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Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices

J. M. Lobo, J.-P. Lumaret and P. Jay-Robert

Laboratoire de Zoogéographie, Université Montpellier 3, Route de Mende, F-34199 Montpellier cedex 5 (France)

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Summary. *1.* The confidence limits and the validity of the results obtained by using dung-baited traps were examined in five sites in southern France, which were very close together and similar for most environmental variables but differed in their pastoral history. Site 1 was a virgin site which had been grazed for only a few months by cattle; site 2 had been grazed for 10 years by cattle but the cattle herd had been removed in the previous year; the other three sites had been grazed by sheep, more or less extensively, for many years.
2. Beetle abundance, biomass or richness were not correlated with temperature and precipitation, but were significantly correlated with radiant energy. The energy necessary for flight activity was probably related to the radiant energy level at the soil surface. This allowed identification of the most favourable periods for sampling.
3. At the sites with at present limited resources, the mean biomass of trapped beetles decreased rapidly when repetitive trappings were carried out over several days. An intense trapping during a continuous period led to an underestimate of the number of beetles, due to site impoverishment. When the cattle herd was removed and dung was therefore not available, the trappings made a few months later overestimated the number of beetles. In contrast, after the establishment of a new, large cattle herd in a virgin site, formerly free of grazing, the baited traps underestimated the number of beetles, due to the amount of dung present in the vicinity of the traps.
4. One trapping session and five traps collected 75–80 % of total local species but 95 % of the abundance and biomass of the community. So, for most of the ecological studies, one trapping session and a few baited traps (five in the Mediterranean area where dung beetle communities are very diverse when compared with more temperate areas) are sufficient to give a sample representing the structure of the dung beetle communities. Conversely, an exhaustive inventory for biogeographical studies need more baited traps. At least 15 traps are necessary to collect 95 % of species present at a site. An abacus allows an estimate of the quality of the sampling.

Key words: Scarabaeidae, dung beetles, pitfall-traps, trapping effort, climatic conditions

Introduction

Randomised sampling from a population or community of insects can be accomplished by many different trapping techniques, including pheromone-, light- and food-baited traps (Southwood 1966; Newton & Peck 1975; Vick et al. 1990; Pinniger 1990). Many beetle spe-

Correspondence to: J.-P. Lumaret, *e.mail:* lumaret@bred.univ-montp3.fr

cies of the Scarabaeidae, Staphylinidae, Hydrophilidae or Histeridae families show a preference for dung (Hanski 1987). Animal droppings constitute a patchy and ephemeral habitat where many similar species live together with severe competition (Hanski & Cambefort 1991). Dung beetles belong to a large and complex community comprising other beetles and flies as well as a multitude of other organisms, for example mites and nematodes (Hanski 1991). Because dung beetles live in discrete patches, they are one animal group which forms a clearly-defined community. The true dung beetles include the family Scarabaeidae, with some 5,000 species, the subfamily Aphodiinae of Aphodiidae, with about 1,850 species, and the subfamily Geotrupinae of Geotrupidae, with about 150 species (Hanski 1991). Dung-baited traps can be used to detect populations of true dung beetles with less effort than exhaustive sampling methods. The main types of dung-baited traps described in the literature were compared by Lobo et al. (1988) who concluded that the CSR type (Veiga et al. 1989) was the most efficient (see in § Materials and Methods a short description of the CSR trap). Doube and Giller (1990) agreed that this CSR type gave the best description of the dung beetle community when compared with a complete census of the community occurring naturally in cow pats. In many situations, the composition of species collected from traps cannot be distinguished from the fresh dung (<72 h old), i.e., before the emigration process which occurs when dung is more than 3 days old (Veiga et al. 1989; Hanski 1980).

Most of temperate dung beetles are heliophilous. Doube (1983) and Menendez & Gutierrez (1996) showed that habitat selection by beetles could depend on the light intensity. The openness of sites, which modifies radiance and microclimate (Lumaret & Kirk 1987; Lobo & Montes de Oca 1994; Galante et al. 1995), affects the activity of beetles and determines their spatial microdistribution. How do environmental variables affect the efficiency of trapping ?

Successive samplings of a community may affect the composition of the samples themselves by eliminating or substituting some elements, especially in cases where the number of individuals is low at the outset. For dung beetles, an important problem is to define what sampling effort may be necessary to obtain the most accurate view of the community with the least distortion possible. What is the optimal number of traps to be set ? What is the optimal frequency of sampling ? Do successive trappings significantly affect the results ?

Lumaret et al. (1992) showed that dung beetle communities react quickly to changes in resource availability and in the nature of the ruminants (cattle vs. sheep) producing dung. The number of beetles reflected the amounts of dung available. For example, an increase in the size of a cattle herd leads to an increase in number and biomass of dung beetles (Lumaret et al. 1992). But what are the short-term and long-term consequences of cattle removal? Do the beetles trapped during this period give an accurate sampling of the present, or of the former, community ?

The aim of this paper is to examine: i) the effects of temperature, rainfall and solar radiation on the trapping efficiency (numbers of beetles and species caught); ii) the effects of regular trapping in optimum climatic conditions on numbers trapped and on the size of the remaining untrapped populations; iii) the optimum number of traps needed to provide a minimum data set in ecological and biogeographical studies.

Materials and Methods

Study area and climatic conditions

All the study sites were very similar for most environmental variables. The substratum in all sites consisted of clay soil. The vegetation corresponded to a low garrigue formation, consisting of an herbaceous pasture dominated by *Brachypodium retusum* with a mixed overstory of evergreen and deciduous oaks, *Quercus ilex* and *Q. pubescens*, respectively.

The experiments were carried out at five contrasting sites near Saint-Martin-de-Londres (43°47′ N; 3°44′ E; elevation 190 to 290 m) about 20 km north of Montpellier (southern France). All sites belonged to the same microecological and biogeographical region (Garrigues of the Montpelliérais) (Lumaret

