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Migration to and from cow droppings by copraphagous beetles

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The patterns of movement between droppings were analysed in six common species of *Cercyon* (Hydrophilidae). The rate of immigration declined exponentially as a function of the age of the dropping, whilst an assumed constant rate of departure descriped the observed rate of emigration well. Interspecific variation in a group of three closely related species was correlated with size, the largest species having the latest successional occurrence. A hypothesis is put forward that these three species (*C. obsoletus, C. impressus* and *C. haemorrhoidalis*) feed on the same resources, the differences in their successional occurrence reflecting the fact that individuals of any shared prey species necessarily grow larger in the course of succession. Mature females of *Aphodius* (Scarabaeidae) show a similar rate of immigration but a slower rate of emigration than immature females. This difference probably reflects differences in the behaviour of immature (feeding) and mature females (copulating and egg-laying). By staying longer in a single dropping, mature females reduce the cost of movements, and can copulate, and if necessary feed, while the dropping is still fresh.

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1. Introduction

I have previously (Hanski 1980a) pointed out that a causal explanation of the patterns of colonization of insects in droppings (and similar microhabitats) is possible only when the patterns of migration to and from the droppings are known. A simple example clarifies the point. Assume that the numbers of individuals of some species remain constant for a certain period of the succession. This means that during that period either immigration exactly balances emigration, irrespective of the absolute values, or there are no movements at all. Although the result is the same, the two alternatives clearly represent very different behavioural patterns, and must have different causes and consequences. (In principle, mortality should be taken into account, but it is ignored here because the relevant time scale of the migrations is relatively fast, because the mortality rate is probably highest during the interdropping movements, and because there is no reason to suppose that it depends on the successional stage of the dropping.)

I believe that three temporal variables are important in understanding the patterns of succession in insects occupying temporary habitats like dung: the seasonal dynamics of the species, successional changes in the microhabitat, and short-term changes in the abiotic conditions, which influence the movements. In the case of droppings, the successional stage is primarily a function of the age of the dropping and the weather, though utilization by the populations also plays a role. Unfortunately, a model incorporating all these three factors would be complicated, especially because it seems difficult at present to model the influence of the weather.

The obvious way to increase our understanding is to perform controlled field experiments. The data on which the present study is based were collected near Oxford in 1977. As is often the case, especially in England, weather conditions were mostly varied, and because the successional stage of the dropping depends on weather, it was almost impossible to repeat an experiment. Therefore, the present analysis must be considered a very preliminary one; I did not aim at quantative results. Nevertheless, even qualitative results are of great interest, because as yet almost nothing is known about the pattern of migration to and from droppings, which I shall analyse in the dung-inhabiting hydrophilid beetles. Results for the carnivorous beetles, which show a different pattern of succession (Hanski & Koskela 1977), will be published elsewhere (Hanski, Koskela & Muona, in prep.).

Table 1. Simultaneous catches of *Cercyon haemorrhoidalis* in pitfall traps baited with a cow dropping, and from natural droppings 1 day old in both cases). Means and standard deviations are given.

	Droppings ($n = 5$)			Traps ($n = 3$)		
	males	females	total	males	females	total
20—21 June	24.2± 7.1	25.6±10.1	49.8±15.9	37.3±14.0	33.3±15.5	70.7±29.5
15—16 July	84.2±20.8	84.6±22.5	168.6±40.1	43.7± 4.2	50.7± 3.1	94.3± 2.3
15—16 Aug.	18.2±11.5	18.8± 8.0	37.0±20.9	3.7± 2.5	4.7± 2.2	8.5± 2.6
06—07 Sept.	4.2± 2.4	6.4± 7.0	10.6± 9.2	2.7± 0.6	3.3± 0.8	6.0± 3.0

2. Experiments

Field experiments were carried out near Wytham Woods (Oxford) in southern England from March to November 1977. The study site was in the middle of extensive fields and pastures, where cattle were present throughout the season (Hanski 1979).

I used two methods to collect beetles. Ten large pitfalls, baited with a standard-sized cow pat (1.5 kg fresh wt), were operated continuously throughout the summer in an area of 20 by 20 m. In most instances, three types of bait, varying in age, were used simultaneously in 3 to 4 traps each, and the old bait was renewed when it ceased to attract beetles (usually 20 to 30 days after deposition). Beetles were collected from the traps 10 to 15 times per month, but at somewhat irregular intervals, partly dictated by the timing of the flotation experiments (see below). Pitfall catches are assumed to reflect the rate of immigration to droppings.

