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Distribution and Relative Abundance of Dipterous Pupae and Their Parasitoids in Accumulations of Domestic Animal Manure in the Southwestern United States

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The native parasitoid complexes associated with four key muscids, *Musca domestica* L., *Stomoxys calcitrans* (L.), *Fannia canicularis* (L.), and *F. femoralis* Stein—and two predatory Diptera, *Muscina stabulans* (Fallen) and *Ophyra leucostoma* (Wiedemann)—are described and shown graphically for the major climatic zones of the southwestern United States. Three geographical groups of the parasitoid species identified were (1) those whose populations extended into most climatic zones below 2,000 meters (*Muscidifurax* species and *Spalangia nigroaenea* Curtis); (2) those whose populations were restricted to the warmer climatic areas (*S. endius* Walker and *S. cameroni* Perkins); and (3) those that were largely restricted to higher latitudes and colder winter climates (*S. nigra* Latreille and *Aleochara* spp.). Considerable yearly, seasonal, and climatic variations were shown in the abundance of both host and parasitoid demes. These factors, combined with others, probably account for the high degree of instability among demes. This instability may be important in determining the panmictic nature of most populations. Some parasitoids such as the Diapriidae and Staphylinidae (*Aleochara* spp.), which exist in small demes, appeared to be local species that may have adapted to invading Diptera. The *Stilpnus* species were specific to *Fannia.* Parasitoid species appear to be irreplaceable mortality factors in the natural control of populations of their dipterous hosts.

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Distribution and Relative Abundance of Dipterous Pupae and Their Parasitoids in Accumulations of Domestic Animal Manure in the Southwestern United States[1,2]

INTRODUCTION

CERTAIN PARASITOID SPECIES are recognized as significant agents in the natural reduction of their fly hosts in accumulations of domestic animal manure. The worldwide distribution of such species has been discussed by Legner *et al.* (1967) and Legner and Olton (1968). Legner and Brydon (1966) and Legner *et al.* (1966) also reported on the use of parasitoids as biological control agents. Parasitoid activity described in these studies was correlated with climate, which tended to limit the occurrence of some species.

Most predominant parasitoids have worldwide distribution. Several narrowly distributed and highly active species have been considered for introduction elsewhere to increase heterogeneity in local biotic complexes (Legner and Olton, 1968; Legner and Bay, 1970).

This paper describes and provides graphs to show the native parasitoid complexes associated with key muscoid and predatory Diptera in the southwestern United States before the intensive introduction of exotic species (Legner and Bay, 1970). An attempt is made to measure the distribution and abundance of viable hosts and parasitoids in a wide variety of climatic zones in the Southwest, which might serve as a comparison with post-introduction data. The results of five survey years are pooled, and average values are derived that transect yearly climatic fluctuations.

MATERIALS AND METHODS

Selection of sample sites

Collection sites chosen in the southwestern United States were in the states of California, Nevada, Utah, Arizona, and New Mexico (fig. 1). Sites were restricted to places where domestic animal manure accumulates: dairies, poultry houses, horse and hog pens. The high humidity and associated chemical stimuli of this type of habitat attract the ovipositing females of both host species and their parasitoids and are necessary for subsequent successful development of their larvae. Data for the Southwest, therefore, are restricted to those climatic zones in which the accumulation of manure was a standard practice and do not include all possible zones.

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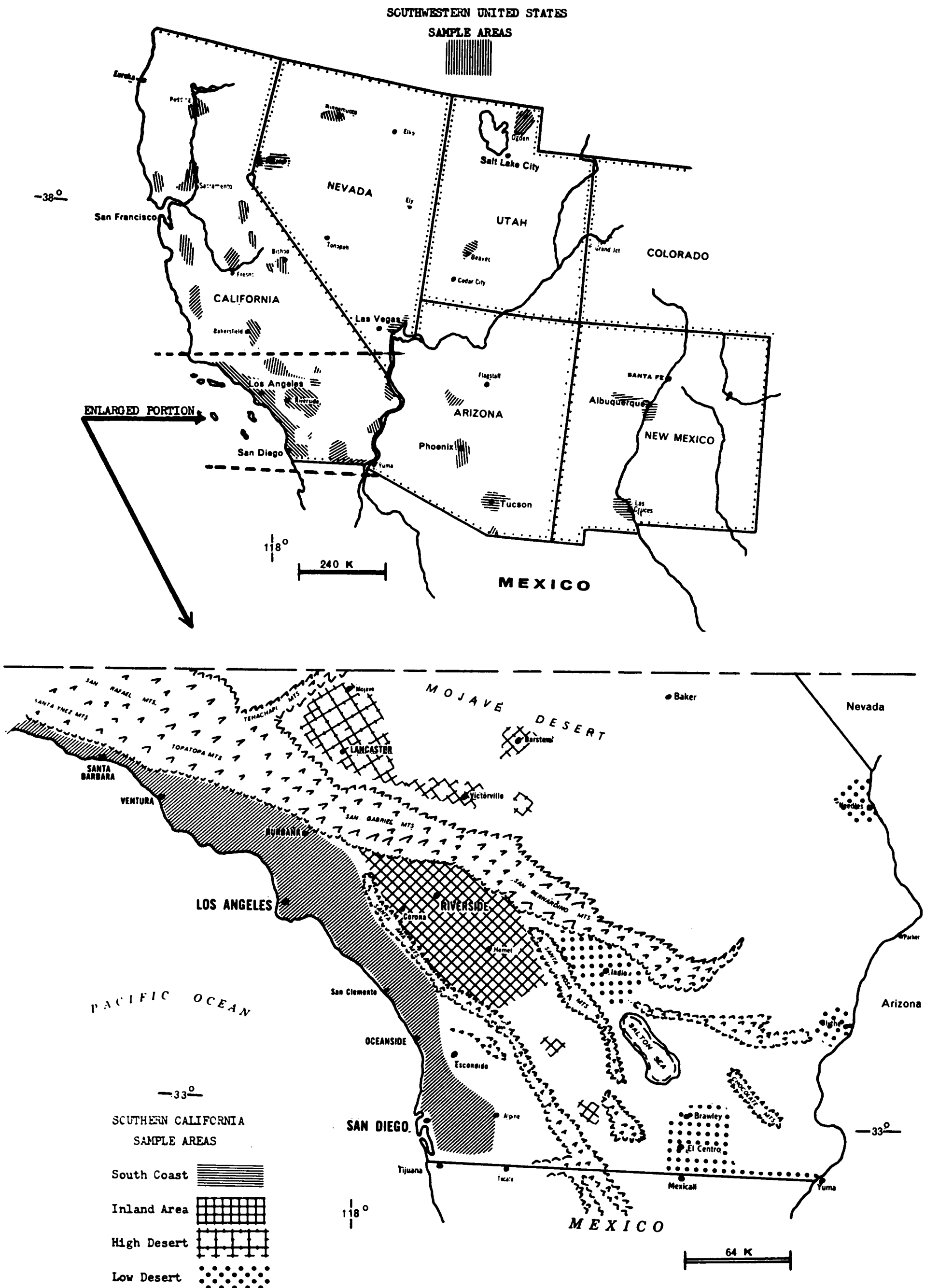

Fig. 1. Major sampling areas for parasitoid species on dipterous hosts in accumulations of domestic animal manure in the southwestern United States. (1964 to 1969.)

In the states other than California, the two major bio-climatic zones sampled were the Great Basin (Upper Sonoran) and Lower Sonoran deserts. In California, however, the distinct areas sampled were in the northern part: (1) Sacramento Valley, (2) San Joaquin Valley, (3) western Sierra foothills, (4) eastern Sierra foothills (Owens Valley), (5) Santa Rosa Valley, and (6) Salinas Valley. In southern California the areas were sampled primarily according to the amount of annual rainfall they received: (1) the South Coast with 450 to 500 mm, (2) Inland area with 250 to 300 mm, (3) the High Desert (the Mojave) with 150 to 200 mm, and (4) the Low Desert (Lower Colorado) with less than 125 mm. Elevations of the South Coast and Inland areas varied from 15 to 300 meters; in the High Desert between 1,000 and 1,500 meters; and 15 meters to below sea level on the Low Desert (fig. 1). Table 1 gives the manure types, collection dates, and number of sites sampled annually for each respective area.

Sample sites chosen in each geographic area consisted of nontreated, accumulated hen, bovine, horse, and hog manure that supported the development of one or all the following fly species: *Musca domestica* L., *Stomoxys calcitrans* (L.), *Fannia canicularis* (L.), *F. femoralis* Stein, *F. scalaris* (F.), *Muscina stabulans* (Fallen), *Ophyra leucostoma* (Wiedemann), *Phormia regina* (Meigen), *Phaenicia sericata* (Meigen), and *Sarcophaga* spp. Sites were chosen at random in each geographical area during the summer period—July *through* September in southern California and July *and* September in other portions of the Southwest. The same sites were sampled once each month during these periods, and no site was sampled containing introduced parasitoid species (Legner and Bay, 1970). In southern portions of California, Arizona, and New Mexico, an additional winter sample was taken from sites selected at random during the months of December through February. Sampling began in 1964 and continued through 1968, with areas in southern California receiving the most intensive examination. During the five-year survey period, six south coastal poultry sites that ceased to produce undisturbed fly breeding habitats were substituted with six new sites selected at random in the same area in 1968. Sites in the other areas sampled remained fixed (table 1).

Extraction of pupae

At each sample site, a minimum of 30 liters of animal manure containing pupae of the several dipterous species was gathered at random with a hand trowel, placed in a receptacle and watered. The pupae that floated to the surface were collected with a 11.8 mesh /cm plastic screen and a camel's hair brush. They were placed in screened, plastic vials with absorbent paper, and stored in an insulated ice chest. Later they were fully dried, separated to obtain intact, apparently viable individuals, and incubated in the vials at 24 to 26°C for the emergence of host flies and parasitoids, as previously described (Legner *et al.,* 1967). The ratio of pupae to the amount of manure in which they were formed was not determined. But during two survey years, an attempt was made to compare different types of animal manure for the amount of viable pupae they contained by measuring as accurately as possible the quantity of manure sampled at each site and the number of viable pupae extracted. Counts were limited to manure that contained viable pupae of the key species under consideration.

The seasonal distribution of emerging adult parasitoids was obtained at three poultry ranch sites on the south coastal plain of California. Pupae were gathered from 30 random samples per day at weekly or greater intervals from manure beneath caged hens. A liter

TABLE 1

SCOPE OF SURVEY FOR PARASITE ACTIVITY ON HOST PUPAE IN DOMESTIC ANIMAL MANURE IN THE SOUTHWESTERN UNITED STATES 1964 TO 1969

Area	Manure type	Sampling period	No. sites sampled per year*
Southern California:			
South Coast	hen	Jul. - Sept. 1964–69	32
	hen	Dec. - Feb. 1964–69	23
	bovine	Jul. - Sept. 1964–69	16
	bovine	Dec. - Feb. 1964–69	11
	horse	Jul. - Sept. 1964–69	4
Inland	hen	Jul. - Sept. 1964–69	22
	hen	Dec. - Feb. 1964–69	16
	bovine	Jul. - Sept. 1964–69	12
	bovine	Dec. - Feb. 1964–69	6
High Desert	hen	Jul. - Sept. 1964–69	5
	hen	Dec. - Feb. 1964–69	9
	bovine	Jul. - Sept. 1964–69	4
	bovine	Dec. - Feb. 1964–69	6
Low Desert	hen	Jul. - Sept. 1964–69	4
	hen	Dec. - Feb. 1964–69	4
	bovine	Jul. - Sept. 1964–69	10
	bovine	Dec. - Feb. 1964–69	8
	horse	Jul. - Sept. 1964–69	10
	horse	Dec. - Feb. 1964–69	8
Northern California:			
Salinas Valley	bovine	Jul. & Sept. 1967–68	6
Santa Rosa Valley	hen	Jul. 1968	2
	bovine	Jul. 1968	3
Sacramento Valley	bovine	Jul. & Sept. 1967–68	6
San Joaquin Valley	hen	Jul. & Sept. 1967–68	2
	bovine	Jul. & Sept. 1967–68	4
Sierra Western Foothills	hen	Jul. & Sept. 1967–68	4
	hog	Jul. & Sept. 1967–68	3
2600 m. High Sierra	horse	Aug. & Sept. 1967–68	6
Owens Valley	bovine	Jul. & Sept. 1967–68	5
Great Basin Region:			
Central Nevada	bovine	Sept. 1968	5
Southern Nevada	bovine	Jan. 1969	3
Logan-Ogden, Utah	bovine	Sept. 1968	5
Beaver	bovine	Sept. 1968	2
Sonoran Desert:			
Cottonwood, Arizona	bovine	Jul. & Sept. 1967–68	4
	bovine	Jan. 1969	3
	horse	Jul. & Sept. 1967–68	2
Phoenix	bovine	Jul. & Sept. 1967–68	4
	bovine	Jan. 1969	5
Tucson	hen	Jul. - Sept. 1967–68	4
	hen	Jan. 1969	2
	bovine	Jul. - Sept. 1967–68	6
	bovine	Jan. 1969	5
Las Cruces, New Mexico	hen	Jan. 1969	2
	bovine	Jul. - Sept. 1967–68	3
	bovine	Jan. 1969	2
Albuquerque	bovine	Jul. - Sept. 1967–68	3
	bovine	Jan. 1969	2
	horse	Jan. 1969	2

* All sites remained the same for the five-year period of sampling except for six poultry sites on the south coast which were substituted in 1968.

cylinder 16 cm long by 8.9 cm diameter was plunged to a depth of 16 cm at an angle of 45° into the side of the ascending manure deposit. The available breeding surface and its age were held relatively constant at 0.9 to 1.1 cm of wet deposit each day during the sampling period through continuous replenishment by the caged hens above. No attempt was made to judge the sizes of host or parasitoid populations on each ranch.

