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Who Steals the Eggs? *Coprophanaeus telamon* (Erichson) Buries Decomposing Eggs in Western Amazonian Rain Forest (Coleoptera: Scarabaeidae)

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Abstract

The necrophagous dung beetle *Coprophanaeus telamon* (Erichson 1847) buried decomposing hen eggs in the rain forest of Ecuador. We suppose that the volatiles 2-butanone, cresol, indole, skatole, and butyric acid are responsible for attracting *Coprophanaeus* because these components of dung odour attract dung beetles and are also present in rotten eggs. A number of them are also produced by bacterial spoilage of raw meat. Abandoned clutches, infertile eggs or eggs with dead embryos of ground-nesting birds may be used as a resource by dung beetles.

Resumen

El escarabajo *Coprophanaeus telamon* (Erichson 1847) enterró huevos de gallina enteros en el bosque humedo tropical del Ecuador. Supponemos que las substancias volátilas 2-butanone, cresol, indol, eskatol y ácido butírico son responsables para atraer *C. telamon* porque éstos componentes químicos de olor de faeces atraen escarabajos que comen faeces y están presentes en huevos en decomposición. La descomposición bacterial de carne tambien produce algunos de ellos. De las aves que anidan en el suelo, huevos abandonados, infertiles o con pollos no eclosionados podrían ser un recurso para escarabajos.

The dung beetles of the superfamily Scarabaeoidea play an important role in dung decomposition, but they also consume such diverse resources as carrion, dead plant material, mushrooms, roots, and humus (Cambefort 1991). Odorous cues guide dung beetles to find patchy resources like dung and carrion (Scholtz and de Villiers 1983). Only Louzada and Vaz-de Mello (1997) have hypothesised that decomposing eggs could be another resource used by dung beetles. They found that decomposing beaten hen eggs used as a lure in pitfall traps attracted five species of Scarabaeidae in a fragment of secondary semideciduous Atlantic forest in Brazil. We present here the first observation of a dung beetle species (*Coprophanaeus telamon telamon* (Erichson, 1847)) burying entire eggs. We obtained these results experimentally with hen eggs in a rain forest in Ecuador.

Table 1. Results of "nest" controls after 4, 8 and 26 days (experimental period: 23.xii.1995–19.i.1996). Values are accumulated over days, except for case "relocated," because moved eggs were repositioned into the "nest." * The activity of beetles was discovered only at the last control day but 3 eggs first classified as "disappeared" on the 8th day were found buried by dung beetles on the 26th day.

Fate of eggs (n = 80) at	4th day	8th day	26th day
Buried by beetles	0*	3*	20 (25.00%)
Disappeared	1	7	31 (38.75%)
Cracked open	1	3	15 (18.75%)
Relocated	9	8	3 (3.75%)
Intact, unchanged	69	59	11 (13.75%)
"Nests" affected (n = 40)	6	13	36 (90.00%)

Material and Methods

Study Area. Old growth terra firme rain forest near Laguna Grande de Cuyabeno, Cuyabeno Wildlife Reserve, Ecuador (0°02′N, 76°15′W, approx. 250 m above sea level).

Experiments. On 23 December 1995, 80 hen eggs were deposited along four transects of 500 m length in terra firme forest. The transects were separated from each other by a linear distance of at least 500 m. Since the experiment was originally designed to examine the risk of predation of unattended tinamou nests (genera *Crypturellus* and *Tinamus*, Tinamidae, Aves), the eggs were grouped in pairs to simulate nests. Ten pairs of eggs were deposited in each transect, with a distance of about 50 m between deposition sites. All simulated "nests" were checked after 4, 8, and 26 days. Relocated but intact eggs were repositioned into the "nest."

Results

During the 26 days of exposure, 90% of the unattended "nests" had been found by different kinds of animals and 82.5% of the eggs were removed (Table 1).

