SPATIAL MICRODISTRIBUTION OF TWO INTRODUCED DUNG BEETLE SPECIES *DIGITONTHOPHAGUS GAZELLA* (F.) AND *EUONITICELLUS INTERMEDIUS* (REICHE) (COLEOPTERA SCARABAEIDAE) IN AN ARID REGION OF NORTHERN MEXICO (DURANGO, MEXICO)

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RESUMEN

Digitonthophagus gazella (F.) y *Euoniticellus intermedius* (Reiche) son dos especies de escarabajos coprófagos que fueron introducidos en el continente americano y, que en la actualidad, constituyen las especies dominantes dentro del gremio en Mapimí (Durango, México). Se analizaron las distribuciones de ambas especies en un ambiente aparentemente homogéneo mostrado a lo largo de transectos constituidos por boñigas de vaca depositadas artificialmente y por trampas pitfall. Ambas especies mostraron distribuciones agregadas, las cuales se presentan a densidades bajas, medias y altas, así como cuando hay o no hay emigración. La agregación intraespecífica observada probablemente se deba a una cierta preferencia de los procesos de inmigración hacia las boñigas (y trampas) seleccionadas repetidamente así como por aquellas boñigas o trampas con mayor número inicial de individuos. A esta escala espacial la correlación negativa mostrada entre *D. gazella* and *E. intermedius* se debe probablemente a tasas de emigración diferenciales. Esta tasa de emigración para cada especie depende del número de individuos de la misma especie que llegan al excremento y no del número de individuos de la otra especie. Concluimos que las interacciones competitivas entre individuos intraespecíficamente agregados son muy probablemente las causas de la emigración diferencial y de la segregación microespacial observada de estas dos especies en esta región.

Palabras Clave: Distribución espacial, agregación, covariación, escarabajos del estiércol, especies introducidas, región árida.

ABSTRACT

The introduced dung beetle species *Digitonthophagus gazella* (F.) and *Euoniticellus intermedius* (Reiche) have become the dominant species into the Scarabaeinae guild of the Mapimí region (Durango, México). The distributions of these two species in an apparently homogeneous environment was analyzed through transects of artificially placed dung pats and pitfall traps baited with cow dung. Both species showed aggregated distributions. Aggregation ocurred at high, moderate and low densities and was not affected by emigration. The observed intraspecific aggregation was probably due to immigration processes: repeated dung beetle selection for the same dung pats and selection of dung pats with larger initial populations. The spatial negative association between *D. gazella* and *E. intermedius* observed at this spatial scale was probably due to differential emigration rates. The rate of emigration of both species depended on the number of the conspecifics into a dung pat, but not on

the number of beetles from the other species. We conclude that the competitive interactions among individuals intraspecifically aggregated likely led to differential emigration rates and caused the observed microspatial segregation.

Key Words: Spatial distribution, aggregation, covariation, dung beetles, introduced species, arid region.

INTRODUCTION

The composition of the dung beetle community in the Mapimí arid region is very simple in comparison with those in tropical and temperate areas and even with those occurring at the edges of the Chihuahuan desert (Lobo, 1996). In fact, it was simpler 20 years ago when it was composed by a very few species. At the present time, at least 3 of the 6 species found in the Mapimí region arrived in the last 13 years, while another 2 were probably introduced very recently (Lobo, *op. cit.*). In this new formed and poor dung beetle assemblage, two species *Digitonthophagus gazella* (F.) and *Euoniticellus intermedius* (Reiche) are dominant both in abundance and biomass.

Digitonthophagus gazella and *E. intermedius* are two Indoafrican dung beetle species which coexist in many African regions (Cambefort, 1991; Doube, 1991; Rougon & Rougon, 1991). These species have been used successfully in the introduction programs carried out in Australia and United States for controlling dung accumulation and dung-breeding flies (Blume, 1984; Blume & Aga, 1978; Doube *et al.*, 1991). *D. gazella* was first collected in Mapimí in 1984 (Zunino & Halffter, 1988), 12 years after its first releases in continental United States. *E. intermedius* was released in 1979-1980 (Blume, 1984) and its presence in La Michilía and Mapimí Biosphere Reserves was recorded in 1992 (Montes de Oca *et al.*, 1994). Accordingly the time elapsed between the release and record dates, the dispersal capability of both species toward Mapimí has been similar.

