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SHORT COMMUNICATION

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Scarabaeolus carniphilus: a necrophagous dung beetle (Coleoptera: Scarabaeinae) buries and feeds on a dead snake

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A rare sighting of two male carrion specialist dung beetles, *Scarabaeolus carniphilus* Deschodt & Davis, 2015, burying a freshly dead Herald snake (*Crotaphopeltis hotamboeia* (Laurenti, 1768)) is documented from its discovery in the field and subsequent reburial under laboratory conditions. The species studied is a member of the telecoprid (dung roller) Scarabaeini, but behaved here like a paracoprid; it deliberately cut into and removed flesh from the dead snake; these pieces were then taken into a feeding burrow; later a pheromone release stance was taken up near an established burrow; and under laboratory conditions the snake was completely buried. These observations, mostly novel for this species and its genus are clearly documented via photographs and an online time lapse video taken every hour for 24-hours during the snake's-(re)burial. This note introduces relevant aspects of dung beetle natural history and new biological information for *Scarabaeolus* and particularly for *Sc. carniphilus*. It records and interprets a carrion specialist Scarabaeini dung beetle burying and feeding on fresh carrion; highlights natural history findings (pheromone release) previously not considered for the evolution of the Scarabaeini; and aims to stimulate behavioural research into this interesting and under studied genus *Scarabaeolus*.

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SUPPLEMENTARY MATERIAL
Supplementary information for this article in the form of a video is available

On 4 Nov. 2014 at 16h14 a dead Herald snake (*Crotaphopeltis hotamboeia*) (Laurenti, 1768) (Graham Alexander pers. comm.), commonly known as a Herald or Red-lipped snake was discovered being buried by two dung beetles (Figure 1). The snake, dung beetles and sand from the same area were then moved (about 2 km) to a field laboratory (26.23′55.1″S 24.19′37.3″E, Stonehenge Farm, near to the town of Vryburg, North-West province, South Africa). The original location (sand road) and field laboratory (camp) are in the same habitat type and would have experienced the same environmental conditions. The dead snake was placed on the surface and the two live dung beetles (*Sc. carniphilus*) were released next to it inside a 10-l rectangular bin containing compacted Kalahari sand from the collection site. A gauze lid (mesh diameter 5 × 5 mm squares) covered the container to prevent other similar sized or bigger beetles from entering the container and its occupants from flying away. On 6 November 2014 at 12h39, we realised that the snake was once again being buried and photographically documented this process using a tripod-mounted Canon G12 SLR camera with hourly photographs for the next 48 hours. Once the snake had completely disappeared from the soil surface the bin was left untouched until it was moved by vehicle (8 November 2014) to a laboratory at the University of the Witwatersrand, Johannesburg, South Africa (26.11′34.116″ S 28.01′56.97″ E). Here (9 November 2014) the bin was placed inside a north facing laboratory, receiving ambient temperatures and a natural day-night cycle. About 250 ml of water was sprinkled over the surface to maintain the sands' moisture content. On 28 November 2014 at 19h48 the bin contents were carefully dug up and sieved (5 × 5 mm mesh) to see what had become of the beetles and snake. Both beetles were buried in the sand and alive. The snake had been completely consumed (one rib remained), and 62 fly pupae were found in the excavated sand. At this point the two dung beetles were killed and preserved for sexing, identification and voucher purposes, and are deposited in the Wits Life Sciences Museum (WLSM) insect collection.

The dung beetles were dissected and following Deschodt et al. (2015) identified by JduGH as two males of *Scarabaeolus carniphilus* Davis & Deschodt, 2015. The specimens match the morphological attributes, male genitalia, feeding preference and geographic location (also near Vryburg) of *Sc. carniphilus*. In addition to this, the specimens' identity was confirmed by A.L.V. Davis and C. Deschodt (the species' authors).

