# DIVERSITY, ABUNDANCE AND SEASONALITY OF DUNG BEETLES (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE) OF BANGALORE

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# CERTIFICATE

This is to certify that the thesis entitled `DIVERSITY, ABUNDANCE AND SEASONALITY OF DUNG BEETLES (COLEOPTERA : SCARABAEIDAE : SCARABAEINAE) OF BANGALORE' submitted by Ms. G. C. Poornima for the degree of MASTER OF SCIENCE (AGRICULTURE) in AGRICULTURAL ENTOMOLOGY of the University of Agricultural Sciences, GKVK, Bangalore, is a record of research work done by her during the period of her study in this university under my guidance and supervision and the thesis has not previously formed the basis of the award of any degree, diploma, associateship, fellowship or other similar titles.

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1 September 1998

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# I. INTRODUCTION

# I. INTRODUCTION

In his presidential address to the "Society of American Naturalists", Hutchinson (1959) posed a simple question, `Why are there so many kinds of animals?' Not only did he pose the question, which to quote the cliche is the most celebrated one liner in ecology, but also went on to elucidate the answer in his inimitable style. He argued that the `finite' resources of planet earth are able to support an `infinite' variety of animals mainly because each species carves out its own niche and avoids comptetion with co-occurring species, especially for food.

Over the years the details of the mechanism of Inter-specific competition have been questioned and even the basic idea of competition itself seriously challenged. However, thanks to nature's oddities, the concept of competition survives. How else is one to explain the evolution of the great diversity of a group which has carved out a niche for itself in the excrement of other organisms! Millions of years ago an odd beetle must have taken to coprophagy and unleashed a radiation (helped along by abundant dinosaur dung perhaps!) leading to more than 5000 species of dung beetles at present.

It is not surprising that the dung beetles (Coleoptera : Scarabaeidae : Scarabaeinae) with their curious behaviour have been the focus of both folklore and scientific literature. The extremely beneficial role of dung beetles in keeping our environment clean was highlighted by Hingston (1923) who declared `...in India during May and June as much as forty to fifty thousand tons of excrement must be carried by scarabs into the soil. And this does not include the dung of animals, which may easily double or treble the amount....'

The value of dung beetles in dung disposal and other ecosystems services that accrue from this act was only realised through the folly of a few Europeans who introduced cattle and sheep into Australia. Intensive cattle ranching led to accumulation of dung heaps which laid waste the pastures. Worse still, parasitic flies bred in the dung heaps and caused more trouble for ranchers. The solution to all these problems lay in introducing dung beetles from Africa and Asia!

The search for suitable species of dung beetles that could be introduced into Australia led to a flurry of research, covering a wide range of issues from taxonomy to ecology of dung beetles worldwide. Further, the dung pats with their associated insects came to be recognised as ecological units (Mohr, 1943) ideal for studies in community ecology. Almost fifty years later, an excellent update on dung beetle ecology was provided by Hanski and Cambefort (1991).

Unfortunately however, the dung beetles have not received adequate attention in India. The only notable work on dung beetles is that of Arrow (1931), and Veena Kumari (1984) and a few other isolated studies. Almost all of these studies have focussed on either the taxonomy or behaviour of dung beetles. The present study was taken up to generate some baseline data on the community ecology of dung beetles particularly on resource partitioning and segregation.

The study was taken up with the following objectives:

1. To study the diversity and abundance of dung beetles associated with cattle dung in Bangalore
2. To study the seasonality of dung beetles associated with cattle dung in Bangalore
3. To study the dung beetlescolonisation pattern in dung of different ages
4. To prepare a faunal list of dung beetles associated with cattle dung in Bangalore.

# II. REVIEW OF LITERATURE

# II. REVIEW OF LITERATURE

Information related to dung beetles are reviewed here mainly to cover the Indian work on Scarabaeinae and community ecology of dung beetles in general on a worldwide basis.

## 2.1 Taxonomic and faunistic studies

The present work is confined to dung beetles belonging to the subfamily Scarabaeinae which comes under the family Scarabaeidae, order Coleoptera. Arrow's (1931) comprehensive taxonomic work on dung beetles of India revealed 354 species in 26 genera that could be grouped into 4 tribes *viz.*, Scarabaeini, Sisyphini, Coprini and Panelini. Few later additions to this list include one species by Gordon and Oppenheimer (1975) and five by Biswas (1978). Thus, a total of 360 species of dung beetles are known from India.

The earliest work on taxonomy of Indian dung beetles was that of Linnaeus who described *Scarabaeus sacer*, an Indian species, in his 10th volume of *Systema Naturae* (1758). Many European entomologists described Indian dung beetles later and these were compiled by Arrow (1931).

From Bangalore, Arrow (1931) recorded 33 species of dung beetles. These include three species each of *Scarabaeus, Gymnopleurus* and *Cacccobius*, one species each of *Sisyphus* and *Heliocopris*, two species of *Catharsius*, four species of *Copris* and thirteen species of *Onthophagus*. Later work by Veena Kumari and Veeresh

(1997b) revealed 61 species which included four species of *Sarabaeus*, six species of *Gymnopleurus*, four species of *Sisyphus*, two species of *Heliocopris* , seven species of *Copris*, two species of *Catharsius*, three species of *Onitis*, one species of *Drepanocerus*, two species of *Oniticellus*, five species of *Caccobius*, one species each of *Phalops*, *Liatongus* and *Tiniocellus* and 24 species of *Onthophagus*. Although 61 species were encountered from different parts of Bangalore, Veena Kumari (1984) reported only 15 species of Scarabaeinae based on a year round survey at the Military Dairy Farm, Hebbal, Bangalore. These were *C. repertus*, *Cat. molossus*, *On. philemon*, *Onit. cinctus*, *D. setosus*, *Ca. vulcanus*, *C. meridionalis*, *O. spinifex*, *O. turbatus*, *O. unifaciatus*, *O. dama*, *O. duporti*, *O. quadridentatus*, *O. rectecornutus*. All these belonged to a single tribe Coprini. Detailed taxonomic description of these species are available in Fauna of British India volume on Coprini (Arrow, 1931).

## 2.2 Biological and behavioral studies

Although taxonomy of dung beetles of India has been well studied, there are a few works on other aspects of these beetles. Hingston (1923) provided the first notes on the ecological importance of these beetles and felt that they are responsible for removing most of the filth of man and other large mammals from the face of the Earth. After this work few scattered publications available on dung beetles are reviewed below.

Gordon and Oppenheimer (1975) studied the seasonal activity, food preference and trap catches of two species of dung beetles in West Bengal. They reported bimodal peaks for *O. bifaciatus* with a major peak during June and minor peak in November.

Rajagopal and Veeresh (1981) reported the occurrence of Scarabaeines in the mounds of *Odontotermes wallonensis*. Verma (1969) described the alimentary canal of *O. catta*. Upadhyaya and Tripathi (1973) studied the food preference of *Cat. molossus*. Mittal and Yadava (1981) documented the burrowing activity and ability of *On. philemon, On. virens and O. catta* to bury dung during different months. He found greater beetle activity for all the three species during August compared to September and October.

At Bangalore, Veena Kumari (1984), Veena Kumari and Veeresh (1996a, b, 1997a) studied the biology of 4 species, viz., *O. gazella, O. rectecornutus, On. philemon* and *C. repertus*. She also studied the seasonal abundance and succession of dung beetles in cattle dung pats. Her study revealed a decreased in the attraction of number of coprophagus species and individuals with increasing age of the dung. She found high activity of dung beetles during the months of May, June, July and August both with respect to number of species and number of individuals. Ravindranath (1994) studied the biology of *O. duporti* and reported that the beetle activity enriched the soil.

## 2.3 Community organization of dung beetles

Dung being an ephemeral habitat the organization of dung insect community follows that of communities in ephemeral habitats such as fungi, carrion, ruderal plants etc. These habitats are characterized by relatively small size, scattered spatial occurrence, short existence or durational stability. Many such microhabitats stand out in the matrix of the surrounding environment as 'islands' of high quality resources.

Further, the dung in itself has no defense against invading organisms (Hanski, 1987a). With this background,community of insects inhabiting dung or other similar ephemeral habitats and the processes that dictate the organization of such communities are reviewed here.

## 2.4 Dung insect community

Animal droppings or dung, is inhabited primarily by members of three insect orders *viz.,* Coleoptera, Diptera and Hymenoptera. Coprophagus insect families in the community include Geotrupidae, Hydrophilidae, Scarabaeidae and Staphylinidae among Coleoptera and Anthomyiidae, Ceratopogonidae, Chironomidae, Muscidae, Psychodidae, Scatophagidae, Scatopsidae, Sciaridae, Sepsidae, Sphaeroceridae and Stratiomyiidae among Diptera. Mycophagus and saprophagus species include Coleoptera of the families, Cryptophagidae, Ptilidae and Staphylinidae. Predators in the community include Muscidae among Diptera and Carabidae, Histeridae, Hydrophilidae and Staphylinidae among the Coleoptera. Insect parasitoids are made of Staphylinidae among Coleoptera, Bombylidae among Diptera and Braconidae, Eucoilidae, Ichneumonidae and Pteromalidae among the Hymenoptera (Hanski and Cambefort, 1991b).

## 2.5 Dung beetle community

Among the insects found in mammalian dung, beetles of the subfamily Scarabaeinae , Family Scarabaeidae are the most dominant worldwide both in terms of number of species and their numerical representation. An estimated 5000 species of dung beetles have been described from different parts of the world. Anderson and Coe

(1974) reported that 16,000 of these beetles arrived at a 1.5 kg heap of elephant dung in East Africa. Upto 200 species have been reported from single elephant dung pats in Africa and these beetles might roll away the dung in matter of few hours. Obviously, much of the literature on ecology of dung inhabiting insects is on dung beetles of the subfamily Scarabaeinae (Hanski and Cambefort, 1991a).

Dung beetles have been the subject of several studies in different parts of the world, from the point of view of community ecology. Aspects of biology, behaviour, population ecology, size differences, spatial processes and patterns, temporal patterns, community patterns, population ecology, resource partitioning etc., have been addressed in great depth in many parts of the world covering North and South temperate regions (Hanski, 1991b; Lumaret and Kirk, 1991), Southern Africa (Doube, 1991), tropical savannas (Cambefort, 1991), South East Asian tropical forests (Hanski and Krikken, 1991), African tropical forest (Cambefort and Walter, 1991), tropical American forest (Gill, 1991), Sahel regions (Rougon and Rougon, 1991), Montane habitats (Lumaret and Stiernet, 1991) and Australia (Doube, *et. al.*, 1991). An overview of these studies is available (Hanski and Cambefort, 1991a).

## 2.6 Mechanisms of community organization

Among the possible mechanisms that mould the community structure of dung beetles, competition, spatial pattern and predation are considered important.

### 2.6.1 Competition

Although,explicit studies of competition in dung beetles are few (Cambefort and Hanski, 1991), its role in ordering the dung beetle communities was illustrated by competitive exclusion of dung feeding flies after the introduction of dung beetles to Australia (Waterhouse, 1974; Ridsdill-Smith, 1990; Doube, 1986). Studies made by Doube *et al.*, (1988) demonstrated interspecific competition among dung beetles. Similarly intraspecific competition both among adults (Kingston, 1977) and among the larvae (Hanski and Cambefort, 1991b) is also demonstrated.

Intraspecific interference competition, largely in grassland situation, has been demonstrated among ball rolling species of several genera such as *Sisyphus, Gymnopleurus* etc., (Hanski and Cambefort, 1991b). Interference competition are also envisaged in tunnelers and cleptoparasitic species of dung beetles (Holter, 1979).

Rapid burial of up to 500g of dung, by many large tunnelers clearly serve as example of exploitative competition among the dung beetles (Edwards, 1986). Even a small number of these beetles in the same dung pat are likely to compete with one another. Many studies have shown such pre-emptive resource competition to be a common feature, across the globe in dung beetle communities. However, many of these are apparent only seasonally (Hanski and Cambefort, 1991c; Kingston, 1977; Heinrich and Bartholomew, 1979).

Competition for resource has also been envisaged among beetles that dwell in the dung pats ( Yasuda, 1987). Alternatively, space might be a limiting factor for many tunneling dung beetles. The evolution of complicated nest structure is generally believed to reflect increased levels of parental care. However, Rougon and Rougon (1991) believe, that stratified nest construction by a few dung beetles of Sahel region serve to reduce the competition for space. Further, higher densities of species under impoverished condition such as montane habitats compared to low elevation habitats are largely considered as indirect indicators of density compensation reflecting competition as the direct process responsible for lower densities in low elevation situations (Hanski and Niemela, 1990).

### 2.6.2 Predation

While predation has been argued as an important mechanism in dictating the abundance of (specific types) species in many communities, there is little evidence to illustrate their effect on dung beetle communities.

There is no evidence of dung beetles themselves serving as predators in cattle pats. Other groups of predacious insects recorded from animal droppings are all believed to be primarily predators of dung inhabiting Diptera (Hanski, 1991a). There is hardly any information on predation of dung beetles themselves. Indeed, very few predators of dung beetles have been recorded so far. This low predation pressure on dung beetles has been suspected to be due to possible extinction of original predators of dung beetles. Nonetheless, mimicry in African rollers and general nocturnal habit of large tunnelers, are possible features that might have evolved in response to predation. Kingston and Coe, (1977) have suggested that great depths of nests of *Heliocopris dilloni* may have evolved in response to predation by ratel. Large concentrations of dung beetles may attract predators. Kumar and Veeresh, (1990), reported repeated raids by the ants *Leptogenys diminuta* to dung pats for collection of Scarabaeines. As an alternative to predation, nesting at greater depths may be a mechanism to reduce cleptoparasitism. Veena Kumari (1984), reported up to 50 per cent loss of broods in dung beetles due to parasitic mites.

### 2.6.3 Spatial processes

A dynamic interaction of resource size, competitive abilities, behaviour of the species, predation *etc.*, leading to condition of intra and inter-specific aggregation of species or complete elimination of many species is the essence of a continuum of lottery dynamics or variance-covariance dynamics. These spatial processes and patterns resulting in observed community structure has been largely championed by Sale (1977,1979) who studied coral reef fishes and Hanski (1981,1991a). Hanski's work particularly dwelt on patchy microhabitats where the resource size might vary as in the case of mammalian dung which varies from few grams to as much as 10 kg. The structure of the community then is dictated by the overall size of the resource patch. Lottery dynamics can operate if a resource patch (or dung) can be exploited by a single or a few individuals of a species such that all the other species are pushed to the margin and become extinct - atleast locally. On the contrary if the resource size, relative to the most competitive species is such that it cannot be harvested to a maximum extent by one or a few individuals, then a mixed community of rich diversity can co-exist. Such a mechanism, mostly identifiable on the basis of relative intra and inter-specific aggregation of species, is termed as variance - covariance dynamics. Communities of patchy micro-habitats are ordered mostly by ensuring competition or predation as consequence of species distribution patterns.

However, ignoring the terminology, conditions for extinction or coexistence of species, depending on the size and density of ephemeral resource has been demonstrated (Kneidel, 1985).

### 2.7 Segregation of species and resource partitioning

Dung apparently being a single resource type, is known to support a large number of species in many habitats of the world. As many as 147 species of Scarabaeidae are expected to live on cattle dung across grasslands of subtropical Africa (Davis *et al.*, 1988). Veena Kumari and Veeresh (1997) reported as many as 57 species of Scarabaeines to inhabit cattle dung in Bangalore. Such a large number of species co-existing on an apparently single resource would demand strong mechanisms of resource partitioning. A large number of studies on a worldwide basis have considered the mechanism of resource partitioning in dung beetle communities. Salient among these are summarized below.

#### 2.7.1 Type of resource

Mammalian dung can be broadly categorised into three major classes: herbivore -dung, omnivore-dung and carnivore-dung. Although specificity of dung beetles to the droppings of any one species of mammals is a rare phenomenon, the specificity or preferential colonization of the above three types of mammalian dung is widespread.

Carnivore dung is known to attract few dung beetles, which comprise a mixture of species that colonize dung and carrion (Hanski, 1987). On the contrary the other two types of dung attract most of the dung beetles. However, majority of the ball rolling species prefer omnivore-dung to herbivore-dung, while tunnelers largely prefer herbivore-dung. By arbitrarily defining a specialist with more than 90% individuals being caught in a particular type of dung, figures for Savanna in Ivory coast were 43 omnivore-dung specialists, 16 herbivore dung specialists and 31 generalists (Cambefort, 1991; Cambefort and Walter, 1991).

Most of the large tunnelers and few rollers are human dung specialists or herbivore dung specialists. Strong specialisation for omnivore dung is a rare phenomenon. But several shifts between herbivore and omnivore dung has been observed in many species of *Pedaria, Caccobius* and *Cleptocaccobius* in Africa. Several shifts between coprophagy and necrophagy has also been noticed among some species of beetles in Barro Colorado Islands in Panama (Young, 1978).

Specialisation is also considered uncommon among the forest dwelling species of dung beetles relative to their counterparts inhabiting grasslands. Possible rich mammalian diversity and abundance in savannas and other grasslands relative to the forests may be one factor that has contributed for this difference. Dung beetles, thus appear to be a major contradictions to the general belief of high degree of specialisation among tropical insect communities (Mac Arthur, 1972 ; Pianka, 1974).

Few exceptional species, among the dung beetles to the above rule are those that feed on scat of sloths of South America (Ratcliffe, 1980), and some Australian *Onthophagus* that breed in macropod pellets (Mathews, 1972).

### 2.7.2 Quality of dung

Quality of dung can be addressed in many different ways and thus may contribute for variation in the utilisation pattern by dung beetles. Seasonal variations in the nutritional quality of elephant dung (Kingston, 1977) is suspected to influence the choice of dung for breeding or feeding by dung beetles. Dung, on the other hand like any other ephemeral resource, changes its quality with time (Southwood, 1977). Changes in the composition of the dung beetles with age has been widely documented (Mohr, 1943; Valiela, 1974; Koskela and Hanski, 1977; Veena Kumari, 1984). The quality of dung with age has been suggested as an important reason for the changing beetle composition both in abundance and species. Three stages of succession, first lasting up to two days, second up to a week after the first and third and infinitely lasting stage, were identified by Koskela and Hanski (1977).

### 2.7.3 Size distribution

Animal size has far ranging consequences to different aspects of ecology of an organism (Peters, 1983). Size as a factor in partitioning of resource between species is also well documented (Hutchinson, 1959). Dung beetle communities however are likely to be effected differently. The following are believed to be some of the ways by which size may influence the structure of the dung beetle communities.

A) Size may affect food selection particularly among the large species, which may have to depend on a narrow range of resources such as only large pats, unlike in the case of predators, where larger size results in wider resource range (Wilson, 1975).

B) Holter (1982) demonstrated utilisation of different parts of cattle dung pats by different species of *Aphodius* and such phenomenon is believed to be a product of size differences among the species involved (Hanski and Cambefort, 1991c).

C) Size of the ball and size of the beetle may determine the extent of inter or intra specific interference competition in ball rollers.

D) Spatial covariance may decrease with increasing size differences. Thus, inter specific aggregation may decrease in relation to intra specific aggregation thus contributing for species coexistence.

Body sizes of dung beetles are known to influence their abundances locally. However, beetles of different body sizes were shown to follow different patterns of abundance at increasing levels of geographical ranges (Cambefort, 1994 ).

### 2.7.4 Method of exploitation (Foraging)

Dung beetles are broadly grouped into four categories based on the dung exploited. They are :

**Rollers:** rollers comprise of those species that make a dung ball and roll it away from the pat. The rollers characteristically belong to two tribes of Scarabaeinae viz., Scarabaeini and Sisyphini.

**Tunnelers**: Many species of dung beetles, particularly in the tribe Coprini, bury the dung by tunneling right beneath the dung pat.

**Endocoprids:** Some species of Coprini feed and breed staying within dung pats. These are also referred to as dwellers.

**Cleptocoprids:** Cleptocoprids are mostly small species of the genera *Caccobius* and *Onthophagus*, which live in the dung stored by larger species of tunnelers or rollers. These functional groups are widely cited in literature as indicators of resource partitioning (See Hanski and Cambefort, 1991a). However, considering body size, stay time in a pat, rate of removal *etc.* Doube (1991) proposed an elaborate structure of dung beetle assemblages where he split the rollers into large and small, tunnelers into fast and slow burying tunnelers, slow burying tunnelers were again spilt into large and small species. Adding endocoprids and cleptoparasites, seven functional groups were assembled by him. These classifications thus reinforce the idea of species segregation on the basis of their ways of exploiting dung.

### 2.7. 5 Temporal partitioning

Temporal partitioning of resources can be on a short or long term basis. Diel activity can be an ideal short term measure of temporal partitioning while seasonality would be a long term measure.

Diel activity among dung beetles is a relatively conservative trait, as many species of most tribes are either diurnal or nocturnal/crepuscular. In Africa, Sisyphini and Oniticellini are diurnal, while Coprini are nocturnal. Majority of Gymnopleurini are diurnal (Hanski and Cambefort, 1991c). Diel activity is also related to functional groups of dung beetles (Doube, 1991; Cambefort, 1991). Most rollers are diurnal, large tunnelers are nocturnal while small tunnelers include both nocturnal and diurnal species. Further diel activity might also be related to the defecation time of concerned mammals. Largest amount of dung is known to be voided at the end of the days feeding period in elephants (Tribe, 1976), thus more nocturnal species of dung beetles are expected to be associated with elephant dung. Many dung beetles have dusk and dawn flight activity, which may coincide with the peak production of dung by diurnal and nocturnal mammals respectively (Gill, 1991). Exceptions to these broad generalisations, may have evolved as mechanisms of avoiding competitions with members of the same guild that represent the functional groups.

### 2.7.6 Habitat selection

Habitats may influence segregation of dung beetles at two spatial scales: at the scale of droppings and macrohabitats scales. These are apparently influenced by the type of soil where the dung is deposited, type and density of vegetation.

Within pat resource partitioning has been shown in the species of *Aphodius,* (Holter, 1982) *Sisyphus* and *Neosisyphus* (Paschalidis, 1974). Functional groups also manifest a microhabitat level spatial segregation (Edwards and Aschenborn, 1987). In essence, the behavioural features and the modes of resource harvesting themselves add a third dimension (within patch) of resource partitioning.

On a lower spatial scale, grasslands are known to be richer in dung beetle species compared to forest areas. But, the primary species of the two ecosystems were found to overlap at different degrees. In general, there was a gradient along the latitude for the extent of overlap between the two assemblages. At higher latitudes, the extent of overlap was greater and there was a little overlap between the grassland fauna and the forest assemblages of dung beetles at lower latitudes.

Soil type indirectly affects the survival and multiplication of dung beetles. Endocoprids, are generally indifferent to soil types. Tunnelers and rollers, which construct underground burrows and nest chambers in the soil, for them the soil type is decisive. A study (Doube, 1991) covering dung beetle assemblages in four soil types of South Africa revealed 73 per cent of variance in dung beetle abundance to be explained by soil types.

## 2.8 Size weight relationships in insects

Biomass estimation of communities is an important parameter for many ecological studies. Biomass estimation of small and numerous organisms such as insects is laborious and time consuming. Further direct weighing may require destruction of specimens that need to be preserved for other studies in future. In order to overcome these problems, size-weight relationships have been established for many invertebrates (Rogers *et al.* 1976; Ganihar, 1997) so that size can be used to estimate biomass.

# III. MATERIAL AND METHODS

# III. Material and methods

## 3.1 Study site

The study was conducted on an unused pasture land (approximately 1.5 ha) at Military Dairy Farm (MDF), Hebbal, Bangalore (12°57' N, 72° 35' E, 916 m MSL) during 1997.

Studies on diversity, abundance, community structure and seasonality of dung beetles were carried out at Bangalore using standard quantitative ecological methods. The materials and methods employed are briefly described here.

The study site was chosen after initial surveys showed that the entire farm with its cattle population supported a teeming community of dung beetles. Further, the security of the farm made it an ideal choice for manipulative field experiments. Beetles were also sampled from other locations around Bangalore and Biligiri Rangaswamy Temple sanctuary in Chamarajanagar for size - weight relationship studies. Veena Kumari (1984) had also previously studied dung beetle communities at this site.

## 3.2 Experimental set up

All quantitative studies were carried out by baited sampling. Sampling was carried out by setting up dung pats of equal volume. Dung pats were laid out using fresh dung collected from cattle stalls. About 1.5 litres of fresh dung was dropped from a height of 1 - 1.25 m on clear ground to serve as pats for colonization by dung beetles. These pats were laid out in four rows of 10 pats each with an inter - pat interval of 10

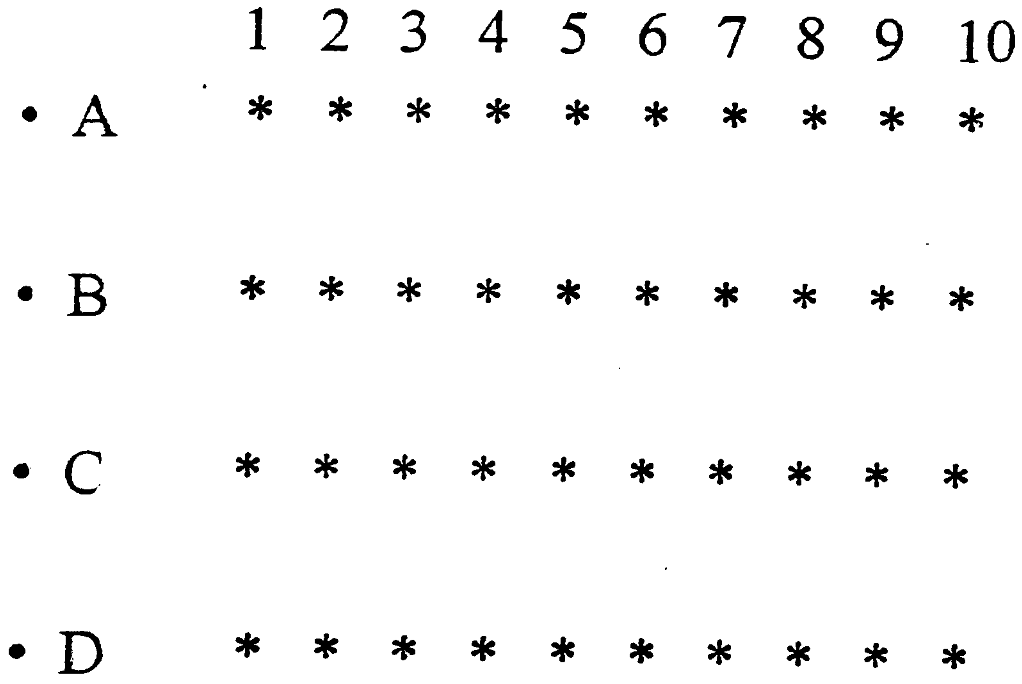

**Fig. 1 SAMPLING LAY OUT**

**PLATE 1. A view of the study site:** The unused pasture land at military dairy farm, Hebbal, Bangalore during monsoon season. The lush green grass grass dries up completely during the dry season between Febraury and June.

PLATE 2. **Dung pats showing dung beetle activity:** A one day old dung pat placed as bait (top left); four day old pat showing burrowing activity of beetles, notice the excavated soil (top right); eight day old pat showing burrow entry holes of large tunnelers like *Cartharsius* sp., and *Copris* sp., (bottom left); a fifteen day old pat showing complete disappearance of dung (bottom right).


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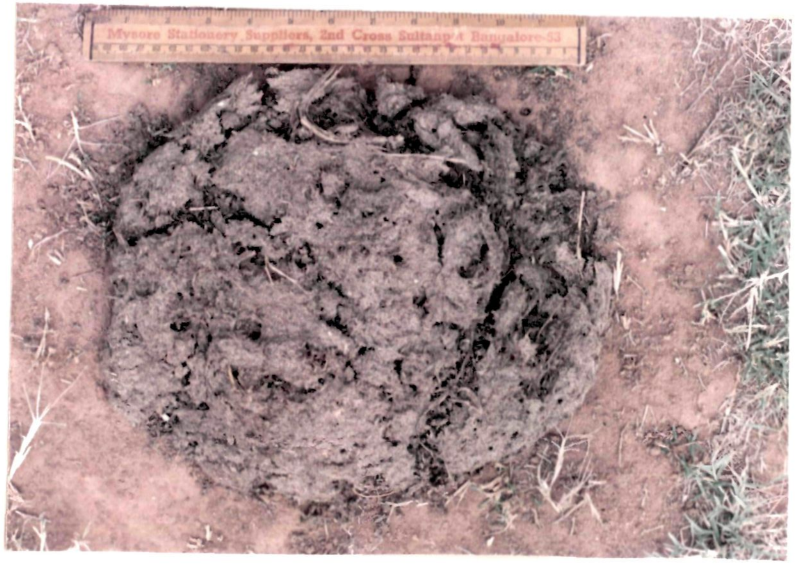
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feet (Fig. 1). For sampling beetles, pats were harvested from this grid of baits at daily intervals upto 10 days and thereafter on 12 and 15 days. Two pats each were harvested on odd days while three pats were harvested on even days and 12 and 15 days. Thus, a total of 31 pats were harvested for each sampling bout lasting fifteen days. Pats after selecting randomly, were harvested along with soil surrounding the pat upto a depth of 5 cm. Harvested pats along with soil were placed in a bucket filled with water and mixed slowly until all beetles floated. This process took 15 minutes. Later, remaining part of the dung was passed through sieves of different sizes to collect any beetle that could not be extracted by the above method (Southwood, 1976; Veena Kumari, 1984). This ensures complete removal of all beetles associated with pat. Beetles harvested from each pat were transferred to 70 % alcohol and appropriately labeled. Entire procedure was repeated twelve times, starting from April 4, 1997, over a period of six months at approximately fifteen days interval. Each sampling bout was designated as a sampling date and numbered serially from 1 to 12.

Beetles collected from each pat were processed using standard taxonomic procedures (Borror and De Long, 1955) and initially sorted upto species level and data on their relative abundances recorded. Attempts were made to identify all species using the taxonomic keys provided by Arrow (1931). However, those that could not be identified were coded as morpho - species or recognisable taxonomic units (RTU's).

### 3.3 Size - weight relationships

Beetles collected from Bangalore (outside MDF) and BRT Sanctuary from March to June, 1998 were used for this study. All collected beetles were initially weighed after thoroughly washing in water. They were later transferred to 70% alcohol after giving a code for each specimen. They were removed after one hour, and transferred to butter paper covers and dried in an hot air oven for 15 days at 35 to 37°C. These were weighed again using electronic balance, with 0.01 mg accuracy. The measurements on body size were made using a stereobinocular microscope fitted with an ocular micrometer. All measurements were converted into millimeters. Elytron length, pronotum length and maximum width of the pronotum were measured. A total of 23 species represented by 232 specimens were used for this study.