The spontaneous arrival of these exotic species to Mapimí provide the opportunity to follow the development of a simple dung beetle community in a distant and biogeographically different region from the species original home (Africa). The purpose of this paper is to describe the spatial distribution of these two introduced species at the level that Hanski & Cambefort (1991) considered the most interesting to analyze, i.e. among nearly dung pats located in an apparently homogeneous habitat. Such a study of the spatial distribution of beetles at this scale in Mapimí can permit to know the processes involved in microhabitat selection level in the formation of the community. With this information we can at a later date observe and analyze the evolution of possible interactions between these species and their role in determining spatial distribution and coexistence.

At the small spatial scale, aggregated distribution seems to be a general trend showed by dung beetles (Holter, 1982; Hanski, 1980; Hanski & Cambefort, 1991)

and other insects (i.e. Diptera) exploiting patchy and ephemeral resources (Hanski & Kuusela, 1977; Shorrocks *et al.*, 1979; Atkinson & Shorrocks, 1981; Kneidel, 1985; Ives 1988, 1991). Some patches have large numbers of individuals while others have only few individuals. One can observe a high spatial variance in the density patch-occupation of one species (intraspecific aggregation) and a covariation in the numbers of two species across a set of patches (interspecific aggregation). The existence of an intraspecific aggregation does not necessarily lead to an interspecific aggregation. Also, two species can be positively or negatively associated with or without the action of the interspecific competition (Hanski, 1986; Hanski & Cambefort, 1991). Hanski (1991) argues that intraspecific spatial aggregation is often much greater than interspecific aggregation facilitating the species coexistence. Such a type spatial distribution between two species promote an increase of intraspecific competition and a decrease of interspecific competition (Shorrocks *et al.*, 1979; Hanski, 1981, 1991; Hanski & Cambefort, 1991; Kouki & Hanski, 1995).

The dynamics and structure of a dung pat beetle community can be considered as the result of the interplay between immigration and emigration processes (Hanski, 1980). Main causes of intraspecific aggregation are related with the immigration process (Hanski & Cambefort, 1991): i) organisms always choose patches with similar suitable conditions (Hanski, 1980); ii) organisms repeatedly choose for colonizing patches containing more individuals, facilitating sexual encounters (Holter, 1982), or iii) due to some other reasons. The first process leads to aggregation as a consequence of environmental heterogeneity undetected by us, which could be a particular case of typical resource partitioning (Ives, 1988). The second highlights the idea of male-female encounters or congregative behavior among individuals. Communication mechanisms like pheromones, whose action has been supposed or proved in the case of some dung beetle species (Tribe, 1975; Bellés & Favila, 1983; Houston, 1986; Pluot-Sigwalt, 1988), perhaps causes attraction to particular dung pats.

On the contrary to the immigration process, the role played by the emigration process in spatial microdistribution is not obvious. Since a high density per patch could increase the degree of intraspecific interactions, an increase of emigration from dung pats must decrease the degree of intraspecific aggregation. Certainly, several studies indicate that the emigration from droppings is often density-dependent at sufficiently high densities (Landin, 1961; Yasuda, 1987; Hanski & Cambefort, 1991). However, a well established property of aggregated distributions is the increasing of spatial variance (aggregation) with the increasing mean abundance (The Taylor Power Law) (Taylor, 1961; Taylor, 1981; Perry, 1988). At all events, the differential emigration processes between two species

also can be responsible of the interspecific spatial covariation among dung-pats, with or without the action of the interspecific competition.

This paper aims to answer the following questions: i) Have *D. gazella* and *E. intermedius* aggregated distributions among apparently homogeneous set of dung-pats?; ii) are the two species negatively or positively associated at this spatial scale?; and iii) are both intraspecific and interspecific aggregations due to immigration or emigration processes?

MATERIAL AND METHODS

Description of the study area

The Mapimí Biosphere Reserve lies within the Bolsón de Mapimí, located in the northern Mexican Plateau, and is part of the Chihuahuan Desert. It includes some portions of the states of Coahuila, Chihuahua and Durango. The climate is dry, midwarm, with a chilly winter, a summer rainy season and annual mean temperatures ranging from 18° to 22 °C. There are two major seasons, a dry season from October to May and a hot and more humid season from June to September. In the Reserve, rains are torrential, of short duration and very localized. The result is a great variability in the spatial distribution of rain in the zone. The meteorological station in this Reserve recorded from 1978-1988 an annual precipitation of 283.8 mm. The flora includes a great variety of life forms dominated by shrub species with small leaves, which give the appearance of xerophitic underbrush.