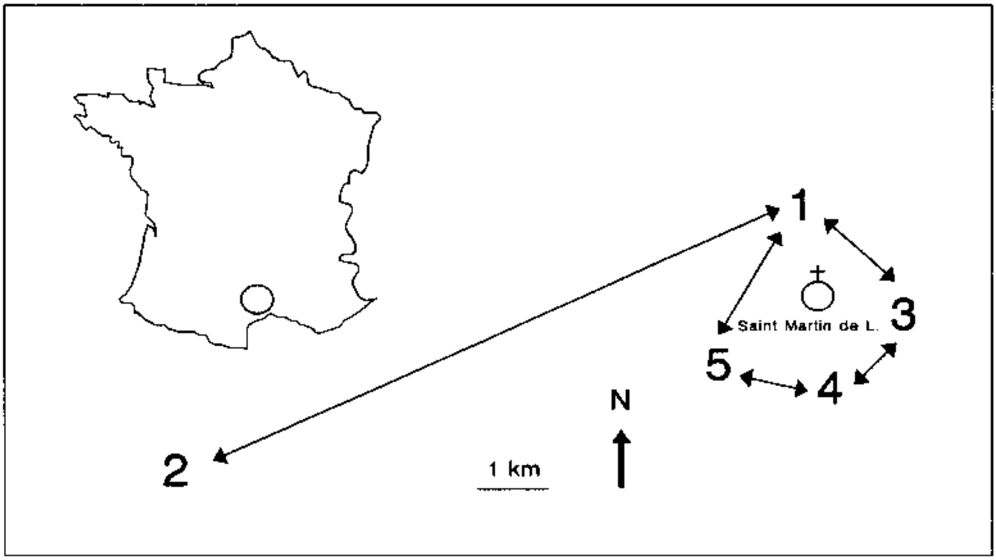

Fig. 1. Schematic diagram of relative location of sampling sites. Site 1 had been grazed by cattle (265 head) since January 1995; site 2 had been grazed by cattle (>100 head) from mid-1984 to mid-1994; sites 3, 4 and 5 were sporadically grazed by sheep (150 head)

1978–79). Four sites were very close to each other (ca. 1.4 km apart), whereas the fifth site was approximately 8.6 km from the others (Fig. 1). The differences in distance between sites were due only to the occurrence of farms supporting cattle herds and sheep flocks.

Temperature (°C), precipitation (mm) and radiant energy (J/cm^2) were measured at the meteorological station of Puéchabon (C.N.R.S. experimental site), 13 km from Saint-Martin-de-Londres, with the presumption of similar climatic conditions at all sites, even if the similarity of climate between the sites was not tested. Total annual precipitation in 1995 was 949.5 mm. The prevailing climate, with two humid phases in autumn and spring, and a dry summer period, corresponds to the cool sub-humid Mediterranean type (Emberger 1955).

History and resource level of the sites

Sites differed in their pastoral history. Site 1 was occupied for the first time in January 1995 by a cattle herd of 265 head grazing freely in several enclosures. Previously this site had remained ungrazed for more than 25 years. Site 2 was grazed permanently from mid-1984 until June 1994 (except in summertime) by a herd of more than 100 head of cattle. The dung beetle community at this site has been well documented previously (site Viols-2 in: Lumaret et al. 1992). Grazing in site 2 stopped definitively in June 1994 when cattle removed. Site 3 has been regularly grazed by sheep (150 head) for more than 50 years (several times a month), whereas sites 4 and 5 have been grazed more sporadically than site 3, but also by sheep.

On average, a mature cow defaecates approximately 12 time a day, i.e. 4.0 kg dry weight (relative humidity RH = 80%) (Waite et al. 1951; Petersen et al. 1956; Marsh & Campling 1970; Whitehead 1970). On average, an adult sheep produces 350 g d.w. day^{-1} of dung (RH = 70%) (Whitehead 1970; Spedding 1971).

In order to estimate the quantity of dung which was available for dung beetles before the experiment started, all the sheep pellets and cattle dung pats were marked at once in the sites and, two weeks later, only the new non marked ones were taken into account. Dung at each site was estimated by counting and weighing the newly deposited 1–15 day-old dung pellets (sheep) and the 1–15 day-old cattle pats collected on the ground along six parallel transects of 80 m^2 each (total 480 m^2). Only site 1 showed a high trophic resource level due to the actual occurrence of cattle (Table 1).

Table 1. Estimated trophic resources per site: numbers of dung pats (cattle grazed sites) and numbers of pellets (sheep grazed sites) per $m^2 \pm$ S.E. Dung pats varied from 50 to 250 g in weight (dry weight) and pellets varied from 0.1 to 9.5 g (dry weight)

Sites	*Altitude (m)*	*Dung density (m^{-2})* (average ± S.E.)	*Origin*
1	240	0.310 ± 0.024	cattle
2	290	0	cattle
3	200	0.011 ± 0.001	sheep
4	200	0.002 ± 0.002	sheep
5	190	0.002 ± 0.002	sheep

Collection of beetles

At each site, five CSR type pitfall traps (Veiga et al. 1989) baited with fresh cattle dung were placed in a straight line at 10 m intervals. Each trap consisted of a plastic basin 210 mm in diameter containing a preservative liquid (water-liquid soap mixture), and buried up to its rim in the soil. Fresh cattle dung (336 ± 2.8 g) was supported on a wire grill on the top of the basin. The traps were cleared after 48 hours and at the same time fresh bait was placed on the grill. All the dung beetles present were collected and counted, and all traps were considered independently.

At site 1, twelve trap-baitings and removals were carried out from 17 April to 24 May, 1995, to give 60 sample units. This five week data set was used to examine the effects of climatic factors (rain, temperature, radiance energy level) on the numbers of beetles caught. In the other four sites however, only five rebaitings were carried out from 17 April to 6 May, 1995, to give 25 sample units for each site. Trapped beetles were identified to species level. Biomass was expressed in milligram (mg) or gram dry weight (g dw) of beetles per trap.

Statistical analyses

As both environmental variables (temperature, precipitation, radiance energy level) and community parameters (abundance, biomass, richness) were not normally-distributed, the Spearman's rank correlation coefficient was used in all measures of covariation.

To help assess whether the mean abundances in each trap were affected by successive baitings, the Kruskall-Wallis one-way analysis by ranking procedure (a non-parametric ANOVA) was used. If a decrease in number was due to overtrapping, this allowed a preliminary estimation of the community size in the different sites by means of a catch-effort method. These calculations were made with the Ricker's method (Krebs 1989).

Results

Species composition

41 dung beetle species and 17,777 specimens were collected from 17 April to 24 May (Table 2). The richness in sites varied from 27 (site 4) to 34 (site 2) species, and the abundance varied from 1,193 (site 4) to 9,334 (site 2) individuals, without correlation between the number of pitfall traps and the richness or abundance. The faunistic composition at all five sites was almost similar. The ten most abundant species made up between 84.5 and 90.5 % of all individuals. The most abundant species (*Onthophagus vacca*) varied between 14.2 and 39.3 % of the total numbers trapped, depending on the sites.

