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Author(s): Ivan Valiela

Source: *American Midland Naturalist*, Vol. 92, No. 2 (Oct., 1974), pp. 370-385

Published by: [The University of Notre Dame](#)

Stable URL: <http://www.jstor.org/stable/2424302>

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Composition, Food Webs and Population Limitation in Dung Arthropod Communities During Invasion and Succession

IVAN VALIELA

*Boston University Marine Program, Marine Biological Laboratory,
Woods Hole, Mass. 02543*

ABSTRACT: Arthropod species invade fresh dung in an orderly pattern and the number of taxa and the complexity of the food web increase as succession takes place. Short-term, local changes in the environment during early succession seem to have a more pervasive effect on species abundance than seasonal changes.

The interactions between burrowing and predatory beetles, and large and small diptera larvae are the core of the food webs in dung succession. Burrowing beetles arrive early and remain throughout succession. Their tunnels riddle the dung and are used by the air-breathing fly larvae to reach the interior of the dropping. Predatory beetles lack adaptations for burrowing but may use burrows already excavated to reach the otherwise unavailable fly larvae. The presence of burrowers, therefore, facilitates predation. The predators involved can feed only on small prey 0.5-6.0 mm long. The larvae of larger flies found early in dung succession are able quickly to outgrow this size range, and escape predation. There is a second group of small fly larvae that then enters this size range and remains exposed to predation for the duration of succession.

Competition for dung is not likely to be a major limitation for dung feeder populations since excess dung seems available. Similarly, estimates of prey needed by predators are smaller than the standing crops of prey available. Predation does not appear to be limiting to prey populations. Similarly, predators themselves are unlikely to be prey-limited. Local, short-term changes in dung and in the immediate environment may be too fast and too erratic to permit fuller use of dung as a resource.

The frequent occurrence of introduced species in dung composition may be related to the lack of competition and predation pressure in dung-inhabiting arthropods. The initial stages of dung succession, as in most other new environments, are largely determined by factors other than competition and predation.

INTRODUCTION

Successional changes in animal communities have been studied for a relatively long time (Odum, 1971). However, there are few studies in which the changes in species composition, as well as the changes in structure of food webs, were followed. Prominent among these are studies on the fauna of ruminant feces.

There has been sustained interest in the invertebrate faunas associated with bovine manure, and several substantial studies have dealt with successional changes in invertebrate communities of dung (Hafez, 1939; Mohr, 1943; Snowball, 1944; Laurence, 1956). The discrete nature of dung droppings, as well as the relative simplicity of the fauna, makes this system amenable to replication and relatively easy to study. The purpose of this paper is to document quantitative and qualitative

changes in species composition and in the structure of food webs during succession in domestic cow droppings and to determine whether food supply or predation could limit populations of dung invertebrates.

METHODS

The methods used are described in detail in Valiela (1969a). A summary is included here. All experiments were conducted within a pasture on a dairy farm near Ithaca, New York.

Manure was collected in a barn while the cattle were being milked. The dung from four or five cows was mixed to decrease heterogeneity. The dung was then taken to the pasture and standard amounts put into 3-cm-high cardboard hoops of about 20-cm diam. A round piece of plastic netting under the hoop prevented the escape of the manure from under the cardboard.

Sixteen of these standard samples were prepared at each of nine trials. Each trial consisted of setting out the 16 samples about 30 cm apart in a square 4 x 4 pattern. Four replicate samples were then collected at intervals of about 1, 2, 3 and 5 days. Preliminary samples showed that after 5 days the animal assemblage found in manure began to contain arthropods belonging to the soil and vegetation fauna. Sampling was therefore limited to time intervals which would show mainly dung arthropods.

The standard droppings were quite similar to natural droppings in regard to temperature, moisture content and fauna (Valiela, 1968).

The samples were placed in plastic bags and taken immediately to the laboratory, where the invertebrates were extracted in Tullgren funnels provided with 200-w lamps. The specimens were preserved in a solution of $\frac{1}{4}$ acetic acid and $\frac{3}{4}$ 75% ethyl alcohol with 5% glycerine. The samples were searched after the end of the extraction period and generally few invertebrates were found. The smaller larvae of diptera, however, were not fully extracted. A regression of per cent efficiency of extraction vs. length of fly larvae was therefore calculated (Valiela, 1969a) and applied as a correction to the extraction data.

Throughout the 4 years of this study, observations were made of food habits. In addition, a number of feeding trials were performed in which potential prey was offered to potential predators. These trials were carried out in petri dishes or other suitable glass containers containing blotting paper soaked with manure fluids.

