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Animal behaviour

From coprophagy to predation: a dung beetle that kills millipedes

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The dung beetle subfamily Scarabaeinae is a cosmopolitan group of insects that feed primarily on dung. We describe the first case of an obligate predatory dung beetle and contrast its behaviour and morphology with those of its coprophagous sympatric congeners. *Deltochilum valgum* Burmeister killed and consumed millipedes in lowland rainforest in Peru. Ancestral ball-rolling behaviour shared by other canthonine species is abandoned, and the head, hind tibiae and pygidium of *D. valgum* are modified for novel functions during millipede predation. Millipedes were killed by disarticulation, often through decapitation, using the clypeus as a lever. Beetles killed millipedes much larger than themselves. In pitfall traps, *D. valgum* was attracted exclusively to millipedes, and preferred injured over uninjured millipedes. Morphological similarities placing *D. valgum* in the same subgenus with non-predatory dung-feeding species suggest a major and potentially rapid behavioural shift from coprophagy to predation. Ecological transitions enabling the exploitation of dramatically atypical niches, which may be more likely to occur when competition is intense, may help explain the evolution of novel ecological guilds and the diversification of exceptionally species-rich groups such as insects.

Keywords: Peru; dung beetle; *Deltochilum valgum*; millipede predation; guild; ecological transition

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1. INTRODUCTION

Although many taxa are trophically diverse, the initial emergence of novel trophic levels from within an ecological guild has rarely been documented in nature. One example is the caterpillars of several species of butterflies and moths, which have evolved predatory habits unlike their close relatives that are entirely herbivorous (Montgomery 1982; DeVries & Penz 2000). Ecological transitions such as these are important for understanding the evolution and diversification of new guilds and may help explain the disproportionately high diversity of insects.

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) feed primarily on the rich bacterial content of vertebrate dung, a trait that presumably evolved from saprophagy (Cambefort 1991). However, with 80 or more species often occurring sympatrically, competition for dung can be intense (Peck & Forsyth 1982). Consequently, species partition resources through different feeding strategies; many dung beetle species have derived necrophagous habits, and others feed on rotting fruit and fungus (Larsen *et al.* 2006). Although no obligate dung beetle predators are known, two dung beetle species that feed on dung and carrion have also been observed to prey on queen leaf-cutter ants *Atta laevigata* (Hertel & Colli 1998). Since dung beetles lack killing mouthparts, the same clypeal teeth used for cutting carrion are used to decapitate the ants.

Since *Deltochilum valgum* has been observed grasping live millipedes (Cano 1998), we decided to examine whether this species might be a predator of millipedes. We used baited pitfall traps to test whether *D. valgum* specialized exclusively on millipedes, and whether they preferred live, injured or dead millipedes. We made behavioural observations to determine whether *D. valgum* preys on millipedes, and, if so, what morphological traits enable this behaviour. We compare and contrast the morphology and behaviour of *D. valgum* with its sympatric congeners. Finally, we discuss factors that might facilitate this type of ecological transition and the role it may play in driving speciation.

2. MATERIAL AND METHODS

See electronic supplementary material for further details on methods.

(a) *Study system*

Research was conducted at multiple sites in wet lowland rainforest of Madre de Díos department, Peru.

(b) *Diet preference*

To examine diet preferences within the dung beetle community, we sampled dung beetles using standardized pitfall traps during 11 months between 1998 and 2000 (see Larsen & Forsyth 2005). We used all bait types known to attract dung beetles in the area, including various kinds of dung, carrion, fungus, fruit and millipedes (appendix in the electronic supplementary material; Larsen *et al.* 2006). We also set paired pitfall traps baited with a comparison of injured and uninjured millipedes. To mimic injuries likely to occur naturally, we made a slight crack in the millipede's exoskeleton.

(c) *Behaviour and morphology*

To observe behaviour, we placed individuals of *D. valgum* at dusk in a large observational arena with live millipedes. Since *D. valgum* is nocturnal, we used weak red light during observation periods and observed behaviour every 30 min for 5 min. If an attack began, we continued the observation period until the attack ended. We measured morphological traits that were used during predation and compared them with sympatric congeners.

3. RESULTS

(a) *Diet preference*

A total of 132 species and 102 639 individuals of dung beetles were collected in pitfall traps ($n=1{,}011$). *Deltochilum valgum* was attracted exclusively to millipedes, and strongly preferred live, injured millipedes over dead millipedes ($t=4.74$, $p=0.001$). Injured millipedes attracted 2.67 ± 0.55 individuals/trap, while dead millipedes attracted only 0.04 ± 0.02 individuals/trap. In paired choice pitfall traps ($n=6$), all *D. valgum* individuals were attracted to injured millipedes over uninjured millipedes ($Z=-2.21$, $p=0.027$). All other *Deltochilum* species were attracted

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to dung and carrion, and sometimes to fungus or dead millipedes (appendix in the electronic supplementary material). Dead millipedes attracted 35 dung beetle species, while live millipedes attracted 5. Except for *D. valgum*, all other species attracted to millipedes were also attracted to dung, carrion and other bait types.