We only observed that eggs were relocated, cracked open, or had disappeared without trace through the second check after 8 days. Relocation of eggs at the first and second check occurred in different "nests." The mean relocation distance was 39.4 cm (range: 5–100 cm, SD: 25.5 cm, n = 16 measurements). Whenever an egg was found to have been cracked open during the experiment, the predators left behind two or three large shell fragments, and in some cases evidence of the use of teeth in cracking the shell was found. This hints to omnivorous mammals such as the common opossum (*Didelphis marsupialis* L.), tayra (*Eira barbara* (L.)), and South American coati (*Nasua nasua* (L.)) (Emmons 1990; pers. comm. of local indigenous people).

After 26 days of exposure, only 14% of the eggs were found intact in the original place and these were all foul. During the last check, four eggs were found half buried in the ground, suggesting that dung beetles could have been responsible for the disappearance of a number of the eggs. Thus all sites were searched again for signs of beetle activity (Fig. 1) in a radius of 1 m around the original deposition site, and another 16 eggs were found to have been completely buried. Three of these had been classified as "disappeared" at the control before (8 days of exposure). A single male of *C. telamon telamon* was found in a cavity (Fig. 2) directly below a buried egg. A tunnel with a diameter of approximately the body width of *C. telamon* met this cavity from the side. Similarly, a single female was found at another "nest" that was approximately 800 meters away from the first one. These two buried eggs were intact but showed soft parts of the shell where the calcium was apparently dissolving. At all other buried eggs

Fig. 1. Superficial traces of burying activity of *Coprophanaeus telamon telamon* (Erichson) directly at a "nest." At other places, burial traces were much less conspicuous.

the same cavity and tunnel as described above (Fig. 2) were present indicating dung beetle activity although the beetles themselves were not found. These buried eggs were destroyed in the process of excavation and were empty or with only a little foul liquid remaining. No beetle larvae were found. Depth of the 16 completely buried eggs was 10 to 15 cm. Seventeen eggs were buried directly at the "nest" site; the remaining three were buried 20 cm, 20 cm and 30 cm away from the original location of the eggs.

Discussion

We have no doubt that *Coprophanaeus telamon* actively approaches eggs in decomposition and tries to make use of them because presumably 25% of the experimentally deposited eggs were buried by this species, and burying activity occurred in a large area of rainforest at sites far away from each other. Although the beetles may bury the eggs without benefiting, we suppose that eggs are used as a food source by *C. telamon*. Since at least some parts of the egg shell seem to weaken during the decomposition process the beetle is, in our opinion, sufficiently strong to open the shell of a buried egg using the surrounding soil for anchorage.

We assume that a large part of the 39% "disappeared" eggs (Table 1) were buried by dung beetles because we identified some of the "disappeared" eggs as having been buried and because some eggs had been relocated before burial. Traces of burial could have been overlooked because changes in the structure of the soil surface caused by beetles were usually much less obvious than in Figure 1. Furthermore, many eggs would not have been found if they had been buried more than 1 m away from the "nest." Since *Coprophanaeus* is a tunneler and not a roller, whether these eggs were relocated by the beetles themselves or by mammals that examined or unsuccessfully tried to open the eggs was not clear. However, there is evidence to show that the beetles are able to handle relatively large objects: Young (1980) found *C. telamon corythus*

Fig. 2. At the same "nest" site, tunnel of dung beetle that leads to the egg.

(Harold 1863) (the northern subspecies) burying vertebrate bones of 10 cm length. Another possible cause of the disappearance of some eggs could be that they were swallowed by snakes. Tiger ratsnakes (*Spilotes pullatus* (Linnaeus 1758), Colubridae) or Neotropical bird snakes (*Pseustes poecilonotus* (Günther 1858), Colubridae) prey on eggs (Robinson and Robinson 2001). However, the time during which eggs are interesting for snakes is likely to be limited by the rotting process, because snakes usually only eat fresh eggs. Since most of the eggs in our experiment disappeared after the 8th day, snakes are probably not the dominant users of this resource.

