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# The Role of Coprophagous Beetles on Dung Decomposition and Enhancement OF Soil Fertility: Effect Of Body Size, Species Diversity and Biomass

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## ABSTRAK

**Peran Kumbang Koprofagus pada Dekomposisi Kotoran Hewan dan Kesuburan Tanah: Pengaruh Ukuran Tubuh, Keragaman Species dan Biomasa**. Penelitian ini bertujuan untuk menganalisis pengaruh keragaman species, ukuran dan biomassa kumbang koprofagus dalam merombak kotoran hewan dan meningkatkan kesuburan tanah. Percobaan dilakukan menggunakan Rancangan Acak Lengkap dengan perlakuan jumlah dan panjang tubuh spesies kumbang koprofagus. Peubah tergantung yang diamati adalah persentase kotoran yang terdekomposisi dan kadar bahan organik serta N,P,K total tanah sebagai indikator kesuburan tanah. Hasil penelitian menunjukkan bahwa persentase kotoran hewan yang terdekomposisi lebih dipengaruhi oleh ukuran dan biomassa kumbang yang terlibat dibandingkan dengan jumlah spesies. Persentase kotoran yang terdekomposisi berkorelasi positif dengan ukuran kumbang koprofagus. Kadar N,P,K total tanah meningkat mengikuti jumlah kotoran hewan yang terdekomposisi yang mengindikasikan bahwa aktifitas perombakan kotoran hewan oleh kumbang koprofagus berpengaruh positif terhadap kesuburan tanah.

**Kata kunci:** *Kumbang koprofagus, komposisi spesies, dekomposisi, kesuburan tanah*

## INTRODUCTION

Coprophagous beetles (Coleoptera: Scarabaeidae) have important ecological roles related to nutrient cycling. Removing and burying dung, either for adult feeding or for oviposition and subsequent feeding of the larvae (Hanski & Cambefort 1991) have important ecological consequences in terms of ecosystem functions such as soil fertilization and aeration (Mittal 1993), increased rates and efficiency of nutrient cycling as well as plant nutrient uptake and yield (Miranda *et al.* 1998; 2001), control of pest flies and enteric parasites of vertebrates (Thomas 2001), and secondary seed dispersal of seeds defecated by frugivorous vertebrates (Andresen 2002; 2003).

Recently, Losey & Vaughan (2006) estimated that the annual value of ecological services provided by native insects in the United States to be more than $ 57 billion including $ 0.38 billion through dung burial activity by coprophagous beetles.

Decomposition of dead organic matter, such as carcasses, leaf litter or dung, is a dynamic process that involves a complex array of physical, chemical and biological interactions that complete the biogeochemical nutrient cycles. This process is largely performed by microbes, but the soil fauna has an important stimulatory role. Insects participate in the decomposition processes, breaking apart or consuming organic matter, and enhancing decomposition rates (Sanchez *et al.* 2004).

The diversity of coprophagous beetles is high (i.e. nearly 5000 species only from subfamily Scarabeinae). They show a pronounced variation in body size and strategies for utilizing dung (Doube *et al.* 1988; Hanski & Krikken 1991; Davis & Scholtz 2001). Both may influence the effectivity of dung processing. Dung burial is the initial step to most of the beneficial functions of tropical coprophagous beetles and has related to the body mass of species in laboratory studies (Doube *et al.* 1988; Doube 1990). Both the amount of dung consumed and the dung burial rate positively correlated with coprophagous beetle size (Lee & Peng 1981; Doube 1990). However, our knowledge on the roles of tropical coprophagous beetles on dung removal as well as the effect on soil fertility is very limited.

This study aimed to analyze the role of some coprophagous beetles species collected from Lore Lindu National Park on dung decomposition and soil fertility. Specifically, the following questions were addressed: (1) How does dung burial activity differ between tropical coprophagous beetle species?, (2) Which traits of coprophagous beetles explain best their importance for dung processing; species richness, size, or biomass (3) How does dung burial activity effect on soil fertility.

