The Requirement for Reassessment of Interactions Among Dung Beetles, Symbovine Flies, and Natural Enemies

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Abstract

Scarab dung beetles continue to be utilized effectively for biological control of cattle dung, but densities of symbovine Diptera remain unacceptably high. It is now apparent that dung dispersion by these beetles does not always automatically lead to diminished fly abundance under natural field conditions. Interference with physical controls and natural enemies may explain the apparent paradox. Regulation of symbovine fly populations below present levels might require additional biological control agents whose densities are reciprocally dependent on and specific to their prey. Central Asia and southern Africa deserve closer investigation as potential sources for effective predators and pathogens. More rigid assessments of a candidate's potential before importation could reduce (1) the frequency of biological control failures and (2) the threat of upsets of existing natural controls.

Symbovine flies that breed primarily in dung droppings of cattle on rangeland and pastures (Povolny 1971), *Haematobia irritans* (L.), *Musca autumnalis* de Geer, and *Musca vetustissima* Walker, are prime targets for biological control, with special emphasis placed on habitat destruction through the activity of scarab dung-burying beetles (Anderson and Loomis 1978, Blume et al. 1973, Fincher 1981, Hughes et al. 1978, Macqueen and Beirne 1975). Although an array of scarab beetle species has become established in pasture and field habitats following introductions in Hawaii, Texas, California, and Australia, it is now clear that densities of these flies have not been greatly reduced in the field, although some control is suggested (Bornemissza 1970, 1976; Fincher 1981; Hughes et al. 1978; Kessler 1983). Recent studies indicate that the interactions between dung burying beetles, symbovine flies, and the latter's natural predators are complex, so that simple habitat reduction or dispersion, as is most often the case, does not automatically lead to a diminished fly abundance (Legner 1978a, Macqueen 1975, Roth et al. 1983, Wallace and Tyndale-Biscoe 1983).

Historical Background

The principal emphasis for biological control of pasture breeding symbovine flies since Albert Koebele first imported dung scavengers and fly predators from Europe to Hawaii in 1909 (Swezey 1911, 1912) has been on scavenger scarab beetles to reduce breeding habitats (Anderson and Loomis 1978, Bornemissza 1976, Ferrar 1975b, Waterhouse 1974). The largest effort took place in Australia, where a goal of equal or greater importance was pasture improvement (Bornemissza 1960, 1976; Ferrar 1975a); but expected widespread significant fly reductions have not occurred (Legner 1978a, Legner and Warkentin 1983, Macqueen 1975).

Laboratory and field studies continue to show that survival of symbovine flies can be experimentally reduced by dung shredding, scattering and burying activities of scarab beetles (Blume et al. 1973, Bornemissza 1970, Moon et al. 1980, Hughes et al. 1978, Ridsdill-Smith 1981, Ridsdill-Smith et al. 1977, Smith 1981, Wallace and Tyndale-Biscoe 1983). However, because of difficulties inherent to gathering data from natural field populations, larvae are not allowed to disperse from the various experimental areas, by the use of screens and other barriers which force their development in a confined space. This results in overcrowding, stunting and, finally, mortality due to the lack of food and abrasion with foraging scarab beetles in the experimental environment. Were larvae allowed instinctively to disperse vertically and horizontally away from intense scarab activity,

a greater survival might result through easing of the crowding effect thereby increasing each individual's chance of finding ample food for development. Such dispersal may be quite common in nature, especially in fields where soil is moist and large populations of dung-burying scarabs have turned underground huge quantities of fresh dung. Macqueen (1975) and Hughes et al. (1978) reviewed several cases *in the field* where bush fly reductions may have resulted from the activities of scarab beetles; and Ridsdill-Smith and Mattiessen (1984) give experimental evidence for some reduction by endemic and imported scarab beetles. However, the degree of control was generally very low. Immigration of bush flies from outside the experimental area often tends to confound the results.

The only apparent reduction of noticeable magnitude in density of symbovine flies as a result of biological control was reported from Fiji involving a single predator, *Hister chinensis* Quensel, that was not imported for control of symbovine flies in the first place (Bornemissza 1968). A minor success apparently occurred in Hawaii, which involved both dung-burying scarab and predatory beetles (Legner (1978b).

