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Patterns of beetle succession in droppings

Ilkka Hanski

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Multispecies patterns in the successional occurrence of beetles in cow droppings are briefly described, and species-specific successional patterns are shown to be similar in the coprophagous species common to two localities in Northern Europe. No important differences were found between males and females, but mature females (of *Aphodius,* Scarabaeidae) tended to occur in older droppings than did immature females. The successional mean occurrence in six groups of dung-inhabiting beetles was related to their size, macrohabitat and seasonal occurrence, and the preferred temperature of their diurnal flight activity. Only two groups, *Philonthus* (Staphylinidae) and Hydrophilidae, showed any evidence of such correlations; in them the successional mean occurrence may have been influenced by size and macrohabitat selection.

New goals for further research are discussed: 1) the precise relationship between the dynamics of resources and consumers in droppings; 2) the pattern of migration to and from droppings; and 3) the causal explanation of 2).

I. Hanski, Animal Ecology Research Group, Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.

1. Introduction

There is every reason to start this introduction by referring to the well-known paper by Mohr (1943) on »cattle droppings as ecological units», in spite of the fact that Mohr's work was the first study of insect succession in droppings: in many respects it is still the best. It is a comprehensive study, too, for it deals with both flies and beetles, the two major taxonomic components of the dung community (see also Legner & Poorbaugh 1972). In his short discussion Mohr admirably summarized several of the key factors: 1) most species present in the beginning of succession are specialists, obligatory dung breeders, whilst the species appearing during the later stages are frequently microhabitat generalists; 2) a dropping is likely to be inhabited by fewer species as it grows older; 3) the earliest species in the succession tend to have the shortest life histories and the shortest occurrence in the droppings; 4) succession is faster in the early stages; 5) the environment of the dropping has a profound influence on the pattern of succession.

In our quantitative study on the beetles inhabiting cow dung in southern Finland (Koskela & Hanski 1977, Hanski & Koskela 1977), where the community is much more diverse than the one studied by Mohr (1943), we confirmed these conclusions for the beetle component of the dung community (our material included 179 species). For instance, among the coprophagous species especially, but also among the carnivores, there is greater niche width (season, macrohabitat, successional occurrence) in early than in late successional species. The average numbers of species in the beginning of the succession were ca. 13 coprophagous (2nd to 4th days) and ca. 17 carnivorous species (2nd to 8th days), whereas after the 20th day the respective figures were 2 to 3 and 4 to 7 species. The contrasts in the successional patterns showed interesting differences between coprophages and carnivores: the crucial contrast in the former was between open field and forest habitats, whilst the carnivores showed more complex contrasts, especially between pine and spruce forest, but also seasonal changes. This emphasizes Mohr's conclusion on the importance of the macrohabitat in determining the general pattern of succession, and demonstrates the existence of differences between different kinds of insects (coprophagous vs. carnivorous beetles).

It thus appears that the study of insect succession on droppings has reached the stage of an adequate description of basic multispecies

