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Coleoptera: Scarabaeidae
Observations on the behavior of a tropical rain forest dung beetle, Megathoposoma candezei (Harold),

by

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ABSTRACT: *Megathoposoma candezei* dung beetles at the southern base of Cerro Nara, 17 km north of the mouth of the Savegre River, on the southern Pacific slope of Costa Rica, are diurnal, in contrast with the Mexican populations; there are from 15 to 19 beetles per 50,000 m² at 760-780 m elevation; below 600 m populations diminish considerably. Among the more obvious protective mechanisms are cryptic coloration and thanatosis which may last over two hours. These beetles avidly seek human excrement which they make into almost perfect balls, coat with mud, and bury in superficial chambers where they spend about 60 hours consuming them.

Copulation takes place over the food pile, which represents the most primitive level of sexual behavior so far known in Scarabaeini; rolling of the dung balls by couples was not observed.

Megathoposoma candezei is a typical dung beetle of the tropical rain forest, never found in open places. It is perhaps, together with some of the *Deltochilum,* one of the largest species of Canthonina found in the tropics. Its color is brownish with greenish tones, with a series of small dark spots on the elytra, and measures from 18 to 28 mm in length (HALFFTER & MARTINEZ, 3; Figs. 1, 2, 3). This species was reported from Chiriquí, Panamá, Chontales, Nicaragua and Palenque, Chiapas, México. Howden, cited by HALFFTER and MARTÍNEZ (3), reported that he had seen specimens from Costa Rica, without mentioning the locality. *Megathoposoma candezei* was a rare species until Halffter collected the first series of 16 specimens in Mexico in 1965, and later I collected more than 50 specimens in 1967 and 1972. The great majority of the forest dung beetles, including *M. candezei* in Palenque, Chiapas, Mexico (3,

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4), are nocturnal, while those collected at Cerro Nara, Costa Rica, are diurnal. They avidly seek human excrement; in a matter of a few seconds, for instance, the first one or two beetles can be heard buzzing and seen flying close to the ground in zigzags or semicircles as they approach the food source. They ignore either cattle or horse dung. It is possible that their natural food is the excrement of wild pigs, *Tayassu tajacu,* one of the most common big mammals in the area, whose dung is apparently similar to that of man (4).

It is interesting to point out that *M. candezei* is very abundant at the southern base of Cerro Nara, at an altitude of 760 to 780 meters. At the northern base of the peak, and at an altitude of 850 meters, no beetles of this species were found. Experiments with human excrement at different altitudes at the southern base of the peak confirmed that the optimum altitude was 760-780 meters, where from 15 to 19 beetles approached each pile of excrement, placed not less than a 50 meters apart. Below 600 meters the number of beetles at the food sources diminished considerably. At 600 meters, for instance, three sources of food were placed, with the following results: Nº 1, one beetle; Nº 2, three beetles; Nº 3, one beetle.

GENERAL BEHAVIOR

PROTECTIVE BEHAVIOR: *Megathoposoma candezei* has two protective mechanisms: cryptic coloration and thanatosis. These two mechanisms are closely related and function as a unit. When a beetle is touched or disturbed it displays a long-lasting thanatosis or death-feigning, and its color blends very neatly with the background (Fig. 4), making it almost impossible to detect. Two specimens at a food source displayed thanatosis before they were picked up, and it was not possible to locate the exact spot where they landed until they began to make their dung balls two hours later. Thanatosis was observed to last, in five beetles touched just once and then left alone (except Nº 2, which was turned on its back), 15, 30, 90, 105 and 140 minutes, with a mean of 76 minutes. This type of protective behavior is, without any doubt, very effective at least against entomologists. We can assume that there is a predator that feeds on these beetles, possibly a bird or a reptile. According to GOLJAN (2) many birds feed on dung beetles in Poland, at least when food is scarce. On the other hand, HALFFTER and MATTHEWS (4) remark that "To escape birds, it is evidently better to get out of sight as quickly as possible, while to escape herptiles it is better to remain immobile".