There is no question that several species of scarab beetles can attain field population densities high enough to cause significant dung removal and pasture improvement (Fincher 1981, Fincher et al. 1981, Kessler 1983, Legner and Warkentin 1983, Waterhouse 1974). But, whether significant symbovine fly reductions are also achieved is not always certain (Legner 1978a, Macqueen 1975). In the case of the *Musca sorbens* Wiedemann group of flies to which the Australian bush fly, *Musca vetustissima*, belongs, this is of special importance from the human annoyance standpoint (Legner 1976, Legner et al. 1974b). Australian studies in 1978–79 and 1983–84 indicate that appreciable buffalo fly control occurred when several species of scarab beetles were particularly abundant, but these situations do not arise regularly each season (A. Macqueen, pers. commun.).

Appraisal of Onthophagus gazella F. in Southeastern California

The apparent ineffectiveness of *O. gazella* to control *Haematobia irritans* in irrigated pastures in the Coachella Valley of southeastern California at first appears enigmatic. In May 1975, I supervised the importation and liberation of 120 pairs of this scarab from Hawaii to California. At present, the species is firmly established at the introduction sites where dung scattering and burying by adult beetles in autumn usually begins within an hour of deposition when pastures are under regular irrigation. Scarab beetles that remain dormant in the sandy soils, in some cases for six months during irrigation-free periods in this largely rainfall-free area, become highly active within *ca.* 1 week following renewed irrigation and cattle stocking. Cattle on these pastures are often stocked at densities exceeding 25 per ha and the amount of dung that is shredded, scattered, and buried daily by the 1–cm long beetles is enormous. By October, beetle density can reach 40 or more per fresh dropping, a density in the range shown by Wallace and Tyndale-Biscoe (1983) where field fly control can result. Initially, ranchers were pleased with the manner in which the cattle dung becomes incorporated into the soil, eliminating the need for mechanical dispersion, even though there was an obvious lack of horn fly control. During warm seasons the cattle sustained continuously high densities of this fly, often exceeding 1,000 per head in autumn. These densities are similar to those attained in pastures where mechanical means are employed to disperse the dung between irrigations. Gradually, some ranchers have become dissatisfied with dung beetle activity alone and have returned to mechanical renovation because pastures in the area are prone to contamination by nongraminaceous weed species when mechanical means are not regularly employed.

An attempt to quantify these field observations was made in November of 1982, a peak time of year for horn fly and *O. gazella* abundance. Random samples were taken of dung pads shredded by established *O. gazella* populations in the Coachella Valley where 40 or more adult beetles attacked a single pad. These were compared to unshredded samples from control pastures in which *O. gazella* was absent. Samples were placed into emergence sleeve cages in a greenhouse, incubated at 26–29 C, 60–55% RH and 14:10–h L:D photoperiod.

The average number and oven-dry weights of horn fly adults emerging per pad from dung collected in both kinds of pastures was calculated. Table 1 shows that horn fly adults were produced

Table 1. Emergence of *Haematobia irritans* Adults from Cattle Droppings Randomly Sampled Among a Standard Size Class in Coachella Valley, California, Irrigated Pastures With and Without *Onthophagus gazella* Populations Present. Sampled 8 November 1982.[1]

Pasture Type	Site No.[3]	Avg. No. Adult Flies Emerged per Pad	s	Avg. O.D. wt. (x 10^{-4} g)	s
Onthophagus[2]	1	9.2	4.1	7.6	0.36
	2	15.4	3.2	7.0	0.36
	3	13.6	3.0	7.0	0.34
Control	1	69.3	30.1	6.2	0.21
	2	37.2	15.3	5.9	0.20
	3	3.0	1.8	8.5	0.38
	4	9.0	3.9	9.7	0.40

[1]Dung pad size = 1.495 cc (s = 374 cc).

[2]ca. 40 *O. gazella* adults present per pad, shredding pronounced.

[3]3 samples.

from all pastures with no significant trend for lower numbers in fields where *O. gazella* beetles were highly active. There was a trend for larger flies to be collected from pads producing the lowest horn fly numbers, based on oven-dry weight data. It is unlikely that the large numbers of horn flies on the cattle in pastures containing high population densities of *O. gazella* was due to the immigration of flies from neighboring ranches, because the pastures under study were isolated. Closer investigation revealed that horn fly immatures were easily extracted from within and below the shredded dung pads in these fields. Further studies in autumn of 1983 and continuing to present show variable results, but a significant horn fly production occurs from all *O. gazella*-inhabited pastures over the entire warm season.