Table 2. Abundance and richness of dung beetle communities at sampling sites

Species	Sampling sites					
	1	2	3	4	5	total
Scarabaeus laticollis L.	19	66	2	0	0	87
Sisyphus schaefferi (L.)	155	66	13	14	10	258
Copris hispanus (L.)	0	7	0	0	0	7
Bubas bubalus (Olivier)	22	193	4	7	3	229
Euoniticellus fulvus (Goeze)	131	341	146	74	57	749
Caccobius schreberi (L.)	53	417	140	61	56	727
Euonthophagus amyntas (Olivier)	174	21	168	63	24	450
Onthophagus taurus (Schreber)	1	0	1	0	1	3
Onthophagus lemur (Fabricius)	386	856	237	138	170	1787
Onthophagus maki (Illiger)	51	213	10	3	6	283
Onthophagus vacca (L.)	489	3672	491	210	215	5077
Onthophagus coenobita (Herbst)	5	12	0	5	1	23
Onthophagus verticicomis (Laicharting)	210	52	232	20	13	527
Onthophagus furcatus (Fabricius)	57	74	154	15	26	326
Onthophagus ovatus (L.)	6	30	4	144	363	547
Onthophagus joannae Goljan	21	7	0	6	4	38
Onthophagus grossepunctatus Reitter	8	3	5	0	0	16
Onthophagus emarginatus Mulsant	27	23	24	10	8	92
Onthophagus semicornis (Panzer)	1	0	0	0	1	2
Aphodius erraticus (L.)	742	233	135	95	93	1298
Aphodius subterraneus (L.)	0	1	0	0	0	1
Aphodius scrutator (Herbst)	0	0	0	0	1	1
Aphodius luridus (Fabricius)	95	9	148	12	13	277
Aphodius haemorrhoidalis (L.)	333	1575	183	212	169	2472
Aphodius constans Duftschmidt	85	44	16	17	38	200
Aphodius satellitius (Herbst)	35	98	26	23	20	202
Aphodius paracoenosus Balthasar & Hrubant	189	328	178	42	51	788
Aphodius pusillus (Herbst)	6	11	0	0	0	17
Aphodius merdarius (Fabricius)	3	4	2	0	0	9
Aphodius sphacelatus (Panzer)	0	0	0	0	1	1
Aphodius granarius (L.)	10	189	5	6	8	218
Aphodius prodromus (Brahm)	1	0	0	1	0	2
Aphodius fimetarius (L.)	16	5	7	2	6	36
Aphodius foetidus (Herbst)	12	619	4	0	11	646
Aphodius scrofa (Fabricius)	30	85	9	4	3	131
Aphodius distinctus (Müller)	0	4	1	1	3	9
Aphodius lividus (Olivier)	0	10	0	0	0	10
Aphodius sturmi Harold	0	4	0	0	0	4
Aphodius biguttatus Germar	61	62	57	7	37	224
Aphodius quadrimaculatus (L.)	2	0	0	0	0	2
Trox hispidus (Pontoppidan)	0	0	0	1	0	
Number of pitfall-traps	*60*	*25*	*25*	*25*	*25*	*160*
Total abundance	3436	9334	2402	1193	1412	17777
Total richness	*33*	*34*	*28*	*27*	*30*	*41*
Total biomass (in g dw)	67.4	251.0	44.3	20.1	19.7	402.5

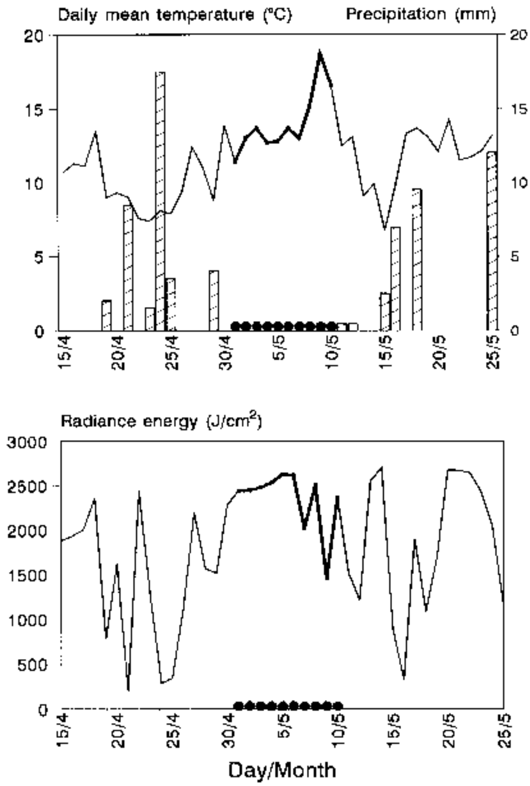

Fig. 2. Variation with time (15 April – 25 May period) of the daily mean temperature (°C) (solid line) and daily precipitation (mm), daily radiant energy level (J/cm²) at sampling sites (meteorological data from the C.N.R.S. site of Puéchabon, 13 km apart from Saint-Martin-de-Londres). The thick dotted line corresponds to the most favourable period to estimate the effect of successive trappings

Effects of climatic factors

Figure 2 shows the daily variation of temperature, precipitation and radiance energy level for the period 15 April – 25 May, 1995. The experiments started on April 17th, after a long dry period (no precipitation since 6th of March) and a dry winter season (25.3 mm in January; 18 mm in February; 9.5 mm in March, concentrated on one day). A rainy period occurred from the 19th to the 29th of April (37 mm in total), the second trapping occurring at the end of this period. From the 11th to the 18th of May, a new rainy period occurred.

Figures 3 and 4 show the variation of beetle biomass with time. In all five sites, a very small biomass of beetles was trapped on the 17–18 April period, which corresponded to the

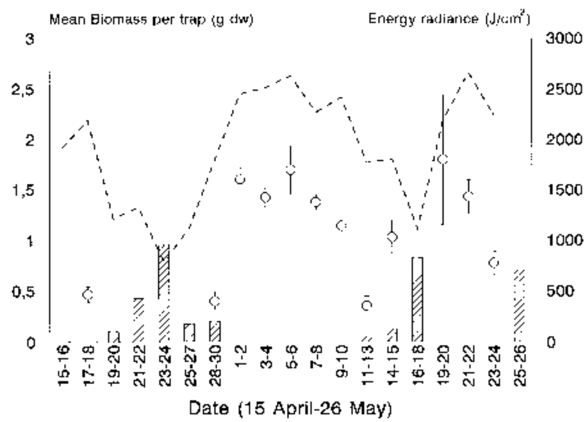

Fig. 3. Variation with time (two day interval) in mean dung beetle biomass per trap (dry weight ± SE) at site 1. The broken line represents the two day interval variation in energy radiance. The bars represent precipitation (see Fig. 2). The two day intervals correspond to the lapse of time between two trap removals