The deposition experiment imitates the natural situation of infertile or abandoned eggs because hen eggs are approximately the size of tinamou eggs. Published data on densities of ground nests in tropical forest are not available but we believe that eggs on the ground occur in considerable numbers. In the Andean foothill forests and the Amazonian tropical rain forests of Ecuador, for instance, there are 26 species of tinamous (Tinamidae), woodquails (Odontophoridae) and nightjars (Caprimulgidae) that lay their eggs on the ground, and some of these species are common (Ridgely *et al.* 1998; Hilty and Brown 1986). Moreover, tinamous have an extended time of breeding (Cabot 1992), theoretically making eggs available for a large proportion of the year. In Costa Rica, *Tinamus major* (Gmelin 1789) breeds from January to October (P. L. R. Brennan pers. comm.). Finally, at least in tinamous and quails, the percentage of eggs that do not develop is quite high. At the study site in Costa Rica, probably 15% of eggs of *T. major* did not hatch (P. L. R. Brennan, pers. comm.). In European and Japanese quails, egg infertility is about 20% and can increase to 60% through inbreeding (Saint-Jalme *et al.* 1986; Sato *et al.* 1984). Thus, abandoned or infertile eggs of ground-breeding birds (containing either egg protein or dead embryos) are likely to be a regularly available resource.

Up to now, *Coprophanaeus telamon* has been described as mainly necrophagous (Kohlmann 1991:126), although it has also been found on dung (Howden and Young 1981:142; Gill 1986:87). *Coprophanaeus* was not among the beetles which Louzada

Fig. 3. Excavated egg and *Coprophanaeus telamon telamon* (Erichson), same "nest" site.

and Vaz-de-Mello (1997) attracted with rotten egg foam. They found *Dichotomius mormon* (Ljungh, 1799), *D.* sp., *D.* (*Parahyboma*) *furcatum* (Laporte 1840), *Eurysternus hirtellus* Dalman, 1824, and *Uroxys* sp., all of which are dung or carrion feeders. *Coprophanaeus telamon* has not been recorded from their study area, but another species of the genus, *C. bellicosus* (Olivier, 1789), was attracted by carrion there (Louzada and Lopes 1997).

Why is *C. telamon* attracted to eggs? We suggest that the bouquet of volatiles produced by decomposing eggs overlaps with the volatile bouquet of dung and that produced by microbial decomposition of meat. Odorous components of faeces that attract dung beetles most efficiently, particularly as a bouquet, are 2-butanone, cresol, indole or skatole, and butyric acid (F.-T. Krell, T. Schmitt, G. Herzner and S. Krell-Westerwalbesloh unpubl.; Inouchi *et al.* 1988). 2-butanone and butyric acid are also among the products of bacterial spoilage of meat, together with acetone, dimethyl disulphide, and esters of fatty acids (Whitfield 1998). Except for 2-butanone, all these volatiles have been identified in fermented suspension of whole egg powder (Bullard *et al.* 1978; Hwang *et al.* 1976), with fatty acids like butyric acid making up the largest fraction of the volatiles. The complete list of volatile substances that might play a role in dung beetle attraction is certainly much longer. However, we conclude from the high efficiency of 2-butanol, indole, skatole and butyric acid in attracting many species of dung beetles, and from the occurrence of these four volatiles in the odour bouquet of either dung, spoiled meat or rotten eggs, that they may be responsible for attracting *C. telamon* to eggs in decomposition.

Fatty acids (C_2-C_5), which are odorous components of fermented eggs, are also present in the scents of many mammals (Bullard *et al.* 1978), and fermented egg products are used to attract coyotes (*Canis latrans* Say) (Linhart *et al.* 1977). Thus, the eggs in our experiment may have attracted some mammals and caused them to relocate or feed on the eggs, acting as potential competitors of the dung beetles.

Further experiments and chemical analysis are needed to clarify exactly how *C. telamon* uses bird eggs, and to confirm our volatile overlap hypothesis. Experiments with small eggs (like those of quails or nightjars) would be interesting to explore whether other, smaller dung beetles species are also using eggs, but could simply not handle hen eggs.

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BOOK REVIEW

KUSCHEL, G. 2003. **Nemonychidae, Belidae, Brentidae (Insecta: Coleoptera: Curculionoidea). Fauna of New Zealand 45**, 100 pp. ISBN 0-478-09348-9. Price: $40.00 US (including packing and postage). Available at the Manaaki Whenua Press Website: www.mwpress.co.nz.

