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A REVIEW OF NATURAL MORTALITY AND ENEMIES OF THE STABLE FLY (DIPTERA: MUSCIDAE) IN MISSOURI

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ABSTRACT

This review article summarizes the most significant results of research on mortality factors affecting populations of the stable fly, *Stomoxys calcitrans* (L.), in Missouri.

RESUMEN

Este artículo revisa y resume los resultados más significantes de la investigación, de los factores de mortalidad que afectan las poblaciones de la mosca de establos, *Stomoxys calcitrans* (L.), en Missouri.

The stable fly, *Stomoxys calcitrans* (L.), is a cosmopolitan ectoparasite that feeds on a broad range of warm-blooded animals including man (Bishopp 1913). Cattle, which are among the preferred hosts (Mitzmain 1913, Sutherland 1978), waste energy by resisting attack. This has been evidenced by reduced weight gain and milk production

in beef and dairy cattle, respectively (Campbell et al. 1977, but cf. Miller et al. 1973). The stable fly has been recognized by the United States Department of Agriculture (USDA) as the most important insect pest of dairy cattle in the U.S. (Anon. 1965). It has been associated with an estimated \$399 million in losses annually to the cattle production industry (Drummond et al. 1981).

The stable fly also affects the comfort of recreationists along the north gulf coast beaches of Florida where it is known to migrate as far as 225 km from livestock production sites. Such movements of large numbers of flies are thought to be associated with north winds located behind cold fronts (Hogsette & Ruff 1985). Losses in tourism revenue up to \$1 million/day have been estimated when control relief is not provided (Newson 1977).

Much information has been reported regarding the stable fly in Missouri (Smith et al. 1985, 1987a, 1987b). This paper serves to summarize the most significant results of these studies which were designed to develop an actuarial database for this pest.

OVERVIEW OF STABLE FLY MORTALITY STUDY METHODS

Egg through adult field mortality was quantified for the stable fly in replicated sentinel breeding sites (protected by rain shelters) exposed at pasture, dairy, and feed-lot cattle farms throughout the 1980-82 fly production seasons (Smith et al. 1985). Sentinels were prepared by using 11.5 l Rubbermaid® dishpans filled with water-saturated ryegrass clippings seeded with immature stages of laboratory reared stable flies. A black puparial strain (Willis et al. 1983), obtained from the USDA Insects Affecting Man and Animals Research Laboratory, Gainesville, Florida, was used to differentiate naturally oviposited stable flies. Eggs, 1st, 2nd, and 3rd instars, and prepupae were used separately as inocula so that mortality estimates could be calculated for each growth stage. Egg hatch was monitored in the laboratory for each egg batch used as an inoculum. Mortality was assessed biweekly in caged (0.8 mm mesh) and noncaged sentinels to quantify the effects of predation and competition. Mortality data were accumulated in life tables similar to Thomas & Morgan (1972) using mortality indices described by Southwood (1978).

Sentinels were removed and replaced with freshly prepared dishpans when the inoculated cohort reached the late pupal stage. This time varied (depending on the stage used as an inoculum) from 2 days for prepupae to 14 days for eggs. Sentinels were processed by water flotation for pupal recovery. All dipterous pupae were held in a rearing room (27°C and 50-60% RH) for adult fly and parasite emergence. Predatory and competitive insects were captured in Tullgren funnels from additional noncaged sentinels. Controlled-access studies employing replicated caged sentinels with screen sizes from 0.8 to 12.8 mm were used to evaluate the importance of these insects.

NATURAL ARTHROPOD ENEMIES AFFECTING STABLE FLY POPULATIONS

Predators

Nineteen different predaceous species representing five arthropod families were recovered from stable fly sentinel breeding sites (Table 1). *Macrocheles* (prob. *muscaedomesticae* (Scopoli)) was the earliest to arrive, most consistent, and most abundant predator. These mites are known to prey upon eggs, first instars (Kinn 1966) and pupae (Kramer 1952) of stable flies and other Diptera. Phoresy is common with this species (Williams & Rogers 1976) and probably accounts for its rapid dispersal ability.