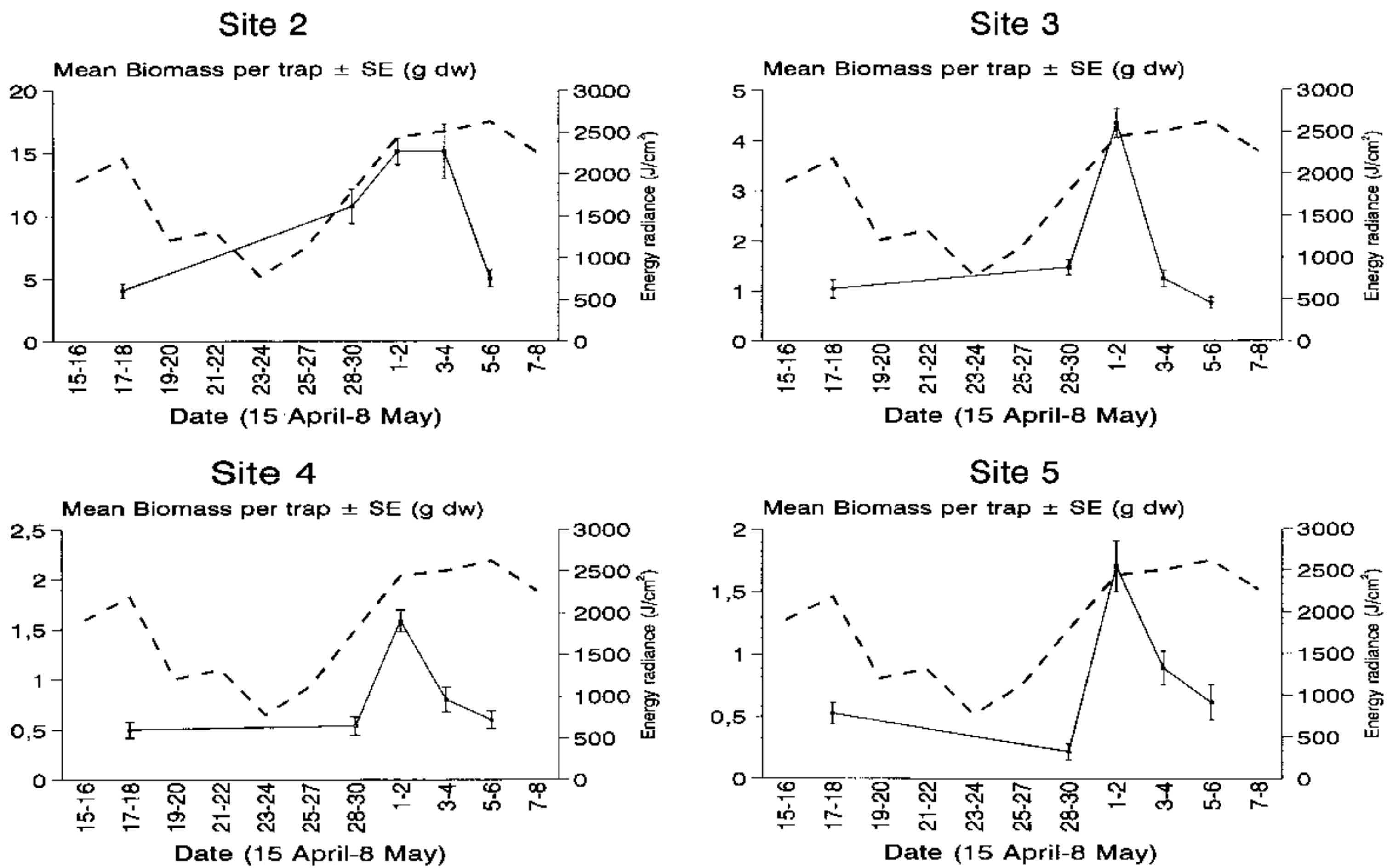

Fig. 4. Variation with time of the mean biomass per trap (dry weight ± SE) at sites 2–5. The broken line represents the variation in energy radiance

Table 3. Spearman's rank correlation coefficients between environmental variables and abundance, biomass and richness of dung beetles collected by trapping at site 1 (period 15 April – 24 May 1995). In all cases df = 10. * = p < 0.05; ** = p < 0.01; NS = non significant

	Temperature	Precipitation	Radiant energy
Mean abundance per trap	0.296 NS	–0.437 NS	0.723 *
Mean biomass per trap	0.291 NS	–0.528 NS	0.708 *
Mean richness per trap	0.371 NS	–0.543 NS	0.885 **

end of the dry period. The two rainy periods with low radiance (overcast) corresponded also to a small biomass of beetles. Conversely, following the rain, there was a large emergence of beetles in all five sites when radiance was high (Figs. 3 and 4).

Temperature and precipitation were not significantly correlated with beetle abundance, biomass or richness (Table 3). Conversely radiance was positively correlated with all three parameters (Table 3). The radiant energy level appeared to be the major factor that explained dung beetle activity and influenced trapping success.

Effect of successive trapping

Between the 15th of April and the 1st of May, the small numbers and biomass of beetles only reflected unfavourable climatic conditions. The largest numbers of beetles were caught when the radiant energy level was highest and precipitation were absent. As the most favourable period for trapping was from the 1st to the 10th of May, so, in order to test the effect of successive trappings, the 1–6 May period was selected. After a peak of biomass occurring at all sites on 1–2 May, the mean biomass of trapped beetles decreased in all sites when successive trappings were carried out, except at site 1 (Fig. 3 and Fig. 4). The mean abundance per trap in each of the five sites for the 1–6 May period varied in the same way (Fig. 5A).

When fresh dung was abundant (site 1), the numbers of trapped beetles were not significantly different (Kruskal-Wallis test = 1.40; p = 0.5) between the three successive trapping occasions (Table 4 and Fig. 5A). Conversely, when dung resources were limited (site 3) or very limited (sites 4 and 5), and even when dung had been abundant previously (site 2), the decrease in numbers between several successive trapping periods was significant (sites 3, 4, 5) (see Table 4). This decrease was all the more important since dung was previously abundant (e. g., site 2).

This analysis was based on three occasions at each site and the comparison of numbers corresponded to these three successive trappings. As the trapping period was very short (6 days), sampling concerned the same dung beetle community in each site, without phenological variations for species. So, independent of climatic conditions (optimal period), the decrease in beetles in sites 2 to 5 for the 1–6 May period was only due to trapping.