Sampling

The data were obtained during two field studies carried out in the same season of two consecutive years: from 21 to 24 August 1992 and from 21 to 25 September 1993. In 1992, seven transects were set near the Laboratory of the Mapimí Biosphere Reserve (transects numbered from 1 to 7). Each transect consisted of ten 1-kg cow dung pats placed 12 m apart. Fresh cow dung was previously collected from the pasture of Rancho La Flor. Amounts of this material were homogeneized and pats were artificially deposited in the afternoon, at 18.00 p.m. The dung pats of four transects were inspected at 6.00 a.m. next morning, whereas the pats of the remaining transects were inspected 24 hours after placement. The difference in the exposure time allowed to determine the activity schedules of the species in the study zone: *Euoniticellus intermedius* is active at noon and *D. gazella* at dawn and dusk (Montes de Oca *et al.*, 1994).

In 1993, six independent transects were studied in the same zone in a west-east direction. Three of them consisted of eight 1-kg dung pats each too, but placed six meters apart (transects numbered 8, 9 and 10). The other three transects

20

consisted of 20 dung baited pitfall-traps of standard design (CSR type) (Lobo *et al.*, 1988; Veiga *et al.*, 1989) placed also six meters apart (transects numbered 11, 12 and 13). The pitfall traps consisted of a plastic basin of 210 mm in diameter buried to its rim in the soil, containing a water soap mixture. Fresh cattle dung was supported on a wire grid on the top of the bucket. The dung used to form the pats as well as the bait for the pitfall traps was fresh and previously collected and homogeneized. So, the attractiveness variation effect within and between transects was intended to minimize.

Each day, only one dung pat transect and one pitfall trap transect were simultaneously conducted two meters apart, so that the spots of the first eight dung pats were front of the position of the last eight western pitfall traps. Both the dung pats and the pitfall traps were always set up in the same place.

In the transects 8, 9, 11 and 12, the dung pats and the pitfall traps were set up in the afternoon at 18.00 p.m. In the transects 10 and 13, the dung pats and the pitfall traps were set up in the morning at 8.00 a.m. The distinct periods of the placement of bait in the transects facilitated the distinct colonization of dung by the two species.

Both the length (108 and 114 m) and the exposure time of dung pats of the 1992 and the 1993 transects, were similar and comparable. Almost all the transects were inspected 24 hours after placement. Beetles trapped in the pitfall traps of the 11 and 13 transects were collected every two hours on 22-23 September and 24-25 September periods, respectively.

Spatial distribution analysis

Aggregation as a concept is difficult to define. Typically its measurement raises several objections (see Hurlbert, 1990). We used the Morisita Index (MI) as the most appropriate aggregation index (Hurlbert, *op. cit.*) as well as the Aggregation Model proposed by Ives (1988). This model provides an intraspecific aggregation measure (*J*) and a interspecific aggregation measure (*C*). Both the Morisita Index and the Aggregation Model are simple and less dependent on variance. They have a higher biological sense than, for example, the variance to mean ratio, commonly used as a dispersion index. The statistical signification of intraspecific aggregation was measured by testing the deviation of the variance to mean ratio from 1.0 using the Chi-Square test statistic. The Spearman rank correlation coefficient was computed to test the interspecific covariation according to Ives (1988).

To know if the immigration rate of beetles was higher in some dung pats than in others, the Pearson correlation coefficients were calculated among the pitfall trap pair abundances for the same site but among the different transects. Beetles collected every two hours from the pitfall traps of transects 11 and 13 allowed to find out the immigration rate was higher in the spots already colonized than in

previously little colonized or uncolonized spots. As traps were efficient at a stretch, and as the two species had different daily activity periods, one can calculate the correlations between the abundance observed when each species was active and the abundance obtained at the end. On the other hand, in order to estimate the importance of emigration processes, the number of beetles found in the pitfall traps and in the dung pats at the same place were compared. The emigration of beetles from the pitfall traps is almost impossible. As from the pitfall traps the emigration was prevented but as it was allowed from the dung pats, the difference between was considered as an estimation of the level of emigration.

