ECOLOGY, BEHAVIOR AND BIONOMICS

First Come, First Serve: "Sit and Wait" Behavior in Dung Beetles at the Source of Primate Dung

Jennifer Jacobs[1], Inés Nole[2], Susanne Palminteri[3] and Brett Ratcliffe[4]

[1]San Francisco State Univ., 1600 Holloway Drive San Francisco, CA 94132, USA; jjacobs@calacademy.org
[2]Univ. Nacional Mayor de San Marcos, Facultad de Medicina Veterinaria, Av. Circunvalación cdra. 29, San Borja, Lima, Peru; inesnole@hotmail.com
[3]Univ. East Anglia, Norwich, Norfolk, NR4 7TJ, UK; spalminteri@earthlink.net
[4]Univ. Nebraska State Museum, W436 Nebraska Hall, Lincoln, NE 68588-0514, USA; bratcliffe1@unl.edu

Neotropical Entomology 37(6):641-645 (2008)

El Primero que Llegue, Primero se Sirve: Comportamiento "Sentarse y Esperar" en los Escarabajos del Estiércol en la Fuente de Excremento de Primate

RESUMEN - Los Escarabajos del estiércol (Coleoptera: Scarabaeidae: Scarabaeinae) compiten intensamente por excrementos, un recurso escaso por el cual muchas especies forrajean en el sotobosque en bosques tropicales. En este artículo describimos el comportamiento particular de una especie de escarabajo del estiércol, *Canthon aff. quadriguttatus* (Olivier), asociado a dos especies de primates en Perú. Observamos esta especie de escarabajo en la región genital y anal de monos "tocones", *Callicebus brunneus* (Wagner), y subsecuentemente cayendo con excrementos que los monos defecaron. De manera similar, observamos individuos de esta especie de escarabajo asociados a monos "huapos", *Pithecia irrorata irrorata* (Gray). Mediante un comportamiento de "sentarse y esperar" a la fuente, *C. aff. quadriguttatus* llega primero a la fuente de excremento y aparentemente supera a otras especies de escarabajos en la competencia por el mismo recurso. Este artículo representa el primer registro de *C. aff. quadriguttatus* en asociación a dos especies de primate en la Amazonía del sureste de Perú. Discutimos este comportamiento en el contexto de competencia y distribución de recursos y especulamos sobre la razón por la cual este escarabajo está asociado a ambas especies de primates.

PALABRAS-CLAVE: Competencia, distribución de recursos, foresia, especialización de nicho

ABSTRACT - Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) compete intensively for dung resources, and most species forage in the understory. Here, we describe the unique behavior of one dung beetle species, *Canthon aff. quadriguttatus* (Olivier), associated with two species of monkeys from Peru. We observed this beetle species on the genital and anal regions of the brown titi monkey, *Callicebus brunneus* (Wagner), and subsequently falling with dung as the monkeys defecated. The same association was also observed with the bald-faced saki monkey, *Pithecia irrorata irrorata* (Gray). Using the "sit and wait" at the source behavior, *C. quadriguttus* may arrive first at the dung resource, possibly out-competing other dung beetle species. This paper is the first report of this behavior for *C. aff. quadriguttatus* on the brown titi monkey and bald-faced saki monkey from southeastern, Amazonian Peru. We discuss this behavior in the context of competition and resource partitioning, and also speculate as to why *C. aff. quadriguttatus* has been found on both monkey species.

KEY WORDS: Competition, resource partitioning, phoresy, niche specialization

Dung beetles play important roles in the decomposition of nutrients stored in herbivore dung, and they are a crucial element for tropical forests in terms of their recycling and seed dispersal abilities (Hanski & Cambefort 1991). Dung beetles are often common, especially in Neotropical forests, where a high number of sympatric species compete intensively for ephemeral resources (Hanski & Cambefort 1991, Herrera *et al*. 2002, Larsen *et al*. 2006). The majority of Neotropical dung beetles opportunistically forage in the understory for mammal dung, though mammal dung in Neotropical forests is limited because there are relatively few large vertebrates (Larsen per. comm., Hanski & Cambefort 1991). Thus, locating a dung resource as quickly as possible is an important foraging strategy, and beetles that first arrive to a dung resource have an advantage over those that later arrive (Herrera *et al*. 2002).