## MATERIAL AND METHODS

### Collection of beetles used in laboratory experiments

Coprophagous beetles were collected alive from natural forest, agroforestry systems and open area from February to March 2006 in the vicinity of Toro at the western margin of Lore Lindu National Park in Central Sulawesi. Dung beetles were collected using pitfall trap baited by cattle dung modified from Larsen & Forsyth (2005). Cattle dung was one of the most effective bait for colleting dung beetles, besides human dung (Jankielsohn *et al.* 2001, Shahabuddin *et al.* 2005a, Shahabuddin *et al.* 2005b).

### Laboratory decomposition study

The experimental studies to quantify the effects of coprophagous beetles on dung decomposition and soil fertility were conducted in the green house (t=29$^{o}$C, RH= 67%) of the Agricultural Faculty, Tadulako University, Palu from March to May 2006. Coprophagous beetles were placed in a bucket (height = 30 cm, diameter = 20 cm) filled with silty loam soil (sand = 36.5%, silt = 53.4%, clay = 10.1%) on which fresh cow dung (fresh weight: ca.170 ± 2.2 g, dry weight: 34.8 ± 2.8 g) was placed. All buckets were covered by gauze to avoid beetles from escaping and to prevent others beetles colonizing the dung.

**Effect of body size of coprophagous beetles on dung decomposition**

To analyze the effect of body size on dung decomposition, eight coprophagous beetle species of various sizes were selected. In all experiments the dung in the buckets was exposed to two individuals of the same species. Per species four replicate experiments were conducted. All beetles were removed from dung and soil after 9 days of dung exposure. Furthermore, body size of specimens was measured with calipers accurate to 0.1 mm. After exposing them to 80$^{o}$C for 48 hours, dry weight was measured using a digital scale (Sartorius MC 410 S) accurate to 0.0001 g (Jankielsohn *et al.* 2001).

To estimate the amount of decomposed dung, the remaining dung piles were weighted after drying them at 100°C for five days (Sanchez *et al.* 2004). The amount of dung removed or consumed by beetles was estimated by the difference between the mean dry weight of 170 g fresh cow dung not exposed to coprophagous beetles (n=8) and the dry weight of the dung exposed to coprophagous beetles.

**Effect of species richness on dung removal and soil fertility**

To quantify the effect of coprophagous beetle species richness on dung decomposition, the number of beetles used for artificially colonizing the dung

**Table 1**. Experimental design to test the effects of species richness and size of coprophagous beetles on dung removal (each treatment: n=4).

| Species[1] | Mean body length ± S.D. (mm) | Treatment<br>1 small (s) species | <br>1 large (l) species | <br>2 species (1s+1l) | <br>4 species (2s+2l) | <br>8 species (4s+4l) |
|---|---|---|---|---|---|---|
| *Aphodius* sp. | 5.2 (±0.95) | | | | 2 ind | 1 ind. |
| *Copris saundersi* HAROLD | 18.5 (±0.64) | | | | . | 1 ind. |
| *C. macacus* LANSBERGE | 12.7 (±1.47) | | | | | 1 ind. |
| *C. punctulatus* WIEDEMANN | 12.8 (±1.49) | | | | 2 ind. | 1 ind. |
| *Onthophagus limbatus* (HERBST) | 6.2 (±0.96) | 8 ind. | | 4 ind. | 2 ind. | 1 ind. |
| *O. ribbei* BOUCOMONT | 10.5 (±0.52) | | | | | 1 ind. |
| *O. scrutator* | 6.5 (±0.55) | | | | | 1 ind. |
| *O. wallacei* | 13.6 (±0.61) | | 8 ind. | 4 ind. | 2 ind. | 1 ind. |
| Total biomass (g) | | 0.072 | 0.779 | 0.426 | 0.524 | 0.904 |

[1] species with body length > 10 mm represent large beetles (l), d" 10 mm small beetles (s)

was standardized to eight individuals while the number of species varied between one and eight following the experimental design presented in Table 1. Four replicates were conducted for each treatment resulting in a total of 24 treatments.