The manure at the three ranches was completely removed twice annually, once in the April to June interval and again in the October to December interval. Such removal was performed so that every other row of manure remained intact for at least two months, allowing predators and parasitoids to move to adjacent fresh deposits that again began to build up. This also insured the continuation of sampling at a minimum depth of 28 to 34 cm of both dry and wet deposit.

Parasitoid rearing

Parasitoids that emerged from pupae were periodically removed from the incubation vials in order to eliminate superparasitization. These were mated and stock cultures established. Virgin females were isolated and compatibility tests performed between cultures of the same species from different geographic areas.

Identification

Diapriidae were identified by C. F. W. Muesebeck, Pteromalidae by B. D. Burks, Ichneumonidae by L. M. Walkley, and Spalangiidae by Z. Boucek and B. D. Burks. We gratefully acknowledge this assistance.

Statistical analyses

The activity of the various parasitoid species in the different geographic areas was calculated using the following methods: For each area the total number of parasitized and unparasitized fly pupae that emerged was taken as the 100 per cent viable fraction of the sample. The percentage of this emergence that was due to parasitoids was recorded. These values were transformed to the arc sin $\sqrt{\%}$ as explained by Steel and Torrie (1960) for each sample site. The standard error of the mean, $s_{\bar{x}}$, was determined among the transformed percentages for each geographic area by the $\surd$ of the formula:

$$\frac{\Sigma X_i^2 - X^2 ../_n}{(n-1)n}$$

Confidence limits around the derived transformed means were calculated with the formula:

$$\bar{x} \pm (t_{05}\, s_{\bar{x}}), \text{ where } df = n - 1$$

The means and confidence limits were retransformed to the original percentage values for text figures and discussion.

Estimates were made of the numbers each parasitoid species contributed to total parasitoid emergence in any given geographical area. It was necessary, however, to recognize that all parasitoid species were not represented at all sample sites. Therefore, percentage emergence figures of each species were gathered, and means and confidence limits were calculated in the manner described above only for those sites where a given parasitoid occurred.

The arc sin $\sqrt{\%}$ transformation was used in these calculations because it tended to reduce errors produced by unequal sample size and by extremely high and low values. Although not completely satisfactory for estimation of parasite emergence, it did provide a more sound basis for comparison of geographic areas.

RESULTS AND DISCUSSION

Distribution and parasitization of Diptera in southern California

Figures 2 to 4 show the distribution of dipterous pupae secured from hen, bovine, and horse manure, respectively, in four major sample areas of southern California from 1964 to 1969. The area of each pie graph illustrates the percentage of sample sites in which live pupae of a particular host species were found. (The shaded portion of each graph represents the average per cent parasitization that these pupae sustained.) The 95 per cent confidence limits around this average are found in the clear portion of most graphs in which data were sufficiently abundant to permit their calculation.

Musca domestica was the most widely distributed species in hen manure, being present at 56.3 per cent of the summer sites and 57.9 per cent of the winter sites on the South Coast. It was equally predominant in summer samples from the Inland and desert areas (fig. 2).

During summer, *Fannia femoralis* was the second most frequently encountered species in hen manure of the coastal and Inland areas, but this species existed in only 25 per cent of sites on the High Desert, and was absent from the Low Desert samples.

Fannia canicularis was the third most frequently encountered species in hen manure during summer in both the South Coast and Inland areas, and second most prevalent in the High Desert. Also, it was absent in breeding sites of the Low Desert.

The fourth species, *Stomoxys calcitrans,* was present in all summer samples except those taken in the Low Desert. The remaining five Diptera, *Ophyra leucostoma, Muscina stabulans, Fannia scalaris, Phaenicia* and *Sarcophaga,* were comparatively poorly distributed in coastal and Inland sites, and did not occur in the desert areas.

Hen manure under winter conditions favored the occurrence of *Fannia femoralis* and *F. canicularis* in all areas except the Low Desert, where *Stomoxys calcitrans* and *Sarcophaga* prevailed. The incidence of the dipterous predators, *Ophyra leucostoma* and *Muscina stabulans,* appeared to be slightly favored by winter conditions on the South Coast; and the occurrence of *Muscina stabulans* was favored in the Inland area (fig. 2).

The distribution of fly species in bovine manure was restricted to six species, with *Fannia scalaris, Phaenicia* and *Sarcophaga* species being absent (fig. 3). *Musca domestica* was again the most widely-distributed species during the summer sampling period. However, it was better distributed in bovine manure than in hen manure on the South Coast (92.9 per cent), Inland area (100 per cent) and Low Desert (87.5 per cent). See figures 2 and 3.

Fannia species were not found in bovine manure outside of the coastal area during summer, and only *F. canicularis* occurred in winter. The predators *Ophyra leucostoma* and *Muscina stabulans* were confined to summer samples of the South Coast.

Musca domestica and *Stomoxys calcitrans* were the only two species that produced live pupae from summer samples of bovine manure outside of the coastal area. During winter, the comparatively greater exposure of bovine manure to low temperatures apparently restricted the incidence of all species (fig. 3).

The lowest numbers of viable dipterous pupae were from horse manure (fig. 4), which yielded only three species, *Musca domestica, Stomoxys calcitrans* and *Sarcophaga.* Only one species, *S. calcitrans,* was found in the Low Desert during the winter sampling interval.

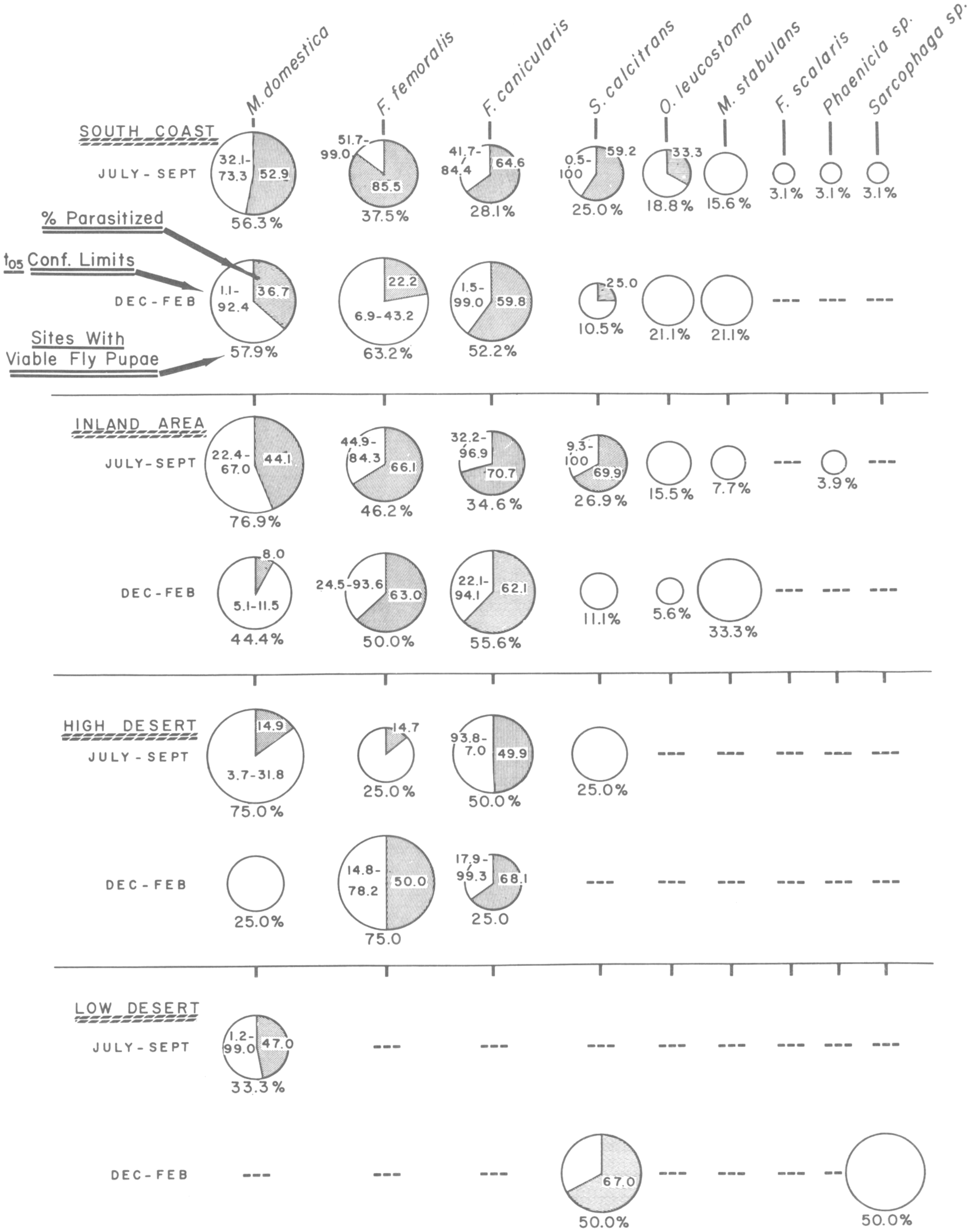

Fig. 2. Distribution of viable fly pupae and average per cent of parasitoids in accumulations of hen manure in southern California. (1964 to 1969.)

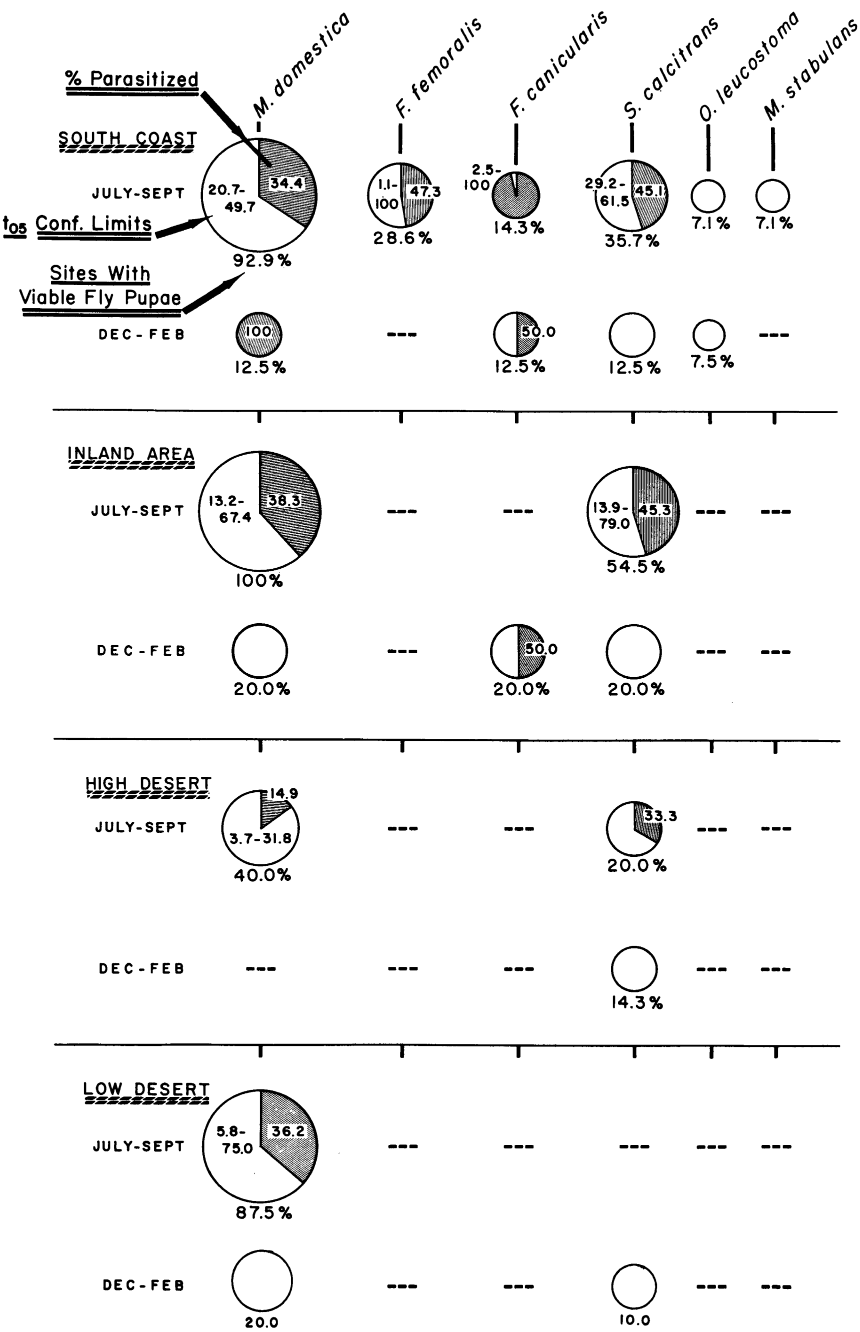

Fig. 3. Distribution of viable by pupae and average per cent of parasitoids in accumulations of bovine manure in southern California. (1964 to 1969.)