Table 4. Values of Kruskal-Wallis one-way analysis by ranks procedure (KW) for analyzing the variation of the mean abundance per trap between three sampling periods (1–2, 3–4 and 5–6 May, 1995). p = associated probability

Site number	KW	p	Signif. level
1	1.40	0.500	NS
2	9.78	0.008	**
3	11.18	0.004	**
4	9.69	0.008	**
5	8.93	0.010	*

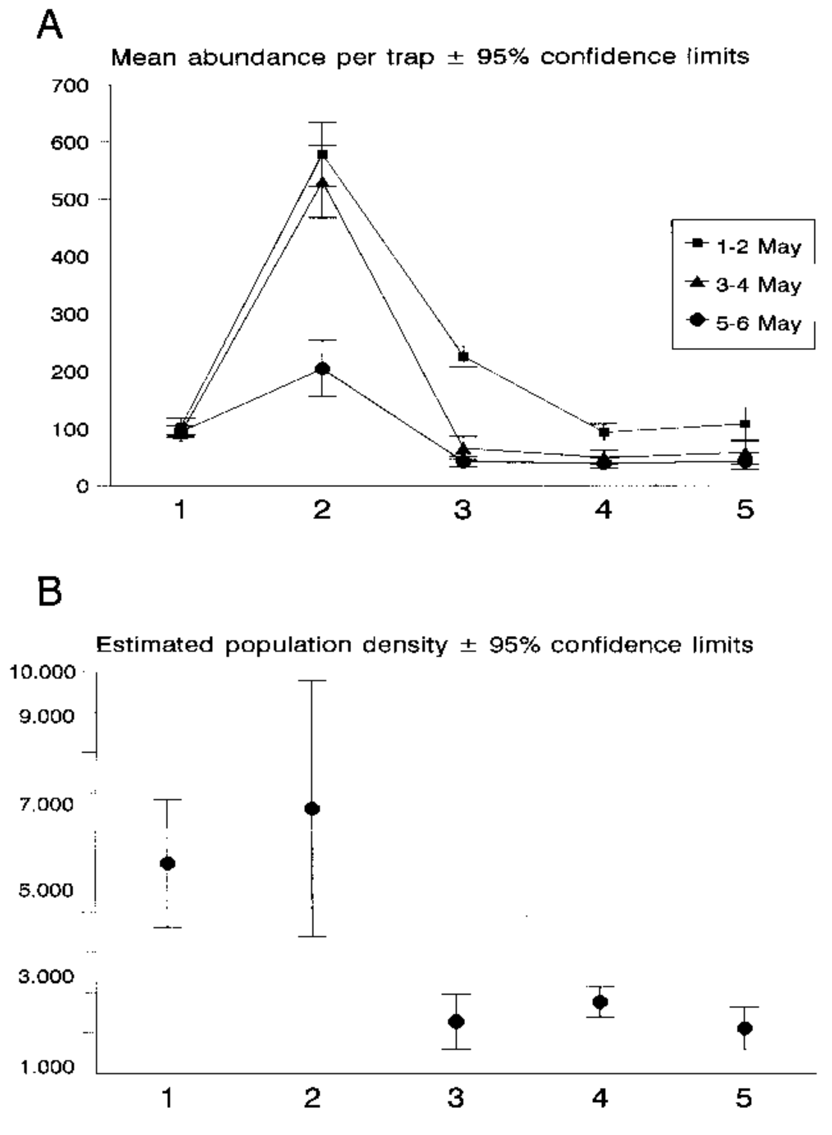

Fig. 5. *(A):* Mean abundance per trap at each of the five sites for the two consecutive samples following the peak of maximum abundance (1–2 May). *(B):* Estimation by means of the Ricker's catch-effort method (Krebs 1989) of the density of dung beetles at each of the five sites. At site 1, data correspond to five successive samplings (1–10 May period); at other sites, data correspond to three successive samplings (1–6 May period)

According to the estimation of the community size in sites by means of Ricker's method, the densities in sites 1 and 2 were not significantly different from one another, and those communities had many more beetles than sites 3, 4 and 5 (Figure 5B).

At sites 2, 3, 4, and 5, the mean abundance per trap (Fig. 5A) was in accordance with the estimated population density (Fig. 5B). Conversely, at site 1, the result was a distortion between the observed abundance (trap data) (Fig. 5A) and the estimation of number of dung beetles obtained after calculation (Fig. 5B)

Optimal number of traps

The estimation of the numbers of beetles could depend both on site history and available resources, but successive trappings or the number of traps used can also modify the number of beetles collected in each trap. The organisation of a beetle community at a site depends both on the number of species and on their relative abundance. How many traps are necessary to obtain a reliable representation of the community?

The mean number of species per trap in this study ranged between the limits $\pm 1.962\ \sigma/\sqrt{n}$ for a 95 % confidence interval, where σ = standard deviation of the number of species and n = number of traps (Snedecor & Cochran 1973). For this 95 % confidence limit, one can define the relative level (L) of precision desired. If $L = 1.962\ \sigma/\sqrt{n}$, then $n = (1.962)^2\ \sigma^2/L^2$.

For the first five trappings made at sites 1 to 5 (17 April – 6 May period), data from 125 samplings (5 traps × 5 successive trappings × 5 sites) allowed the calculation of the values of n for e.g. 4 desired values of L (5 %, 10 %, 15 % and 20 % of the mean species per trap, respectively). Figure 6 shows that when using 4 traps, the number of species per trap fluctuated about ±15 % against the mean. For example, if the mean observed richness was 20 species per trap, the limits were ±3 species using 4 traps (20 ± 3 species). If 8 traps had been used, the gain would only have been one species (20 ± 2 species). Using 3 traps allowed the collection of between 58.6 % and 61.8 % of all dung beetle species present at a site (local species) (Table 5) and about 41 % of all species present at all 5 sites (regional species) (Fig. 7A). With 5 traps, between 70 % and 72.8 % of local species (Table 5) and about 50 % of regional species were collected (Fig. 7A). Figure 7A shows that at least 15 traps are necessary to collect 95 % of species at a site. Conversely, using only 2 traps gives ca. 53 % of the species of a site but these correspond to 86 % of total beetle abundance (Fig. 7B) and 85 % of the total biomass (Fig. 7C and Table 5).

Table 5. Variation of the share of the total number of species collected by trapping (95 % confidence interval) and their relative abundance and relative biomass according to the number of traps used at a site

Number of traps	% of local species	% abundance	% biomass
2	51.08–55.27	85.72	84.97
3	58.64–61.83	89.27	88.93
5	70.04–72.83	93.97	94.01
7	78.20–81.02	96.65	96.78
10	89.17–86.69	98.68	98.77

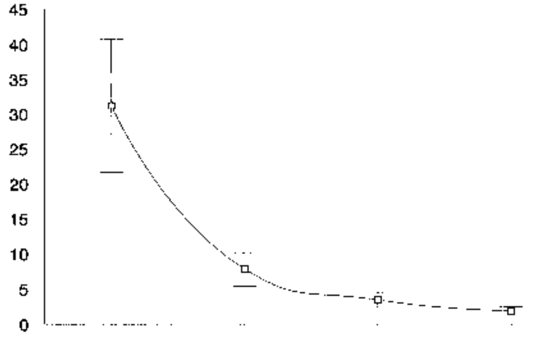

Fig. 6. Number of pitfall traps required (n) at four values of the relative level of precision (L) desired (5 %, 10 %, 15 % and 20 % of the mean number of species per trap). The error bars correspond to the n variation between the five sites

