Food relocation and nesting behavior of the Argentinian dung beetle genus *Eucranium* and comparison with the southwest African *Scarabaeus* (*Pachysoma*) (Coleoptera: Scarabaeidae: Scarabaeinae)

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■ **ABSTRACT.** The food relocation and nesting behavior of the South American genus *Eucranium* Brullé is described based on observations carried out under natural conditions. Food preference, food transportation, period of surface activity, and habitat preference are described for two species, *E. arachnoides* Brullé and *E. planicolle* Burmeister. The biology and food relocation behavior of *Eucranium* is compared with that of the morphologically similar South African subgenus *Scarabaeus* (*Pachysoma*) MacLeay. The convergent adaptations to psamophilous habitats of *Eucranium* and S. (*Pachysoma*) are discussed.

KEY WORDS. Behavior, dung beetles, food relocation, endemism, xeric habitat.

■ **RESUMEN. Comportamiento de reubicación del alimento de *Eucranium*, escarabajo estercolero endémico de la Argentina y comparación con *Scarabaeus (Pachysoma)* del sudoeste de África (Coleoptera: Scarabaeidae: Scarabaeinae).** Se describe el comportamiento de reubicación del alimento del género sudamericano *Eucranium* Brullé basado en observaciones en su ambiente natural. La preferencia de alimento, el modo de transportarlo, preferencia de hábitat, y período de actividad en la superficie son discutidos para dos especies: *E. arachnoides* Brullé y *E. planicolle* Burmeister. La biología y comportamiento de relocación del alimento de *Eucranium* es comparado con la biología y comportamiento del subgénero del sudoeste de África *Scarabaeus* (*Pachysoma*) MacLeay, el cual es similar morfológicamente. La convergencia adaptativa a los ambientes áridos de *Eucranium* y *S*. (*Pachysoma*) son discutidas.

PALABRAS CLAVE. Comportamiento, escarabajos estercoleros, reubicación del alimento, endemismo, ambientes áridos.

INTRODUCTION

The genus *Eucranium* Brullé is a relatively small genus of dung beetles belonging to the Eucraniini (Coleoptera, Scarabaeidae), a morphologically and behaviorally unique New World tribe endemic to the Chaqueña and Monte Biogeographic provinces in Argentina (Zunino *et al.,* 1991; Philips *et al*., 2002). Members of the Eucraniini are unusual in that they occur only in specific thorn-desert habitats and have very specialized ecological adaptations (Ocampo, 2004, 2005). Unusual behaviors include excavating burrows before foraging and feeding on dry dung, traits once thought limited to the southwest African subgenus *Scarabaeus* (*Pachysoma*) MacLeay. Presently, the tribe Eucraniini consists of four genera: *Anomiopsoides* Blackwelder (five species) (Ocampo, 2005), *Ennearabdus* van Lansberge (one species), *Eucranium* Brullé (seven species) (Ocampo, in prep.), and *Glyphoderus* Westwood (three species) (Ocampo, 2004).

The taxonomic placement of the tribe has been enigmatic due to their unusual biology and external

morphology. Recently it was hypothesized that Eucraniini is a monophyletic group related to the Phanaeini with both derived from Dichotomiini (Philips *et al*., 2002; 2004; Ocampo *et al*., in prep.). The species-level taxonomy of the genus *Eucranium* has been enigmatic; seven species were recognized for this genus, but probably, based on an ongoing revision, the genus consists on more species (Ocampo, in prep.).

The genus *Eucranium* is restricted to the Monte and Chacoan biogeographic provinces in Argentina from 26°- 43° latitude South and between 200-2,800 m elevation (Roig Juñent and Flores, personal communication). The climate in this area is temperate-arid with little rainfall (80-250 mm per year) (Roig-Juñent *et al*., 2001). The northern and central regions of the Monte and southern portion of the Chacoan province receive rain in summer, but in the south it is colder and rainfall is distributed throughout the year (Morello, 1958; Cabrera, 1976). The dominant vegetation of this region is open scrubland (Figs. 1-2). The landscape consists of sandy plains and plateaus and is characterized by the presence of mountains that define several elongated valleys. All species studied prefer sandy, or clay soils with a 20-60% vegetation cover.