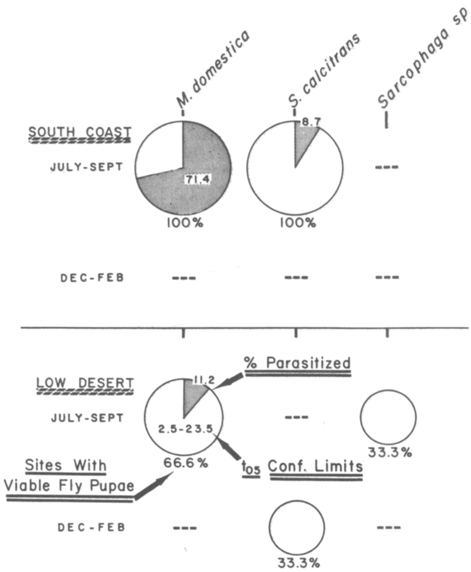

Fig. 4. Distribution of viable fly pupae and average per cent of parasitoids in accumulations of horse manure in southern California. (1964 to 1969.)

Density of dipterous pupae in southern California

Estimates of the density of viable pupal production of key species in various manures were made in southern California in 1964–1965 and 1968. The mean number of fly pupae per liter of manure was plotted as the area of the circle between the inner and outer circles of each circle graph in figure 5. The 95 per cent confidence limits around the mean are shown as the inner and outer circles.

The distribution data in figures 2 to 4 correlate closely with the density data of figure 5. The most widely distributed fly species were almost invariably those that occurred at the highest densities in the 1964–1965 and 1968 surveys.

The data in figure 5 also suggest that certain manures accumulated more pupae of some fly species than did others. However, speculation on differential productivity of flies would not be warranted, because clumping patterns of pupae varied in different manures. It is probable, nevertheless, that bovine manure was most productive of *Musca* pupae on the South Coast and in Inland sample areas during summer, and that in the same areas, *Stomoxys* pupae were more dense in bovine and horse manure than in hen manure. During winter, the relatively greater cover afforded by the poultry house environment probably caused hen manure to sustain the highest pupal density for most species (fig. 5).

In the Low Desert, however, summer *Musca* pupal production was higher in hen manure than in either bovine or hog manure. This probably is a result of the relatively cool habitat afforded by the latter two types of manure. Poultry are frequently cooled in summer in the hotter areas of southern California by a water spray over the rooftops of their houses, and horses are usually corralled in shady, irrigated areas. Pupal production of all species was especially low in the Low Desert during winter.

Summarizing three climatic areas of southern California, the greatest production of *Musca* occurred in the Low Desert in summer. *Musca, Stomoxys* and *Fannia* were relatively prominent on the South Coast and in the Inland areas. In winter, pupal production was highest in the comparatively moderate coastal environment, with *Musca, Fannia* and *Ophyra* being the most dense. *Fannia femoralis* was especially numerous on the coast (fig. 5).

Distribution of parasitoids in southern California

Figures 6 to 8 show the distribution of parasitoids on four key host species, *Musca domestica, Fannia femoralis, F. canicularis* and *Stomoxys calcitrans,* that were sampled from hen and bovine manure in southern California. Data from other manures were too few for plotting in this manner. The area of each pie graph illustrates the per cent

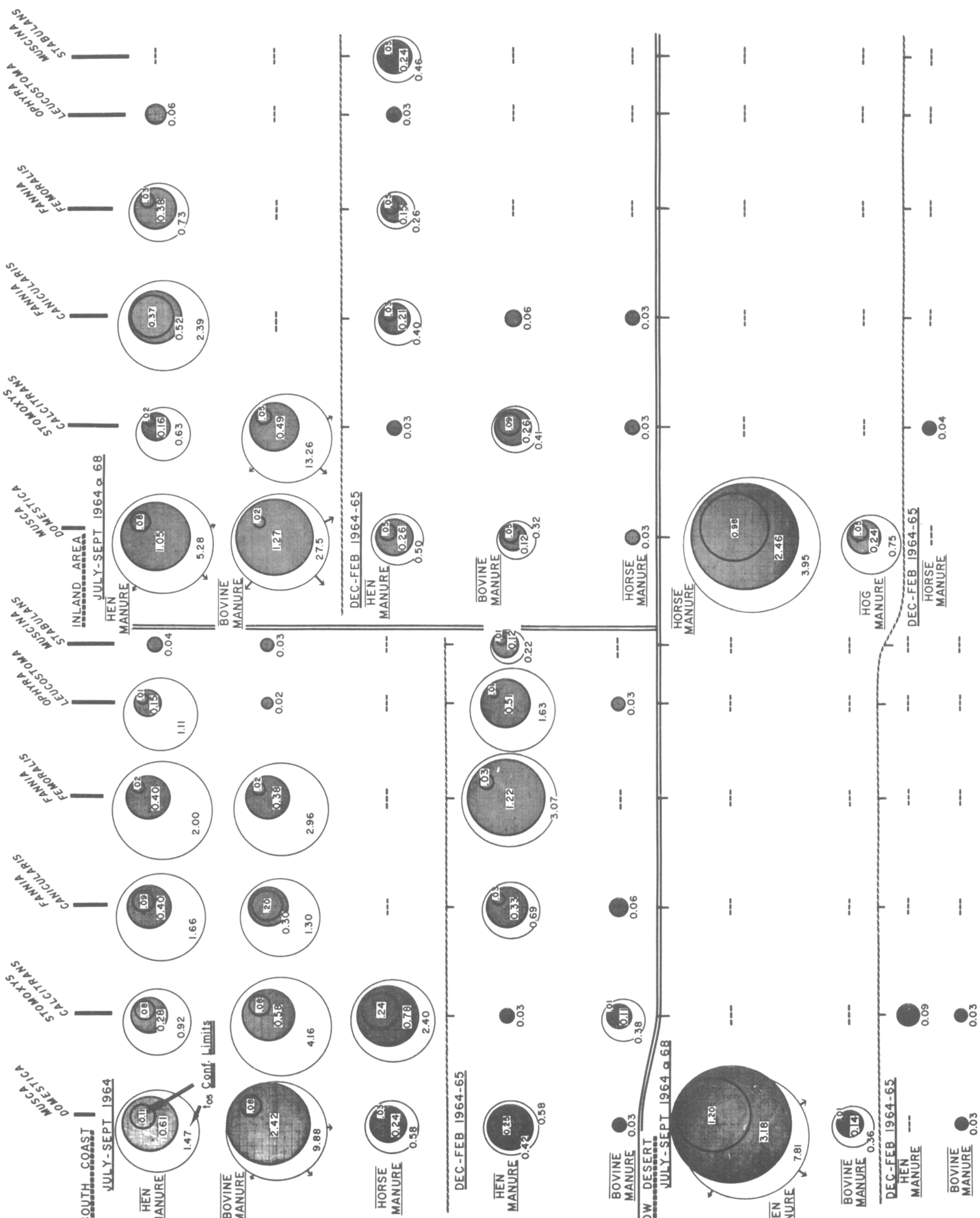

Fig. 5. Mean number of viable pupae of the principal dipterous species found in per-liter accumulations of animal manure in southern California. The shaded inner and unshaded outer circles represent the 95 per cent confidence limits around the mean—which is the shaded circle between. (1964–1965, 1968.)

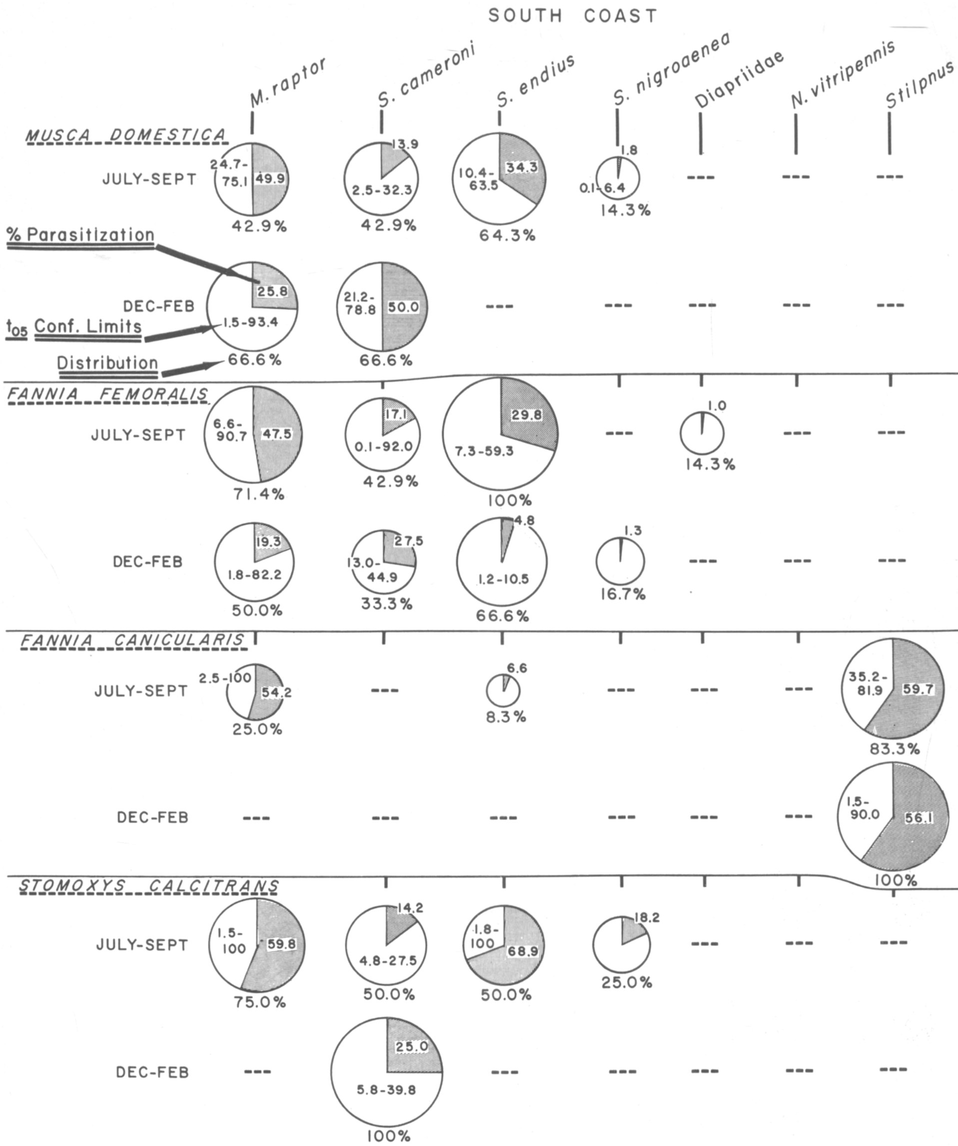

Fig. 6. Distribution of parasitoids of four principal dipterous hosts in accumulations of hen manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Southern California coast, 1964 to 1969.)

of host collection sites at which a parasitoid species was present. The shaded portion of each graph represents the average per cent parasitization caused by that species in each area of distribution. The 95 per cent confidence limits around each average are printed in the clear portion of most graphs, whenever their calculation was possible.