### 3.4 Data analyses

A total of 372 pats were sampled across 144 sampling days in 12 age groups of dung spread across 12 sampling dates. Data on dung beetle abundance, number of species, specieswise abundances were tabulated across all the four levels of sampling viz., pats, days, age of dung and dates of sampling. Standard statistical measures such as mean and standard deviation were calculated for each parameter.

Two diversity indices *viz.*, Shannon's and Simpson's index were used following Magurran,(1988).

Shannon's Index was computed as :

$$H' = - \Sigma p_i \ln p_i$$

Simpson's Index was computed as:

$$D = 1 - \Sigma p_i^2$$

Where: $p_i$ = Proportion of the $i^{th}$ species in a pool of S species

Niche breadth was calculated using the Shannon-Wiener formula for information (Shannon and Weaver, 1949) following Levins (1968). The formula as indicated by Colwell and Futuyma (1971) is given by :

$$B'_i = -\Sigma p_{ij} \ln p_{ij}$$

where $p_{ij} = N_{ij} / Y_{ij}$ , the proportion of the individuals of species 'i' which is associated with resource state 'j'.

Niche overlap was calculated following the measure developed by Schoener (1974). The proportional niche overlap for any two species is given by :

$$C_{ih} = 1 - 1/2 \, \Sigma \, | p_{ij} - p_{hj} |$$

where $p_{ij}$ is as given above and

$p_{hj} = N_{hj}/Y_{hj}$, the proportion of the individuals of the second species 'h', which is associated with resource state 'j'.

Pearson's product moment correlation (Snedecor and Cochran, 1967) was used where necessary. Power functions of size weight relationship were deduced from log transformations of the data and then computing the correlations (Rogers *et al.,* 1976 and Ganihar, 1997).

Principal component analyses (PCA) technique was employed to identify the clusters of species. Unrotated data sets were used for all these analyses and clusters of species were identified by obtaining plot of species in the space of two principal components. This part of the analyses was carried out following the technique employed by Doube (1991) and using a Windows based statistical package - Statistica.

In order to understand the distribution of diversity at different levels of sampling hierarchy the diversity was partitioned at the pat, day, age of dung, date of sampling and pooled sample following Joshi *et al.*,(1997). They suggested the weighted means of Simpson's index as a measure of partitioning variance, alternative to standard analysis of variance. The technique is easy and simple to apply. Both weighted and unweighted means always increase in value with the level of sampling. The values themselves indicate proportional variance and multiplied by 100 yield per cent variance.

# IV. RESULTS

# IV. RESULTS

## 4.1 Species assemblage of dung beetles

Cattle dung pats sampled from April 4, 97 to October 20, 97 at Military Dairy Farm (MDF), Hebbal, Bangalore yielded a total of 1901 individuals belonging to 32 morpho species (or Recognisable Taxonomic Units), representing eight genera and a single tribe Coprini.

Genus *Onthophagus* Latr. was represented by 21 morpho species, of which three could be identified to species level. They are *O. dama* F., *O. truncaticornis* Schall. and *O. rectecornutus* Lansb. The remaining 18 species were coded and are yet to be identified. The next most abundant genus was *Copris* Geoffroy which was represented by four species and all could be identified (Table 1). Of the remaining seven species, two species belonged to the genus *Oniticellus* Serv., while *Caccobius* Thomson, *Drepanocerus* Kirby, *Onitis* Fabricius, *Liatongus* Reitter and *Catharsius* Hope were represented by a single species each.

The analysis of the data gathered during the course of this study over a period of six months are presented in the following sections.

## 4.2 Patterns of diversity in the dung beetle community at MDF

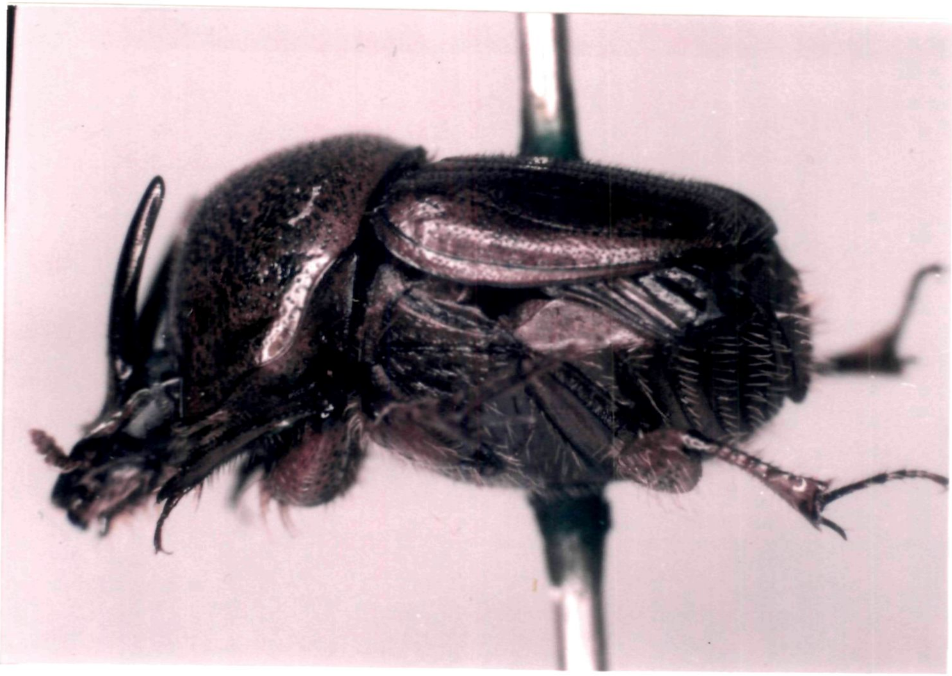
The community of dung beetles associated with cattle dung at MDF, encountered during the course of study, was examined at different levels. The variation in size of the dung beetle community at the level of individual pat, day of sampling , age

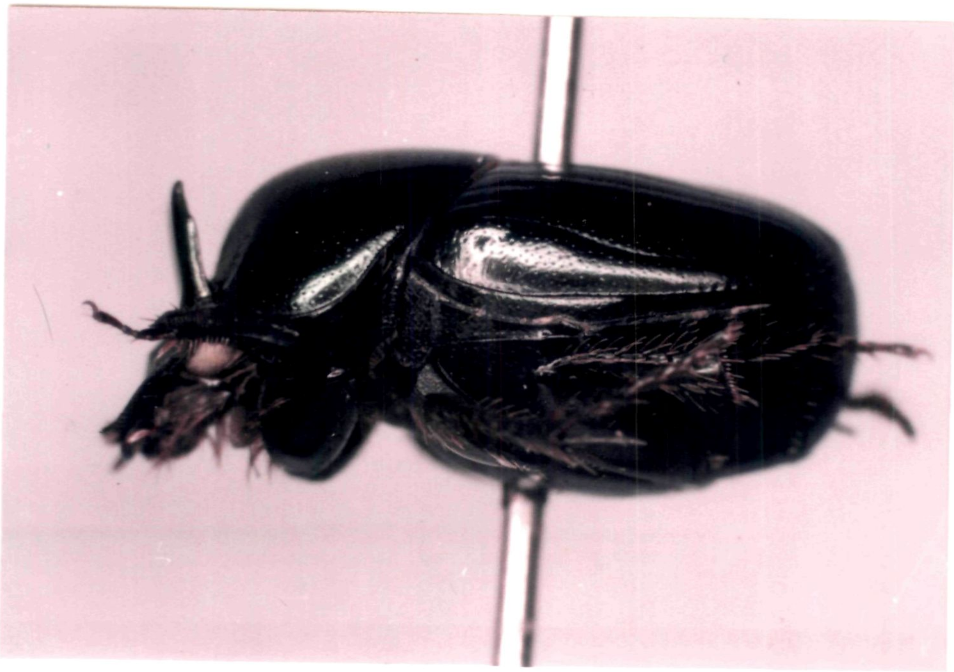
Table: 1. **List of species of Scarabaeinae dung beetles encountered at MDF, Bangalore during 1997**

| **Sl. no.** | **Genus** | **Species** |
|---|---|---|
| 1 | *Drepanocerus* Kirby | *Drepanocerus setosus* (Wied.) |
| 2 | *Onthophagus* Latreille | *Onthophagus dama* (F.) |
| 3 | | *Onthophagus truncaticornis* (Schall.) |
| 4 | | *Onthophagus rectecornutus* Lansb. |
| 5 | *Caccobius* Thomson | *Caccobius vulcanus* (F.) |
| 6 | *Oniticellus* Serv | *Oniticellus cinctus* (F.) |
| 7 | | *Oniticellus spinipes* (Roth.) |
| 8 | *Onitis* Fabricius | *Onitis philemon* F. |
| 9 | *Liatongus* Reitter | *Liatongus rhadamistus* (F.) |
| 10 | *Copris* Geoffray | *Copris repertus* Walk. |
| 11 | | *Copris numa* Lansb. |
| 12 | | *Copris bengalensis* Gillet. |
| 13 | | *Copris sacontala* Redt. |
| 14 | *Catharsius* Hope | *Catharsius molossus* (L.) |
| 15 | | *Onthophagus* sp.B |
| 16 | | *Onthophagus* sp.C |
| 17 | | *Onthophagus* sp.D |
| 18 | | *Onthophagus* sp.E |
| 19 | | *Onthophagus* sp.F |
| 20 | | *Onthophagus* sp.H |
| 21 | | *Onthophagus* sp.I |
| 22 | | *Onthophagus* sp.J |
| 23 | | *Onthophagus* sp.K |
| 24 | | *Onthophagus* sp.P |
| 25 | | *Onthophagus* sp.O |
| 26 | | *Onthophagus* sp.R |
| 27 | | *Onthophagus* sp.S |
| 28 | | *Onthophagus* sp.T |
| 29 | | *Onthophagus* sp.V |
| 30 | | *Onthophagus* sp.W |
| 31 | | *Onthophagus* sp.Y |
| 32 | | *Onthophagus* sp.Z |

**PLATE 3.**
**Dung beetles**

| | |
|---|---|
| *Onthophagus rectecornutus* Lansby | (12.5x) |
| *Onthophagus dama* (Fabricius) | (15x) |





### PLATE 4.
### Dung beetles

| | |
|---|---|
| *Oniticellus cinctus* (Fabricius) | (15x) |
| *Onitis philemon* Fabricius | (7x) |

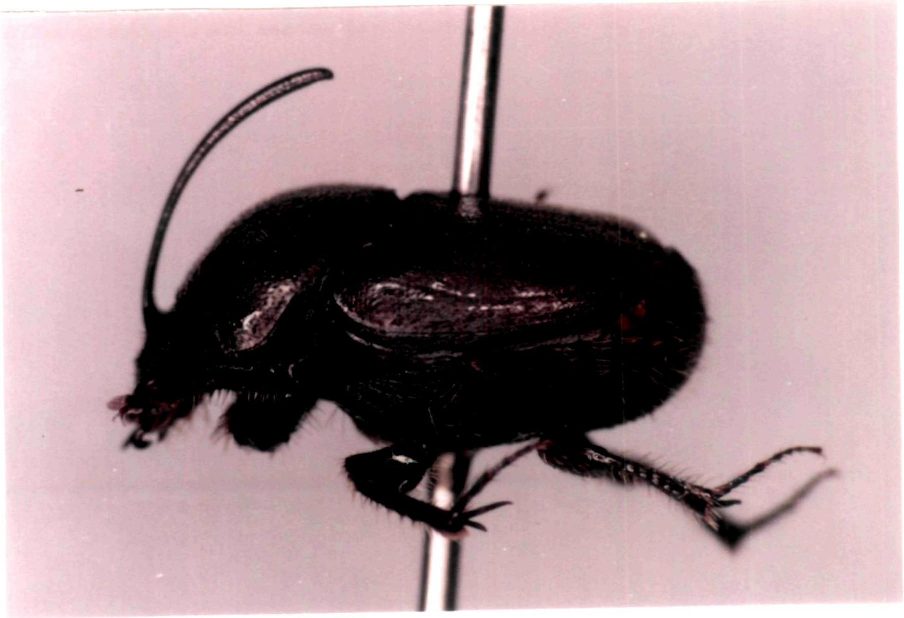
**PLATE 5.**
**Dung beetles**

| | |
|---|---|
| *Liatongus rhadamistus* (Fabricius) | (10x) |
| *Copris repertus* Walker | (10x) |

## PLATE 6.

**Dung beetles**

| | |
|---|---|
| *Onthophagus* sp. E | (15x) |
| *Onthophagus* sp. P | (15x) |



of dung (at the time of sampling) and at different sampling bouts (sampling dates) are summarised in table 2. The diversity indices varied considerably at these four levels and ranged from 0 to 3.78 and 0 to 0.972 for Shannon's and Simpson's index, respectively.

### 4.2.1 Diversity across pats

Analysis of the community, on the basis of individual pats indicated that the number of species ranged from 0 to 10 species, with a mean (± sd) of 1.699 ± 2.01 species per pat. The number of individuals ranged from 0 - 65 per pat with a mean (± sd) of 5.11 ± 9.29 suggesting an aggregated distribution of species across pats. It is important to note that as many as 36.3 per cent of the 372 pats sampled did not yield any beetles.

The Shannon's diversity index ranged from 0.00 to 1.96 per pat with a mean (± sd) of 0.398 ± 0.568; while the range for the Simpson's index was from 0.00 to 0.83 with a mean (± sd) of 0.223 ± 0.229 (Table 2). These results clearly suggest considerable pat to pat variation in number of individuals, number of species and the diversity indices.

### 4.2.2 Diversity across days

The day to day variation in species richness was computed by pooling the data from all pats for each of the 144 sampling days. Up to a maximum of 11 species were encountered with a mean (± sd) of 3.00 ± 2.92 species of dung beetles per day. The total number of individuals encountered ranged from zero to 117 individuals with a

**Table : 2. Species richness, relative abundance and diversity of dung beetles collected at MDF, Bangalore during 1997. The data from 372 pats presented across different sampling categories.**

| Sl. no. | Category | Sample size | No. of individuals | | No. of species | | Shannon's index | | Simpson's index | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd |
| 1. | Dung pat | 372 | 0 - 65 | 5.11 ± 9.29 | 0 - 10 | 1.70 ± 2.01 | 0 -1.96 | 0.40 ± 0.57 | 0 - 0.83 | 0.223 ± 0.229 |
| 2. | Day of sampling | 144 | 0 - 117 | 13.20 ± 20.94 | 0 - 11 | 3.00 ± 2.92 | 0 - 3.78 | 0.65 ± 0.64 | 0 - 0.97 | 0.349 ± 0.318 |
| 3. | Age of dung at sampling | 12 | 23 - 597 | 158.22 ± 192.44 | 4 - 23 | 12.75 ± 6.62 | 0.97 - 2.33 | 1.77 ± 0.48 | 0.58 - 0.85 | 0.74 ± 0.1 |
| 4. | Date of sampling | 12 | 58 - 290 | 158.42 ± 73.47 | 8 - 18 | 13.25 ± 2.89 | 1.46 - 2.28 | 1.91± 0.24 | 0.69 - 0.87 | 0.79 ± 0.06 |
| 5. | Community (pooled) | 372 | 1901 | | 32 | | 2.402 | | 0.878 | |

mean ( ± sd) of 13.20 ± 20.94 beetles per day. As many as 20.14 per cent of the days did not yield a single beetle. High variance to mean ratio (33.22) suggested an aggregative distribution of beetles, across days of sampling.

The diversity was 0.65 ± 0.64 (mean ± sd) by Shannon's index and 0.35 ± 0.32 (mean ± sd) by Simpson's index with a range of 0 to 3.78 and 0 to 0.97 per day respectively. The observed range was higher on the basis of day compared to any other method of pooling the data, suggesting the variation to be greatest on day to day basis (Table 2).

### 4.2.3 Diversity across dung age

Data on dung beetles sampled from dung pats, one to 15 days old were pooled across number of pats sampled per day and number of days sampled for (12 days for 12 sampling bouts) each of the 12 dung ages considered i.e. 1 to 10, 12 and 15 days old dung pats. An analysis of the data, pooled for each of the 12 dung age catagories considered are also presented.

#### 4.2.3.1 Patwise variation in diversity across dung age

Summary of the data collected patwise for each of the 12 dung age groups and pooled across the 12 sampling bouts is presented in table 3. The total number of pats sampled for each of the 12 dung age catagories are indicated in the table. The range of number of individuals recorded per pat on each of these age groups varied from 0 to 65

**Table: 3. Diversity and abundance of dung beetles (patwise) in dung pats of different age categories at MDF, Bangalore. The data were pooled for each category from 12 sampling bouts.**

| Sl. no | Age of dung in days | No. of pats sampled | No. of individuals/pat | | No. of species/pat | | Shannon's index | | Simpson's index | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd |
| 1. | 1 | 24 | 0 - 65 | 21.04 ± 19.9 | 0 - 10 | 4.29 ± 2.68 | 0 - 1.93 | 0.99 ± 0.59 | 0 - 0.81 | 0.52 ± 0.27 |
| 2. | 2 | 36 | 0 - 47 | 16.5 ± 11.84 | 0 - 8 | 4.50 ± 2.35 | 0 - 1.92 | 1.15 ± 0.56 | 0 - 0.83 | 0.58 ± 0.26 |
| 3. | 3 | 24 | 0 - 28 | 8.04 ± 7.63 | 0 - 6 | 3.00 ± 2.09 | 0 - 1.83 | 0.77 ± 0.64 | 0 - 0.83 | 0.42 ± 0.32 |
| 4. | 4 | 36 | 0 - 17 | 5.25 ± 4.25 | 0 - 7 | 2.44+/-1.70 | 0 - 1.96 | 0.66 ± 0.58 | 0 - 0.80 | 0.37 ± 0.29 |
| 5. | 5 | 24 | 0 - 12 | 3.42 ± 3.45 | 0 - 5 | 1.63 ± 1.41 | 0 - 1.58 | 0.35 ± 0.51 | 0 - 0.78 | 0.20 ± 0.29 |
| 6. | 6 | 36 | 0 - 13 | 3.39 ± 3.76 | 0 - 6 | 1.42 ± 1.38 | 0 - 1.63 | 0.34 ± 0.47 | 0 - 0.78 | 0.21± 0.27 |
| 7. | 7 | 24 | 0 - 15 | 1.33 ± 3.04 | 0 - 2 | 0.58 ± 0.65 | 0 - 0.69 | 0.06 ± 0.19 | 0 - 0.50 | 0.04 ± 0.14 |
| 8. | 8 | 36 | 0 - 12 | 1.69 ± 2.69 | 0 - 4 | 1.00 ± 1.17 | 0 - 1.22 | 0.20 ± 0.37 | 0 - 0.66 | 0.13 ± 0.24 |
| 9. | 9 | 24 | 0 - 7 | 1.83 ± 2.24 | 0 - 3 | 0.83 ± 0.87 | 0 - 0.69 | 0.15 ± 0.29 | 0 - 0.50 | 0.10 ± 0.20 |
| 10 | 10 | 36 | 0 - 6 | 0.94 ± 1.35 | 0 - 3 | 0.61± 0.84 | 0 - 1.09 | 0.10 ± 0.30 | 0 - 0.67 | 0.07 ± 0.19 |
| 11 | 12 | 36 | 0 - 6 | 0.69 ± 1.33 | 0 - 2 | 0.44 ± 0.69 | 0 - 0.69 | 0.08 ± 0.22 | 0 - 0.50 | 0.05 ± 0.16 |
| 12 | 15 | 36 | 0 - 10 | 0.58 ± 1.86 | 0 - 2 | 0.25 ± 0.55 | 0 - 0.69 | 0.04 ± 0.16 | 0 - 0.50 | 0.03 ± 0.12 |

beetles per pat. Highest range and consequently the maximum number of beetles recorded from any one pat was from one day old dung. The lowest range was for the 10 and 12 days old dung pats. However, in all dung age categories a few pats without any beetles were encountered during the course of sampling. The mean (± sd) for number of beetles recorded per pat was 21.04 ± 19.9, which was highest for one day old pats and the values decreased monotonously upto 15 day old dung pats which recorded the lowest mean (± sd) number of beetles per pat. A similar trend was observed for number of species recovered per pat. Upto 10 species were recovered per pat on one day old dung while a maximum of only 2 species were recovered on 15 day old dung. However, highest number of species (mean ± sd) 4.5 ± 2.35 were recovered per pat from the two day old dung while the lowest 0.25 ± 0.55 (mean ± sd) number of species were recovered from 15 day old dung. The mean (± sd) diversity of 1.15 ± 0.56 and 0.58 ± 0.26 by Shannon's and Simpson's index respectively were also recorded for the two day old pats (Table 3). There was a continuous decline in diversity beginning from 3 day old dung pats reaching a low of 0.04 ± 0.16 and 0.03 ± 0.12 respectively for Shannon's and Simpson's indices for 15 day old pats (Table 3).

The data thus suggest a continuous decrease in the number of individuals, species and diversity from one day old pats to 15 day old pats. Interestingly, two day old dung pats when compared to one day old pats recorded higher values for number of species and the two diversity indices (Table 3).

### 4.2.3.2 Daywise variation in diversity across dung age

The data from all pats sampled were pooled within each category to examine day wise variation in diversity of dung beetles. This data represents 12 days of observations from 12 sampling bouts for each of the 12 age categories of dung pats.

Even when expressed as number of dung beetles collected per day, one day old dung pats recorded the highest number of beetles (Table 4). One to five day old dung pats yielded at least one beetle per day while it was not always the case for dung pats of six or more day old. The number of individuals encountered per day was 49.75 ± 27.17 (mean ± sd ) in two day old dung while it was 42.00 ± 36.41 beetles (mean ± sd) for one day old dung. These values were found to be considerably high compared to dung of three or more days old. The three day old dung yielded 16.08 ± 14.87 beetles (mean ± sd) per day and almost a continuous decrease was evident from thereon upto 15 day old dung. The lowest value of 1.92 ± 3.10 beetles (mean ± sd ) per day was recorded for 12 day old dung with a similar value for 15 day old dung.

Number of species of dung beetles recovered per day followed a similar pattern with a maximum of 11 species per day on one and two day old dung. Older dung yielded fewer number of species although the reduction was not always continuous. The number of species per day was 6.33 ± 3.11 (mean ± sd) on the first day followed by 7.83 ± 2.66 species (mean ± sd) per day on two day old dung. The lowest number of species 0.67 ± 0.84 (mean ± sd) per day was recorded for 15 day old dung .

**Table: 4. Diversity and abundance of dung beetles (daywise) in dung pats of different age categories at MDF, Bangalore. The *data were pooled for each category from 12 sampling bouts.***

| Sl. no. | Age of dung (days) | No. of individuals/day | | No. of species/day | | Shannon's index | | Simpson's index | |
|---|---|---|---|---|---|---|---|---|---|
| | | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd |
| 1 | 1 | 1- 117 | 42.00 ± 36.41 | 1 - 11 | 6.33 ± 3.11 | 0 - 1.91 | 1.20 ± 0.61 | 0 - 0.84 | 0.60 ± 0.28 |
| 2 | 2 | 10 - 93 | 49.75 ± 27.17 | 3 - 11 | 7.83 ± 2.66 | 0 - 1.92 | 1.50 ± 0.36 | 0.34 - 0.81 | 0.70 ± 0.13 |
| 3 | 3 | 0 - 54 | 16.08 ± 14.87 | 0 - 8 | 4.33 ± 2.9 | 0 - 2.0 | 0.90 ± 0.63 | 0 - 0.86 | 0.49 ± 0.32 |
| 4 | 4 | 2 - 32 | 14.63 ± 8.49 | 2 - 7 | 5.0 ± 1.81 | 0.53 - 2.17 | 1.21 ± 0.51 | 0 - 0.83 | 0.59 ± 0.18 |
| 5 | 5 | 2 - 18 | 7.42 ± 5.87 | 1 - 6 | 2.5 ± 1.57 | 0 -1.6 | 0.64 ± 0.58 | 0 - 0.77 | 0.36 ± 0.32 |
| 6 | 6 | 0 - 32 | 10 ± 9.96 | 0 - 8 | 2.58 ± 2.11 | 0 - 1.91 | 0.71 ± 0.61 | 0 - 0.81 | 0.39 ± 0.32 |
| 7 | 7 | 0 - 16 | 3.0 ± -4.47 | 0 - 2 | 0.83 ± 0.83 | 0 - 0.69 | 0.16 ± 0.29 | 0 - 0.50 | 0.11 ± 0.21 |
| 8 | 8 | 0 - 16 | 4.83 ± 5.39 | 0 - 6 | 2.33 ± 1.87 | 0 - 1.55 | 0.59 ± 0.59 | 0 - 0.75 | 0.34 ± 0.32 |
| 9 | 9 | 0 - 13 | 3.83 ± 4.34 | 0 - 3 | 1.33 ± 1.15 | 0 - 1.05 | 0.36 ± 0.41 | 0 - 0.64 | 0.23 ± 0.26 |
| 10 | 10 | 0 - 11 | 2.83 ± 3.10 | 0 - 3 | 1.33 ± 1.07 | 0 - 0.95 | 0.29 ± 0.37 | 0 - 0.56 | 0.18 ± 0.23 |
| 11 | 12 | 0 - 10 | 1.92 ± 3.10 | 0 - 4 | 0.92 ± 1.16 | 0 - 1.28 | 0.15 ± 0.38 | 0 - 0.70 | 0.08 ± 0.21 |
| 12 | 15 | 0 - 15 | 1.92 ± 4.25 | 0 - 2 | 0.67 ± 0.89 | 0 - 0.69 | 0.16 ± 0.29 | 0 - 0.50 | 0.12 ± 0.21 |

Diversity indices also followed a similar pattern. Two day old dung recorded the highest values for Shannon's and Simpson's indices. Although discontinuous, a decreasing trend was observed for both the diversity indices with age of the dung (Table 4).

### 4.2.3.3 Variation in diversity across dung age

Data pooled from all the 12 sampling bouts for each dung age category indicated a higher recovery of beetles during the first two days of age of dung and the pattern of decrease was similar to data pooled across pats or days (Table 5). A total of twenty three species, the highest, were recorded from two day old pats followed by 19 from one and three days old pats. There was a continuous decrease in the number of species encountered with the exception of eight day old dung pats which yielded 16 species. All the 32 species encountered at MDF were recovered at least once before the dung was 7 days old and there was no addition of species thereafter. More importantly, 28 of the 32 species were encountered in dung pats aged three days or less and only four species were added between 5 and 7 days of age to complete the list. These results suggest that a majority of species of dung beetles are early colonizers and only four species colonize the dung of 5 or more days of age.

Number of individuals recorded per species for all the 12 age categories of dung indicated high variance to mean ratios (6.88 - 102.61) suggesting dominance by a few species. This was best reflected in high standard deviations for number of individuals in dung of all age groups (Table 5). The highest number of individuals of 18.66 ± 39.60 (mean ± sd) was recorded for the two day old dung while the lowest

**Table: 5 Species richness, relative abundance, diversity and species accumulation across age of dung pats for pooled data from 12 sampling bouts at MDF, Bangalore, 1997.**

| Sl.no. | Age of dung (days) | Individuals | | Species | | Shannon's index | Simpson's index |
|---|---|---|---|---|---|---|---|
| | | Total | Mean ± sd/species | Total | Added | | |
| 1 | 1 | 504 | 15.75 ± 40.20 | 19 | 19 | 1.86 | 0.77 |
| 2 | 2 | 597 | 18.66 ± 39.60 | 23 | 7 | 2.16 | 0.83 |
| 3 | 3 | 192 | 6.0 ± 13.31 | 19 | 2 | 2.11 | 0.82 |
| 4 | 4 | 179 | 5.59 ± 11.36 | 17 | 0 | 2.17 | 0.84 |
| 5 | 5 | 89 | 2.78 ± 5.52 | 17 | 2 | 2.26 | 0.85 |
| 6 | 6 | 120 | 3.75 ± 8.65 | 13 | 1 | 1.93 | 0.81 |
| 7 | 7 | 36 | 1.13 ± 3.92 | 04 | 1 | 1.07 | 0.60 |
| 8 | 8 | 58 | 1.81 ± 3.53 | 16 | 0 | 2.28 | 0.85 |
| 9 | 9 | 46 | 1.44 ± 4.01 | 07 | 0 | 1.53 | 0.73 |
| 10 | 10 | 34 | 1.06 ± 3.32 | 08 | 0 | 1.41 | 0.67 |
| 11 | 12 | 23 | 0.72 ± 2.56 | 05 | 0 | 1.18 | 0.59 |
| 12 | 15 | 23 | 0.72 ± 2.34 | 05 | 0 | 1.25 | 0.65 |

was 0.72 ± 2.34 (mean ± sd) for the 15 day old dung. Twelve day old dung also recorded the lowest mean values for number of individuals per species.

Diversity indices calculated across age for the pooled data presented different picture with higher values being observed on 8 day old dung for the Shannon's and Simpson's indices (Table 5). Six day old dung also recorded the highest diversity indices of 0.85 by Simpson's index on par with the 8 day old dung. The lowest diversity values were for the 12 day old dung.

The foregoing observations clearly suggest dung age to be an important factor in influencing the structure of the dung beetle community. Dung age has a significant impact on the number of individuals and number of species that colonise a dung pat and consequently the diversity. Further, all dung beetles occurring in MDF, Bangalore colonise dung which is 7 or less days old. All species occurring in older dung are persistent species since no fresh colonisations of dung were observed by any species beyond seven days.

### 4.2.4 Species richness and diversity across time (Julian date or season)

Dung beetles sampled at MDF from 4 - April - 97 to 20 - October - 97 in twelve sampling dates (bouts), each lasting fifteen days, were pooled ignoring dung age and analyzed in different ways to reflect the variation across time (season). The results of these analyses are presented below.

### 4.2.4.1 Patwise variation in diversity across time

A total of 31 pats were sampled during the fifteen days period in each of the twelve sampling bouts. Number of individuals collected per pat ranged upto 65 beetles per pat in the June 6 sample. However, pats with out beetles were encountered in all the sampling dates. There was no apparent trend in the maximum numbers of beetles recovered per pat. The lowest maximum per pat of 16 beetles was encountered in the August 12 sample (Table 6). The lowest number of beetles per pat was 1.87 ± 5.13 (mean ± sd) and found during the II fortnight of May. The highest of 9.35 ± 9.86 mean (± sd) beetles per pat was recorded during April I fortnight. There was again a lack of clear trend across sampling dates in the mean number of dung beetles recovered per pat.

The number of species recovered per pat ranged from 0 - 10, the highest, which was observed during April - I fortnight and the lowest of 0 - 5 was observed during II fortnight of May and September. Mean (± sd) number of species recovered per pat ranged from a high of 3.1 ± 2.56 during April I fortnight to a low of 0.77 ± 1.28 per pat during the second fortnight of May. Except for a large peak during April - I fortnight, no clear pattern was discernible in the number of species per pat during the twelve sampling dates.