This monograph is an important and welcome contribution by a world authority of curculionoid paleontology, phylogeny, and evolution. Its author has enjoyed an impressively long and productive career, working on weevils of predominantly the southern hemisphere since the mid 1940s (Zimmermann 1993). The present volume will only add to this legacy. It is a *tour de force* of related yet also partly independent results and conclusions, reminiscent of Kuschel's influential 1995 analysis of Curculionoidea. The range of information presented within the 100 pages could easily constitute a series of articles. With respect to the treated subject areas it will be a reference framework for generations to come.

Kuschel provides a comprehensive overview of three of the four orthocerous weevil families occurring in New Zealand: Nemonychidae, Belidae, and Brentidae. Holloway (1982) revised the remaining family Anthribidae in an earlier volume from the same series. The monograph includes keys to genera and species with detailed descriptions of all taxa, and a key to the families of adult New Zealand Curculionoidea. A total of 17 species are treated in this work: one genus and four species of Nemonychidae; six species in four genera of Belidae; and seven species in six genera of Brentidae. Three of the genera and six of the species are new. The book includes 187 illustrations, with habitus drawings for 12 of the species, numerous additional drawings including side views, drawings of the head, mouthparts, hind wings, genitalia, and several photographs and scanning electron micrographs. Distribution maps are provided for each species.

In addition to the revision, Kuschel discusses host plant relationships of orthocerous weevils in New Zealand, gives a brief overview of fossil weevil families, and contributes information about glands associated with the female reproductive tract of many weevils. Finally, a phylogenetic analysis of the genera of Belinae is included in an appendix written by Kuschel and R. Leschen.

In his section on host-plant information, Kuschel notes that in New Zealand, Australia, and Chile over 50% of weevils having host-specific relationships with conifers are orthocerous. This contrasts remarkably with 2.5% of weevils in Europe specializing on conifers being orthocerous. The author hypothesizes that this dissimilarity between Orthoceri in the southern versus the northern hemisphere could be due to differences in the level of climate change between them, as well as the loss of Araucariaceae and Podocarpaceae and the great success of Scolytinae in temperate northern zones. A list of known host plants for each of the 17 revised species is also included.

Kuschel discusses the general patterns of distribution for each of the four families of orthocerous weevils occurring in New Zealand, as well as their levels of endemicity. Apparently, these taxa are most closely related to genera from New Caledonia, then from Australia, the area northwest of New Caledonia to Sulawesi, and finally Chile.

The section entitled "Fossil Evidence" is not specific to New Zealand, and contains information relevant to anybody interested in the taxonomy of fossil weevils. The author provides evidence for the exclusion of the fossil family Obrieniidae from the Curculionoidea. Characters considered important for the placement of Eobelidae, Ulyanidae, and Eccoptarthridae are discussed, and relationships among these and extant taxa are suggested.

Based on their phylogenetic analysis of the genera of Belinae, Kuschel and Leschen propose that Agnesiotidini (*sensu lato*) and Pachyurini are paraphyletic. Belini and Agnesiotidini (*sensu stricto*) are monophyletic yet their positions within the phylogeny are still ambiguous. Pachyurini is paraphyletic and should be recognized only for convenience. Clearly these insights will form a basis for further discussions at the upcoming Phytophaga symposium in Brisbane, Australia.

In light of such a wide scope and the duration of the study it is understandable that some idiosyncrasies will occur. We have noticed that the quality of the illustrations is inconsistent, ranging from excellent to somewhat ambiguous. Most of them lack scale bars. In our view it is also useful to complete a cladistic analysis by selecting a particular cladogram and optimizing the included characters along its branches, even if the overall consensus is less resolved. Character optimization is the most efficient way to convey the diagnostic achievements and problems inherent in a character matrix, particularly when morphological characters are used. Apparently the author also omitted results from recent and critical publications on fossil weevils by Gatshev and Zherikhin (R. Oberprieler, pers. comm.).

These minor issues notwithstanding, we strongly recommend Kuschel's authoritative and wide-ranging monograph to anyone interested in the fauna of New Zealand. For experts and students of phylogeny and evolution it represents a valuable step towards the understanding of the origins of the Curculionoidea as a whole. The shipping costs are conveniently included in the moderate price for this paperback edition.

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