Four nonspecific parasitoid species which predominated in southern California were *Muscidifurax raptor* Girault and Sanders, *Spalangia cameroni* Perkins, *S. endius* Walker and *S. nigroaenea* Curtis (figs. 6 to 8). A fifth species, *Stilpnus anthomyidiperda* (Viereck) was specific on *Fannia canicularis*. Two or more diapriid para-

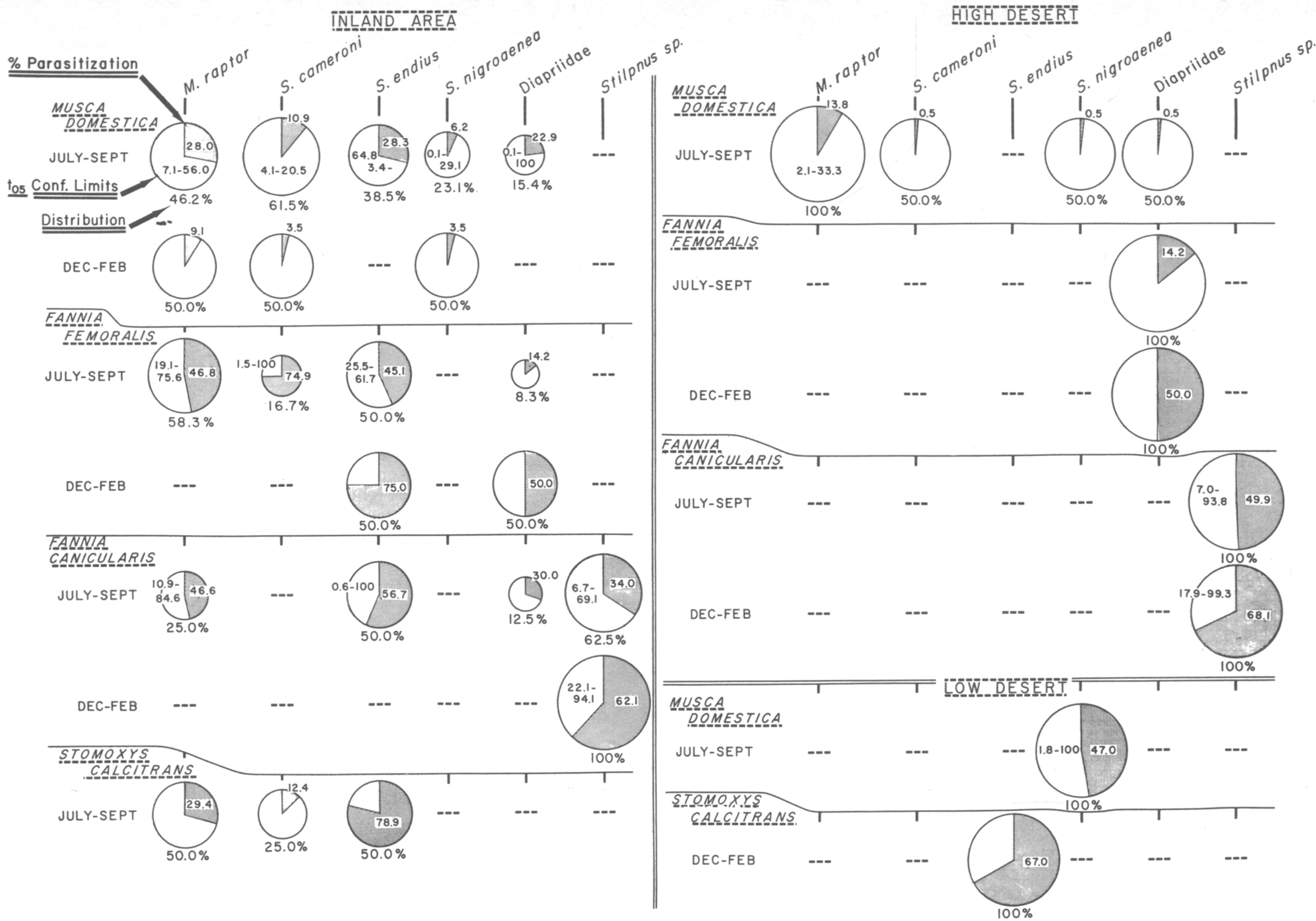

Fig. 7. Distribution of parasitoids of four principal dipterous hosts in accumulations of hen manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Inland and desert portions of southern California, 1964 to 1969.)

sitoids, *Trichopria* and *Phaenopria* spp., were also present. *Nasonia vitripennis* (Walker) was known to parasitize *Fannia* pupae in southern California (Legner, 1967; Legner and Brydon, 1966), but it was not collected during the survey months shown in the graphs.

Winter conditions apparently did not restrict the presence of some parasitoids in hen manure as much as in bovine manure, where exposure to low temperatures was more common (figs. 6 to 8). No parasitized hosts were found in horse manure during winter (fig. 4).

The amount of parasitization by each parasitoid species was not correlated with its distribution. For example, the more widely distributed *Spalangia endius* on *Musca domestica* and *Fannia femoralis* in hen manure on the South Coast (fig. 6) contributed in its range an average parasitization of only 34.3 per cent and 29.8 per cent, respectively. *Muscidifurax raptor,* although more narrowly distributed, showed a greater parasitization on these hosts, 49.9 per cent and 47.5 per cent, respectively.

The first species shown in figures 6 to 8, *Muscidifurax raptor,* is now known to consist of two separate but sympatric species, *M. raptor* Girault and Sanders and *M. zaraptor* Kogan and Legner (Legner, 1969; Kogan and Legner, 1970). The combined distribution of these two species, which were indistinguishable earlier, shows them to be well distributed on all hosts in hen manure of the South Coast and Inland areas during summer. On the High Desert, *Muscidifurax* was found only on *Musca.* The genus was not found to occur in the Low Desert. Winter conditions restricted them to *Musca domestica* and *Fannia femoralis* in hen manure in other areas (figs. 6 and 7).

In bovine manure, *Muscidifurax* species were also conspicuous on the four hosts during summer on the South Coast. However, they occurred only on *Musca* in the Inland area and on *Musca* and *Stomoxys* on the High Desert. They were completely absent in the Low Desert, and from all hosts in bovine manure in winter (fig. 8).

Muscidifurax also attacked *Musca domestica* in horse manure on the South Coast during summer.

The second species, *Spalangia cameroni* (figs. 6 to 8), was notably absent from *Fannia canicularis;* however, it was well distributed on the other three hosts and occurred more widely and was more active during the winter months on the South Coast (figs. 6 and 8). It also parasitized *Musca domestica* in horse manure on the South Coast during summer. In the comparatively colder winter conditions of the Inland and Desert areas, *S. cameroni* either did not occur or was not active (figs. 7 and 8).

Spalangia endius, the third species in figs. 6 to 8, was widespread in hen manure on all hosts collected on the South Coast and Inland sampling areas during summer (figs. 6 and 7). During winter, *S. endius* in hen manure was restricted to *Fannia femoralis* pupae only in these areas (figs. 6 and 7). Figure 7 shows that its distribution was decreased, but activity appeared to increase in the Inland area on hosts in hen manure; *Spalangia endius* was present in hen manure in the Low Desert only in winter.

In bovine manure, *Spalangia endius* was well represented in both coastal and Inland areas, but it was absent on the High Desert and occurred at very low density on the Low Desert (fig. 8). *Spalangia endius* was also present on *Musca domestica* and *Stomoxys calcitrans* in horse manure on the South Coast during summer.

The fourth species, *Spalangia nigroaenea,* had a comparatively narrow distribution compared with that of the other species, and its activity was less. During the summer months, it did not occur on *Fannia,* but was restricted rather to *Musca* and *Stomoxys. Spalangia nigroaenea* was the only species

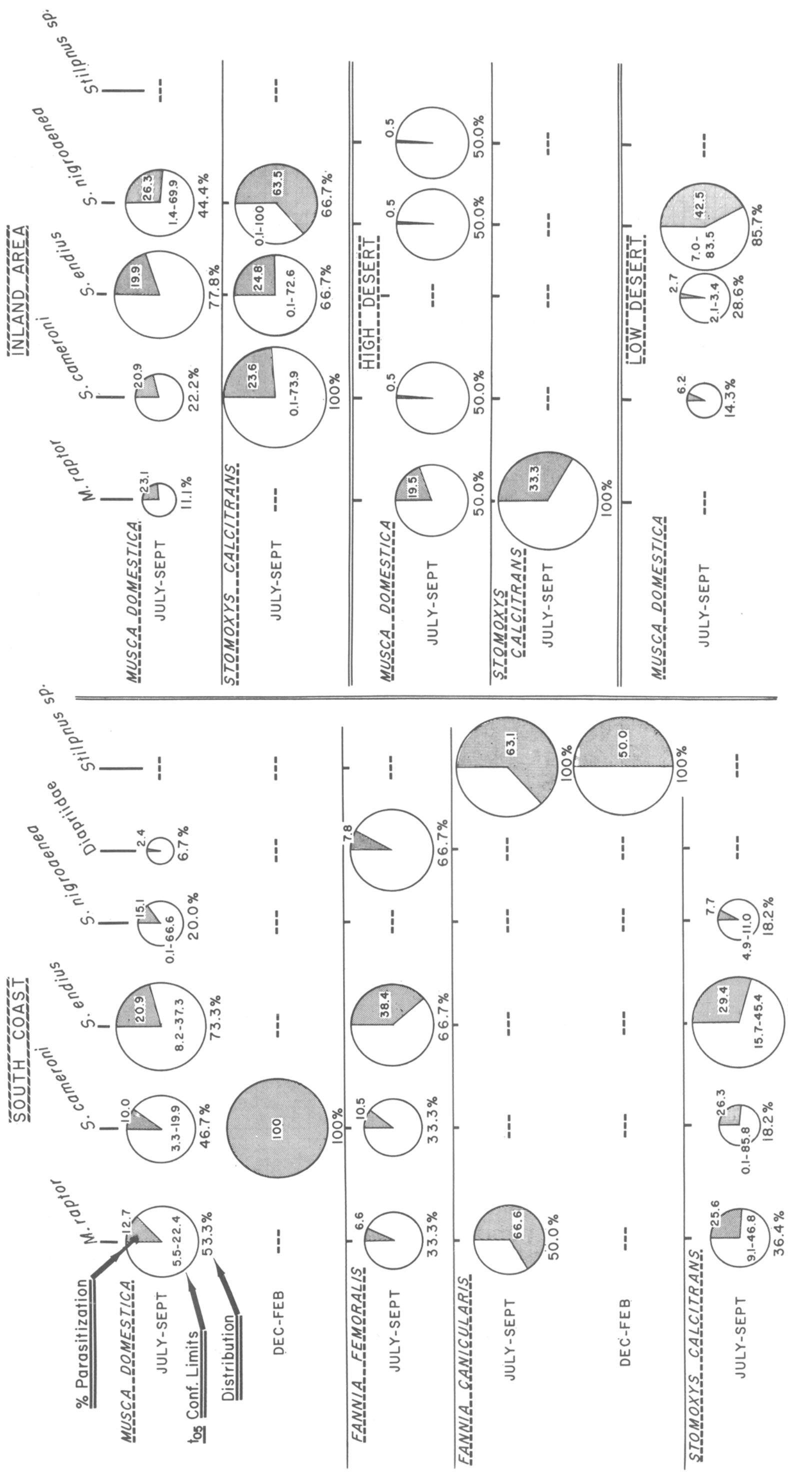

Fig. 8. Distributions of parasitoids of four principal dipterous hosts in accumulations of bovine manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Southern California, 1964 to 1969.)

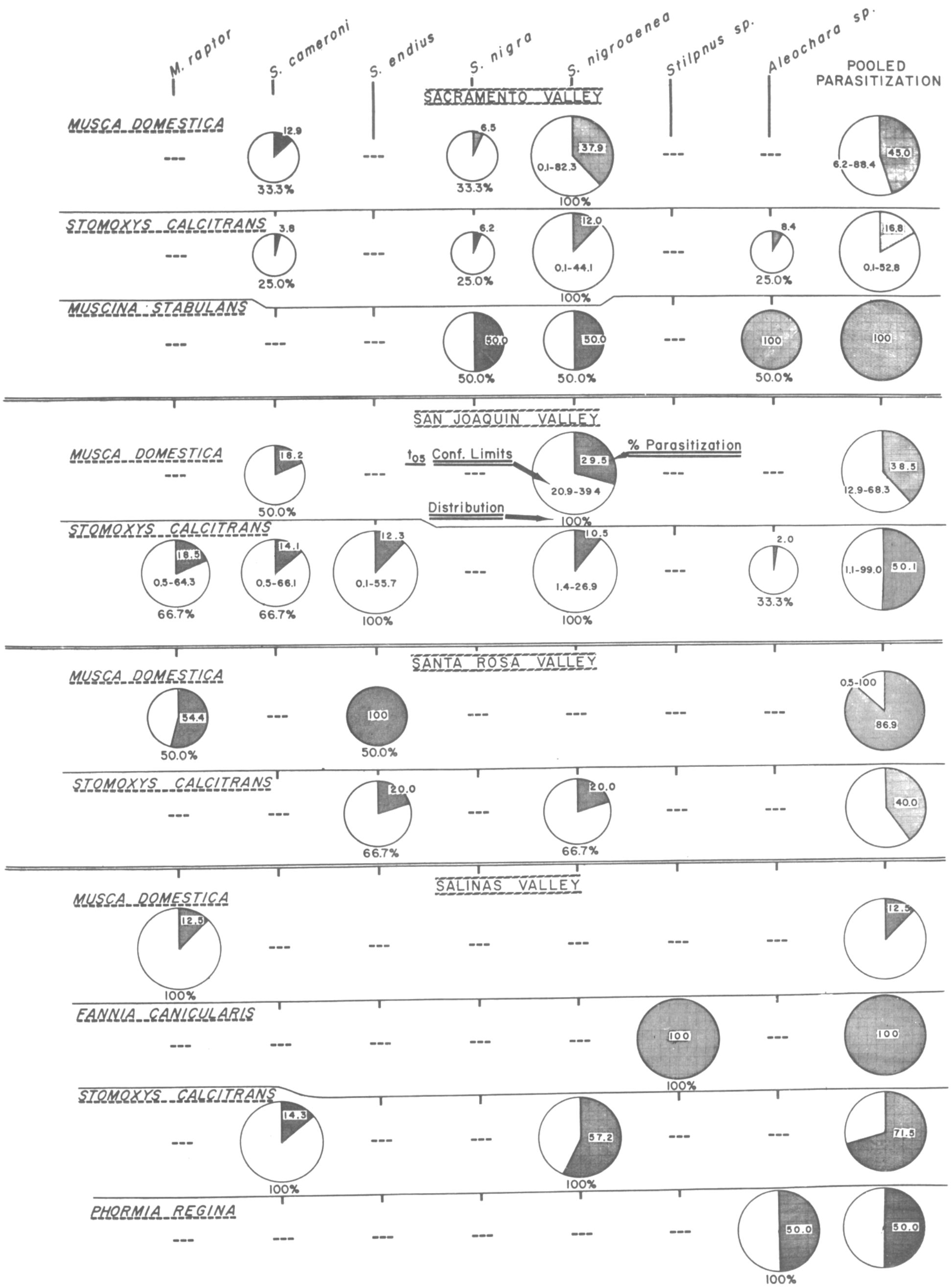

Fig. 9. Distribution of parasitoids of principal dipterous hosts in accumulations of bovine manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Central and northern California, 1967–1968.)