Shannon's index ranged from 0 - 1.96 per pat, the highest, during April - I fortnight, while the lowest range of 0 - 1.33 was noticed during the sampling bout that began on August 28. The highest mean diversity was recorded during April - I fortnight (0.78 ± 0.64) and the lowest diversity was 0.13 ± 0.37 and observed during

**Table: 6. Patwise variation in species richness, abundance and diversity across dates of sampling. Data pooled from all pats from each sampling bout lasting 15 days each. Data from MDF, Bangalore collected during 1997.**

| Sl. no | Date of sampling | No. of pats sampled | Individuals/pat | | Species/pat | | Shannon's index | | Simpson's index | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd |
| 1 | 4 - 4 - 97 | 31 | 0 - 40 | 9.35 ± 9.86 | 0 - 10 | 3.10 ± 2.56 | 0 -1.96 | 0.78 ± 0.64 | 0 - 0.83 | 0.43 ± 0.31 |
| 2 | 20 - 4- 97 | 31 | 0 - 46 | 6.81 ± 10.85 | 0 - 6 | 2.13 ± 2.22 | 0 -1.70 | 0.51 ± 0.65 | 0 - 0.80 | 0.28 ± 0.33 |
| 3 | 5 - 5 - 97 | 31 | 0 - 47 | 6.32 ± 11.25 | 0 - 8 | 2.10 ± 2.60 | 0 -1.79 | 0.45 ± 0.65 | 0 - 0.80 | 0.24 ± 0.33 |
| 4 | 19- 5- 97 | 31 | 0 - 27 | 1.87 ± 5.13 | 0 - 5 | 0.77 ± 1.28 | 0 -1.42 | 0.13 ± 0.37 | 0 - 0.72 | 0.75 ± 0.21 |
| 5 | 6 - 6 - 97 | 31 | 0 - 65 | 5.52 ± 14.50 | 0 - 9 | 1.32 ± 2.10 | 0 -1.86 | 0.21 ± 0.47 | 0 - 0.81 | 0.12 ± 0.25 |
| 6 | 25 -6 -97 | 31 | 0 - 36 | 6.77 ± 10.60 | 0 - 8 | 1.90 ± 2.13 | 0 -1.89 | 0.42 ± 0.57 | 0 - 0.82 | 0.24 ± 0.29 |
| 7 | 11- 7 - 97 | 31 | 0 - 35 | 3.30 ± 6.54 | 0 - 6 | 1.42 ± 1.69 | 0 -1.67 | 0.34 ± 0.55 | 0 - 0.78 | 0.19 ± 0.29 |
| 8 | 26 -7 - 97 | 31 | 0 - 17 | 2.87 ± 4.67 | 0 - 6 | 1.61 ± 1.86 | 0 -1.72 | 0.44 ± 0.58 | 0 - 0.82 | 0.26 ± 0.32 |
| 9 | 12 -8 -97 | 31 | 0 - 16 | 3.90 ± 4.43 | 0 - 7 | 1.84 ± 1.75 | 0 -1.83 | 0.47 ± 0.56 | 0 - 0.83 | 0.29 ± 0.31 |
| 10 | 28 -8 -97 | 31 | 0 - 63 | 8.13 ± 12.58 | 0 - 7 | 1.90 ± 1.70 | 0 -1.33 | 0.36 ± 0.47 | 0 - 0.70 | 0.21 ± 0.27 |
| 11 | 15 - 9- 97 | 31 | 0 - 21 | 3.00 ± 4.60 | 0 - 5 | 1.19 ± 1.62 | 0 - 1.58 | 0.37 ± 0.53 | 0 - 0.78 | 0.22 ± 0.30 |
| 12 | 5 -10 -97 | 31 | 0 - 28 | 3.48 ± 7.07 | 0 - 6 | 1.10 ± 1.90 | 0 -1.36 | 0.27 ± 0.50 | 0 - 0.74 | 0.14 ± 0.26 |

the II fortnight of May. There was no clear pattern in the diversity across the sampling dates. Simpson's index closely followed the Shannon's index in its variation and the mean values.

### 4.2.4.2 Daywise variation in diversity across time

Each of the twelve sampling bouts included twelve days of sampling, each with two or three pats sampled. Thus the data pooled according to the day of the sampling could also be analyzed to record the extent of variation on day by day basis for each of the twelve sampling bouts. A summary of these results are indicated in table 7.

A range of 0 - 117 beetles per day was recorded during June I fortnight. During April I fortnight and the second sample in June yielded atleast one beetle on every day of sampling. A maximum of only 29 beetles per day was recorded during the May 19 and August 12 sampling bouts. Mean number of beetles recorded per day was 24.16 ± 21.46 during April 4 sampling bout while a low of 4.83 ± 8.39 mean (± sd ) number of beetles per day was recorded during the II fortnight of May.

A maximum of 11 species were recorded per day in atleast three of the twelve sampling bouts. While only six species per day was the maximum recorded for two sampling bouts during II fortnights of May and September. The lowest (1.92 ± 2.1 species per day; mean ± sd) number of species recovered per day was the May 19 sample while the maximum (4.83 ± 3.3 species per day ; mean ± sd) species per day was during the I fortnight of April (Table 7). However, there was no clear trend either

**Table : 7. Daywise variation in species richness, abundance and diversity across dates of sampling. Data pooled from samples collected over 144 days in 12 sampling bouts at MDF, Bangalore during 1997.**

| Sl. no. | Date of sampling | Individuals/day | | Species/day | | Shannon's index | | Simpson's index | |
|---|---|---|---|---|---|---|---|---|---|
| | | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd | Range | Mean ± sd |
| 1 | 4 - 4 - 97 | 3 - 71 | 24.16 ± 21.46 | 1 - 11 | 4.83 ± 3.30 | 0 -1.92 | 1.15 ± 0.56 | 0 - 0.80 | 0.60 ± 0.23 |
| 2 | 20 -4 - 97 | 0 - 77 | 17.58 ± 24.52 | 0 - 9 | 3.50 ± 3.23 | 0 - 1.91 | 0.73 ± 0.71 | 0 - 0.81 | 0.38 ± 0.35 |
| 3 | 5 - 5 - 97 | 0 - 93 | 16.33 ± 27.70 | 0 - 11 | 3.75 ± 3.60 | 0 - 1.75 | 0.82 ± 0.68 | 0 - 0.77 | 0.43 ± 0.33 |
| 4 | 19 -5 - 97 | 0 - 29 | 4.83 ± 8.39 | 0 - 6 | 1.92 ± 2.10 | 0 - 1.44 | 0.44 ± 0.52 | 0 - 0.78 | 0.28 ± 0.31 |
| 5 | 6 - 6 - 97 | 0 - 117 | 14.25 ± 32.60 | 0 - 10 | 2.17 ± 2.72 | 0 - 1.76 | 0.31 ± 0.34 | 0 - 0.79 | 0.21 ± 0.26 |
| 6 | 25 - 6 -97 | 1 - 88 | 17.50 ± 27.38 | 1 - 11 | 3.58 ± 3.06 | 0 - 1.82 | 0.75 ± 0.58 | 0 - 0.81 | 0.42 ± 0.30 |
| 7 | 11 - 7 -97 | 0 - 41 | 8.50 ± 12.71 | 0 - 9 | 2.50 ± 2.78 | 0 - 1.86 | 0.51 ± 0.70 | 0 - 0.81 | 0.27 ± 0.33 |
| 8 | 26 -7 -97 | 0 - 34 | 7.42 ± 10.0 | 0 - 8 | 3.30 ± 3.03 | 0 - 2.00 | 0.84 ± 0.81 | 0 - 0.86 | 0.42 ± 0.35 |
| 9 | 12 -8 -97 | 0 - 29 | 10.10 ± 9.27 | 0 - 8 | 3.30 ± 2.64 | 0 - 1.68 | 0.74 ± 0.63 | 0 - 0.79 | 0.42 ± 0.33 |
| 10 | 28- 8- 97 | 0 - 100 | 21.00 ± 26.80 | 0 - 7 | 2.78 ± 2.00 | 0 - 1.22 | 0.52 ± 0.44 | 0 - 0.66 | 0.28 ± 0.24 |
| 11 | 15 -9 - 97 | 0 - 38 | 7.75 ± 11.27 | 0 - 6 | 2.08 ± 2.54 | 0 - 1.33 | 0.53 ± 0.66 | 0 - 0.82 | 0.29 ± 0.36 |
| 12 | 5 -10 - 97 | 0 - 61 | 9.00 ± 8.43 | 0 - 9 | 2.25 ± 3.49 | 0 - 1.88 | 0.44 ± 0.68 | 0 - 0.85 | 0.21 ± 0.32 |

with range or with respect to mean number of individuals and species per day across the twelve sampling dates. The diversity index by Shannon's index ranged from 0 to 2.00 per day for the dung beetles of MDF. This range was noticed during the II sampling bout in July. The lowest range of 0 to 1.22 was recorded for Shannon's index during the August 28 sampling bout. The highest diversity index (1.15 ± 0.56; mean ± sd) was observed during April - I fortnight and the lowest was 0.31 ± 0.34 during June 6 sampling. The highest (0.86) Simpson's diversity index in a day was noticed during July 26 sampling. The highest diversity index per day (0.60±0.23; mean ± sd) was recorded during April I fortnight, while the lowest (0.21 ± 0.26) mean (± sd) diversity index by Shannon's index was recorded for June 6, sample. There was no apparent trend across the twelve dates of sampling either for the range or for the means per day for the two diversity indices.

#### 4.2.4.3 Variation across time : pooled data

The twelve sampling bouts yielded 58 to 290 beetles and 8 to 18 species of Scarabaeinae dung beetles per sampling bout. Although there was no clear pattern in number of species recorded per sampling bout, the number of species added over successive sampling bouts tapered off to zero from the ninth sample onwards (Table 8). Thus, clearly suggesting the possibility of occurrence of more than 32 species at MDF, Bangalore to be extremely low.

**Table: 8. Number of individuals and species, species added and the diversity indices for dung beetles of MDF, Bangalore collected in 12 sampling bouts, each lasting for 15 days during 1997.**

| Sl. no. | Date of sampling | Individuals | | Species | | Shannon's index | Simpson's Index |
|---|---|---|---|---|---|---|---|
| | | Totals | Mean± sd | Total | Additional species | | |
| 1 | 4 - 4- 97 | 290 | 9.06 ± 16.10 | 18 | 18 | 2.28 | 0.87 |
| 2 | 20- 4- 97 | 211 | 6.59 ± 16.63 | 14 | 6 | 1.85 | 0.78 |
| 3 | 5 - 5 - 97 | 196 | 6.13 ± 15.31 | 15 | 1 | 1.98 | 0.78 |
| 4 | 19- 5 -97 | 58 | 1.81 ± 3.90 | 8 | 0 | 1.87 | 0.83 |
| 5 | 6 - 6 - 97 | 171 | 5.34 ± 11.39 | 13 | 1 | 2.02 | 0.83 |
| 6 | 25- 6 -97 | 210 | 6.56 ± 15.40 | 16 | 3 | 1.98 | 0.80 |
| 7 | 11- 7 -97 | 102 | 3.19 ± 9.64 | 14 | 2 | 1.67 | 0.69 |
| 8 | 26- 7 -97 | 89 | 2.78 ± 5.17 | 14 | 1 | 2.24 | 0.86 |
| 9 | 12- 8 -97 | 121 | 3.78 ± 7.79 | 14 | 0 | 2.10 | 0.84 |
| 10 | 28 -8 -97 | 252 | 7.88 ± 23.34 | 9 | 0 | 1.46 | 0.70 |
| 11 | 15- 9- 97 | 93 | 2.91 ± 8.02 | 10 | 0 | 1.65 | 0.74 |
| 12 | 5 -10 -97 | 108 | 3.38 ± 8.71 | 14 | 0 | 1.86 | 0.77 |

The diversity indices by Shannon's and Simpson's index were highest during the April 4 sampling bout while the lowest were during August 28 for Shannon's index and July 11 for Simpson's index. Again there was no discernible pattern in the diversity indices across the dates of sampling.

### 4.2.5 The structure of dung beetle communities: Partitioning diversity

The dung beetles of the subfamily Scarabaeinae, collected at MDF, Hebbal, Bangalore over a period of six months in twelve sampling bouts of fifteen days each could be grouped on the basis of their representation, according to pats, days of sampling, age of the dung and dates of sampling. Clearly, there was a significant declining trend in the number of individuals and the species encountered with age of the dung. There was also a declining trend in the diversity along the same gradient. However, no discernible trend could be recognized in sampling dates for any of the four parameters verified. Thus it appeared that the greatest variation in the organizational parameters of the dung beetle community at MDF is contributed by the age of the dung sampled. An attempt to partition the variance according to the levels of sampling might help us test the above possibility. The simplest and easiest way of partitioning the variances is by using weighted means of Simpson's index for each of these levels of sampling. Unweighted means for the Simpson's index suggested 0.223, 0.349, 0.74 and 0.79 as the mean diversity indices for the four sampling levels viz., pats, days, age of dung and sampling dates (Table 9). Further, the unweighted means also suggested a difference of 39.1 per cent between the days of sampling and age of dung suggesting dung age to be the primary factor in influencing the variances for the

**Table: 9. Partitioning the diversity of dung beetles across sampling hierarchy using weighted and unweighted mean Simpson's index for the dung beetles of MDF, Bangalore.**

| Sl.no. | Sample category | Sample size | Mean Simpson's index | | % variance explained | |
|---|---|---|---|---|---|---|
| | | | Unweighted means | weighted means | Pooled | Addition |
| 1. | Pats | 372 | 0.223 | 0.556 | 55.6 | 55.6 |
| 2. | Days | 144 | 0.349 | 0.593 | 59.3 | 3.7 |
| 3. | Dung age | 12 | 0.740 | 0.703 | 70.3 | 11.0 |
| 4. | Sampling dates | 12 | 0.790 | 0.792 | 79.2 | 8.9 |
| 5. | Community | | 0.878 | 0.878 | 87.8 | 8.6 |

dung beetle occurrence. While these results upheld the previous view, the weighted means for Simpson's index clearly demonstrated pat to pat variation to subsume most of the observed variation in the dung beetle occurrence pattern. As much as 55.6 per cent of variance in dung beetle occurrence pattern could be explained on the basis of differences between the pats and at all the higher levels of grouping of the data, only 3.7 (for days) to 11.0 (dung age) per cent of variation could be explained (Table 9).

The above results have helped to describe the dung beetle community at MDF, Bangalore and their levels of organization, on the basis of the sampling approach followed. On the strength of these results, an attempt is made to understand the inter - relationships between the various parameters of the community in the following section.

## 4.3 Characteristics of the community of dung beetles at MDF, Bangalore

### 4.3.1 Relative abundance of species

The 32 species of dung beetles that made up the community at MDF, Bangalore were found to vary greatly in their abundances. As many as six species were represented by just a single individual, while *Onthophagus dama* was found to be the most abundant with 394 individuals out of 1901 individuals encountered during the course of study amounting to nearly 21 % of the population. Only 25 % of species were represented by more than 50 individuals (Fig. 2A) and the total contribution of these individuals accounted 87.32% of the total population. The most abundant

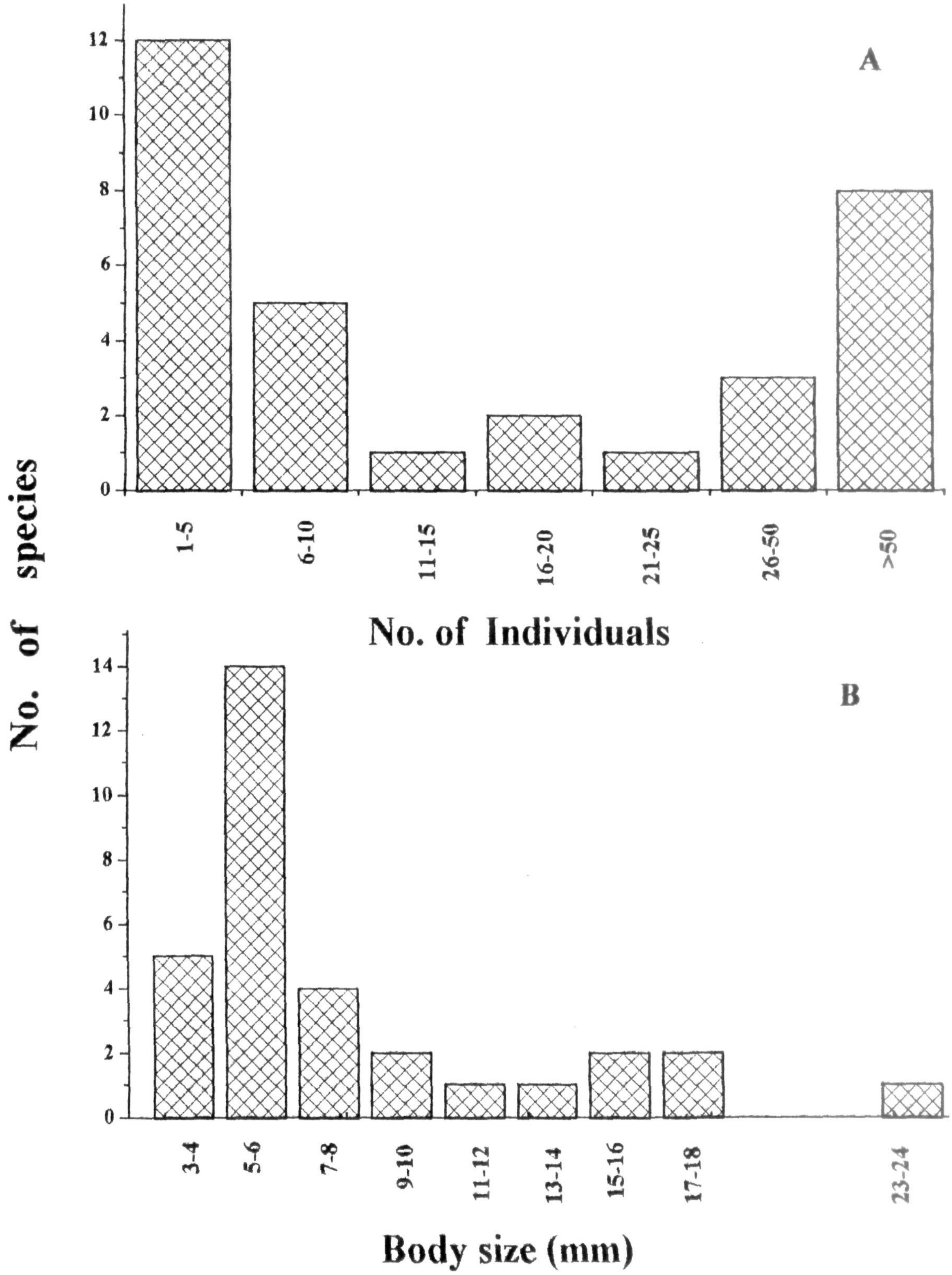


Fig. 2. Frequency distribution of 32 species of dung beetles collected at MDF, Bangalore during 1997 on the basis of their abundance (A) and body size (B)

species in the descending order of abundance were *O. dama, O. truncaticornis and Caccobius vulcanus.*

### 4.3.2 Body size distribution

Of the 32 species, the smallest was *Onthophagus* sp. R with 3.37 mm of combined length of elytron and pronotum, which was used as an index of body size. The largest species was *Catharsius molossus*, measuring 23.67 mm and was more than 7 times the smallest species encountered. Nearly 60% (19 of the 32) of the species were less than 5 mm in length (Fig. 2B). Two species of *Copris* measured more than 15 mm and were next only to *Catharsius molossus*, with a gap in the body size distribution of scarabaeines at MDF. Mean (± sd) body size of the 30 species was 7.724 ± 4.844 mm.

### 4.3.3 Relationship between body size and abundance

The overall abundance of species was independent of their body sizes ($r = 0.019$; $n = 32$; $p > 0.9$) in the community (Fig 3).

### 4.3.4 Beetle abundance and species recovery

Number of species recovered in any community is expected to be influenced by the sampling effort. Using number of beetles recovered as a proxy for the sampling effort, an attempt was made to understand the number of species recovered using

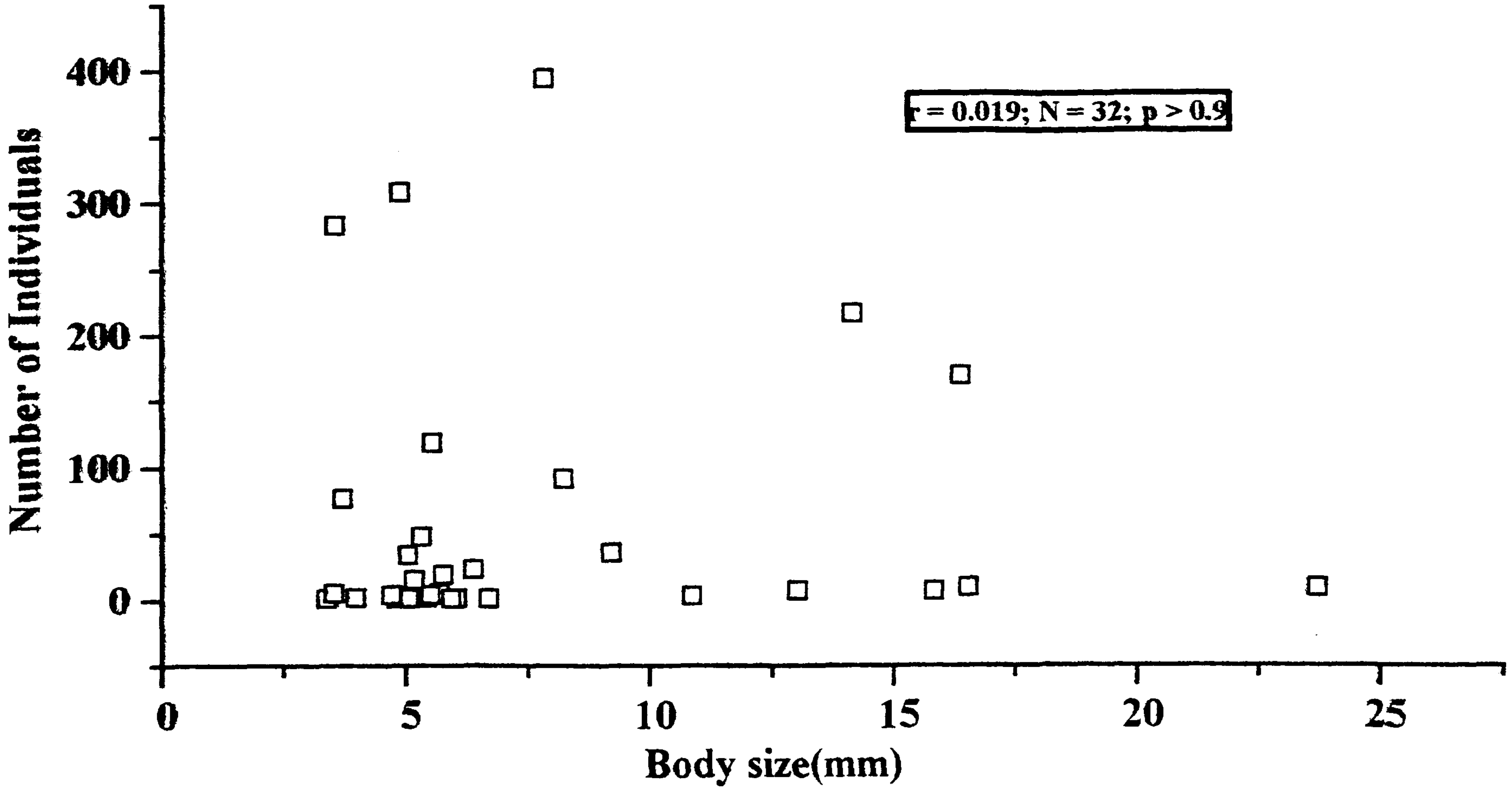


Fig. 3. Relationship between body size and abundance for the 32 species of dung beetles encountered at MDF, Bangalore during 1997.

Pearsons product moment correlation at all the four levels of sampling employed. The 372 pats sampled had 0 - 65 individuals with up to 10 species per pat. The scatter plot of individuals against species recovered (Fig. 4A) clearly indicated a strong and positive correlation ($r = 0.794$; $n = 372$; $p << 0.01$). The linear relationship could be explained by the equation : $y = 0.81 + 0.174\,x$ where y is the number of species and x is number of individuals recovered per pat. A similar positive relationship was evident even for the samples based on the 144 days of sampling (Fig. 4B). Number of beetles recovered per day ranged from 0-117 while the number of species ranged up to 11. The linear relationship could be explained by the equation : $y = 1.56 + 0.11x$ ($r = 0.783$ ; $n = 144$ ; $p << 0.01$) where y is the number of species recovered and x the number of individuals collected in a day.

The relationship was found to hold even at higher levels of grouping (Fig 4C) when the data pooled across age of the dung was plotted. The linear relationship could be given by the equation $y = 8.6 + 0.026x$ ($r = 0.764$; $n = 12$; $p < 0.01$) where y and x are as stated above. However, the data grouped according to the dates of sampling was not found to hold the above relationship (Fig 4D) ($r = 0.449$; $n = 12$; $p > 0.14$). One extra- ordinary outlier was the August 28, sampling bout which could yield only nine species from 250 specimens, which might have contributed to the low correlation encountered.

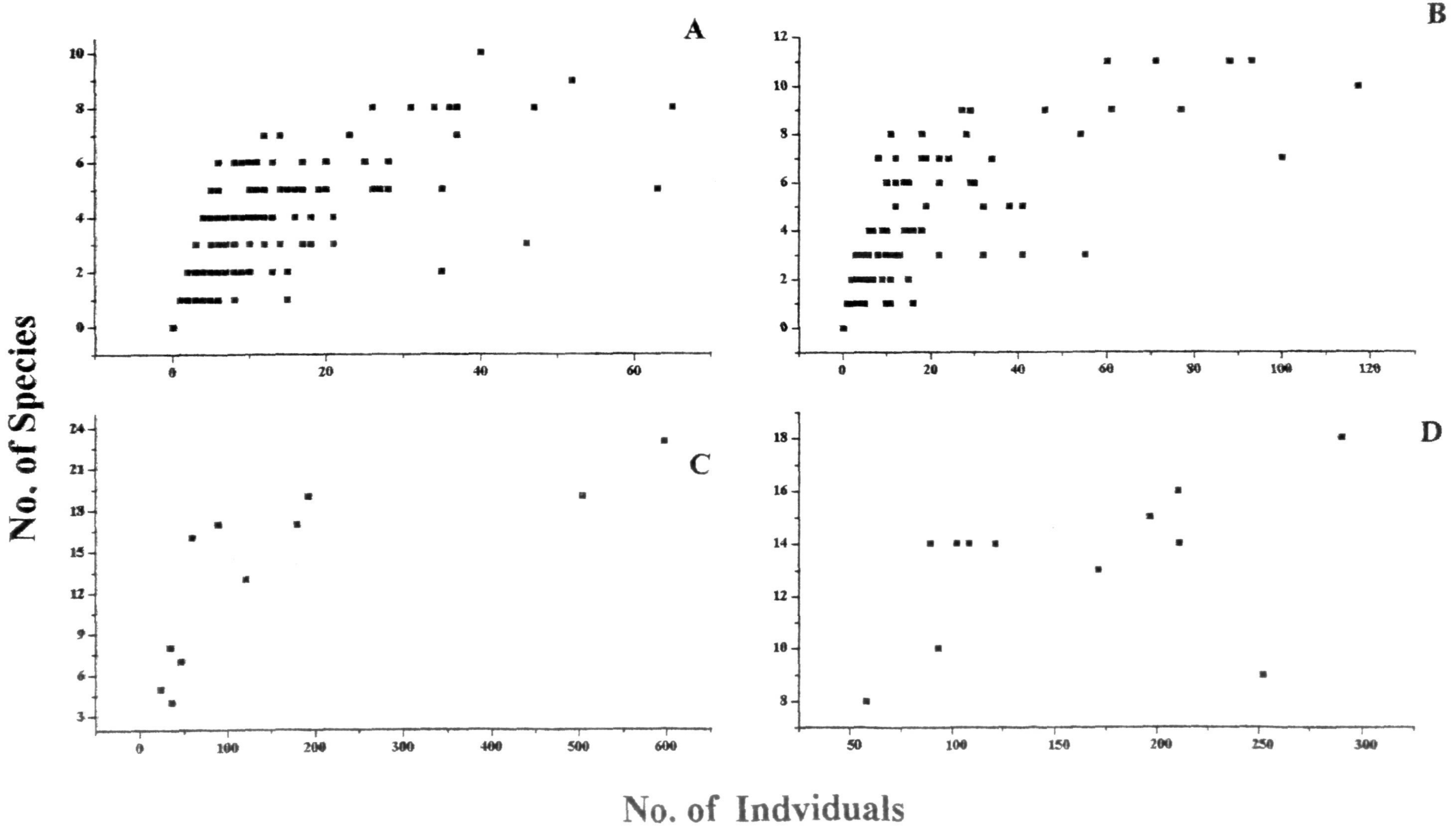


Fig. 4. Relationship between number of individuals and number of species collected across pats (A), days (B), age of dung (C) and dates of sampling (D) at MDF, Bangalore during 1997.

### 4.3.5 Diversity index as a function of number of individuals

Shannon's diversity index calculated for each of the 372 pats collected, varied with the number of individuals (Fig 5A). The relationship between the index and the number of individuals could be given by the equation $y = 0.187 + 0.041x$, where y is the Shannon's index and x is the number of beetles per pat, with a correlation coefficient of 0.677 ($n = 372$; $p << 0.01$).

The relationship between the above two parameters calculated for the days was also highly significant and was found to be positive ($r = 0.559$; $n = 144$; $p << 0.01$) (Fig. 5B). This relationship could be given by the equation $y = 0.427+0.017x$, where y, is the Shannon's index and x, the number of beetles per pat.

However, similar strong relationship was not evident when the data were pooled across the age of dung ($r = 0.456$; $n = 12$; $P >0.136$; Fig. 5C) or the dates of sampling ($r = 0.094$; $n = 12$ ; $p >0.750$; Fig. 5D). These poor correlations notwithstanding, the two strong and positive relations observed clearly suggest number of individuals as one of the factors that influence the value of diversity index.

