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Are fungivorous Scarabaeidae less specialist?

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Abstract. In a tropical forest patch of Southeastern Brazil, adult Scarabaeidae beetles were used to test the hypothesis that fungivorous guilds have a higher proportion of generalist species than either frugivorous, necrophagous or coprophagous ones. No significant differences were found between guilds in relation to either the proportion of generalists or niche breadths of the component species. Only two fungivorous specialist species were sampled. These results indicate that sporocarps eaten by Scarabaeidae are not as rare as literature suggests. Fungi may help maintain high species diversity of Scarabaeidae in tropical forests.

[Keywords: mycophagy, fungivory, dung beetles, food resource, rainforest]

Resumen. ¿Son los escarabeidos fungívoros menos especialistas?: En un fragmento de bosque tropical en Minas Gerais, sureste de Brasil, se estudió la proporción de generalistas en escarabajos adultos de la familia Scarabaeidae. A partir de los resultados obtenidos, se rechazó la hipótesis de que el gremio de los fungívoros de escarabeidos adultos tendría una mayor proporción de generalistas que los gremios frugívoro, necrófago o coprófago. No se encontraron diferencias significativas entre los gremios, ni en relación a la proporción de generalistas, ni en la amplitud de nicho de sus especies componentes. Solo dos especies fungívoras especialistas se encontraron en este estudio. Aunque se trata de un caso puntual, este resultado indicaría que los esporocarpos consumidos por miembros de la familia Scarabaeidae no son tan raros como lo sugiere la literatura. Posiblemente, los hongos ayuden al mantenimiento de la diversidad de Scarabaeidae en bosques tropicales americanos, donde no hay abundancia de excrementos de grandes mamíferos.

[Palabras clave: micofagía, fungivoría, escarabajos estercoleros, recurso alimentario, bosque tropical]

Introduction

Adult stages of Scarabaeidae beetles species, though mainly coprophagous, can be found feeding on a variety of food items such as carrion, rotting fruits and fungi, especially in the Neotropics (Halffter & Matthews 1966). Many Scarabaeidae adults have got a generalist diet, though they may need more specific food resources for nesting. The use of a given food resource by the adult does not mean that it is essential to its survival; an absent resource can be sometimes substituted by another one. Indeed, food generalism is a characteristic of some adult beetles; larvae tend to have a more re-

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stricted diet involving only one resource derived from the nesting material which is not necessarily the same as eaten by the adult. Although in some cases the resource preferred by the adult is different to those used for nesting, such cases are not common (Anduaga & Halffter 1993).

According to Halffter & Matthews (1971), adult Scarabaeidae beetles feed on fluids, or more specifically, on the microorganisms that accompany the putrefaction of the observed resources, a fact that can be deduced from the beetles soft and fragile oral pieces. If the beetles feed predominantly on the microorganisms, their source of microorganisms and the observed resources may be less important than appears at first glance (Anduaga & Halffter 1993).

However, as some Scarabaeidae species feed exclusively on fungi, the latter may represent an important resource for both adults and larvae of Scarabaeidae beetles (Matthews 1972; Cambefort 1984; Anduaga & Halffter 1991; Anduaga 2000).

In the Neotropical Region, the exclusively fungivorous Scarabaeidae species are usually found feeding on the sporocarps of the family Poliporaceae, either decomposing or underground, or on live sporocarps of other groups (Anduaga & Halffter 1991). Although they seem to use decomposing sporocarps in more advanced states of decomposition, there are few studies regarding their preferences (Navarrete & Galindo 1997).

According to Hanski (1991), there may be a trend in fungivorous insects to be more generalist owing to the relative rareness of sporocarps in the field. Finding sporocarps may be time consuming, which would contribute to the assumed high degree of polyphagy in fungivorous insects in general. However, a species using a rare (small abundance) resource may have relatively few individuals so that relatively small quantities of the resource can be sufficient for the entire population.

The aim of this work is to test if the fungivorous guild of Scarabaeids in tropical forest presents more generalist species than coprophagous, necrophagous and frugivorous guilds.