RESULTS

Intraspecific aggregation

The higher was the mean abundance of both species, the higher was is the variance (Fig. 1). For mean densities above than five individuals per dung pat, the Morisita index (MI) and the intraspecific aggregation measure (J) values indicated aggregated patterns. Nevertheless, several MI and J values indicated aggregation even when population densities were less than five ind./pat (Table 1 and Fig. 1).

For both species, the mean abundances were significantly higher from pitfall traps than from dung pats ($D. gazella$: dung pats 10.71 ± 8.69 (mean ± SD), pitfall traps 15.90 ± 14.27; $t = 2.035$; $P < 0.05$; $E. intermedius$: dung pats 3.17 ± 2.60; pitfall traps 9.22 ± 8.11; $t = 5.153$; $P < 0.001$). As the mean densities were higher for pitfall-traps, all the variance to mean ratios as well as the MI and J values indicated a significant aggregation for $D. gazella$ (Table 1). However, the magnitude of the MI and J indices did not differ with regard to their values from the dung pats (Kolmogorov-Smirnov two-sample test; $DN = 0.40$; $P = 0.85$). The intraspecific aggregation indices for $E. intermedius$ were also significant in the two pitfall trap transects with higher densities (transects 12 and 13, Table 1), but their magnitude did not differ with regard to those from dung pats (Kolmogorov-Smirnov two-sample test; $DN = 0.50$; $P = 0.70$).

The number of individuals of $E. intermedius$ captured in the pitfall traps located in the same place was significantly correlated once (Fig. 2). Presumably, when the $E. intermedius$ numbers increased (transects 12 and 13), the beetles tended to colonize the western pitfall traps. In the case of $D. gazella$, the spatial arrangements were variable and there were even significant negative correlations between the abundances in transects 11 and 13, and in transects 11 and 12 (Fig. 2). For $D. gazella$, there were no significant correlations at $P - 0.05$ between the abundance observed during the period when the species was active and the abundance finally obtained (transect 11: $r = 0.420$, $df = 18$; transect 13: $r - 0.121$, $df = 18$). However, in transect 11 the correlation was nearly significant

(0.05 < P < 0.1). For *E. intermedius*, the correlation was negative but not statistically significant in transect 11 ($r = -0.345$, df = 18), and positive and significant in transect 13 ($r = 0.546$, df = 18, 0.01 < P < 0.02).

Table 1

Values of mean (μ), variance (σ^2), variance-mean ratio (σ^2/μ), Morisita index (MI), intraespecific aggregation (J) and interspecific aggregation (C) from dung pat (1-10) and pitfall trap (11-13) transects, carried out in a physiognomically homogeneous area of the Mapimi Biosphere Reserve. T = transect number. n = number of sampling units. Dg = *Digitonthophagus gazella* and Ei = *Euoniticellus intermedius*. P = statistical significance of χ^2 values: NS- no significant, * P<0.05; **- P<0.01; *** P<0.001.