Mean dry weights were obtained for all the species. In the case of fly and beetle larvae, where substantial growth took place during the 5-day period of study, length-weight regressions were obtained. These data were used to obtain estimates of dry weight standing crops for each of the species.

A list of the species of arthropods found in the samples with information on their natural history has been published (Valiela, 1969b). The number of species involved made it awkward to deal here with individual species. Plots of the number of species occurring in 1, 2, 3, . . . n samples were prepared (Hairston and Byers, 1954) to identify

the relative numerical importance of the species and eliminate those numerically unimportant. These curves are found in Appendix 2 in Valiela (1969a). From these graphs a large group of species which were found in fewer than six samples could be identified. Since this group of species consisted of rare members of the dung community plus accidentals from other habitats, these species were not considered further. The remaining species are listed in Table 1.

To further simplify the presentation of the data the species of Table 1 were grouped into trophic "guilds" (Root, 1967), groups of species which feed on more or less similar foods with more or less similar feeding behavior. Both taxonomic and feeding criteria were used to define the groups or "guilds," but the main source of information used was the results of the food habit studies shown in Appendix 3 in Valiela (1969a) plus laboratory and field observations. Nevertheless, the groups chosen are still somewhat arbitrary. All predators found in dung are capable of feeding on dung itself. The "small staphylinid predator" category includes *Oxytelus*, considered a predator in the literature (Mohr, 1943) but not observed to feed on prey during the present study. Larvae of *Sargus cuprarius* were placed in the "miscellaneous" group rather than in "small dipteran dung feeders," because *S. cuprarius* larvae, with their very thick calcareous cuticle, are not fed upon by any predators and thus differ from all other small-fly larvae. The term "dung feeder" itself is vague since fly larvae apparently feed on the microorganisms growing on organic matter rather than on the organic matter itself (Baumberger, 1919; Muirhead Thompson, 1937; Dowding, 1967). Larvae of *Sphaeridium* were classified as "larval hydrophilid predators," on the basis of morphology of mouthparts and unpublished reports. However, feeding was not observed in these larvae and it was not possible to evaluate their role in the community.

Table 2 shows the duration of the sampling intervals for the various trials throughout the summer season. Samples were usually set out in the pasture by 0900-1000 hr. Although an effort was made to sample at similar times, it was not always possible to do so. The samples in Trial 7, for example, were set out in the pasture later in the morning than in the other trials. It appeared that in that instance colonization took place without any hindrance even though the period of exposure was shorter than usual. The variation in the mean times of exposure for the four intervals was relatively small (Table 2).

Estimates of biomass were obtained by applying the dry weight estimates and length-weight regressions (Table 1) to the census data from the samples. The data on the biomass of each trophic group through the 5 days of succession for each of the nine trials were subjected to two-way analyses of variance and the results are summarized in Table 3.

RESULTS AND DISCUSSION

Sequence of species and trophic groups in succession.—Figure 1 shows the mean standing crops of the various trophic groups and prin-

TABLE 1.—Invertebrate taxa found in more than six samples. The specialists who did the determinations are acknowledged in Table 1 in Valiela (1969a). The identifications are for larvae unless indicated otherwise. The species are classified into the following groups: large burrowers (LB); small burrowers (SM); large staphylinid predators (LP); small staphylinid predators (SP); larval hydrophilid predators (HP); large dipteran dung-feeders (LD); small dipteran dung-feeders (SD); parasitic hymenoptera (PH); predatory mites (PM); and a miscellaneous (MS) category including all other forms. For the adult forms the average total length and weight are included. For the larval forms which grew during the period of study the range in size is included as well as the regression equation which was used in predicting weight (W) from measured lengths (L.)

	Length (mm)	Weight (mm)	Trophic group
SCARABAEIDAE			
<i>Aphodius haemorrhoidalis</i> (L.)	5.1	3.28	LB
<i>A. erraticus</i> (L.)	8.5	13.07	LB
<i>A. fimetarius</i> (L.)	8.0	7.27	LB
<i>A. stercorosus</i> Melsh.	5.5	2.10	LB
<i>A. prodromus</i> (Brahm)	3.0	1.97	LB
<i>A. fossor</i> (L.)	11.8	33.00	LB
<i>A. larvae</i>	2.0	0.21	LB
STAPHYLINIDAE			
<i>Philonthus cruentatus</i> Gmelin	9.7	2.29	LP
<i>Aleochara bipustulata</i> (L.)	10.2	2.57	LP
<i>Hyponigrus obsidianus</i> Melsh.	8.9	1.14	LP
<i>Platystethus americanus</i> Erichson	4.0	0.21	SP
<i>Aleochara</i> sp.	5.7	0.82	SP
<i>Atheta sordida</i> Marsh	4.3	0.36	SP
<i>Atheta</i> sp.	2.5	0.23	SP
<i>Oxytelus tetracarminatus</i> Block.	2.5	0.11	SP
<i>Falagria dissecta</i> Erichson	2.8	0.21	SP
<i>Oxytelus larvae</i>	2.0	0.14	SP