METHODS

The sampling was carried out in Viçosa, Minas Gerais state, Brazil (20°45'S; 42°50'W). The region was originally covered by a mesophilic forest heavily fragmented, creating patches of pasture and cultivated fields. Some of these patches have regenerated into secondary forests during the last decades. The work was carried out on a 300 ha patch regenerated from a coffee plantation.

Sampling was carried out in October 1998 at the beginning of the rainy season. Forty pitfall traps and four types of bait were used: decayed bovine spleen, human dung, rotted banana and an abundant, yet unidentified, mushroom species of the family Tricholomataceae in an advanced state of decay (stage IV of decomposition – following the classification of Navarrete & Galindo 1997). Due to unpredictable availability of the fungal bait and to previous work in the site that showed no seasonal succession of scarabaeids inside the rainy season (Louzada et al., unpubl. data), no temporal replicates were done.

In all traps, bait was placed on ground level protected by a rain cover and the fluid used in its bottom was soaped water with a few formalin droppings, in a quantity not sufficient to alter attraction as evidenced by previous tests. Each trap was placed at a two square meters corner in a set of four traps. Distribution of baits in each set was random, but each square always had the four kinds of bait. Ten trap sets were arranged at thirty meter intervals along a transect. Each trap set presented all four baits with each trap containing only one type of bait. Traps were left in the field for one week. Each trap had a quantity of about 50 g of bait, a standardized size successfully used in several occasions in the area.

Two different analyses were carried out. In the first analysis, the proportion of generalist species in each trap was calculated, considering as a generalist every species caught in more than one type of bait. The proportion of generalist species in each bait type was compared using a generalized model of analysis of variance employing binomial error structure and logit link function (Crawley 2002). The model used considered a nested design in which the baits were nested within each plot. In this approach, a species was considered as generalist when it was caught only once in one bait and many times in only one other bait. The advantage of this approach is that no data transformation is necessary.

In the second analysis, the niche breadth was calculated using the non-standardized Levins' method (Krebs 1989) which is given by:

$$B = \frac{1}{\sum p_j^2}$$

where B is Levins' index of niche breadth and p_j is the proportion of individuals found in the resource j ($\Sigma p_j = 1$). This index has the advantage of differentiating species that use different numbers of resources. The standardized index was not used because it gives similar niche breadth values for species that occur in only one resource and for those occurring in equal abundance in several different resources. In our analysis, the latter are considered to be more generalist than the former.

The niche breadths of the species caught in each bait were compared by a generalized linear model, using normal errors, followed by residual analysis. In order to avoid giving the same weight in the average of rare and abundant species, the total number of individuals was used to weight the abundance of each species. If fungivorous species are generalists, as hypothesized by Hanski (1991), species caught in fungus baits will present larger niches than other guilds.

All analyses were carried out under R (Ihaka & Gentleman 1996) and were followed by residual analyses to check the suitability of the models and error distributions.

RESULTS

Nine hundred ninety two specimens belonging to 33 species in 12 genera were captured (Table 1). The percentage of generalist species (Table 2; $F_{3,36} = 0.47$, $p = 0.71$) and niche breadths (Table 1; $F_{3,64} = 1.53$, $p = 0.21$) were not significantly different between baits. Residual analyses confirmed the models and the error distributions used. This test showed no evidence of a higher proportion of generalist species in the fungivorous guild than in frugivorous, necrophagous or coprophagous ones.

DISCUSSION

An enhanced generalism in species that use fungi as a resource is expected if fungi are a rarer resource than carrion or dung, or if there are no specialist species in the guild. If fungivorous species are specialists, then they have been under sampled in several works of scarab species richness.

Only two species were exclusively collected in the fungus traps: *Canthidium gigas* and *Dichotomius* sp. (both with only one specimen captured). However, this does not prove the exclusive fungivory of these two species when compared to the number of species exclusive to the other tested resources (Table 1). These two species are apparently exclusive fungivorous because they have been also collected several times in flight interception traps, showing that they are not rare. However, in intensive sampling carried out in the same forest patch during 8 years, they have never been collected in traps other than those baited with fungus (Vaz-de-Mello & Louzada, unpubl. data)

In tropical mesophilic forests of Southeastern Brazil, it is easier to find sporocarps than either dung or carrion (pers. obs.), notwithstanding the possibility that the observed large numbers of Scarabaeidae in tropical forests may quickly utilize the latter. Our results suggest that sporocarps are just as abundant as other resources to Scarabaeidae beetles, and are frequently exploited. If fungi are an important and abundant resource, they may equally help maintain the observed high diversity of Scarabaeidae in tropical forests along with other resources such as fruit and carrion studied in the Neotropics (Pereira & Halffter 1961; Anduaga & Halffter 1991; Gill 1991; Louzada & Vaz-de-Mello 1997).