| T	n	Species	μ	σ^2	σ^2/μ	χ^2	P	MI	J	C
1	10	Dg	2.2	8.18	3.72	33.46	***	2.165		
2	10	Dg	1.7	2.23	1.31	11.82	NS	1.176		
3	9	Dg	1.56	1.53	0.98	7.86	NS	0.989		
4	10	Dg	3.9	14.32	3.67	33.05	***	1.633		
5	9	Dg	1.22	0.94	0.77	6.18	NS	0.818	-0.138	-0.718 NS
		Ei	2.67	26.75	10.03	80.25	***	4.14	8.314	
6	10	Dg	2.3	3.12	1.36	12.22	NS	1.146	0.25	-0.014 NS
		Ei	1.6	2.71	1.69	15.25	0.08	1.417	0.522	
7	10	Dg	2	4.67	2.33	21	*	1.632	0.633	0.222 NS
		Ei	2.2	2.4	1.09	9.82	NS	1.04	0.046	
8	8	Dg	10	34.57	3.46	24.20	**	1.218	0.260	-0.339 *
		Ei	1.63	1.41	0.868	6.08	NS	0.923	-0.085	
9	8	Dg	13.50	160.86	11.92	83.41	***	1.714	0.479	-0.289 *
		Ei	3.13	8.98	2.87	20.12	**	1.55	0.588	
10	8	Dg	9.25	37.64	4.07	28.49	***	1.294	0.750	0.258 NS
		Ei	4.75	6.21	1.31	9.16	NS	1.058	0.084	
11	20	Dg	7.45	23.84	3.20	60.80	***	1.282	0.343	-0.057 NS
		Ei	4.35	4.24	0.975	18.52	0.5	0.994	0.000	
12	20	Dg	28.25	322.83	11.43	217.12	***	1.351	0.438	-0.042 NS
		Ei	6.05	18.47	3.05	58.01	***	1.325	0.360	
13	20	Dg	12.00	34.10	2.84	54.00	***	1.146	0.171	-0.012 NS
		Ei	17.25	78.20	4.53	86.13	***	1.195	0.216	
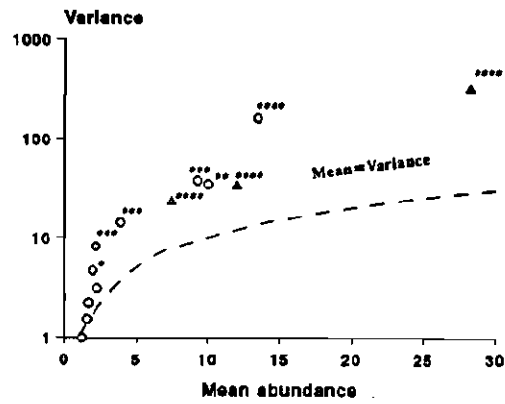
D. gazella

E. intermedius.
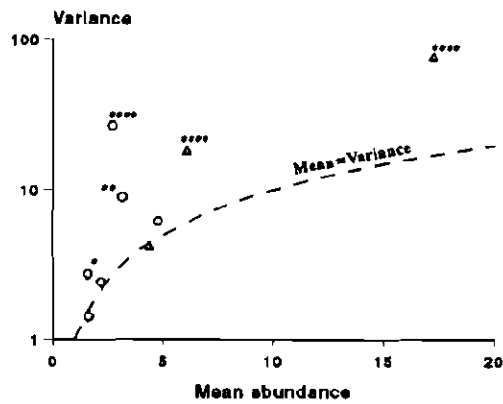
Figure 1

Relationship between the mean abundance and the variance for *Digitonthophagus gazella* and *Euoniticellus intermedius* from dung pat (circles) and dung baited pitfall-trap (triangles) transects. χ^2 values were calculated for the variance-to-mean ratio, where * P<0.05, ** <0.01, *** P<0.001, **** P<0.0001.