In response to intense competition for limited resources, many species of dung beetles have evolved specialized

niches or behaviors for obtaining food (Larsen *et al*. 2006), including positioning themselves at the source of vertebrate dung. Phoretic behavior of dung beetles on mammals has been described for various genera of dung beetles in different regions of the world. Six species of beetles from the genus *Onthophagus*, possessing modified claws for grasping mammal fur, have been reported on some Australian marsupials (Matthews 1972). These beetles have been observed to drop with feces when the marsupials defecate. It is thought that this phoretic relationship evolved due to the rapid desiccation of dung in the arid Australian environment in combination with widespread marsupial populations (Matthews 1972). In the Neotropics, some species from the dung beetle genera *Uroxys* and *Pedaridium* (formerly *Trichillum*) have been found to inhabit the fur of sloths, where the adult beetles hang onto the fur until the sloth defecates. The beetles then drop with the feces and subsequently use the dung as food or ovipositing material (Halffter & Mathews 1966, Ratcliffe 1980, Howden & Young 1981, Waage & Best 1985). One species from central South America, *Zonocopris gibbicollis* (Harold), is phoretic on large South American ground snails and is reported to exclusively feed on their mucus (Gill 1991, Vaz-de-Mello 2007). Addtionally, *Canthon proseni* (Martínez) was reported on the American tapir, *Tapirus terrestrius* (L.), in Bolivia, though no additional information on dung resource use exists for that account (Pereira & Martínez 1956)

There have also been accounts in the last century reporting dung beetles phoretically associated with monkey species in the Neotropics, but unfortunately the majority of these accounts are vague and do not include much, if any, information on the ecological and behavioral interactions of the beetles and the mammal host. Luederwaldt (1922) reported that the dung beetle, *Canthon* (formerly *Glaphyrocanthon*) *quadriguttatus* (Olivier), was found on recently killed howler monkeys, *Allouatta* sp., in Para, Brazil. Pereira & Martínez (1956) also reported that a closely related dung beetle, *Canthon* (formerly *Glaphyrocanthon*) *subhyalinus* (Harold), was found on the brown titi monkey, *Callicebus brunneus* (Wagner), in Guapore, Brazil. A more recent study conducted by Herrera *et al*. (2002) includes one of the only detailed accounts of phoretic dung beetles on monkeys in the Neotropics. In northeastern Amazonian Perú, Herrera *et al*. (2002) found dung beetles of *Canthidium* sp. near *metallicum* sitting in the fur around the anus of red titi monkeys, *Callicebus cupreus* (Spix), and observed the dung beetles attaching to and dropping with the monkey feces.

Here, we report observations and photo-documentation of what Herrera *et al*. (2002) termed "sit and wait at the source strategy" for *Canthon aff. quadriguttatus* (Olivier) on both the brown titi monkey, *Callicebus brunneus* (Wagner) and the bald-faced saki monkey, *Pithecia irrorata irrorata* (Gray), in southeastern Amazonian Peru.

Material and Methods

Observations of *C. aff. quadriguttatus* associated with brown titi monkeys and bald-faced saki monkeys were made incidental to behavioral and ecological studies of these two monkey species during February-May 2007. All field observations in this study were conducted at the Los Amigos Field Station in Madre de Dios department, Manu province, Peru. Los Amigos field station is located at 12˚34'07"S 70˚05'57"W at 268 masl. The study area is located in lowland Amazonian rainforest with a variety of habitat types, including floodplain forest, upland terra firme forest, bamboo forest, palm swamps, and successional riparian forest (Pitman 2006).

Five family groups of brown titi monkeys and four family groups of bald-faced saki monkeys were studied. Family group size for both monkey species was approximately three to six individuals. Researchers waited below individual family groups on the forest floor to collect freshly defecated monkey dung. Observations of *C. aff. quadriguttatus*, attached to brown titi monkey and bald-faced saki monkeys' fur and genital region, were made both with and without binoculars, and dung beetle specimens were observed and collected from both monkey species' dung. Voucher specimens of *C. aff. quadriguttatus* were deposited in the California Academy of Sciences, USA and in the Museo de Historia Natural Universidad Nacional Mayor de San Marcos in Peru.