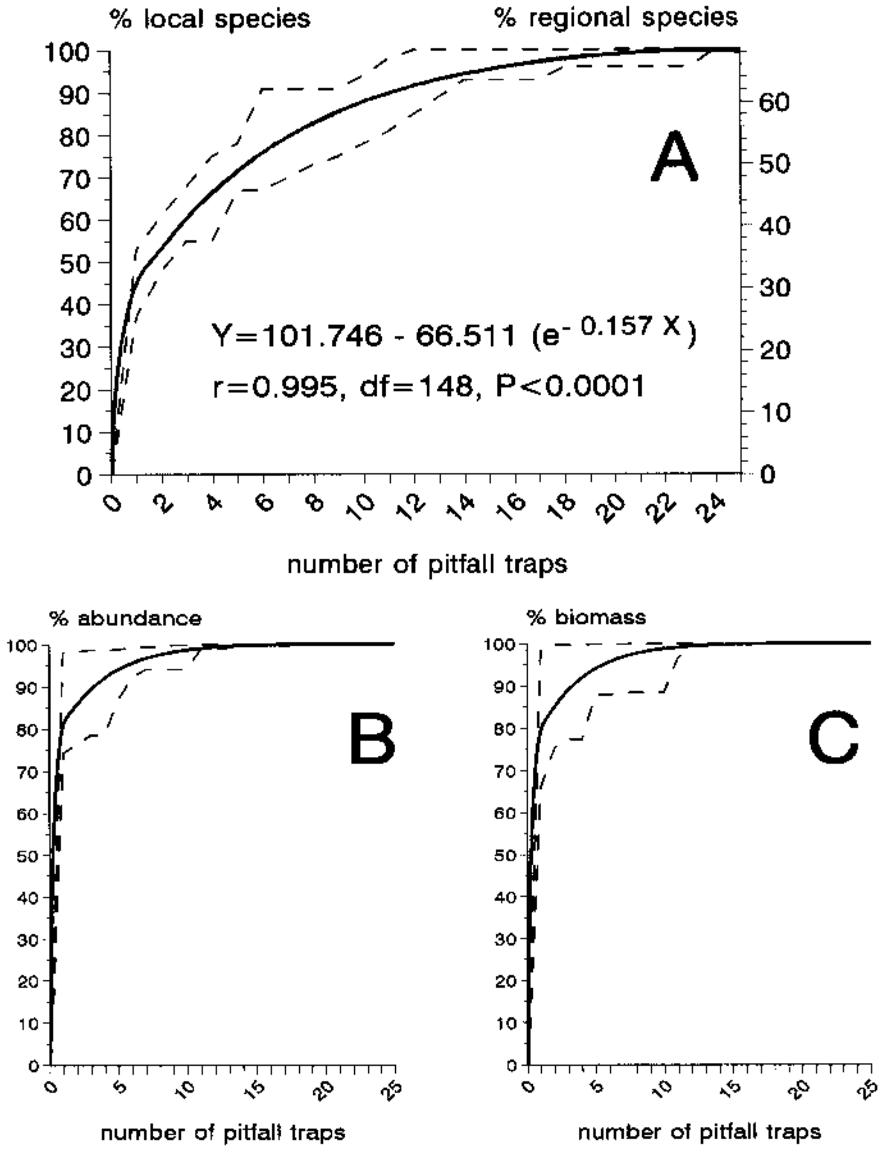

Fig. 7. (A): Local and regional variation of the percentage of species trapped according to the number of pitfall traps used. Asymptotic adjustment of data ($Y = A - B\ (e^{cx})$), with maximum and minimum of species numbers (dotted line). Relative abundance (%) (B) and relative biomass (%) (C) of dung beetles according to the number of pitfall traps used

The calculation of the power regression ($Y = aX^b$) between the mean richness per trap and the number of traps allows the building of curves giving the proportion of the number of species which have been trapped against the total number of species present at a site (trapped percentage = TP) (Fig. 8). Results showed that the number of traps depends on the number of active species when the traps are set up at a site. Figure 8 corresponds to an abacus which allows an estimation of the quality of the sampling in the French Mediterranean area. For

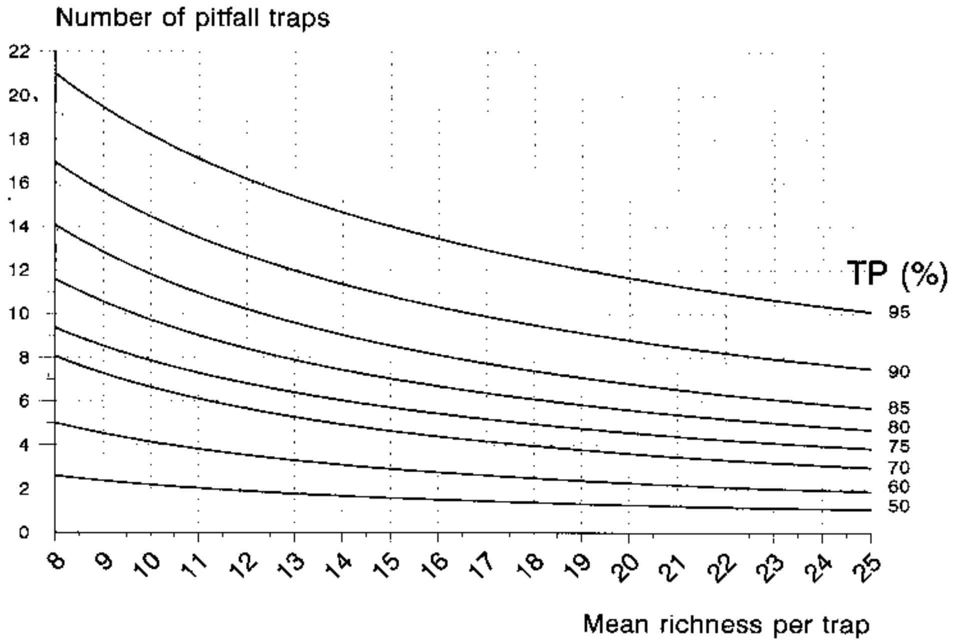

Fig 8. Variation in the number of pitfall traps required for different trapped percentage (TP) according to the mean richness of dung beetles per trap. The curves have been drawn by means of power regression ($Y = aX^b$) between the mean number of species per trap and the number of traps required to obtain the trapped percentage desired

example, in sites where 20–25 species are commonly collected per trap, using 5 traps encompasses 75–80 % of the total species (Fig. 8). These in turn represent about 94 % of abundance and biomass in the dung beetle community (Table5).

Discussion and Conclusion

The relevance of studies on animal communities directly depends on the sampling quality (Frontier 1983; Magurran 1988). In such conditions, dung beetle communities constitute a good model as they concern well structured zoocoenoses (Hanski 1991) and as actual trapping methods look very efficient (Doube & Giller 1990). Nevertheless, several parameters can affect sampling results.