(**b**) ***Behaviour and morphology***

During 15 trials (556 min observation time), we observed 37 attacks on millipedes by males and females of *D. valgum*. We directly observed one successful kill and found seven millipedes that had been killed outside direct observation periods. Two of these eight killed millipedes had been injured by us previously. Two out of 3 (66%) injured millipedes were killed, while 6 out of 39 (15%) uninjured millipedes were killed. *D. valgum* killed millipedes much larger than themselves; beetles ranged in size from 7.2 to 8.0 mm (elytra width), while killed millipedes ranged from 25 to 110 mm (body length). We observed six aggressive encounters (inter- and intra-sexual) among individuals of *D. valgum*. Beetles pushed each other with their heads and legs, and chased each other away from millipedes.

Deltochilum valgum has several distinct morphological traits that played a role in millipede predation (figure 1; video in the electronic supplementary material). Attacks began with the beetle grasping the millipede's body with its mid and hind legs. The hind tibiae of *D. valgum*, which wrapped tightly around the millipede's body, are elongated and more strongly curved than those of its congeners (figure 1*c*,*d*). Millipedes responded either by coiling their body before the beetle established a firm grip or by flailing their body. Beetles frequently waited until millipedes uncoiled to renew their attack, pulling the millipede forwards in the meantime with one hind leg inserted inside the coils (figure 1*e*).

When flailing slowed down, beetles moved themselves into a ventral position and inserted their clypeal teeth into a joint between body segments. Beetles appeared to pry upwards with the head while simultaneously sawing and prying at the same joint with their foretibial teeth. The clypeus, which acted as a lever, is elongated and more strongly angled than in its sympatric congeners (figure 1*a*,*b*). Many attacks were focused behind the head capsule or behind the sixth body segment, the location of the male gonopods where legs are absent. During the one kill that we observed, the force of the beetle's prying severed the millipede's head from the rest of its body. Examination of killed millipedes showed that three kills were by decapitation, two at an apparently arbitrary location on the millipede's body and one behind the sixth body segment. Both injured millipedes that were killed had been severed at the location of the injury. One uninjured millipede was found alive the next day, but was missing all of its legs.

We never observed any ball rolling by *D. valgum*. Instead, the beetle transported a killed millipede by pinning it with one hind tibia against the surface of the pygidium and walking forwards using its other five legs. The millipede was supported by the dorsally reflexed apical margin of the pygidium, a trait not shared with sympatric congeners (figure 1*c*,*d*). After moving a killed millipede, beetles pried apart the rest of its body into several smaller pieces and placed their head entirely inside the segments, apparently feeding (figure 1*f*). The head of *D. valgum* is very narrow relative to its congeners (figure 2). Food was not buried as with most dung beetle species, and empty disarticulated pieces of millipede exoskeleton were later found underneath dead leaves, entirely cleaned of soft inner tissue.

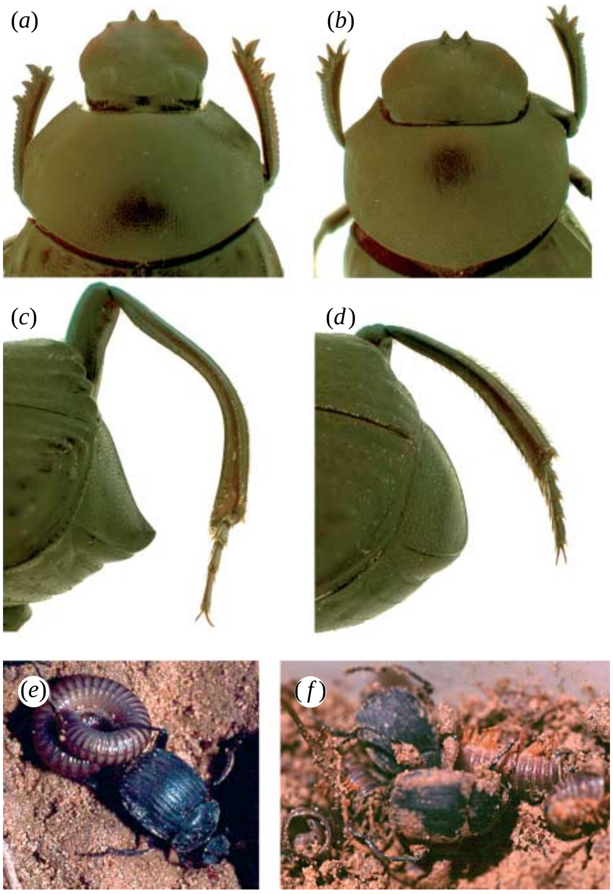

Figure 1. Comparison of morphological traits adapted for millipede predation in *Deltochilum valgum* against those of a typical coprophagous sympatric congener. (*a*) Dorsal view of *D. valgum* head. Sharp clypeal teeth and angled clypeus act as a lever to disarticulate millipede. Narrow, elongate head permits feeding inside millipede; (*b*) dorsal view of *Deltochilum peruanum* head, lacking characters described in (*a*), head used to mould dung balls; (*c*) lateral view of *D. valgum* pygidium and hind tibia. Dorsally reflexed pygidial lip is used to support millipede during transport. Elongate, strongly curved hind tibia is used to grip millipede. (*d*) Lateral view of *D. peruanum* pygidium and hind tibia, lacking characters described in (*c*), hind tibia used for rolling dung balls. (*e*,*f*). Predation strategy by *D. valgum*. (*e*) Dragging live, coiled millipede with one hind leg, walking forwards; (*f*) feeding on killed millipede with head inside segments; disarticulated empty millipede pieces nearby.