Eight different species of staphylinids were recovered. The first five (Table 1) were most abundant and were collected commonly at all study sites. These insects are well

TABLE 1. PREDACEOUS ARTHROPODS ASSOCIATED WITH STABLE FLIES DEVELOPING IN RYEGRASS CLIPPINGS IN CENTRAL MISSOURI.¹

Family	Species
Macrochelidae	<i>Macrocheles</i> sp. (prob. <i>muscaedomesticae</i> (Scopoli))
Staphylinidae	<i>Belonuchus rufipennis</i> Fabricius <i>Lithocaris ardenus</i> Sanderson <i>Philonthus rectangulus</i> Sharp <i>Philonthus brunneus</i> (Gravenhorst) <i>Platystethus americanus</i> Erichson <i>Philonthus hepaticus</i> Erichson <i>Philonthus sericans</i> (Gravenhorst) <i>Staphylinus maculosus</i> Gravenhorst
Hydrophilidae	<i>Cercyon praetextatus</i> (Say)
Carabidae	<i>Calosoma externum</i> Say <i>Anisodactylus ovularis</i> Casey <i>Harpalus caliginosus</i> F. <i>Scarites subterraneus</i> F. <i>Pterostichus chalcites</i> Say
Histeridae	<i>Peranus bimaculatus</i> Linnaeus <i>Hister abbreviatus</i> F. <i>Phelister vernus</i> Say <i>Saprinus</i> sp.

¹From Smith et al. (1987b).

known predators (in both larval and adult stages) of fly larvae (Hammer 1942). Some *Philonthus* spp., such as *Philonthus theveneti* Horn have been found to be particularly effective egg and early instar predators of the stable fly (Campbell and Hermanussen 1974). *Philonthus rectangulus* Sharp is a common inhabitant of pastured cattle dung in Missouri (Thomas & Morgan 1972). It has also been recovered in chicken manure and was found to have a wide distribution and high relative abundance in comparison to other predators collected in a world-wide survey of accumulated animal manure (Legner & Olton 1970). Our recovery in grass clippings substantiates the multiple habitat searching capability of this predator.

Cercyon praetextatus (Say) was the only hydrophilid collected. It was found frequently after late June. Close relatives of this species are known to be predaceous as larvae (Geetha Bai & Sankaran 1977). As adults, they are known to be scavengers (Sanders & Dobson 1966) and may compete with developing fly populations for space and food.

Five species of carabids were recovered in much fewer numbers than the previous predators. *Scarites subterraneus* F. and *Calosoma externum* Say were both observed feeding on late instar fly larvae. These insects tended to be most numerous in June and July.

Four histerid species were collected infrequently, with *Peranus bimaculatus* Linnaeus and *Hister abbreviatus* F. being the two most commonly collected. Feeding habits vary greatly within this group. Some species prey upon early fly instars, while others feed on all stages (Geetha Bai & Sankaran 1977).

The macrochelids, staphylinids and the hydrophilid were the most abundant predaceous arthropods recovered. They were recovered from all sentinels from 2 days after field placement and throughout the remainder of the 14 day exposure period.

Competitors

Twenty-six insects representing 16 families in 4 orders were associated with stable fly sentinel breeding sites (Table 2). The relationship of these insects to survival of developing stable flies is not fully understood. Some of the Coleoptera and most of the Diptera collected in these studies were thought to compete with stable flies for available food and space. Scarabaeids are known to promote desiccation of fly breeding habitats by foraging activities (Hammer 1942). *Ataenius* spp. was collected abundantly in these studies. This scarabaeid and the anthicid, *Anthicus floralis* L., which was also collected frequently, are known to occupy many different fly breeding sources (Legner & Olton 1970).

Diptera in the genus *Muscina* may be predaceous as late instars on other fly larvae occupying the same habitat (James 1948). *Muscina stabulans* (Fallen) (the false stable fly) and *Muscina assimilis* (Fallen) were the most commonly collected flies associated with the stable fly. Other species were collected much less. Surprisingly, few *Musca domestica* (L.) were found in sentinels, although numerous adult house flies were observed at the experimental sites. In laboratory studies, *M. domestica* was found to not survive well in grass clippings.