### 4.3.6 Diversity index as a function of number of species

In all the four hierarchical sampling regimes followed, the Shannon's index was found to vary with the number of species (Fig. 6). For pats, the correlation coefficient

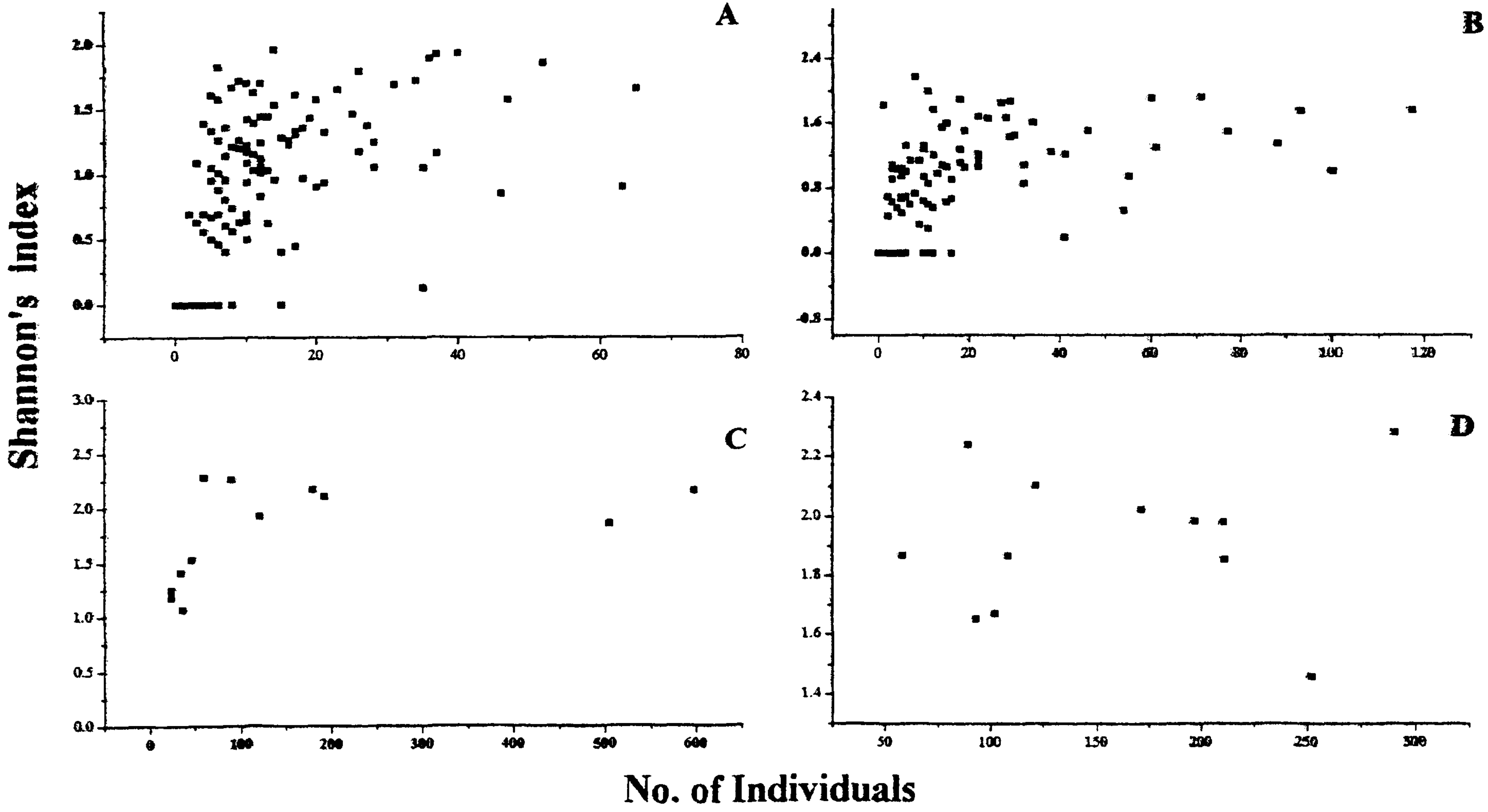


Fig. 5. Relationship between number of individuals and Shannon's index across pats (A), days (B), age of dung (C) and dates of sampling (D) at MDF, Bangalore during 1997.

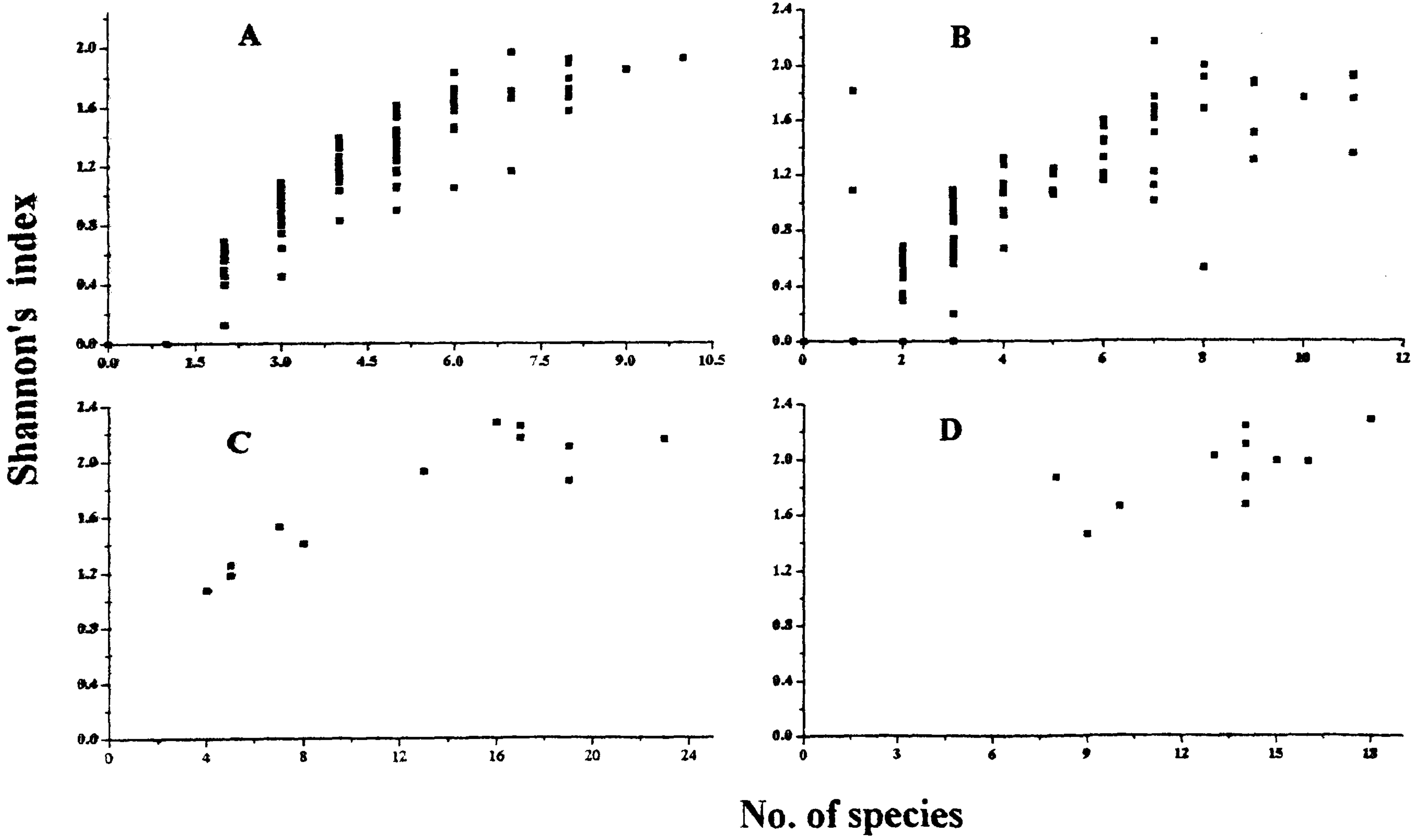


Fig. 6. Relationship between number of species and Shannon's index across pats (A), days (B), dung age (C) and dates of sampling (D) at MDF,Bangalore,during 1997.

was 0.947 ($n = 372$; $p << 0.01$) and the relationship could be given by the equation $y = 0.26x - 0.049$, where y is the Shannon's index and x the number of species per pat. The relationship for the days could be given by $y = 0.074 + 0.19x$ ($r = 0.876$; $n = 144$; $p << 0.01$) where, y is the Shannon's index and x, the number of species of dung beetles recorded in a day. Number of species recorded at different ages of dung ($r = 0.909$; $n = 12$; $p << 0.01$) and at different dates of sampling ($r = 0.67$; $n = 12$; $p < 0.02$) were also found to vary with diversity index.

Thus the above observations clearly establish the number of species recorded as one of the important factors that influence the diversity index values.

### 4.3.7 Relationship between the two diversity indices

While the above observations clearly establish Shannon's index to be a function of number of individuals and the number of species encountered, the Simpson's index was found to be strongly correlated with the Shannon's index at all the four levels of sampling (Fig. 7) *viz.*, pats ($r = 0.977$ ; $n = 372$ ; $p << 0.01$), days ($r = 0.97$; $n = 144$; $p << 0.01$), age of dung ($r = 0.986$; $n = 12$; $p << 0.01$) and the dates of sampling ($r = 0.925$; $n = 12$; $p << 0.01$). Thus, it is likely, that Simpson's index is also a function of number of individuals and species found in a sample.

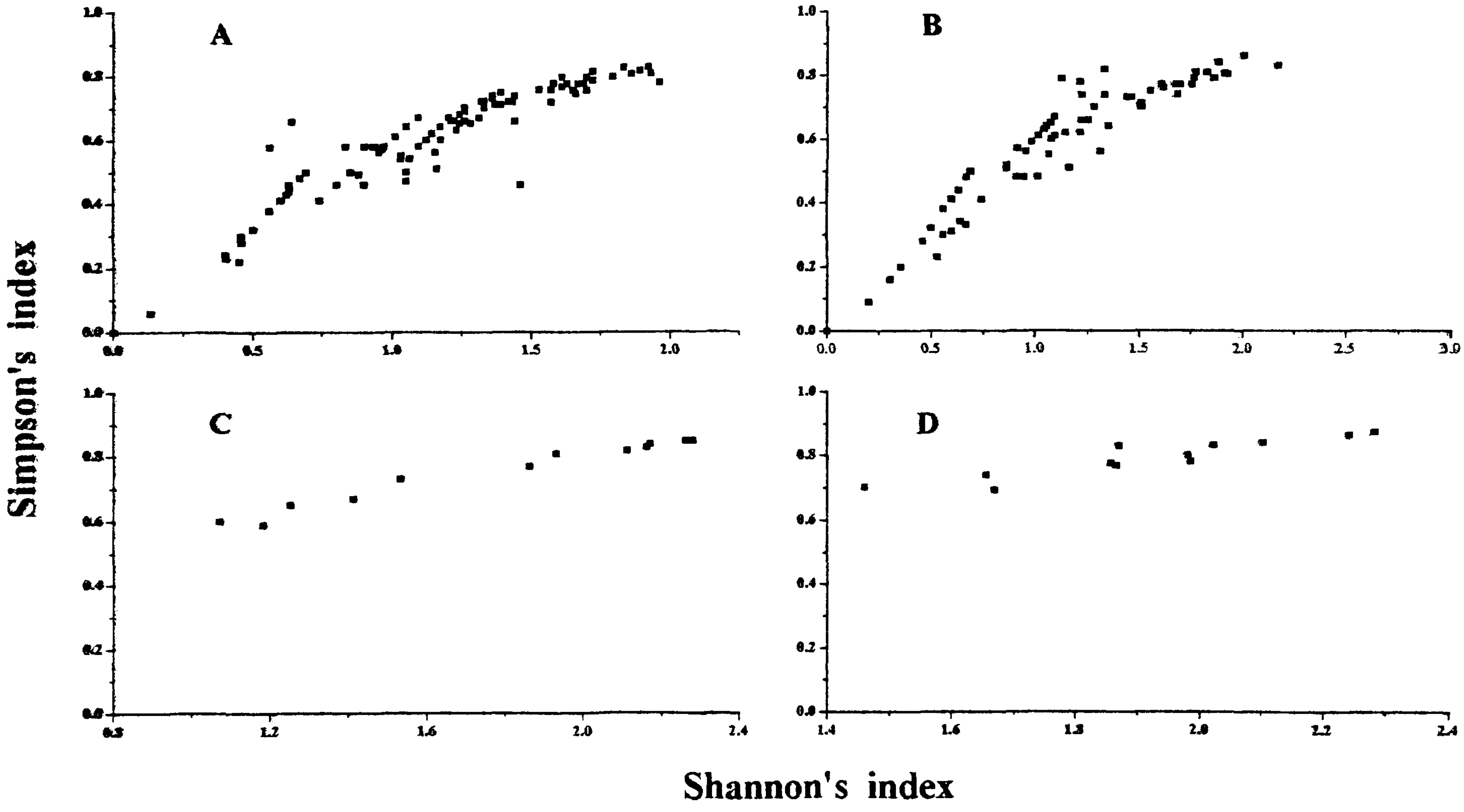


Fig. 7. Relationship between the Shannon's and Simpson's indices measured across pats (A), days (B), age of dung (C) and dates of sampling (D) at MDF, Bangalore during 1997.

### 4.3.8 Occurance pattern of dung beetle species across age of dung and sampling dates

The variability in the occurrence pattern of dung beetle species of MDF could be assessed at two levels viz., age of dung and sampling dates. As many as ten species of dung beetles were encountered in only one or two of the twelve age groups of dung considered, amounting to nearly 30 per cent of the total species encountered. Further six species each were found in age groups of seven or eight and nine or ten of the possible 12 ages of dung considered. All others recorded lower values than these. The graphs (Fig. 8A) clearly indicate bimodal distribution of the 32 species in respect of their representation in different numbers of age groups of dung. Those species that are more frequently encountered are obviously indifferent to the age of dung and can be termed as core species. These included *O. dama, Oniticellus cinctus, Onitis philemon, Copris repertus* and *Onthophagus* sp. B.

A similar bimodal distribution was evident when plotted according to their occurrence in numbers of sampling dates (Fig. 8A). Although, 14 species were found only in one or two sampling bouts, as many as 5 species were encountered in more than 10 of the 12 sampling dates. These five species *viz., O. dama, O. truncaticornis, Ca. vulcanus, Onit. spinipes* and *Onthophagus* sp. C appear to be insensitive to sampling dates (season) and constitute core species.

This obviously raises the question, are core species across age of dung also the core species across sampling dates?. The correlation between the frequency of

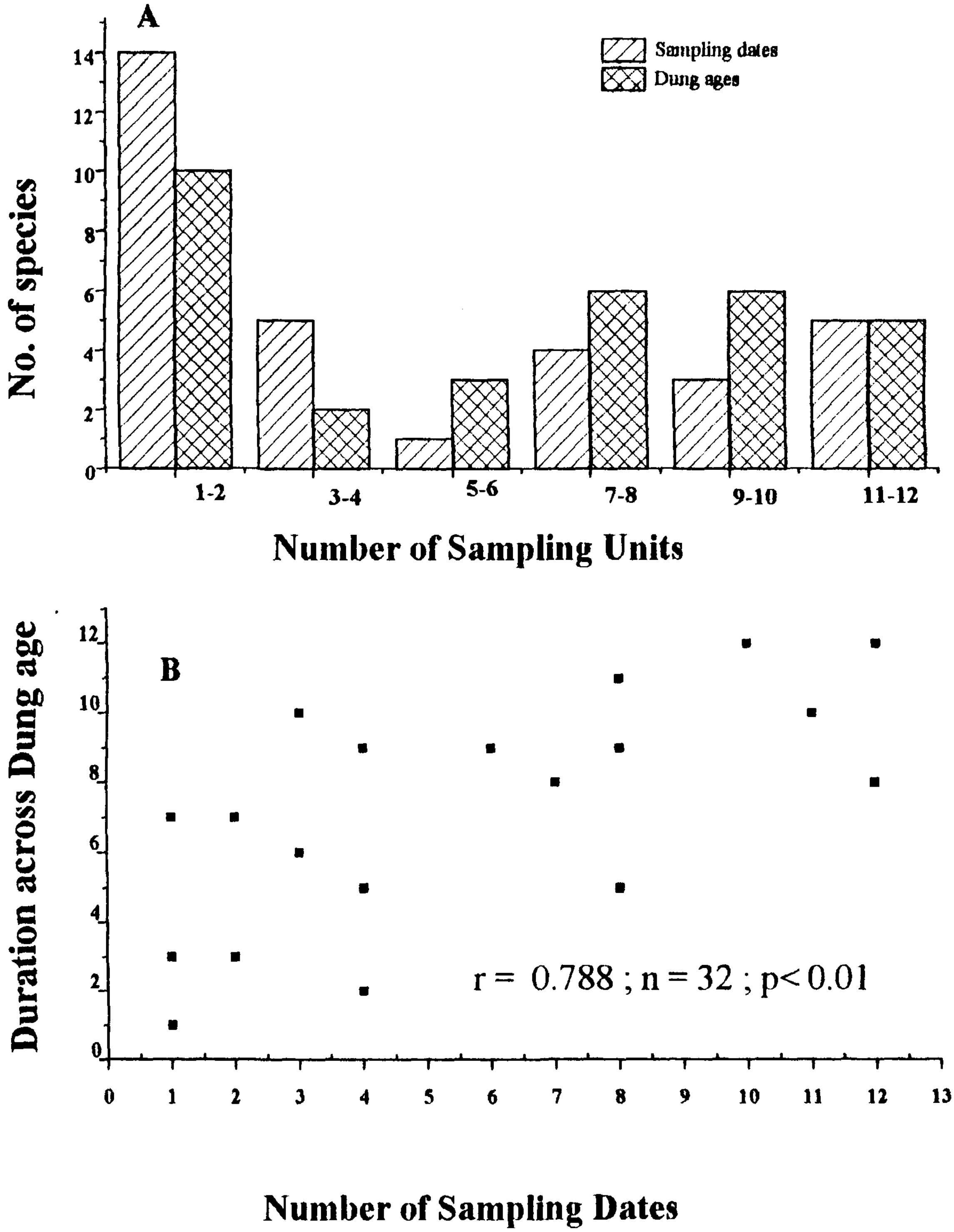


Fig. 8. Frequency distribution of species of dung beetles occurring for different numbers of days of dung age and sampling dates (A) and the relationship between the duartion of occurrence across different sampling dates and dung ages (B) for the thirty two species of dung beetles encountered at MDF, Banga;ore during 1997

occurrence across 12 ages of dung and 12 sampling dates considered for the 32 dung beetle species of MDF was found to be highly significant ($r = 0.788$; $n = 32$ ; $p << 0.01$) and positive (Fig. 8B). Clearly the species that are indifferent to age of dung also tend to be indifferent to date of sampling (season) and vice-versa. As a testimony to this, it was observed that out of eight species that were indifferent to date of sampling (season) six species were indifferent to age of dung. Conversly, of the 10 species that were sensitive to age of dung nine were also found sensitive to date of sampling (season). Thus these six species *viz.*, *O. dama, O. truncaticornis, Onit. cinctus, Onit. spinipes, On. philemon* and *C. repertus* form the overall core species in the dung beetle community at MDF.

### 4.4 Parameters of co-existence

The mechanism of co - existence in the dung beetle community comprising 32 species was investigated using the occurrence pattern across dung age and sampling date (seasons) as the primary dimensions.

#### 4.4.1 Dung age as a factor of resource partitioning

In order to consider age of dung as a factor of resource partitioning, the frequency distribution of each of the 32 species was worked out across age of dung. The possible role of body size in resource segregation was also examined. Resource partitioning was examined using the standard measures of niche breadth and niche overlap. Further, the occurrence pattern of dung beetles across dung age was parameterised and eight parameters were used to identify 'guilds' using multivariate statistical procedures.

#### 4.4.1.1 Occurrence pattern across age of dung

More than 50 per cent of the species occurred on one day old dung. These included *D. setosus, O. dama, O. truncaticornis, O. rectecornutus, Ca. vulcanus, Onit. cinctus, Onit. spinipes, On. philemon* (Fig 9), *C. repertus, C. bengalensis, Cat. molossus, Onthophagus* sp. B, *Onthophagus* sp. C (Fig. 10), *Onthophagus* sp. H, *Onthophagus* sp. P (Fig. 11), *Onthophagus* sp. R, *Onthophagus* sp. S, *Onthophagus* sp. T, and *Onthophagus* sp. W. (Fig. 12). Among these, *C. vulcanus, Onit. spinipes, C. bengalensis, Cat. molossus, Onthophagus* spp. C, H, P, R, S, T and W colonized the one day old dung in their highest numbers and all of them tended to decline in older dung. Other eight species continued their colonization to reach peaks on two day (5 spp.) six day (2 spp.) and seven (1 spp.) day old dung. Likewise one species each occurred in the dung age category of two, six and 11 days, two spp. each for five, nine and 10, three spp. for eight ages of dung while four species were represented at all ages.

Seven additional species *viz*., *C. numa*, *Onthophagus* spp. - E, F, K, V, Y and Z were encountered in the dung which was two day old or more, with three of these occurring in their highest numbers. Among the other four, two had peaks on the four day old dung while the other two had peaks on five and eight day old dung. Two of

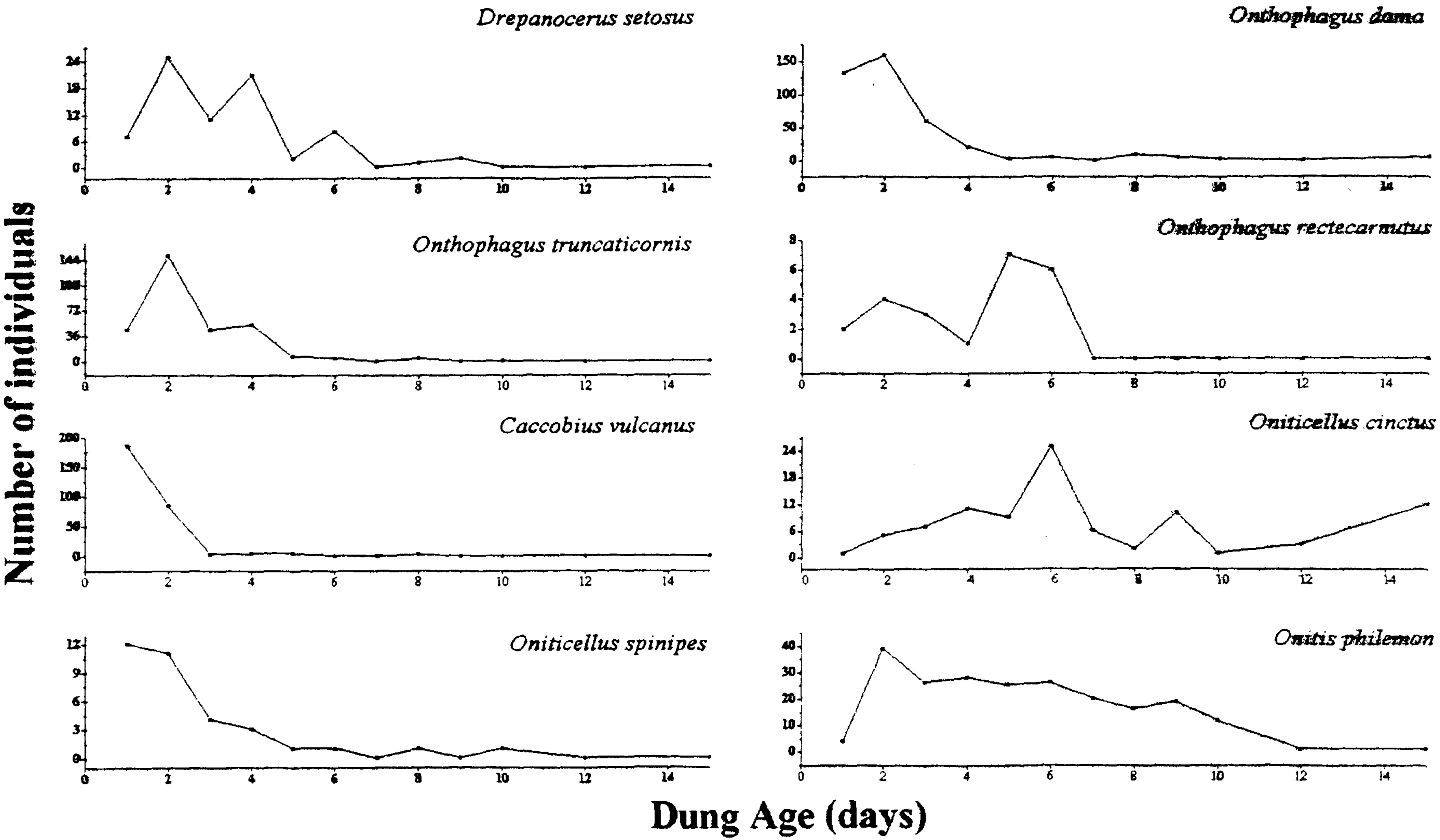


Fig. 9. Occurrence pattern of 32 species of dung beetles encountered at MDF, Bangalore during 1997 in cattle dung of different age categories.

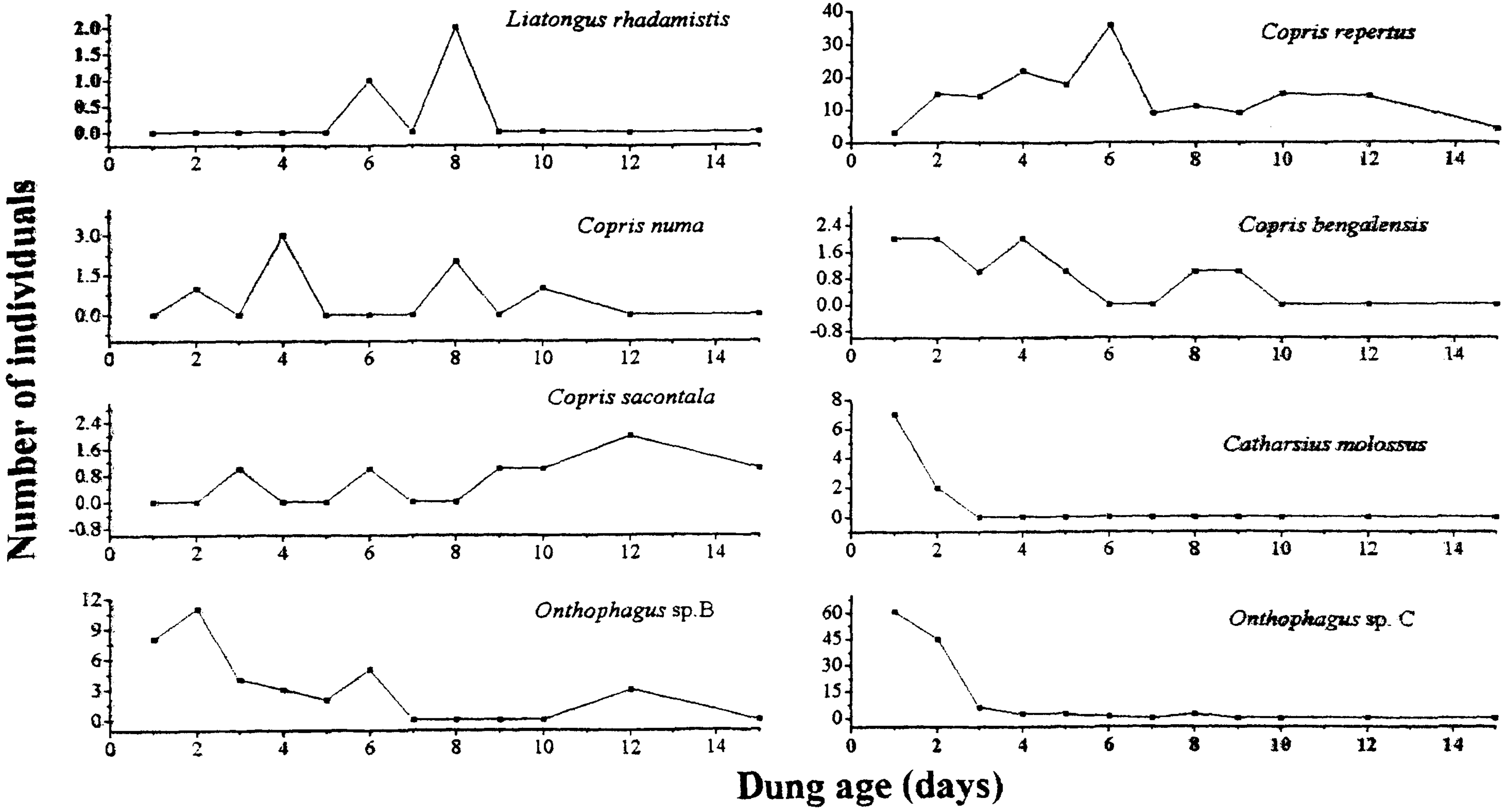


Fig. 10. Occurrence pattern of 32 species of dung beetles encountered at MDF, Bangalore during 1997 in cattle dung of different age categories.

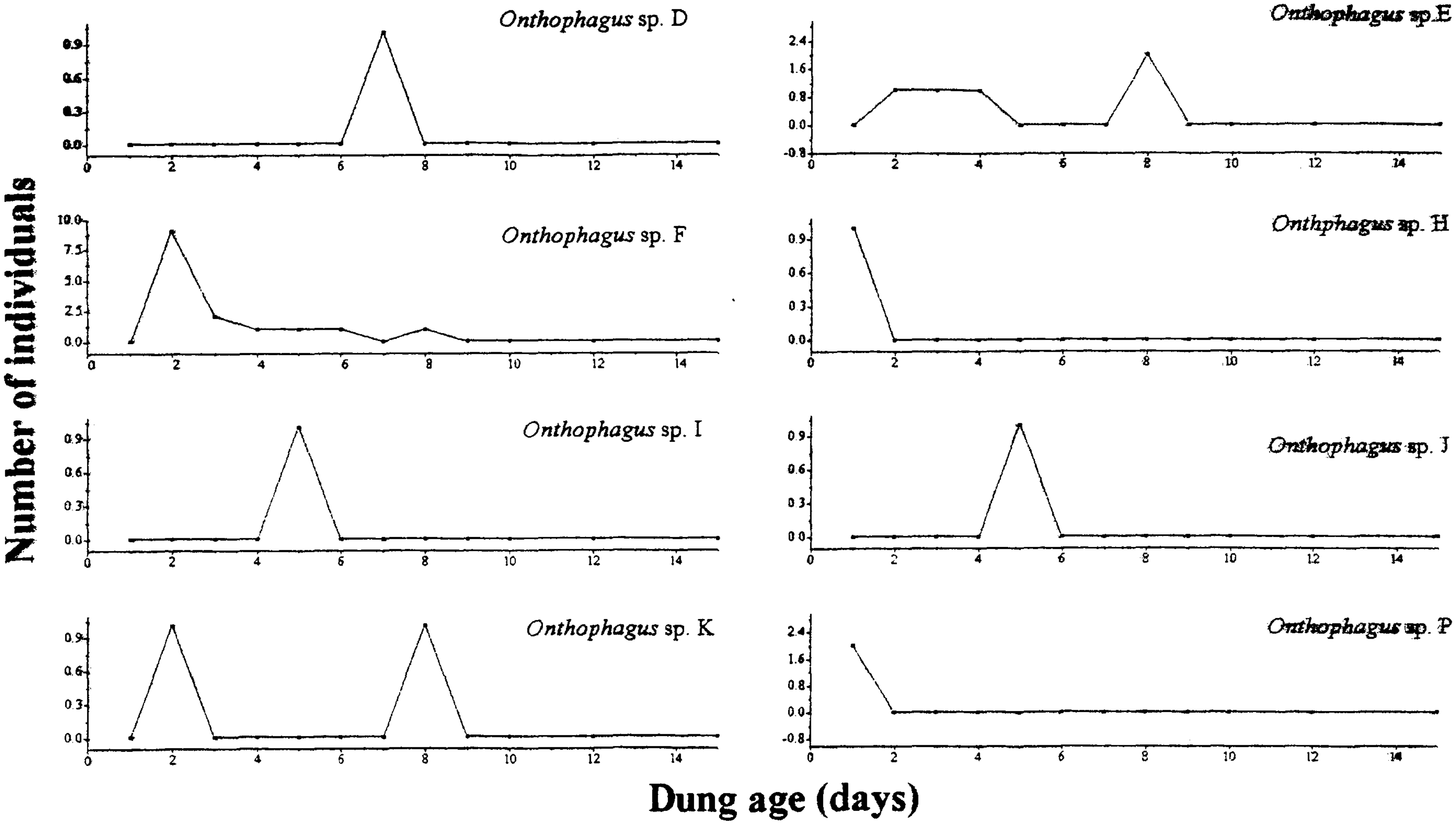


Fig. 11. Occurrence pattern of 32 species of dung beetles encountered at MDF, Bangalore during 1997 in cattle dung of differen
age categories.