As their name implies, dung beetles feed predominantly on dung (coprophagy) but will also feed on both dung and carrion (copro-necrophagous) or only carrion (necrophagous, including both invertebrate and vertebrate carrion) (Halffter and Matthews 1966; Scholtz et al. 2009). A few taxa are obligate feeders on fungi (fungivores), detritus or millipedes (as necrophages or even carnivores) while others are associated with land snails (Vaz-de Mello 2007) or predacious on live ant alates (Halffter and Matthews 1966; Halffter and Halffter 2009; Hertel and Colli 1998). Dung beetles from the tribe covered here (Scarabaeini), have been recorded feeding on wet dung (*Pachylomerus*, *Scarabaeus*, *Kheper* and *Scarabaeolus*), dry dung (*Pachysoma*), detritus (*Pachysoma*), carrion (*Pachylomerus*, *Scarabaeus* and *Scarabaeolus*) and millipedes (*Sceliages*) (Tribe 1976; Mostert

Figure 1. Fresh Herald snake (*Crotaphopeltis hotamboeia*) road kill on Kalahari sand at Stonehenge Farm, Vryburg, South Africa (4 November 2014, 18:08). (**A**) The cloacal region of the snake has already been penetrated by one or two male *Scarabaeolus carniphilus* dung beetles, with fresh sand "push-up" as evidence of their digging. Cocktail ants (Formicidae: *Crematogaster* sp.) can also be seen feeding on the snake "A and C". (**B**) The central region of the snake (flattened and internally ruptured by vehicle tyre) also has dung beetle push-ups. (**C**) The head of the snake has already being eaten away by another group of *Crematogaster* ants. Photograph 4 November 2014, 18:08 by JduGH. Scale bar = 50 mm.

and Scholtz 1986; Scholtz 1989; Forgie et al. 2002; Harrison and Philips 2003; Harrison et al. 2003; Scholtz et al. 2004). In a comparative study of the mouthparts of 12 dung beetle species Mathikge (2021) found that *Sc. carniphilus* and a generalist feeder have similar mouthparts to wet dung feeding species, which she assumed was a pre-adaption to liquid-type foods.

On the basis of their dung relocation behaviour, dung beetles have been divided into four main functional groups following the papers of Halffter and Matthews (1966); Bornemissza (1969, 1976); Hammond (1976) and Klemperer (1983), which include:

(i) paracoprids construct their nests at the end of tunnels under the dung;
(ii) endocoprids create a nest chamber within or immediately under the dung;
(iii) telecoprids detach a portion of dung from the mass, roll it some distance away from the source and then bury it (or place it above ground in a grass tussock), and
(iv) kleptoparasites use dung that has already been buried by geotrupine or scarabaeine dung beetles.

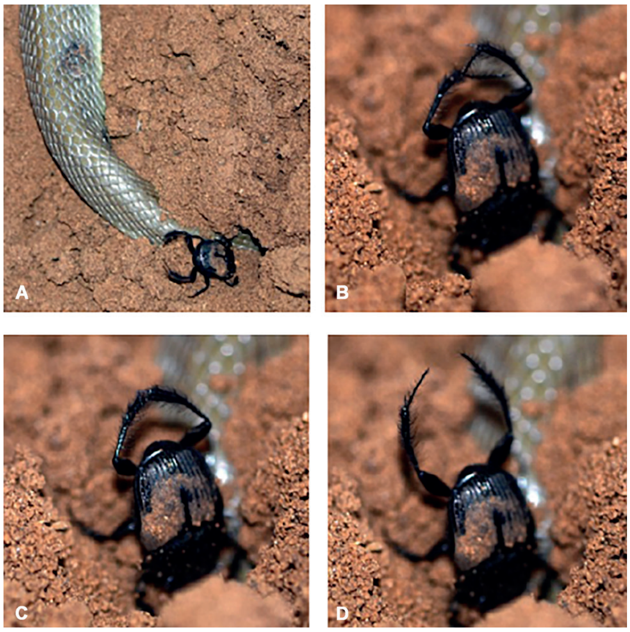
Doube (1990) refined this classification into seven functional groups. Known Scarabaeini food relocation behaviour is generally of the telecoprid style, with some taxa modifying this by altering the body posture (or direction) which the beetle uses to relocate the food item: *Sceliages* push millipede pieces forwards (Forgie et al. 2002), *Pachysoma* drag dry dung and detritus forwards (Scholtz 1989; Harrison et al. 2003; Harrison and Philips 2003), *Scarabaeus galenus* and *Scarabaeus vicinus* (after Deschodt et al. 2017) push fragments of wet dung or pellets backwards (Dacke et al. 2020; JduGH pers. obs.), *Scarabaeus*, *Kheper*, *Scarabaeolus* and *Pachylomerus* make and roll wet-dung-balls backwards (Byrne et al. 2003), but *Pachylomerus* will also head-butt dung into a burrow close to the dung source, in more of a paracoprid style of nest provisioning (Tribe 1976; Mostert and Scholtz 1986). To date all known species of *Scarabaeolus* are assumed to use the telecoprid style of food relocation.

