrtaceae) with 700 species distributed throughout the world (Batish et al. 2008). Galli et al. (2018) analyzed the repellent and insecticidal effects of *E. globulus* Labill oil nanoemulsion and nanocapsules against *Musca domestica* L. (Diptera: Muscidae) and *H. irritans* flies. The insecticidal effect was observed by counting the number of dead flies at intervals of 30, 60, 120, 360, and 750 min post-treatment. The nanoemulsion resulted in 100% mortality after 750 min and significantly reduced horn fly numbers (66.7%) after 24 h.

Geraniol is an acyclic isoprenoid monoterpene isolated from essential oils of aromatic plants including *Cinnamomum tenuipilum* J. Sugimoto (Lauraceae: Cinnamomum), *Valeriana officinalis* L. (Dipsacales: Caprifoliaceae), and other plants (Lei et al. 2019). Pasture cattle treated with geranium essential oil in a 5% concentration of sunflower oil had 93% fewer horn flies than those on untreated control cattle at 24-h post-treatment (Lachance and Grange 2014). In a laboratory feeding deterrent study of 0.2, 2, and 20 mg concentrations of geraniol, horn fly feeding was reduced by 85–95% over a 24 h period (Zhu et al. 2015). In a corresponding field study, 30% geraniol in light mineral oil applied to cattle provided residual activity against the horn fly for 24 h. The limited residual effectiveness may be due to the high volatility of geraniol (Zhu et al. 2015). Mullens et al. (2017) observed 2% geraniol in mineral oil applied at 125 ml per adult animal provided 1–3 d of horn fly control and reduced blood-feeding success and reproductive fitness of horn flies relative to untreated controls (Mullens et al. 2018a).

Lemongrass oil is obtained from the aerial parts of *Cymbopogon citratus* (DC.) Stapf. (Poaceae: Panicoideae) (Oyedele et al. 2002). Pastured cattle treated with lemongrass oil diluted in 5% sunflower oil had fewer horn flies than the untreated control for a 24-h period (Lachance and Grange 2014). Organic dairy cows treated with 2.5% geranium oil and 2.5% lemongrass oil in 95% sunflower oil applied weekly, reduced horn fly numbers by 84.9% compared to an untreated control (Woolley et al. 2018). In a laboratory study, contact exposure of horn flies to 5.8% laboratory grade limonene, a component of lemongrass oil, and 2.9% Orange Guard (d-Limonene), a commercially available product, provided up to 100 and 88% knockdown (immobilization), respectively (Showler et al. 2019).

Tea tree oil is a complex mixture of terpene hydrocarbons and tertiary alcohols distilled from tea tree *Melaleuca alternifolia* (Maiden. and Betche.) Cheel. (Myrtales: Myrtaceae). Laboratory studies conducted by Klauck et al. (2014) demonstrated that both 1 and 5% concentrations sprays of tea tree oil provided 100% horn fly mortality 3 h post-treatment. A 5% concentration of tea tree oil applied to cows reduced horn fly numbers for 24 h, but after 48 h horn fly numbers were equal to the control animals (Klauck et al. 2014).

Fatty acids are abundant organic ingredients in nature such as oils from plants or fats from animals (Seo et al. 2015). Equal mixtures of three medium chain fatty acids (C₈, C₉, and C₁₀) patented as C8910 (Reifenrath 2005) repelled horn flies for 3 d in a laboratory study (Mullens et al. 2009). Zhu et al. (2015) found that C8910 provided horn fly repellency and feeding deterrence for up to 3 d in the lab and for 24 h in the field. However, in another study C8910 in mineral oil provided 1–3 d of horn fly control in the field (Mullens et al. 2017) and Mullens et al. (2018b) documented reduced blood-feeding success and reproductive fitness of horn flies exposed to C8910 on pastured cattle. Another medium

chain fatty acid mixture, derived from coconut, repelled 90% of horn flies tested in a lab study compared to a 70% repellency rate for DEET (Zhu et al. 2018).