Possible mechanisms to explain horn fly breeding in irrigated pastures where *O. gazella* is active may be found in the dynamics of scarab beetles with horn flies and their natural enemies in the dung habitat. When *O. gazella* scatters and buries cattle dung, a great quantity of fresh fly larval habitat is incorporated into the soil before it has had a chance to become fully aerated and decomposed (compost to a degree unsuitable for fly larval development). Horn flies oviposit in fresh dung prior to colonization by scarab beetles and some eggs hatch before beetle disturbance reaches a level where pad destruction begins. The ensuing fly larvae may either remain in the dung pad that is being shredded, or they may disperse at large through the damp soil, finding ample food from previous scarab dung dispersion to complete their development. Horn fly larvae are known to develop satisfactorily in the soil just below a cattle dropping (March and Bay 1983, Legner 1978b), so that with the dung dispersed, a major behavioral change in the fly larvae is not required. In this way, horn fly development may be actively favored by the larvae encountering greater amounts of food material partially sealed from oxygenation and rapid decomposition in the soil, in a manner shown for *Hippelates collusor* Townsend, whose population density soars when natural food material is cultivated into the soil (Legner 1970; Legner et al. 1966, 1970).

Natural enemy habitats are probably altered or destroyed by the dung shredding process. Although horn flies are a continuous and vexing problem of cattle in California, a number of natural enemies do forage in their breeding habitat (Poorbaugh et al. 1968), which by their cohabitation and laboratory feeding studies are suspected of contributing to the natural control in certain seasons. Any disturbance of this control could guarantee the survival of an even greater number of horn flies. Some of the principal staphylinid predators of horn flies in the Coachella Valley, *Philonthus discodeus* Gravenstein and *Philonthus longicornis* Clark (Legner and Warkentin 1983), are practically eliminated from dung in pastures where *O. gazella* has been active, probably because the dung scattering activity of the beetles reduces habitat configuration and/or moisture content to a level unsuited for staphylinid oviposition and larval development. This is similar to the effects of cultivation on the natural breeding habitat of *Hippelates* eye gnats, which causes a marked reduction in the effectiveness of natural enemies (Legner and Olton 1969). Recently, Roth et al. (1983) also gave evidence that *Philonthus* species were involved in horn fly reductions, and declines in these

predators' abundance were shown during summer months in the presence of dense scarab populations.

A scenario of horn fly production in irrigated and natural rainfall pastures containing well established populations of *O. gazella* may be hypothesized as follows: Some horn fly mortality may initially be caused by the dung scattering activities of beetles shown in laboratory studies for both horn and bush flies (Blume et al. 1973, Bornemissza 1970). However, surviving fly larvae may encounter unlimited food which is distributed by the scarabs throughout the continuously moist soil, so that they may escape the natural predation of native predators because of habitat alteration. The net result could be a greater horn fly abundance than in pastures where *O. gazella* is absent. However, in pastures where cattle are stocked at high densities (25+/ha), and where mechanical pasture renovation is necessary, the result is also a high fly abundance, probably from the same causes of having food mixed at large in the soil and predator curtailment. Thus, the difference is negligible, giving a strong argument for the use of scarabs in such situations, as less energy and cost are required to maintain productive pastures. Fly control, nevertheless, is not achieved to a satisfactory level.

On range land where cattle usually are not stocked at densities exceeding 5–7 head per ha, and where mechanical dung spreading and mixing is not practiced, horn fly densities are characteristically much lower. Dung under the lower herd densities generally decomposes at rates which are fast enough to preclude harmful accumulations (Legner 1978a, McKinney and Morley 1975). The introduction of new predatory natural enemies here may afford a positive means for lowering horn fly densities. However, introducing scarabs such as *O. gazella* could result in habitat disruption to the point of predator exclusion, and increased fly densities. Similar dangers may exist in the bush fly, *M. vetustissima*, ecosystem in Australia (Tyndale-Biscoe et al. 1981).