There are two serious sources of error here. First, some beetles may conceivably have stayed, at least occasionally, in the bait, which was not covered. Nevertheless, in preliminary experiments I found only a few beetles in the bait 1 and 3 days after deposition. This still leaves the possibility that some individuals visited the bait very briefly, and managed to emigrate, instead of falling into the pitfall. The second problem is the probably somewhat faster rate of evaporation from droppings above the trap than from those on the ground: in the trap droppings were exposed both above and below, instead of only from above. My impression was that this did not introduce a major difference, though no actual comparisons were made. The crust formation typical of cow dung will diminish the difference.

The second method used to collect beetles was to place droppings in the field near the traps for a certain number of days (1, 2, 3, 4, 6, 8, 12, 20, and 30 days). After the dropping was removed, beetles were extracted by flotation in water (see Koskela 1972, Koskela & Hanski 1977). Each month 5 x 9 droppings were deposited between the first and the fifteenth day of the month (5 replicates), in such a way that droppings of different ages could be removed on the same dates in the latter half of the month. Droppings were always deposited and removed, and traps rebaited, in the morning (0900 to 1100), when the flight activity of most of the species is minimal (Koskela 1979). These results give the numbers of beetles in droppings of different ages, i.e. the values for plotting the colonization curve, which is the net result of immigration and emigration. Naturally, if the rate of immigration and the colonization curve are known, the rate of emigration can be calculated.

The present analysis includes only the more common species of *Cercyon* (Hydrophilidae). *Aphodius* species occurred in smaller numbers, and the great variability of the results, which was due to changing weather conditions, would make a similar analysis less profitable in their case. Nevertheless, information is given about the rate of immigration of *Aphodius* females, to show the difference between mature and immature individuals. The rate of immigration in *Sphaeridium* is dealt with elsewhere (Hanski 1980b).

Table 1 shows a comparison between the results obtained by the two methods after exposure for 1 day; one may assume that during the first 24 hours emigration is not important. There is reasonable agreement, though a systematic bias may be present, since in 3 out of 4 cases the trapping result is smaller than the result given by flotation.

3. Models and their evaluation

My trapping results come in the form of numbers of individuals caught between times t_1 and t_2, where t_1 and t_2 indicate the number of days after the exposure of the dropping ($t_1 < t_2$). To derive the rate of immigration, $i(t)$, I used the following procedure.

A priori, there are four conceivable simple forms for the rate of immigration (Fig. 1), but two

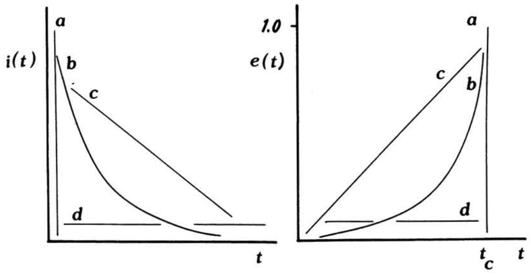

Figure 1. Four conceivable simple forms of the rate of immigration, $i(t)$, and four conceivable forms of the rate of emigration, $e(t)\mathcal{N}(t)$, where $\mathcal{N}(t)$ is the number of individuals present at time t. Note that $i(t)$ gives the absolute rate of immigration, whilst $e(t)$ is the probability of departure for a single individual (therefore, $e(t) \leq 1$ for any t).

Table 2. Statistics for the models of the rate of immigration, Equations 1) and 2).

	Linear decline, $i(t) = a - bt$				Exponential decline, $i(t) = \alpha \exp(-\beta t)$				
	a	b	SE	r	α	β	SE	r	n
C. obsoletus	2.19	0.16	4.80	.657	11.60	1.12	3.38	.848	11
C. impressus	5.58	0.55	10.62	.788	63.08	2.72	6.08	.936	12
C. haemorrhoidalis	11.15	0.71	24.62	.614	430.47	6.64	15.26	.872	36
C. melanocephalus	8.03	0.60	10.20	.887	64.91	2.04	6.69	.953	15
C. pygmaeus	3.07	0.25	3.35	.866	12.62	1.06	2.22	.944	27
C. lateralis	2.65	0.16	6.04	.805	23.30	1.43	7.10	.721	22

of these may be disregarded after a preliminary examination of the data: beetles do not invade a dropping immediately after it is deposited (a in Fig. 1), nor is the rate of immigration constant (d). This leaves either a linearly or exponentially decreasing rate of immigration,