Nontarget Effects of Insecticides

Insecticides are the primary pest management tactic for horn fly control; however, nontarget effects are observed and use of insecticides creates safety and sustainability challenges around food animal products. Specifically, Lumaret et al. (2012) did a thorough literature review of nontarget effects of several feed-through active ingredients; while horn fly populations were controlled other invertebrates in terrestrial and aquatic environments were adversely affected. Other nontarget effects have been noted for many beneficial insects (Khan et al. 2008, Fishel 2019) including pasture invertebrates such as dung beetles (Fincher 1991, Strong 1993). Public concern about possible residue contaminants, including pesticide residues in animal products entering the human food chain, is encouraging practices and standards to lower or achieve zero tolerance of pesticide residues in food products (Lee et al. 2001).

Resistance to Insecticides

The Food and Agriculture Organization of the United Nations (FAO 2004) defines resistance as 'a reduction in susceptibility of a parasite to the acaricide or insecticide when it is used at the recommended concentration and according to all of the recommendations for its use'.

The rate at which insecticide resistance develops is dependent on three factors: 1) Genetics (frequency of resistance gene, gene dominance, past selection, and fitness of genotypes), 2) Biological (generations per year, progeny per year, and behavior), and 3) Operational factors (insecticide, residual activity, application rate, and frequency of use; Georghiu and Taylor 1977, FAO 2004). Horn flies have a high potential to develop resistance to commonly used insecticides because they are highly host-specific to cattle, remain on the host almost constantly, have a high biotic potential (up to 400 eggs/female), and have a short life cycle (about 9–12 d) resulting in 6–30 generations per year depending on the climate.

Horn Fly Resistance to Insecticides in the US

The first report of horn fly resistance to insecticides in the United States was in 1960 to DDT and toxaphene (McDuffie 1960). Resistance to organophosphates was first reported in 1962, after 3 yr of intense use of fenclorophos in backrubbers in Louisiana (Burns and Wilson 1963). In the late 1970s, Sheppard (1983) reported that ear tags impregnated with tetrachlorvinphos (stirofos) failed to control horn fly on herds in Georgia and a similar report noted unsatisfactory control in Kansas (Harvey et al. 1984). In Kentucky, resistance to tetrachlorvinphos was related to the use of a feed-through for three consecutive years, while in Arkansas, resistance to diazinon was related to the use of organophosphates as sprays and/or dust bags (Cilek et al. 1991). Steelman et al. (2003) also reported resistance to diazinon-impregnated ear tags and coumaphos dusts, sprays, and impregnated ear tags in Arkansas. A low level of resistance to the organophosphates fenthion and diazinon was reported in Wyoming, consistent with low organophosphate use in the state (Kaufman et al. 1999). The use of a 20% diazinon-impregnated ear tag for four consecutive years reduced horn fly control from >20 to 1 wk in Louisiana (Barros et al. 2001). These authors also reported cross-resistance between organophosphate insecticides namely diazinon, ethion, fenthion, pirimiphos-methyl, tetrachlorvinphos, and fenthion (Barros et al. 2001).

Pyrethroid-impregnated ear tags provided excellent control of horn flies when first introduced but effectiveness declined after 2–4 yr of use in many areas, particularly in the southeastern United States. This situation may have been accelerated by the cross-resistance between pyrethroids and DDT and the use of ear tags (Sheppard 1984, Byford et al. 1985, Bull et al. 1988). Resistance to several pyrethroids (permethrin, fenvalerate, cypermethrin, flucythrinate, and deltamethrin) including cross-resistance to DDT was reported in Louisiana (Quisenberry et al. 1984b, Byford et al. 1985). In Georgia, 8% fenvalerate ear tags failed to control horn flies after 3 yr of consecutive use (Sheppard 1984) and lambda-cyhalothrin ear tags controlled horn fly for 14 wk or longer from 1986 to 1988, but for 4 wk or less in 1989 and 1990 because of high levels of pyrethroid resistance (Sheppard and Joyce 1992). Resistance to pyrethroids was reported in Kentucky (Cilek et al. 1991), Florida (Schmidt et al. 1985, Holderman et al. 2018), and Wyoming (Kaufman et al. 1999).