Predators Capable of Regulating Densities of Symbovine Flies

Regulation of symbovine fly densities to levels below that presently and commonly experienced may require the involvement of biological control agents which are more specific to their prey, and which possess a reciprocal density relationship with it. In other words, natural enemies of the caliber of *Rodolia cardinalis* (Mulsant), *Metaphycus helvolus* (Compere), *Apanteles flavipes* (Cameron), *Tachinaephagus stomoxicida* Subba Rao; and to go a bit more afield, *Cactoblastis cactorum* (Berg), *Microlarinus* spp., and *Chrysolina hyperici* (Forster), to mention just a few (Clausen 1978; DeBach 1964, 1974; Greathead and Monty 1982), which are capable of regulating their hosts more or less permanently at low, non-economic densities. Such organisms have caused the most successes in biological control. Acarid predators, *Macrocheles glaber* (Muller) and *M. peregrinus* Kranz which are disseminated by adult scarab beetles as they seek out freshly deposited dung were studied in Australia (Wallace and Holm 1983, Wallace et al. 1979); but results of translocations for widespread practical control are not encouraging (M.M.H. Wallace, pers. commun.). Ridsdill-Smith et al. (1977) suggest other biological control candidates for bush fly. Fay and Doube (1983) have shown that certain staphylinids and histerids caused significant mortality of immature stages of *Haematobia thirouxi potans* (Bezzi) in southern Africa.

A comprehensive appraisal of the capabilities of a dung fly predator to effectively reduce its host was given by Bornemissza (1968) with *Hister chinensis* Quensel in tropical regions of the South Pacific. This predator was originally introduced there from Java for *Musca domestica* L. control (Simmonds 1958). Bornemissza also became interested in similar introductions in Australia for the biological control of buffalo fly, *Haematobia irritans irritans*, bush fly, *M. vetustissima*, and a ceratopogonid, *Culicoides boevitarsis* Kieffer, using other species of climatically adapted predators. Although later emphasis turned to scarab beetles and fly habitat reduction, his earlier work involved the importation of two southern African beetles, *Hister caffer* Erichson and *Hister nomas* Erichson, from Hawaii. After demonstrating a great voracity for fly eggs and young larvae in laboratory trials, both species were field released. However, only *H. nomas* established in northern Queensland at elevations up to 1,000 m (G.F. Bornemissza, pers. commun.). A fly-attacking nematode, *Heterotylenchus* sp., accidentally became established in Australia (Nicholas and Hughes 1970), but bush fly densities were not significantly affected.

In California, symbovine fly problems exist primarily in temperate climates where regular periods of frost occur in winter. Subtropical species of scarab beetles and predatory insects that were being utilized in Australia were thus unsuitable for the greater portion of cattle lands in California. However, there was more encouragement for the adaptation of the two predatory histerids, *H. caffer* and *H. nomas*, especially as the latter had already colonized frosty portions of the Atherton Tableland in northeastern Australia. These and a European staphylinid, *Aleochara tristis* Gravenhorst, and the parasitic nematode were also good candidates and introductions were begun (Table 2).

Finally, a group of histerid predators was imported from northwestern Pakistan that was reportedly associated with low *Haematobia irritans* and *Musca autumnalis* densities (M.A. Ghani, pers. commun.). Laboratory and field studies with two species, *Santalus parallelus* (Redtenbacher) and *Peranus maindroni* (Lewis), showed that adult beetles usually occupy the soil below and surrounding the dung pad to ca. 10–13 cm. Feeding occurs on both the eggs and young larvae of *H. irritans* and *M. autumnalis* within the dung pad and on emigrating older larvae as they disperse into the surrounding soil to pupate. Feeding behavior on other dipterous species in this habitat is presumed possible, but the largest biomass of Diptera in dung pads in southeastern California irrigated pastures is usually contributed by *H. irritans* during warm seasons. Other species of Sepsidae and Phoridae predominate in cool seasons and could serve to carry beetles in these horn

Table 2. Natural Enemies Introduced in California for the Control of *Musca autumnalis* and *Haematobia irritans* During 1968–1983.