TABLE 2. COMPETITIVE INSECTS ASSOCIATED WITH STABLE FLY BREEDING SITES¹ IN CENTRAL MISSOURI.²

Order	Family	Species
Diptera	Muscidae	<i>Muscina stabulans</i> (Fallen) ³
		<i>Muscina assimilis</i> (Fallen) ³
		<i>Fannia canicularis</i> (L.)
		<i>Fannia manicata</i> (Meigen)
		<i>Brontaea arcuata</i> (Stein)
		<i>Thricops coquillettii</i> (Malloch)
		<i>Ophyra leucostoma</i> (Wiedemann)
		<i>Musca domestica</i> (L.) ³
		<i>Syrphididae</i>
		<i>Syrphididae</i>
Coleoptera	Syrphidae Sepsidae Otitidae Sarcophagidae Scarabaeidae Anthicidae Tenebrionidae Elateridae Mycetophagidae Rhizophagidae Cucujidae Curculionidae	Unidentified species ³
		<i>Euxesta</i> sp. ⁴
		<i>Ravinia querula</i> (Walker) ⁴
		<i>Ataenius</i> sp.
		<i>Trox suberosus</i> (F.)
		<i>Anthicus floralis</i> Linnaeus
		<i>Tenebrio obscurus</i> F.
		<i>Neatus tenebrioides</i> (Palisot)
		<i>Conoderus bellus</i> (Say)
		<i>Aeolus mellillus</i> (Say)
Dermaptera	Labiidae	<i>Typhaea stercorea</i> (L.)
		<i>Monotoma americana</i> Aube
		<i>Telephamus velox</i> (Haldeman)
		<i>Sphenophorus parvulus</i> Gyllenhal
		<i>Labia minor</i> (Linnaeus)
Hemiptera	Cydnidae	<i>Pangaeus bilineatus</i> (Say)
		<i>Xylocoris sordidus</i> (Reutor)

¹Breeding sites consisted of moistened ryegrass clippings or a 23:23:1 volumetric mixture of wheat bran, horticultural vermiculite, and fish meal.

²From Smith et al. (1987b).

³Collected from both wheat bran mixture and grass clippings.

⁴Collected from wheat bran mixture only.

It has been demonstrated that in cattle dung the effect of interspecific competition among dipterans is minimized through successional differences in species' utilization of the habitat as it ages (Mohr 1943). Seasonal abundance data from the present studies indicate considerable overlap in species presence in grass clippings. As such, stable fly populations may have been affected.

Parasites

Ten insect species and one nematode species were found to parasitize the stable fly (Table 3). The nematode was collected from adult flies while the others were recovered from puparia. At least two morphologically distinct species of both *Muscidifurax* and *Trichopria* were recovered. Specific identifications could not be provided due to the taxonomic status of these genera. *Spalangia haematobiae* Ashmead, *Diplazon laetatorius* (F.), and the mermithid nematode were new parasitic associations for the stable fly. *Spalangia nigra* Latreille was the dominant parasite accounting for 84 and 47% of the total parasitism from sentinel stable fly breeding sites in 1981 and 1982, respectively. This species may have been highly attracted to the grass clipping habitat. It was not collected as frequently from natural stable fly production sites as was *Spalangia nigroaenea* Curtis and *Muscidifurax* spp. (prob. *raptor* and *zaraptor*).

Total seasonal parasitism seldom exceeded 10%. However, weekly parasitism was found to be substantial (i.e., approaching or exceeding 50%) during July; during other months, it rarely surpassed 15-20%.

LIFE TABLES FOR THE STABLE FLY

Theoretical life tables were formulated for the stable fly using mortality data accumulated from laboratory and field experiments conducted in 1981 (Table 4) and 1982 (Table 5). Total egg-to-adult mortality was substantial (95.1 and 97%, respectively). Unknown causes, which probably included desiccation, adverse environmental conditions, pathogens, physiological anomalies, and delayed temperature effects (Larsen 1943) during the larval instars, accounted for the largest proportion (51.1 and 62.6%) of the real mortality (the number of individuals dying expressed as a percentage of the original cohort). Predation of eggs and larvae was found to be important as measured by apparent (the number of individuals dying expressed as a percentage of the number of surviving individuals entering that stage) and indispensable (the percentage of indi-

TABLE 3. STABLE FLY PARASITES (LISTED IN ORDER OF PREVALENCE) COLLECTED IN MISSOURI.¹

Order	Family	Species
Hymenoptera	Pteromalidae	<i>Spalangia nigra</i> Latreille
		<i>Spalangia nigroaenea</i> Curtis
		<i>Muscidifurax</i> spp.
		(prob. <i>raptor</i> and <i>zaraptor</i>)
		<i>Spalangia endius</i> Walker
		<i>Spalangia haematobiae</i> Ashmead
	Ichneumonidae	<i>Diplazon laetatorius</i> (F.)
	Diapriidae	<i>Trichopria</i> spp.
Coleoptera	Staphylinidae	Aleocharinae
Nematoda	Mermithidae	Unidentified species

¹From Smith et al. (1987a).