Mechanisms of Resistance

Insecticide resistance has been shown to evolve by two main genetic mechanisms, metabolic resistance or detoxification and target-site insensitivity (Fournier and Mutero 1994, Scott 1995, Li et al. 2007a, Bass and Field 2011, Dong et al. 2014). Metabolic resistance or detoxification is characterized as drug inactivation by detoxifying enzymes such as esterases, cytochrome P450 monooxygenases (P450s) and glutathione-S-transferase (GSTs; Li et al. 2007a, Bass and Field 2011). Target-site insensitivity is the structural alteration of a drug's target site, which prevents the interaction between the drug and its target site and consequently reduces the drug's pharmacological effects (Fournier and Mutero 1994, Scott 1995, Dong et al. 2014). Behavioral resistance is another type of resistance mechanism that has been described in insects and it refers to avoidance of a treated area by the resistant organism (Sparks et al. 1989). Although stimulus-dependent behavioral resistance, irritancy, and repellency have been demonstrated in pyrethroid-resistant horn flies in laboratory and field conditions, the genetic and molecular mechanisms related to this type of resistance have not been elucidated (Quisenberry et al. 1984b, Lockwood et al. 1985, Byford et al. 1987, Zyzak et al. 1996).

In horn flies, resistance to organophosphates seems to be related to metabolic resistance due to enhanced esterase activity (Guerrero et al. 1999, Guerrero 2000, Barros et al. 2001, Li et al. 2007b) and target-site insensitivity due to a point mutation in the structural gene encoding acetylcholinesterase (AChE), the target site of organophosphate insecticides (Temeyer et al. 2008, 2012; Foil et al. 2010; Holderman et al. 2018). A shift from glycine to alanine in the mature AChE amino acid sequence at position 262 (G262A) results in an altered enzyme with decreased inhibition by organophosphates (Fournier and Mutero 1994, Temeyer et al. 2008). Although the G262A mutation contributes to organophosphate resistance in horn flies, this mutation alone did not fully explain the phenotypic resistance observed in bioassays with diazinon (Foil et al. 2010). The authors speculate additional amino acid substitutions in the AChE in combination with G262A and/or metabolic resistance mechanisms as provided by esterases may further increase resistance to organophosphates (Foil et al. 2010, Temeyer et al. 2012).

For pyrethroids, target-site insensitivity known as knockdown resistance or '*kdr*', is thought to be the main cause of resistance, but metabolic resistance is also important. Due to the cross-resistance between DDT and pyrethroids and the lack of high levels of cross-resistance to organophosphates and carbamates, the first studies concluded that *kdr* was the main mechanism of resistance to pyrethroid

in horn flies and that it was inherited as a single, incompletely recessive gene (Byford et al. 1985, Roush et al. 1986, McDonald and Schmidt 1987). Guerrero et al. (1997) described two mutations (*kdir* and *super-kdir*) in the voltage-gated sodium channel, the target site of pyrethroids, in pyrethroid-resistant laboratory colonies of horn fly. The *kdir* mutations had been previously described as pyrethroid-resistant genes in other arthropods (Dong et al. 2014). The *super-kdir* mutation is a replacement of a methionine by threonine (M918T) in the S4-S5 transmembrane segment of domain II of the voltage-gated sodium channel, and the *kdir* mutation is a replacement of a leucine by phenylalanine (L1014F) in the S6 transmembrane fragment of domain II of the voltage-gated sodium channel (Guerrero et al. 1997, Dong et al. 2014). Both mutations have been found in wild populations of horn fly in the states of Florida, Georgia, Louisiana, Texas, and Washington, with *super-kdir* being more common in laboratory populations than in wild populations with equivalent resistance levels (Jamroz et al. 1998; Guerrero et al. 2002; Foil et al. 2005; Oremus et al. 2006; Li et al. 2009; Foil et al. 2010; Domingues et al. 2014, 2019; Holderman et al. 2018). Interestingly, the *super-kdir* has never been detected in the absence of the *kdir* mutation (Jamroz et al. 1998, Guerrero et al. 2002, Foil et al. 2005, Foil et al. 2010, Domingues et al. 2019). By comparing the allelic frequencies of the *super-kdir* and *kdir* mutations in field populations of horn flies, Foil et al. (2005) found that pyrethroid susceptibility increased from (*super-kdir-kdir*) SS-SS<SS-SR<SS-RR<SR-SR<SR-RR<RR-RR (SS: homozygous susceptible, SR: heterozygous; RR: homozygous resistant), confirming that the *kdir* is indeed an incompletely recessive gene.