$$i_l(t) = a - bt \qquad 1)$$

$$i_e(t) = \alpha \exp(-\beta t). \qquad 2)$$

Let us denote by $I(t_1, t_2)$ the number of individuals arriving between t_1 and t_2,

$$I(t_1, t_2) = \int_{t_1}^{t_2} i(t)\, dt \qquad 3)$$

Integration gives

$$I_l(t_1, t_2) = (t_2 - t_1)\,[a - b\,(t_1 + t_2)/2] \qquad 4)$$

$$I_e(t_1, t_2) = \alpha\beta^{-1}[\exp(-\beta t_1) - \exp(-\beta t_2)], \qquad 5)$$

for Equations 1) and 2), respectively. I used Marquardt's iterative algorithm (Conway et al. 1970) to fit 4) and 5) to my data.

The results are conclusive. With one exception the exponential function (Eq. 2)) gave a much better fit than a straight line (Eq. 1)) (Table 2). The exception was *Cercyon lateralis* (Marsh), in which the rate of immigration decreased more slowly than in the other species. My conclusion, then, is that these beetles show an exponentially declining rate of immigration of the type depicted in Figure 1 (case c).

From Table 2 it is clear that, in all the species except *C. lateralis,* most of the individuals arrived during the first 2 days, the predicted proportion varying from 88 % (*C. pygmaeus* (Ill.)) to almost 100 % (*C. haemorrhoidalis* (Fabr.)). In *C. lateralis* the predicted proportion was less, though the estimate of 23 % from the linearly decreasing rate of immigration (Eq. 1)) is certainly an underestimate. (Unfortunately, there is no simple way of expressing the corresponding values for the proportions observed.) As most individuals arrive within the first 2 days, something can be said about the rate of emigration simply by examining the changes in the numbers after the first 2 days (i.e. the colonization curve, $N(t)$, the numbers of individuals in a dropping t days old).

I fitted an exponential function to the colonization curves of the more common species of *Cercyon* in both England and Finland (data from Hanski & Koskela 1977, see also Hanski 1980a); the first few days were excluded to remove the effect of immigration. Clearly, the fit is very good (Table 3), though the very high values of the correlation coefficients are largely due to the nature of the data (some of these colonization curves are included in Fig. 5 in Hanski 1980a). In other words, excluding the first few days, a valid description is,

$$N(t) = \alpha \exp(-\beta t), \qquad 6)$$

Table 3. Statistics for the standardized colonization curves in *Cercyon* in England and in Finland, excluding the first few days (indicated in the table: start, in days). The parameters are for the equation, $N(t) = \alpha \exp(-\beta t)$.

	England						Finland					
	α	β	SE	r	n	start	α	β	SE	r	n	start
C. obsoletus	43.1	−0.26	3.92	.961	6	3						
C. impressus							121.5	−0.46	1.18	.999	7	2
C. haemorrhoidalis	184.5	−0.62	0.69	.999	5	3	556.5	−1.01	1.32	.999	3	2
C. melanocephalus	118.5	−0.61	2.40	.990	8	2	231.5	−0.70	0.92	.999	6	2
C. quisquilius	42.4	−0.29	1.98	.994	9	1	261.3	−0.67	0.37	.999	7	2
C. unipunctatus	90.9	−0.45	3.35	.999	6	2	136.0	−0.43	6.37	.980	6	2
C. pygmaeus	50.9	−0.23	1.32	.990	7	4	40.8	−0.13	5.92	.929	8	4
C. lateralis	33.2	−0.11	8.37	.904	7	4	38.1	−0.11	2.09	.991	8	4

from which, by differentiation,

$$\frac{dN}{dt} = -\alpha\beta \exp(-\beta t) = -\beta N. \quad 7)$$

The simplest interpretation of the patterns observed is that each individual leaves the dropping with a constant probability, β (d in Fig. 1). To be sure, my results do not allow conclusions to be drawn about the rate of emigration during the first few days.

I shall next examine interspecific variation in β_i and β_e, the parameters defining the rates of immigration (Eq. 2)) and emigration (Eq. 7)), respectively. The simplest hypothesis is that the β s are positively correlated: this would be the case if the changes in the rates of immigration and emigration are determined by the same factors. The following conclusions are suggested by the data in Tables 2 and 3.