Species	Origin	County in Which Liberated	Approx. No. Released
COLEOPTERA			
Histeridae			
Atholus coelestis Mars.	NW Pakistan	Imperial	30
Hister caffer Erichson	southern Africa	Humboldt	25
		Shasta	30
		Imperial	25
Hister chinensis Quensel	Java	Imperial	25
Hister nomas Erichson	southern Africa	Del Norte	27
		Humboldt	150
		Modoc	50
		Shasta	108
		Siskiyou	100
		Tehama	50
Hister scissifrons Mars.	NW Pakistan	Imperial	20
Peranus maindroni (Lewis)	NW Pakistan	Imperial	660
		Tulare	1246
		S.L. Obisop	1100
		San Diego	230
		Ventura	600
Santalus parallelus (Redtenbacher)	NW Pakistan	Imperial	425
		Tulare	332
Staphylinidae			
Aleochara tristis Gravenhorst	France	Del Norte	6500
		Humboldt	5500
		Modoc	5500
		Shasta	6500
		Siskiyou	2300
		Tehama	10000
NEMATODA			
Heterotylenchus autumnalis Nickle [infected adult flies]	east U.S.A.	Del Norte	10100
		Humboldt	22000
		Modoc	8250
		Shasta	6500
		Siskiyou	1500
		Tehama	12000

fly-reduced periods. Egg laying by the histerids under experimental conditions is related to horn fly numbers, occurring two to three days after having fed on fly eggs or larvae, and in quantities related to the number of hosts consumed. Predator movement into the dung pad is stimulated by the presence of fly eggs and larvae. In the field, considerable dispersal away from the dung pad and into the surrounding moist soil may be expected of crowded fly larvae as has been observed with the previously mentioned chloropid flies (Legner 1966, Legner and Olton 1969) and as reported by March and Bay (1983) for *H. irritans*. An effective predator at this point would add to the total mortality of the fly population, albeit intraspecific competition among horn fly larvae would undoubtedly be reduced and larger, more viable surviving flies would be expected, as visualized by Macqueen (1975). Several species of predators with seasonal activity preferences may be necessary for optimum biological control, in a manner obviously required for endophilous flies (Legner et al. 1975). However, the kinds of predatory species in the symbovine fly habitat should be quite different [compare Legner and Olton (1970) with Poorbaugh et al. (1968)].

Results from releases of the histerids in warm winter areas in southeastern California showed initially significant adult horn fly mortality in selected irrigated pastures where the histerids were liberated and became active. However, overwintering has not been recorded due to removal of the experimental area in this extremely hot, almost rainless region. Introductions have been extended to more permanent grazing lands in other portions of south California; but as the histerids currently available are subtropical, it is uncertain if they will be able to establish in the California environment.

Parasitic Hymenoptera for Symbovine Flies

Parasitic Hymenoptera do not seem to play a prominent role in the natural regulation of symbovine flies (Hughes et al. 1974; Legner, unpub. data), although research conducted in very humid areas shows very high activity. It is an accepted fact that the different species of synanthropic Diptera have different favored habitats as exemplified by the oviposition preferences of the face fly, *M. autumnalis*, and the horn fly, *H. irritans*, in field dung of cattle versus the barnyard accumulated excrement habitat sought out by the common house fly, *M. domestica* L., stable fly, *Stomoxys calcitrans* (L.), and the poultry fly, *Fannia canicularis* (L.). Because their breeding habitats are so different (Snowball 1941), these two groups of Diptera are usually assigned to different categories of synanthropy (Legner et al. 1974a, Povolny 1971).

For each category of host synanthropy, there are also different groups of associated natural enemies (Legner et al. 1974a). Until recently, predatory arthropods were considered to be of prime importance in the natural regulation of Diptera breeding in isolated deposits of cattle dung in pastures, primarily by inferences made from the large numbers present (Hammer 1941, Legner 1978b, Mohr 1943, Poorbaugh et al. 1968). However, predatory, parasitic, and scavenger arthropods appear to interact to regulate populations of Diptera breeding in accumulated animal wastes and garbage (Legner 1971; Legner and Olton 1970, 1971; Legner et al. 1974a, 1975). Although some natural enemy species overlap into both the pasture and accumulated dung habitats, there are many species which are mostly confined to either one or the other habitat (Legner and Olton 1970, Poorbaugh et al. 1968). The highest levels of parasitism are characteristically observed in the larger accumulations of dung (Legner and Brydon 1966, Legner and Greathead 1969, Legner and Olton 1971, Legner et al. 1974a).