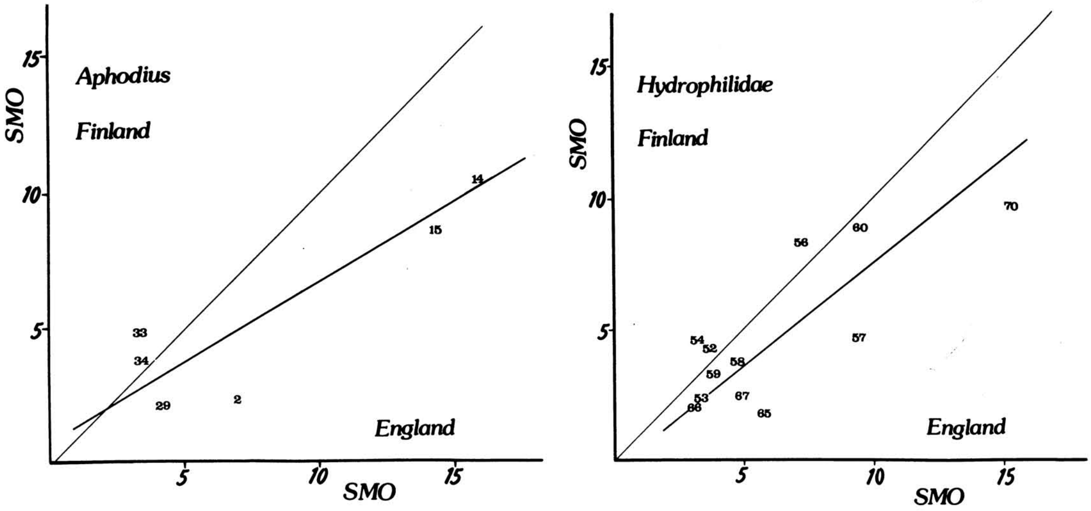

Fig. 1. The successional mean occurrence (*SMO*) in *Aphodius* and in the hydrophilids in southern England and southern Finland. *SMO* has been defined in the text. Symbols for the species are:

Aphodius: 2 = *A. ater* DeG., 14 = *A. fimetarius* (L.), 15 = *A. fossor* (L.), 29 = *A. prodromus* (Brahm), 33 = *A. rufescens* Fabr., 34 = *A. rufipes* (L.).

Hydrophilidae: 51 = *Cercyon obsoletus* (Gyll.), 52 = *C. impressus* (Stm.), 53 = *C. haemorrhoidalis* (Fabr.), 54 = *C. melanocephalus* (L.), 56 = *C. pygmaeus* (Ill.), 57 = *C. terminatus* (Marsh.), 58 = *C. quisquilius* (L.), 59 = *C. unipunctatus* (L.), 60 = *C. lateralis* (Marsh.), 65 = *Sphaeridium bipustulatum* (Fabr.), 66 = *S. scarabaeoides* (L.), 67 = *S. lunatum* (Fabr.), 70 = *Cryptopleurum minutum* (Fabr.), 85 = *Megasternum boletophagum* (Marsh.).

patterns. At the same time, however, this stage is becoming unsatisfactory, and provides a nice example of the importance of having a theoretical basis for empirical research. The theory of optimal foraging in a patchy environment (e.g. MacArthur & Pianka 1966, Pyke et al. 1976, Krebs 1978) calls for a more detailed single-species approach to an evolutionary ecological explanation of the successional patterns.

My aim in this paper is to analyse the constancy of successional patterns between two localities (Section 2), to compare the successional occurrence of males and females (Section 3), and to analyse the importance of size and of some abiotic factors in creating interspecific differences in the successional occurrence of beetles (Section 4). I shall conclude by formulating some important questions for further research (Section 5).

2. The constancy of interspecific differences

Before a causal explanation of the successional patterns is likely to succeed, one needs to know whether the patterns are repeated in space and time; otherwise it would be difficult to know what to explain. My data from southern Finland and southern England are suitable for such a comparison in Scarabaeidae (*Aphodius*) and Hydrophilidae, two of the three important beetle families inhabiting dung (the third is Staphylinidae).

I shall first define the successional mean occurrence, abbreviated *SMO*, as the »mean» of the colonization curve (which gives the numbers of individuals of a species present in droppings of different ages). The formula for the calculation of *SMO* is

$$SMO = \sum_{i=1}^{n} p_i \, (t_i - t_{i-1}) t_i \Big/ \sum_{i=1}^{n} p_i \, (t_i - t_{i-1}),$$

where p_i is the number of individuals extracted from droppings of age t_i (in days), and n the number of »sampling points» along the succession. The unit of *SMO* is »days». In the present calculations I used either monthly or annual results of experiments carried out in southern Finland by Hanski & Koskela (1977; for methods see also Koskela 1972), and near Oxford in 1977 by me. The Finnish results have been recalculated, as the method used in our previous paper (Hanski & Koskela 1977) was different. For a full account of the methods used in the field in