Like dung, carrion is a spatially and temporally fragmented food resource (Halffter and Mathews 1966; Hanski and Cambefort 1991; Scholtz et al. 2009; Simmons & Ridsdill-Smith 2011). However, unlike dung, carrion is also eaten by a host of vertebrate scavengers and predators, further reducing its availability. African vertebrate scavengers include birds (e.g., crows, hornbills, kites, raptors and vultures), small to medium sized predators (e.g., jackals and hyenas (Mills and Mills 2010)) and even hungry lions (McBride 1990) which, directed via smell or sight, quickly locate and eat such meals. Consequently, any dung beetle species feeding on carrion compete with these larger animals for this resource. Additionally, the frequency and availability of carrion is dependent on something being killed or dying, unlike defecation, which African herbivores do many times per day, for example, "African elephants defecate about 14–20 times per day in the wet season, and about 10 times per day during the dry season. An adult elephant produces between 6 kg and 11 kg of faeces per defecation on average, depending on its size. On average, the total quantity of faeces produced per day would amount to about 150 kg wet mass, or 35 kg dry mass" (Owen-Smith 1988).

The advantage of using carrion as a food resource is that it has a higher nutritional value, particularly its nitrogen content, in comparison to dung (Scholtz et al. 2009). Its disadvantage is its scarcity in comparison to dung and competition for it from vertebrate scavengers and other carrion-associated insects (Scholtz et al. 2009).

To replicate the biological sequence of events the figures are arranged in chronological order. Two male *Sc. carniphilus* had already started burying the snake when it was discovered (Figure 1). The first in residence (based on the size of its sand push-ups), was working on the cloacal region of the snake (Figure 1A), the second about 60 mm back from the head (Figure 1B). As one would expect (from forensic entomological knowledge) the insects initially focussed their attention on sections of the snake where the skin had been ruptured (where the vehicle crushed it). On collection of the snake, cocktail ants (Formicidae: *Crematogaster* sp.) present (Figure 1C) were removed and subsequently no further ants were involved in the decomposition process.

Under field laboratory conditions the snake was reburied by being pulled into the sand, i.e., the beetles buried it from underground. During the latter stages of the snake's reburial, the beetles were observed on the surface walking around the periphery of the container. Alternatively, they were observed just below or just out of a tunnel dug right next to the snake, for example, during the pheromone release stage (Figures 2A–D). Within 48



Figures 2A–D. In the field laboratory a male *Sc. carniphilus* at an entrance hole to a portion of the buried snake releasing pheromone to attract a female (unfortunately both beetles in the container were male). (**A**) Beetle at burrow entrance, standing on its front four legs and with its hind legs held outwards just after having "brushed" off a plume of pheromone, (**B**) close up of the beetle as it brings its hind legs back in again, (**C**) mid-action as its legs move outwards once more, (**D**) after pheromone release, and now in a static sit-and-wait posture. Photographs taken between 06:42–06:45 am on 6 November 2014 by JduGH.

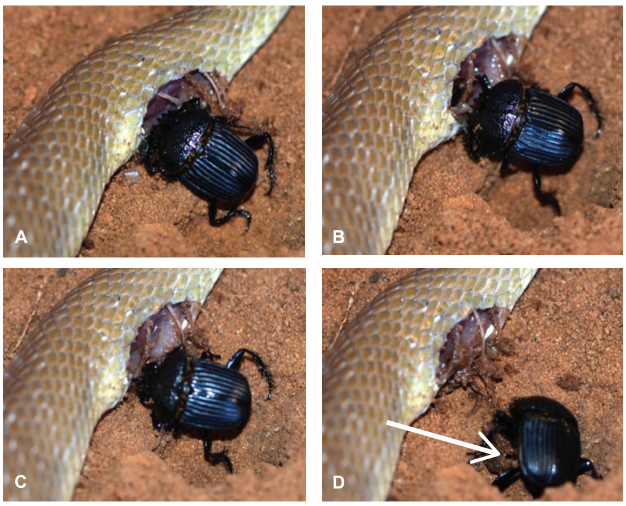
hours of being placed in the field laboratory the snake had been completely buried. An online time lapse video condensing the snake's reburial is available as supplementary material.