Studies using synergists such as esterase inhibitors (S,S,S-tributyl phosphorotrithioate), P450 mixed function oxidases (piperonyl butoxide), carboxylesterases (triphenyl phosphate), and glutathione-S-transferases (GST, diethyl maleate) have demonstrated that metabolic resistance is also important in horn fly resistance to pyrethroids (Byford et al. 1985, Bull et al. 1988, Sparks et al. 1990, Sheppard and Joyce 1992, Guerrero et al. 1997, Jamroz et al. 1998, Li et al. 2009). However, it seems that metabolic resistance is secondary to target-site insensitivity in pyrethroid-resistant flies and is more accentuated in highly resistant laboratory strains (Bull et al. 1988, Guerrero et al. 1997).

Studies suggest that pyrethroid-resistant flies are more susceptible to the organophosphate, diazinon, and the halogenated pyrethrin, chlorfenapyr, than pyrethroid-susceptible flies (Sheppard and Marchiondo 1987, Byford et al. 1988, Cilek and Knapp 1993a). This phenomenon is likely caused by increased activity of mixed function oxidases (P450s) in the pyrethroid-resistant flies, which convert diazinon to its more potent form, diazoxon, and chlorfenapyr (a pro-insecticide) to its insecticidal form, increasing the efficacy of these insecticides (Cilek et al. 1995, Sheppard and Joyce 1998).

Target-site insensitivity has also been implicated in horn fly resistance to endosulfan, a cyclodiene organochlorine. Cyclodiene insecticides inhibit chloride ion transport regulated by the gamma-aminobutyric acid subtype A (GABA_A) receptor and thus block functional insect neuronal GABA receptors (Wafford et al. 1989). The *Rdl* mutation (*Rdl*, resistance to dieldrin) is a single amino acid substitution in the GABA_A receptor locus: the replacement of an alanine with a serine at the position 302 (A302S; French-Constant et al. 1993). The *Rdl* mutation conferred resistance to field populations poorly controlled by endosulfan-impregnated ear tags and in bioassay (Domingues et al. 2013). A multiplex polymerase chain reaction assay is available that can simultaneously detect resistance to pyrethroids (L1014F, *kdir* mutation), organophosphates (G262A, acetylcholinesterase mutation) and cyclodienes (A302S, *Rdl* mutation) in horn fly populations (Domingues et al. 2014).

Management of Horn Fly Resistant Populations

Laboratory and field assays have demonstrated that the consecutive use of the same insecticide or insecticides with the same mode of action accelerates development of resistance (McKenzie and Byford 1993, Byford et al. 1999, Barros et al. 2001, Domingues et al. 2019). For horn fly populations resistant to pyrethroids, lack of exposure to them for 2 or 3 yr is of limited value in reestablishing susceptibility (Weinzierl et al. 1990, Domingues et al. 2019), especially if target-site insensitivity is the main mechanism of resistance in the population. That is because although the *super-kdir* mutation is significantly affected by absence of insecticide pressure, the *kdir* mutation is not, and thus continues to affect pyrethroid efficacy (Guerrero et al. 2002, Oremus et al. 2006, Domingues et al. 2019). Thus, several resistance management strategies have been proposed to delay or prevent insecticide resistance, including the use of mixtures of insecticides and/or synergists (two or more insecticides or insecticides and synergists are used in the same animal at the same time), mosaics (different treatments for different groups of cattle of the same herd), and rotations (two or more insecticides with different mode of action are alternated each year or season; Byford et al. 1987).

Studies with colony flies showed that insecticide mixtures (permethrin and diazinon) or rotation (permethrin and ivermectin or permethrin and diazinon) better delay the rate and magnitude of development of resistance than the consecutive use of single insecticides (McKenzie and Byford 1993, Byford et al. 1999). Cilek and Knapp (1993b) demonstrated that acceptable control of horn fly was achieved with ear tag mixtures (cyhalothrin, PBO, and DEF or cypermethrin, PBO, and chlorpyrifos), but the frequency of pyrethroid-resistant individuals increased substantially after 14 wk. Barros et al. (1999) demonstrated that yearly rotation of pyrethroid (lambda-cyhalothrin and PBO) and organophosphate (pirimiphos-methyl) ear tags for control of pyrethroid-resistant horn flies for 7 yr did not improve pyrethroid efficacy or prevent further development of resistance to pyrethroid or organophosphates. A midseason treatment with doramectin in addition to pyrethroid ear tags increased the number of weeks of control provided by the pyrethroid ear tags, but the increase was rapidly reversed in the following years (Oremus et al. 2006).