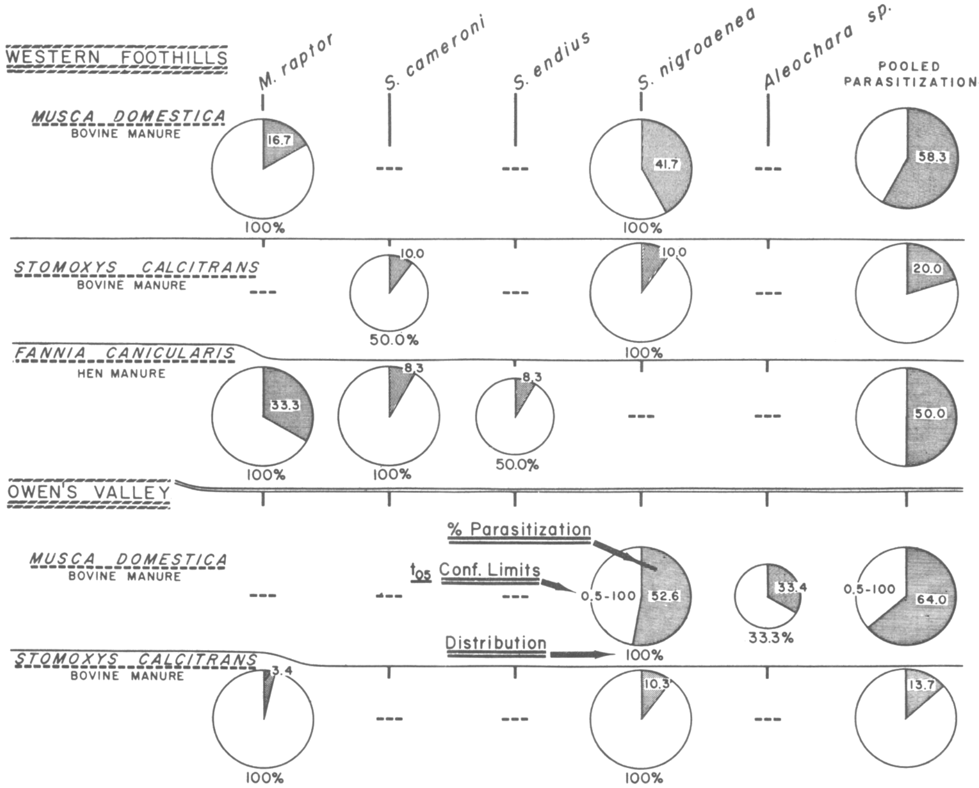

Fig. 10. Distribution of parasitoids of three principal dipterous hosts in accumulations of bovine and hen manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Western foothills of the Sierra and Owens Valley, 1967–1968.)

active in hen and horse manures on the Low Desert during summer (fig. 7). It was scarce or nonexistent during winter in all sample areas (figs. 6 to 8).

The fifth group of parasitoids, the Diapriidae, was highly inactive compared to the other species just discussed. Their occurrence and parasitization appeared to be more favored in winter of the Inland and High Desert areas. The greatest activity was demonstrated on *Fannia femoralis* in the Inland and High Desert areas (fig. 7).

Stilpnus anthomyidiperda, specific to *Fannia canicularis,* was the only ichneumonid parasitoid found in the southern California area on any fly species. Loomis *et al.* (1968) list a second species, *S. gagetes* Gravenhorst, which was not collected in the present study. *Stilpnus* was well distributed throughout the range of *Fannia canicularis,* in most cases occurring at all collection sites (figs. 6 to 8). It was also the predominantly active species on *F. canicularis,* and the only parasitoid reared from this host during the winter months (figs. 6 to 8). The per cent of parasitization by *Stilpnus* was high, usually surpassing 50 per cent.

Parasitization of key hosts in northern and central California

Summer collections of key host species in portions of California north of the Tehachapi Mountains, showed all southern California parasitoid species with the exception of the Diapriidae

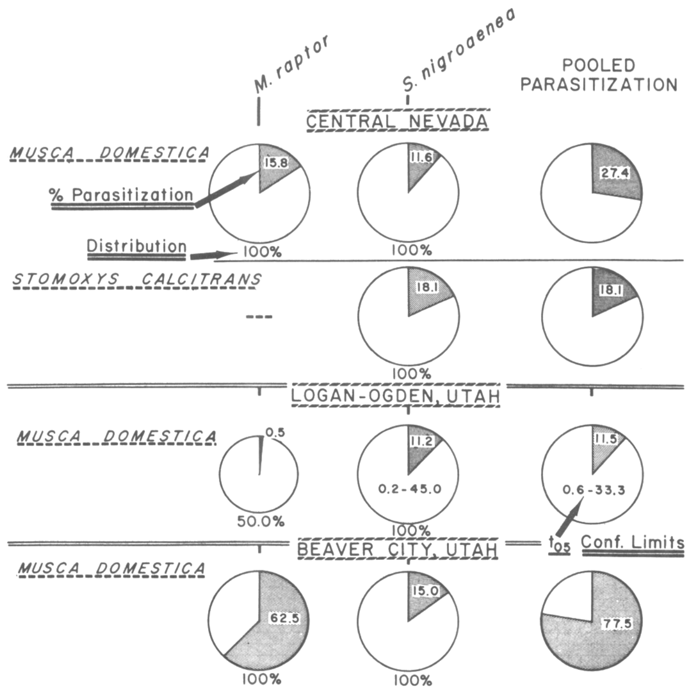

Fig. 11. Distribution of parasitoids of two principal dipterous hosts in accumulations of bovine manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Portions of the Great Basin (Upper Sonoran Desert), 1968.)

(figs. 9 and 10). Two additional species that appeared in the northern collections were the pteromalid *Spalangia nigra* Latreille and the staphylinid *Aleochara* sp. *Stilpnus anthomyidiperda* was again the only specific species encountered, attacking only *Fannia canicularis. Spalangia nigroaenea* was the only parasitoid found active on *Musca* and *Fannia* pupae in the Eureka area (not shown in figures).

Why a particular parasitoid species was absent from some hosts in the north is not known, although the missing species was often known to occur in the area on other hosts in the same habitat. One species, however, *Spalangia endius,* might be considered as more effective in the south, since it was not encountered in exposed bovine manure north of the San Joaquin Valley (fig. 9). Its existence in poultry manure in the north was also not established. *Spalangia nigra* in the present survey obviously was restricted to more northern latitudes (fig. 9). Parasitoid species were clearly scarce at the higher elevations and latitudes (figs. 9 and 10). Extensive sampling of *Musca* and *Stomoxys* pupae above 2,600 meters at horse and mule pack stations of the High Sierra during August and September of 1967 and 1968 did not reveal any parasitoids.

Parasitization of key hosts in portions of the Great Basin (Upper Sonoran) and Lower Sonoran deserts

Only two species of parasitoids, *Muscidifurax* (*M. raptor* and *M. zaraptor* were detected later) and *Spalangia nigroaenea* were present in samples from the Great Basin (fig. 11), although

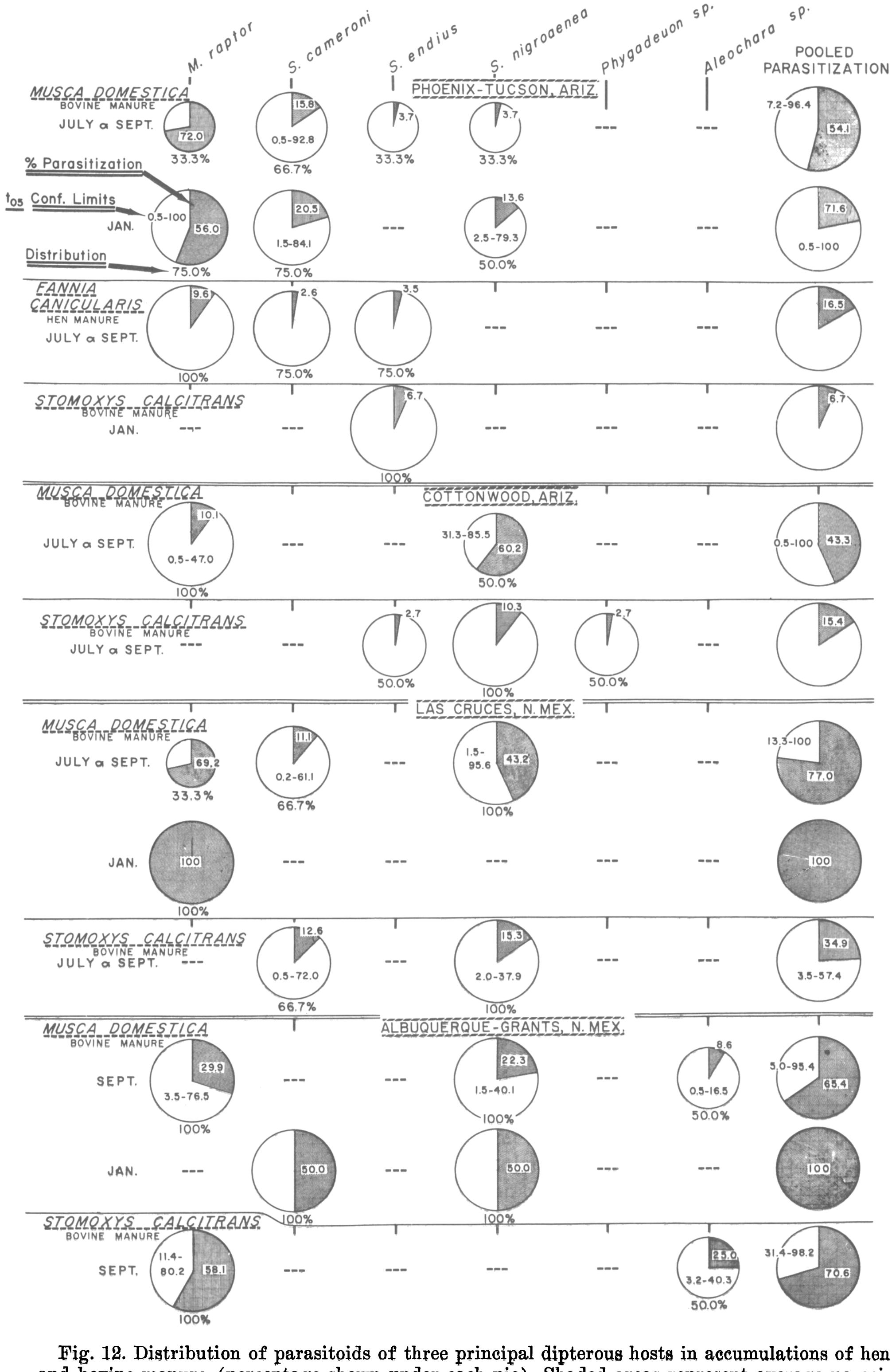

Fig. 12. Distribution of parasitoids of three principal dipterous hosts in accumulations of hen and bovine manure (percentage shown under each pie). Shaded areas represent average parasitization among sites of occurrence. (Portions of the Lowern Sonoran Desert, 1967–1968.)

Muscidifurax did not occur on *Stomoxys calcitrans.*

Figure 12 shows that as collections were made further south in warmer portions of the Sonoran Desert, additional species became evident, until all species that occurred in California, except the Diapriidae, were active. An additional ichneumonid, *Phygadeuon* sp., was also slightly active here.

