Chapter 8
CO-OCCURRENCE AND AGGREGATION OF DUNG BEETLES COMPETING FOR EPHEMERAL RESOURCES IN FOUR HABITATS

8.1. INTRODUCTION

Dung pats are discrete, ephemeral patches or 'islands' of highly concentrated energy, which are widespread throughout a variety of habitats over the surface of the landscape. These units exist only until the energy they contain has been consumed or dispersed. One would expect these dung pats to be colonized by a great number of species taking advantage of a resource with such a high energy content. Because of the temporary nature of dung a scramble for this resource can be expected. In ecosystems where dung beetles are less abundant this would pose no problem. In many biotopes in southern Africa, however, dung beetles are often very abundant, especially in the warm rainy season, and there is potential for strong competition for dung here. According to Hanski & Cambefort (1991b) intraspecific and interspecific competition occur at least occasionally in nearly all communities of dung beetles and in some situations competition is severe and undoubtedly greatly influences the structure of communities. Ridsdill-Smith (1990) states that competition occurs when resources become limiting, and would be expected to be particularly important in populations living in dung. He also agrees that competition is one of the important regulating factors in determining the size of the population. Hudson & Stiling (1997) found that in a phytophagous insect community *Trirhabda bacharidis* played a major role, depressing densities of the most common insect herbivores on *Baccharis halimifolia*. They ascribed the reduced densities to interspecific, exploitative competition facilitated by *T. bacharidis* herbivory. Ward & Seely (1996) found that in a detritivorous tenebrionid community in the Namib desert interspecific competition was an important organizing force. Reeve *et al.* (1998) state that although competition is not the most important force in the dynamics of the southern pine beetle, *Dendroctonus frontalis*, in the southern U.S.A., intraspecific competition could be a source of immediate density dependence in the beetle's population dynamics.

Competition for dung can take a number of forms, ranging from direct combat, in which beetles fight over the possession of dung, through resource pre-emption, in which priority of access determines the winner, to scramble competition, in which the beetles' activity at high densities prevents most individuals acquiring sufficient resources for breeding (Doube, 1991). Competition can either be intraspecific or interspecific and may be either symmetric or asymmetric. Symmetric interspecific competition occurs when both species are negatively effected, while asymmetric competition has a negative effect on one species, but no detectable effect on the other (Ridsdill-Smith, 1990). Competition in dung beetle assemblages is mostly asymmetric, with a superior competitor occurring dominantly and many inferior competitors occurring less abundantly.

If competition is so strong in dung beetle assemblages, how can we then explain the often high species diversity of assemblages that exploit this discrete ephemeral resource? One would expect that in these situations the superior competitors would cause the weaker competitors to become extinct, resulting in lower species diversity. Because there are large numbers of species in most dung communities there are numerous potential interspecific interactions, but there is frequently much variation in the behaviour of different species, which might influence the outcome of competition. Differences in diel activity, time of colonization, seasonality, habitat preference and dung preference can enable weaker competitors to co-exist with stronger competitors. Doube (1987) found that the majority of interactions occur only infrequently, if at all, because most species are relatively rare, are restricted to particular habitats in specific seasons of the year and have specific diets. Dung is, however, a relatively homogenous resource and thus presents beetles with little opportunity for specialization within a single resource patch (Giller & Doube, 1989) and despite a high level of niche partitioning in dung beetles on various scales there are still species with similar biological characteristics that occur together. Dung is patchily distributed in both time and space. Patchy environments may be unstable at one spatial scale, but stable on another scale. The instability of populations in habitat patches may contribute to stability on a larger scale in competitive and predator-prey systems (Hanski, 1987b). Species must occupy the same pat in order to compete with one another and some species show independently aggregated spatial distributions among patches, which reduces the probability of potential competitors occurring together on the same resource. Aggregation refers to the degree to which insects are clumped among the patches. If most of the individuals of one species occur in a few of the patches, causing a high variance in the number of dung beetles per patch, then the distribution is intraspecifically aggregated, while interspecific aggregation is the degree to which two different species occur in the same patches, producing positive covariance between the distributions of the two species (Ives, 1991). Several authors agree that the patchiness of dung and the aggregation of dung beetles in discrete habitat patches will reduce interspecific competition and facilitate co-existence of different species, resulting in higher species diversity. Ives (1991) considers aggregation a general mechanism that may explain co-existence in any insect community in which species compete for patchily distributed resources. Doube (1987) suggests that the independent aggregated distribution of species over discrete patches of resource favours the co-existence of competing species by reducing the intensity of interspecific competition. Atkinson & Shorrocks (1981) also found that two processes could lead to more prolonged coexistence, viz. increasing patchiness of resources and increased aggregation of the competitor. They found that the maximum time of co-existence between competitors resulted when both the degree of their aggregation over sites and patchiness of the resource were at their maximum. Hanski (1990) reasons that many dung and carrion communities are exceptionally rich in species because habitat patchiness facilitates coexistence. Patchiness leads to independently aggregated spatial distributions in the competitors and differences in foraging behavior affect the probabilities of colonization of individual habitat patches. Hanski & Cambefort (1991b) argue that when habitat patchiness increases and the durational stability of individual patches decreases, the level of spatial aggregation in the insect populations further increases. Further to this Kneidel (1985) found that under high patchiness, where aggregation was high and the species were distributed independently, overlap was reduced, the effect of interspecific competition was reduced and the level of intraspecific competition was increased.