24

Figure 2
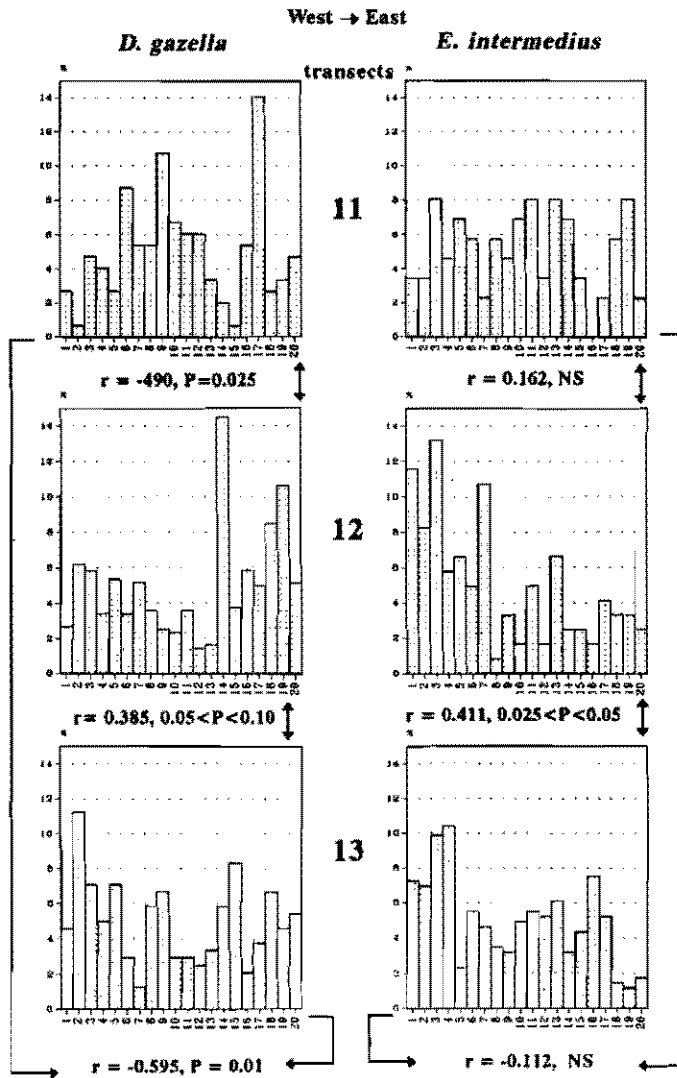Percentage of individuals attracted per trap in each 1993 transect. The Pearson correlation coefficients (r) of abundance per trap in the same site among the pairs of transects are indicated.
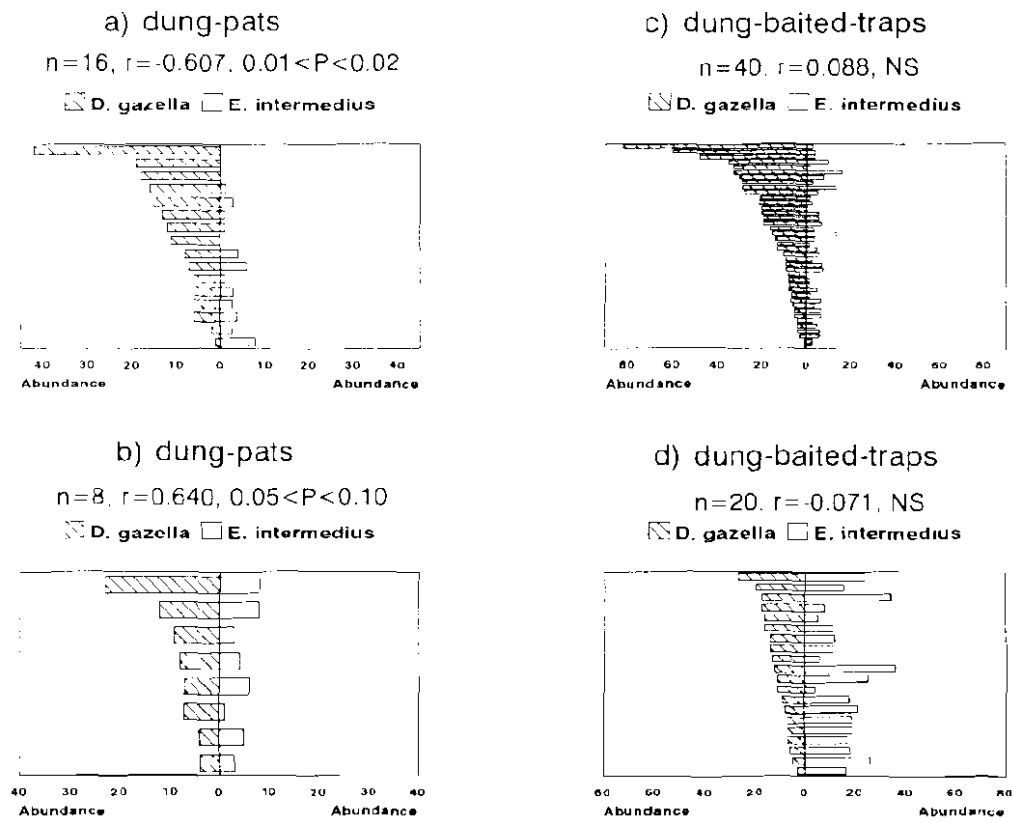
Figure 3

Abundance of *D. gazella* and *E. intermedius* i) per dung pat, in transects 8 and 9 (a) and in transect 10 (b); ii) per dung baited pitfall trap, in transects 11 and 12 (c) and in transect 13 (d). The Pearson correlation coefficients (r) between the abundances of the two species are indicated.