To analyze the effects of dung burial activity on soil fertility, the nutrient content of soil below the dung artificially colonized by coprophagous beetles was analyzed. Soil samples were taken four weeks after coprophagous beetles were placed on the bucket. The two control treatments were (1) soil without dung and coprophagous beetles (control 1) and soil with dung but no coprophagous beetles (control 2).

N total, P total, K total, C/N ratio and total organic content (%) were used as indicator for soil fertility. Soil analyses were conducted by the Laboratory Analytic of Agricultural Faculty Tadulako University and the STORMA laboratory unit in Palu. The total N of soil was measured following Kjeldahl methods, total organic phosphor (P) and potassium (K) were quantified by extraction using concentrated hydrogen chloride (HCL 25%). Furthers P and K concentrations were determined by Spektrofotometer UV-VIS and. Atomic Absorption Spectrometer, respectively. Total C organic in soil was quantify using method develoved by Walkley & Black. Later on, organic matter of soil was estimated through multiplying the organic C value by Van Bemmelen factor 1.724 (Sparks *et al.* 1996).

Kruskal-Wallis (KW) nonparametric analyses followed by pairwaise comparisons of means were used to test the effects of body size, species richness and biomass on dung decomposition quantified as the percentage of removed dung (Zar 1999). Additionally, relation between number of decomposed dung and soil fertility were analysed using Spearman's or Pearson's Correlation depend on the data distribution (Zar 1999).

## RESULTS

### Effect of beetle sizes on dung removal

The size and dry weight of eight species selected for the experiments as well as amount of dung removed are given

**Table 2**. Mean body length (±S.D.) and dry weight (±S.D.) of coprophagous beetles species as well as amount of dung removed (±S.D.) after 9 days

| Species | Body length (mm) | Dry weight (g) | Decomposed dung (%) |
|---|---|---|---|
| *Copris saundersi* | 18.48(1.92) | 0.47(0.18) | 55.09 (5.43) |
| *Onthophagus wallacei* | 14.01(3.04) | 0.10(0.02) | 35.42 (4.86) |
| *C. macacus* | 12.74(0.79) | 0.11(0.11) | 35.26 (5.00) |
| *C. punctulatus* | 12.49(0.77) | 0.15(0.15) | 32.35 (7.65) |
| *O. ribbei* | 10.49(0.54) | 0.06(0.06) | 25.59 (9.35) |
| *O. scrutator* | 6.48(0.55) | 0.01(0.01) | 18.23 (4.22) |
| *O. limbatus* | 6.78(0.84) | 0.01(0.00) | 14.34 (4.31) |
| *Aphodius* sp. | 5.23(0.81) | 0.002(0.00) | 13.28 (3.09) |

in Table 2. Percentages of removed dung significantly related to the size of coprophagous beetles involved (KW-$H_{7,31}$ = 24.71, $p$ < 0.01). The largest percentage of decomposed dung was recorded for the largest beetle species (*C .saundersi*) while the smallest amount of dung was decomposed by the two smallest species (*O. limbatus* and *Aphodius* sp.) (Figure 1).

The size of beetles positively correlated to the percentage of removed dung (Spearman's $r = 0.88, p < 0.001$).

**Effect of species richness and biomass on dung removal**

The amount of dung removed differed significantly between coprophagous beetle species assemblages (KW: $H_{(4,20)}$=14.28, $p$ < 0.01). However the percentage of dung removed did not relate to the number of species involved. The largest amount of dung was removed when the dung was exposed to only one, but the largest species. The lowest amount of dung was removed when the dung was exposed to the smallest species. Species assemblages, which consisted of 2, 4, and 8 species, decomposed intermediate amounts of dung. In general, the percentage of dung removed did not relate to the number of species involved (Figure 2).

In contrast, the percentage of removed dung positively correlated with the total biomass of coprophagous beetles (*Spearman* r = 0.55, $p$ < 0.05). These results indicate coprophagous beetle biomass as a better predictor for dung removal than species richness of coprophagous beetles.