Species of *Eucranium* and *S.* (*Pachysoma*) are morphologically similar, having undergone convergent adaptations for survival in xeric habitats. Both taxa have completely different modes of transporting dung, which is an indication of the descent of each from two unrelated lineages within the Scarabaeinae.

This paper is a continuation of our work on the taxonomy and evolution of the food relocation and nesting behavior of the genera of Eucraniini. The aim of this paper is to provide a qualitative description of the behavior of the species of *Eucranium* and to compare it to the species in the southwestern African *S.* (*Pachysoma*). Images and videos on the food relocation behavior and natural history of the tribe Eucraniini are available on the World Wide Web page at http://www.museum.unl.edu/research/entomology/Eucraniini/Eucraniini1.html.

METHODS

Observations on the biology and food relocation behavior of two species of *Eucranium*, *E. arachnoides* Brullé and *E. planicolle* Burmeister were carried out under natural conditions in Mendoza, La Rioja, and Neuquén provinces, Argentina (Mendoza: Reserva Telteca, Reserva Provincial La Payunia, and Pata Mora; La Rioja: Anillaco), for a period of ten days in January 2002 and seven days in January 2003. During our observations, air temperature varied from 18 to 38 °C in the shade, with the hottest temperature recorded at 13:00-15:00 hr and the coolest temperature at night.

Food relocation and nesting behavior of *Eucranium* Brullé

Under natural conditions, the period of surface activity of *E. arachnoides* and *E. planicolle* is from 10:00-13:00 hr, and from 18:00-20:00 hr, depending on the air and soil temperatures. Nocturnal surface activity was observed for *E. arachnoides* in Reserva Talteca, Mendoza from 22:00-23:30 hr. Nocturnal activities of *E. arachnoides* consisted of walking in an apparently random manner in what we presume is a search for mates, because no beetles were observed carrying dung or walking rapidly (speed may be temperature dependent) like they do when foraging in the daylight and several individuals were observed sitting on the sand with their antennal club open. *Eucranium* species, as in most other members of the Eucraniini, specialize trophically on dehydrated dung pellets. Individuals of *E. arachnoides* and *E. planicolle* were observed carrying pellets of «goat» (*Capra hircus* L.), and *E. planicolle* was observed carrying pellets of «guanaco» (*Lama guanicoe* Cuvier). *Eucranium arachnoides* and *E. planicolle* were also observed using dry horse or cow dung (Fig. 3) but they were not attracted to dung traps baited with fresh human or cow dung. Generally, *Eucranium* species are not found directly associated with rodent nests, which is often the case in the other two flightless genera of Eucraniini, *Anomiopsoides* and *Glyphoderus*. One of us (Ocampo) observed an association of *Eucranium arachnoides* with a guanaco dung midden in Mendoza province. To carry dung, the beetles grasp it with the foretibiae and run forward using only their middle and hind legs (Fig. 3). This unique behavior is known only for members of the tribe Eucraniini.

One species, *E. arachnoides*, was also observed moving a large piece of horse dung by butting it. To do this, the beetles used their forelegs and head to push dung while walking forward. Sometimes after several unsuccessful attempts to transport a large piece to their burrow, the beetle decided to dig a new burrow, then fragmented the piece of dung by using the clypeus and forelegs, and then buried it. The method of food relocation by butting the dung piece was also observed in the Eucraniini *Ennearabdus lobochephalus* (Harold) (Ocampo, personal observation), in various species of *Phanaeus* MacLeay (Phanaeini), and in *Dichotomius nisus* (Olivier) (Dichotomiini) (Halffter & Matthews, 1966; Halffter & Edmonds, 1982). Species that also carry food with their front legs are found in the Australian genus *Cephalodesmius* Westwood. In contrast though, *Cephalodesmius* species walk backwards while holding food and gather fresher and moister food particles, such as leaves and flowers, in its humid forest habitat (Monteith & Storey, 1981). *Coptorhina* Hope is another genus that has been recorded carrying food (mushroom pieces) with its front legs while moving backwards (Tribe, 1976).