It is noteworthy that some cases of 100 per cent parasitoid emergence were recorded from *Musca domestica* in the New Mexico area during winter, and that *Spalangia endius* was restricted wholly to the Arizona collections (fig. 12).

Seasonal distribution of parasitoids on hosts in hen manure

The seasonal distribution of dipterous pupae in hen manure and the per cent emergence and distribution of their parasitoids are shown in figures 13 to 22 for three coastal poultry ranches in southern California. The data are quantitative values for the slope of hen manure accumulations as described in "Methods." Figure 13 shows meteorological data for ranch I. Meterological conditions at ranch II—only 16 kilometers distant, and ranch III, 3 kilometers distant, on the same south coastal plain—were similar to those at ranch I.

Five principal host pupae on ranches I and II were, *Musca domestica, Fannia femoralis, F. canicularis, Ophyra leucostoma* and *Muscina stabulans.* Ranch III had all species present except *Fannia canicularis* and *Muscina.*

Fannia femoralis predominated on ranch I, the largest facility, which supported a maximum of 280,000 birds during the sample period. Its highest pupal densities were attained during the winter and spring months (fig. 14). *Fannia canicularis,* also an important species, did not attain as high a density during the second sample year as the first. Its numbers were characteristically highest during the months of spring (fig. 14). This species was building up in higher numbers in spring of 1967 just before sampling ceased. *Musca domestica* pupae appeared sporadically at low densities once in summer of 1964 and again in January of 1965 (fig. 14).

Parasitization of *Fannia femoralis* was highest during the warmer months of late spring, summer and autumn, often claiming over 90 per cent of the pupae collected. *Fannia canicularis* parasitization was characteristically highest following peaks of host abundance. The summer population of *Musca* sustained a very high parasitism, especially when compared to the complete absence of any parasitoid activity from this host in January (fig. 14).

The parasitoid species responsible for the per cent parasitization observed on these hosts at ranch I are shown in figure 15. *Muscidifurax* was most active on all hosts from early spring through the summer months, while *Spalangia endius* was active through most seasons, with predominance demonstrated in the autumn and winter months on *Fannia femoralis.* It was not found to attack *Musca. Spalangia cameroni* and *S. nigroaenea,* restricted to *Fannia* species, appeared infrequently during cooler seasons and were conspicuously absent during 1965.

Stilpnus anthomyidiperda, specific to *Fannia canicularis,* accounted for most of the observed parasitization of this host during the latter's population peaks (fig. 15).

Figure 16 shows that the two predators, *Ophyra leucostoma* and *Muscina stabulans,* occurred at comparatively lower densities than the other hosts, and that *Ophyra* sustained a significantly higher parasitization during the warmer months of its abundance, while *Muscina* did not yield any parasitoids. Figure 17 shows that the three parasitoid species attacking *Ophyra* were *Muscidifurax, Spalangia cameroni,* and *S. endius,* with the latter appearing

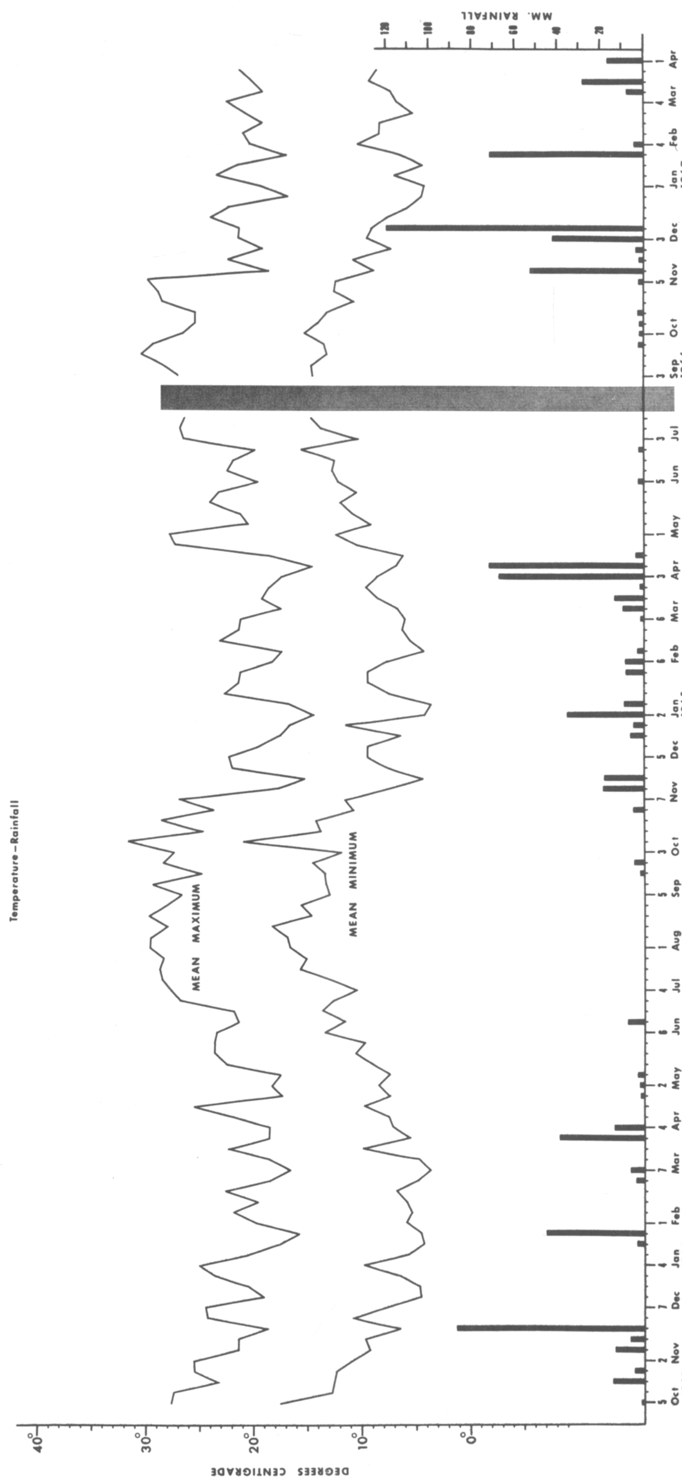

Fig. 13. Mean maximum and minimum temperatures and total rainfall near surface of accumulations of hen manure on Ranch I. (1963 to 1967.)

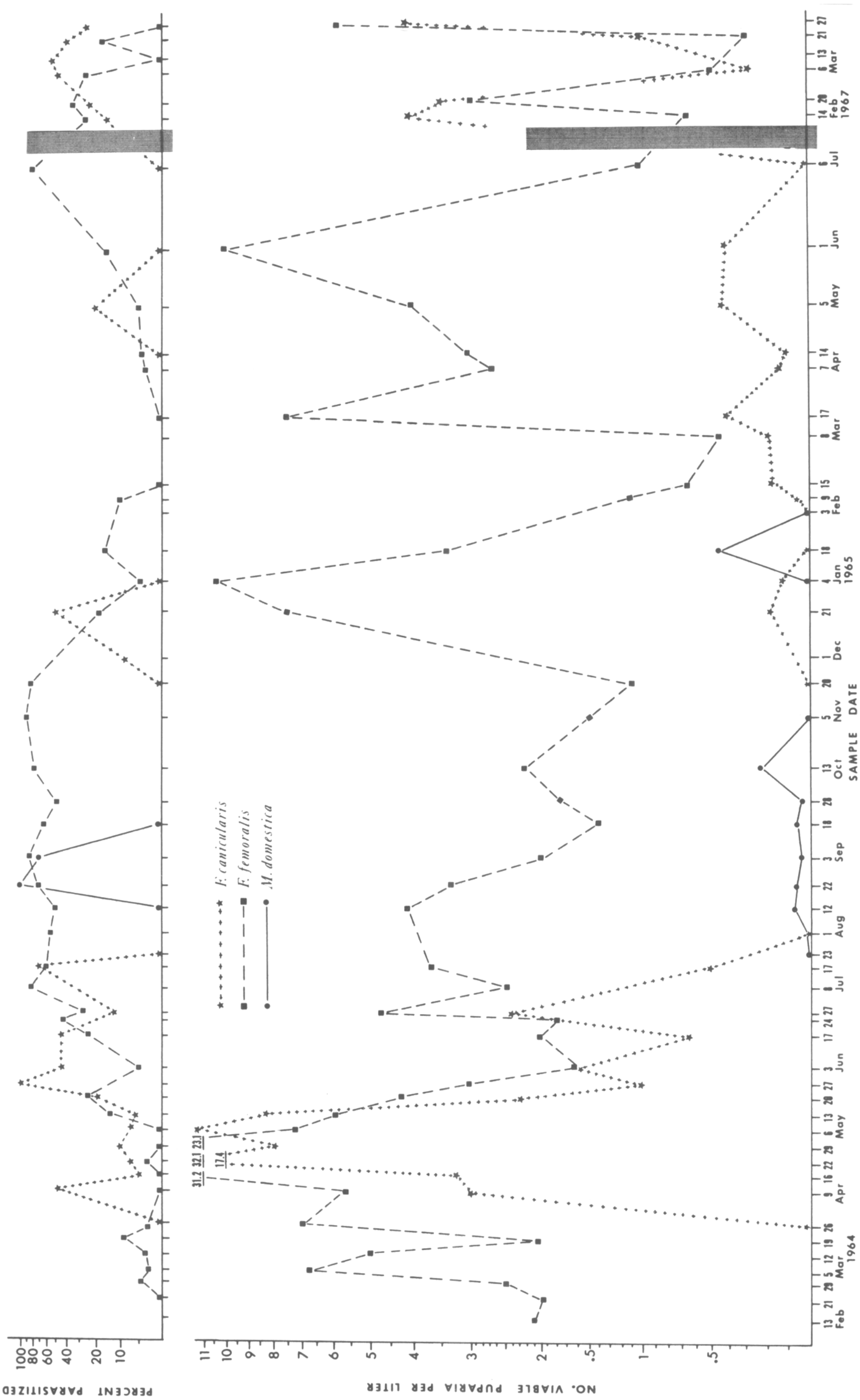

Fig. 14. Seasonal distribution and per cent parasitization of pupae of three principal noxious Diptera in accumulations of hen manure at Ranch I. (Southern California coast, 1964–1965, 1967.)

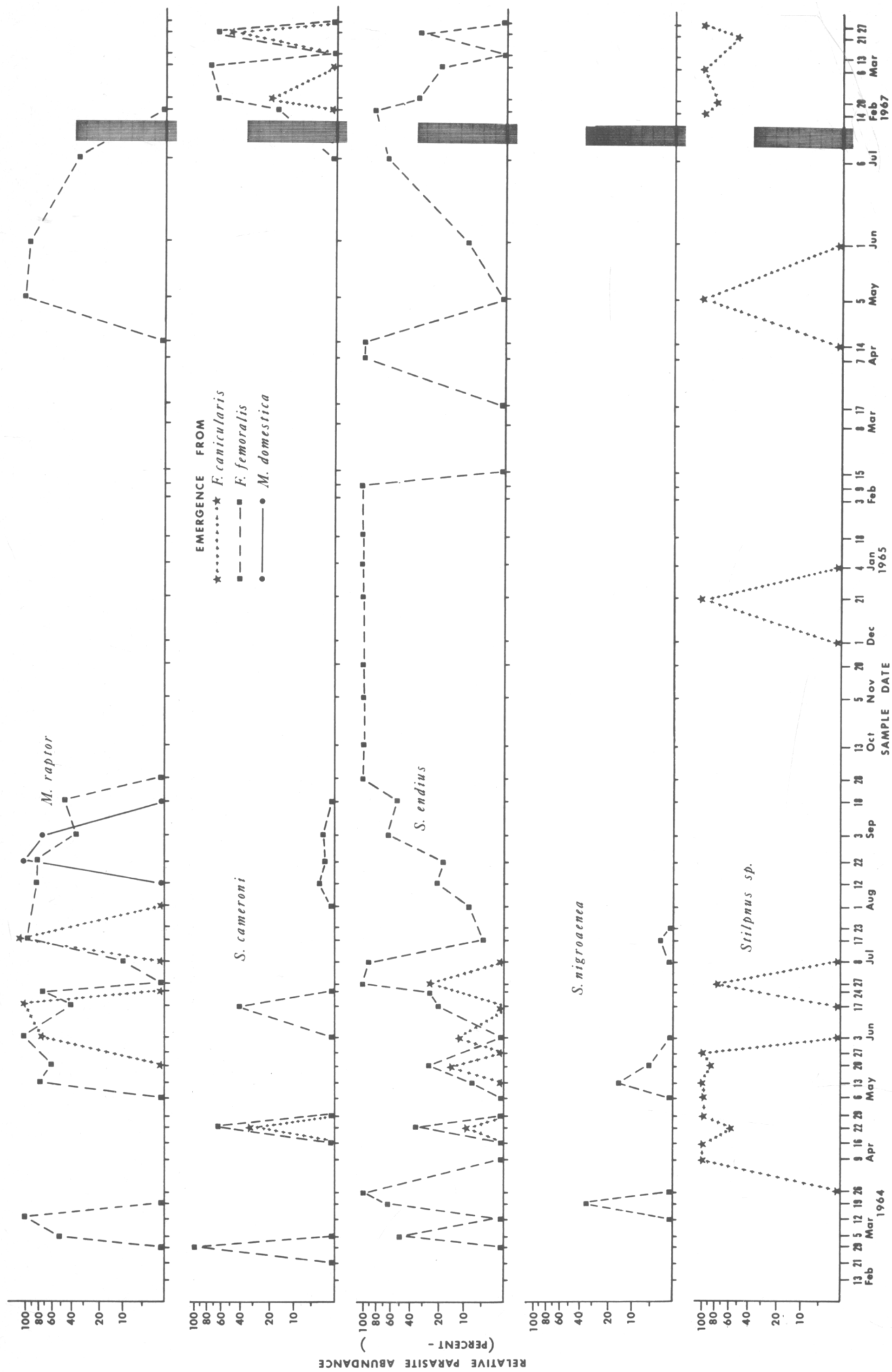

Fig. 15. Seasonal distribution of five parasitoids that emerged from dipterous hosts at Ranch I. (See also fig. 13.)