**Dung decomposition and soil fertility**

There was a significant effect for all treatments on the total content of Nitrogen (one-way ANOVA: $F_{(5,18)}$ = 5.36, $p$<0.01), phosphor (one-way ANOVA: $F_{(5,18)}$ = 79.0, $p$<0.001) and potassium (one-way ANOVA: $F_{(5,18)}$ = 2443, $p$<0.001) of soil. While other indicators of

**Table 3.** Mean soil nutrient content of Nitrogen (N), Phosphor (P) and Kalium (K) as well as the C/N ratio and organic content after 4 weeks (n=4).

| Treatment | Soil nutrient content | | | | |
|---|---|---|---|---|---|
| | N total (%) | $P_2O_5$ (mg/100 g soil) | $K_2O$ (mg/100 g soil) | C/N ratio | Total organic content (%) |
| Control 1 (no dung and beetles) | 0.160[b] | 12.280 [e] | 12.268[f] | 9.205 | 2.531 |
| Control 2 (no beetles) | 0.164[b] | 13.793 [de] | 14.270[e] | 9.188 | 2.589 |
| 1 L | 0.179[a] | 20.830 [a] | 27.505[a] | 8.859 | 2.735 |
| 2 (L+S) | 0.169[ab] | 18.242 [b] | 24.100[b] | 9.086 | 2.645 |
| 4 (L+S) | 0.167[ab] | 16.175 [c] | 20.565[c] | 9.149 | 2.635 |
| 8 (L+S) | 0.166[b] | 14.178 [d] | 15.682[d] | 9.173 | 2.626 |

Differents letter in the same column indicate significant differences between means Tukey HSD Test (á=0.05). For treatment abbreviations see Table. 1.

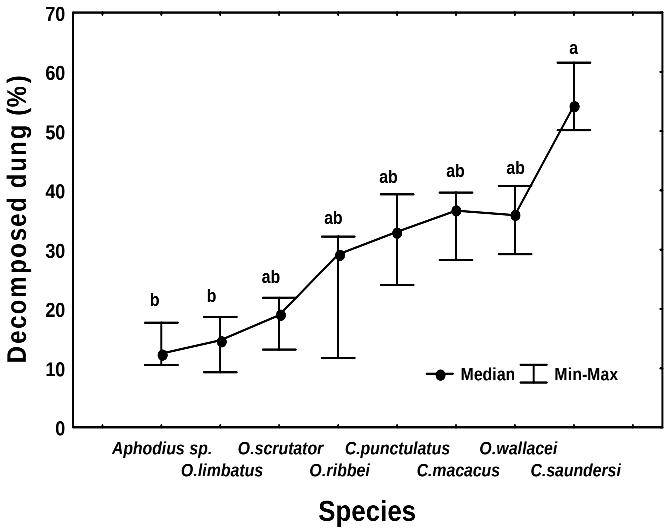


**Figure 1.** Percentage of dung decomposed by several coprophagous beetles species after 9 days. Ranking of species is based on their body size from small (left side of x-axis) to large size (right side of x-axis). Different letters indicate significant differences using Kruskal-Wallis All-Pairwise Comparisons Test (α=0.05).