TABLE 1.—(continued)

	Length (mm)	Weight (mm)	Trophic group
SEPSIDAE			
<i>Saltella sphondylii</i> (Schränk)	3.0-8.5	$\log W = 3.975 + 0.065 (L - 7.328)$	SD
<i>Sepsis neocynipsea</i> Melandier and Spuler	4.0-7.0	$\log W = 0.538 + 0.357 (L - 5.268)$	SD
<i>S.</i> sp. B	2.0-5.7	$\log W = 0.054 + 0.727 (L - 3.394)$	SD
Sepsid adult	5.0	0.55	MS
SPHAEROCERIDAE			
<i>Leptocera</i> sp. adult	2.0	0.10	MS
<i>Leptocera</i> larvae	2.0	0.12	SD
STRATIOMYIDAE			
<i>Sargus cuparius</i> (L.)	0.48	MS
PSYCHODIDAE			
<i>Psychoda</i> sp.	0.09	SD
Diptera B66	0.03	SD
Diptera C66	0.12	SD
CYNIPIDAE			
<i>Cothonaspis</i> sp. adults	0.22	PH
PTILIIDAE			
<i>Acrotrichis</i> sp. (n. sericans)	0.8	0.022	MS
HYDROPHILIDAE			
<i>Sphaeridium scarabaeoides</i> (L.)	8.3	7.16	LB
<i>S. bipostulatum</i> Fabricius	6.5	4.27	LB
<i>S. lunatum</i> Fabricius	8.3	7.16	LB
<i>S. bipostulatum</i> larvae	2.5-8.2	$\log W = 0.829 + 3.304 (L - 5.639)$	HP
<i>S. scarabaeoides</i> larvae	2.5-7.7	$\log W = 0.251 + 2.564 (L - 3.855)$	HP

TABLE 1.—(continued)

	Length (mm)	Weight (mm)	Trophic group
<i>Cercyon</i> sp. A	1.9	0.197	SB
<i>C.</i> sp. B	3.0	1.067	SB
<i>C.</i> sp. C	2.0	0.181	SB
<i>C.</i> sp. F	3.3	0.553	SB
Hydrophilid A65 (<i>Cercyon</i> ?)	3.5	0.488	SB
<i>Cercyon</i> larvae	2.0	0.135	MS
MUSCIDAE			
<i>Musca autumnalis</i> De Geer	3.6-13.9	$\log W = 9.012 + 0.673(L - 1.297)$	LD
SARCOPHAGIDAE			
<i>Sarcophaga</i> sp. A.	4.5-18.6	$\log W = 1.795 + 1.995(L - 15.263)$	LD
<i>Ravinia pherminieri</i> (Desvoidy)	4.3-12.1	$\log W = 1.334 + 0.137(L - 8.614)$	LD
FORMICIDAE			
<i>Lasius flavus</i> adults	0.27	MS
PODURIDAE			
<i>Hypogastrura glasgowi</i> (Folsom)	0.032	MS
MAGROCHELIDAE			
<i>Macrocheles</i> sp.	0.070	PM
PARASITIDAE			
<i>Parasitus</i> sp.	0.049	PM
UROPODIDAE			
Uropodid sp.	0.010	PM
ACARIDAE			
Acarid sp.	0.008	PM
Unidentified mites	0.008	?

cial species for the 5-day periods during which succession took place, averaging over all the trials. The standard errors of these averages show the variation which could be found through the summer season.

The large burrowers are composed mainly of *Aphodius*, with *Sphaeridium* present in the first days but nearly disappearing by the 5th day. Burrowing beetles as a whole are present very early and do not significantly change density through the 5 days in question, since the "time" mean square for large burrowers is not significant in Table 3. The considerable size of the standard errors is due substantially to a trial-to-trial variation (Fig. 1) rather than to broad seasonal changes. This accounts for the significant mean squares for "trials" and interaction in Table 3. This reflects the fact that short-term, localized but undefined conditions occurring during succession can greatly affect the course of events in these small communities, particularly if such environmental changes occur in the initial few hours.