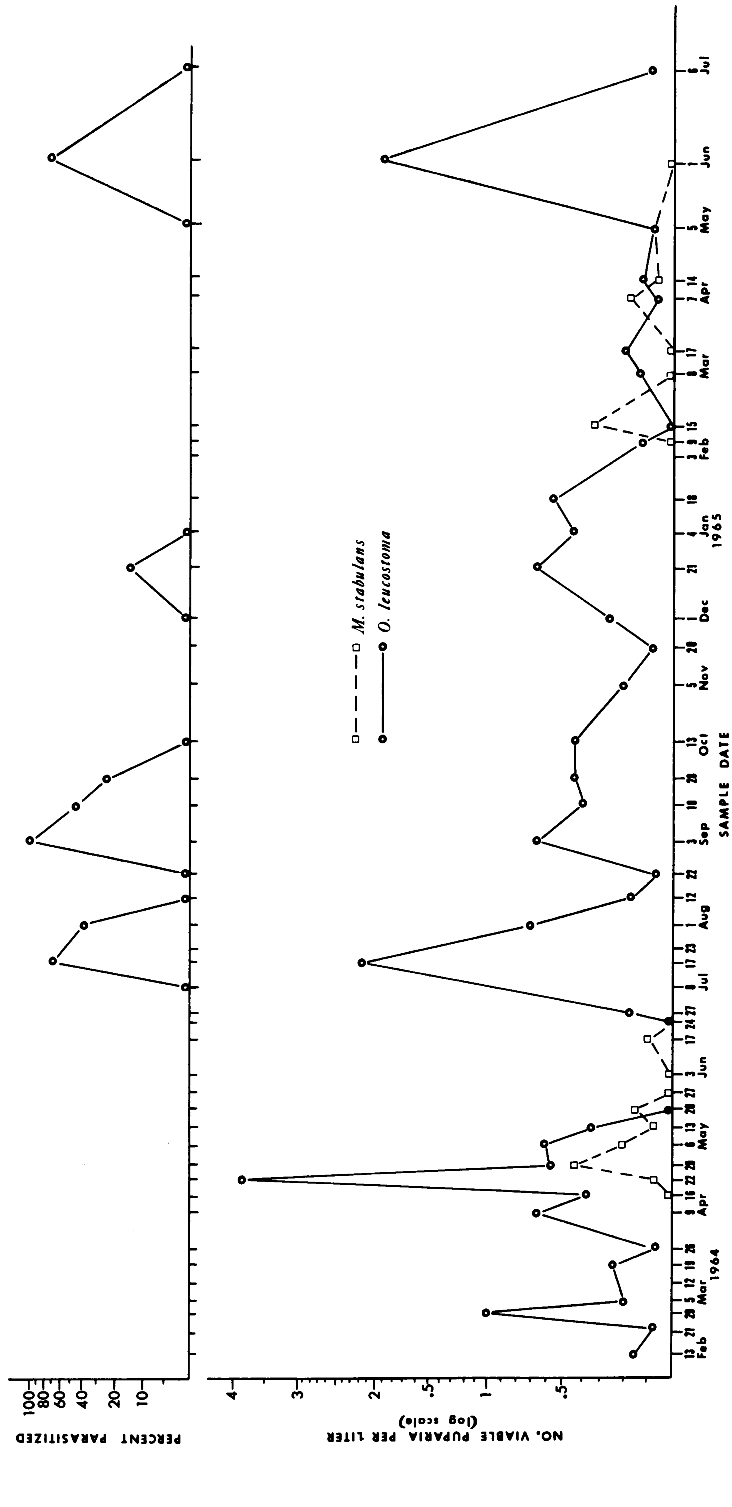

Fig. 16. Seasonal distribution and per cent parasitization of pupae of two predatory Diptera in hen manure at Ranch I. (1964–1965.)

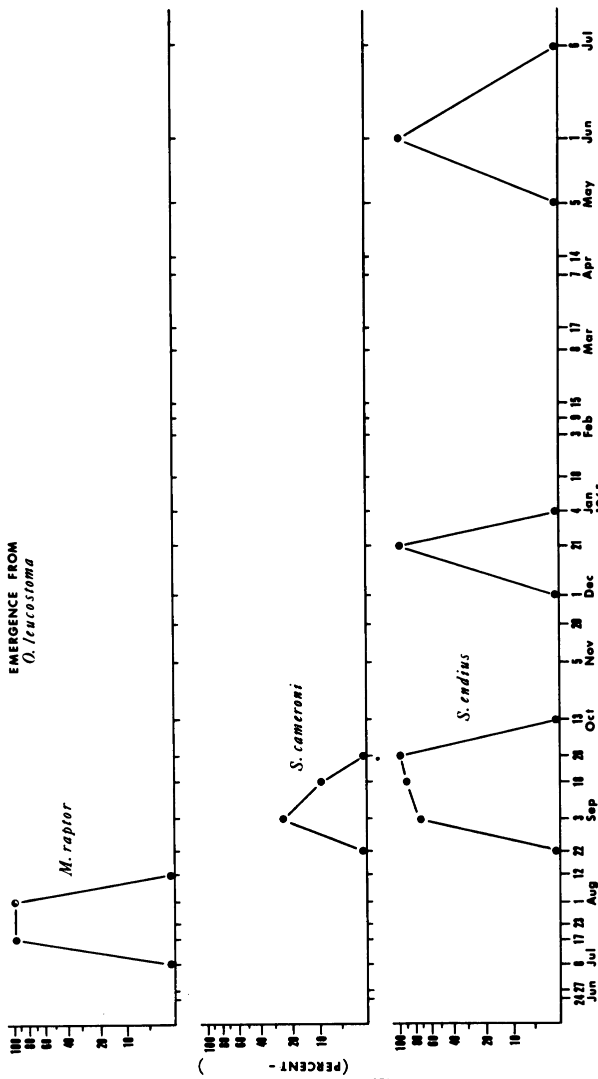

Fig. 17. Seasonal distribution of parasitoids that emerged from pupae of predatory Diptera at Ranch I. (See also fig. 15.)

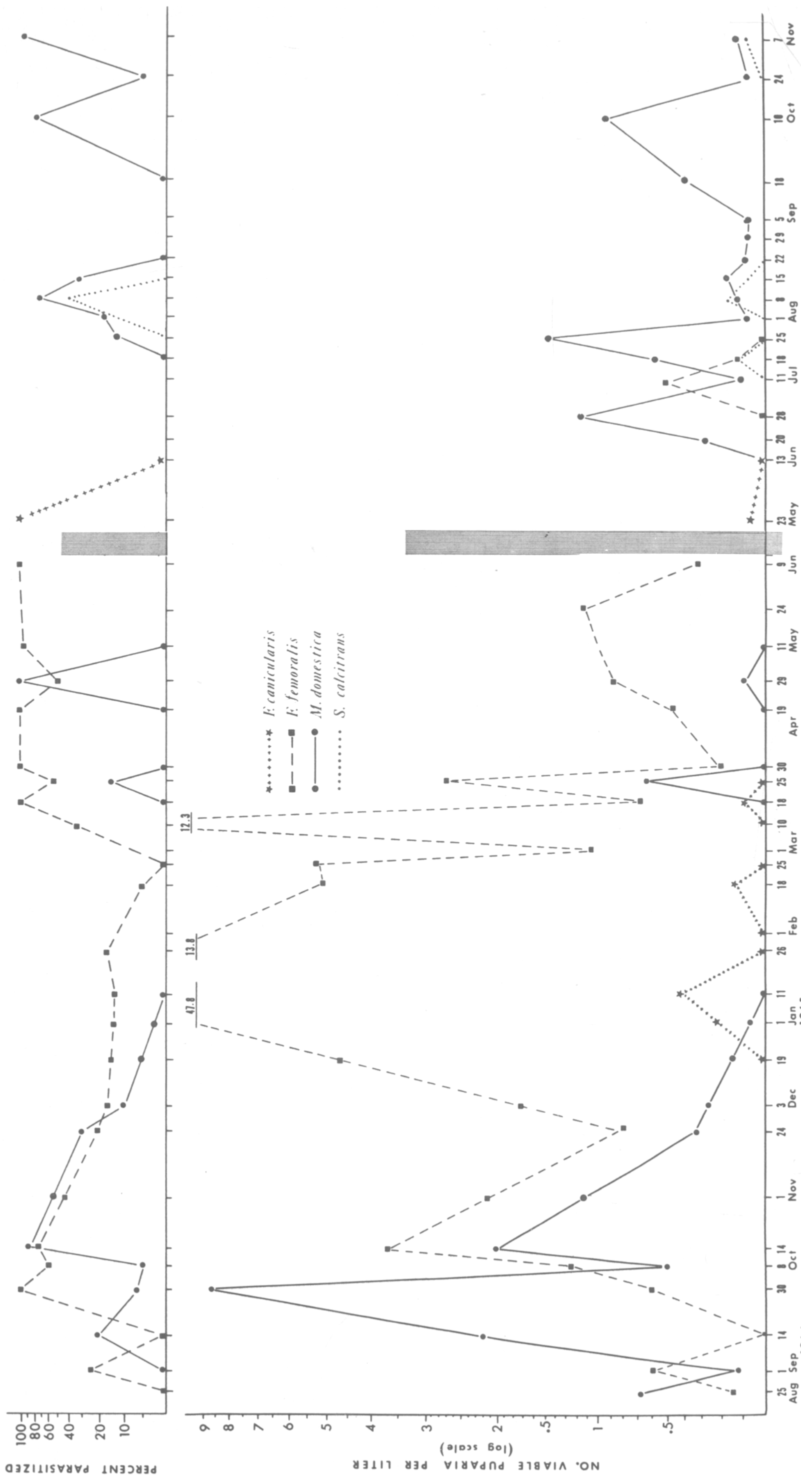

Fig. 18. Seasonal distribution and per cent parasitization of pupae of four principal noxious Diptera in hen manure at Ranch II. (1964–1965, 1968.)

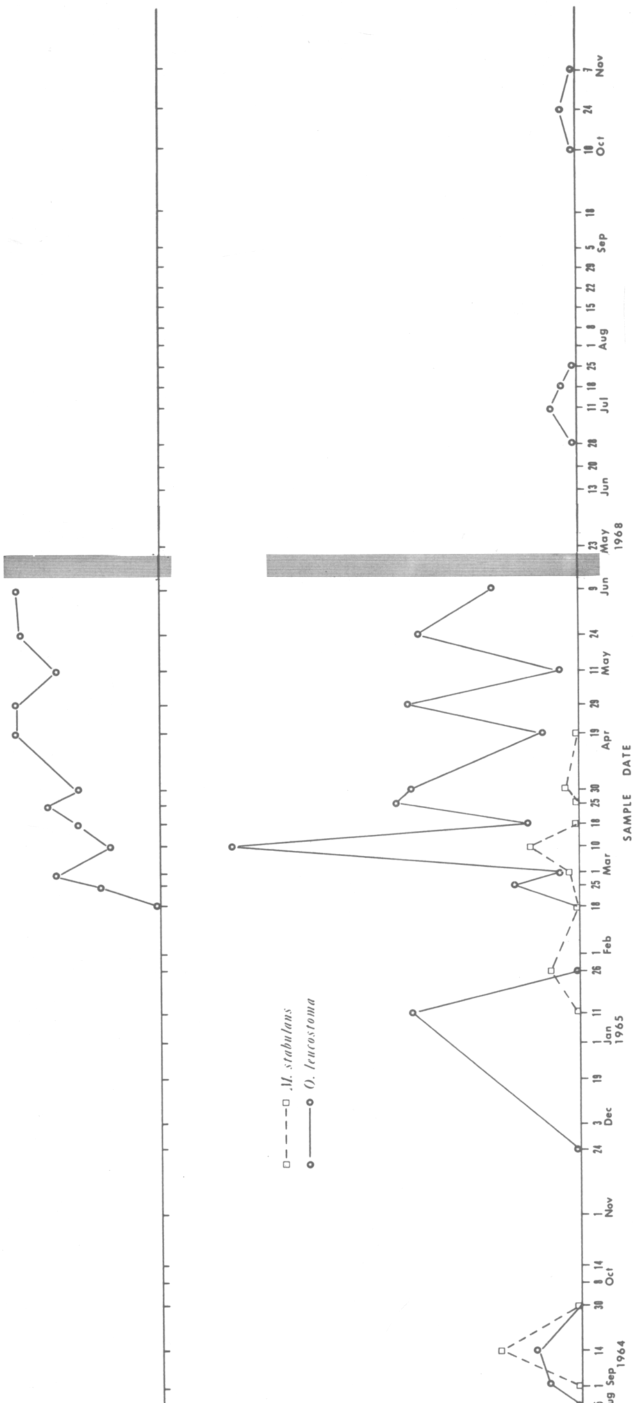

Fig. 19. Seasonal distribution and per cent parasitization of pupae of two predatory Diptera in hen manure at Ranch II. (1964–1965, 1968.)