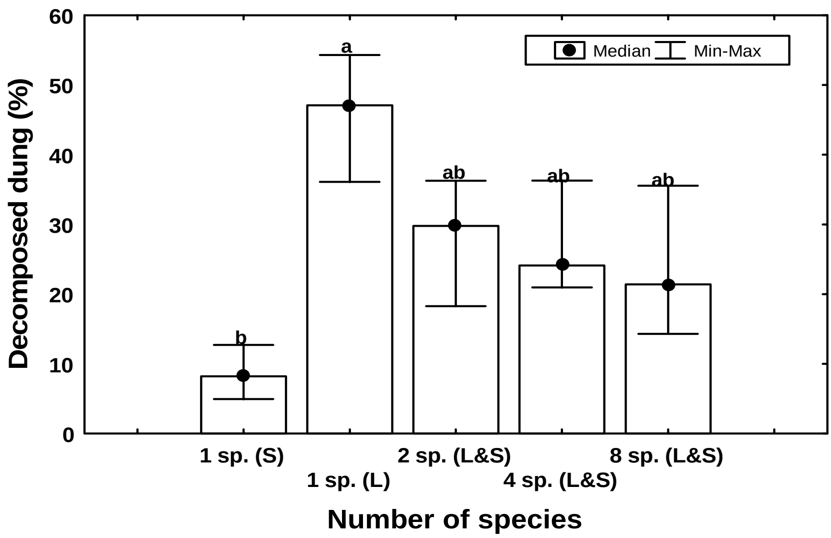


**Figure 2.** Percentage of dung decomposed by different coprophagous beetle number after 9 days. Different letters indicate significant differences using Kruskal-Wallis all-pairwise comparisons test (á=0.05). For treatment abbreviations see Tab. 1.

soil quality, the C/N ratio and the total organic content, different not significantly between treatments

The highest content of N, P and K was recorded for soil on which surface dung was exposed to only one large coprophagous beetles species (treatment 1L), followed by treatments with 2, 4, and 8 species beetles, respectively. In all these treatments N, P and K contents of the soils were higher than in the control without dung and with dung but no beetles (Tab. 3).

### Soil nutrient content and dung removal

As expected, dung burial activity has a significant effect on soil nutrient contents. The total content of N P and K in the soil was positively correlated with the percentage of dung removed (N: Spearman's $r = 0.56$, $p < 0.05$, n=16; P: Spearman's $r = 0.60$, $p < 0.05$, n=16; K: Pearson's $r = 0.71$, $p < 0.01$, n=16) indicating the significant contribution of dung burial activity for maintaining soil fertility.

## DISCUSSION

The present study showed a significant contribution of coprophagous beetles to dung decomposition. Body size and biomass were the best predictors for the amount of removed dung, while the number of species involved was just of minor importance. The larger the size of coprophagous beetle species, the higher the amount of dung they are able to remove. This result corresponded to previous studies, which reported that the amount of dung consumed and the burial rate positively correlated with coprophagous beetle size (Lee & Peng 1981; Doube 1990; Mittal 1993; Larsen *et al*. 2005). Furthermore, Horgan (2005) emphasized that dung decomposition in the field is best predicted by the biomass and not by the species richness of coprophagous beetles. However, in the present study the highest amount of dung was not removed by beetles representing the highest biomass.

The body size of beetles involved in dung decomposition showed the strongest relationship with dung removal while biomass and species richness were less important. It is known that there is a high interspecific competition between coprophagous beetles for dung resources although their way in utilizing dung varies to avoid competition potential (Hanski & Cambefort 1991). However, competition between species may reduce the importance of species richness and biomass. To quantify such kind of effects, additional experiments should be conducted using varied number of specimens per species across a wider range.

With respect to the diversity-ecosystem function hypothesis, these results did not support the *rivet hypothesis*, which stated that the provided ecological service a group of species is increasing with species number. However this study should not be taken as evidence of functional redundancy since the present study excluded natural variability by standardizing dung pads where the type and volume of dung as well as the dung exposure time did not vary. In the field, species might respond functionally to natural variability in resource patches (i.e. Rosenfeld 2002). The *keystone species* hypotheses (Mills *et al*. 1993) may better explain the results of the present study. The large species (particularly large tunnellers) had the most significant effect on dung decomposition. Therefore, the rate of dung removal highly depending on the existence of this group. Recent field studies also reported that the contribution of the large tunnellers in dung removal was significantly higher compared to the other groups of coprophagous beetles, large beetle species are functionally more efficient than smaller ones. The loss of these species may cause a significant decrease in function (Larsen *et al*. 2005). Consequently, in natural ecosystems the amount of dung decomposed by beetle communities consisting of many larger species is most likely to be higher than those removed by communities consisting of mostly small species. Even when smaller species has a similar biomass, large beetles are more effective since they remove dung faster than smaller ones.