Fungivory in Scarabaeidae may result either from adaptive radiation, or shifting from coprophagy by originally coprophagous species

Table 1. Number of specimens of species collected using banana, carrion, fungus and feces as bait. NB: Levins' non standardized niche breadth.

Tabla 1. Número de ejemplares de especies colectadas utilizando banana, carroña, hongos y heces como cebo. NB: Amplitud de nicho no estandarizada de Levins.

Species	Banana	Carrion	Fungi	Feces	Total	NB
Ateuchus sp.	2	2	3	0	7	2.88
Canthidium sp.1	1	0	1	1	3	3.00
Canthidium sp.2	1	4	10	69	84	1.45
Canthidium sp.3	6	5	6	21	38	2.68
Canthidium prox. *gigas*	0	0	1	0	1	1.00
Canthidium sp.4	0	1	1	0	2	2.00
Canthidium sp.5	71	0	14	0	85	1.38
Canthon ibarragrassoi	0	6	3	0	9	1.80
Chalcocopris hespera	0	2	0	29	31	1.14
Coprophanaeus bellicosus	0	58	0	1	59	1.03
Coprophanaeus jasius	0	2	0	0	2	1.00
Deltochilum morbillosum	0	21	0	1	22	1.10
Dichotomius ascanius	1	0	0	0	1	1.00
Dichotomius assifer	0	26	1	6	33	1.53
Dichotomius fissus	3	0	0	0	3	1.00
Dichotomius luctuosus	0	1	0	0	1	1.00
Dichotomius mormon	0	3	0	5	8	1.88
Dichotomius muticus	0	2	3	11	16	1.91
Dichotomius quadrinodosus	0	2	0	1	3	1.80
Dichotomius aff. *mundus*	43	9	21	7	80	2.64
Dichotomius sp2	0	0	1	0	1	1.00
Eurysternus calligrammus	0	20	0	2	22	1.20
Eurysternus cyanescens	0	16	1	5	22	1.72
Eurysternus parallelus	0	9	0	1	10	1.22
Canthon sp. nov.	0	0	1	8	9	1.25
Deltochilum aff. *pseudoicarus*	0	11	0	0	11	1.00
Ontherus azteca	0	1	0	0	1	1.00
Deltochilum furcatum	2	159	0	16	177	1.23
Sylvicanthon foveiventre	0	0	0	3	3	1.00
Trichillum hirsutum	0	53	0	9	62	1.33
Trichillum sp. nov.	0	1	1	0	2	2.00
Uroxys sp.1	0	0	0	3	3	1.00
Uroxys sp.2	0	2	0	109	111	1.04

occurring after the extinction of most of the large mammals in South America during the Pleistocene. With fewer animals, the availability of mammal dung was greatly reduced. The adaptive radiation idea is supported by the high number of frugivorous and necrophagous species among the neotropical Scarabaeidae when compared to the absolute dominance of coprophagous species in the Palaeotropics, especially Africa, where an equivalent extinction of mammals has not occurred. However, in this case the high proportion of coprophagous species may be a result of collecting bias, as few studies prospected for other resource

Table 2. Number of species trapped and mean percentage of generalists (± SE) per resource.

Tabla 2. Número de especies capturadas y porcentaje medio de generalistas (± ES) en cada recurso.

Resource	Number of species	%Generalists (mean ± ES)
Banana	10	90 ± 16.42
Fungi	15	95 ± 11.47
Carrion	24	91 ± 10.89
Dung	20	96 ± 6.37

users (Walter 1978; Walter 1983; Cambefort 1984). Southeast Asia, where large mammals are scarce, is the only biogeographic region which is comparable, with the presence of many necrophagous beetles (Halffter & Matthews 1966; Gill 1991; Halffter 1991).