On farms there is normally an unlimited supply of dung because of a concentration of large herbivores in a small area. This is usually not the case in a nature reserve where dung is distributed randomly because of a larger area through which the large herbivores are able to move. This will probably influence the aggregation of dung beetles in an area and subsequently the outcome of competition.

3.2. MATERIAL & METHODS

Sampling procedure

During the sampling period the species richness, total abundance of dung beetles and the maximum number of individuals were highest during February 1997 in all four habitats. The interspecific and intraspecific interaction in the dung beetle assemblages can be expected to be most pronounced during this time and data collected during this month was therefore used to determine the aggregation of dung beetles in the four different habitats. Dung beetle sampling was done in four different localities within two different habitat types, comprising a grassveld area and a bushveld area. In these two habitat types dung beetle assemblages in a natural habitat (Sandveld Nature Reserve) and on farms (where habitats were disturbed by overgrazing) were compared. The farm Rietvlei represented a grassveld area and the farm Josina a bushveld area. Three sites, spaced 1km apart, were chosen in each of the four localities. In each site three plots, spaced 50m apart, were chosen. Each plot contained four pitfall traps, spaced 1m apart. The beetles from these four traps were pooled and statistically treated as a single sample. 1l plastic pitfall traps were used for sampling. The traps were buried up to the rim and the bottom filled with salt water. Dung preference studies showed that dung beetles in all the habitats were most strongly attracted to cattle dung (Geyser, 1994). Cattle dung was therefore used as bait in all the localities to ensure that dung beetles were equally attracted to traps in all the localities and that dung type did not affect the differences in dung beetles caught between the different habitats. A container with 200g of fresh cattle dung was put inside the trap to attract the dung beetles and was considered sufficient to attract both flying and walking dung beetles. Dung beetles attracted by the dung fell into the traps and could be collected later. Freshly dropped cattle dung, used to bait the traps, was collected on the dairy farm Bospré, near Bloemfontein (26°,00'S; 29°,00'E). The dung was transported in plastic buckets, covered tightly with lids to avoid desiccation and oxidation of the dung. After baiting the traps with fresh dung they were left for 24 hours after which the dung beetles in the traps were collected and preserved in 70% alcohol for later identification.

Analytical Methods

Intraspecific aggregation was determined between plots, which were spaced 50m apart and between sites, which were spaced 1 km apart. Ives' measure of aggregation (J) (Ives, 1991) was used to determine the intraspecific aggregation of species of dung beetles attracted to pitfall traps:

$$J=\{[\Sigma\, n_i (n_i - 1/(NL)] - N\}/N$$

Where L is the number of traps, n_i the number of dung beetles attracted to trap i (i = 1 to L), and N the mean number of dung beetles. A value of J=0.75 indicates a 75% increase in the expected number of conspecifics attracted to the same trap above what the expected number would be if dung beetles were randomly and independently distributed. J=0.75 thus means an increase in crowding by 75% (Ives, 1991).

Interspecific aggregation was determined between sites, which were spaced 1 km apart. To measure interspecific aggregation between sp. A and sp. B Ives' measure of interspecific aggregation (C) was used (Ives, 1991):

$$C_{A,B}=\{[\Sigma\, n_i m_i/(NL)]-M\}/M$$

Where L is the number of traps, n_i and m_i are the numbers of dung beetles of each species attracted to trap i (i = 1 to L), and N and M the mean number of dung beetles. A value of $C_{A,B}$=0.5 indicates that there is a 50% increase in the expected number of heterospecific competitors in the same trap above the expected number if sp. A and sp. B were distributed independently.

The size range among dung-inhabiting beetles is large (Koskela & Hanski, 1977). In the present study dry mass was used as an indicator of size. The dry mass per species was obtained by calculating the mean mass of 20 specimens (10 males and 10 females) of each species. These were dried at 80°C for 48 hours and were subsequently weighed on a precision balance. The biomass of beetles in each trap was calculated by summing the results derived from multiplying the abundance of each species by its mean dry mass (g) per individual.

To determine significant linear relationships between size and abundance of different dung beetle species and level of intraspecific aggregation in a species Pearson's correlation coefficient, which measures the linear association of two data sets, was used. A value of r near or equal to 0 implies little or no linear relationship exists between the two lists of numbers. A value of r near or equal to 1 or -1 indicates a very strong linear relationship.