Byford et al. (1999) reported when both a pyrethroid and organophosphate were used in a combination strategy the efficacy of treatments did not change over a 3-yr period, while when a single class was used consecutively over the same period, the efficacy (as weeks of control) dropped significantly. In a field trial, Domingues et al. (2019) compared the impacts of four long-term insecticide treatment regimens (consecutive use of pyrethroid ear tags for 6 yr; 3 yr of consecutive use of pyrethroid ear tags, followed by 1 yr with no treatment, followed by 2 yr with organophosphate ear tags or endosulfan ear tags; mosaic with pyrethroids, organophosphates, avermectins and/or cyclodienes for 6 yr) on the *super-kdir* and *kdir* pyrethroid resistance alleles. They found that although lack of pyrethroid use significantly reduced the *super-kdir* mutation, none of the four treatments provided satisfactory results for the management of the *kdir* mutation. Unfortunately, the study did not include an assessment of the number of weeks of control or number of flies observed in the animals, so a practical conclusion on which treatment was more efficient in reducing the number of flies could not be achieved.

Animal Genetics

Selection and use of cattle with resistance or tolerance to horn flies could provide an alternative approach to conventional chemical control. Several authors (Tugwell et al. 1969, Holroyd et al.

1984, Brethour et al. 1987, Cocke et al. 1989) have indicated different breeds of cattle respond differently to the horn fly. Most of these studies examined the effects of horn flies on Zebu (*B. indicus* L.) or Zebu crossbred cattle. Tugwell et al. (1969) in a comparison of purebred Angus, Charolais, and Brahman heifers and mixed breeds showed that the higher the level of Brahman genetics the lower the number of horn flies regardless of animal color. Steelman et al. (1991) in a comparison of European cattle breeds determined the Chianina breed had horn fly densities that were 50% or less that of Angus, Hereford, Polled Hereford, Red Poll, and Charolais cattle. The authors also indicated cows within each breed may have a factor or factors that contribute to innate resistance to the horn fly. A study by Brown et al. (1992) estimated repeatability and heritability for resistance to horn flies. Their estimates suggested that breed selection as a nonchemical tool for managing horn fly populations is possible. In Argentina, Criolla (Iberian *B. taurus*) cattle were reported to be more resistant than other breeds to horn fly infestations. This finding has been attributed to the small size of Criolla, which is suggested to be a factor involved in host preference (Guglielmo et al. 2000).

Phenotypic traits associated with horn fly resistance are reported to include cattle body color (Steelman et al. 1991, Pruett et al. 2003), body size (Steelman et al. 1996) and individual variation in immune systems (Stear et al. 1984). Oliveira et al. (2013) compared *B. indicus* (Nelore) and three-cross animals ($\frac{1}{2}$ Angus + $\frac{1}{4}$ Canchim + $\frac{1}{4}$ Nelore) for their susceptibility/resistance to parasites of cattle in tropical conditions in Brazil. Over the 24-mo study period, cattle in Nelore group (*B. indicus*) had more abundant horn fly infestations than those in a three-way cross group with $\frac{1}{4}$ Nelore genetics, suggesting horn flies prefer animals with darker colored hair coats and male animals.

The efficacy of horn fly anticoagulation mechanisms may vary by host and can be a mechanism of cattle resistance to horn flies (Pruett et al. 2003, Untalan et al. 2006). Ling et al. (2020) found estimates of heritability of horn fly abundance ranged between 0.14 and 0.22 and varied between sire families, suggesting a potential to improve cattle genetic resistance to horn flies. To estimate producer acceptability of horn fly resistance, McKay et al. (2019) surveyed grower willingness to purchase fly resistant bulls to improve herd welfare and they found producers were willing to pay a premium of 51–59% more for horn fly resistance if other quality traits were maintained.