The factors determining the composition of dung beetle communities have been reviewed by Doube (1987). Many factors influence the readiness of beetles to fly and therefore to be available to be caught. Short-term fluctuation in weather, particularly solar radiation and ambient temperature, is an important determinant of dung beetle activity. But in the present case, only the solar radiant energy level appeared to be the factor that explained the dung beetle activity and influenced the trapping success, whereas air temperature and precipitation were not correlated with beetle abundance, biomass or richness.

In tropical conditions, several crepuscular and nocturnal dung beetles elevate their body temperature by endogenous heat processes (e.g., pre-flight warm-up). The rates of specific energy metabolism of these species can approach and even exceed that of active mammals of similar size at the same ambient temperature (Bartholomew & Casey 1977a, b). Large tropical dung beetles often maintain thoracic temperatures of 40 °C or more in an ambient temperature of only 25–26 °C. Such highly elevated body temperatures during terrestrial activity are probably selectively advantageous in the competitive foraging for food in tropical regions (Bartholomew & Heinrich 1978). Conversely, in temperate regions, Landin (1961) concluded that fluctuation in populations of dung beetles mostly depended on abiotic factors rather than on competition. In temperate regions, although crepuscular beetles such as Geotrupes species also elevated their body temperature by endogenous heat processes (Galante, pers. comm.), most species have diurnal activity, and if these beetles do not elevate body temperature by endogenous heat production, our hypothesis is that the energy necessary for flight activity can be linked to the radiant energy level at the soil surface. The surface layers of soil and dung may become considerably warmer than the ambient air during hot, sunny days (Landin 1961). This could explain both why this factor was significant whereas air temperature was not, and also why, when many dung beetles were active during the periods of clear sunlight, the flight activity declined markedly in overcast conditions. Examination of literature clearly shows that both temperature and rainfall have a major effect on dung beetle activity in many situations (Holter 1982; Davis 1987, 1990; Lumaret & Kirk 1987). Present results appear to contradict previous data. This discordance is only apparent as it is due to the scale of time: seasonal scale for previous works; day scale for present work. Indeed, Figures 3 and 4 show that the trapping of the 17–18 April period, which followed a long dry period, gave few beetles even when radiance was high.

In all sites, except site 1, intense and successive trapping during a continuous period led to an impoverishment of sites. At site 2, all traps attracted many beetles and two successive trappings had no effect on the numbers collected. However, the third trapping session led to a significant decrease ($p < 0.01$) in beetle abundance (Fig 5A). At sites 3, 4 and 5, two successive trapping periods led to a high decrease in abundance of trapped beetles. For the second trapping (3–4 May), the numbers of beetles per trap were close to those obtained at site 1 (Fig 5A). However, the estimated number of beetles at sites 3, 4 and 5 was few, contrary to site 1 (Fig. 5B).

Repetitive trapping had various effects according to the level of available trophic resources. At site 1, where a large cattle herd (265 head) had been present full-time for 4 months, several hundred dung pats were deposited daily. These pats competed with the five baited traps, and traps had no opportunity to attract more beetles than any one of natural pats. So, baiting could underestimate the number of beetles active at the site. Conversely, site 2 was grazed continuously during a ten-year period by a large cattle herd of more than 100 head (Lumaret et al. 1992). Many dung beetles still remained even when no dung was available, since the cattle had been removed several months before. The five baited traps constituted the only resource available to the dung beetles at that time. As a consequence, baiting overestimated the number of beetles present at the site. At sites 3, 4 and 5 dung was limited but steadily available, due to the regular passage of a flock of sheep. So, trapping drained the sites of most of their beetles (Fig. 5A), and the total number of trapped beetles from successive trappings was close to the estimation of the entire beetle population at those sites. This explains the shape of the curves in figure 4 for the period 16 May. When the size of the entire beetle population was small, sites were quickly emptied of all their beetles and those which were trapped subsequently may be due to the arrival of some immigrants from surrounding areas. When beetles were numerous at a site, the number of beetles collected for the first time seemed to be sufficient to give a good estimation of the organisation of the beetle community.

So, the representation of communities by the use of dung-baited pitfall traps is variable and depends on the equilibrium (or lack thereof) between available trophic resources and population size. In a state of equilibrium, the total number of dung beetles closely follows the level of trophic resources (Lumaret et al. 1992). Conversely, the lack of dung beetles adapted to local dung types may lead to the accumulation of dung for prolonged periods, even in intensively grazed areas (Lumaret & Iborra 1996). An example of this situation has been well documented in Australia before the intentional introduction of foreign dung beetles (Doube et al. 1991; Kirk & Lumaret 1991).

In the present study, two examples of non-equilibrium have been found. i): After a regular increase of dung beetle populations linked to regular and abundant dung supply (e.g. site 2; see

Lumaret et al. 1992), the resource was stopped suddenly when the cattle herd was taken away (present study). Trappings, made a few months later, overestimated the number of beetles present at the site, as dung in the traps constituted the only dung present for several months. The numbers of beetles actually trapped was much greater than needed to remove the entire resource, and exploitative competition may be intense at the site. ii): In contrast, the establishment of a new, large cattle herd in a virgin site, formerly free of grazing led to an Australian-like situation (Doube et al. 1991), with too much dung in comparison with the number of dung beetles present (e.g., site 1). The efficiency of traps baited with fresh cattle dung was reduced, due to the high competition between traps and dung pats at the site (e.g., 5 traps versus several thousands dung pats at site 1). Traps gave an underestimation of the number of beetles active at the site. In such conditions, the numbers of trapped beetles may be considered as being roughly equivalent to the sum of beetles immigrating toward a natural dung pat.

When equilibrium occurred between numbers of dung beetles and resources (sites 3, 4 and 5), trapping seemed to give a good estimation of beetle numbers, especially when populations were small, provided that only one session of trapping was carried out.

Our study also showed that the sampling-effort must be adjusted to the objectives of the experimentation. The use of only two to five baited traps gives a good idea of the structure and organisation of a dung beetle assemblage and may be sufficient for most of ecological studies, even when rare species are excluded from these studies. However, in biogeographical works which need exhaustive samplings a high trapping-effort is required and 15 traps are necessary to collect 95 % of species at a site.

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References

Bartholomew, G. A., Casey, T. M. (1977a) Endothermy during terrestrial activity in large beetles. Science **195**, 882–883.

Bartholomew, G. A., Casey, T. M. (1977b) Body temperature and oxygen consumption during rest and activity in relation to body size in some tropical beetles. J. Therm. Biol. **2**, 173–176.

Bartholomew, G. A., Heinrich, B. (1978) Endothermy in African dung beetles during flight, ball making, and ball rolling. J. Exp. Biol. **73**, 65–83.

Davis, A. L. V. (1987) Geographical distribution of dung beetles (Coleoptera: Scarabaeidae) and their seasonal activity in south-western Cape Province. J. ent. Soc. sth. Afr. **50** (2), 275–285.