Interspecific aggregation

When pitfall traps were used, the interspecific aggregation indices were not statistically significant (see *C* in Table 1). The only significant values of interspecific aggregation between *D. gazella* and *E. intermedius* were obtained for data from the two dung pat transects number 8 and 9 (Table 1). The values were negative, indicating a segregation between the two species. In these transects the mean densities of *D. gazella* per dung pat were high. The abundances of the two species in dung pats was negatively correlated in transects 8 and 9 when take them together (n = 16; r = -0.607; 0.01 < P < 0.02) (Fig. 3a). In the transect 10, the correlation between the abundances of two species was almost significant (Fig. 3b). On the contrary, when the pitfall traps were considered the correlations between the abundances of the two species were distant from a statistically significant level (Fig. 3c and d).

The emigration rate (difference between pitfall trap and dung pat abundances) increased for the two species as the immigration rate (abundance in pitfall traps) increased (Fig. 4a). The emigration rates of the two species were not correlated (Fig. 4b). The high *D. gazella* immigration rates were not correlated with the high *E. intermedius* emigration rates (Fig. 4c), as well as the high *E. intermedius* immigration rates were not correlated with the high *D. gazella* high emigration rates (Fig. 4d).

DISCUSSION

In Mapimí, *D. gazella* and *E. intermedius* showed aggregated distribution at a small spatial scale (an area of 200 m^2) in which environmental heterogeneity was difficult to detect. At this microspatial scale, the intraspecific aggregation seemed to be a general trend for the two species as it occurred for other dung beetles (Hanski & Cambefort, 1991). Aggregated distribution appeared when population densities were high and when emigration was prevented (pitfall traps), but also existed when population densities were low and when emigration occurred (dung pats). Therefore, intraspecific aggregation usually occurred at high population densities, but it was also frequent and of similar intensity at moderate or low densities (less than five individuals per dung pat).

The aggregated distribution observed in the two species seemed to be a consequence of differential immigration rates but their cause was still not clear. Was the immigration rate higher in some patches than in others? Was the immigration rate higher in those pitfall traps that had an initial abundance higher than those with a low abundance?. Presumably, when the mean population of *E. intermedius* increased, the individuals tended to colonize the pitfall traps of the western part of the site.
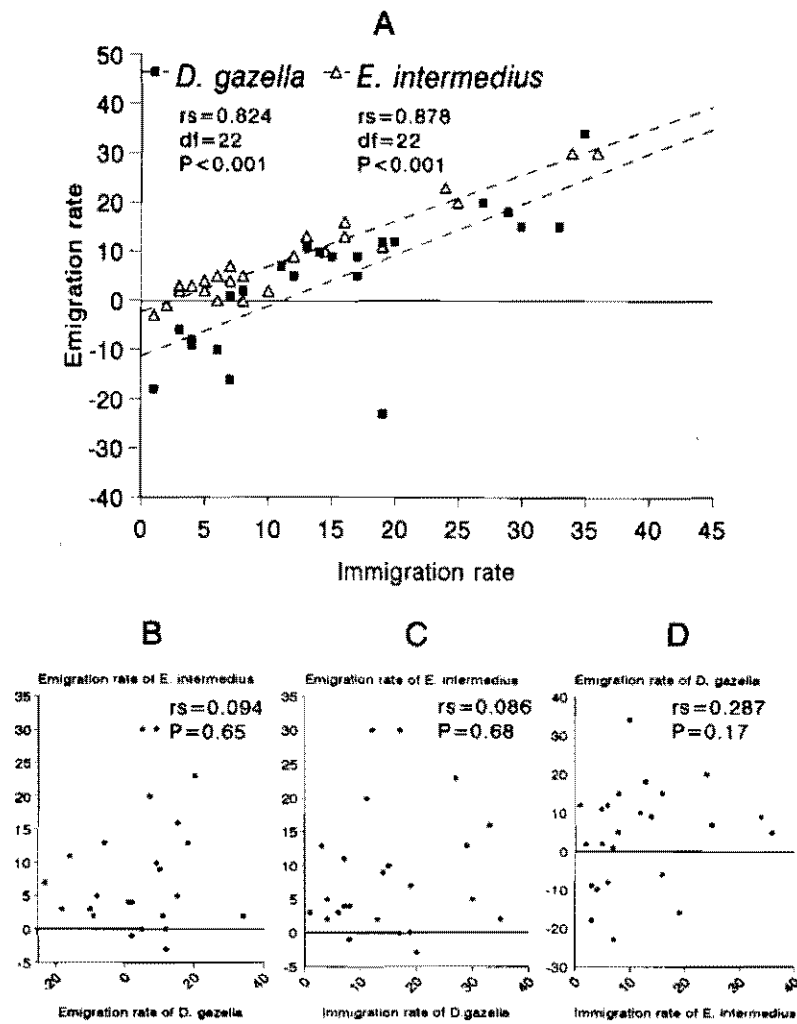
27