When the entrance of the burrow is reached, the observed specimens of *E. arachnoides* and *E. planicolle* entered by walking forward rather than backward. Observations published by Zunino *et al.* (1989) suggested that the beetles drop the dung pellet and turn back and enter the nest walking backward while dragging the pellet. We never observed this for Eucraniini species under natural conditions (see Ocampo, 2004, in press) but one of us (Philips) observed this alternative behavior under laboratory conditions. The burrow is always dug prior to provisioning. It is variable in depth (usually between 0.2-0.8 m long) and variable in slope (between 35-60° with respect to the ground surface). The tunnel may be straight or curved. The depth of the burrow is probably associated with the depth where beetles find a certain level of soil moisture. Burrows are sometimes bifurcated near the end and in those cases only one chamber was observed provisioned with dung. Beetles store the food at the end of the burrow, and no special chamber was prepared for it. The number of dung pellets or dung pieces found stored is variable, and ranges from three to 193 for *E. arachnoides*, each pellet is carried independently to the burrow. Sexual cooperation has been observed, and it follows the same behavior as that for individuals. Occasional vigilance at the entrance of the burrow was noted and this is done by one of the members of the couple. No special brood chambers were observed in burrows constructed by pairs. During the hours with no surface activity, it is common to observe the entrance of the burrow obscured with sand or other substrate.

Comparison with the South African flightless *Scarabaeus* (*Pachysoma*)

Species of the subgenus *Scarabaeus* (*Pachysoma*) MacLeay are found only in southwest Africa and range from Cape Town, South Africa, north to near Walvis Bay, Namibia from approximately 34º to 23º S latitude (Harrison & Philips, 2003). They are found along coastal sands from near sea level to approximately 1,500 m in altitude (near Aus, Namibia). Species are distributed in the predominantly winter rainfall areas where at least 2/3 of the precipitation occurs during this cooler season (Goldblatt, 1978). The amount of rainfall varies from 400-500 mm in the lowland southwest Cape region decreasing to no more than 100 mm per annum in the Namib Desert.

Thirteen species are now included in the subgenus (Harrison *et al.,* 2003). Similar to *Eucranium*, S. *(Pachysoma*) is a denizen of areas with sandy soils. The vegetation density in their habitat ranges from bare loose sand dunes to firmer sandy-gravel areas (mainly in Namibia) to vegetated scrub landscapes of varying sand firmness in Namaqualand to the Cape region in South Africa. The habitat varies from flat to various undulating topologies, such as river banks and dry beds, coastal hummocks, and vegetated dunes (Harrison *et al.,* 2003; Philips, personal observation).

The peculiar foraging behavior for *S. (Pachysoma*) was first recorded by Holm & Scholtz (1979). Species of S. (*Pachysoma*) use their posterior legs to grasp either dung or detritus, depending upon the species, in a pincher-like manner. Individuals walk forwards dragging food to burrows. In a slight variation, *S. (Pachysoma*) *denticollis* (Péringuey) reportedly picks up detritus with its hind legs and presses this material against the ventral abdominal surface (Holm & Scholtz, 1979). In contrast, species of *Eucranium* use their front legs to hold food, which is often held well above the ground surface while they transport it.

Foraging behavior of *S. (Pachysoma) striatum* (Castelnau) was recorded by Scholtz (1989). He found that beetles are active on the surface from 9:00-18:00 hr with the most intense activity from 10:00-12:00 hr and 15:00-17:00 hr. Temporary burrows were sometimes excavated at midday and also in mid-afternoon when the temperature was decreasing. Harrison *et al.* (2003) noted foraging of *S. (Pachysoma) aesculapius* Olivier as occurring slightly earlier (ca. 7:00-9:00 hr) and slightly later (ca. 16:00-18:00 hr) than the previous species. Except for the earlier activity of *S. (Pachysoma) aesculapius*, activity periods are similar to *Eucranium* and nocturnal activity is not known in *S.* (*Pachysoma*) species.