Vaccines

Since horn flies feed so persistently and have a close relationship with its host (Lancaster and Meisch 1986), vaccines may be a unique approach to fly management in cattle. Differently from other blood-feeding arthropods, horn fly saliva has a lower diversity of anti-hemostatic compounds (Cupp et al. 1998, 2000), and thrombostasin, a thrombin-inhibiting protein, seems to be responsible for all clot-inhibiting activity observed in horn fly saliva (i.e., disruption of platelet aggregation and coagulation; Cupp et al. 1998, 2000; Zhang et al. 2002). Recombinant thrombostasin was evaluated as a candidate for anti-horn fly vaccine and yielded promising results: flies that fed on vaccinated cattle or vaccinated rabbit acquired a smaller bloodmeal than flies fed on control animals, and egg development was delayed (Cupp et al. 2004, 2010). However, the deleterious effects were not uniform across all tested populations due to the presence of different thrombostasin isoforms in the flies. Thus, a vaccine mixture including more than one isoform would be needed for effective horn fly control. (Cupp et al. 2010).

Baron and Lysyk (1995) studied cattle antibody response to horn fly salivary gland antigens and found no correlation between antibody response and fly abundance, suggesting that horn fly salivary antigens may have an immunomodulatory effect on the host. Breijo et al. (2016) identified two immunomodulatory proteins in the salivary gland of horn flies: irritans 5, an immunoglobulin-binding protein (Ameri et al. 2008) that counteracts the host's immunoglobulins present in the blood (Sá-Nunes and Oliveira 2010), and hematobin, a macrophage inhibitor (Breijo et al. 2018). In a field study, vaccination of cattle with recombinant hematobin reduced horn fly numbers by 30% (Breijo et al. 2017).

Bautista et al. (2004) reported that animals vaccinated with a crude intestine antigen produced specific antibodies to the antigen, which in turn affected fly oviposition but not adult fly survival. Future use of these or other vaccines against the horn fly, either alone or in concert with integrated pest management programs is a promising strategy.

Sterile Insect Technique

The sterile insect technique was successfully used to eradicate screwworms from northern and central America (Wyss 2000), and more recently from Libya (Vargas-Terán et al. 1994). This tactic consists of sterilizing reared insects using irradiation or other techniques and then releasing mass numbers of sterile insects into the field where they compete with fertile insects for mates thereby reducing offspring (Knipling 1955, Klassen and Curtis 2005). In the 1970s the use of a sterile insect technique to control horn flies was evaluated under field conditions and showed promising results when the ratio of sterile to wild flies was 10–1 (Eschle et al. 1973, Kunz et al. 1974). Eschle et al. (1977) used methoprene in combination with sterile insect technique to successfully eliminate a wild population of horn flies from a ranch on the island of Molokai, Hawaii. The authors suggested that the control system could be used to implement a suppression-eradication program for the island of Molokai and ultimately, the entire state of Hawaii. However, despite the promising results, the use of sterile insect technology for controlling horn fly populations has not been implemented.

One of the main conditions for the success of sterile insect technology is that the released sterile males outnumber the wild-type males, preferably by at least a 10:1 ratio and that the population size of the pest species is low, as fewer sterile flies are required for release. Horn fly populations can reach high numbers and this pest can be found from southern Canada all the way to South America. Thus, the implementation of a horn fly control program using sterile insects would require an extremely large number of flies to be reared and released to be successful. Although horn fly rearing is well established (Lohmeyer and Kammlah 2006), the cost associated with such endeavor is another limitation to the use of sterile insect technologies for horn fly control.

More recently, Concha et al. (2016) developed transgenic 'male-only' screwworm strains that carry a conditional female lethal trait such that, under permissive conditions, both sexes can be efficiently reared and under restrictive conditions, only males are produced. The use of transgenic 'male-only' strains in a sterile insect release program would not only reduce production costs but also provide more efficient population suppression making a genetic control program more economically feasible (Concha et al. 2016). Konganti et al. (2018) identified eight gene loci in the horn fly genome with functional annotations related to sex determination. These and similar loci could be explored for development of a 'male-only' horn fly strain like those developed for screwworm flies, and maybe bring

back the possibility of using a sterile insect technology project for horn fly control.

Future Needs for Ecological Management of Horn Flies

Horn fly management has long relied on insecticides for prophylactic and reactive fly control. However, gains in preventative tactics to decrease the impact of horn fly populations are being created. Vaccines offer a promising, preventative approach to horn fly management (Oyarzún et al. 2008, Torres et al. 2011, Breijo et al. 2017). The availability of a partial horn fly genome (Konganti et al. 2018) as well as several transcriptomes (Guerrero et al. 2008, 2009; Torres et al. 2011; Domingues et al. 2018; Ribeiro et al. 2019) offer opportunities for identifying new vaccine targets, improving our understanding of the molecular basis of insecticide resistance, and discovering new chemotherapeutics and methods of control.