8.3. RESULTS & DISCUSSION

Species richness, abundance and dominance in four different habitats

Because of a concentration of large mammals in a small area on the farms Rietvlei and Josina there is an unlimited supply of dung. One would therefore expect that these farms would support more species and higher abundance of dung beetles than in the nature reserve where dung is more widely distributed across a larger area. This is, however, not the case. The highest number of species occurred in the grassveld area at SNR and the species richness is higher in both the grassveld and bushveld areas in the nature reserve (Table 8.1). The total abundance and maximum number of individuals are higher in the grassveld area than the bushveld area and also higher in the nature reserve than on the farms (Table 8.1).

Table 8.1: Species richness (S); number of individuals (N) and maximum number of individuals (Nmax) in four different habitats: Sandveld Grassveld – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; Sandveld bushveld – natural bushveld habitat; Josina – disturbed bushveld habitat.

	S	N	Nmax
Sandveld Grassveld	31	3657	1588
Rietvlei	22	1402	1016
Sandveld Bushveld	28	979	364
Josina	25	718	312

Although many species occurred in the study area only a few species were dominant, with many rare species. In the grassveld area at SNR seven species were dominant, making up 88.9% of the total abundance (Fig. 8.1.a). *Scarabaeus flavicornis* was the most dominant species making up 43.4% of the total population (Fig. 8.1 a). In the disturbed grassveld area (Rietvlei) six species were dominant, making up 91.8% of the total abundance. There was a much higher dominance in this area than in the natural grassveld area, with *Caccobius seminulum* making up 72.8% of the total population (Fig. 8.1. b). In the natural bushveld area at SNR there were seven dominant species, making up 83.1% of the total abundance. *Onthophagus variegatus* was dominant making up 36.3% of the total population (Fig. 8.1. c). Five dominant species occurred in the disturbed bushveld habitat, making up 72.5% of the total abundance. *Onthophagus variegatus* was dominant, making up 44.1% of the total population (Fig. 8.1 d). Due to the dominance of a single species in all the habitats we can expect competition, if it occurs, to be asymmetric. Denno *et al.* (1995) found that interspecific competitive interactions in phytophagous insects were also mostly asymmetric. They ascribed the tendency for intraspecific competition to diminish interspecific interactions to this asymmetry. In the present study there was a high dominance of one species in all the habitats but the degree of dominance and the dominant species varied between the habitats. There is a clear difference between the different functional groups in their ability to compete for dung. The best competitors are the large telocoprids (FG I) and the fast-burying paracoprids (FG III), whilst the small telocoprids (FG II) are also good competitors because they remove the dung soon after arrival at the pat (Doube, 1991). Compared to these groups the paracoprids (FG IV and V) are subordinate and the endocoprids (FG VI) are especially likely to have their breeding activities disrupted by members of the other functional groups, while kleptocoprids (FG VI) use the dung buried by other groups (Doube, 1991). The natural grassveld habitat was dominated by a superior competitor belonging to FG II, which removes large amounts of dung at a fast rate, while the disturbed habitat was dominated by an inferior competitor belonging to FG VI, which use the dung buried by other dung beetles as food source. Both the bushveld habitats were dominated by an inferior competitor belonging to FG V, which is small and removes dung at a slow rate.

In the natural grassveld habitat the dominant species has a competitive advantage through its ability to rapidly gain control over dung, causing resources to be limiting in this area. Although *P. femoralis* were not as abundant as *S. flavicornis*, this was a large superior competitor, removing large amounts of dung at a fast rate. There was pre-emptive competition between these two species where the resource was limited, with one species utilizing all the dung voided at certain times of the day leaving no resource for the other species. Despite abundance of superior competitors in the natural grassveld habitat there were many other species able to co-exist with them (Table 8.1). There must be some mechanism, which enables these species to occur together in the same area despite strong interference. The dung beetle assemblages here are structured by variance-covariance dynamics, where many species occupy the same dung pat. In assemblages obeying variance-covariance dynamics, regional species richness may be high in spite of competition.