On 28 November 2014 (24 days after its initial discovery) the bin containing the snake and beetles was excavated and all that remained of the snake was a single rib (no photograph), two live male *Sc. carniphilus* beetles and 62 fly pupae. The fly pupae were returned to the sand and covered with moist sand, and when checked again on 22 December 2014 most of the flies had emerged including three parasitic hymenopterans, from a genus (*Brachymeria* sp.) known to parasitise *Sarcophaga* pupae (Delvare and Huchet 2017). It goes beyond the intended scope of this paper to discuss the other insects involved (ants, flies and parasitic wasps), but their presence does show how necrophagous dung beetles compete with other insects for this nutritious food resource. The 62 fly pupae account for what became of the snakes tissue and bones, namely they were converted by *Sarcophaga* maggots into the pupal cases and another generation of flesh flies.

Figures 3A–D provide the first photographic evidence of a *Scarabaeolus* species feeding on carrion and behaving like a paracoprid rather than like a telecoprid at the food resource. Further work is needed to determine if this is a common behaviour (no food relocation) among carrion feeding *Scarabaeolus* species. No attempt was made (by the two male beetles) to make and roll a carrion ball either in the field, or in the storage container. Many other species of larger telecoprid dung beetles will make and roll dung balls in these same containers.

Figures 3A–C shows how a *Sc. carniphilus* beetle cuts (this species is equipped with sharply pointed clypeal and protibial teeth) into the snake and provisions its adjacent feeding burrow with fresh carrion as food (Figure 3D). We did not observe if the snake was opened up before or after the feeding burrow was dug. Finally, after being provisioned with snake carrion, the feeding burrow was sealed off, leaving the rest of the snake still on the surface.

The first record of a dung beetle releasing pheromone was made by Tribe (1975) for the African Scarabaeini species (*Kheper nigroaeneus*), but more generally he also mentioned that "various ball rolling species have specific rhythmic patterns of brushing behaviour and certain features such as a criss-crossing of the extended [hind] tibiae in *Scarabaeus* is specific to that genus. No comparable release stance has been observed in any female [dung]



Figures 3A–D. In the field laboratory. Male *Sc. carniphilus* cutting into, extracting and burying some fresh, wet snake tissue to presumably feed on. (**A**) beetle cuts into the snake using its clypeal teeth and protibia, (**B**) pulling snake tissue out with its right protibia, (**C**) moving backwards, with snake tissue held in its pro and mesotibia, (**D**) about to disappear into its tunnel (dug immediately next to the snake like a paracoprid) carrying with its pro and mesotibia some snake tissue (arrowed). Photographs taken between 17:21–17:27 on 6 November 2014 by JduGH.

beetles" (Tribe 1976). Tribe's (1976) thesis on dung beetles mentions these Scarabaeini taxa with respect to pheromone release: *Kheper lamarcki*, *K. nigroaeneus*, *K. subaeneus*, *Pachylomerus opaca*, *Scarabaeus ambiguus* and *S. galenus*), but makes no mention of pheromone release by any species of *Scarabaeolus*, although other aspects of the breeding biology of *Scarabaeolus bohemani* are covered. Following from Tribe's (1975, 1976) findings, Burger *et al*. (1983, 1990, 1991, 1995, 2002a,b, 2008) expand on the chemical aspects of dung beetle pheromone release in various species of *Kheper* and *Pachylomerus*, but unfortunately did not include any *Scarabaeus* or *Scarabaeolus* species in their analyses. In a series of papers, Pluot-Sigwalt (1982, 1983, 1986, 1991, 1995) examined the abdominal pheromone glands of the following Scarabaeini species: *Kheper cuvieri*, *K. festivus*, *Pachylomerus femoralis*, *Scarabaeolus palemo*, *Scarabaeus furcatus*, *S. goryi*, *S. laticollis*, *S. radama*, *S. sacer*, *S. semipunctatus* and *S. typhon*. These glands showed intraspecific sexual dimorphism for all species and the distribution of the glands on the abdominal sternites of the four main groups studied (*Scarabaeolus*, *Scarabaeus*, *Kheper* and *Pachylomerus*) also varied. Of particular interest was the finding that female *Scarabaeolus palemo* lacked abdominal pheromone glands, in contrast females of the other Scarabaeini mentioned earlier had pheromone glands.

Perhaps this scientific note raises more questions than answers, but it is our hope that it will stimulate further study of the natural history of *Scarabaeolus* and other related Scarabaeini genera.

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