TABLE 2.—Duration of the sampling intervals (hours:minutes) and dates for the various trials during the summer of 1966

	Trial 1 (27 May- 1 June)	Trial 2 (2 June- 8 June)	Trial 3 (13 June- 19 June)	Trial 4 (27 June- 1 July)	Trial 5 (7 July- 12 July)
T ₁	25:30	25:30	24:00	29:00	21:15
T ₂	51:00	50:00	51:00	48:00	42:20
T ₃	77:00	80:00	97:00	72:00	60:20
T ₄	127:00	145:30	150:00	124:30	110:30
	Trial 6 (21 July- 25 July)	Trial 7 (2 Aug.- 12 Aug.)	Trial 8 (7 Aug.- 12 Aug.)	Trial 9 (6 Sept.- 12 Sept.)	Mean \pm s.e.
T ₁	22:30	7:10	26:30	25:25	22:59 \pm 2:07
T ₂	46:30	35:50	50:00	49:30	47:08 \pm 1:41
T ₃	70:20	62:05	75:15	73:00	74:07 \pm 3:35
T ₄	93:00	105:20	123:15	99:00	119:47 \pm 6:39

TABLE 3.—Results of two-way analysis of variance for the biomass of the various groups of species. The values tabled are the calculated F values. All tests had 8 df for trials, 3 df for time, 24 df for the interaction and 72 df for the error term. Single asterisks denote significant F values at the 0.05 level; double asterisks indicate significance at the 0.01 level. The remaining values are not significant

	Value of F-test for sources of variance		
	Trials	Time	Interaction
Small burrowers	6.76**	2.03	2.26**
Large burrowers	10.73**	10.41*	2.69**
Large predators	7.77**	17.41**	4.00**
Small predators	93.93**	10.32**	9.93*
Larval hydrophilid predators	2.63*	7.62**	2.38**
Large dipteran dung-feeders	2.98**	1.57	1.34
Small dipteran dung-feeders	1.46	13.60**	1.41
Parasitic hymenoptera	1.81	11.88**	1.40
Predatory mites	10.74**	35.83**	4.07**
Miscellaneous	5.06**	2.73**	2.49**

The small burrower group, composed of species of *Cercyon*, shows a steady increase in biomass during the 1st 3 days, followed by a decrease (Fig. 1). There is a weak seasonal effect and an interaction explainable as in the case of the large burrowers.

The large staphylinid predators (*Philonthus*, *Aleochara* and *Hyponigrus*) steadily increased in biomass through the 5-day succession (Fig. 1). The significant trial and interaction terms in Table 3 are again due to short-term variations affecting individual trials rather than to seasonal trends.

The biomass of small staphylinid predators was the most heterogeneous of all the groups of species. *Oxytelus tetracarinatus*, the most

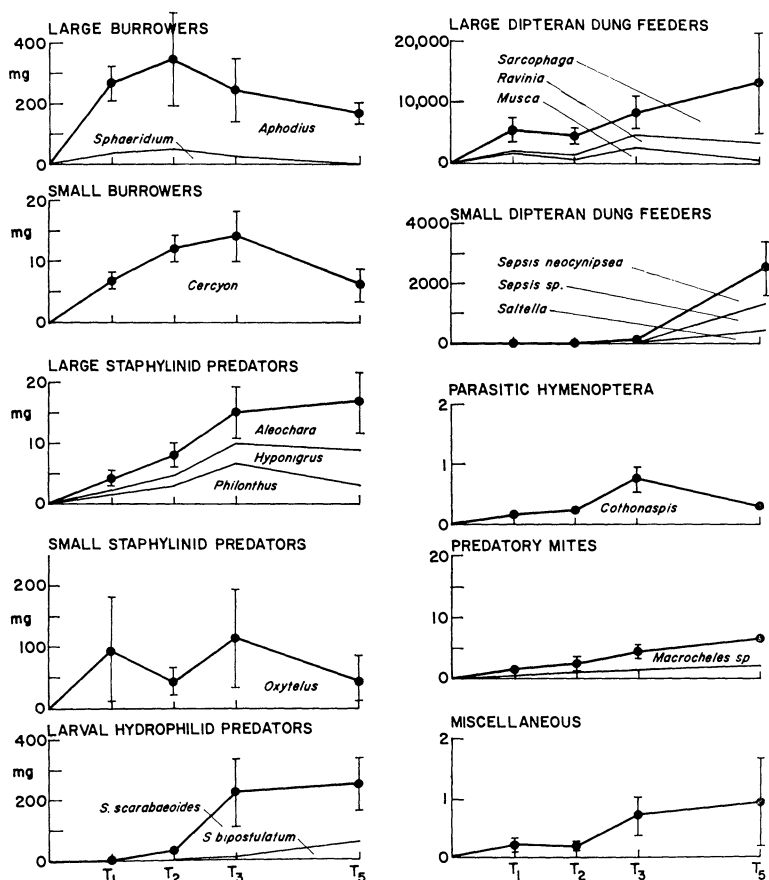


Fig. 1.—Dry weight standing crops ($\bar{x} \pm \text{s.e.}$) of trophic groups through the first 5 days of succession in dung communities. The total standing crops are broken down into the principal taxa where possible. T₁, T₂, T₃, T₄ correspond to the periods described in Table 2