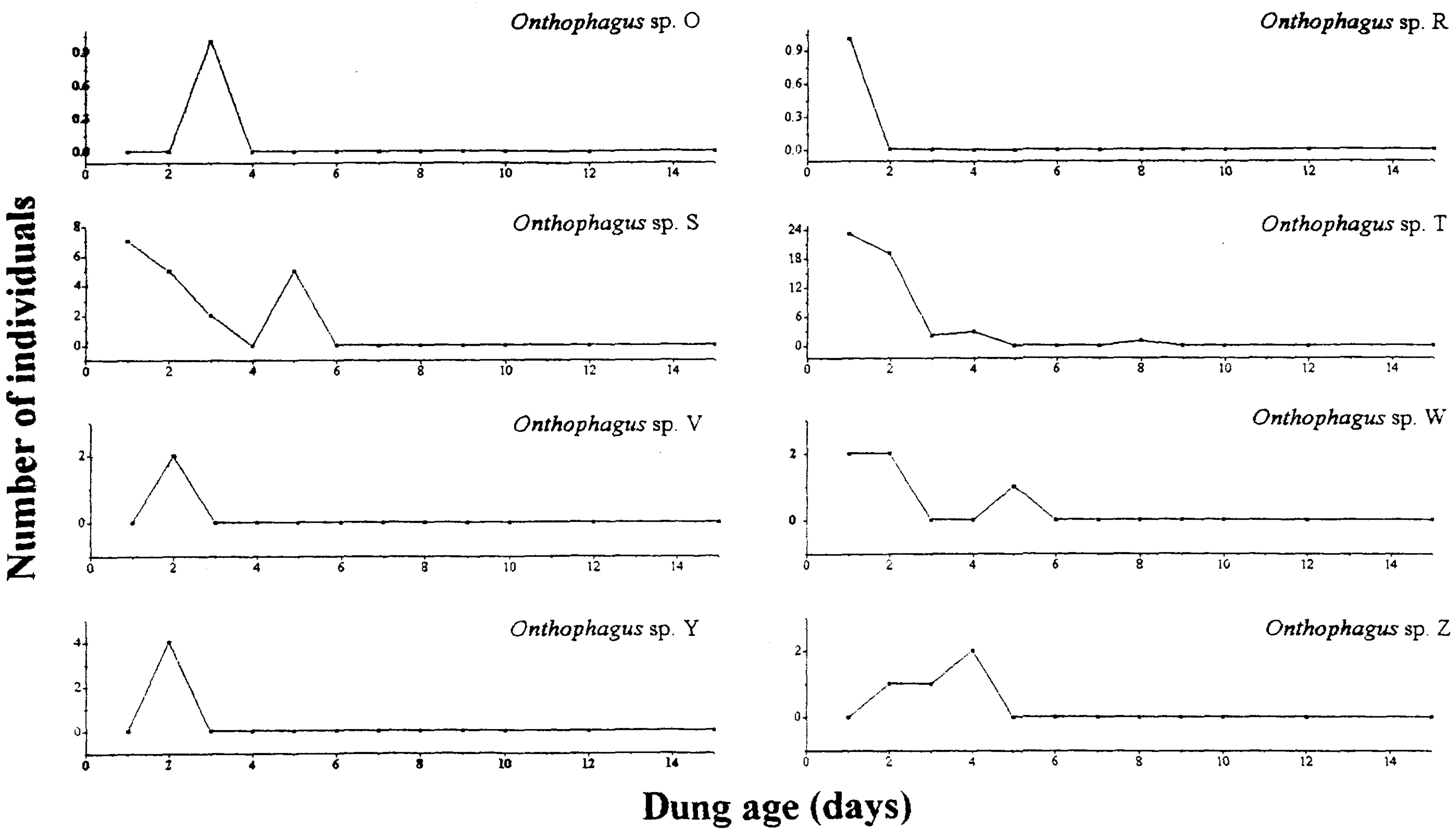


Fig. 12. Occurrence pattern of 32 species of dung beetles encountered at MDF, Bangalore during 1997 in cattle dung of different age categories.

these species were not encountered again, while one, three and one species were represented in the age categories three, seven and nine.

*Copris sacontala* and *Onthophagus* sp. O were encountered in dung aged three days or more only. The former had its peak on 12 day old dung and occurred on all the ages of the dung considered beyond its first occurrence. On the other hand, *Onthophagus* sp. O was found only on the three day old dung.

Two additional species, *Onthophagus* spp. J and I, were found only on five day old dung and were not recovered later. *Liatongus rhadamistus* was found for the first time on six day old dung and occurred in its peak on eight day old dung. The last of the species, *Onthophagus* sp. D was recovered on seven day old dung only.

In general, fewer species were encountered in older dung and there was no recruitment of new species beyond seven days upto 15 days. However, dung of all ages considered (upto 15 days) hosted dung beetles.

From the above results, certain broad categories or `guilds' of species could be identified based on their occurrence pattern. These are tentatively grouped as follows:

**Guild I** : Species that occurred on one, two or three day old dung and were not encountered in dung of older age categories *viz.*, *Cat. molossus, Onthophagus* spp. H, K, P, O, R, V and Y.

**Guild II** : Species that occurred for the first time on one, two and three day old dung and were represented in older dung with a declining trend *viz.*, *D. setosus, O. dama, O. truncaticornis, Ca. vulcanus, Onit. spinipes, On. philemon, C. bengalensis, Onthophagus* spp. B, C, F, S, T and W.

**Guild III** : Species that occurred for the first time on one, two or three day old dung and had their peaks on older dung *viz.*, *O. rectecornutus, Onit. cinctus, C. repertus, C. numa, C. sacontala, Onthophagus* spp. E and Z.

**Guild IV** : Species that occurred for the first time on dung of more than 3 days of age *viz., L. rhadamistus, Onthophagus* spp. D, I and J

The most intriguing of these four categories of beetles are those that make up the last group. All these species occurred in five to seven days old dung and were encountered only for a short time thereafter, signifying a high fidelity to dung of a specific age. This perhaps, is also true of a few species that constitute the first group.

### 4.4.1.2 Size vs occurrence pattern

If each of the 32 species were to segregate independently and randomly across dung age there would be 384 possible combinations of occurrence across dung age. However, only 152 combinations were realized. In order to investigate the possible factors which influence the occurrence pattern of species across age, the size distribution of species was examined in these 152 combinations. A plot of the body size of dung beetles against age of dung is provided in Fig. 13. It was observed that the size of beetles varied with the age of dung ($r = 0.254$; $n = 152$; $p < 0.002$), although the relationship explained only 6.45 per cent of the variation.

Commensurate with the diversity of species observed in the earlier dung age categories, there was greater diversity of sizes among the species encountered. An interesting feature was the maximum size of the beetles encountered being negatively correlated ($r = -0.66$; $n = 12$; $p = 0.019$) while the minimum size of the species positively correlated ($r = 0.79$; $n = 12$; $p = 0.003$) with the age of the dung. The observed association for the maximum size may be an artefact of the species size distribution, the minimum size of beetles clearly indicated the limitation of smaller species to colonize the dung of older ages. However, the above observations clearly substantiate the reduction in the diversity of body size for dung beetles with age of the dung along with the absence of larger and the smaller species from the dung of older age.

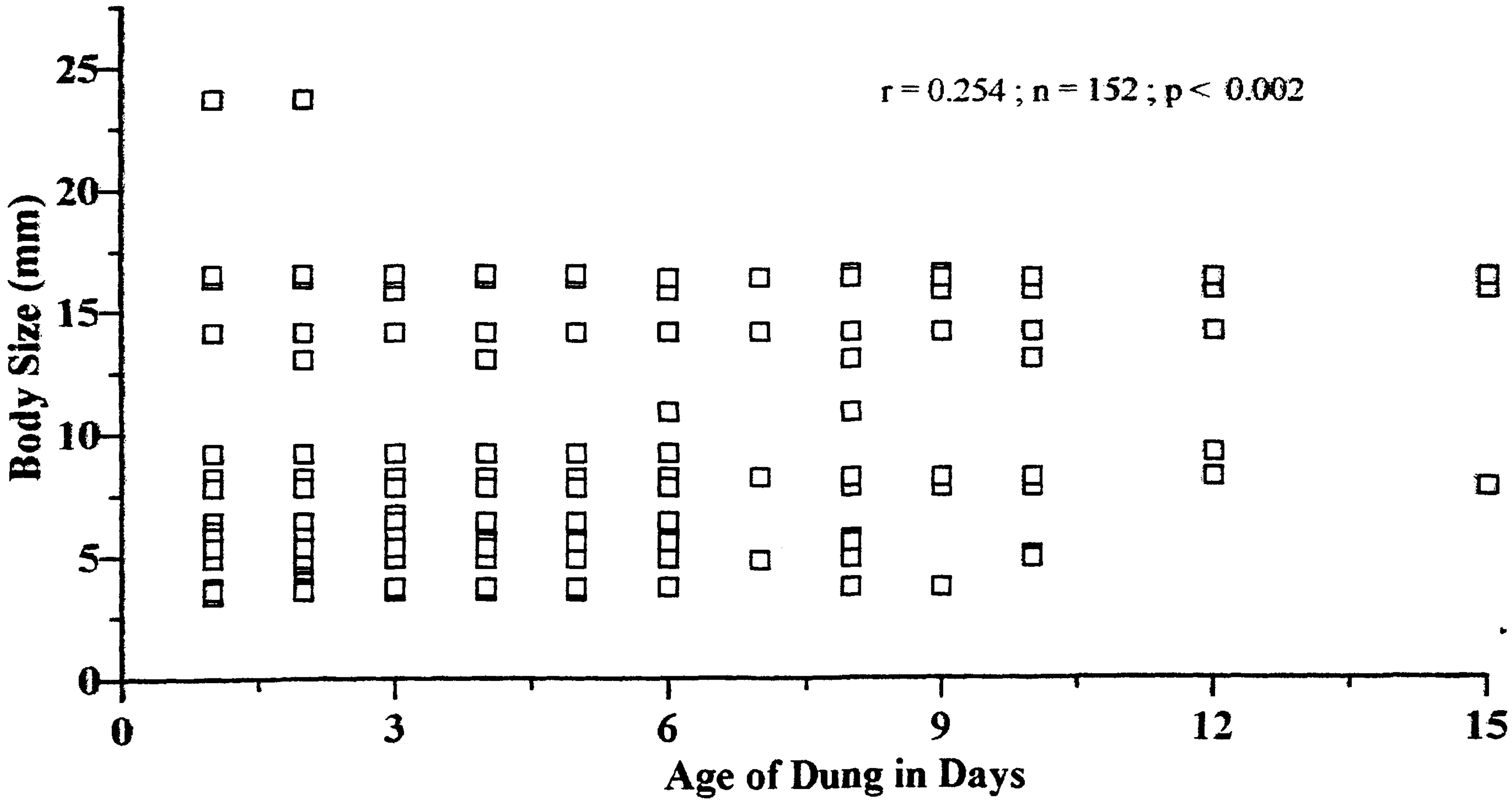


Fig. 13. Distribution of species based on their body size across dung pats of different age categories sampled at MDF, Bangalore during 1997.

### 4.4.1.3 Niche breadth of dung beetles based on the age of dung colonized

Niche breadth computed for each of the 32 species varied from 0 to 2.318 (Fig. 14A). As many as nine species had zero niche breadth, since they occurred in only one dung age category. Three species *viz.*, *C. repertus* (2.318); *On. philemon* (2.238); and *Onit. cinctus* (2.168) closely approached the highest possible niche breadth of 2.48. All these species were characterized by occurrence in all age groups of the dung, and had moderate to high abundance (92 - 217 individuals).

### 4.4.1.4 Niche overlap for all species combinations

A distribution of all possible pairwise combinations of the 32 species (n = 496) revealed as many as 88 (17.74%) combinations to be of zero value indicating complete segregation of the species involved (Fig. 14B). Further 59.27 per cent (294) pairs were found to have less than 0.5 niche overlap while 21.98 per cent (109) pairs had 0.5 to 1.0 niche overalp. Complete niche overlap was observed in five pairs *viz.*, *Onthophagus* spp. V & Y; *Onthophagus* spp. P & R; *Onthophagus* spp. I & J; *Onthophagus* spp. H & P and *Onthophagus* spp. H & R. These combinations involved a total of seven species and all these species were characterized by overall densities of four or less.

Clearly, resource partitioning was strong even considering a single dimension of dung age and only a relatively small proportion of the species pairs exhibited overlap exceeding 0.5.

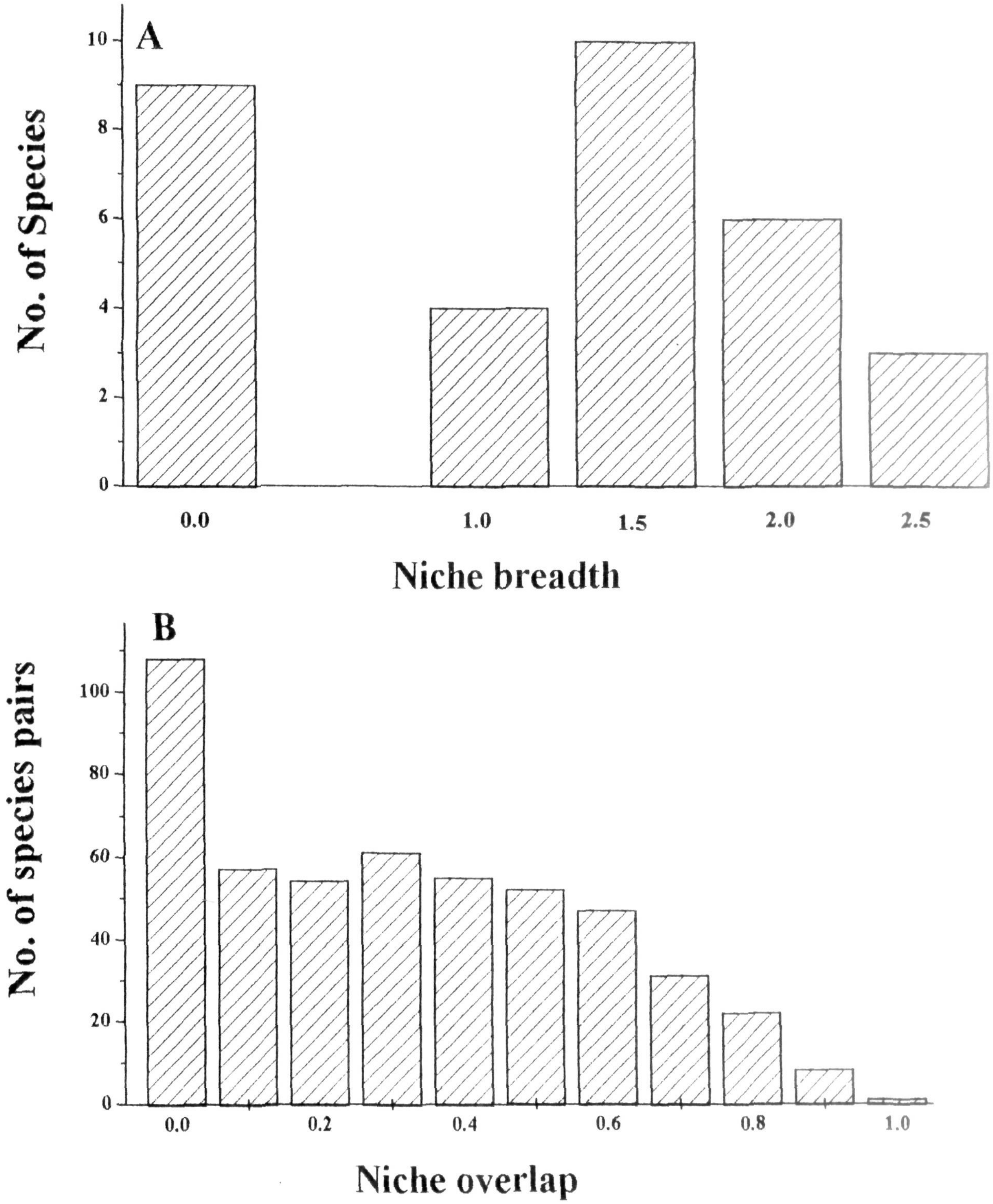


Fig. 14. Frequency distribution of niche breadth (A) for 32 dung beetle species and niche overlap (B) for 496 species pairs calculated on the basis of their occurrence in dung pats of different age categories at MDF, Bangalore, 1997.

#### 4.4.1.5 Species groups on the basis of dung age colonized

Using the data of individual species distribution across age of dung, a new set of parameters were identified for each species. These are tabulated along with overall abundance, body size and niche breadth in table 10. Utilizing these eight parameters an attempt was made to identify the species clusters using Principal Component Analysis. The distribution of the thirty two species, identified by their serial number in table 10, across two major factors is given in fig. 15. The first principal component accounted for 48.34 % of the variance while the second principal component accounted for 34.50 % and the cumulative variance explained by the two components was 82.84 %. Three major clusters were identified when the 32 species were plotted in the space of the first two principal components.

**Cluster I** : A distinct cluster comprising species, *D. setosus* (serial number 1), *O. dama* (2), *O. truncaticornis* (3), *O. rectecornutus* (4), *Ca. vulcanus* (5), *Onit. cinctus* (6), *Onit. spinipes* (7), *On. philemon* (8), *C. repertus* (10), *Onthophagus* sp. B (15), *Onthophagus* sp. C (16), *Onthophagus* sp. F (19), *Onthophagus* sp. S (27), *Onthophagus* sp. T (28). Fourteen species that made up this group were all found to be represented by fifteen individuals or more. Except for *Onthophagus* sp. E, which was first encountered on two-day old dung and all the others colonized the fresh dung of less than two days of age for the first time. Further, all these species were found in dung of atleast upto five days of age.

**Cluster II** : A second cluster consisting of species *Onthophagus* spp. W (30), Y (31), *C. bengalensis* (12), *Onthophagus* sp. Z (32), *C. numa* (11), *Cat. molossus* (14), *Onthophagus* sp. P (24), *Onthophagus* sp. V (29), *Onthophagus* sp. R (26),

**Table: 10 Distribution parameters of 32 species of dung beetles across age of dung as observed at MDF, Bangalore during 1997 along with the overall abundance, body size and niche breadth.**

| Sl. No. | Species name | I day of occurence | Mean day of curence | Mean/day | Day of peak occurence | Body size | Niche breadth | Total duration of occurence |
|---|---|---|---|---|---|---|---|---|
| 1 | *D. setosus* | 1 | 3.35±1.78 | 6.42±8.6 | 2 | 3.7 | 1.697 | 9 |
| 2 | *O. dama* | 1 | 2.38±2.12 | 32.83±54.94 | 2 | 7.81 | 1.458 | 12 |
| 3 | *O. trunaticornis* | 1 | 2.56±1.32 | 25.66±44.14 | 2 | 4.88 | 1.430 | 10 |
| 4 | *O. rectecornutus* | 1 | 4.09±1.76 | 1.92±2.54 | 5 | 6.38 | 1.631 | 6 |
| 5 | *Caccobius vulcanus* | 1 | 1.49±0.98 | 33.52±56.26 | 1 | 3.16 | 0.843 | 8 |
| 6 | *Oniticellus cinctus* | 1 | 7.01±3.82 | 7.67±6.68 | 6 | 8.22 | 2.168 | 12 |
| 7 | *Oniticellus spinipes* | 1 | 2.56±2.08 | 2.83±2.24 | 1 | 5.04 | 1.614 | 10 |
| 8 | *Onitis philemon* | 1 | 5.25±2.67 | 18.08±11.82 | 2 | 14.13 | 2.238 | 12 |
| 9 | *Liatongus rhadamistus* | 6 | 7.33±1.15 | 0.25±0.62 | 8 | 10.86 | 0.637 | 3 |
| 10 | *Copris repertus* | 1 | 6.35±3.2 | 14.17±8.77 | 6 | 16.66 | 2.318 | 12 |
| 11 | *Copris numa* | 2 | 5.71±2.93 | 0.58±1.00 | 4 | 13.02 | 1.277 | 9 |
| 12 | *Copris bengalensis* | 1 | 3.90±2.77 | 0.83±0.83 | 1 | 16.52 | 1.887 | 9 |
| 13 | *Copris sacontala* | 3 | 9.57±4.04 | 0.58±0.67 | 12 | 15.82 | 1.748 | 10 |
| 14 | *Catharsius molossus* | 1 | 1.22±0.44 | 0.75±2.05 | 1 | 23.70 | 0.530 | 2 |
| 15 | *Onthophagus* sp. B | 1 | 3.60±3.06 | 3.00±3.57 | 2 | 9.20 | 1.790 | 11 |
| 16 | *Onthophagus* sp. C | 1 | 1.76±1.21 | 9.92±20.48 | 1 | 5.53 | 1.107 | 8 |

............ contd...

Table 10 .........contd

| Sl. No . | Species name | I day of occurence | Mean day of curence | Mean/day | Day of peak occurence | Body size | Niche breadth | Total duration of occurence |
|---|---|---|---|---|---|---|---|---|
| 17 | *Onthophagus* sp.D | 7 | 7.00±0.00 | 0.08±0.29 | 7 | 4.81 | 0.00 | 1 |
| 18 | *Onthophagus* sp.E | 2 | 5.00±2.83 | 0.42±0.67 | 8 | 5.70 | 1.332 | 7 |
| 19 | *Onthophagus* sp.F | 2 | 3.13±1.85 | 1.25±2.53 | 2 | 5.17 | 1.297 | 7 |
| 20 | *Onthophagus* sp.H | 1 | 1.00±0.00 | 0.08±0.29 | 1 | 6.04 | 0.00 | 1 |
| 21 | *Onthophagus* sp.I | 5 | 5.00±0.00 | 0.08±0.29 | 5 | 5.94 | 0.00 | 1 |
| 22 | *Onthophagus* sp.J | 5 | 5.00±0.00 | 0.08±0.29 | 5 | 5.07 | 0.00 | 1 |
| 23 | *Onthophagus* sp.K | 2 | 5.00±4.24 | 0.17±0.39 | 5 | 5.41 | 0.693 | 7 |
| 24 | *Onthophagus* sp.P | 1 | 1.00±0.00 | 0.17±0.58 | 1 | 5.44 | 0.00 | 1 |
| 25 | *Onthophagus* sp.O | 3 | 3.00±0.00 | 0.08±0.29 | 3 | 6.70 | 0.00 | 1 |
| 26 | *Onthophagus* sp.R | 1 | 1.00±0.00 | 0.08±0.29 | 1 | 3.37 | 0.00 | 1 |
| 27 | *Onthophagus* sp.S | 1 | 2.53±1.65 | 1.58±2.57 | 1 | 5.77 | 1.307 | 5 |
| 28 | *Onthophagus* sp.T | 1 | 1.80±1.23 | 4.00±8.05 | 1 | 5.33 | 1.106 | 8 |
| 29 | *Onthophagus* sp.V | 2 | 2.00±0.00 | 0.17±0.58 | 2 | 3.97 | 0.00 | 1 |
| 30 | *Onthophagus* sp.W | 1 | 2.20±1.64 | 0.42±0.79 | 1 | 3.53 | 1.055 | 5 |
| 31 | *Onthophagus* sp.Y | 2 | 2.00±0.00 | 0.33±1.15 | 2 | 4.71 | 0.00 | 1 |
| 32 | *Onthophagus* sp.Z | 2 | 3.30±0.96 | 0.33±0.65 | 4 | 5.51 | 1.040 | 3 |

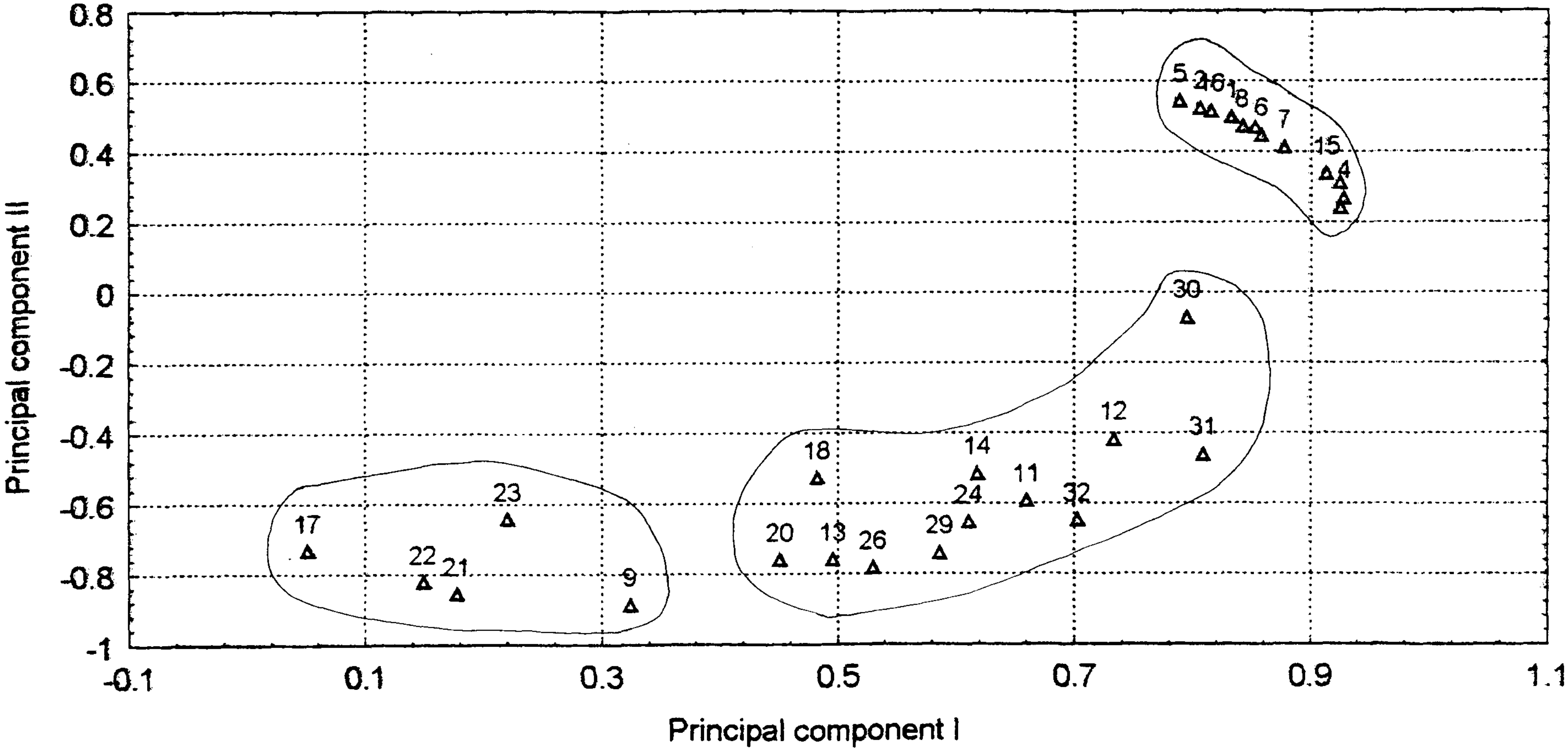


**Fig. 15. Clustering of 32 species of dung beetles encountered at MDF, Bangalore in dung of different ages using principal components analysis.**

*C. sacontala* (13), *Onthophagus* sp. E (18), and *Onthophagus* sp. H (20). These species were represented by overall numbers ranging from one, as in spp. H and P of *Onthophagus*, to ten individuals as observed in *C. bengalensis* and all of them were first encountered within the three days of dung age.

**Cluster III** : The third cluster consisted of species *L. rhadamistus* (9), *Onthophagus* sp. K (23), *Onthophagus* sp. I (21), *Onthophagus* sp. J (22), *Onthophagus* sp. D (17) and *Onthophagus* sp. O (25). These species were characterized by very low overall abundances of less than three individuals. *Onthophagus* sp. K occurred for the first time on two day old dung, *Onthophagus* sp. O occurred on three day old dung and all other species were encountered in dung of five, six or seven days old.

### 4.4.2 Temporal (seasonal) resource partitioning in dung beetles

Utilizing the twelve sampling dates as units of seasons, the segregation of dung beetles encountered at MDF, Bangalore was studied to understand the temporal (seasonal) partitioning of resources.

#### 4.4.2.1 Occurrence pattern across sampling dates

The twelve sampling dates starting from April 4, 1997 spread over six months approximately at fifteen day intervals were serially numbered and occurrence patterns of 32 Species of dung beetles studied.

Eighteen species of dung beetles were recorded in the first sample. This was followed by six additional species in the second, one in the third, one in the fifth, three in the sixth, two in the seventh and one in the eighth sample. Distribution of all the 32 species of dung beetles are plotted across the 12 dates of sampling in Figs. 16 to 19. This data on the distribution of the individual species were used for comparison between the species and for grouping. On the basis of this exercise four categories of species distributions could be identified. They were:

**Category 1.** Species that are represented in only one sample: This group consisted of twelve species of *Onthophagus viz.*, D, E, H, I, J, K, P, O, R, V, Y and Z. These were characterized by extremely low overall abundances of 1 - 5 individuals. Three of these species were found in the first sample while 4 in the second, 2 in the sixth, 2 in the seventh and 1 in the eighth sample .