4. DISCUSSION

This is the first known case of what appears to be an obligate predatory dung beetle species. We believe that this study is based on the most exhaustive dung beetle trapping effort with the broadest variety of bait types yet conducted, yet we never recorded a single

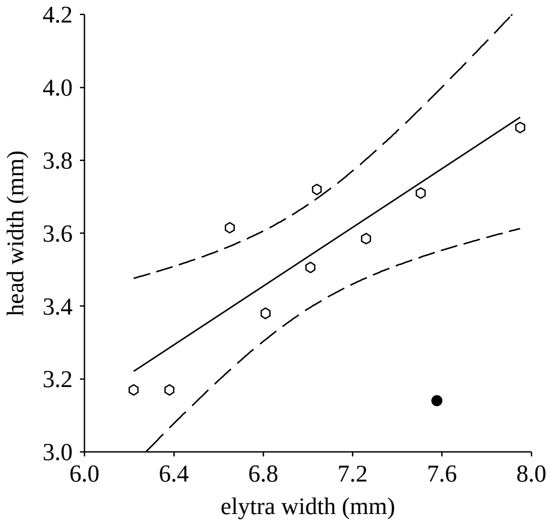

Figure 2. Relative head width of *D. valgum* (filled circle) compared with nine sympatric *Deltochilum* congeners (open circles), mean ± 1 s.e. Regression line represents the nine non-predatory congeners with 99% C.I.

individual of *D. valgum* with any food other than millipedes. Although it was once believed rare, *D. valgum* has been abundantly captured with millipedes in Guatemala and Brazil, but never with any other food (Cano 1998). This is a remarkable transition for a guild with adult mouthparts adapted to extract bacteria from dung and carrion.

Competition is likely to drive this kind of phenotypic divergence (Darwin 1859). Sympatric congeners of *D. valgum* were attracted to dead millipedes, in addition to dung and carrion, suggesting that these diversified feeding habits helped facilitate a transition to predation. Villalobos *et al.* (1998) observed a species of Canthonini feeding on the putrefied wound of a live millipede, providing further evidence as to how this shift might occur.

Olfactory detectability may partially explain why *D. valgum* is specialized on millipedes and not on other arthropods. Some carrion-feeding dung beetle species can be attracted by the defensive chemical secretions of millipedes, an adaptation allowing them to use freshly dead carcasses (Schmitt *et al.* 2004; Bedoussac *et al.* 2007). A switch in olfactory cues from carrion to defensive secretions is likely to be a prerequisite for predation of millipedes by dung beetles, which otherwise may have difficulty in finding their prey. The preference of *D. valgum* for injured millipedes may be because injured millipedes emitted much more powerful odours than uninjured millipedes (T. H. Larsen 2000, personal observation) and may have been simpler to kill because they were weakened and beetles were able to attack at the injury site. It is not clear how *D. valgum* is able to avoid harm from the defensive chemicals produced by millipedes to deter predators. The predatory larva of a phengodid beetle is known to paralyse millipedes before feeding in order to prevent chemical discharge, and the millipede's glandular sacs are not eaten (Eisner *et al.* 1998).

Relatively minor morphological adaptations to the head, hind legs and pygidium enabled behavioural innovations in *D. valgum*. Despite its close relationship with dung-feeding species in the same subgenus, *D. valgum* has entirely abandoned ancestral ball-rolling behaviour and instead uses its hind tibiae to grasp millipedes and pull them while walking forwards. The broad head and clypeus used by most dung beetle species to push and mould dung are instead narrowed and elongated for feeding inside a millipede's exoskeleton, in a similar fashion to the specialized heads of some ground beetles and harvestmen that are adapted to reach inside snail shells (Nyffeler & Symondson 2001).

This study provides an example of an unusual leap across trophic levels for species within a single ecological guild. Intra- and interspecific competition is intense among dung beetles, a situation that could promote this kind of shift (Simpson 1953). Ecological transitions are more likely to occur if relatively minor morphological and physiological changes enable large behavioural changes, such as those documented here. These changes might occur rapidly, especially since the relationship between ecological similarity and phylogenetic relatedness can be very weak (Losos *et al.* 2003). Ecological transitions provide the potential for rapid speciation, and may be one way in which new guilds of organisms have evolved (Levin 2004).

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