abundant small staphylinid, had a marked peak in abundance from late June to early July. This fluctuation is reflected in the very large standard errors seen in Figure 1, which shows values averaged over the whole summer. The data for each succession are not shown, but, except for periods of very high densities, the biomass of small predators increased during succession as a result of immigration of adult beetles. At high densities, immigration rates may have been high enough so that density asymptotes were reached within a few hours.

The hydrophilid beetles of the genus *Sphaeridium*, dealt with in the large burrower group, entered droppings early in dung succession and oviposited. The larvae hatched in 1-2 days and became substantial contributors to biomass by the end of the 5-day period (Fig. 1).

Sarcophaga sp., *Ravinia l'herminieri* and *Musca autumnalis*, the large dipteran dung-feeder group, increased in combined biomass as time passed (Fig. 1) but this increase is not significant (Table 3). The decrease in biomass of *M. autumnalis* between the 3rd and 5th days was due to emigration of mature larvae during the 4th day for pupation outside the dropping. These fly larvae did show a significant seasonal pattern (Table 3), with very low populations during the cooler period of late May to early June. Later in the summer the populations of fly larvae built up to considerable levels so that this group became the major contributor to biomass in the dung community. However, standing crops of large diptera larvae showed very high variability, with standard errors reaching 100% of the means. This is likely due to the sensitivity of adult flies to small changes in local environmental conditions. If, for example, a cloud covers the sun during the 2-3-hr period during which the dung is attractive to ovipositing female flies, far fewer eggs will be deposited and the cohort of larvae in that set of droppings will be small. This is another example of the importance of short-term meteorological events in the establishment of dung communities.

The three principal components of the small dipteran dung-feeders are larvae of the sepsids *Sepsis neocynipsea*, *Sepsis* sp. and *Saltella sphondylii* (Fig. 1). Although adult flies may be seen on the surface of fresh dung, sepsid larvae do not appear until late in succession. Oviposition, hatching and growth of larvae do not seem to take place as rapidly as in other dung flies. It may also be that the Tullgren extraction procedure is inadequate for the smallest larvae, resulting in a delay in the appearance of these larvae in our data. The analysis of variance shows a striking effect of time in the F values of Table 3, while there is no significant seasonal trend in biomass for small dipteran larvae.

A number of parasitic hymenoptera have been found in dung communities (Valiela, 1969b). Adults of *Cothonaspis* sp. were the most abundant form found, but the sampling technique may have underestimated the importance of other parasitic wasps (*Aphaereta pallipes*, *Eucoila* sp., *Xyalophora quinquelineata*) since fly larvae

were not dissected to find internal parasites. *Cothonaspis* did not show any seasonal fluctuations but was most abundant during the 3rd day. Perhaps adult *Cothonaspis* were attracted to the growing populations of sepsid larvae (Laurence, 1954) found at that time.

Macrocheles sp. were the dominant form of predatory mites (Fig. 1) but *Parasitus* sp. and uropodid mites were also present. Although the mean squares for trials and for interaction (Table 3) were significant, the most obvious trend is a uniform increase in standing crops of predatory mites in the course of the 5-day time period (Fig. 1). From observations it seems likely that the increase was due to immigration, but in situ reproduction could have taken place.

The miscellaneous category is included in Figure 1 mainly to show that the amount of biomass not accounted for in the previous groups was quite small.

Changes in food webs during succession.—Figures 2 and 3 show the mean standing crops for the major components of the dung community during the 1st and 5th days of succession. The arrows show the feeding relations among the members of the community. Similar diagrams for the 2nd and 3rd days have been omitted for simplicity. The number of taxa increases as time goes on (24, 37, 41 and 44 taxa in the 1st, 2nd, 3rd and 5th days, respectively). Along with an increase in the number of taxa, there is an increase in the complexity of the food web, as can be seen by comparing Figures 2 and 3.