BALL-MAKING BEHAVIOR: About 50 per cent of the beetles observed landed directly on the food source, and proceeded to make their balls immediately. Most of the others, which landed a few centimeters away, walked directly under the excrement, where they spent about 10 to 30 minutes, after which they made their balls. Most beetles started to cut the excrement at the edge with the clypeus and the fore legs. Since the ball-making behavior of these

beetles is essentially the same as that of other dung beetles, references should be made to those authors describing these events in detail (COMIGUAN, 1; HALFFTER and MATTHEWS, 4). The beetles very rapidly build up a mass of dung (Fig. 5) which is quickly made into an almost perfect ball. The whole process takes from 2 to 5 minutes, usually less than 5, then they may roll the ball from the food source to a distance of about 30 to 40 cm, where they proceed to coat the surface with mud. This is done by simple rotation of the ball against the soil with the fore legs for about 8 minutes. A few beetles coat the balls while they are under the excrement. Twelve coated balls were measured and found to vary from 17 to 26 mm in diameter (Figs. 6, 7), the size apparently differs according to the size of the beetle. HALFFTER and MATTHEWS (4) report that the middle and hind legs are used as calipers to estimate the size of the ball.

Theft of the dung ball by a larger beetle or through temporary carelessness of the victim was observed twice. In these cases combats my easily develop, but usually the larger beetle wins. The beetles readily accept any dung ball, providing that size and weight are within their normal range. When the dung ball is taken away from a beetle, it spends a short time looking for it but soon starts to make a new one.

ROLLING AND BURIAL OF THE BALL: When rolling the ball the beetle holds it with the middle and hind legs and pushes backward with the fore legs, with the head down (Fig. 8, 9, 10, 11). One beetle per ball was always observed. On encountering an obstacle the beetle may temporarily leave the ball in order to investigate the situation. All the beetles observed rolled the balls from 40 to 180 cm away from the food source, where they proceeded to excavate superficial chambers to bury them. Figure 14 shows the relative paths, directions and distances taken by several dung beetles from two different food sources and the places where they buried their balls (marked with an X). When the beetles are ready to bury their balls they may either dig around and under them, or to one side, or they may abandon them from 30 minutes to more than two hours while they search for a more suitable place to dig. In either case they dig using the clypeus as a shovel and the fore legs to push the debris out. They usually excavate a very superficial chamber, just big enough to accomodate the ball and themselves (Fig. 15). Sometimes they may go under a stone or take advantage of natural cavities. Beetles have been observed pulling the ball inside of the chamber with the hind legs with a head-up position (Figs. 12, 13). Usually the forest floor is strewn with litter, and therefore their activities are performed under cover. It was necessary to clear the ground beforehand to observe the whole process.

Observations revealed that the buried dung balls were eaten by the beetles in about 60 hours and were not used for egg-laying. It is interesting to point out that the next day, after all the beetles in a particular area had made their chambers and were busy eating, only one beetle approached a new source of

fresh food. This seems to show that actually there is a maximum of 15 to 19 beetles per 50,000 m² at the optimum altitude.

COPULATION: According to HALFFTER and MATTHEWS (4) it is quite unusual to observe copulation of the Scarabaeinae group of dung beetles. I was, however, lucky enough to witness the whole process in *Megathoposoma candezei.* It is perhaps advisable to transcribe directly the field notes.

> January 9, 1972: Food source placed at 8:04 AM. First beetle arrived at 8:11 and almost immediately started to make a ball. At 8:12 a second beetle arrived, slightly smaller than the first, went directly under the excrement where it stayed for several minutes, then came up at 8:20 and mounted the first beetle, as if trying to copulate with it. As the first beetle (possibly the female) was making a dung ball, it stopped doing so while the second one (possibly the male) climbed on its back. They stayed in this position, without actually copulating, for 7 minutes. At 8:27 copulation started, the aedeagus was inserted into the female gonopore (Fig. 16). It is interesting to note that the female continued working on the dung ball during copulation, although at a slower rate.