Our results also suggest that a higher proportion of fungivorous Scarabaeidae in the Neotropics will be found than in most of the Palaeotropics where the large mammal fauna has not suffered a major extinction.

Further work is necessary to find if some Scarabaeidae show a preference for certain species of fungi to parallel the observed preference of Scarabaeidae beetles for dung of particular mammal species (Halffter 1959).

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REFERENCES

ANDUAGA, S. 2000. Escarabajos coprófagos (Coleoptera: Scarabaeoidea) asociados a hongos en la Sierra Madre Occidental, Durango, México: con una compilación de las especies micetófagas. *Acta Zoológica Mexicana* **80**:119-130.

ANDUAGA, S & G HALFFTER. 1991. Micofagía en Scarabaeidae. Pp. 151-169 e*n:* JL Navarrete-Heredia & GA Quiroz-Rocha (eds.). *I Simpósio Nacional sobre la Interacción Insecto-Hongo. Memórias.* SME, FC-UNAM, IGU. Veracruz.

ANDUAGA, S & G HALFFTER. 1993. Nidificación y alimentación en *Liatongus rhinocerulus* (Bates) (Coleoptera: Scarabaeidae: Scarabaeinae). *Acta Zoológica Mexicana* **57**:1-14.

CAMBEFORT, Y. 1984. Étude écologique des Coléoptères Scarabaeidae de Côte d'Ivoire. *Travaux des Chercheurs de la Station de Lamto* **3**: VIII+294+13 pp.

CRAWLEY, MJ. 2002. *Statistical computing: an introduction to data analysis using S-plus*. John Wiley & Sons (ed). Chichester, England.

GILL, BD. 1991. Dung beetles in tropical american forests. Pp. 221-229 in: I Hanski & Y Cambefort (eds.). *Dung Beetle Ecology.* Princeton University Press. Princeton.

HALFFTER, G. 1959. Etología y Paleontología de Scarabaeinae (Coleoptera: Scarabaeidae). *Ciencia (Mex.)*:**19**:165-178.

HALFFTER, G. 1991. Historical and ecological factors determining the geographical distribution of beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomológica Mexicana* **82**:195-238.

HALFFTER, G & EG MATTHEWS. 1966. The Natural History of dung beetles of the Subfamily Scarabaeinae (Coleoptera-Scarabaeidae). *Folia Entomológica Mexicana* **12-14**:1-312.

HALFFTER, G & EG MATTHEWS. 1971. The Natural History of Dung Beetles. A Supplement on associated biota. *Revista Latinoamericana de Microbiología* **13**:147-164.

HANSKI, I. 1991. The dung insect community. Pp. 5-21 in: I Hanski & Y Cambefort (eds). *Dung beetle ecology*. Princeton University Press. Princeton.

IHAKA, R & R GENTLEMAN. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphics Statistics* **5**:229-314.

KREBS, CJ. 1989. *Ecological Methodology*. Harper & Row. New York.

LOUZADA, JNC & FZ VAZ-DE-MELLO. 1997. Scarabaeidae (Coleoptera, Scarabaeoidea) atraídos por ovos em decomposição em Viçosa, Estado de Minas Gerais, Brasil. *Caldasia* **19** (3):521-522.

MATTHEWS, E.G. 1972. A revision of the Scarabaeinae dung beetles of Australia I. Tribe Onthophagini. *Australian Journal of Zoology, Supplementary Series* **9**:3-330.

NAVARRETE-HEREDIA, JL & NE GALINDO-MIRANDA. 1997. Escarabajos asociados a Basidiomycetes en San José de los Laureles, Morelos, México (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana* **99**:1-16.

PEREIRA, FS & G HALFFTER. 1961. Nuevos datos sobre Lamellicornia mexicanos con algunas observaciones sobre saprofagía. *Revista Brasileira de Entomologia* **10**:53-66.

WALTER, P. 1978. *Recherches écologiques et biologiques sur les scarabéides coprophages d'une savane du Zaïre.* Thèse Docteur d'État, Université des Sciences et Techniques du Languedoc. Montpellier, France.

WALTER, P. 1983. La part de la nécrophagie dans le régime alimentaire des Scarabéides coprophages afro-tropicaux. *Bulletin de la Société Zoologique de France* **108**(3):397-402.