The taxa making up the miscellaneous category have been entered separately in Figures 2 and 3 because of the differences in food habit and role as prey. In general, the small size and low standing crops of

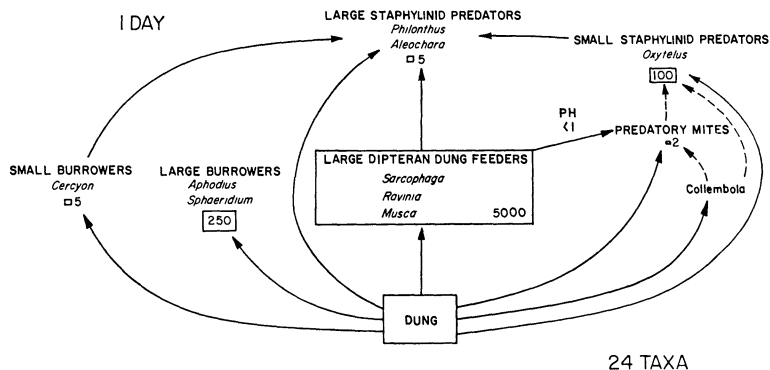


Fig. 2.—Food web of the dung community during the 1st day of succession. The trophic groups are indicated in capital letters. The size of the boxes are proportional to the mean biomass and the number is the approximate biomass of each trophic group. The major taxa are shown in lower case. The box representing dung is not drawn to scale. The mean amount of dry dung per dropping was about 13,600 mg. The continuous arrows show established feeding relations. The dashed arrows indicate presumed feeding. PH is an abbreviation for parasitic hymenoptera.

collembola, *Acrotrichis*, adult *Leptocera*, larvae of *Aphodius*, *Cercyon* and oxyteline beetles probably indicate that these taxa are unimportant, since there is no evidence that their turnover rates are greater than the other species of dung communities. Hymenoptera may parasitize the small as well as the large dipteran dung-feeders. Another parasitic relation of interest not shown in the data is that large dipteran dung-feeders, especially sarcophagids, were frequently hosts to larvae of the staphylinid *Aleochara* (Thomas and Wingo, 1968; Turner *et al.*, 1968). These beetles feed only on young fly larvae, while the young larvae of *Aleochara* seek older fly larvae to parasitize, apparently thus partitioning fly larvae into prey and hosts with little overlap.

Adult flies appear on the surface of a dropping almost immediately after defecation by a cow. The female *Musca autumnalis* and other muscoids oviposit while the larviparous sarcophagids leave larvae on the surface of the dung, all in the first moments of succession (Figs. 1, 2).

Burrowing beetles (*Sphaeridium* and *Aphodius*) also make an early appearance (Figs. 1, 2) and begin to riddle the dung with tunnels. These burrows allow the newly hatched fly larvae to penetrate and feed within the dropping. Since the larvae need to obtain air through their spiracles, feeding would be restricted to the periphery of the dropping if the burrows were not present. However, burrowing beetles were found in every dropping examined during 4 years of study, and therefore the network of burrows was a constant feature of dung environments.

Staphylinid predators are also found quite early in succession (Figs. 1, 2) and feed on small larvae and eggs of flies. These beetles do not have any morphological adaptations for burrowing such as found in *Sphaeridium* and *Aphodius*. Since fly larvae avoid exposed surfaces

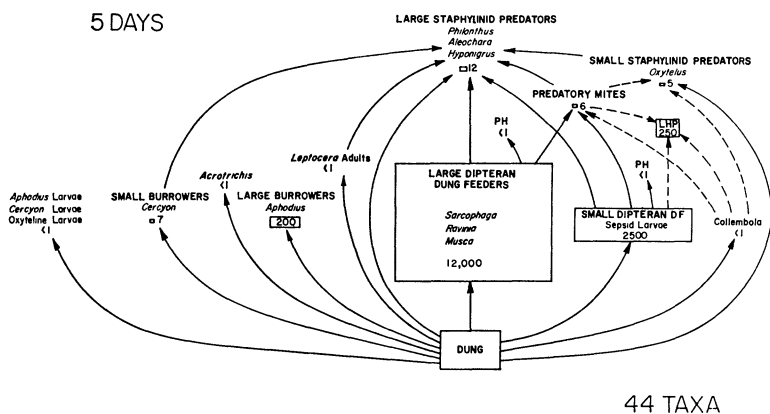


Fig. 3.—Food web of the dung community during the 5th day of succession. All the additional comments of the legend on Figure 2 are also applicable here. PH means parasitic hymenoptera; LHP refers to larval hydrophilid predators and DF is an abbreviation for dung-feeders

of the dung, staphylinid predators could have difficulty finding prey after the initial period of exposure following oviposition or release of larvae. From experiments conducted in the laboratory, however, it seems that the presence of burrowing beetles and, consequently, burrows, increases the mortality of larvae due to predation (Valiela, 1969a). Staphylinid beetles are able to use the ever-present network of burrows to reach and prey upon fly larvae that had sought protection inside the dropping, thus increasing mortality due to predation.