A

B **C** **D**

Figure 4

(A) Relationship between immigration rate (pitfall trap abundance) and emigration rate for each dung beetle species (1993 data). The emigration rate was calculated as the difference between the abundance in pitfall-traps and dung pats. (B) Relationship between emigration rate of the two species. (C) Relationship between the immigration rate of *Digitonthophagus gazella* and the emigration rate of *Euoniticellus intermedius*. (D) Relationship between the immigration rate of *E. intermedius* and the emigration rate of *D. gazella*. rs is the Spearman rank correlation coefficient.

On the contrary, *D. gazella* did not show any preference for particular dung pats. On the other hand, sometimes the individuals of the two species tended to colonize patches with a larger initial number of beetles. Our results are not conclusive. The spatial microlocalization of dung pats can influence dung beetle colonization degree on some occasions (Hanski, 1987). There is always a certain degree of environmental heterogeneity that cannot be observed. A suitable microenvironment and its perception by individuals may lead to the spatial distribution observed on this scale, but several other experiments would be necessary to confirm this hypothesis. Other factors, such as wind direction, the location of the main source (pool) of beetles, or inclusive, differences on the attraction capability of dung used for dung pats and pitfall traps, also may influence the results. It could be possible that the previously treatment of homogoneization of the fresh dung collected was not as effective to reduce the attractiveness variation effect. But it is also possible that without heterogeneity, repeated choice of more densely populated patches could give rise to a pattern of intraspecific aggregation.

The present data suggest that the two species show a covariation in the number of the two species when emigration was not prevented. This interspecific aggregation was negative, indicated by a negative correlation between the distributions of species at this spatial scale. Yasuda (1987) found that the emigration of the dung beetle species *Liatongus phanaeoides* depended on the numbers of another species, *Aphodius haroldianus*. Is it possible that one of the two species was dominant and prevented the immigration of the other species or induced its emigration from the patches?. Are interspecific interactions the main responsible factors for the differential emigration of species from the pats?. The more individuals was attracted and arrived to the pitfall traps (immigration rate), the higher was the emigration from the dung pats. Others experiments also demonstrated that emigration from droppings was density dependent at sufficiently high densities (Landin, 1961; Yasuda, 1987). However, the immigration rate of *D. gazella* did not influence the emigration rate of *E. intermedius*, nor did the immigration rate of *E. intermedius* influenced the emigration rate of *D. gazella*. The emigration rate of both species was not spatially correlated and, perhaps, the responsible factors of emigration were not the same for both species. This suggests that neither of the two species induces the emigration by the other. In fact, *E. intermedius* was the first species attracted by the traps of transect 13 set up in the morning and, for that reason, its mean abundance was higher than that obtained with traps set up in the afternoon (transects 11 and 12) (17.25 $\pm$ 8.84 vs 5.20 $\pm$ 3.44; t = 14.57, P < 0.001). *Digitonthophagus gazella* arrived later, at dusk and again at dawn. The probability of emigration due to competitive interactions between the two species is low,

unless the arrival of *D. gazella* led *E. intermedius* to emigrate from pats between dusk and dawn, when its normal activity period falled out. The intraspecific competition exerts a great influence on the emigration process, but the interspecific competition (or other factors such as microenvironmental dung pat changes, for example) cannot be disregarded. The competitive interactions among individuals intraspecifically aggregated could lead to the generation of differential emigration rates and microspatial segregation. At this scale, it is not necessary to suppose that extant environmental heterogeneity gives rise to spatial partitioning. Immigration as well as emigration can generate aggregated distributions in the absence of environmental heterogeneity.

ACKNOWLEDGEMENTS

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32