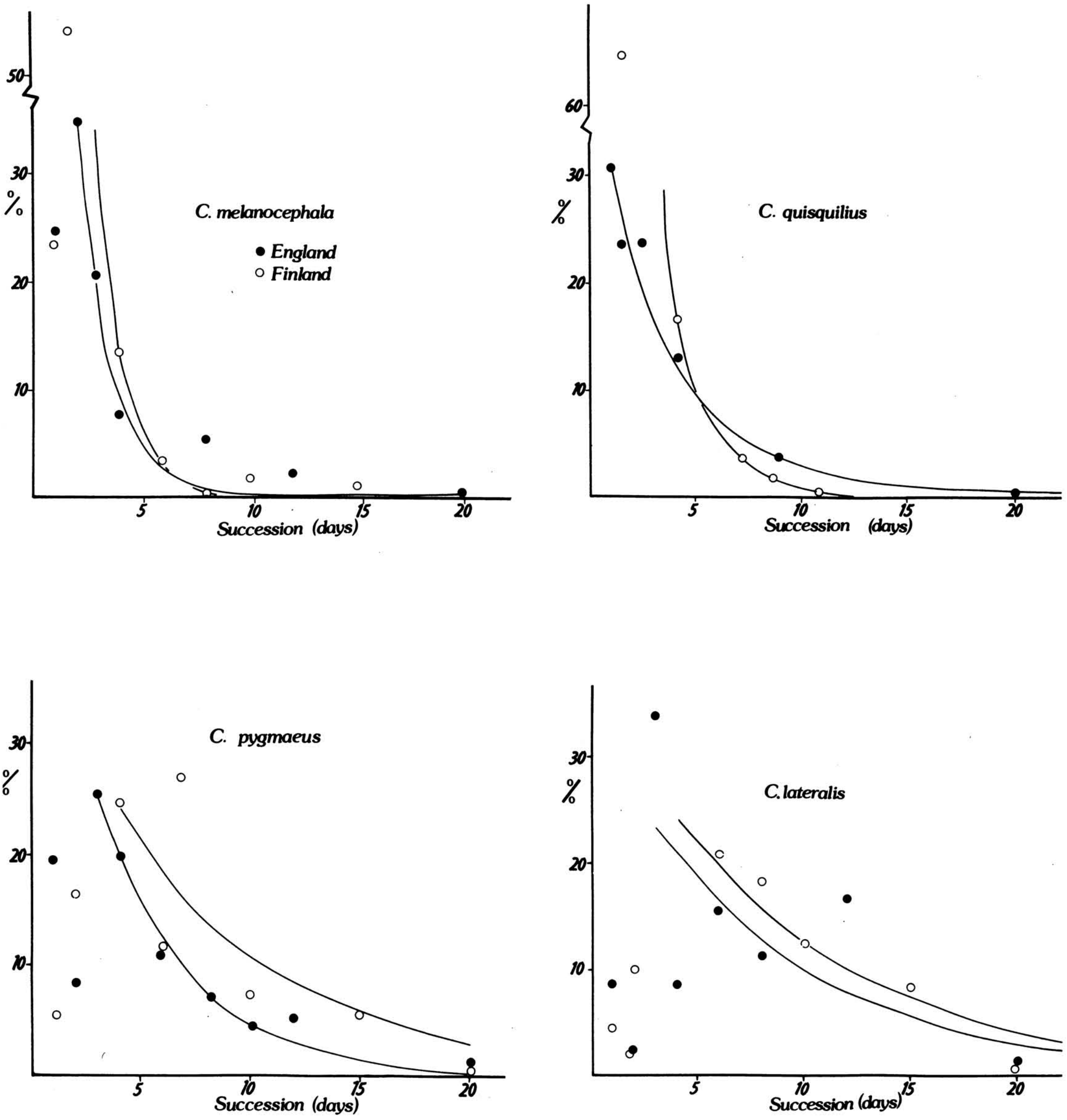

Fig. 2. Colonization curves for four species of *Cercyon* (Hydrophilidae) in southern England and in southern Finland. See Table 1 for the statistics. The *y* axis gives the relative frequency of individuals associated with the successional stage indicated.

Oxford, see Hanski (1980b). Briefly, every month from April to September 1977 I deposited altogether 5 x 9 = 45 droppings in the study pasture, removed 5 of these after 1, 2, 3, 4, 6, 8, 12, 20 and 30 days, and extracted the beetles (in the Finnish study the incubation periods were: 1, 2, 4, 6, 8, 10, 15, 20, 25 and 30 days).