The larvae of flies associated with dung show very fast growth rates relative to those of other habitats. The outcome of predator-prey relationships often depends on the relative size of prey and predator (Brooks and Dodson, 1965; Hall *et al.*, 1970; Landenberger, 1968). *Philonthus cruentatus*, the most numerous and active of the staphylinid beetles found in the dung community, is incapable of killing fly larvae over 6 mm long, although attack may take place. Similarly, invertebrates under about 0.5 mm are overlooked by *Philonthus*. Figure 4 shows the biomass of fly larvae 0.5 to 6.0 mm long. Although the biomass of large dipteran larvae is substantial (Figs. 1 and 4), only up to 10% of that biomass is available to predators during the 1st day. The larvae of these diptera largely escape predation by outgrowing the period of exposure. However, the larvae of small diptera appear after the 2nd day and provide, on the average, about 1600 mg of available prey biomass in the dung community. Some sepsid larvae do outgrow the size susceptible to predators, but this still leaves about 75% of the small larvae biomass available for feeding (Figs. 1 and 4).

Oxytelus may be a potential contributor to prey biomass (Valiela, 1968), but this would only occur early in succession and only during the brief midsummer period of peak abundance of *Oxytelus*.

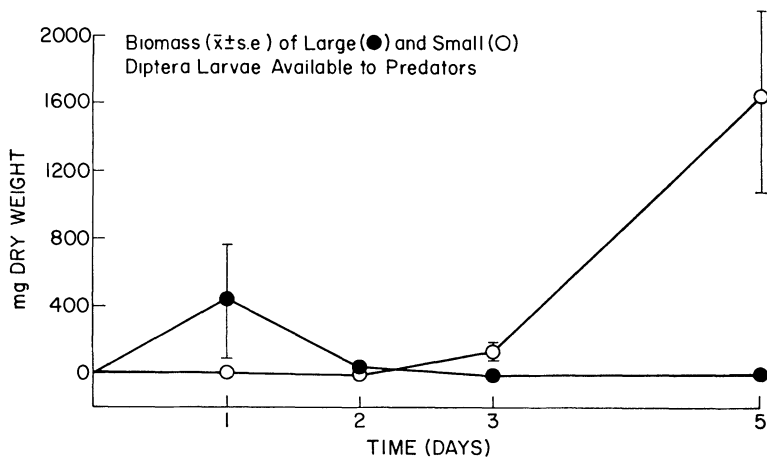


Fig. 4.—Biomass ($\bar{x} \pm \text{s.e.}$) of large and small dipteran dung-feeders between 0.5 and 6.0 mm in length and, therefore, available to predators through 5 days of succession

Predatory mites are shown in Figures 2 and 3 as feeding on dipteran larvae. However, these mites, particularly macrochelids and uropodids, feed principally on the fly eggs rather than on larvae.

Feeding by large staphylinids on *Cercyon* was observed but these small hydrophilids did not seem to be a preferred prey for staphylinids.

Limitation of population abundance in dung communities.—A previous paper (Valiela, 1969a) concluded that competition for food among dung-feeders was not likely to affect mortality of *Musca autumnalis*, one of the major larval dung-feeders. Table 4 shows the total biomass of dung-feeding invertebrates during the sampling periods, including fly larvae as well as dung-feeding burrowing beetles. The average amount of dung in an experimental dropping was 136.15 ± 3.64 g dry weight. The weight of dung per weight of dung-feeder could therefore be calculated (Table 5). Competition for food in fly larvae is initially expressed as a reduction in pupal size, and only if exploitation of the resource is severe is mortality affected (*cf.* Valiela, 1969a, and references therein). Experiments in which densities of diptera larvae were manipulated showed a threshold at about 5 mg dry dung/mg of larvae below which pupal size would decrease sharply in *M. autumnalis*. Table 4 shows that field populations of dung-feeders exhibit dung/dung-feeder ratios above this threshold. The calculated ratios are probably too low, since dung-feeding beetles were included in the total biomass for dung-feeders. Beetles are likely to consume only a fraction of the dung ingested by fast-growing fly larvae. Reduction in size in field-collected fly pupae is very rare (Valiela, 1969a), an observation which supports the contention that

TABLE 4.—Biomass of dung-feeders and ratio of dung to dung-feeders. Dung-feeder biomass is the sum of mean values from Table 3 for large and small diptera larvae, large and small burrowers. The average dry weight of dung per experimental dropping was 136.15 ± 3.64 g. A ratio of 5 is taken as a threshold below which competition for food reduces pupal size (Valiela, 1969a)