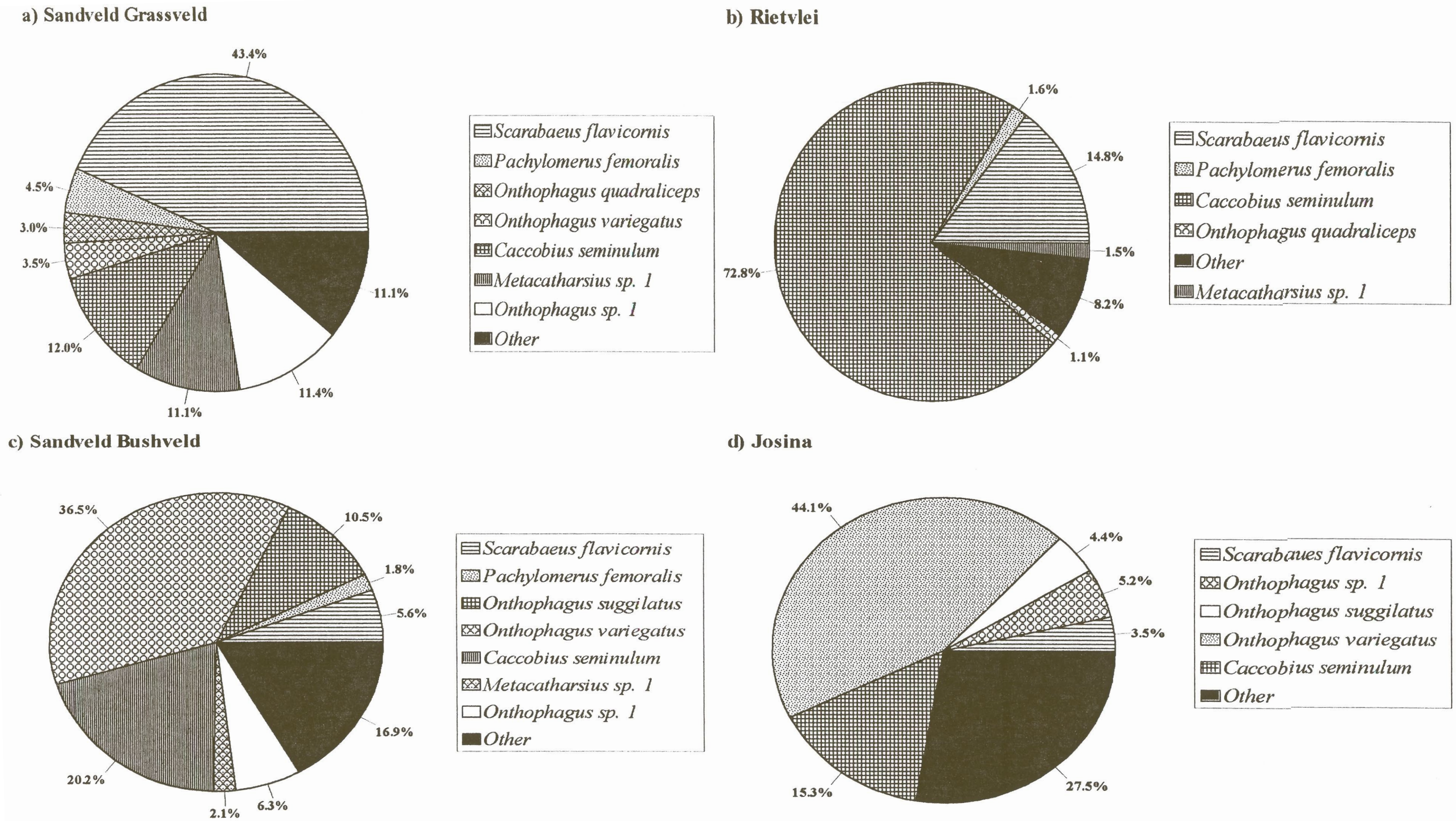

Fig. 8.1:Distribution of dominant species in dung beetle assemblages in four different habitats: a) Sandveld Grassveld – natural grassveld habitat; b) Rietvlei – disturbed grassveld habitat; c) Sandveld Bushveld – natural bushveld habitat; d) Josina – disturbed bushveld habitat.

Intraspecific and interspecific aggregation of dung beetle species in four different habitats