In both *Aphodius* and Hydrophilidae there was a positive correlation in *SMO* between southern Finland and southern England (Fig. 1), though succession proceeded somewhat faster in Finland than in England. This must have been due to the weather conditions during the respective experiments. An exception was *Megasternum bole-*

tophagum (Marsh.) (Hydrophilidae, No. 85 in Fig. 1), which had an *SMO* of 17.5 days in Finland but of only 14 days in England. This can be explained by the difference in its habitat occurrence in the two localities: in Finland *M. boletophagum* was present throughout the macrohabitat spectrum, whilst in England it was usually found in open habitats (Hanski 1979). Second, in spite of the good general agreement between the *SMO*s, there is still a considerable scatter, especially in species with *SMO*s of less than 5 days (Fig. 1). The data available are not sufficient to show whether these deviations represent real differences between the two populations.

Four species of *Cercyon* (Hydrophilidae) were common enough in both localities (more than 300 individuals, usually more than 1000) to allow a comparison of their respective colonization curves, and not only their *SMO*s. The agreement is good (Fig. 2), and in fact is probably even better than the curves suggest, because some allowance should be made for some exceptional points (especially in *C. pygmaeus* (Ill.)). The only real difference is perhaps in *C. quisquilius* (L.), which showed an earlier but less steep decline in England than in Finland (Fig. 2). Another point is the generally good fit of the observations to a negative exponential falling-off of numbers in the latter part of the succession (Table 1).

My third example is the guild of three very similar species of *Sphaeridium*. I have analysed elsewhere (Hanski 1980a) their coexistence in Europe and North America. Table 2 gives the *SMO*s for four localities, two in Europe and two in North America. The data for *S. bipustulatum* (F.) are not extensive enough to allow conclusions (Hanski 1980a), but the two more common species show a clear pattern: *S. lunatum* (F.) always had a greater *SMO* than *S. scarabaeoides* (L.)

The above comparisons indicate that a species usually shows the same successional occurrence in widely separated localities. From this it follows that interspecific differences in successional occurrence call for an evolutionary and/or ecological explanation.

3. Are there successional differences between males and females?

Besides interspecific variation in successional occurrence one would expect to find intraspecific differences: the successional occurrence is not necessarily the same in males and females. The two sexes are likely to be searching for different things in droppings: males are looking for females, whilst females primarily need places for feeding and egg-laying, males being available in any case (see e.g. Parker 1978, Hanski 1980c).

Table. 1. Statistics for Figure 2. The fitted equation is of the form $y = ae^{bx}$, where y is the proportion of individuals associated with the xth successional stage, and a and b are constants. Curves were fitted, starting from the given day ("start") after the beginning of the succession, using Marquardt's iterative algorithm (Conway et al. 1970). Standard error (SE in the table) of the estimate (y) and standard errors of the parameter estimates are given. The latter are for linear confidence limits.

		England	Start and SE	Finland	Start and SE
C. melanocephalus	*a*	118.5±25.2	2	231.5±11.7	2
	b	−0.605±0.086	2.40	−0.704±0.023	0.70
C. quisquilius	*a*	42.4±3.3	1	261.3±5.2	2
	b	−0.290±0.033	1.98	−0.674±0.009	0.35
C. pygmaeus	*a*	50.9±5.2	4	40.8±15.6	4
	b	−0.231±0.024	1.32	−0.129±0.056	5.92
C. lateralis	*a*	33.2±14.6	4	38.1±4.6	4
	b	−0.113±0.077	8.37	−0.110±0.016	2.09

Table 2. The successional mean occurrence (*SMO*, in days) of *Sphaeridium* in two localities in Europe and two localities in North America. F = southern Finland (Hanski & Koskela 1977), E = southern England (the present study), A1 = Missouri, U.S.A. (Wingo et al. 1974), and A2 = Dakota, U.S.A. (Kessler & Balsbaugh 1972).

	F	E	A1	A2
S. lunatum	2.15	4.93	1,89	1.95
S. scarabaeoides	1.90	2.93	1.54	1.59
S. bipustulatum	1.94	5.77	1.96	1.77

Nevertheless, there are no consistent differences in *SMO* between males and females, either in *Aphodius* or in the hydrophilids (Fig. 3). Although there is variation, this is not related to the overall value of *SMO*, nor is it correlated with abundance. It may seem that there is less variation in the hydrophilids than in *Aphodius*, but this is probably due to the larger samples of the former.