	T ₁	T ₂	T ₃	T ₄
Total biomass of dung-feeders	5419.0	4688.1	8601.3	17284.7
mg dry weight dung/mg dung-feeder	25.1	29.0	15.8	7.9

TABLE 5.—Available prey biomass and food demands by predators. Available prey biomass calculated by adding means in Table 3 for small staphylinid predators, available large and small dipteran dung-feeders and predatory mites. The calculated food demands by the large staphylinid predators are overestimates because it was assumed that the feeding rate of 0.042 mg prey consumed/mg predator per hour was carried out 24 hr a day

	T ₁	T ₂	T ₃	T ₄
Total biomass of prey available to predators (mg)	556.8	71.5	348.0	223.3
Total food demands of standing crops of predators (mg/day)	4.6	8.2	15.8	17.3

competition for food is not very important. In some instances, especially late in succession, the threshold ratio of 5 mg dung/mg dung-feeder may be reached. In such cases, and probably to some extent in all instances, reuse of dung and microbial regrowth are likely to be of importance in preventing competition. An evaluation of microbial activity with and without dung-feeders would be of interest, but, in general, competition for dung does not appear to be a major limitation of populations of dung-feeders.

The ability of the large staphylinid predators to limit densities of prey populations can be roughly evaluated. Table 5 shows the total biomass of potential prey available during the 5-day period, taking the data from Figures 1, 2 and 3. Using a feeding rate estimated in Valiela (1969a), the predation pressure on the prey can be calculated (Table 5). The weight of prey demanded by the weight of predators present is always about one order of magnitude less than the weight of prey available for any 1-day period. This suggests that predators are unable to limit prey abundance and, in turn, that predators are not food-limited in communities of dung invertebrates.

Neither food nor predators seem, therefore, likely to limit populations of dung-feeders. Similarly, there seems to be more than adequate prey biomass to support the predators present. Potentially, dung-feeders and predators could be more abundant.

It may be, however, that physicochemical changes in the dung itself proceed too fast and are too erratic to allow larger populations of dung invertebrates. For the large dung flies, as an example, all oviposition must occur within 2-3 hr, since dung ceases to be attractive to ovipositing females after this period. Decreases in density cannot be compensated for by increased individual growth because even at the highest densities observed fly larvae achieved maximum growth. Perhaps there are simply not enough gravid females available to furnish eggs. This seems unlikely in view of the large populations of dung insects found in pastures, but there could be factors outside the dung habitat responsible for limiting populations of gravid females. However, the 5-day period studied here comprises only a portion of the life cycle of the species involved. The larvae of staphylinid predators, for example, are found in dung up to 1 month old. Food limitations in such cases may in fact occur during periods other than the 5-day span dealt with here.

During the period in which succession has been studied, neither food limitation nor predation appears to be limiting to dung invertebrates. Rather, multiple, unidentified and small local alterations in the environment and in the dung itself may set some upper thresholds on the number of predators and prey. These small-scale changes may also be responsible for the very large variability observed on what appeared to be similar experimental droppings.

Underlying, and in spite of, these variations there is a successional pattern. The appearance of certain taxa allows or facilitates feeding interactions, such as the burrower-predator-prey relationship. The

timing of oviposition and growth also affects the structure of food webs, as in the relative appearance of large- and small-fly larvae and the escape from predation due to size.

Faunas of dung arthropods are markedly cosmopolitan (Valiela, 1969b) and often contain many introduced species (Brown, 1940). Notable among these is the recent introduction of the face fly, *Musca autumnalis* De Geer, into North America (Smith *et al.*, 1966; Smith and Linsdale, 1967). Such invasions seem to occur easily and with no major alterations in dung faunas. It may be that the apparent excess in dung or prey biomass available in dung communities is a major factor in the zoogeographical distribution of arthropods associated with dung.

The absence of biologically mediated limitation of dung arthropod populations agrees with MacArthur and Wilson's (1963) explanation of the process of colonization of empty substrates. In the initial stages of invasion, nonbiological processes determine the number of colonizing units, and biological regulation may only be expressed later when the environmental resources are more fully utilized (Simberloff and Wilson, 1969). In the case of dung communities, at least during the 1st 5 days of colonization and succession, no biological regulation seems to occur.

Acknowledgments.—D. J. Hall and W. E. Cooper provided manifold support and criticism. This work was done with the help of a predoctoral fellowship from the National Institutes of Health while the author was at Cornell University and N.I.H. postdoctoral traineeship 1T01GM01751-01 while at Michigan State University.

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