Davis, A. L. V. (1990) Climatic change, habitat modification and relative age of dung beetle taxa (Coleoptera: Scarabaeidae, Hydrophilidae, Histeridae, Staphylinidae) in the south-western Cape. Ph. D. thesis, Univ. of Cape Town, South Africa.

Doube, B. M. (1983) The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. Bull. Entomol. Res. **73**, 357–371.

Doube, B. M. (1987) Spatial and temporal organization in communities associated with dung pads and carcasses. In: Gee, J. H. R., & Giller, P. S. (eds.) Organization of communities, past and present. 27th Symposium of the British Ecological Society. Blackwell, Oxford, pp. 255–280.

Doube, B. M., Giller, P. S. (1990) A comparison of two types of traps for sampling dung beetle populations (Coleoptera: Scarabaeidae). Bull. Entomol. Res. **80**, 259–263.

Doube, B. M., Macqueen, A., Ridsdill-Smith, T. J., Weir, T. A. (1991) Native and introduced dung beetles in Australia. In: Hanski, I., & Cambefort, Y. (eds.) Dung Beetle Ecology. Princeton University Press, Princeton, N. J. pp. 255–278

Emberger, L. (1955) Projet d'une classification biogéographique des climats. Annals biol. **31**, 249–255.

Frontier, S. (1983) Stratégies d'échantillonnage en écologie. Masson, Paris, 494 p.

Galante, E., Mena, J., Lumbreras, C. (1995) Dung beetles (Coleoptera, Scarabaeidae, Geotrupidae) attracted to fresh cattle dung in wooded and open pasture. Environ. Entomol. **24** (5), 1063–1068.

Hanski, I. (1980) Migration to and from cow droppings by coprophagous beetles. Ann Zool. Fenn. **17**, 11–16.

Hanski, I. (1987) Nutritional ecology of dung- and carrion-feeding insects. In: Slansky, Jr., & Rodriguez, J. G. (eds.) Nutritional Ecology of Insects, Mites, and Spiders. Blackwell, Oxford, pp. 837–884.

Hanski, I. (1991) The Dung Beetle Community. In: Hanski, I., & Cambefort, Y . (eds.) Dung Beetle Ecology. Princeton University Press, Princeton, N. J., pp. 5–21.

Hanski, I., Cambefort, Y. (1991) Competition in dung beetles. In: Hanski, I., & Cambefort, Y. (eds.) Dung Beetle Ecology. Princeton University Press, Princeton, N. J., pp. 305–329.

Holter, P. (1982) Resource utilization and local coexistence in a guild of scarabeid dung beetles (Aphodius spp.). Oikos **39**, 213–227.

Kirk, A. A., Lumaret, J. P. (1991) The importation of Mediterranean adapted dung beetles (Coleoptera: Scarabaeidae) from the northern hemisphere to other parts of the World. In: Groves, R. H., & Di Castri, F. (eds.) Biogeography of Mediterranean Invasions. Cambridge University Press, U.K., pp. 409–420.

Krebs, C. J. (1989) Ecological Methodology. Harper and Row publish., New York.

Landin, B. O. (1961) Ecological studies on dung-beetles (Coleoptera Scarabaeidae). Opusc. Ent., suppl. XIX, 1–227.

Lobo, J. M., Martin-Piera, F., Veiga, C. M. (1988) Las trampas pitfall con cebo, sus posibilitades en el estudio de las comunidades coprofagas de Scarabaeoidea (Col.). I. Caracteristicas determinantes de su capacidad de captura. Rev. Ecol. Biol. Sol **25** (1), 77–100.

Lobo, J. M., Montes de Oca, E. (1994) Distribucion local y coexistencia de *Digitonthophagus gazella* (Fabricius, 1787) y *Onthophagus batesi* Howden & Cartwright, 1963 (Coleoptera: Scarabaeidae). Elytron **8**, 117–127.

Lumaret, J.-P. (1978–79) Biogéographie et écologie des Scarabéides coprophages du sud de la France. II. Analyse synécologique des répartitions. Vie Milieu, C, 28–29, 179–201.

Lumaret, J.-P., Kadiri, N., Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. J. Appl. Ecol. **29**, 349–356.

Lumaret, J.-P., Kirk, A. A. (1987) Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeinae). Acta Zool. Mex. (n.s.) **24**, 11–55.

Lumaret, J.-P., Iborra, O. (1996) Separation of trophic niches by dung beetles (Coleoptera, Scarabaeoidea) in overlapping habitats. Pedobiologia **40** (6), 1–13.

Magurran, A. E. (1988) Ecological Diversity and its Measurement. Princeton University Press, N. J., 179 p.

Menéndez, R., Gutiérrez, D. (1996) Altitudinal effects on habitat selection of dung beetles (Scarabaeoidea: Aphodiidae) in the northern Iberian peninsula. Ecography **19**, 313–317.

Marsh, R., Campling, R. G. (1970) Fouling of pastures by dung. Herbage Abstracts **40**, 123–130.

Newton, A., Peck, S. B. (1975) Baited pitfall traps for beetles. Coleopts. Bull. **29** (1), 45–46.

Petersen, R. G., Lucas, H. L., Woodhouse, W .W. Jr. (1956) The distribution of excreta by freely grazing cattle and its effects on pasture fertility. I. excretal distribution. Agron. J. **48**, 440–449.

Pinniger, D. B. (1990) Food-baited traps; past, present and future. J. Kansas ent. Soc. **63** (4), 533–538.

Snedecor, G. W., Cochran, W. G. (1973) Statistical Methods. 6th ed. Iowa State Univ. Press, Ames, Iowa, USA.

Southwood, T. R. E. (1966) Ecological methods with particular reference to the study of insect populations (reprinted 1976). Chapman and Hall Ltd., London.

Spedding, G. R. W. (1971) Grassland ecology. Grazing, Oxford, 1–101.

Veiga, C. M., Lobo, J. M., Martin-Piera, F. (1989) Las trampas pitfall con cebo, sus posibilitades en el estudio de las comunidades coprofagas de Scarabaeoidea (Col.). II: Analisis de efectividad. Rev. Ecol. Biol. Sol **26** (1), 91–109.

Vick, K. W., Mankin, R. W., Cogburn, R. R., Mullen, M., Throne, J. E., Wright, V. F., Cline, L. D. (1990) Review of pheromone-baited sticky traps for detection of stored-product insects. J. Kansas ent. Soc. **63** (4), 526–532.

Waite, E., Mac Donald, W. B., Holmes, W. (1951) Studies in grazing management. III. The behaviour of dairy cows grazed under the close folding and rotational systems of management. J. Agric. Sci. **41**, 163–173.

Whitehead, (1970) The role of nitrogen in grassland productivity. Bull. 48. Commonwealth Bureau Pastures Field Crops, Berkshire, England.