Differences in *SMO* between males and females are smaller than those between mature (fully developed ovaries) and immature females and, most importantly, the differences between the two latter categories are consistent (Table 3). I had suitable data for four species of *Aphodius*. In each case, mature females tended to occur in older droppings than did immature females. On the basis of the present data it is impossible to decide between two alternatives: either mature females prefer to colonize older droppings, or they stay longer in a single dropping than immature

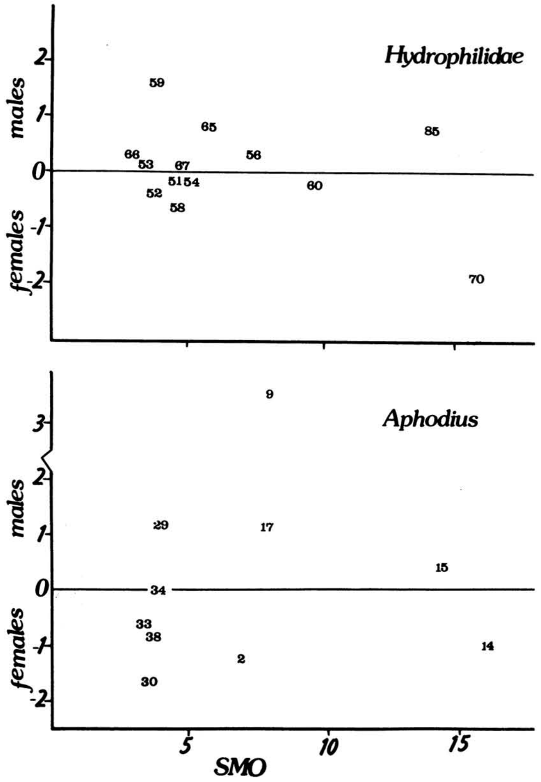

Fig. 3. Difference in the successional mean occurrence (*SMO*) of males and females in *Aphodius* and in the hydrophilids. The difference is given as the *SMO* (in days), which is defined in the text. Symbols for the species are given in Fig. 1; the missing ones are (all *Aphodius), 9 = A. contaminatus* (Hbst.), 17 = *A. haemorrhoidalis* (L), 30 = *A. pusillus* Hbst., 38 =*A. sphacelatus* (Panz.).

females (this question is given a preliminary answer in favour of the latter alternative in Hanski 1980b).

4. Successional mean occurrence: the significance of size and abiotic factors

Our previous study in southern Finland (Hanski & Koskela 1977) included six groups of taxonomically related species (in parentheses, numbers of species represented by more than 25 individuals): *Atheta* (19), *Tachinus* (5), *Philonthus* (9), *Oxytelinae* (6), Hydrophilidae (12) and *Aphodius* (11). The first three groups consist of carnivorous beetles, and hydrophilids are predators as larvae whereas the others are coprophagous. We have analysed elsewhere (Hanski & Koskela 1979) the niche patterns in these guilds in relation to time (season), place (macrohabitat) and food resources (size of the species). In the present section, I shall relate the interspecific variation in *SMO* (from Hanski & Koskela 1977) within these guilds to three factors: the size of the beetles (from Koskela & Hanski 1977), their macrohabitat selection (from Hanski & Koskela 1977), and their preferred (observed median) temperature for diurnal flight activity (from Koskela 1979). Moreover, I shall analyse seasonal intraspecific changes in the *SMO* of the hydrophilids, using my data from Oxford. Of course, a necessary assumption in all these analyses is that within each of these six guilds the species are sufficiently similar in their ecology to make comparisons meaningful (cf. Hanski & Koskela 1979).

Table 3. The successional occurrence of immature (im) and mature (ma) females of four species of *Aphodius*. Half individuals are due to "splitting" of intermediate females between two groups. *SMO* is the successional mean occurrence, defined in the beginning of Section 2.

		Incubation period in days									*SMO*	χ^2
		1	2	3	4	6	8	12	20	30		
A. ater	ma	—	0.5	12.5	3.0	8.5	1.0	2.0	—	—	6.2	14.78*
May-June	im	—	8.5	14.5	1.0	2.5	—	—	—	—	3.3	
A. fossor	ma	1.0	0.5	2.0	3.0	2.5	4.5	2.0	3.5	—	13.8	5.98
June-July	im	—	0.5	1.0	—	3.5	1.5	—	0.5	—	9.7	
A. haemorrhoidalis	ma	—	—	0.5	—	19.0	8.5	1.0	1.5	—	9.1	20.70***
June	im	—	—	19.5	—	17.0	3.5	—	0.5	—	6.2	
A. rufescens	ma	6.5	6.0	17.5	6.5	2.0	—	1.0	—	—	3.8	5.40
Aug-Sept	im	5.5	3.0	12.5	0.5	—	—	—	—	—	2.4	

*P < 0.05, **P < 0.01, ***P < 0.001.