According to G. Halffter (personal communication) copulation at this stage represents the most primitive level of sexual behavior in Scarabaeini. While these events were taking place other beetles arrived, one at 8:15, another at 8:17 and a third at 8:37. The female in copulation finished a perfect ball, uncoated, at 8:42 (30 minutes later). At 8.55 copulation ended, the whole process lasted 23 minutes. The male, after wandering about came back to the female and took away her dung ball, she did not fight, but made a new one in 10 minutes, coated it and went away. In this case the female was larger than the male.

CONCLUDING REMARKS

Although the present paper must be considered as a preliminary study of *Megathoposoma candezei,* some interesting observations can be made. While the population observed by HALFFTER and MARTÍNEZ (3) in Palenque, México, was nocturnal, that studied in Costa Rica was diurnal. This phenomenon could be interpreted as representing two subspecies, morphologically identical but ecologically different. We can assume that the diurnal condition is a secondary adaptation, and that there must be an ecological advantage in being diurnal in Costa Rica. To my knowledge, the most likely reason is that in the area of study there is an abundant population of *Bufo marinus,* and possibly other species of large toads, like *Bufo haematiticus,* both nocturnal feeders; if our beetles were nocturnal, there is no doubt that they would soon become the main food-source of these toads. The new adaptation of our beetles has apparently avoided them this problem. Another important protective behavioral adaptation is death-feigning or thanatosis. It would be intersting to learn whether the Mexican populations undergo long-lasting thanatosis as do ours.

As mentioned before, we can assume that there is a predator that feeds on these beetles, the problem is to find a suitable diurnal candidate in Costa Rica. Among herptiles the most suitable ones are the toads, which may also be among the major predators of these beetles in Mexico, but in Costa Rica this is not the case; snakes are out of the question. Among the lizards the only ones abundant in our study area are those of the genus *Anolis,* which are too small, or live in trees several meters above the forest floor and therefore do not constitute a real danger to *M. candezei.* Apparently this would leave us only with small mammals and birds as possible predators.

Among the mammals the most likely ones in our area are nocturnal, while the birds may offer several possibilities: The tinamous (Tinamidae) are terrestrial birds of the forest floor, and can eat insects and other small animals. The trogons (Trogonidae) are forest birds that feed on large insects, and are abundant in our area. The antbirds (Formicariidae), some of which are terrestrial forest species, are mainly insectivorous. These insectivorous birds seem to be the most suitable candidates as predators of dung beetles. However, further research is needed in order to arrive at definite conclusions.

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RESUMEN

El presente trabajo consiste en una serie de observaciones sobre *Megathoposoma candezei* (Coleoptera: Scarabaeini), llevadas a cabo en la base sur del Cerro Nara (17 km norte de la desembocadura del río Savegre, en la costa del Pacífico de Costa Rica). Entre los hechos más interesantes se pueden destacar los siguientes: la población de Costa Rica es diurna, en contraste con las observadas en México que son nocturnas. Se encontró de 15 a 19 abejones en una área de media hectárea aproximadamente, a una altura de 760-780 metros; más abajo de los 600 metros el número de abejones disminuyó considerablemente. Entre las formas de defensa más evidentes están la coloración críptica y la tanatosis, que puede durar más de dos horas.

Estos abejones hacen bolas casi perfectas de excremento humano, las cubren con una delgada capa de barro; luego excavan cámaras superficiales, donde las entierran y en donde pasan dos días consumiendo esta provisión.

Entre los hechos más sobresalientes observados está el de que la copula-

ción se lleva a cabo sobre el montón de alimento, lo que representa el nivel más primitivo de comportamiento sexual hasta ahora conocido en los Scarabaeini; no se observó el rodamiento de las bolas por parejas de *Megathoposoma candezei.*

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Figs. 1, 2, 3. General aspect of *Megathoposoma candezei* showing a series of small dark spots on the elytra.

Fig. 4. Cryptic coloration of the beetle.