Results and Discussion

During the brown titi-monkey study, *C. aff. quadriguttatus* beetles were found in phoretic associations with three of the five family groups. All individuals from one of the five family groups each had a conspicuous load of dung beetles on their fur, and *C. aff. quadriguttatus* beetles were consistently found in their dung immediately after defecation. In this family group, phoretic dung beetles were also observed falling with the dung, and fresh dung was never observed without *C. aff. quadriguttatus*. Each individual monkey from the infested family group dropped approximately 1-3 dung pellets, with between 2-3 individual dung beetles attached to each pellet. For the remaining four titi monkey family groups, only one dung beetle, on a single individual monkey, was observed in two titi monkey family groups. Thus, only one of the five family groups of brown titi monkeys studied had a large number of dung beetles inhabiting the tail and genital region. Initially, we thought these particular monkeys were ill or carrying parasites, but their behavior, diet, size of group, and all other characteristics were normal and no different from other family groups in the area (I. N., unpublished data).

From a distance, the beetles attached to the monkeys appeared as jewels or shiny water droplets (Fig. 1). With binoculars, we clearly identified the shiny objects on the monkeys as dung beetles. We observed many individuals (20+) of *C. aff. quadriguttatus* in the fur above and around the tail area, in addition to the genital and anus region (Fig. 2), on every individual monkey from the infested family group throughout the entire observation period. Photos and binocular observations of dung beetles on the titi monkeys match the species identification of those specimens collected from fresh dung pellets and positively identified by B.C.R. as *C. aff. quadriguttatus* (Fig. 3). The brown titi monkeys did not appear to react to the presence of the dung beetles and were rarely observed removing beetles from their fur, but on

Fig. 1. Brown titi monkey from the infested family group with many *C. guadriguttatus* attached to the fur above the tail. Photo by J. Aben.

Fig. 2. Genital region of a brown titi monkey from the family group infested with *C. guadriguttatus* beetles. Photo by J. Aben.

Fig. 3. *Canthon aff. quadriguttatus*. Photo by B. Ratcliffe.

at least two occasions the juvenile from the populated group was observed picking a dung beetle out of its fur and flicking it off its body. However, the dung beetle was observed flying back onto the monkey.

While bald-faced saki monkeys typically use higher levels of the forest canopy than brown titi monkeys and feed primarily on seeds rather than fruits, *C. aff. quadriguttatus* beetles were also found together with bald-faced saki monkey dung pellets. *C. aff. quadriguttatus* beetles were consistently found on bald-faced saki monkey dung as soon as it fell from the canopy. Individual beetles were also observed around the tail region of monkeys of both sexes and different ages from all four focal groups monitored during the bald-faced saki monkey study. The actual species identity of the phoretic

beetles on the bald-faced saki monkeys was impossible to discern directly in the field due to the great height at which the monkeys occur in the forest. The monkeys were never observed removing the dung beetles from their fur or otherwise reacting to the beetles' presence. One research assistant reported that a fecal pellet from a bald-faced saki monkey, with dung beetles attached, fell directly into his shirt pocket as he was observing the monkeys in the canopy overhead (E. Collado, pers. comm.). These particular beetles were not collected, but all other specimens of beetles collected with bald-faced saki dung were identified as *C. aff. quadriguttatus*. Though the circumstantial evidence of a phoretic association between *C. aff. quadriguttatus* and the bald-faced saki monkeys is strong, clear photographs are needed to confirm the sit and wait behavior of this dung beetle species on bald-faced saki monkeys, as they do for brown titi monkeys.

Our observations at the Los Amigos Field Station provide evidence for a highly specialized behavior by dung beetles in order to rapidly obtain an ephemeral resource in high demand by many organisms. After hours of monitoring family groups of the two monkey species, we observed only *C. aff. quadriguttatus* on the monkeys' fur, and it was this beetle species that was always documented arriving first to brown titi monkey and bald-faced saki monkey dung. Other dung beetle species have been observed on brown titi monkey dung, but they were only seen arriving to the dung after *C. aff. quadriguttatus*. We do not know why many individuals of *C. aff. quadriguttatus* were only observed on one of the five family groups of brown titi monkeys. This family group was utilizing the same habitat as other titi monkey groups and did not exhibit any strange behavior that would suggest the presence of disease. Further studies, including parasite analyses (in progress I.N.), of brown titi monkeys at Los Amigos are necessary to determine why only one family group had a high number of phoretic dung beetles, when the other family groups had few beetles or none at all.