Three species of *S.* (*Pachysoma*) have been observed in what appears to be pheromone releasing behavior at the burrow entrance (Harrison *et al.,* 2003). This has not been observed in any Eucraniini. The degree of sexual cooperation, if any, is unknown. Scholtz (1989) reported only one burrow out of 21 for *S. (Pachysoma) striatum* had an individual of each sex. Based on field work with several other species, finding two individuals (of unknown sex) in a single burrow was even less common (Philips, personal observation).

Like in *Eucranium* species, the burrow was always excavated before gathering dung. It was dug at a angle of about 45° to the surface and variable in depth with a total length of 45-60 cm. The burrow usually had several abrupt turns on the way down to the dung chamber (Scholtz, 1989; Philips, personal observation). As in *Eucranium*, the depth of the burrow was apparently associated with a certain level of soil moisture that is sometimes manifested as a distinct damp zone horizon below dry sand. In contrast to *Eucranium* species, but like many other Scarabaeini (see Halffter & Matthews, 1966), *S.* (*Pachysoma*) species excavate dung chambers. The first chamber excavated is for temporary storage, while a second, deeper chamber below the moisture line, was where feeding and brood rearing apparently occurred. As in *Eucranium*, the number of dung pellets or the amount of detritus stored is variable and pellets are carried one by one into the burrow. Based on 14 burrows, Scholtz (1989) found an average mass of 1.4 g of air-dried rodent dung (range = 0.53-2.57 g). Once sufficient dung was collected, burrow entrances were blocked with sand pushed up to the entrance by the inhabitant.

As with *Eucranium* species, fresh wet dung was not very attractive to S. (*Pachysoma*) species and would be ignored until it partially dried out (Scholtz, 1989). Native dung used as food included that of many rodent species (Scholtz, 1989), oryx or gemsbok (*Oryx gazella* L.), species of *S.* (*Pachysoma*) have also been observed utilizing sheep and hare pellets, ostrich dung, dead insects, and mice and chameleon droppings (Holm, 1970; Holm & Scholtz, 1979). It is likely that dung from the Greater Kudu (*Tragelaphus strepsiceros* Pallas), Grey Duiker (*Sylvicapra grimmia* L.), Springbok (*Antidorcas marsupialis* Zimmermann), Zebra (*Equus zebra* L.), and undoubtedly many other small antelope species could also be utilized as a food resource. Like *Eucranium* species, there is no evidence that *Pachysoma* species were associateed with rodent nests.

Some species of *Pachysoma*, such as *S. (Pachysoma) hippocrates* (MacLeay) and *S.* (*Pachysoma*) *glentoni* Harrison, Scholtz, and Chown feed on detritus, although the former will feed on dung if available. Six of seven excavated nests of *S. (Pachysoma) endroedyi* Harrison, Scholtz, and Chown were found to contain a combination of detritus and pellets, eight of 17 nests of *S. (Pachysoma) gariepinus* (Ferreira) contained only detritus or a mixture of detritus and dung, and the single excavated nest of *S. (Pachysoma) bennigseni* (Felsche) contained a mixture. *Scarabaeus* (*Pachysoma*) *schinzi* (Fairmaire) is known to feed on vegetable matter (Harrison *et al.,* 2003) and dung (Philips, personal observation). Although *Eucranium* species are known to use dung only, there are at least two species of the closely related genus *Anomiopsoides* that also use detritus, seeds, and other plant material as food (Ocampo, in press).

Larvae of *S.* (*Pachysoma*) are reported for two species (Harrison *et al.,* 2003). There is no use of a brood pear or ball of dung, and the larvae appear to be open-nest feeders as they lack the characteristic dorsal hump found in other ball-confined larvae. Lack of a brood ball is also appears true in lab colonies of *Eucranium*. In the closely related *Anomiopsoides*, pupae in lab colonies were enclosed in cells composed of organic material and

sand. In contrast, *S.* (*Pachysoma*) species are known to pupate in fragile sand cases.