The three species *C. obsoletus* (Gyll.), *C. impressus* (Stm.) and *C. haemorrhoidalis* (Fabr.) support the above hypothesis: the first colonizer is *C. haemorrhoidalis,* which also leaves the droppings earlier than the others; *C. obsoletus* is the slowest to colonize the droppings, and it shows the slowest rate of emigration, too. Table 4, which gives the successional mean occurrences (for the calculation of *SMO* see Hanski 1980a), confirms this pattern: the mean occurrence is earliest in *C. haemorrhoidalis,* and latest in *C. obsoletus.* Interestingly enough, the increase in the *SMO* coincides with an increase in size (Table 4).

C. melanocephalus (L.), although resembling the above three species in appearance (in fact, these four species seem to comprise a morphologically and taxonomically (cf. Vogt 1968) uniform group), deviates from the pattern described. It is the smallest of the four (Table 4), yet shows a later *SMO* than *C. haemorrhoidalis,* or even perhaps *C. impressus* (Table 4). It seems clear that in *C. melanocephalus* the successional decline in the rate of immigration is slow, next only to that of *C. obsoletus* (Table 2), whereas the rate of emigration is approximately that of *C. haemorrhoidalis* (Table 3). I draw two final conclusions.

Table 4. The successional mean occurrence (*SMO*) and dry weight in the six species of *Cercyon* presented in Table 2 (for calculation of the *SMO* see Hanski 1980a). The weights are from Koskela & Hanski (1977), except the one for *C. obsoletus,* which is based on length-weight regression.

	SMO (in days) Finland	*SMO* (in days) England	Weight ($\bar{x}\pm$SD)
C. obsoletus	—	4.36	2.60
C. impressus	3.18	3.73	1.90±0.34
C. haemorrhoidalis	2.03	3.23	1.13
C. melanocephalus	2.44	4.16	0.82±0.20
C. pygmaeus	6.39	7.08	0.18±0.04
C. lateralis	7.03	9.51	1.03±0.21

Of the four species, *C. obsoletus, C. impressus,* and *C. haemorrhoidalis* show a positive correlation in changes in the rates of immigration and emigration during the succession, and these changes are related to size, the heaviest species having the latest *SMO.* This supports the hypothesis that the same factors determine the rates of both immigration and emigration. *C. melanocephalus* is exceptional; for some reason or other it colonizes older droppings than one would expect from a knowledge of the three other species. On the other hand, the rate of emigration in *C. melanocephalus* is in accordance with the general pattern. It is worth mentioning that in Northern Europe all these species, except perhaps *C. haemorrhoidalis,* are dung specialists (P. Hammond, pers. comm.).

Another type of question is raised by the two remaining species, *C. lateralis* (Marsh.) and *C. pygmaeus* (Ill.), which are both dung specialists, but which do not seem to be closely related to each other or to the above four species; *C. pygmaeus* is a very small *Cercyon,* whilst *C. lateralis* is larger than *C. melanocephalus* (Table 4). In spite of this difference, the two species show a similar and very late *SMO,* about one week (Table 4, see also Hanski & Koskela 1977). The rate of emigration declines more slowly in *C. lateralis* than in *C. pygmaeus* (Table 3), and it seems (although this is not quite clear) that older droppings are more frequently colonized by *C. lateralis* than by *C. pygmaeus* (Table 2). In fact, I suggested above that *C. lateralis* is exceptional in having a different pattern of immigration from the others (a linearly, not an exponentially declining rate of immigration), which would mean that the rate of emigration depicted in Table 3 is still influenced by immigration. In this case, the conclusion would be the same as in the exceptional case of *C. melanocephalus*: the rate of immigration rather than the rate of emigration is of a deviating type. Whatever the correct answer to this question, it is still clear that both *C. lateralis* and *C. pygmaeus,* especially the latter, behave in a very different way from the above four species.

4. Mature and immature females: Aphodius

In my earlier analysis of successional patterns (Hanski 1980a), I had suitable data to compare the successional occurrence of mature and immature females in four species of *Aphodius*; in

Table 5. The rate of immigration in mature (m) and immature (i) females in four species of *Aphodius*. The numbers are given for three successional periods, the first being the earliest, and the third the latest (the intervals were not fixed).