Brown titi monkeys do not interact with bald-faced saki monkeys, because they typically occupy different forest types and levels of the forest canopy, and have distinct foraging patterns and behavior. However, both species of monkeys have long, dense fur and produce dung pellets that are similar in size and consistency. The hardness and size of the titi and saki monkeys' dung pellets appear optimal for a small dung beetle, because the beetle can grasp and fall with the pellet and successfully roll the pellet away without further modification. We hypothesize that two of the reasons *C. aff. quadriguttatus* is found on these different monkey species are the similarities of the monkeys' dung as well as the presence of thick fur providing a substrate to which the beetles can cling. Unlike the phoretic dung beetles from Australia, there are no obvious morphological adaptations in *C. aff. quadriguttatus* that are modified for grasping mammal fur.

The behavior of *C. aff. quadriguttatus* appears exploitative, commensalist, and highly-specialized. *C. aff. quadriguttatus*, along with *C. subhyalinus* and other closely related species of *Canthon*, are probably canopy specialists as suggested by Vaz-de-mello (pers. comm.) and Larsen *et al*. (2006), who trapped *C. aff. quadriguttatus* (*Canthon* sp. 2 in Larsen *et al*. 2006) and *C. subhyalinus* significantly more often at 25 m in the canopy compared to the ground ($t = 9.4$, $P < 0.001$; $t = 3.9$, $P < 0.001$ respectively). However, *C. aff. quadriguttatus* also forages opportunistically because this same species has been collected in pitfall traps baited with human dung placed in the understory and in the canopy (Larsen *et al*. 2006), and unbaited pitfall traps in the understory (J.J.) at the Los Amigos field station. As is the case with some other dung beetle species, *C. aff. quadriguttatus* occurs on several monkey species from different localities (Pereira & Martinez 1956, Halffter & Matthews 1966). The report by Luederwalt (1922), documenting *C. aff. quadriguttatus* on recently killed monkeys, and the revision by Pereira and Martinez (1956) documenting this species on live howler monkeys suggests that *C. aff. quadriguttatus* may also have phoretic associations with howler monkeys (*Alouatta* sp.). The majority of dung beetle species reported on monkeys belong to the genus *Canthon*, with the exception of the study by Herrera *et al*. (2002) documenting primate associations with beetles from the genus *Canthidium*., Many of these *Canthon* are probably closely related, and their taxonomy and systematic position within the genus *Canthon* is currently being analyzed (Larsen pers.comm.,Vaz-de-Mello pers. comm.).

The "sit and wait" strategy of *C. aff. quadriguttatus* may limit interspecific competition, but given the large number of individual beetles that can be present on one monkey (Fig. 1), it may increase intraspecific competition. It is possible that intense competition at the source of dung prevents the majority of individual beetles from obtaining a sufficient amount of resource and discourages other dung beetle species from employing this strategy, or that species such as *C. aff. quadriguttatus* must additionally utilize the more active searching methods typical of other dung beetle species.

Phoretic behavior has been observed in a number of different and distantly related genera of Scarabaeinae and thus has probably evolved more than once within particular lineages (Vaz-de-Mello & Louzada 1997,Vaz-de-Mello pers.comm.). However, the degree to which particular dung beetle species exhibit phoretic behavior varies. Some species of Neotropical *Uroxys* and *Pedaridium* and Australian *Onthophagus* are always or almost always found on their host, but *C. aff. quadriguttatus* and *C. subhyalinus* have often been caught in pitfall traps at various heights within the forest (Larson *et al*. 2006, Vaz-de-Mello pers.comm.), suggesting their arboreal tendencies but not strictly phoretic behavior.

One hypothesis, put forward by Vaz-de-Mello & Louzada (1997) and Louzada (1998), to explain why *C. aff. quadriguttatus* and closely related *Canthon* species have been observed on monkeys is that this phoretic behavior evolved from the ability to perch on leaves in the canopy and forage in a multi-dimensional space, as opposed to only foraging on the ground. Once a group of dung beetles evolved the ability to forage within the canopy and at various vertical levels in the forest, a new niche to exploit dung resources was available for these species. If particular *Canthon* species, those of which are good fliers and forage in the canopy (Vaz-de-Mello & Louzada 1997), are able to fly from various perches throughout the canopy onto which monkey dung has fallen, it is a logical next step that they would learn to fly directly to the source of the dung rather than wait for it to fall.