Populations of *S.* (*Pachysoma*) vary in density that is perhaps dependent upon the amount of available dung and the harshness of the environmental conditions (Philips, personal observation). Unfortunately, there is little available data to substantiate the sizes and densities of populations, and false impressions may be created due to the degree of above-ground or tunneling activity observed. It is apparent that most dung is encountered by chance and, at least for some populations, is plentiful and not limiting to population size (Scholtz, 1989). Additionally, interspecific competition (within the subfamily Scarabaeinae) is reduced or even lacking because most other scarabaeines are not attracted to dry dung. It is possible that reduced amounts of dung for nesting in some habitats may have been the selective force improving the fitness of those individuals that use detritus.

It is not clear how beetles find their way back to the burrow along the shortest possible route. As described by Byrne *et al*. (2003) and Dacke & Warrant (2002) for the South African winged dung beetles *Scarabaeus rugosus* (Hausman), *S. rusticus* (Boheman), *Kheper nigroaeneus* (Boheman) and *Pachylomerus femoralis* (Kirby) (Scarabaeinae: Scarabaeini), and suggested for the Eucraniini genera *Anomiopsoides* and *Glyphoderus* (Ocampo, 2004), the beetles rely on the pattern of polarized light as a compass bearing that can be used to «calculate» the direction to the burrow. Dacke *et al*. (2003) documented the use of polarized moonlight by the African *Scarabaeus zambesianus* Péringuey that forages at night for fresh dung. We cannot infer the same adaptation for *E. arachnoides*, since observations of nocturnal activity of this species were conducted during the dark phase of the moon (Ocampo personal observation).

Species of *Eucranium* and *S.* (*Pachysoma*) are dry dung (or dry detritus) feeders. *Scarabaeus* species formerly placed in the genus *Mnematium* MacLeay and *Neomnematium* Janssens, (*S. silenus* (Grey), *S. ritchiei* (MacLeay), and *S. cancer* (Arrow)) may also have similar food feeding and relocation strategies of dragging or carrying as evidenced by common ancestry (Harrison & Philips, 2003). Unfortunately, there is no information available on the feeding habits of these species although their mouthpart structure appears to be intermediate between wet dung and dry dung feeders (Harrison *et al.,* 2003).

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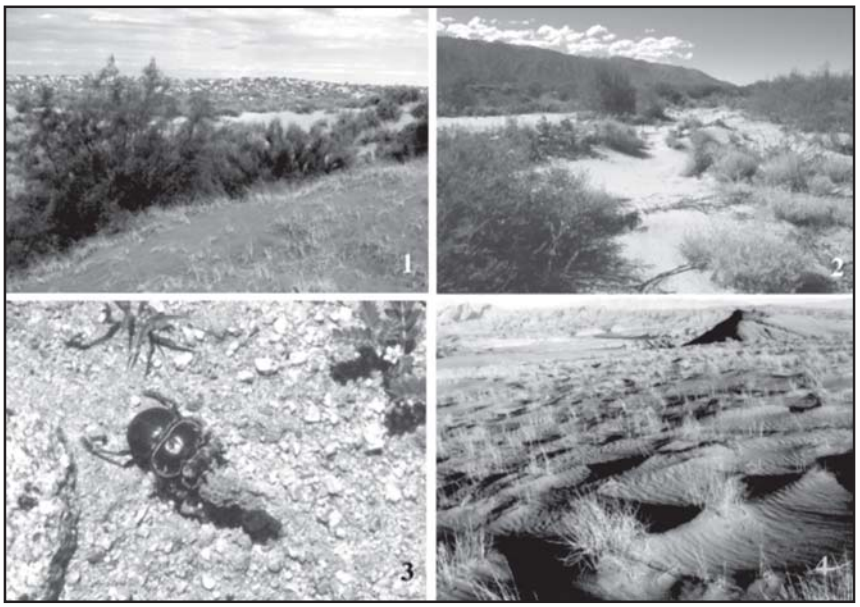

Figs 1-4. 1-2. Typical habitat of *Eucranium* species in 1. Mendoza and 2. La Rioja provinces, Argentina. 3. *Eucranium arachnoides* carrying a dry piece of horse dung. 4. Typical habitat of the southwest African *Scarabaeus* (*Pachysoma*).

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