The reason for correlating *SMO* with size is the cost of migrations from dropping to dropping, which I except to be higher in the smaller species, because the distances are relatively larger for them than for the large species, and they are more dependent on the prevailing winds (Koskela 1979). Moreover, from studies with *Drosophila*, Roff (1977) concluded that »the energetic and reproductive cost of dispersal decreases with increasing body size.» The prediction then is that, in smaller species, the frequency of migration between droppings is smaller, and the *SMO* consequently greater. (It should be noted that the *SMO* correlates with the width of the successional occurrence, because almost every species starts to occur from the first few days of the succession; cf. Hanski & Koskela 1977, Figs. 6 and 11).

Macrohabitat selection enters into the analysis because the rate of succession in droppings is faster in open habitats, where the rate of evaporation is higher than in forests (Koskela & Hanski 1977, Kuusela, Koskela & Hanski in preparation). On the other hand, macrohabitat »selection» in these beetles is primarily selection of suitable microenvironmental conditions (Hanski & Koskela 1977, Thiele 1977, Koskela 1979). If the decisive factor initiating migration is the declining suitability of the dropping occupied, and especially the decreasing moisture content, one would expect that species inhabiting forests would stay longer in droppings than their relatives in open habitats.

The extensive study by Koskela (1979) on flight activity in dung beetles provides data dor testing the extent to which temperature determines the *SMO*. One might reason as follows. Under continuously changing weather conditions, beetles are unable to initiate migration whenever they »like», but presumably have to wait for suitable weather conditions, especially a sufficiently high temperature. Species that can only fly at high temperatures would be expected to be more constrained than others, because the higher the preferred temperature, the lower presumably is the frequency of suitable weather conditions. Species that prefer high temperatures would therefore be expected to show a greater *SMO* than the others. This tendency would be reinforced if a preference for high temperatures is linked with a high tolerance of desiccation, as it is in at least some species (of *Aphodius,* Landin 1961).

Because there are seasonal changes in the rate of drying of the droppings, due to higher temperatures and usually a lower rainfall in the middle of the summer, one would expect that in species present throughout the season the *SMO* would be at a minimum in the middle of the summer.

The results of the analyses are clear-cut but somewhat difficult to interpret. None of the six groups studied showed any indication of a correlation between the *SMO* and the temperature preferred for diurnal flight activity. The hypothesis about the significance of the frequency of suitable weather conditions for dispersal is not supported. In two of the six cases there seemed to be a correlation of the type predicted between macrohabitat selection and *SMO*, and similarly in two cases *SMO* was negatively correlated with size, as was predicted (Fig. 4). In both cases the two "well-behaved" groups were *Philonthus* and Hydrophilidae.