**Category 2.** Species that are represented in 2-6 contiguous sampling dates : This group represented a slightly wider occurrence pattern, where a species occurs in atleast two farthest sampling dates separated by less than six sampling dates. This group included species with relatively small representations of 3-15 individuals. *C. sacontala, L. rhadamistus* and *Onthophagus* sp. F were grouped in this category.

**Category 3.** Species that are represented in more than six contiguous sampling dates with a single peak in their abundances: The group consisted of *D. setosus*, *On. philemon*, *Onit. cintus*, *Cat. molossus* and *Onthophagus* sp. T. In order to identify these groups, the peaks were approximated as contiguous if more than one peak was observed. These species were represented by 9-217 individuals.

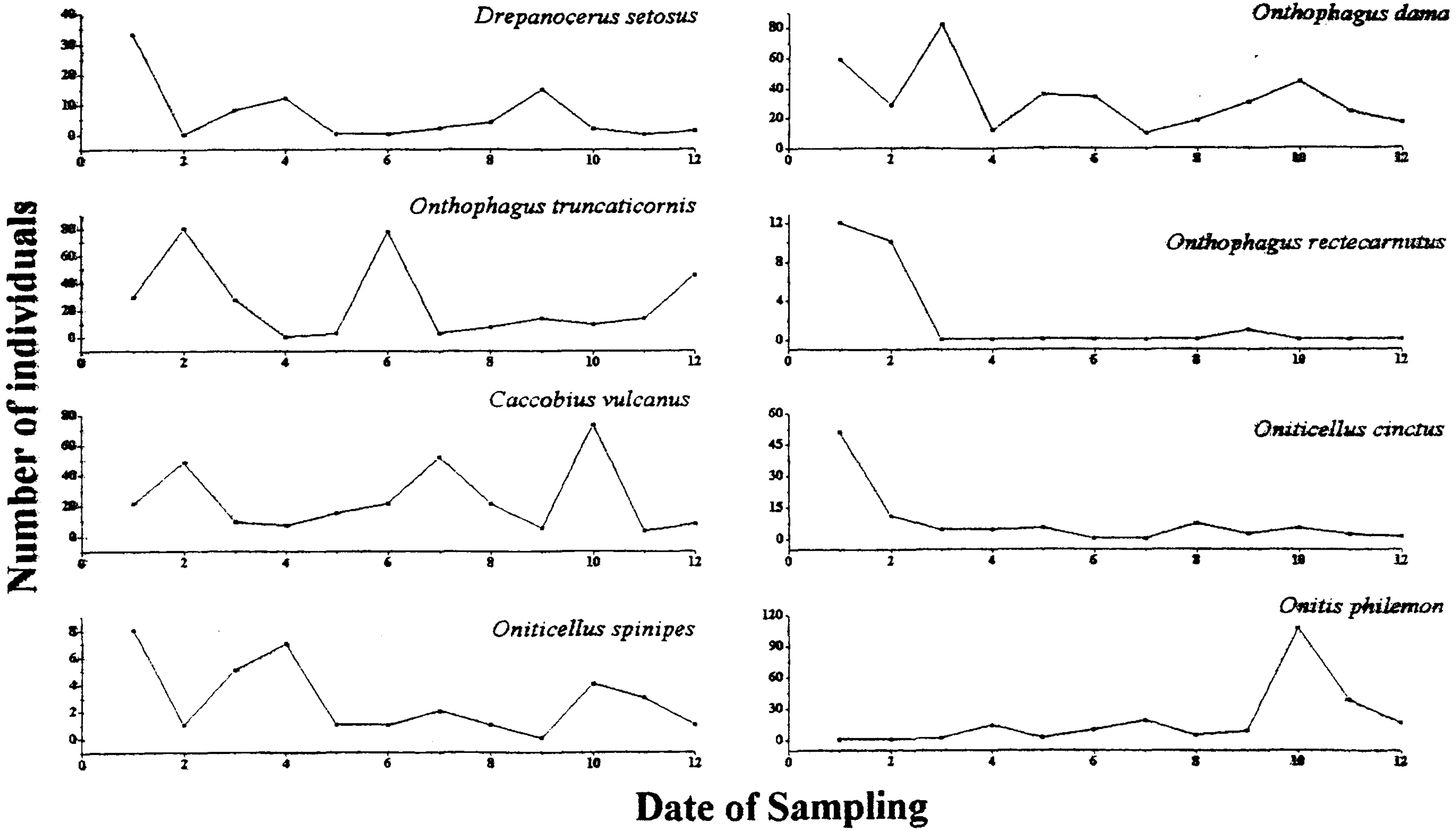


Fig. 16. Occurence pattern of 32 species of dung beetles at MDF, Bangalore during 1997on different sampling dates.

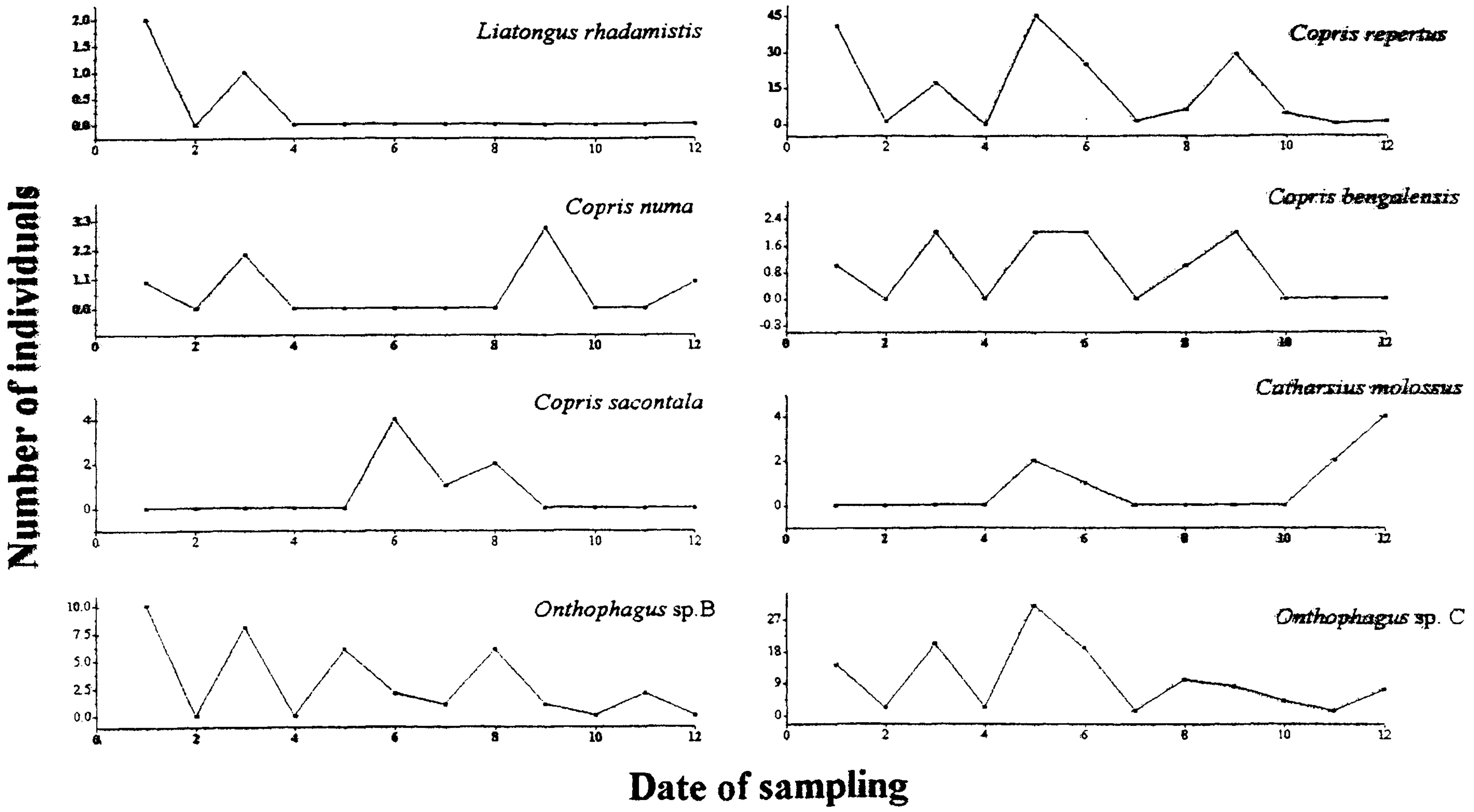


Fig. 17. Occurence pattern of 32 species of dung beetles at MDF, Bangalore during 1997on different sampling dates.

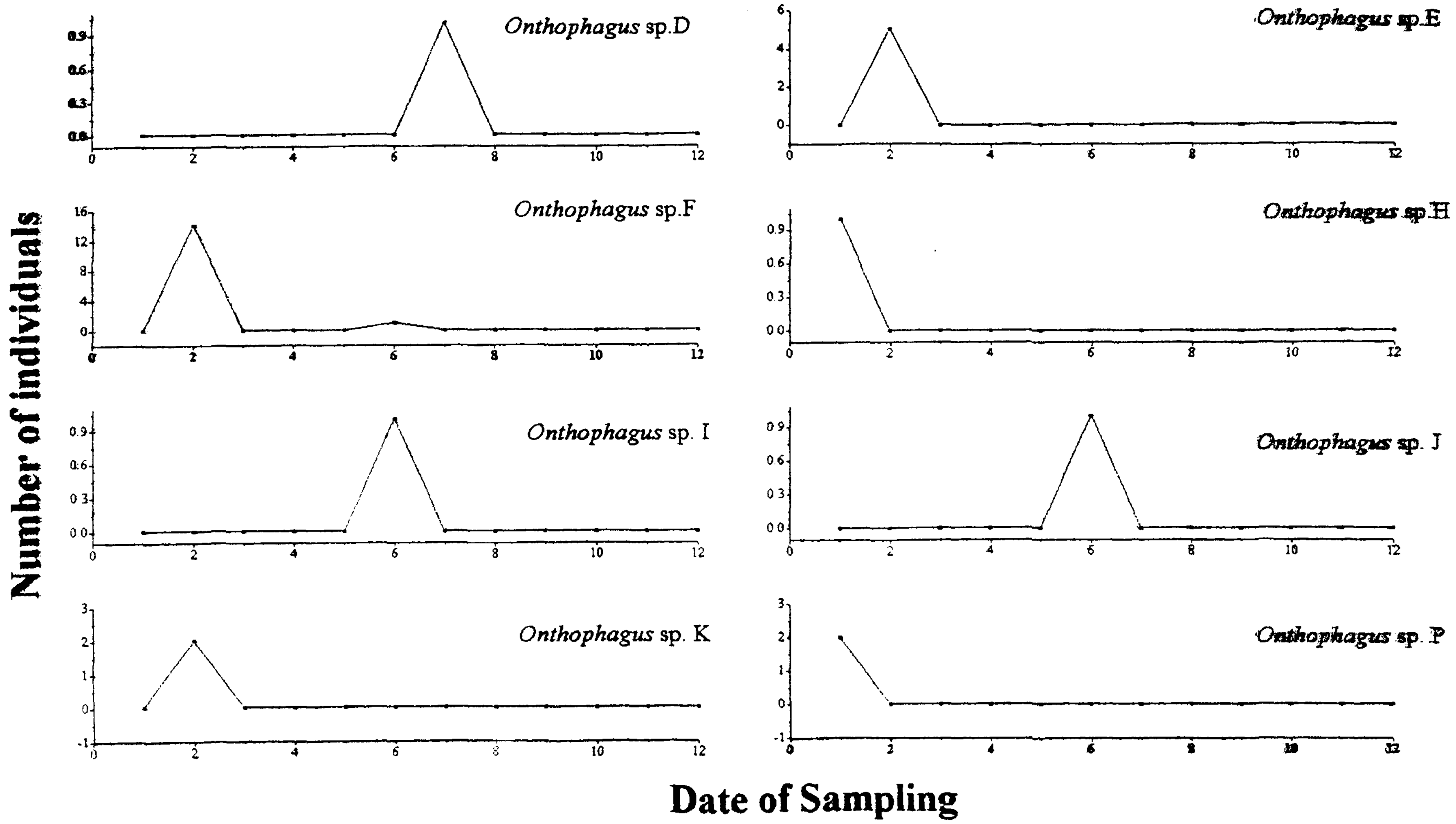


Fig. 18. Occurence pattern of 32 species of dung beetles at MDF, Bangalore during 1997on different sampling dates.

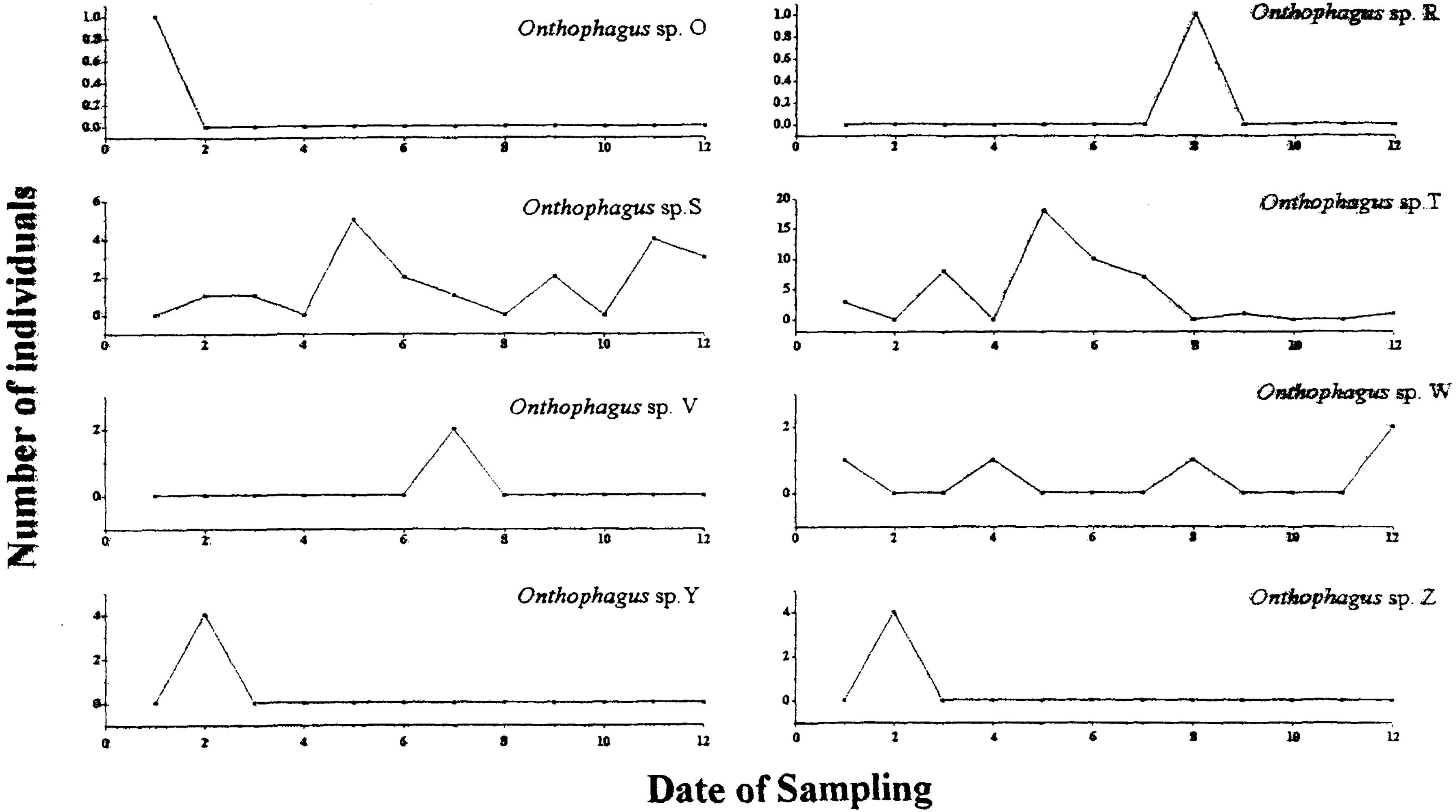


Fig.19. Occurence pattern of 32 species of dung beetles at MDF, Bangalore during 1997on different sampling dates.

**Category 4.** Species that are represented in more than six sampling dates with multiple peaks : Twelve species *viz.*, *O. dama, O. truncaticornis, O. rectecornutus, Ca. vulcanus, Onit. spinipes, C. repertus, C. numa, C. bengalensis, Onthophagus* sp. B, C, S and W were grouped in this category. The species were characterized by abundances ranging from 10-394 except *Onthophagus* Sp. W which yielded only 5 specimens.

The abundances of all these species across different sampling dates are presented in Figs. 16 to 19. The observed patterns and the consequent grouping of the species clearly demonstrates the variations across species even in short duration sampling of dung beetles in a locality.

#### 4.4.2.2 Body size versus seasonal occurrence pattern.

In all, a total of 159 combinations of species versus sampling dates were realized. The 159 observations when plotted across sampling dates (Fig. 20), indicated a random distribution of species based on their body sizes ($r = 0.071$; $n = 159$; $p > 0.37$). Clearly the seasonality of dung beetles at MDF, Bangalore is not determined by their body sizes.

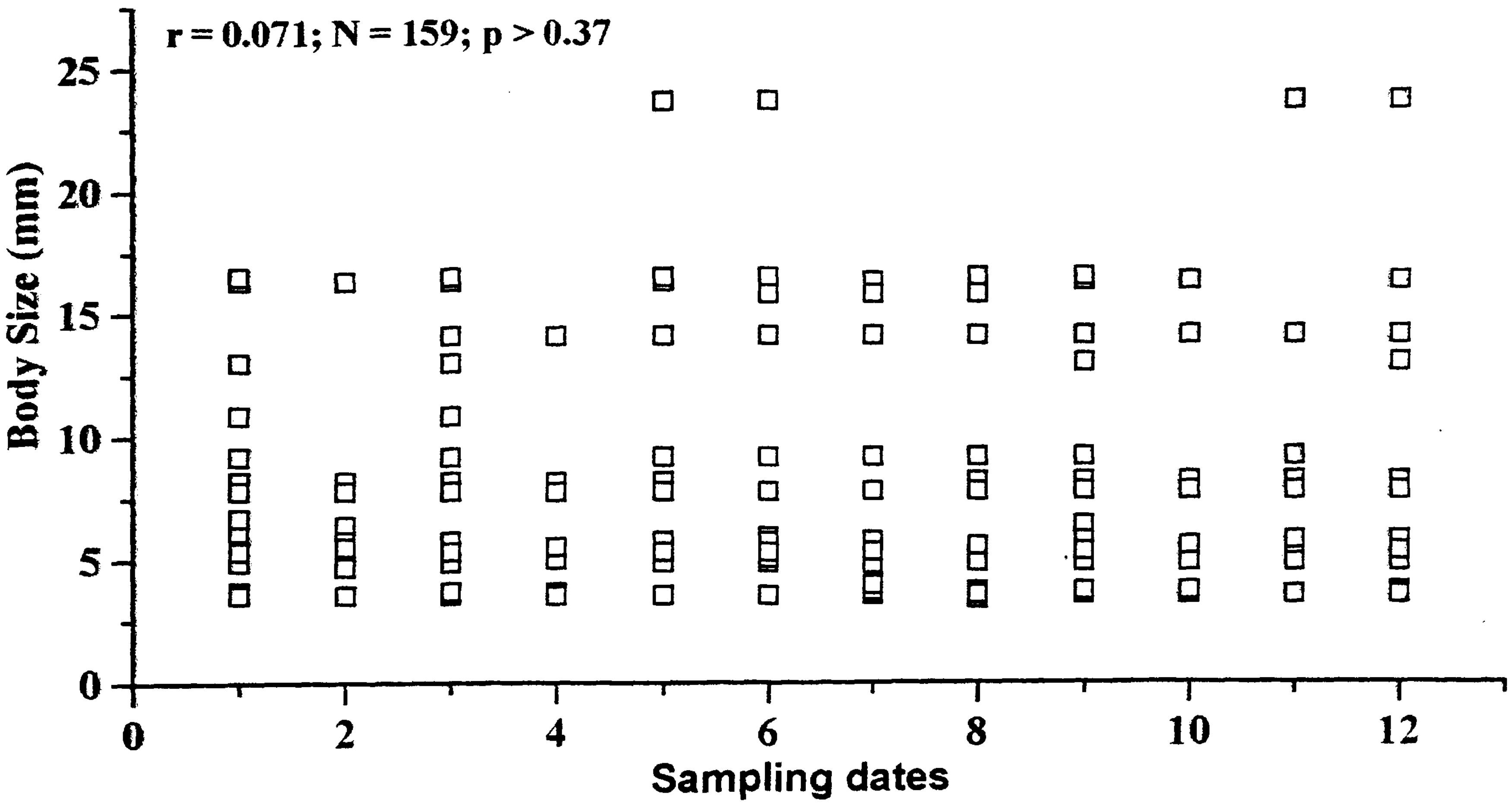


Fig. 20. Distribution of species based on their body size across different dates of sampling at MDF, Bangalore during 1997.

#### 4.4.2.3 Niche breadth of dung beetles based on their representation in different sampling dates.

Niche breadth of 32 species calculated on the basis of their representation in the twelve sampling dates varied from 0-2.316. As many as 12 species (Category 1) had zero niche breadth indicating their occurrence in only one sampling date (Fig. 21A). All these species were characterized by very low abundances. However, as many as four species had niche breadth values of more than two. These were *O. dama*, *Ca. vulcanus* *Onit. spinipes* and *Onthophagus sp.* C. These were represented in 11-12 sampling dates. All these species belonged to the Category 4, classified on the basis of their occurrence pattern (Section 4.4.2.1). More than 25% (9 species) were found to have niche breadth in the range of 1.5-2.0 indicating a wider representation across sampling dates for these species also; most of these species belonged to Categories 3 and 4.

#### 4.4.2.4 Niche overlap for species pairs based on their representation in different sampling dates

Distribution of niche overlap calculated for all possible pairs of species, on the basis of their representation in the 12 sampling dates are given in Fig 21B. It was observed that 132 pairs (26.61%) had complete segregation demonstrating zero overlap values. As many as 305 pairs (61.49 %) of species indicated an overlap range of 0 - 0.5 while only 9.68 per cent (48 pairs) accounting for overlap values in the range of 0.5 - 1.0. However, 11 combinations represented complete overlap with a value of 1.00. These combinations were all observed in the species of *Onthophagus viz.*, spp. D & V, I & J, H & P, P & O, H & O, E & K, E & Y, E & Z, K & Y, K & Z and Y & Z. The

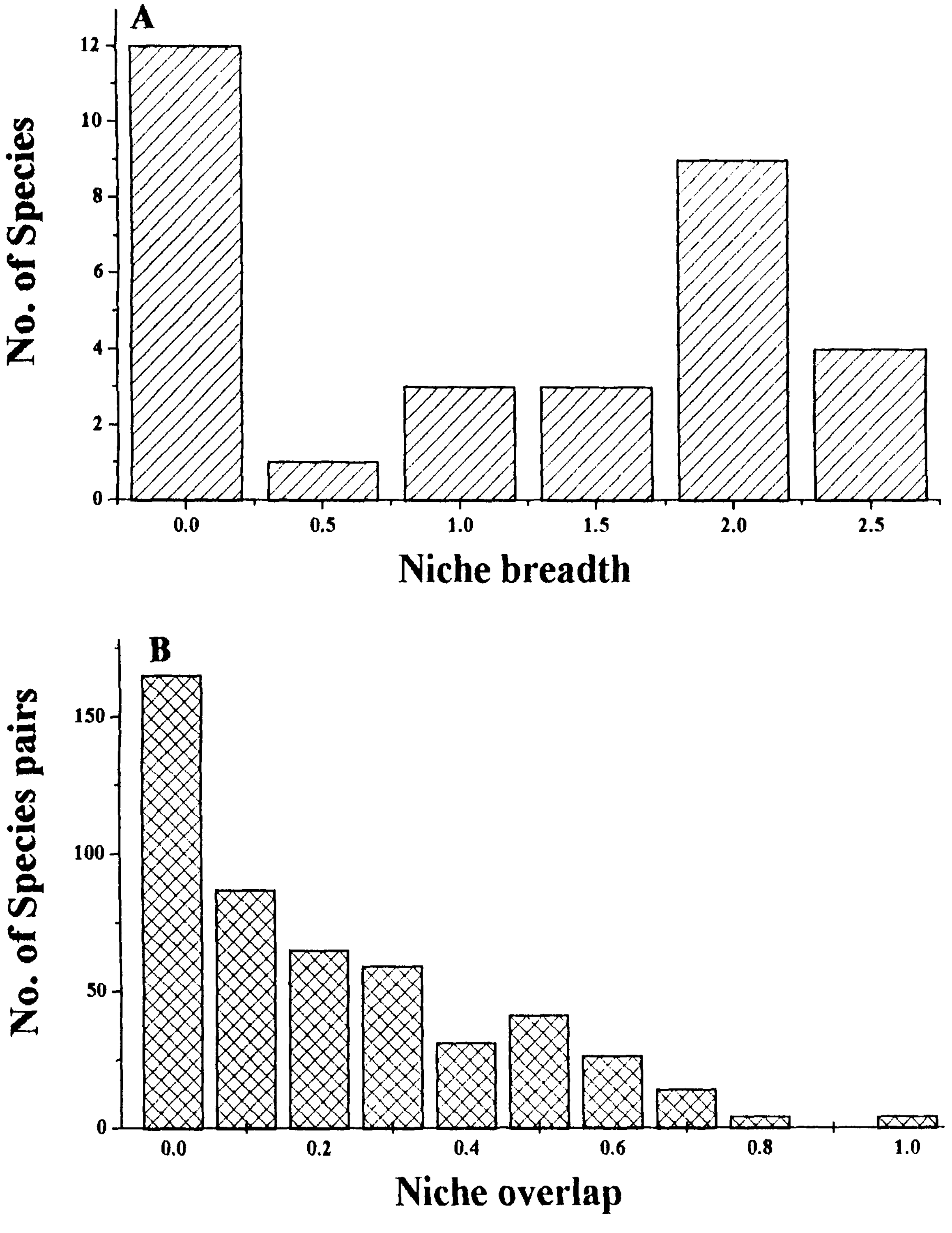


Fig. 21. Frequency distribution of niche breadth (A) for 32 dung beetle species and niche overlap (B) for 496 species pair calculated on the basis of their representation on different sampling dates at MDF, Bangalore during 1997.

11 species involved all belonged to category 1 mentioned under section 4.4.2.1 and were represented by very low number of individuals (less than four).

The above results suggest segregation of a large number of pairs of species considered amounting to (305 + 132) 88 per cent of the 496 possible combinations. Therefore sampling dates themselves appear to influence temporal (seasonal) resource partitioning among the dung beetles.

### 4.4.2.5 Species groups on the basis of occurrence in different sampling dates

The abundance and distribution of the 32 species of dung beetles across sampling dates were used to generate a new set of parameters as indicated in table 11. These parameters were similar to those developed for the 32 species on the basis of their occurrence across age of dung . Clustering of the species was attempted using this data set by following the principal component analyses. The plot of the 32 species (Fig. 22) in the space of two components (PC I and PC II) clearly indicated four clusters.