Intraspecific aggregation may play an important role in structuring dung beetle assemblages. In northern Germany Hirschberger (1998) found that intraspecific competition played an important role in the small dung beetle species *Aphodius ater*. She found that this species aggregate, possibly to facilitate mate finding, but between-pat distribution was more even in older pats, leading to a more even distribution of eggs and minimal larval competition. In southern Africa the dung beetle assemblages differ from those in temperate climates. There is an abundance of larger dung beetle species and intraspecific aggregation may play a completely different role to enable smaller species to co-exist with larger, superior competitors. In the present study intraspecific aggregation differed between plots and sites and also between habitats. Hanski & Cambefort (1991b) found that average distance between traps or dung pats affects the level of aggregation. In the present study and depending on the species, the level of aggregation differed with varying degrees between plots and sites (Table 8.2). Between both plots and sites *Pachylomerus femoralis* was more aggregated in the disturbed grassveld habitat than in the natural habitat (Table 8.2). The level of aggregation for this species was higher between sites than plots, indicating that it tended to be more aggregated over larger than smaller areas (Table 8.2). *Scarabaeus flavicornis,* which was the dominant species in the natural grassveld habitat, was more aggregated over a small area, while they were more aggregated over a larger area in the disturbed habitat (Table 8.2). This species was also more aggregated over a larger area in the disturbed bushveld habitat than in the natural bushveld habitat (Table 8.2). *Metacatharsius sp. 1* also showed a higher level of aggregation over a small area in the natural grassveld habitat and a higher level of aggregation in the disturbed grassveld habitat (Table 8.2). Between sites the level of aggregation for *Onthophagus quadraliceps* was higher in the natural grassveld habitat than in the disturbed grassveld habitat (Table 8.2). Both between plots and sites *Onthophagus variegatus, Onthophagus sugillatus* and *Onthophagus sp. 1* all showed a higher level of aggregation in the disturbed bushveld habitat than the natural bushveld habitat (Table 8.2). *Caccobius seminulum* showed a higher level of aggregation in the natural grassveld habitat than the disturbed habitat, both between plots and sites and also showed a higher level of aggregation between plots in the disturbed bushveld habitat than the natural bushveld habitat, whilst between sites there was similar aggregation in these two habitats (Table 8.2). *Scarabaeus flavicornis* showed a high level of aggregation over small areas in the natural grassveld habitat. This species was dominant here and the aggregation probably enabled smaller less effective competitors to utilise the resource where this species did not occur over a small area. According to Giller & Doube (1994) co-existence is facilitated by increased aggregation of the competitively superior species, as this leaves more low density or empty sites in which the inferior species can breed. Atkinson & Shorrocks (1981) argue that co-existence should depend much more on the aggregation of the superior competitor than on the inferior one. Over a larger area in the natural grassveld habitat, however, the opposite was found in the present study, where there seemed to be a smaller level of aggregation of larger superior competitors, while the level of aggregation for the smaller species seemed to be larger. This might be explained by a better dispersal ability of the inferior competitors. Giller & Doube (1994) state that species may co-exist either due to good dispersal or good competitive abilities and Keough (1984) found that the best competitors tended to exclude other species from large patches, while the latter species, usually good dispersers, survive in small patches. The smaller inferior competitors in the present study therefore probably have good dispersal abilities enabling them to locate the few patches not colonised or carrying a lower density of superior competitors over a large area. The inferior competitors can therefore adjust their own spatial distribution to minimise the effects of competition with larger superior competitors. In the disturbed grassveld habitat the situation seemed to be reversed. The larger more effective competitors seemed to be more aggregated than the smaller less effective competitors. In this habitat the co-existence seemed to be dependent on the aggregation of the superior competitor allowing the inferior competitor to become more dominant. This might explain the dominance of the small cleptocoprid *Caccobius seminulum* in this habitat. There seemed to be a higher level of intraspecific aggregation over a large area in the disturbed grassveld habitat than in the natural grassveld habitat. The level of intraspecific aggregation was also higher in the disturbed bushveld habitat than in the natural bushveld habitat. It would seem therefore that the habitat influences the level of intraspecific aggregation and consequently also the structure of the assemblage. This is reflected by the difference in dominance of different species in the different habitats (Fig. 8.1).

In the natural grassveld habitat interspecific aggregation was stronger between the smaller, less effective competitors belonging to FG IV and FG V, while the larger superior competitors belonging to FG I and FG II did not show such strong interspecific aggregation (Table 8.3 a). Interspecific aggregation was, however, stronger between the larger species than between the larger and smaller species (Table 8.3 a). Cambefort (1991) found that the greater the size difference between two species, the lower their spatial correlation. In the present study small species of similar habits and size, like the species belonging to FG IV and V, compete for breeding space in the soil underneath the dung pat and therefore affect the spatial distribution of one another. According to Hanski & Cambefort (1991b) paracoprids have two essential requirements for successful breeding, namely food for the larvae and a space in the soil, below the dung, to construct their nest. The larger species belonging to FG I and FG II are unaffected by this because dung is buried at a distance from the dung pat. The intraspecific aggregation of the larger competitors was also stronger than the interspecific aggregation between larger, superior competitors and smaller inferior competitors. According to Hanski (1991) increasing intraspecific aggregation amplifies intraspecific competition relative to interspecific competition. Co-existence will depend on the relative magnitudes of intraspecific and interspecific competition and increasing intraspecific aggregation of the superior competitor relative to interspecific aggregation between this competitor and inferior competitors will facilitate co-existence. In the disturbed grassveld habitat the interspecific aggregation was stronger between species belonging to FG I and FG II than in the natural grassveld habitat (Table 8.3 b). Trampling and overgrazing of the habitat probably influences the breeding space of these species in the habitat resulting in a more aggregated distribution. In the natural Bushveld habitat there was also stronger interspecific aggregation between smaller species belonging to FG V (Table 8.3 c), while interspecific aggregation was stronger between larger superior competitors in the disturbed bushveld habitat than in the natural bushveld habitat (Table 8.3 d).