The surface layer of most cultivated soils contains between 0.06 and 0.5 % N. The total of P concentration in soils is generally between 2000 and 5000 mg P kg $^{-1}$ with an average 600 mg P kg$^{-1}$, while the total K content of soils ranges from 3000 to 100.000 mg K kg ha$^{-1}$ in the upper 0.2 m of the soil profile (Sparks *et al*. 1996). A higher amount of removed dung corresponded to a higher concentration of soil nutrients represented by N, P, and K. The total N obtained from all treatment was in low level category (Anonim 1980). Nonetheless, the treatment without dung and coprophagous beetles was significantly lower than the soil with dung and large beetles. While the existence of coprophagous beetles could increase the level of P total from low to intermediate as well as the K total from intermediate to high level (Anonim 1980).

This result clearly demonstrated the importance of dung burial activity by coprophagous beetles in increasing soil fertility. Omaliko (1984) also reported that dung decomposition increased concentrations of nitrogen, photassium, phosphor, magnesium and calcium of soil up to 42-56 days after dung exposure. Furthers, dung burial activity altered environmental conditions, reduced pH of dung, sped it incorporation into the soil and greatly reduced loss of Nitrogen as ammonia gas ($NH_3$) (Yokohama *et al*. 1991).

Dung burial activity proved to be not only important for maintaining or increasing soil fertility (see Wilson 1998, Miranda *et al*. 1998), but also has several other advantages such as enhancing total nitrogen and phosphorus of plants as well as its yield (Miranda *et al*. 2001), improving plant regeneration through dungseed dispersal activity by coprophagous beetles (Andresen 2002; 2003), reducing parasite populations on dung (Tyndale-Biscoe & Vogt 1996; Thomas ML 2001) and increasing plant palatability by reducing plants fouled with dung (Fincher 1981; Gittings *et al*. 1994). Therefore, in natural ecosystems the reduction of coprophagous beetle populations most likely has cascading and longterm effects throughout the ecosystem (Klein 1989; Larsen *et al*. 2005).

## CONCLUSION

This study indicated that coprophagous beetles had a significant contribution to dung removal activity. Additionally, they showed that size of coprophagous beetles has a stronger effect than biomass and species number on dung removal. Larger species removed more dung than the smaller ones indicating the functional importance of large species for dung decomposition. Furthermore, the soil nutrient contents (N, P, K) positively correlated with the percentage of removed dung indicating the high importance of dung burial by coprophagous beetles for soil fertility. In conclusion dung burial activities differ between tropical coprophagous beetles and it was mainly depend on the size and biomass of dung beetles involved on dung decomposition.

## REFERENCES

Anonim. 1980. *Pemetaan Tanah dan Survei Lingkungan*. Term of Reference Type B. Lembaga Penelitian Tanah. Jakarta.

Andresen, E. 2002. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology* 27: 257-270.

Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26(1): 87-97.

Davis, ALV & CH Scholtz. 2001. Historical vs. ecological factors influencing global patterns of scarabaeine dung beetle diversity. *Diversity and Distributions 7:* 161–174.

Doube, BM., PS. Giller, & F. Moola. 1988. Dung burial strategies in some South African coprine and onitine dung beetles (Scarabaeidae: Scarabaeinae). *Ecological Entomology* 13: 251–261.

Doube, BM. 1990. A functional classification analysis of the structure of dung beetle assemblages. *Ecological Entomology* 15: 371–383.

Fincher, GT. 1981. The potential value of dung beetles in pasture ecosystems. *Journal of the Georgia Entomological Society* 16: 301-316.

Gittings T, PS. Giller & G. Stakelum. 1994. Dung decomposition in contrasting temperate pastures in relation to dung beetle and earth worm activity. *Pedobiologia* 38: 455-474.

Hanski, I & Y. Cambefort, editor. 1991. *Dung beetle ecology*. Princeton University Press. Princeton.