Period	*ater*		*fossor*		*haemorrhoidalis*		*rufescens*	
	m	i	m	i	m	i	m	i
1	56	33	40	20	22	31	98	55
2	44	18	44	11	17	12	13	9
3	21	13	22	11	3	8	3	2
χ^2	1.25		3.01		3.86		0.23	

χ^2_{05}= 5.99 for df. = 2

each species I found that the mature females had a later *SMO* than the immature ones. In other words, mature females tended to occur in older droppings. Nevertheless, this result itself does not tell much about the patterns of movements. It is therefore imperative to compare the rates of immigration of mature and immature females. I have restricted this comparison to the same four species of *Aphodius* and the same months as before (Hanski 1980a).

This comparison shows that there is no difference between mature and immature females in the rate of immigration (Table 5). The logical conclusion must be that mature females have a lower rate of emigration, i.e. mature females stay longer in a single dropping than immature ones, at least in these four species of *Aphodius*. It is interesting that this result holds both for *A. ater* DeG. and *A. fossor* (L.), which have relatively late *SMO*s, and for *A. haemorrhoidalis* (L.) and *A. rufescens* Fabr., which show earlier *SMO*s (Table 5, see also Hanski & Koskela 1977, Hanski 1980a).

It makes ecological sense that mature females stay longer in a single dropping than immature ones. First, the immature females feed in the droppings, which is best done in the very fresh ones, whilst the mature females lay eggs, which is best done in older droppings, because *Aphodius* larvae are adapted to utilize old droppings (cf. Mohr 1943, Landin 1961). Second, by arriving early and staying a long time in a single dropping mature females become less vulnerable to the risks entailed by migration; they can copulate and, if necessary, feed while the dropping is still fresh. On the other hand, it does not seem very prudent to lay all one's eggs in one dropping. I repeat here that the reproductive tactics in *Aphodius*, which vary greatly, seem to influence the spatial distribution in the populations (Hanski 1979), and may thereby influence their abundance (Hanski 1979). It is not clear how many droppings the eggs should be laid in.

5. Discussion

Comparison between the Finnish and English data (see also Hanski 1980a) indicated that interspecific variation in the movement patterns in *Cercyon* is consistent enough to call for an ecological explanation. I shall argue that this is not possible, however, before more is known about the feeding biology and resources of these species.

The correlations between size and movement patterns in the group of *C. obsoletus*, *C. impressus* and *C. haemorrhoidalis* do not support a simple model of optimized movements (e.g. Parker & Stuart 1976, Hanski 1979; see also Hanski 1980a), for small species, for which the cost of migration is probably higher (e.g. Roff 1977, Koskela 1979, Hanski 1980a), stay a shorter time in one dropping, i.e. move more frequently, than large species. However, in postulating this hypothesis I have made the implicit assumption that the resource dynamics are the same for all these species, which is not necessarily true, for though the adults are coprophagous the larvae are carnivorous. Indeed, assuming that the larvae of these three species are actually feeding on the same prey species, the pattern observed is what one might expect, because every prey species may be assumed to increase in size in the course of succession. If larval feeding biology is crucial, and if competition occurs, these three similar species coexist in spite of the very asymmetric competitive situation: the smallest species always has an advantage because, on average, it feeds on the shared prey before the other species.

Table 6 shows a quantitative comparison (same amount of effort in collecting) between the abundances of these three species in southern Finland and southern England (see Hanski 1980a for further comparisons). The striking difference is that *C. haemorrhoidalis* was extremely common in England, but rare in Finland. Both *C. obsoletus* and *C. impressus* were uncommon in England; in Finland, on the other hand, *C. impressus* was very

Table 6. A quantitative comparison of abundances in four species of *Cercyon* between southern Finland and southern England. *SMO* is here the successional mean occurrence in England.

	Finland	England	*SMO*
C. haemorrhoidalis	45	4910	3.23
C. impressus	1752	303	3.73
C. obsoletus	—	290	4.36
C. melanocephalus	805	1639	4.16

common and *C. obsoletus* absent (in reality it was extremely rare, H. Koskela, pers. comm.). This pattern could be explained by the above hypothesis of asymmetric competition between similar species, but obviously only actual data on the feeding biology could improve our understanding. Similar data are needed to test my conjecture that *C. melanocephalus* feeds on something different from the above three species. Finally, I must emphasize that the present data are really too meagre for definite conclusions on the abundance relations. Although our analysis (Hanski & Koskela 1978) indicated that *C. impressus* and *C. melanocephalus,* the two common Finnish species, were among the numerically stable dung-inhabiting beetles, the spatial and temporal variation in the numbers of any of these species should not be forgotten (Hanski 1979).

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