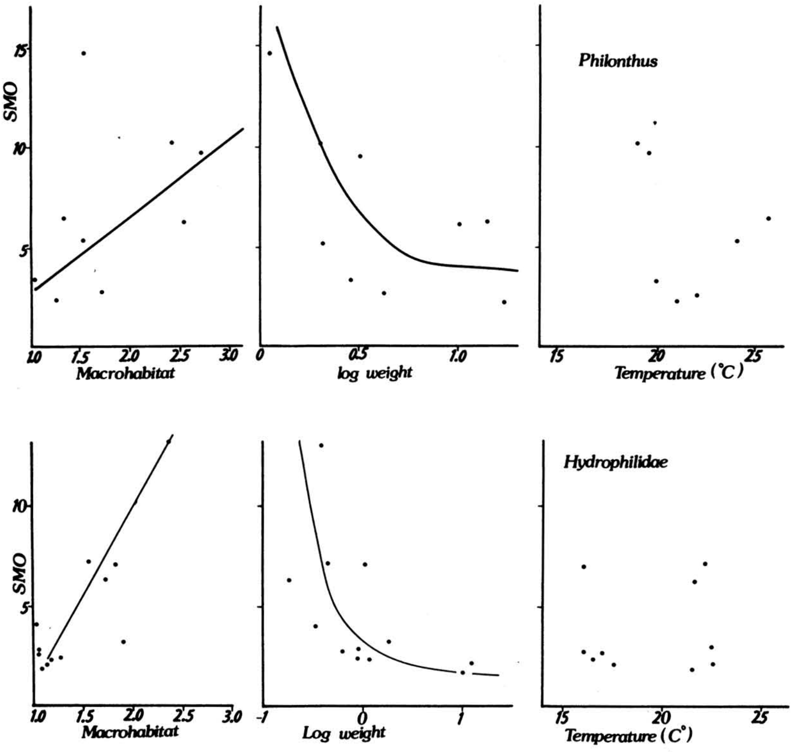

Fig. 4. Relationships between the successional mean occurrence (*SMO*) and macrohabitat selection, size, and preferred temperature for diurnal flight activity in two groups of dung-inhabiting beetles: *Philonthus* (Staphylinidae) and Hydrophilidae. *SMO* has been defined in the text. The macrohabitat spectrum has been coded from 1 (open field) to 3 (dense forest) (data from Hanski & Koskela 1977); size data are from Koskela & Hanski (1977), and data on temperatures from Koskela (1979).

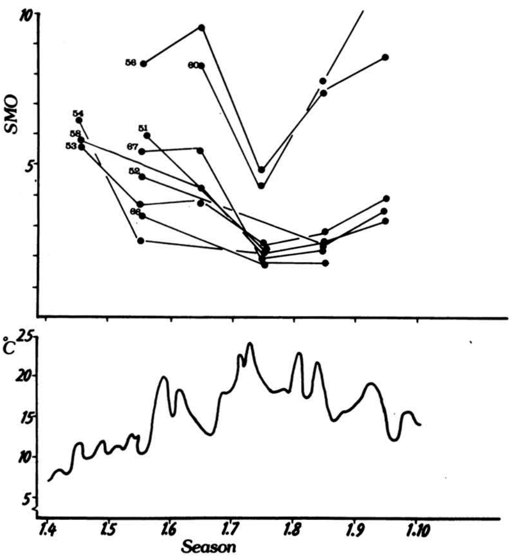

Fig. 5. Seasonal changes in successional mean occurrence (*SMO*) in the hydrophilids. The lower part of the figure gives the sliding 5-day averages for the temperature at 1500 hours. *SMO* has been defined in the text, and the symbols for the species are given in Fig. 1.

Although the same two guilds were involved in the suggested correlations, which moreover were of the type predicted, there is the difficulty that *Philonthus* consists of large carnivorous species, whilst the hydrophilids are small coprophagous species. Nevertheless, hydrophilids have predatory larvae, which suggests that the tendencies predicted may be more important in predators than in coprophages. If, in the course of succession, there is a slow change in the size distribution of the prey, as there may well be (Koskela, personal communication), predators would be less constrained by their food resources than coprophages. But *Tachinus* and *Atheta*, though also predators, definitely did not show any such correlations.

Intraspecific seasonal changes in *SMO* were analysed in the hydrophilids, which are multivoltine, occurring throughout the summer. In this group the original expectation was confirmed (Fig. 5): the *SMO* attained a clear minimum in July, which was the warmest month.

5. Discussion

The present results indicate that the interspecific differences in the successional patterns are consistent enough to call for an ecological explanation. On the other hand, there were no differences between males and females, though mature females of *Aphodius* tended to occur in older droppings than immature females. This is probably related to the late successional occurrence of *Aphodius* larvae in droppings (Landin 1961); females prefer to lay eggs in relatively old droppings (?). Rather surprisingly, the successional mean occurrence showed no correlation with the size, macrohabitat occurrence or preferred flight temperature of the species, with some possible exceptions, which I was not able to explain adequately.

There are several possible explanations for the absence of these correlations. Most importantly, the *SMO*, the succesional mean occurrence, is a crude indicator of the type of successional occurrence. The major problem is that the *SMO* is derived from the colonization curve, which is the result of the rate of migration to and from the droppings.