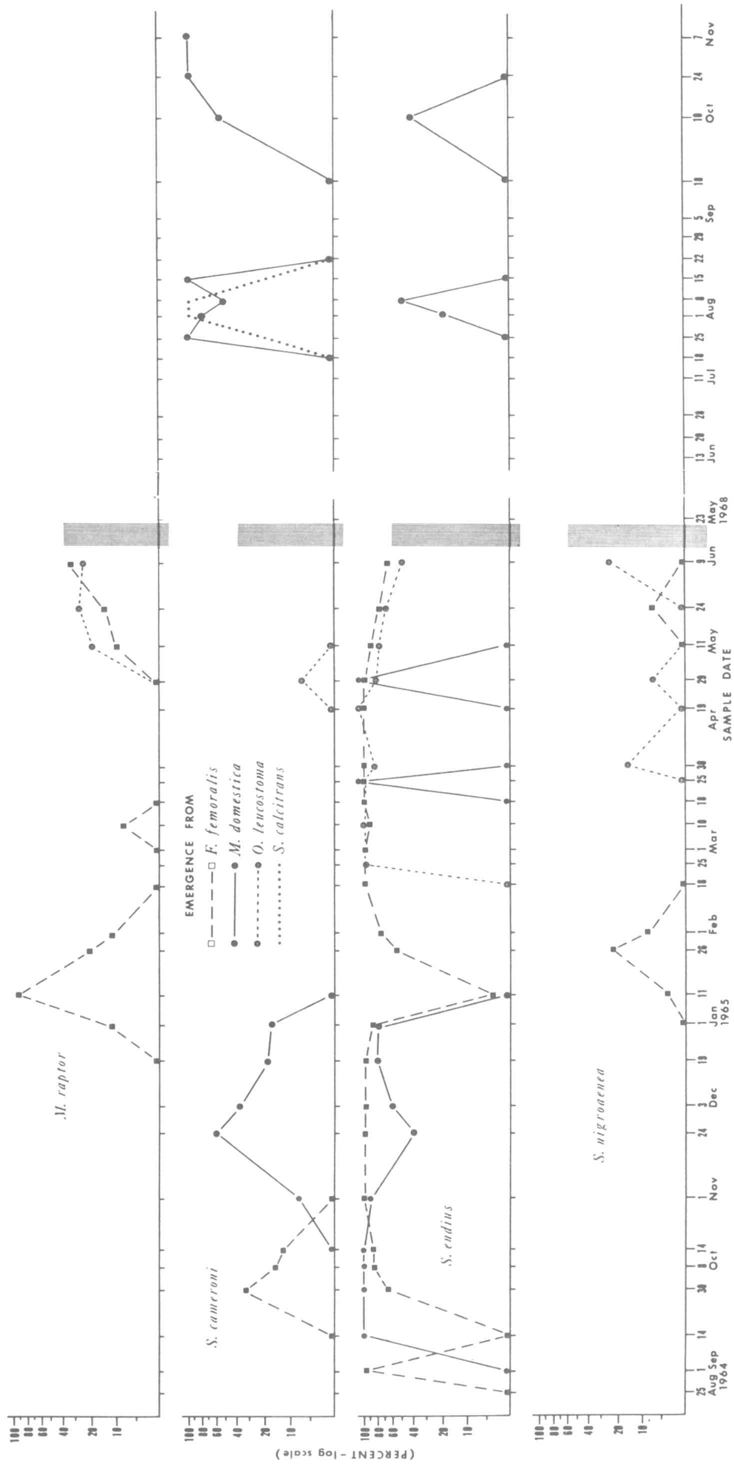

Fig. 20. Seasonal distribution of parasitoids that emerged from all dipterous pupae in manure accumulations at Ranch II. (See also figs. 18 and 19.)

over the entire sample period; the first two species were recovered from *Ophyra* only during the first sample year.

Ranch II, a smaller facility supporting a maximum of 50,000 birds during the sample interval, had a distribution of *Fannia femoralis* similar to that observed on ranch I on common dates (figs. 14 and 18). By 1968, however, *F. femoralis* had diminished to a comparatively low density (fig. 18). Parasitization of this host was also most pronounced during the spring to autumn of the early sample period, but was absent altogether in 1968 (fig. 18). The density of *Fannia canicularis* on ranch II was even lower than on ranch I, although it was present during similar seasons (figs. 14 and 18). Parasitization of this species was, however, absent in 1964–1965, and slight in 1968 (fig. 18). In contrast to the first ranch, *Musca domestica* occurred at a high density on ranch II, and sustained a high parasitization during the autumn months of 1964 (fig. 18). By 1968, five years after the study began, its average density was considerably diminished with the coincidental regulation of manure removal and subsequent cessation of manure treatment with chemicals.

Figure 19 shows the seasonal distribution of the dipterous predators, *Muscina stabulans* and *Ophyra leucostoma* on ranch II. *Ophyra* was more widely distributed throughout the year than *Muscina,* and its peaks of abundance coincided with those observed on ranch I (figs. 16 and 19). By 1968, only *Ophyra* remained on the ranch at extremely low densities. Parasitization was observed during later winter and spring months on *Ophyra* only (fig. 19). *Muscina* was found to occur at very low densities in late summer and during the winter and early spring (fig. 19), and was not parasitized. The failure to detect parasitism of this species might have been due to sampling error at this low density.

Parasitoid species responsible for the parasitization on Ranch II are shown in fig. 20. *Muscidifurax* and *Spalangia nigroaenea* emerged only from *Fannia femoralis* and *Ophyra* during the winter and spring months; *Spalangia cameroni* and *S. endius* were found on most parasitized hosts during all seasons, with the latter predominating (fig. 20). Neither *Muscidifurax* nor *S. nigroaenea* were present in the 1968 samples.

Ranch III was the smallest experimental site in the present study, supporting only a maximum of 2,000 birds. *Musca domestica* was the most abundant host species found during a comparatively short sample period (fig. 21). The presence of *Musca* on this ranch in late summer and autumn coincided largely with that observed on

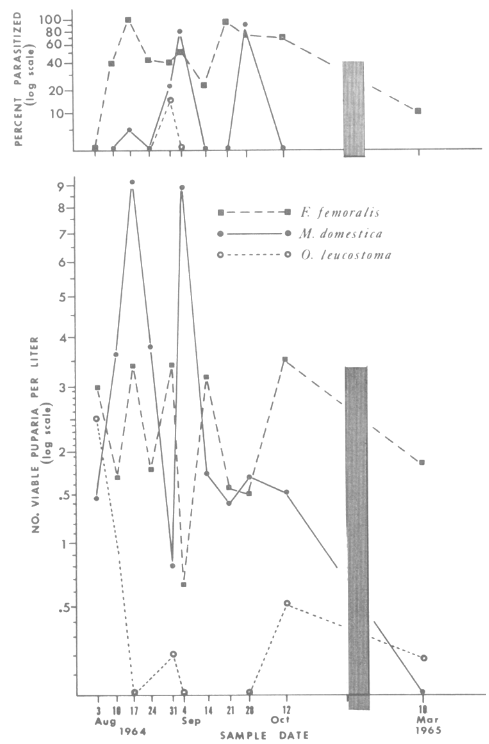

Fig. 21. Seasonal distribution and per cent parasitization of pupae of three principal Diptera in accumulations of hen manure at Ranch III. (1964–1965.)

Ranch II (figs. 18 and 21). The parasitization curves for *Musca* are also similar on both ranches. *Fannia femoralis* and *Ophyra leucostoma* were also present on ranch II at lower densities (fig. 21), with a high degree of parasitization observed on *Fannia.*

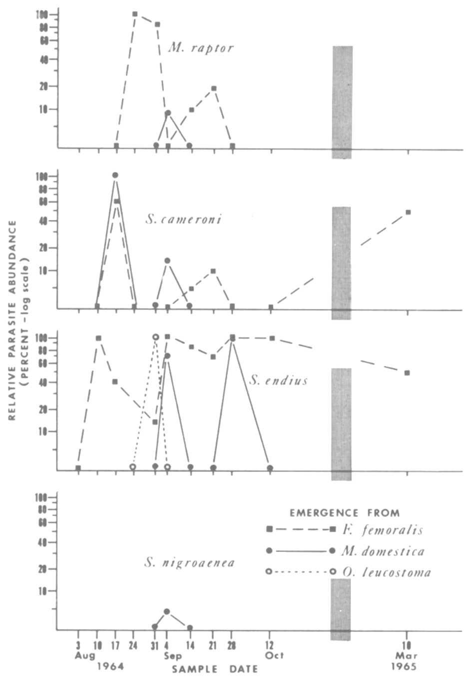

Fig. 22. Seasonal distribution of parasitoids that emerged from dipterous pupae in hen manure accumulations at Ranch III. (1964–1965.)

All principal parasitoids were present on ranch III (fig. 22). However, *Muscidifurax* was confined to the late summer as was the case on ranch I (figs. 14 and 22). *Spalangia cameroni* and *S. endius* predominated during the entire sample period, as they did on ranch II (figs. 20 and 22), while *S. nigroaenea* was extremely rare.

Results of reciprocal crosses

Cultures of parasitoid species were secured from all portions of the southwestern United States, and reciprocal crosses were performed with the same species occurring in southern California. The only reproductive isolation found was interspecific, and it was complete. Experimental crosses performed coincidentally between strains secured in other parts of the world (Legner and Greathead, 1968), in fact, showed no reproductive isolation between any strains. Further tests are being conducted to detect heterosis resulting from such crosses.

This worldwide intercompatibility among species might be explained by (1) recent colonization, (2) slow rate of evolution, and (3) panmictic population. We favor panmictic population, especially in light of the discontinuous morphological variation apparent in most species.

CONCLUSIONS

Populations of the parasitoid species attacking dipterous hosts in accumulations of domestic animal manure in the southwestern United States may be divided into three major geographical groups, (1) those widespread in areas below 2,000 meters, (2) those restricted to the warmer climatic areas and (3) those restricted to higher latitudes and colder winter climates.

The first group contains the two species of *Muscidifurax* and *Spalangia nigroaenea.* Group II contains *Spalangia endius* and *S. cameroni;* and Group III, *Spalangia nigra* and *Aleochara* species.

It is not known if one of the restricting factors in species distribution is a direct or an indirect effect of climate on manure composition. Also, within each parasitoid and host population, considerable yearly variation occurs in the abundance of "demes" (Mayr, 1965; Wright, 1955), as evidenced by seasonal studies of hen manure. Parasitoid demes also vary in abundance according to the availability of hosts at any particular site. Therefore, since most host-breeding sites are in themselves very unstable, differing in composition as animal diets differ, as breed and age of animals change, and as weather conditions vary, so instability occurs among parasitoid demes. Some cease to exist where they were large in a previous year. Others appear where they had not existed before. Much of this appearance and disappearance may be due to migration—an important element in the panmictic nature of most populations.

Some parasitoids, such as the Diapriidae and the Staphylinidae, appear to be local species that have adapted to some of the dipterous pupae. Species in these groups change among localities and probably consist of small demes.

Fannia canicularis is presently Holarctic in distribution, but most certainly did not originate in the southwestern United States (Chillcott, 1961; Legner and McCoy, 1967). Either *Stilpnus* followed its host out of another portion of the Nearctic or Palearctic, or it became adapted to *F. canicularis* from some related native *Fannia* species. Yet *F. femoralis,* an apparent invasion from South America (Legner, 1966), has not acquired any similar specific parasitoid. Evidence appears to favor the theory of invasion of both host and parasitoid into the Southwest.

The obvious function of parasitoid species as irreplaceable mortality factors (in the sense of Thompson, 1929) in the populations of their dipterous hosts, indicates their value as natural control agents. Consideration of their presence is indispensible if their dipterous hosts are to be deliberately reduced.

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