According to Giller & Doube (1994) co-existence is facilitated by increased aggregation of the competitively superior species. This was true for dung beetles in the disturbed habitats, but in the natural habitats the inferior competitors were more aggregated than the superior competitors. Atkinson & Shorrocks (1981) suggest two processes, which can lead to more prolonged coexistence, increased patchiness of resources, and increased aggregation of competitors. According to Begon, *et al.* (1995) the heterogeneous nature of the environment can facilitate co-existence without the presence of a marked differentiation of niches. They argue that interspecific competition often proceeds not in isolation, but under the influence of, and within the constraints of, a patchy, impermanent or unpredictable world. Gittings & Giller (1998) reason that dung quality preferences can also lead to reduced interspecific aggregation in naturally dropped dung pats of varying moisture and nitrogen content. In the present study there were differences in the habitats and these differences influenced the distribution of resources and consequently the distribution of dung beetle species. In the natural habitats the resources were more randomly distributed than in the disturbed habitats, probably facilitating co-existence even if species were less aggregated. The habitat seems to have a very strong effect on the level of intra-and interspecific aggregation of species, competition and co-existence. Atkinson & Shorrocks (1981) found that the outcome of competition is as much determined by the way the individuals respond to the environment as by the competitive interactions between species. Dung beetle species tended to be more intra- and interspecifically aggregated in the disturbed habitats than in the natural habitats. The larger superior competitors were more aggregated in the disturbed habitats than in the natural habitats. This enabled the smaller less effective competitors to become more dominant in the disturbed habitats. Trampling and overgrazing in the disturbed habitat might influence the distribution of the species here, forcing them to become more aggregated, and thereby influencing the structure of the assemblage. The more aggregated distribution of dung beetles in the disturbed habitats may also be explained by the movement of cattle and the resultant pat-deposition between camps. Giller & Doube (1994) argue that cattle are moved between paddocks several times per year and some paddocks are not stocked for a substantial period of time, resulting in instantaneous density of potential colonist beetles emerging from previous resource patches.

Table 8.2: Level of intraspecific aggregation (J) of dung beetle species distributed between plots and sites in four different habitats: S.G. – natural grassveld habitat; Rietvlei – disturbed grassveld habitat; S.B. – natural bushveld habitat; Josina – disturbed bushveld habitat.

Species	Dry mass (g)	Intraspecific aggregation (J)							
		Between Plots				Between Sites			
		S.G.	Rietvlei	S.B.	Josina	S.G.	Rietvlei	S.B.	Josina
F.G. I:									
Pachylomerus femoralis	1.49 ± 0.27	0.01	0.18	TS	TS	0.18	1.17	TS	TS
F.G. II:									
Scarabaeus flavicornis	0.158 ± 0.31	1.82	0.02	-0.04	0.09	0.19	1.14	-0.01	0.35
F.G. IV:									
Metacatharsius sp. 1	0.028 ± 0.002	0.16	0.04	0.07	TS	0.18	0.39	0.24	TS
Onthophagus quadraliceps	0.014 ± 0.005	0.08	0.07	TS	TS	0.66	0.306	TS	TS
F.G. V:									
Onthophagus sugillatus	0.003 ± 0.0008	TS	TS	0.49	1.04	TS	TS	0.24	0.46
Onthophagus variegatus	0.003 ± 0.0006	1.14	TS	0.47	0.6	1.39	TS	0.74	1.4
Onthophagus sp. 1	0.005 ± 0.001	0.58	TS	0.09	1.04	0.33	TS	-0.02	0.83
F.G. VI:									
Caccobius seminulum	0.001 ± 0.003	0.31	0.28	0.09	0.35	0.1	0.02	0.36	0.3

***TS – Samples to small**

Table 8.3: Average association values (C) between individual species between sites in four different habitats

a) Sandveld Grassveld –natural grassveld habitat

Species	**Interspecific aggregation (C)**						
	FG I	FG II	FG IV		FG V		FG VI
	Pachylomerus femoralis	*Scarabaeus flavicornis*	*Onthophagus quadraliceps*	*Metacatharsius sp. 1*	*Onthophagus variegatus*	*Onthophagus sp. 1*	*Caccobiu seminului*
F.G. I:							
Pachylomerus femoralis		0.19	0.19	0.19	0.07	0.07	0.03
F.G. II:							
Scarabaeus flavicornis			0.12	0.18	-0.06	0.01	0.01
F.G. IV:							
Onthophagus quadraliceps				0.23	0.89	0.46	0.15
Metacatharsius sp. 1					0.14	0.11	0.04
F.G. V:							
Onthophagus variegatus						0.68	0.21
Onthophagus sp. 1							0.11
F.G. VI:							
Caccobius seminulum							

Table 8.3. Continued: Average association values (C) between individual species between sites in four different habitats

b) Rietvlei – disturbed grassveld habitat

Species	**Interspecific aggregation (C)**					
	FG I	FG II	FG IV		FG V	FG VI
	Pachylomerus femoralis	*Scarabaeus flavicornis*	*Onthophagus quadraliceps*	*Metacatharsius sp. 1*	*Onthophagus sp. 1*	*Caccobius seminulum*
F.G. I:						
Pachylomerus femoralis		-0.61	-1.73	-0.6	-0.87	-0.06
F.G. II:						
Scarabaeus flavicornis			-0.27	0.72	1.5	-0.7
F.G. IV:						
Onthophagus quadraliceps				-0.31	-0.8	-0.05
Metacatharsius sp. 1					1.00	2.12
F.G. V:						
Onthophagus sp. 1						-0.9
F.G. VI:						
Caccobius seminulum						