The first principal component accounted for 48.50 per cent variance, while the second accounted for 33.36 per cent (81.86 per cent cumulative variance). The four clusters consisted of the following species :

**Cluster 1**: *Drepanocerus setosus* (1), *O. dama* (2), *O. Truncaticornis* (3), *O. rectecornutus* (4), *Ca. vulcanus* (5), *Onit. cinctus* (6), *Onit. spinipes* (7), Table: 11 Distribution parameters of 32 species of dung beetles across date of sampling as observed at MDF, Bangalore during 1997 along with the overall abundance, body size and niche breadth.

| Sl.No. | Species name | Date of I occurence | Mean date of ccurence | Mean/ Date | Date of peak occurence | Body size | Niche breath | No. of dates |
|---|---|---|---|---|---|---|---|---|
| 1 | *D. setosus* | 1 | 4.13±3.43 | 6.42±9.78 | 1 | 3.7 | 1.606 | 8 |
| 2 | *O. dama* | 1 | 5.55±3.82 | 32.83±20.83 | 3 | 7.81 | 2.316 | 12 |
| 3 | *O. trunaticornis* | 1 | 5.63±3.82 | 25.67±27.89 | 2 | 4.88 | 1.974 | 11 |
| 4 | *O. rectecornutus* | 1 | 1.78±1.65 | 1.92±4.27 | 1 | 6.38 | 0.838 | 3 |
| 5 | *Caccobius vulcanus* | 1 | 6.39±3.31 | 23.58±22.24 | 10 | 3.16 | 2.118 | 12 |
| 6 | *Oniticellus cinctus* | 1 | 3.09±3.21 | 7.67±14.00 | 1 | 8.22 | 1.580 | 10 |
| 7 | *Oniticellus spinipes* | 1 | 5.03±3.65 | 2.83±2.62 | 1 | 5.04 | 2.099 | 11 |
| 8 | *Onitis philemon* | 1 | 9.36±2.11 | 18.08±29.98 | 10 | 14.13 | 1.635 | 10 |
| 9 | *Liatongus rhadamistus* | 1 | 1.67±1.15 | 0.25±0.62 | 1 | 10.86 | 0.637 | 2 |
| 10 | *Copris repertus* | 1 | 4.92±2.91 | 14.17±16.81 | 5 | 16.66 | 1.806 | 10 |
| 11 | *Copris numa* | 1 | 6.57±4.16 | 0.58±0.99 | 9 | 13.02 | 1.277 | 4 |
| 12 | *Copris bengalensis* | 1 | 5.50±2.68 | 0.83±0.94 | 6 | 16.52 | 1.748 | 6 |
| 13 | *Copris sacontala* | 6 | 6.70±0.95 | 0.58±1.24 | 6 | 15.82 | 0.956 | 3 |
| 14 | *Catharsius molossus* | 5 | 9.56±3.20 | 0.75±1.29 | 12 | 23.70 | 1.273 | 4 |
| 15 | *Onthophagus* sp. B | 1 | 4.50±3.08 | 3.00±3.54 | 1 | 9.20 | 1.808 | 8 |
| 16 | *Onthophagus* sp. C | 1 | 5.45±2.94 | 9.92±9.42 | 5 | 5.53 | 2.083 | 12 |

......... contd

Table 11 ..... contd

| Sl.No. | Species name | Date of I occurence | Mean date of ccurence | Mean/ Date | Date of peak occurence | Body size | Niche breath | No. of dates |
|---|---|---|---|---|---|---|---|---|
| 17 | *Onthophagus* sp.D | 7 | 7.00±00 | 0.083±0.29 | 7 | 4.81 | 0.000 | 1 |
| 18 | *Onthophagus* sp.E | 2 | 2.00±00 | 0.42±1.44 | 2 | 5.70 | 0.000 | 1 |
| 19 | *Onthophagus* sp.F | 2 | 2.27±1.03 | 1.25±4.25 | 2 | 5.17 | 0.245 | 2 |
| 20 | *Onthophagus* sp.H | 1 | 1.00±00 | 0.083±0.29 | 1 | 6.04 | 0.000 | 1 |
| 21 | *Onthophagus* sp.I | 6 | 6.00±00 | 0.083±0.29 | 6 | 5.94 | 0.000 | 1 |
| 22 | *Onthophagus* sp.J | 6 | 6.00±00 | 0.083±0.29 | 6 | 5.07 | 0.000 | 1 |
| 23 | *Onthophagus* sp.K | 2 | 2.00±00 | 0.17±0.58 | 2 | 5.41 | 0.000 | 1 |
| 24 | *Onthophagus* sp.P | 1 | 1.00±00 | 0.17±0.58 | 1 | 5.44 | 0.000 | 1 |
| 25 | *Onthophagus* sp.O | 1 | 1.00±00 | 0.083±0.29 | 1 | 6.70 | 0.000 | 1 |
| 26 | *Onthophagus* sp.R | 8 | 8.00±00 | 0.083±0.29 | 8 | 3.37 | 0.000 | 1 |
| 27 | *Onthophagus* sp.S | 2 | 7.74±3.30 | 1.53±1.68 | 5 | 5.77 | 1.909 | 8 |
| 28 | *Onthophagus* sp.T | 1 | 5.15±1.97 | 4.00±5.69 | 5 | 5.33 | 1.609 | 7 |
| 29 | *Onthophagus* sp.V | 7 | 7.00±00 | 0.17±0.58 | 7 | 3.97 | 0.000 | 1 |
| 30 | *Onthophagus* sp.W | 1 | 7.40±4.90 | 0.42±0.67 | 12 | 3.53 | 1.332 | 4 |
| 31 | *Onthophagus* sp.Y | 2 | 2.00±00 | 0.33±1.15 | 2 | 4.71 | 0.000 | 1 |
| 32 | *Onthophagus* sp.Z | 2 | 2.00±00 | 0.33±1.15 | 2 | 5.51 | 0.000 | 1 |

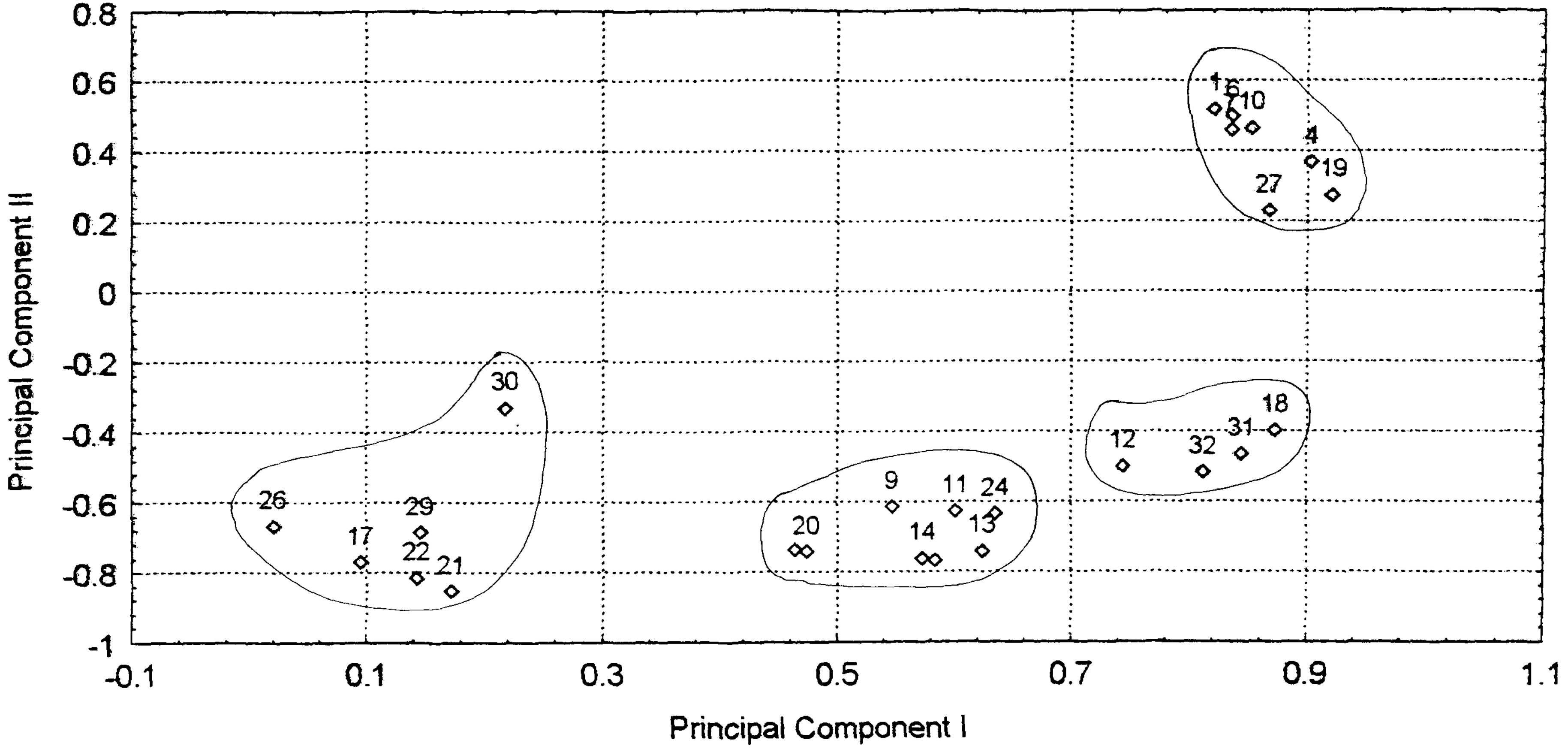


Fig. 22. Clustering of 32 species of dung beetles encountered on different sampling dates at MDF, Bangalore during 1997 using principal components analysis.

*On. philemon* (8), *C. repertus* (10), *Onthophagus* sp. B (15), *Onthophagus* sp. C (16), *Onthophagus* sp. F (19), *Onthophagus* sp. S (27), *Onthophagus* sp. T (28). These fourteen species contained all species with 15 or more beetles and were represented in 2 or more sampling dates.

**Cluster 2**: This was made up of four species *viz.*, *C. bengalensis* (12), *Onthophagus* sp. E (18), *Onthophagus* sp. Y (31), and *Onthophagus* sp. Z (32) and ranged in abundance from 4 to 10 individuals per species.

**Cluster 3**: This cluster contained *L. rhadamistus* (9), *C. numa* (11), *C. sacontala* (13), *Cat. molossus* (14), *Onthophagus* sp. H (20), *Onthophagus* sp. K (23), *Onthophagus* sp. P (24) and *Onthophagus* sp. O (25). These were represented by 1 - 9 individuals per species in one to four sampling dates.

**Cluster 4**: The fourth cluster was made of six species viz., *Onthophagus* sp. D (17), *Onthophagus* sp. I (21), *Onthophagus* sp. J (22), *Onthophagus* sp. R (26), *Onthophagus* sp. V (29) and *Onthophagus* sp. W (30). Again these species were of low abundance with 1 - 5 individuals per species and were represented in 1 or 4 (*Onthophagus* sp. W) sampling dates.

This exercise demonstrated the possibility of 32 species clustering into four separate units, on the basis of the parameters of distribution across sampling dates. However, these clusters did not represent any gradient across a single or a set of characters as the qualifying factors.

### 4.4.3 Species segregation along two dimensions

While single dimensions of age of dung or sampling date showed considerable proportions of species to segregate, they did not indicate a complete segregation. Obviously, species are segregated on more than one dimensions. To verify this aspect an attempt was made utilising both the dimensions of dung age and the season to work out niche breadth, niche overlap and clustering of species similar to the attempts made on single dimensions.

#### 4.4.3.1 Niche breadth : along two dimensions

The 32 species of dung beetles at MDF, had their niche breadth ranges from 0 - 4.00 when both dung age and sampling dates were considered for the calculation of niche breadth. Nine of the 32 species showed zero niche breadth (Fig. 23A) and these were *Onthophagus* spp. D, H, I, J, P, O, R, V and Y. Only one species , *viz.*, *C. repertus,* on the contrary, had the highest value of 3.78. Further, two to five species occurred in class intervals of 0.5 to 1.0, 1.0 to 1.5, 1.5 to 2.00, 2.0 to 2.5, 2.50 to 3.00 and 3.00 to 3.50 indicating a more or less equitable distribution of species within this range. Although, more of the species crossed the possible value of > 4.00 (maximum possible = 4.48), the results nonetheless indicate smaller niches on wider scales. Therefore, the possibility of segregation of species becomes greater.

#### 4.4.3.2 Niche overlap across two dimensions

Niche overlaps calculated for 496 pairs of the 32 species of dung beetles indicated a strong declining trend with increasing value of the niche overlap (Fig. 23B).

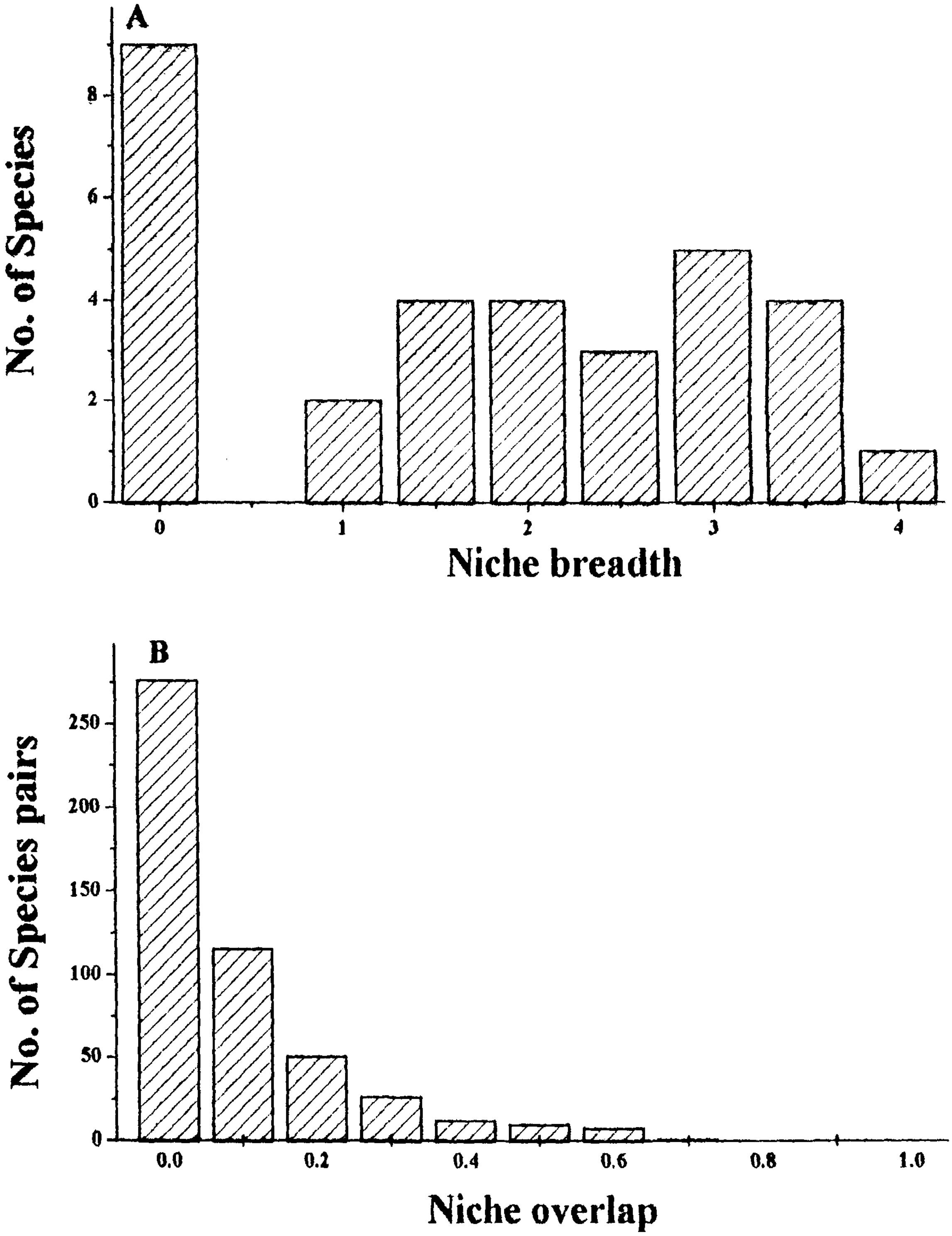


Fig. 23. Frequency distribution of niche breadth(A) for 32 dung beetle species and niche overlap (B) for 496 species pairs calculated on the basis of their representation on different days of sampling at MDF,Bangalore,1997

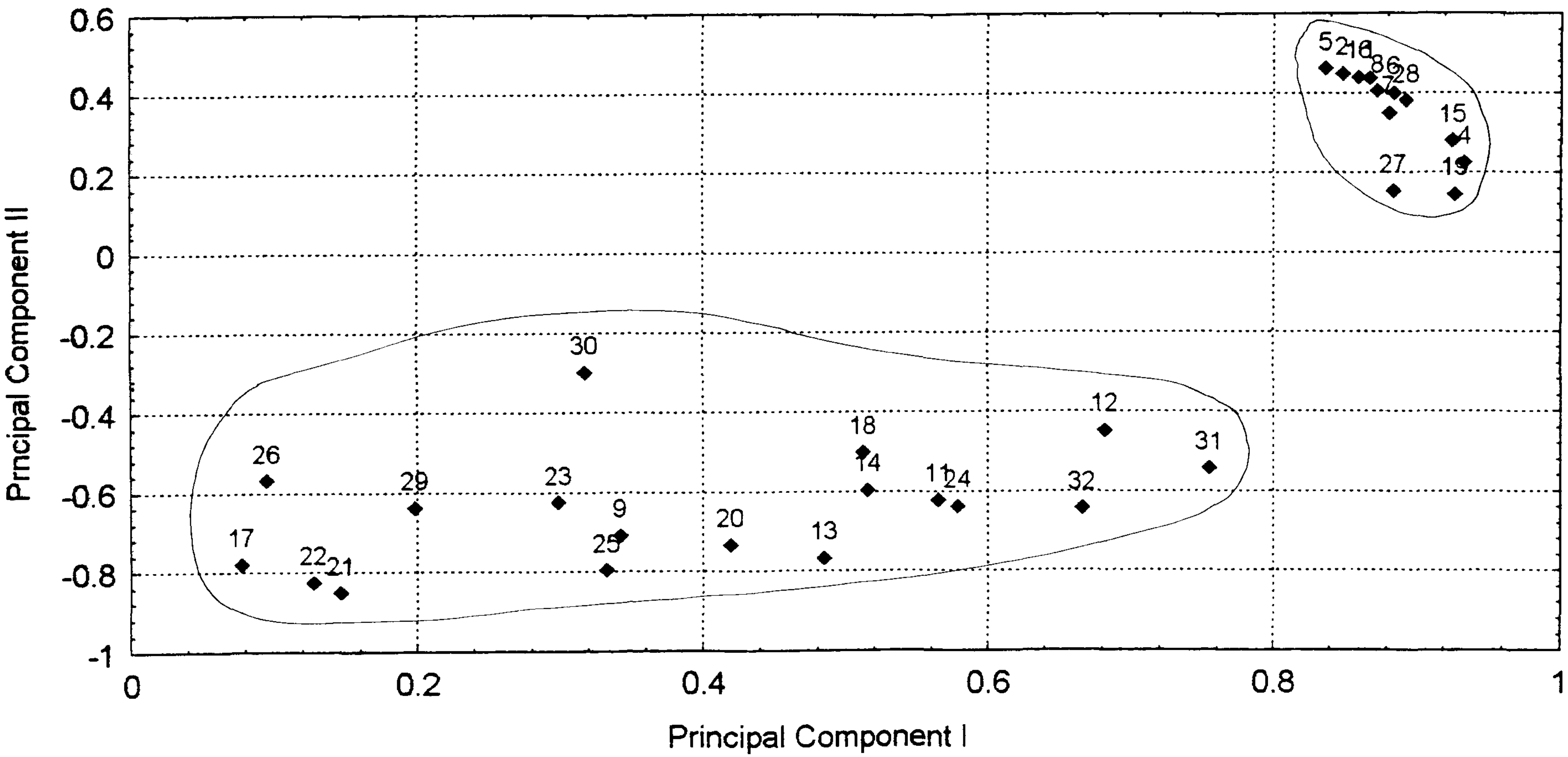


Fig. 24. Clustering of 32 species of dung beetles using principal components analysis of 14 variables charaterising their occurrence across dung age and sampling date.

As many as 144 pairs (29.03%) recorded zero values and 342 pairs (68.95%) recorded 0 - 0.5. Together they accounted for 97.98 per cent of all possible pairs of species. Among the remaining 10 species, seven recorded values of 0.5 - 0.6, one pair > 0.6 and only two pairs recorded a complete overlap value of 1.00. These pairs were *Onthophagus* sp. H & *Onthophagus* sp. P and *Onthophagus* sp. I & J, comprising of species with only one or two beetles. It is likely that low abundances among the samples is a limitation for understanding their segregation. Barring this limitation, two dimensions of the resource considered appear to be sufficient for allowing the segregation of dung beetles of MDF, so that they can co-exist.

#### 4.4.3.3 Clustering of species on the basis of two dimensions

Using the data distribution of 32 species generated for dung age and sampling dates, avoiding the duplications, an attempt was made to generate a scatter plot of 32 species (Fig. 24). The scatter plot indicated two possible clusters. One of the clusters contained 14 species represented by 15 or more individuals. The second cluster, with a sparse distribution of individuals consisted of 18 species, all represented by 10 or less number of individuals. Clearly the primary segregating variable appeared to be their overall abundances.

PC I explained 45.2% variance with abundance (3.639) and standard deviation for mean distribution across age of dung (1.19) as the most important variables with the highest factor scores. PC II accounted for 30.28% of the variances with the above two variables again bearing the highest factor scores of 1.624 and 2.488 respectively.

By increasing the dimensions, of resource state, PCA shows lower number of species clusters. Reduction in the number of clear clusters shows that segregation of species is complete and that it may not be possible to identify 'guilds' of dung beetles in the dung beetle community studied, by increasing the number of dimensions of the resource.

## 4.5 Size - weight relationships for Scarabaeinae dung beetles

Four measurements, viz., elytron length, pronotum length, pronotum width and combined length of pronotum and elytron were verified for their association with fresh and dry weights utilizing the data on 232 specimens representing 19 species of dung beetles.

All the four parameters of body size were strongly and positively correlated ($r > 0.77$; $p << 0.01$) on both linear and logarithmic dimensions (Table 12). Therefore, any one of the four selected linear measurements can be used for estimating biomass on either fresh weight or dry weight basis for dung beetles. Fresh and dry weights were also correlated among themselves on both linear and logarithmic dimensions (Fig. 25A).

**Table 12. Intercorrelation matrix between parameters of size and weight for the Scarabaeiane dung beetles. Data is based on 232 specimens collected from Bangalore and B.R.T. sanctuary during March - June 1998. All correlations are significant ($p<< 0.01$). Top right corner represents linear and bottom left corner the double log correlations.**

| | **Fresh weight** | **Dry weight** | **Elytron length** | **Pronotum length** | **Pronotum + Elytron length** | **Pronotum width** |
|---|---|---|---|---|---|---|
| **Fresh weight** | - | 0.99<br>$p<<0.001$ | 0.89<br>$p<<0.001$ | 0.79<br>$P<<0.001$ | 0.86<br>$p<<0.001$ | 0.87<br>$p<<0.001$ |
| **Dry weight** | 0.98<br>$p<<0.01$ | - | 0.87<br>$p<<0.001$ | 0.77<br>$p<<0.001$ | 0.84<br>$p<<0.001$ | 0.86<br>$p<<0.001$ |
| **Elytron length** | 0.96<br>$p<<0.001$. | 0.95<br>$p<<0.001$ | - | 0.94<br>$p<<0.001$ | 0.99<br>$p<<0.001$ | 0.98<br>$p<<0.001$ |
| **Pronotum length** | 0.96<br>$p<<0.001$ | 0.95<br>$p<<0.001$ | 0.93<br>$p<<0.001$ | - | 0.98<br>$p<<0.001$ | 0.97<br>$p<<0.001$ |
| **P ronotal+ Elytral length** | 0.98<br>$p<<0.001$ | 0.97<br>$p<<0.001$ | 0.98<br>$p<<0.001$ | 0.98<br>$p<<0.001$ | - | 0.99<br>$p<<0.001$ |
| **Pronotum width** | 0.98<br>$p<<0.001$ | 0.96<br>$p<<0.001$ | 0.97<br>$p<<0.001$ | 0.97<br>$p<<0.001$ | 0.99<br>$p<<0.001$ | - |

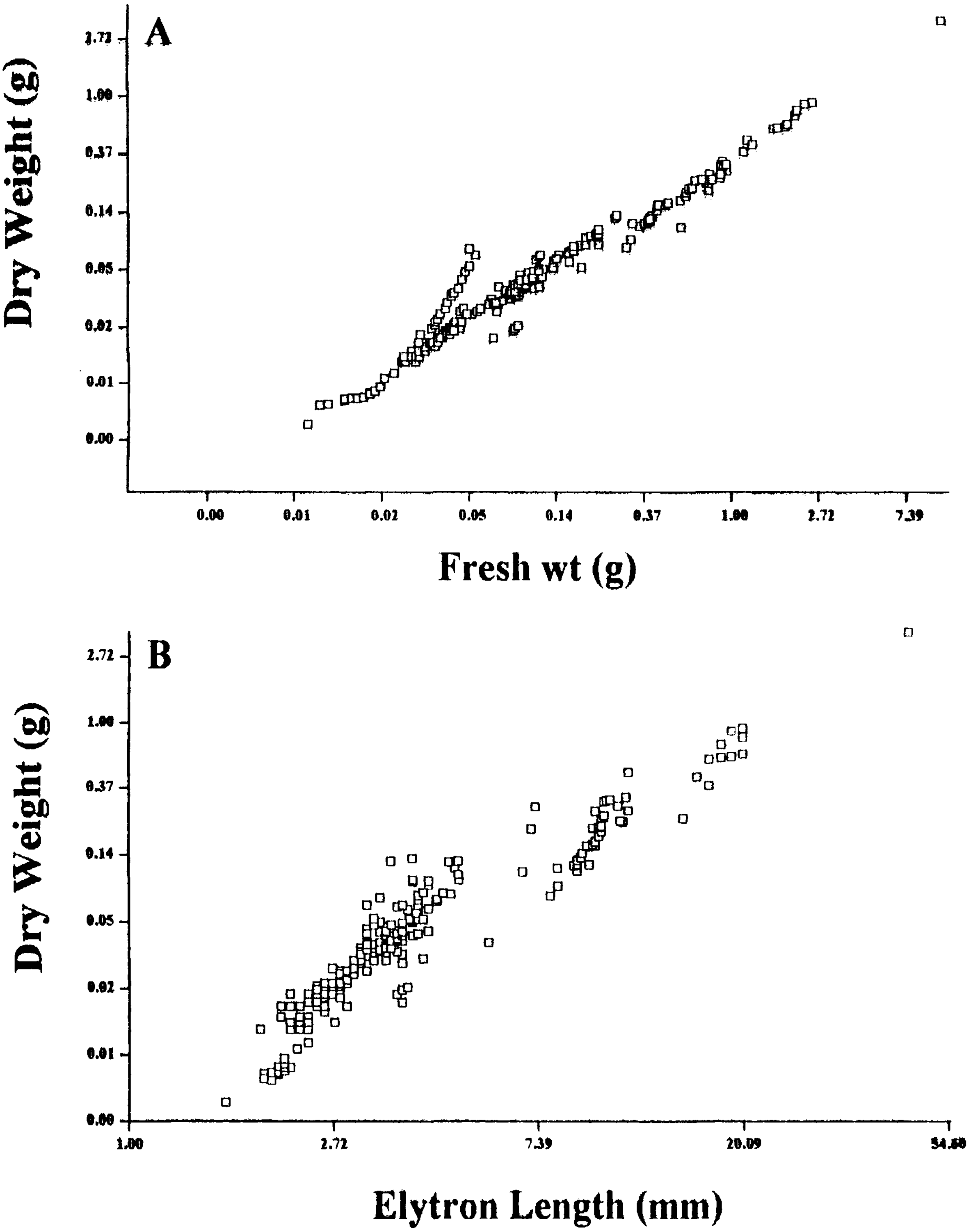


Fig. 25. Relationship between dry weight and fresh weight (A) or elytron length (B) for Scarabaeine dung beetles. Data gathered from 232 specimens collected from Bangalore and Biligiri Rangaswamy Temple sanctuary during 1998.

The power function of the relationship between fresh weight and elytron lengths was :

$$Wt_F = 0.604\ E^{(2.106)}$$

Where

$Wt_F$ = fresh weight of the dung beetles in g. and

E = length of elytron along the mid line measured in mm.

Similarly the relationship between the elytron length and the dry weight (Fig. 25B) was given by

$$Wt_D = 0.844\ E^{(0.054)}$$

where

$Wt_D$ = dry weight of dung beetles in gm and E as mentioned above.

These power functions based on a range of linear dimensions from the smallest species of Scarabaeinae dung beetles *viz.*, *Caccobius meridionalis* Boucomont which measured 1.6 mm in elytron length to a maximum of 45 mm elytron length of *Heliocopris gigas* (L).

# V. DISCUSSION

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## 5.1 Species assemblage of dung beetles at MDF

As many as 61 species of dung beetles belonging to 3 tribes were reported by Veena Kumari and Veeresh (1997b) from Bangalore. Four of these were not found by them to feed on cattle dung. However, Veena Kumari (1984) found only 15 species of dung beetles at MDF, during a year round survey of cattle dung of different ages. Present study revealed 32 species of dung beetles at the same site, Military Dairy Farm (MDF), over a six month study. All these species were of a single tribe Coprini. Among the 15 species reported by Veena Kumari (1984) eight species were of *Onthophagus* genus while the present study revealed as many as 18 species in the same genus. Among the 3 species of *Onthophagus* identified, two, *Onthophagus dama* and *Onthophagus rectecornutus* were also reported by her from MDF. *Caccobius vulcanus*, *Onit. cinctus*, *D. setosus*, *On. phiemon*, *Catharsius molossus* and *Copris repertus* were also common to the two studies while, *C. numa, C. bengalensis, C. sacontala*, *Onit. spinipes* and *O. truncaticarnis* were not reported previously either at MDF or from other parts of Bangalore (Veena Kumari and Veeresh, 1997b). *Liatongus rhadamistus*, although, reported from Bangalore, was not recorded at MDF. Considering the six remaining species of *Onthophagus* in the previous study at MDF, to be among the list of unidentified species of the present study atleast 13 species of *Onthophagus* can be added to the list of dung beetles of MDF. Thus, a total of 20 species of dung beetles are new records for MDF.

However, only five of the identified species in the present study were new records for Bangalore and it is possible that all the 18 species of *Onthophagus* collected at MDF and yet to be identified are known previously from Bangalore. Therefore adding five species to the list of 61 dung beetles reported by Veena Kumari and Veeresh(1997), Bangalore has 66 species of dung beetles from among the 360 species reported from India (Appendix I).

### 5.2 Diversity across pats and days

The primary features of dung beetle occurrence in the community at MDF revealed a maximum 10 and 11 species of dung beetles to occur in any given pat and given day respectively. Consequently any mechanism relevant to avoidance of competition among so occurring species perhaps operates on this assemblage of 10 - 11 species. Very high standard deviations (section 4.2.1 and 4.2.2) observed for the number of beetles per pat or per day suggests aggregative distribution of the beetles. Although, aggregation across individual species were not addressed on pat to pat basis, the above observation is a sufficient evidence to suggest high variance in the distribution of dung beetles across resource patches. This data coupled with low mean species observed per pat and per day, clearly suggest the possibility of getting and variance-covariance dynamics to be the ordering force in the organism of dung beetle community of MDF (Hanski, 1991a). However, variance-covariance for the species involved are needed to be worked out after carefully ascertaining the sampling units to be selected for such a study. But, the structure of present data set (maximum of 3 pats per day) does not permit a meaningful evaluation of these mechanisms. Therefore, large scale sampling of dung beetle communities spread across different sessions is required for more detailed analysis of variance and covariance in the distribution of species of dung beetles in and around Bangalore. Thus, the present analyses provides a broad indication of the possibility of lottery, variance-covariance dynamics to be underlying mechanism for the organisation of dung beetle communities. Unweighted mean diversity for both Shannon's and Simpson's indices were low on pat to pat and day to day basis. However, the ranges of these indices were considerably high. This was possibly because as much as nearly 33% of the species of the community were encountered in single pats or a single day while many pats and many days of the sampling were free of beetles (sections 4.2.1 & 4.2.2). Such detailed studies on the dung beetle abundance, species richness and diversity indices have not been reported previously to document pat to pat or day to day variation in India. In fact virtually such detailed studies are lacking for any community of insects in India. The documentation of dung beetle communities which hopefully pave the ways for addressing conceptual issues in community ecology using the dung beetle as model system.

### 5.3 Diversity pattern across age of dung

Age of dung was found to have a significant impact on number of species, number of individuals and the diversity of dung beetles recorded at MDF in general a declining trend was observed for all the above parameters with increasing dung age. Data considered across pats ( Table 3), days of sampling (Table 4) and overall pooled data (Table 5) all depicted similar patterns.

Many previous studies have also indicated a similar declining trend in abundance, species richness and diversity with the age of dung (Mohr, 1943; Valiela, 1974; Koskela & Hanski, 1977; Veena Kumari, 1984). Dung may be removed in part or consumed by organisms that inhabit it. In addition, drying results in encrustation on the surface of the pat resulting in effective loss of quantity of dung (Veena Kumari, 1984; Doube, 1991). Therefore, it appears that quantitative loss of available dung may have influenced the observed drop in abundance of beetles on pats of increasing age. However, if the quantity in itself is a limitation, the decreasing abundance can be explained on this factor alone. But, for this to be true, the 32 species of dung beetles encountered at MDF should occur randomly in dung of all ages and a priori there is no reason to suspect that large many species should occur only in early age categories of the dung. Only four species were encountered at all ages of the dung sampled (Table 10; Fig. 9 to 12) and the remaining 28 species were not encountered on all days and indeed on most of the days sampled, indicating the preference of these beetles to certain specific age of the dung. Consequently it appears that the quantity of the dung remaining in the pat does not affect the beetle abundance and species richness with age. Alternatively, dung is known to lose moisture with age. The loss of moisture may make the dung less friable. Dung also tends to be less odorous with age (Evans, 1975) indicating reduced biological activity, particularly microbial activity which may attract less and less beetles. Activity of insects and other organisms within the dung, may change the physio-chemical properties of the dung. In essence with age, the dung undergoes a qualitative change. This change appears to be the primary reason that has contributed for the observed reduction in the abundance and diversity of beetles. Similar conclusions were drawn by previous worker (Valiela,1974; Southwood, 1977; Veena Kumari 1984).