Significant technological advancements are expanding the potential of sterile insect technologies as a fly management strategy. Genetic technologies (Konganti et al. 2018) and infections with sterilizing *Wolbachia* strains (Zhang et al. 2015, Nikolouli et al. 2018) being investigated for use in sterile insect technologies with other dipteran species are potentially useful as a promising preventative tactic for horn fly management.

Genetic improvements to the U.S. beef breeds during this period may have altered the economic impacts of horn fly biting, particularly as it is estimated 60% of the U.S. cattle going to slaughter are now crossbred animals with an Angus influence (Drouillard 2018). One of the most important measures of cow-calf productivity is calf weaning weights, which have steadily increased for most U.S. breeds since 1980 (USDA NAHMS 2010, Kuehn and Thallman 2016). There is a need for studies investigating the impact of horn flies on the efficiency of the current cattle breeds, e.g., the effects of variable horn fly populations on forage consumption and consequent milk production and calf weaning weights. Additional linkages between horn fly injury and cattle productivity based on animal breed and other parameters such as vaccination technologies, management systems, regional variation, and other stressors will further improve horn fly management and are needed to improve our understanding of the impacts of horn flies on cattle productivity. Cow-calf producers in Tennessee and Texas recognize horn flies as a production problem and have expressed interest in purchasing genetic cattle breeds with horn fly resistance to improve cattle welfare and reduce input and management costs (McKay et al. 2019).

As an alternative or supplement to advances in horn fly assessments (discussed earlier in the Monitoring section), precision livestock farming, including the use of smart technologies applied to range systems, is allowing remote measurement of cattle activity patterns, including defensive behaviors (Zambelis et al. 2019) and other deviations from normal behaviors and physiological stress (Rutter 2014, 2017). See Jukan et al. (2017) and references therein for a review of the behavioral and animal health applications and technologies being developed for monitoring group farm animal welfare. Various wearable sensors are being used in precision animal agriculture to measure heartbeat, temperature, movements, and animal activity patterns (see Karthick et al. 2020 and references therein).

As these technologies become more available and accurate, they will aid in horn fly management research. Sensor technologies will also provide producers quick and accurate information to determine whether a reactive, suppressive technique is needed when preventative tactics are overwhelmed by high horn fly populations.

In situations where horn fly populations are considered injurious, fly control will continue to largely depend on immediate applications of insecticides. Innovations in pesticides includes promising research on biopesticides that can be integrated with other products as components of an insecticide resistance management plan (Feng and Isman 1995). Feed-through insecticides, while not new, are advancing with new chemistries (Dell' Porto et al. 2012) and the potential use of biopesticides formulated as feed-throughs (Miller and Chamberlain 1989, Mulla and Su 1999) needs to be reconsidered. Repellents have long been used to protect against bites of medically important arthropods (Kalita et al. 2013, Rehman et al. 2014) and plant-based and other natural product repellents are efficacious against Muscid flies (Mullens et al. 2009, Cook 2020) including the horn fly (Showler 2017, Zhu et al. 2018). Descriptions of horn fly chemosensory gene family members provides a promising avenue for identifying receptors or accessory binding proteins that are activated by repellent compounds and can assist in designing behavior modifying compounds targeting horn flies (Olafson and Sasaki 2020).

Innovative technologies such as the Cow Vac horn fly trapping system offer a non-pesticide intervention strategy to mechanically remove flies (Denning et al. 2014, Kienitz et al. 2018). Using assistive or Zero Effort systems as described in Mudziwepasi and Scott (2014) to couple technologies such as the Cow Vac or automated sprayers with smart sensors will increase fly management precision and reduce input and operational costs.

To conclude, advances in biological control, vaccination technologies, new insecticide modes of action, repellents, and cattle genetics will greatly increase producer ability to limit horn fly population development. Improved economic injury levels reflecting local conditions and expected management innovations will be critical to facilitate decision making and increase capacity to quickly implement intervention tactics when needed.

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