TABLE 4. A LIFE TABLE FOR THE STABLE FLY IN MISSOURI, 1981.¹

Stage	No. alive at beginning of time interval	Factor responsible for death	# Dying	% Apparent mortality	% Real mortality	% Indispensable mortality
Eggs & Larvae	6000	Egg sterility	606	10.1	10.1	0.6
	5394	Unknown causes	3067	56.9	51.1	6.6
	2327	Predation	1638	70.4	27.3	11.8
Pupae	639	Parasitism	29	4.2	0.5	0.2
	660	Unknown causes				
		—pupal death	245	37.1	4.1	2.9
		—adult death	117	28.2	2.0	2.0
Adults	298 (5.0% survival)				Total = 95.1	

¹From Smith et al. (1985).

TABLE 5. A LARVAL GROWTH STAGE SPECIFIC LIFE TABLE FOR THE STABLE FLY IN MISSOURI, 1982.¹

Stage	No. alive at beginning of time interval	Factor responsible for death	# Dying	% Apparent mortality	% Real mortality	% Indispensable mortality
Egg	1200.0	Egg sterility	112.8	9.4	9.4	0.3
	1087.2	Unknown causes	99.0	9.1	8.3	0.3
	988.2	Predation	13.0	1.3	1.1	0*
Larval	975.2	Predation	110.0	11.3	9.2	0.7
	865.2	Unknown causes	751.0	86.8	62.6	20.6
1st instar	975.2	U.C. & Predation	469.0	48.1	39.1	2.9
2nd instar	506.2	U.C. & Predation	162.0	32.0	13.5	1.5
3rd instar	344.2	U.C. & Predation	207.0	60.1	17.3	4.7
Prepupal	137.2	U.C. & Predation	23.0	16.8	1.9	0.6
Pupal	114.2	Parasitism	8.6	7.5	0.7	0.3
	105.6	Unknown causes	68.1	64.5	5.7	5.7
Adult	37.5 (3.1% survival)				Total = 97.0	

¹From Smith et al. (1985).

* < 0.1%

viduals that would not die if the given mortality factor was removed from the model) mortality indices during 1981. Smaller staphylinids (capable of entering 1.6 mm screen cages) were the most important predators.

Specific mortality measurements were made for each growth stage of the stable fly in 1982 (Table 5). The most significant proportion of mortality affected first and third instars and was associated with unknown causes. Pupal death attributed to unknown causes, as measured by apparent mortality, was also important. Probable causes were as listed previously and were thought also to include parasite host-feeding on pupae, a behavior common among *Spalangia* spp. (Legner 1967).

DISCUSSION

These studies were designed to improve understanding of factors regulating stable fly populations in the field. Mortality for each developmental stage was quantified, and natural enemies were identified and their impact assessed. Vulnerable points in the life cycle of the stable fly were identified so that steps could be taken toward developing more efficient and effective biological control initiatives.

We encourage use of this information to formulate mathematical models to simulate stable fly population dynamics. Such models could be used not only to simulate the effects of various control strategies on developing populations, but also specifically to identify future research needs and priorities.

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RESISTANCE IN CONSTANT EXPOSURE LIVESTOCK INSECT CONTROL SYSTEMS: A PARTIAL REVIEW WITH SOME ORIGINAL FINDINGS ON CYROMAZINE RESISTANCE IN HOUSE FLIES

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ABSTRACT

Insecticide resistance development in three continuous exposure livestock insect control systems is discussed. These include residual pyrethroid sprays and cyromazine feed-through for house flies, and insecticide cattle ear tags for horn flies. All three of these systems selected for resistance problems in the field within two years. Other discontinuous use patterns of these same chemicals have been used on the same insects in the field and selected for much lower or no resistance. The conclusion is that these systems waste the resource of insect susceptibility, especially with mobile insects with short generation time such as the flies discussed here.

RESUMEN

Se discute el desarrollo de resistencia a insecticidas en tres exposiciones continuas de sistemas de control en ganado. Estos incluyen rocios residuales de piretroides y de criomisina "alimentos-a-través" para la mosca común, e insecticidas en etiquetas puestas en las orejas del ganado para los tábanos. Estos tres sistemas seleccionaron problemas de resistencia en el campo en dos años. Otros patrones de uso discontinuados de estos