There is a specific complication in the analysis of the relation between size and *SMO*. If (as I have assumed) the congeneric species within my six guilds are closely similar ecologically, they may be expected to feed on the same kind of prey. As any particular prey species almost necessarily grows larger in the course of succession, one would expect the large species to have a greater *SMO* than the small species (see Hanski 1980b). Nevertheless, it must be emphasized that the average prey size does not necessarily increase during the succession; Koskela (pers. comm.) has in fact found that the size distribution of the prey remains more or less constant. Muscid larvae are among the largest insects in droppings, yet they complete their development during the first few days of the succession (Hammer 1941, Mohr 1943). My results on the hydrophilids may point to the correct explanation. In a group of three very similar species of *Cercyon*, which could feed on the same prey species, the *SMO* was roughly proportional to size (Hanski 1980b), but among all the species of Hydrophilidae, the *SMO* seemed to decrease with increasing size (Fig. 4), as predicted in Section 4.

It is unfortunate that for most species the *SMO* is the only information available. I found no consistent differences in *SMO* between males and females, but this does not conclusively prove that none exist. Parker (1970) has shown that the males of the dung fly *Scatophaga stercoraria* L. arrive earlier in droppings than the females, yet there is no important difference in *SMO* between the sexes (Parker 1970, Fig. 1).

Which factors, then, if not the three analysed here (size, habitat, and preferred temperature for flight), cause the observed interspecific differences in *SMO*? "Differences in food resources", though a plausible hypothesis, seem unlikely to be the sole factor. In any case, much more should be known about the feeding biology of these beetles. If deteriorating microclimatic conditions in ageing droppings are important in determining the time of departure, as they probably are, the possibility remains that the behaviour observed in many species is not "optimal" in the present environment, but rather reflects the evolutionary history of the species.

The present results emphasize the need for information on the following three interrelated points: 1) the precise relationship between the dynamics of prey (resource) and predator (consumer) in droppings; 2) the patterns of migration to and from droppings; and 3) the causal explanation of 2).

The general picture is clear: in the case of beetle succession in dung, the numbers of coprophagous species reach a peak earlier than the numbers of the carnivorous species because the resources of the former appear earlier; in other words, resource dynamies determines consumer dynamics. But before one is in a position to discriminate between different hypotheses on the successional occurrence of beetles (point 3)), one needs more quantitative information at the resource level. It seems that the best way to achieve this is to collect comparable data from different localities, from the same locality at different times, and for comparisons between different groups of species.

Aside from the fact that the temporal dynamics in resources must be described quantitatively before an adequate causal explanation of the successional patterns can be reached, more detailed information is needed on the succession of the consumers, too. What is known is merely the pattern of colonization, i.e. the numbers of individuals and species against the stage of the succession (e.g. Hanski & Koskela 1977, Koskela & Hanski 1977), whereas what should be known are the processes that create these patterns: immigration and emigration. The reason for this is obvious: any successional pattern may be a result of entirely different rates of immigration and emigration, which, nevertheless, are exactly those behavioural variables with which a causal explanation must be concerned.

I thus come to my last point 3), which can be framed as two questions. a) Given that the animal is present in a particular microhabitat (dropping), when does it leave and why? b) Given that the animal is moving between microhabitats, where does it go and why? I wish to emphasize that I do not pose these questions in the narrow sense of what the animal "should" do (to behave "optimally"). I shall offer preliminary information on point 2) in a separate paper (Hanski 1980b), as far as the coprophagous dung beetles are concerned, and I shall discuss point 3) further elsewhere (Hanski 1980c). I conclude by returning to the present results.

The two tentative correlations between size and *SMO* suggest that in some cases at least the cost of migrations may be an important factor, whilst the difference observed between mature and immature females shows that the successional patterns result from some other factors besides migration and the microclimatic conditions in the droppings. Other results are compatible with one or other of two hypotheses: 1) Individuals respond in a stereotypic (i.e. evolutionarily fixed) way to physical changes in the droppings, particularly to changes in moisture content. 2) Successional patterns reflect "optimal" movement patterns, i.e. individuals readily adjust their behaviour according to ecological circumstances. The fact that in most species movements are restricted to a few hours each day (Koskela 1979) suggests that a discrete model should be used to describe the movement patterns.

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