Table 8.3. Continued: Average association values (C) between individual species between sites in four different habitats

c) Sandveld Bushveld – natural bushveld habitat

Species	**Interspecific aggregation (C)**					
	FG II	FGIV	FG V			FG VI
	Scarabaeus flavicornis	*Metacatharsius sp. 1*	*Onthophagus variegatus*	*Onthophagus sugillatus*	*Onthophagus sp. 1*	*Caccobius seminulum*
F.G. II:						
Scarabaeus flavicornis		-0.1	-0.08	0.05	-0.02	-0.07
F.G. IV:						
Metacatharsius sp. 1			-0.1	-0.3	0	-0.2
F.G. V:						
Onthophagus variegatus				0.27	0.16	0.53
Onthophagus sugillatus					0.05	0.26
Onthophagus sp. 1						0.1
F.G. VI:						
Caccobius seminulum						

Table 8.3. Continued: Average association values (C) between individual species between sites in four different habitats

d) Josina – disturbed bushveld habitat

Species	**Interspecific aggregation (C)**				
	FG II	FG V			FG VI
	Scarabaeus flavicornis	*Onthophagus variegatus*	*Onthophagus sugillatus*	*Onthophagus sp. 1*	*Caccobius seminulum*
F.G. II:					
Scarabaeus flavicornis		-0.71	-0.41	0.54	0.1
F.G. V:					
Onthophagus variegatus			0.88	-0.48	-0.49
Onthophagus sugillatus				-0.22	-0.34
Onthophagus sp. 1					-0.19
F.G. VI:					
Caccobius seminulum					

Correlation between the size and abundance of different dung beetle species and the level of intraspecific aggregation in a species

In the natural grassveld habitat there was a negative correlation between the dry mass of a species and the level of aggregation, with the smaller species tending to be more aggregated (r=-0.27; Fig. 8.2). The opposite was true for dung beetle species in the disturbed grassveld habitat. There was a very high positive correlation between the dry mass of a species and the level of aggregation, with the larger species more aggregated (r=0.68; Fig. 8.2). In both the natural and disturbed bushveld habitats there was a negative correlation between the dry mass of species and the level of aggregation (r=-0.51; r=-0.47; Fig. 8.2). Hanski & Cambefort (1991b) found that large Coprini interfere with one another and become distributed more evenly among the dung pats than the small paracoprids Onthophagini and Oniticellini, and Giller & Doube (1994) also found that in West Africa the larger Coprini tend to be more evenly distributed than the smaller tunnelling species. Hanski & Cambefort (1991b) concluded that the size of the beetle, not the tribe, significantly affects aggregation. From the present study it can be concluded that the habitat influences species of different sizes differently and consequently influence their distribution and aggregation differently.

The correlation between abundance and aggregation (J) also differed between the habitats. In both the natural and disturbed grassveld habitats there was a negative correlation between the abundance and aggregation with aggregation increasing with decreasing abundance (r=-0.335; r=-0.534; Fig. 8.3). The most abundant species probably utilised most of the resource, while the less abundant species tended to be aggregated in the patches less occupied by the more abundant species. In both the natural and disturbed bushveld habitats the situation was reversed. There was a very high positive correlation between abundance and aggregation in both habitats, with the more abundant species being more aggregated (r=0.89; r=0.81; Fig. 8.3). Tree cover might influence the distribution of the more abundant species causing a more aggregated distribution of abundant species in the bushveld habitats than in the grassveld habitats.