Hanski, I & J. Krikken. 1991. *Dung beetles in tropical forests in South-East Asia*. In: Hanski, I. & Y. Cambefort, (eds.), *Dung Beetle Ecology*. Princeton University Press. Princeton.

Horgan, FG. 2005. Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slopes of the Peruvian Andes. *Forest Ecology and Management* 216: 117–133.

Jankielsohn, A., CH. Scholtz, & S. Louw. 2001. Effect of habitat transformation on dung beetle assemblages: A comparison between a south african nature reserve and neighboring farms. *Environmental Entomology* 30 (3): 474-483.

Klein, BC. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* 70: 1715-1725.

Larsen, TH & A. Forsyth 2005. Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica* 37(2): 322–325.

Larsen, TH., NM. Williams, & C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8: 538–547.

Lee, JM. & YS. Peng 1981. Influence of adult size of *Onthophagus gazella* on manure pat degradation, nest construction, and progeny size. *Environmental Entomology* 10: 626–630.

Losey, JE. & M.Vaughan. 2006. The economic value of ecological services provided by insects. *Bio-Science* 56 (4): 311-323.

Mills, LS., ME Soul & DF Doak. 1993. The Keystone Species Concept in Ecology and Conservation. *BioScience*, 43 (4): 219.

Miranda, CHB., JC. Do Santos & I. Bianchin. 1998. Contribution of *Onthophagus gazella* to soil fertility improvement by bovine fecal mass incorporation into the soil. 1. Greenhouse studies. *Rev. Brasil. Zootec.* 27: 681-685.

Miranda, CHB., JC. Do Santos & I. Bianchin. 2001. The role of *Digitonthophagus gazella* in pasture cleaning and production as a result of burial of cattle dung. *Pasturas Tropicales.* 22 (1):14-18.

Mittal, IC. 1993. Natural manuring and soil conditioning by dung beetles. *Tropical Ecology* 34: 150-159.

Omaliko, CPE. 1984. Dung decomposition and its effects on the soil component of a tropical grassland ecosystem. *Tropical Ecology* 25: 214-220.

Rosenfeld, JS. 2002. Functional redundancy in ecology and conservation. *Oikos* 98: 156–162.

Sanchez, MAB., AA.Grez & JA Simonetti. 2004. Dung decomposition and associated beetles in a fragmented temperate forest. *Revista Chilena de Historia Natural*. 77: 107-120.

Shahabuddin, Schulze CH, Tscharntke T. 2005a. Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures. *Biodiversity and Conservation* 14: 863–877

Shahabuddin, Hidayat P, Noerdjito WA, Manuwoto S. 2005. REVIEW: Penelitian Biodiversitas Serangga di Indonesia: Kumbang Tinja (Coleoptera: Scarabaeidae) dan Perannya dalam Ekosistem. Biodiversitas *Journal of Biological Diversity* 6 (2): 141-146

Sparks, DL., AL. Page, PA. Helmke, RH. Loeppert, PN. Soltanpour, MA.Tabatabai, CT. Johnston & ME. Summer. 1996. Methods of soil analysis Part 3. Chemical methods. Soil Science Society of America, Inc. Madison USA.

Thomas, ML. 2001. Dung beetle benefits in the pasture ecosystem. NCAT Agriculture Intern. www.attra.org/attra-pub/PDF/dungbeetle.pdf [Januari 2003].

Tyndale-Biscoe, M. & WG. Vogt 1996. Population status of the bush fly and native dung beetles in south-eastern Australia in relation to establishment of exotic dung beetles. *Bulletin of Entomological Research* 86: 183-192.

Yokohama, K., H. Kai, & H. Tsuchiyama. 1991. Paracoprid dung beetles and gaseous loss of nitrogen from cow dung. *Soil Biology and Biochemistry* 23 (7): 643-647.

Wilson, J. 1998. A summary of interaction in Dung beetle-soil-plant relationship. http://www.esb.utexas.edu/wilson/Bot394/index.htm.

Zar, JH. 1999. *Biostatistical Analysis. 4th edition*. Prentice-Hall Inc. New Jersey.USA