More importantly, Koskela & Hanski (1977) and Hanski (1987) suggested that dung may undergo a series of successional changes with respect to the fauna it supports. They identified 3 phases: The first phase of rapid turnover of species lasting for two days. The present study also indicated the rapid turnover route to last for two days as one day old dung attracted 19 species and the two day old dung attracted 23 species in all, adding in the process seven species to the earlier 19. But Koskela and Hanski (1977) also reported a further period approximately one week, which they reffered to as the stable phase and then an indefinite third phase. However, the present study clearly revealed addition of new species upto one week of dung age and next 8 days also recorded the repetition of species. Nonetheless, upto the 10 day old dung, the overall species abundance tended to fluctuate and also 12 to 15 days old dung recorded a constant number of five species each. It is not clear how having this static situation would remain. Thus, the results strongly support the possibility of species turnover upto 10 days of dung age, although new species are not added beyond seven days of age. Therefore, Koskela and Hanski's (1977) classification does not seem to hold under South Indian conditions. Further, the present study, appears to have insufficient data to into the possibility of such a classification. Irrespective of these considerations, the study clearly shows dung age as an important factor in regulating the abundance, species richness and diversity of dung beetles. The changes in the quality of dung with age might be the major contributing factor for the above observations.

## 5.4 Seasonal variations in diversity patterns

Phenology of any insect is expected to be strongly tied with the seasons. Dung beetles are no exceptions to this. But, dung beetles are different from many other insects, primarily because many species exhibit prolonged adult activity (Hanski & Cambefort, 1991c) thus, different kinds of phenological patterns can be expected from dung beetles. On the contrary, long adult life may favour reduced impact of seasonal associative features on their phenology. This aspect has been extensively examined in many different ecosystems of the world. The results are unequivocally in favour strong season based phenological trends for dung beetles of that exhibit both short (one month or less) and long (one year or more) adult life span (Hanski & Cambefort, 1991b). Although the duration of the present study was limited to only six months, considerable variation was noticed between the 12 samples with respect to abundance, species richness and diversity.

Both species richness and abundance were low during the 19 May sampling, while the maximum were observed during 4 April sampling for both these parameters (Table 6) according to patwise comparisons. The mean diversity indices were observed to be low almost throughout the sampling period and the maximum range in diversity between the pats were observed during the 4 April, sampling as also the mean maximum diversity for pat, both by Shannon's and Simpson's measures.

The pattern was similar on per day basis. Highest range in number of species recovered per day was on 4 April, 5 May, 6 and 25 June, samplings (Table 7). However , the mean maximum per day was observed during the 4 April sampling. Highest range in the number of individuals recorded per day was during 6 June sampling and the maximum per day was observed in 4 April sampling. However, the highest range in diversity was observed during the 26 July sampling. The mean maximum diversity per day, both by Shannon's and Simpson's indices were again on 4 April.

The data, pooled over the sampling bout indicated 8 to 18 species per sampling bout (Table 8). The addition of species was observed during II April and I May fortnight samplings in the beginning. Again during June and July more species were observed in the collections. The last four samples did not yield any species. Thus,it appears most, if not all, of the species occurring in MDF, Bangalore are encountered during the course of sampling. It is important to stress that as against report of 15 species at the same location by Veena Kumari (1984) which was based on a year round survey, the present study indicated as many as 32 species of the dung beetles during the six months of survey.

What was striking in these studies is the lack of pattern in the occurrence of beetles, with respect to number of species, number of individuals or diversity indices. This may be because as pointed out by Koskela and Hanski (1977) and Hanski and Cambefort (1991c), the dung beetle abundance, species richness and the diversity are largely influenced by the prevailing weather conditions at any time of the year.

Veena Kumari (1984) observed that the highest number of coprophagous species to be present in Bangalore during June - July with a clear single peak. The basis for this data (the sampling technique) was not clear from her studies, as the data depicted upto 55 species and the systematic sampling done at MDF and at UAS dairy by her indicated only 33 species. The present study did not depict any such peak when systematic sampling was done from April 14 to October 5. However, the possibility of a peak during the above mentioned months cannot be ruled out as these encompass the maximum rainy months at Bangalore.

### 5.5 Partitioning the variance in dung beetle diversity

A comparison of the weighted and unweighted means for Simpson's index calculated for different levels of sampling clearly indicated the disparity between the two approaches (Table 9).

Weighted means for Simpson's index have been recommended as indicators of variance by Joshi *et al.*, (1997). The variance was observed to be maximum for diversity of dung beetles at the pat level. As much as 55.6 per cent of the variance was explained by pat to pat variation and the next highest level of 11.0 per cent was explained by the data pooled according to age of dung. The community as a whole explained only 87.8 per cent indicating the possibility of certain extraneous unaccounted factors. Such a pattern of the lowest sampling unit to explain most of the variance is not uncommon and Joshi *et al.*, (1997) reported that the smallest sampling unit in a linear transect survey of plants accounted for more than 75 per cent of the variance when four higher grades of pooling the data were attempted. Thus, the observed results suggest that the variance explained by a sampling level may possibly be a function of species - area curves for the individual groups of organisms.

### 5.6 Characteristics of the community of dung beetles at MDF

The six months of sampling efforts at MDF yielded 32 species of which as many as 12 species were extremely rare (less than 5 individuals) and five species were rare (<10 individuals). Again among the remaining species, only eight species contributed for more than 50 individuals (Fig. 2A). Clearly, the observed patterns fit most of the communities. Rare species accounting for large proportions is not uncommon among dung beetles (Hanski and Cambefort, 1991a). Further, the body size distribution (Fig. 4.1B) of the dung beetles of MDF followed the typical pattern observed for dung beetles from Africa and South America (Hanski and Cambefort, 1991c). The gaps in the distribution towards the largest size and peaks in smaller sizes followed by little uneven distribution in the range of body sizes was demonstrated in rollers, tunnellers at both species and genus level grouping for dung beetles by

Hanski and Cambefort (1991a). The present observations also confirmed the results of their studies with respect to the relationship between body size and abundance among dung beetle communities. As shown by them, there was no relationship between the body size and abundance of species (Fig. 3) even in the dung beetle community of MDF.

Number of species recovered in any community is expected to be influenced by the sampling effort. A verification of this aspect by checking for the relationship between the numbers of individuals encountered and the consequent recovery of species yielded linear correlations (Fig. 4). Although, the relationship was not found to be valid when data was pooled according to sampling dates, the other observed relationships were strong enough to point to this possibility. Such an attempt at examining the species recovery by sampling effort is widely prevalent in ecological studies of different communities (Magurran, 1988). However, such studies were not observed for dung beetle community (Hanski and Cambefort, 1991). The present study thus,appears to be the first of its kind for dung beetles of the subfamily Scarabaeinae.

Similarly, the relationships between the number of individuals and the diversity or the number of species and the diversity index are lacking on communities of dung beetles. The present effort has shown that the diversity is possibly a function of number of individuals (Fig. 5), but is definitely a function of number of species that constitute a community (Fig. 5) of dung beetles. Many previous studies that examined this relationship have clearly indicated the diversity, irrespective of the measure employed, to be a function of species (Magurran, 1988). It is all the more meaningful for both Shannon's and Simpson's measures of diversity were observed to be strongly related at all levels of pooling the data (Fig. 7). Similar strong correlations between the Simpson's and Shannon's indices have been recorded for different communities of plants and animals (Magurran, 1988).

The idea of core-satellite hypothesis, is largely based on geographic representation of species. Species that are widely represented geographically are reffered to as 'core' while those that are geographically restricted in their distribution are called 'satellites' (Hanski, 1982). Representation of the 32 species of dung beetles at MDF when pooled across sampling units either across numbers of age categories of dung or sampling bouts in which they are represented clearly indicated bimodal distributions (Fig. 8A). Obviously, some species are indifferent to age categories of dung while a few are indifferent to time of sampling. A good majority were sensitive to the age or sampling time and tended to occur in restricted numbers (<2) of sampling units. Therefore, the data clearly points to a logical extension of core and satellite species hypothesis on resources state and temporal scales. Thus the present study is the first demonstration of the possibility of existence of core and satellite species along these two dimensions.

More interestingly, temporal core species also appear to be the core species along the dimension of resource state. Because, the correlation between the frequency of occurrence across 12 age categories of cattle dung and 12 sampling dates considered for the 32 dung beetle species at MDF was found to be positive and highly significant (Fig. 8B). On the basis of these results, *O. dama*, *O. truncaticornis*, *Onit. cinctus*, *Onit. spinipes*, *O. philemon* and *C. repertus* can be considered as the core species of dung beetles at MDF. More detailed studies on their morphological behavioural and biological features in comparison with a few satellite species would be enlightening to appreciate the causes for a species to become core or satellite in a community.

### 5.7 Resource partitioning across age of dung

Literature on dung beetles is replete with their classification according to functional groups. The ecology of each of these groups are generally addressed separately as they are expected to constitute distinct guilds. The four primary categories are rollers, tunnelers, endocoprids and cleptocoprids (Doube, 1991; Hanski and Cambefort, 1991). Rollers, cleptocoprids and some tunnelers are known to get attracted to fresh dung, while some tunnelers and endocoprids may be capable of colonising dung of different ages. Rollers, for sure, were not encountered at MDF, as all the rollers belong to the tribes Scarabaeini and Sisyphini. Coprini consists of all the tunnelers, endocoprids and cleptocoprids. Such a classification of Indian species is lacking. Consequently, the 32 species encountered at MDF could not be categorised into tunnelers, endocoprids or cleptocoprids. Thus the present discussion on the dung beetle community is independent of this categorisation.

Nevertheless, dung of a specific age can constitute a resource state and all species that are utilising it by rolling away, burying or by any other mechanism are competing for the same resource. Abundance patterns are perhaps the best indicators of resource utilisation. Thus the four guilds of dung beetles identified at the MDF represent the extent of utilisation of dung of different age categories (Section 4.4.1.1). As stated above similar grouping has been attempted on the basis of functional groups by several workers (Hanski and Cambefort, 1991a). Further, the largest and the smallest species predominate the fresher dung. Largest species are likely to be fast burying tunnelers while many of the smallest species may be cleptocoprids (Doube, 1991). Large many species being small, it is difficult to gauge their possible functional roles in the cattle dung. However, the loss of these size categories of beetles in older dung signifies their inability to utilise older dung. Therefore, the persistent species may be either slow burying tunnelers or endocoprids (dwellers: Doube, 1991). Irrespective of these considerations, the fact that the four distinct occurrence patterns can be identified in dung of different age categories clearly point to the possibility of understanding the mechanisms that allow variability in exploiting dung of different ages. Similar classifications of dung beetles are completely lacking on dung beetles of India. Further, the observations help to separate out groups that can be addressed individually to understand the mechanisms of resource partitioning in detail, while the present study established four broad categories of exploitation of cattle dung by dung beetles.

More importantly, distribution of species by their niche breadths calculated on the basis of their ability to exploit dung of different ages, suggested nearly 25 per cent of the species to exhibit total isolation with zero niche breadth and only three species exhibited the near maximum possible niche breadth (Fig. 14A). This was further substantiated by the fact that large many species were well segregated along the gradient of dung age from one another as over 77 per cent of species pairs exhibited niche overlap values of less than 0.5. Further, as Hanski and Cambefort (1991c) have pointed out the species that exhibited complete overlap were all rare species. Thus, their overlap may not have great significance in organising the community. Further, it is likely that such species might depend on totally different resource as cattle dung is only one of the many possible resources for Scarabaeines (Arrow, 1931).

Although on the basis of visual observations, four different guilds could be identified, attempts to develop a comprehensive structure for the guilds using principal component analysis yielded three possible clusters from 32 species. The first of these clusters consisted of species from the second and third guilds identified previously.

The second cluster consisted of species from first , second and third 'guilds'. The species from the first and the fourth 'guilds' were represented in the third cluster. Thus, only the fourth guild was completely represented in the third category and no 'guild' was unique to any of the three clusters identified. A clear basis was difficult to make out for the three observed clusters as of now. More detailed analysis by eliminating individual parameters may help to understand the meaning of these clusters better.

The PCA, has been used previously in the study of dung beetle communities (Doube, 1991; Hanski and Cambefort, 1991c) to understand the pattern of resource segregation. However, no attempt has been made to identify ecological units of species but has been used for identifying the factors that contribute most for structuring the communities of dung beetles.

Veena Kumari (1984) also attempted the segregation of species of dung beetles at MDF. But she made comparisons of niche-overlap between pairs of species using body weights and also grouped species for comparison arbitrarily as possible guilds and did not provide a sound reason for the grouping of species. *A priori* there is no reason to believe that body weights may have a role to play in dung beetle ecology. As dung beetle communities are always loaded with many species within a small range of body size (Hanski and Cambefort, 1991c).

More importantly, identification of guilds is a questionable aspect in most dung beetle communities as little is known about 'what eats what' within the dung (Hanski, 1987). Therefore, the attempt in the present study to identify the guilds is based on the relative abundance of a species across age categories of cattle dung.

### 5.8 Partitioning of resources across time

Various kinds of seasonal patterns have been identified for dung beetle communities. The major types involve abundance pattern, breeding schedules and switching in food habits (Hanski and Cambefort, 1991c). The present study, however addressed only the abundance pattern in a structured sampling schedule at MDF. Similar study was carried out by Veena Kumari (1984), at MDF, over a period of one year. However, she did not attempt a detailed study on abundance patterns of individual species and their consequences for resource partitioning.

Four clear distribution patterns could be identified for the 32 species of dung beetles at MDF (see section 4.4.2.1) largely based on representation across time frame and in abundance. These visual classifications were based on their distribution patterns (Figs. 16 to 19). The possibility of such grouping clearly showed that species vary in their exploitation of cattle dung and each group serves to indicate the manner in which the concerned resource is being exploited along the temporal dimension. However, the grouping or the seasonality of dung beetles at MDF was not influenced by their body sizes.

Seasonality of dung beetles has been attributed for two major reasons. One, the changes in weather factors and the consequent influence on the soil moisture (Hanski and Cambefort, 1991c; Gill, 1991; Davis, 1995). Secondly the changes in the quality of dung and consequently the changes in the ability of dung beetles to exploit it (Macqueen *et al.*, 1986). These two aspects were not investigated in the present study. However, considerable variations observed in the abundance and composition of species of dung beetles (Table 8) suggests a significant role for an unidentified factor that did not have a discernible pattern. One such possible factor is the rainfall.

Irrespective of these considerations seasonality or temporal segregation of species of dung beetles was shown by several workers to be the major factor in resource partitioning (Hanski and Cambefort, 1991; Doube, 1991).

In order to verify this possibility, niche breadths of all the 32 species were calculated using their occurrence pattern across the 12 sampling bouts (Fig. 21A). More number of species (12 species) exhibited zero niche compared to the niche breadth calculated across age categories of dung. Further, the remaining species exhibited a tendency to spread out across other class intervals and fewer species exhibited higher values for niche breadth. As an apparent offshoot of this distribution, the distribution of niche overlap categories demonstrated a steeper declining trajectory compared to the niche-overlaps based on the age categories of dung. As many as 88 per cent of the 496 pairs of species recorded niche overlap values of less than 0.5 and the eleven pairs that exhibited complete overlap were all among the rare species. Thus the resource partitioning across temporal scale seems to be much stronger than the scale of resource state (age of dung) for the dung beetle community at MDF.

This was also evident from the fact that as many as four apparent clusters could be identified from the PCA based on the secondary parameters developed from individual species distributions across sampling dates. Cluster 1 was made up of beetles represented by visual groups, two, three and four; cluster 2 was made up of beetles from the first and fourth visual groups; cluster 3 contained elements of first, third and fourth visual groups while the category 4 contained members of visual groups one and four. However, four clusters could not be clearly categorised. Detailed analyses are necessary to understand the reasons for mix up in the two kinds of groupings generated.

### 5.9 Resource partitioning along two dimensions

Dung beetle species at MDF were found to get distributed more evenly across the different class intervals of niche breadth. When two dimensions *viz.*, age categories of dung and sampling dates were considered together (Fig. 23A). Coupled with a wider niche breadth domain (by the property of the Shannon's index), the segregation of species was expected to be clearer. The distribution of niche overlaps testified to this possibility as nearly 98 per cent of the possible 496 pair of species indicated a niche overlap value of less than 0.5 and nearly 29 per cent of all pairs exhibited zero niche overlap (Fig. 23B). Only two pairs of species, an insignificant proportion, exhibited complete overlap. Again these were pairs of rare species. Thus, if could be demonstrated that although dung beetle community at MDF consisted of 32 species feeding on an apparently single resource - cattle dung - the segregation of the species involved was near complete. Such a clear partitioning of a single resource was possible when only two dimensions were considered for the resource availability.

Attempt to identify possible clusters among these dung beetle species along the two dimensions only indicated two clusters, while three and four possible clusters were evident when a single dimension of the resource availability *viz*, age of dung or sampling date were considered. Although the reasons for this poor clustering was not clear, two facts emerged from this exercise. First, it is likely that by increasing the dimensions for the consideration of a resource state (or a sampling unit), the tendency for clustering together may disappear among the constituent species. In other words, if more dimensions are considered for characterising the community, then it is likely that separation of 'guilds' may disappear and a single set of species may emerge representing the 'global set', where each species is segregated from every other species. Although, the meagre evidence and the availability of data is insufficient to prove this point, biologically the emergence of global set may be meaningful at least in the context of dung beetle species. Then one may ask what are the other possible dimensions? Many possibilities exist. Hanski and Cambefort (1991c) showed that four dimensions *viz.*, food type (dung type), log body size, diel activity and seasonality were more than sufficient to generate a 'global set' of species of dung beetles even when as large a community as that of African Savannas (119 species) is considered.

Secondly, abundance and the standard deviations for mean abundances were the primary characters that accounted for maximum weights along both the axis. Therefore, it is likely that the spatial distribution and abundance may be the primary factors that are regulating the structure of dung beetle communities. This aspect has been repeatedly stressed by Hanski (1987b) and Hanski and Cambefort (1991a). Studies on this aspect are lacking on an insect communities in India.

### 5.10 Size weight relationships for dung beetles

The present study revealed that accurately measurable charecters of dung beetles such as elytron length, pronotum length, combined length of elytron and pronotum and pronotum width can be used for assessing the weights - fresh or dry. All these characters were found to be strongly correlated with both fresh and dry weights. This was becausse the fresh and dry weights were correlated among themselves (Fig. 25A).

In a recent study Ganihar (1997) showed that body lengths of beetles are related to the fresh weights by a power function where the slopes of the double log linear equation was 2.46 for dung beetles, the present study indicated a much lower value of 2.106 (Fig. 25B) that too when only the elytron length was used. The reason for this discrepancy was not clear.

## 5.11 Synthesis

Dung beetles have attracted the attention of man since time immemorial. Perhaps the oldest entomological record is that of *Scarabaeius sacer* from the Egyptian civilisation. Although the reasons for the Egyptian record are differnt (Cambefort, 1991), the dung beetles have attracted the attention of community ecologists due to their sheer size of the assemblages. Dung beetle community are also exceptional in that their resource, the dung pats have no defense against the invaders (Hanski, 1987).

Many different factors have been tested to understand the organisation of dung beetle community, food types, diel activity, log of body size and seasonality have been considered as the most important factors apart from their aggregative distribution. In India Veena Kumari (1984) have studied the seasonality, species richness, dung type colonised, diversity and segregation of species. However, she studied these aspects at the levels coprophagous guild which included many non Scarabaeines.

Present investigation has attempted to describe species assemblage, richness, preference of age of dung, abundance and diversity of Scarabaeinae dung beetles at MDF, Bangalore. Attempts have also been made to broadly charecterised the dung beetles community at MDF. Further, using the occurrence pattern of individual species across age categories of dung and sampling dates, attempts have been made to understand the organisation of dung beetles. This was done by following different approaches. Niche breadth and niche overlap were calculated for all species and species pairs at different levels of sampling. Further, broad groups were identified visually on the basis of their abundance pattern across sampling units - age categories of dung or sampling dates. These groups were considered to present guilds of species. The grouping of these guilds were verified by principal component analyses. However, two methods of grouping did not overlap, suggesting the need for in-depth analyses and larger data sets.

However, considerable segregation of the 32 species of dung beetles encountered at MDF was evident when age categories of dung and sampling dates (seasonality) were considered as two dimensions of resource partitioning.

# VI. SUMMARY

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Dung beetles (Scarabaeidae: Scarabaeinae) are a rich and diverse group of coprophagous insects. These beetles provide important ecosystem services by aiding degradation of animal and human excrement. Extensive studies of dung beetles covering diverse aspects such as taxonomy, zoogeogrophy, biology, behaviour and ecology have been carried out in different parts of the world. However, studies on even the most basic aspects of dung beetles are woefully inadequate from India. The present study carried out on an unused pasture land in Hebbal, Bangalore, is an attempt to understand the organisation of dung beetle community associated with cattle dung.

Sampling for dung beetles in an unused pasture land at MDF, Hebbal, Bangalore led to identification of an assemblage comprising 32 species of dung beetles associated with cattle dung. Five species were added to the faunal list of dung beetles of Bangalore.

Thirty one dung pats (laid out as baits in pasture land) were sequentially sampled over a period of 15 days to represent 12 dung age categories. This sampling cycle was repeated 12 times over a period of six months to yield data on a total of 372 pats. Data on number of species and number of individuals encountered in each of these dung pats was analysed to understand patterns of diversity across pat, day of sampling, age of dung and date of sampling and resource partitioning.

The pooled data from 372 pats, revealed interesting patterns in diversity at level of individual pats, day of sampling, age of dung and season (time of sampling). The mean (± s.d.) number of dung beetle species encountered was 1.69± 2.01, 3.0 ± 2.92, 12.75 ± 6.52 and 13.25-± 2.98 on per pat, per day, age of dung and sampling date respectively. The number of individuals encountered per pat and per day also showed a similar high mean to variance ratio suggesting aggregated distribution pattern of both species and individuals.

A closer examination of diversity pattern across dung age revealed that highest mean number of species (4.5 ± 2.35 per pat) and mean number of individuals (21.04 ± 19.9 per pat) were recorded for one day old and two day old dung,respectively. The mean Shannon diversity index was 1.15 ± 0.56 per pat for any dung age category. There was a continuous decline in the number of species, number of individuals and diversity from 2 day old dung to 15 day old dung. Although not significant, there was an increase in the number of individuals on 2 day old dung. However, the highest Shannon diversity index was recorded from 8 day old dung. The lowest index of 0.04 ± 0.16 was recorded for 12 and 15 day old dung. These results underscore the importance of dung age in determining the structure of dung beetle communities associated with cattle dung. Season or sampling also had a discernible influence on species compositon and diversity. The mean number of species recorded per pat ranged from 0.77 ± 1.28 to 3.1 ± 2.56 and the mean number of individuals recorded per pat ranged from 1.87 ± 5.13 to 9.35 ± 9.86. The Shannon index ranged from 0.13 ± 0.37 to 0.78 ± 0.64. None of these parameters had any correlation with 12 different sampling dates over a period of six months; nevertheless indicated sufficient changes in the composition from one sampling date to other. The variation in the species composition across the sampling hierarchy was sought to be understood by partitioning the variance across respective sampling hierarchy. The Simpson's index which has been recently shown to approximate variance was employed to establish the hierarchy of variance in diversity. The mean Simpson's index (weighted) for the four sampling levels, viz., pats, days, dung age, sampling date and the entire community was 0.556, 0.593, 0.703, 0.792 and 0.878,respectively.

Weighted means for Simpson's index showed that as much as 55.6 per cent of variance in dung beetle occurrence could be explained on the basis of differences between pats. Dung age accounted for 11.6 per cent variance while the day of sampling accounts for only 3·7 per cent of variance. The relative abundance of species followed a characteristic `hollow curve' with many species being represented by one or very few individuals. However, the overall abundance of species was independent of their body size. A strong positive correlation between number of individuals and the number of species was observed at three levels *viz.*, pat, days and dung age. The number of individuals and number of species in a sample were observed to strongly influence the diversity index and the two diversity indices *viz.*, the Shannon's index and the Simpson's index were strongly correlated.

How are 32 species of dung beetles able to co-exist on a single and apparently homogenous resource like cattle dung? An attempt was made to answer this question by analysing the data to reveal segregation patterns in the species across two variable, viz., the age of dung and season (sampling date). At the simplest level the occurrence pattern of species across dung age and sampling date was used to identify `guilds' of co-occurring species. Frequency of occurrence across dung age and sampling date was used to qualitatively rank the species. Four `guilds' of species were identified according to occurrence across age with 8, 13, 7 and 4 species respectively. The four guilds based on occurrence across sampling date had 12, 3, 5 and 12 species, respectively. Alternatively, the frequency of occurrence of species in sampling units was found to be distributed bimodally and the species occurring in two modes can be identified as satellites and core species respectively at both sampling hierarchies namely dung age and sampling date.

The data on occurrence of dung beetles across age of dung and date of sampling were used to compute niche breadth and niche overlap. Only 3-4 species were found to have high niche breadth and more than 60 per cent of species pairs had an overlap of <0.05 for both dung age and sampling dates as separate dimensions. Computation of niche breadth and overlap along the two dimensions combined showed that more than 97 per cent of species pairs had an overlap of less than 0.05. Interestingly, the core species tended to have a wide niche breadth and the rare satellite species tended to have greater overlap.

A more rigorous quantitative approach, using multivariate statistics was attempted to identify clusters of species. A principal components analysis of the data for dung age could delineate three clusters and a similar analysis for sampling date yielded four clusters of species. However, the pooled data for both dung age and sampling date could separate out the species into only two categories.

The results of the present study have established diversity patterns of dung beetles across sampling hierarchy. Further two clear lines for future investigations have been established. First, the biological and ecological correlates of the 'guilds' of species need to be established. Secondly, the 'guilds' themselves can be investigated in detail for resource partitioning and niche segregation.

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# APPENDIX - I

# APPENDIX I

## DUNG BEETLES OF BANGALORE

| Sl. No. | Species | Veena Kumari (1997) | This study |
|---|---|---|---|
| | **Tribe Scarabaeini** | | |
| 1. | *Scarabaeus sanctus* (Fabricius) | + | - |
| 2. | *S. gangeticus* (Castelnau) | + | - |
| 3. | *S. brahminus* Catelnau | + | - |
| 4. | *S. erichsoni* (Harold) | + | - |
| 5. | *Gymnopleurus cyaneus* (Fabricius) | + | - |
| 6. | *G. spilotus* (Macleay) | + | - |
| 7. | *G. koenigi* (Fabricius) | + | - |
| 8. | *G. dejeani* Castelnau | + | - |
| 9. | *G. gemmatus* Harold | + | - |
| 10. | *G. miliaris* (Fabricius) | + | - |
| | **Tribe Sisyphini** | | |
| 11. | *Sisyphus crispatus hirtus* (Wiedemann) | + | - |
| 12. | *S. longipes* (Oliver) | + | - |
| 13. | *S. neglectus* Gory | + | - |
| 14. | *S. hirtus* Wiedemann | + | - |
| | **Tribe Coprini** | | |
| 15. | *Heliocopris bucephalus* (Fabricius) | + | - |
| 16. | *H. gigas* (Linnaeus) | + | - |
| 17. | *Copris signatus* Walker | + | - |
| 18. | *C. repertus* Walker | + | + |
| 19. | *C. fricator* Fabricius | + | - |
| 20 | *C. andrewsi* Waterhouse | + | - |
| 21. | *C. indicus* Gillet | + | - |
| 22. | *C. numa* Lansby | - | + |
| 23. | *C. bengalensis* Gillet | - | + |
| 24. | *C. sacontala* Redt. | | + |
| 25. | *Catharsius molossus* (Linnaeus) | + | + |
| 26. | *C. pithecius* (Fabricius) | + | - |
| 27. | *Onitis philemon* Fabricius | + | + |
| 28. | *O. subopacus* Arrow | + | - |
| 29. | *O. siva* Gill | + | - |

| Sl. No. | Species | Veena Kumari (1997) | This study |
|---|---|---|---|
| 30. | *Drepanocerus setosus* Wiedemann | + | + |
| 31. | *Oniticellus pallipes* (Fabricius) | + | - |
| 32. | *Onit. cinctus* (Fabricius) | + | + |
| 33. | *Onit. spinipes* (Roth.) | - | + |
| 34. | *Caccobius meridionalis* (Boucomount) | + | - |
| 35. | *C. vulcanus* (Fabricius) | + | + |
| 36. | *C. unicornis* (Fabricius) | + | - |
| 37. | *C. inermis* Arrow | + | - |
| 38. | *C. indicus* Harold | + | - |
| 39. | *Onthophagus gazella* (Fabricius) | + | - |
| 40. | *O. rectecornutus* Lansberge | + | + |
| 41. | *O. duportii* Boucomont | + | - |
| 42. | *O. amplexus* Sharp | + | - |
| 43. | *O. ramosus* (Wiedemann) | + | - |
| 44. | *O. dama* (Fabricius) | + | + |
| 45. | *O. pactolus* (Fabricius) | + | - |
| 46. | *O. unifasciatus* Schaller | + | - |
| 47. | *O. turbatus* Walker | + | - |
| 48. | *O. spinifex* (Fabricius) | + | - |
| 49. | *O. quadridentatus* (Fabricius) | + | - |
| 50. | *O. igneus* Vigors | + | - |
| 51. | *O. truncaticornis* | - | + |
| 52. | *O. pygmaeus* (Schaller) | + | - |
| 53. | *O. tarandus* (Fabricius) | + | - |
| 54. | *O. centricornis* (Fabricius) | + | - |
| 55. | *O. laevigatus* (Fabricius) | + | - |
| 56. | *O. ludio* Boucomont | + | - |
| 57. | *O. pusillus* (Fabricius) | + | - |
| 58. | *O. tritinctus* Boucomont | + | - |
| 59. | *O. ephippioderus* Arrow | + | - |
| 60. | *O. kchatriya* Boucomont | + | - |
| 61. | *O. gratus* Arrow | + | - |
| 62. | *O. abrewi* Arrow | + | - |
| 63. | *Phalops divisus* (Wiedemann) | + | - |
| 64. | *Liatongus rhadamistus* (Fabricius) | + | + |
| 65. | *Tiniocellus modestus* Arrow | + | - |
| 66. | *Onthophagus* sp.(18 yet to be identified) | - | + |