Sampling for Parasitism

An important requirement for appraising the value of parasitic insects in the natural control of synanthropic Diptera is the natural extraction of samples from the undisturbed habitat. Immature hosts (larvae and pupae) must be removed directly from the habitat in which they were naturally formed, admittedly entailing painstaking labor. Changing the breeding situation to facilitate collection, and gathering field deposited dung into heaps in order to concentrate pupation sites of fly larvae developing therein, attracts those parasitic species which range in *accumulated* dung for

their hosts. Consequently, as most parasites of synanthropic Diptera are not host specific but habitat specific, the pasture breeding fly species in the altered habitat may then sustain parasitism by species and at rates rarely if ever encountered naturally.

The importance of host habitat to parasite searching has been emphasized for many years (Flanders 1937, Laing 1937, Salt 1935, Vinson 1976). Particular attention to the kind of habitat is required when an accurate appraisal of parasite performance is desired. Simmonds (1948) concluded that, "to avoid misleading results care must be taken to secure samples of host material in the field with due consideration to the habits of both host and parasite." In this way, the host-exposure method acclaimed by Bartlett and van den Bosch (1964) is not always a well suited technique, neither for the qualitative nor the quantitative evaluation of parasites of synanthropic flies. The artificial exposure of host pupae can, as in the case of *Hippelates* eye gnats, attract parasites that would not normally parasitize the host in nature (Bay et al. 1964, Legner and Bay 1965). A careful study of the breeding situation can, however, result in the development of techniques whereby the host may be exposed more naturally (Legner and Bay 1964).

For reasons evident from the previous discussion, many of the reports of high levels of parasitism of symbovine flies are probably in error. In many cases where the sample method was detailed, it was evident that the habitat had been altered by investigators to facilitate fly collection or collections were made in dung pads adjacent to large accumulations of dung, as is characteristically found in barnyards and from which parasitic insects could easily disperse. There is one example from a very humid and tropical area of northern Australia where a species of *Spalangia* appears to have exerted significant impact on a symbovine fly species (Legner et al. 1974a). However, over the greater expanse of cattle rangeland, there is little evidence to suggest a high level of parasitism of symbovine flies. Thus, with the possible exception of very humid areas, the commonly reported species of *Spalangia*, *Muscidifurax*, and *Pachycrepoideus*, are probably incapable of evoking significant parasitism of symbovine flies, their natural instincts being to seek out hosts in accumulated dung habitats (see Legner et al. 1974a).

Future Emphasis in Biological Control

The continued importation of different species of scarab beetles to control dung on our range and pasture lands will probably greatly aid agriculture by reducing operating costs and guaranteeing the availability of a larger grazing area. It may also aid in the reduction of gastrointestinal parasites of livestock (Durie 1975, Fincher 1981). However, it cannot be considered a wholly satisfactory approach for reducing symbovine fly densities significantly, if past trends are indicative. The economic importance of such species as *H. irritans* and *M. autumnalis* may be slight (Harvey and Brethour 1979, Haufe 1982, Kunz et al. 1984, Palmer and Bay 1981, Shugart et al. 1979), and control is still attainable with insecticide-impregnated ear tags in the absence of strong resistance, so that the major concern of ranchers will probably continue to focus on the quality of grazing land. To this end we should pay heed to observations of Wallace and Tyndale-Biscoe (1983) that single-species populations may attain higher densities and so disperse dung pads as well as, or better than, several species in combination. Also, the native dung beetle fauna may be quite numerous in undisturbed habitats as recently shown in California (Anderson et al. 1984), and both numerous and effective as witnessed in Australia (Ridsdill-Smith and Matthiessen 1984, Ridsdill-Smith et al. 1983). Therefore, the need for further importations in the wilderness could be minimal. On the other hand, the native species may not be common in pastures (Ridsdill-Smith and Hall 1984). Thus, A. Macqueen (pers. commun.) believes that dung burying beetle species with other types of activity might be seriously considered if testing showed that they would be advantageous.