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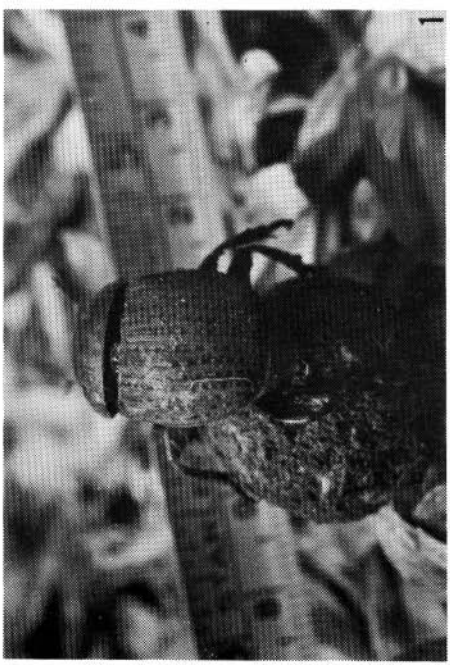
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Fig. 5. Beetle building up a mass of dung which is quickly made into an almost perfect ball.


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Figs. 6, 7. Size of the coated dung ball. Fig. 6 shows some toilet paper which was included when the ball was coated.

Figs. 8, 9. Typical position when rolling the ball.

Figs. 10, 11. Typical position when rolling the ball.
Figs. 12, 13. Beetles pulling the ball inside the chamber.


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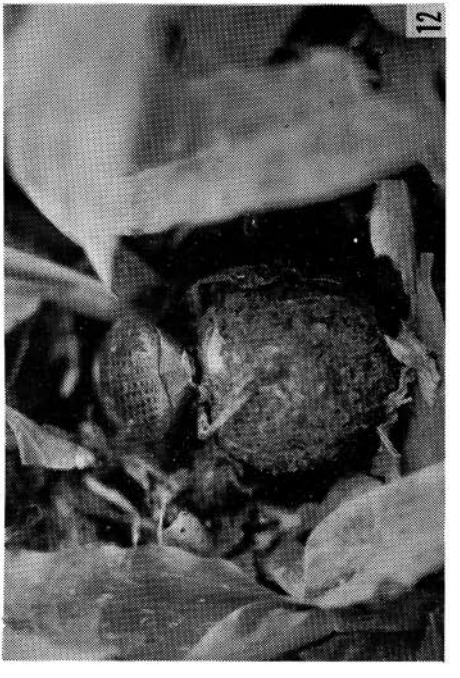
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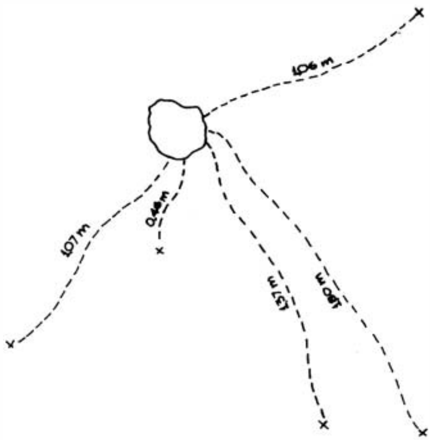
Fig. 14. Relative paths, directions and distances taken by several dung beetles from two different food sources and the places where they buried the dung balls (marked with an **X**).

Fig. 15. Superficial chamber, just big enough to accomodate the ball and the beetle.



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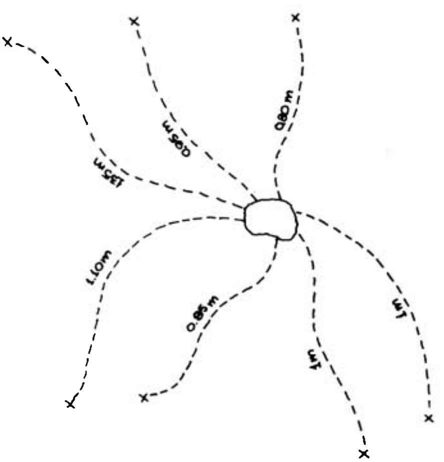

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Fig. 16. *Megathoposoma candezei* copulating on top of the food source.


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