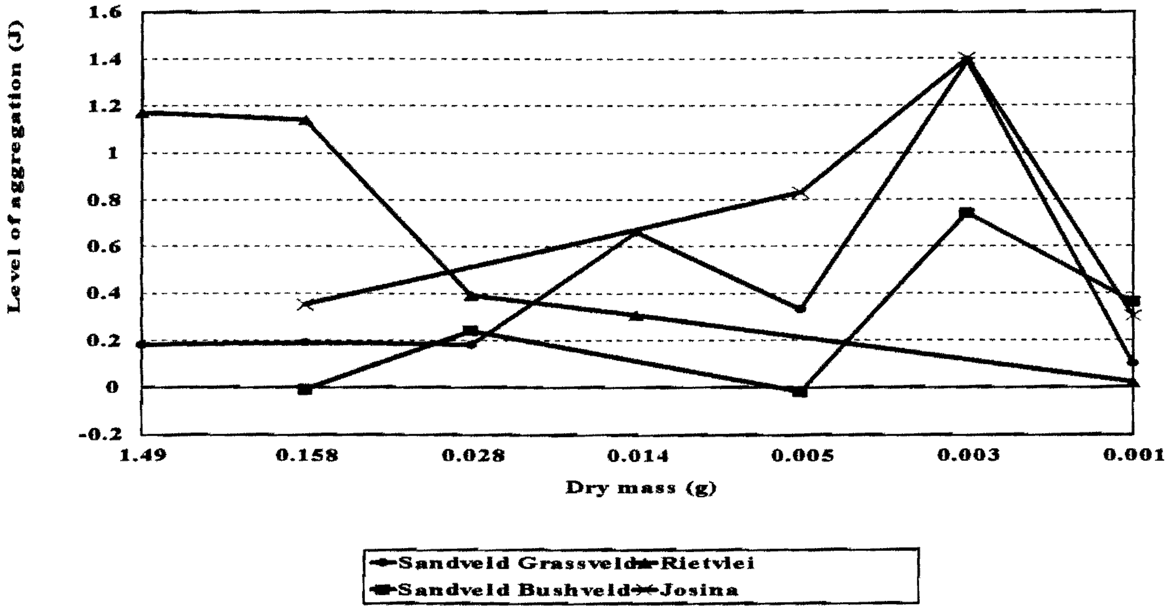

Fig. 8.2: Correlation between dry mass (g) of dung beetles and level of aggregation (J) in four different habitats: Sandveld Grassveld – natural grassveld habitat (r=-0.27); Rietvlei – disturbed grassveld habitat (r=0.68); Sandveld Bushveld – natural bushveld habitat (r=-0.51); Josina – disturbed bushveld habitat (r=-0.47).

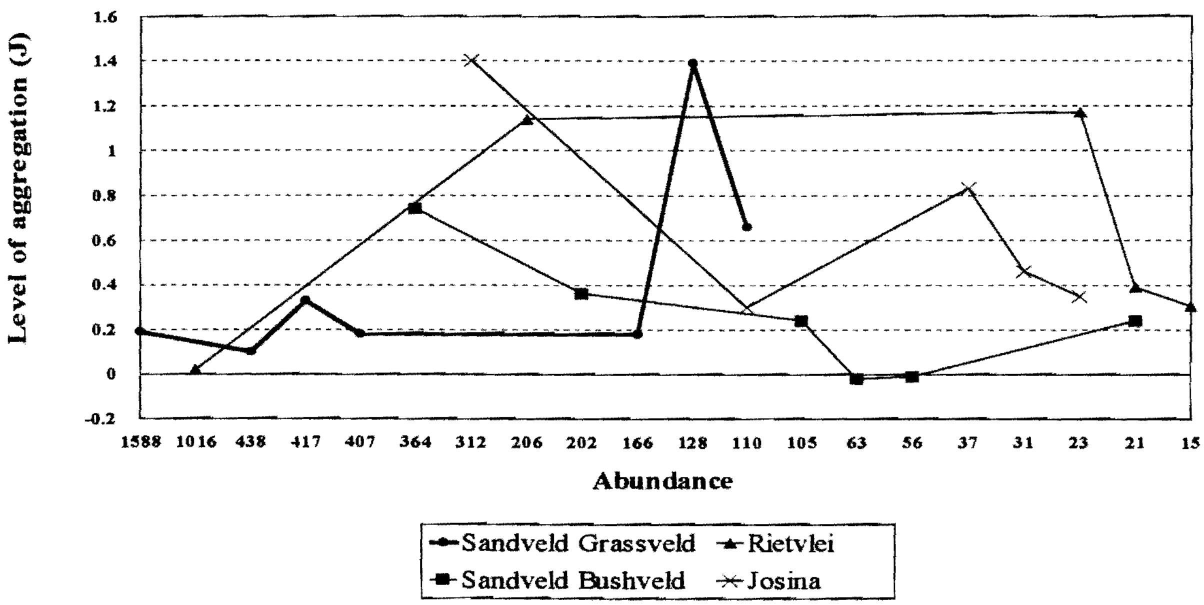

Fig. 8.3: Correlation between abundance of dung beetles and level of aggregation (J) in four different habitats: Sandveld Grassveld – natural grassveld habitat (r=-0.355); Rietvlei – disturbed grassveld habitat (r=-0.534); Sandveld Bushveld – natural bushveld habitat (r=0.89); Josina – disturbed bushveld habitat (r=0.81).

8.4. CONCLUSION

Aggregated distribution of dung beetle species and patchiness of resources is just one of the many mechanisms allowing the co-existence of inferior competitors with superior competitors in a dung beetle assemblage. It is, however, an important mechanism determining the structure of the assemblage in a particular habitat. The habitat seems to have an important effect on the aggregation of dung beetle species. In the present study the degree of dominance and also the dominant species differed with different habitats. In the natural grassveld habitat the assemblage was dominated by a superior competitor belonging to FG II, while the assemblages in the disturbed grassveld habitat was dominated by an inferior competitor belonging to FG VI. The assemblages in both the bushveld habitats were dominated by an inferior competitor belonging to FG IV. In the natural grassveld habitat the larger, superior competitors showed a lower level of intraspecific aggregation, while in the disturbed grassveld habitat these competitors were more aggregated intraspecifically and there was also stronger interspecific aggregation between superior competitors, allowing a higher dominance of the smaller inferior competitors. There was a correlation between size and level of aggregation with aggregation decreasing with increasing size in the natural grassveld habitat and aggregation increasing with increasing size in the disturbed grassveld habitat. Size thus seems to have a significant effect on aggregation. Different habitats influence dung beetles of different sizes differently. Larger, superior competitors are more severely effected in disturbed habitats than in the natural habitats. This will influence the aggregation of these species and subsequently the structure of the whole assemblage.