For fly species that are obnoxious to humans, such as *M. vetustissima* in Australia and to a lesser extect *M. autumnalis* in the Holarctic, there is an equal or greater need to reduce fly population densities. Because chemical control is costly and of limited value in the continuously available breeding sites, biological control offers a possible practical solution. Until now there has been proportionately little effort to import new species of predators, parasites, and pathogens against these flies. Wallace and Tyndale-Biscoe (1983), however, question whether the maximum level of

overall mortality has already been reached and that any additional factors introduced into the system will simply be substitutes for one of those already existing. Reasons for this center around our unawareness of more effective natural enemies; this in turn is to some measure due to our attentions usually having been confined to these flies where they are persistent problems. Those species which have been tried, such as *Aphaereta pallipes* Say, *Aleochara tristis* Gravenhorst, and *Spalangia* spp. (Hughes and Woolcock 1978, Hughes et al. 1974, Legner 1978a,b, Legner et al. 1974a), might never have been expected to succeed in the first place, if basic information about their habits were considered earlier. For example, *A. tristis* is apparently unable effectively to locate isolated cattle droppings in America; other natural enemy species were imported from humid to dry climates where they could not adapt; and in any case all originated in areas where symbovine fly abundance was unacceptably high. Obvious good natural enemies (e.g., *Macrocheles* spp.) which failed should be measured for temporal significant impact, such as in certain seasons, and not serve as reasons for abandoning further exotic natural enemy importation.

The status quo, in my view, is perpetual coexistence with hordes of flies. Past biological control successes were evoked by researchers who were never satisfied with the density of their target organisms until suitable natural enemies *had been found*. Biological control successes are proportional to the amount of effort expended in the search for good natural enemies (DeBach 1974). I do not feel that sufficient time nor effort has been given to the procurement of suitable candidates. In California, for instance, most research funds were diverted exclusively to the importation of dung burying scarab beetles when earlier attempts at importation of nonadapted predators failed. There were only weak attempts to extend the search for appropriate climatically adapted predators and pathogens on an acceptable scale. The token effort made by the research group at Riverside would at best fit the label of preliminary studies. Establishment of exotic beneficial species is often difficult and usually requires larger number releases than were possible to carry out without adequate funds (see Table 2).

There is, for example, one portion of Central Asia that has been understressed as a source of natural enemies. This region includes northwestern Pakistan and extends into the western Soviet Union and possibly western China. A fly fauna exists there with some species characteristic of two or three geographic regions: Palearctic, Ethiopian and Oriental (Sytshevskaya 1970, Sytshevskaya and Vtorov 1969). Some pasture breeding species, including a close relative of the Australian bush fly, *Musca sorbens* (Wiedemann, apparently occur there at comparatively low densities (Commonwealth Institute of Biological Control 1970–72; Sytshevskaya 1963, 1970, 1972; Sytshevskaya and Vtorov 1969; M.A. Ghani, pers. commun.). Studies in Pakistan show that the presence of certain predatory Histeridae could account for considerable natural mortality of symbovine flies (Legner 1978a). Because of climatic similarities, these have been most recently stressed in California (Table 2). Further explorations in Asia should be conducted for natural enemies possessing the necessary climatic tolerances and behavioral characteristics that could produce the desired significant drop in symbovine fly densities.

Similarly, searches in southern Africa, which have previously stressed dung burying scarabs, might be extended to include such entomophagous organisms as revealed by Fay and Doube (1983).

Conclusions

In conclusion, several points need to be emphasized as follows: (1) the *status quo* density of *Musca autumnalis*, *Haematobia irritans*, and *Musca vetustissima* is presently unacceptable over most of the range of these flies; (2) there are no practical non-biological alternatives to reduce their average density; (3) relying exclusively on dung burying scarab beetles to reduce these fly densities has not been successful so far; (4) the addition of more scarabs to the ecosystem might not be wise, as it is possible that, through interspecific competition and interference with existing natural biological controls, fly densities could rise; and (5) further worldwide searches should be intensified to secure more effective natural enemies, principally predators and pathogens.

However, extremely careful assessments of the attributes and potential of any candidate, whether parasite, predator, pathogen, or dung beetle, should be made beforehand to reduce the generation of further biological control failures and possible ecosystem upsets.

Acknowledgements

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