Primate researchers at the Los Amigos Field Station have reported only one species of dung beetle, *C. aff. quadriguttatus,* on monkeys, and only this species has been observed arriving first to brown titi monkey and bald-faced saki monkey dung. It may be possible that *C. aff. quadriguttatus* "sits and waits at the source" of dung from other species of primates or other mammals such as tapirs or sloths. More investigation is needed to determine how many dung beetle species, especially within the genus *Canthon*, exhibit the "sit and wait" behavior, from which mammal species they obtain dung, and what fraction of the total time spent foraging they employ this strategy. In addition, more rigorous field sampling and phylogenetic hypothesis testing regarding the evolution of phoresy in dung beetles is necessary to help explain the behavior within the context of the Scarabaeinae subfamily. Finally, additional field research is needed to help explain the fascinating biology of *C. aff. quadriguttatus*, such as where their larvae reside and if the adults have other methods for obtaining dung resources. The information described in this study is important for understanding the roles of competition and resource partitioning in the maintenance of high biodiversity in tropical forest ecosystems.

Acknowledgments

We thank Job Aben, Department of Animal Ecology and Ecophysiology, Radboud University Nijmegen, The Netherlands, for providing excellent photos of the brown titi monkeys. We thank INRENA and the Museum of Natural History San Marcos in Lima, Perú for providing the collecting and export permits. Additionally, we thank Fernando Z. Vaz-de-Mello, Edward Connor, Wendy Moore, Rudolf von May, Trond Larsen, and Jeremy Miller for reading drafts of the manuscript and providing helpful comments and suggestions. We thank the Amazon Conservation Association, San Francisco State University, and the ARCS organization for providing us the opportunity and funding to work at Los Amigos.

References

Gill, B.D. 1991. Dung beetles in tropical American forests, p.211-229. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. Princeton University Press, Princeton, New Jersey, 520p.

Halffter, G. & E.G. Mathews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mex. 12-14: 1-312.

Hanski, I. & Y. Cambefort (eds.). 1991. Dung beetle ecology. Princeton University Press, Princeton, New Jersey, 520p.

Herrera, E.R.T., K. Vulinec, C. Knogge, & E.W. Heymann. 2002. Sit and wait at the source of dung – an unusual strategy of dung beetles. Ecotropica 8: 87-88.

Howden, H.F. & O.P. Young. 1981. Panamanian Scarabaeinae: Taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). Contrib. Am. Entomol. Inst. 18: 1-204.

Larsen, T., A. Lopera & A. Forsyth. 2006. Extreme trophic and habitat specialization by Perúvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Coleopt. Bull. 60: 315-324.

Louzada, J.N.C. 1998. Considerations on the perching behavior of tropical dung beetles (Coleoptera, Scarabaeidae). Revt. Bras. Ent. 41: 125-128.

Luederwaldt, H. 1922. Ein *Canthon* (Coleoptera, Lamellicornia. Coprinae) auf Affen. Deutsher Ver. Wiss. Kunst São Paulo 2: 226.

Matthews, E.G. 1972. A revision of the scarabaeine dung beetles of Australia II. Tribe Scarabaeini. Aust. J. Zool. Suppl. Ser. 9: 3-330.

Pereira, F.S. & A. Martínez. 1956. Os generos de Canthonini americanos. Rev. Bras. Entomol. 6: 91-192.

Pitman, N.C.A. 2006. An overview of the lost Amigos Watershed, Madre de Dios, Perú [on line]. Accessed on 15 September 2007.URL: http://www.amazonconservation.org/home/docs/los-amigos-overview6.pdf.

Ratcliffe, B.C. 1980. New species of Coprini (Coleoptera: Scarabaeidae: Scarabaeinae) taken from the pelage of three toed sloths (*Bradypus tridactylus* L.) (Edentata: Bradypodidae) in central Amazonia with a brief commentary on scarab-sloth relationships. Coleopt. Bull. 34: 337-350.

Vaz-de-Mello, F.Z. 2007. Revision and phylogeny of the dung beetle genus *Zonocopris* Arrow 1932 (Coleoptera: Scarabaeidae: Scarabaeinae), a phoretic of land snails. Ann. Soc. Entomol. Fr. 43: 231-239

Vaz-de-Mello, F.Z. & J.N.C. Louzada. 1997. Considerações sobre forrageio arbóreo por Scarabaeidae (Coleoptera, Scarabaeoidea), e dados sobre sua occorrência em floresta tropical do Brasil. Acta Zool. Mex. 72: 55-61.

Waage, J.K. & R.C. Best. 1985. Arthropod associates of sloths, p.319-322. In G.G. Montgomery (ed.), The evolution and ecology of armadillos, sloths, and vermilinguas. Smithsonian Institution Press, Washington, D.C., 462p.

Received 13/II/08. Accepted 26/IX/08.