ECOTROPICA 15: 35–41, 2009

TEMPERATURE-DEPENDENT KLEPTOPARASITISM IN A NEOTROPICAL DUNG BEETLE

Orrey P. Young

Department of Zoology, University of Maryland, College Park, Maryland, USA

Abstract. On Barro Colorado Island, Panama, a competitive interaction between *Canthon septemmaculatus* (Coleoptera: Scarabaeidae) and other members of the diurnal dung beetle community is postulated to be facultative kleptoparasitism. The occurrence of this interaction is dependent on the frequency of contact between species, ambient temperature, and the presence or absence of sunlight. On cool mornings *C. septemmaculatus* is likely to perch on sunlit leaves and then attempt the pirating of rolled balls or butted chunks of dung from other species in areas peripheral to the dung source, particularly if many individual beetles are already on the dung source. During warmer afternoons movement directly onto a dung source is most likely, without perching on sunlit leaves and without pirating. This behavior is best explained by the energetic needs of an ectothermic beetle and its competitive relationship with the numerically dominant dung beetle on the island, *Canthon angustatus*. *Accepted 27 May 2009.*

Key words: Barro Colorado Island, Canthon septemmaculatus, *ectothermy, competition*, Canthon angustatus.

INTRODUCTION

The study of the beetles that acquire dung for food and nesting has a long and fruitful history. In the Neotropics, numerous studies have documented the composition and characteristics of dung beetle communities (e.g. Andresen 2005, Horgan 2007, Larsen *et al*. 2008). Some of the particularly interesting aspects of these communities are the mechanisms by which each species is able to sustain itself in the face of both intra- and interspecific competition. On Barro Colorado Island (BCI), Panama, I looked at those mechanisms and discovered that behavioral thermoregulation by some dung beetles may play an important role in determining their success or failure in acquiring dung material. One species in particular, *Canthon septemmaculatus* (Latreille) (= *Csep*) (Coleoptera: Scarabaeidae), has previously been documented to perch on leaves in the sun in the morning but not later in the day, suggesting a need to "warm up" before competing at a dung source (Young, 1984a). Not surprisingly, the situation is not that easily described. The following report describes some of the other parameters that affect the behavior of this species at food resources.

* e-mail: ory2pam@verizon.net

METHODS

Observations of naturally occurring dung and its consumers were conducted on Barro Colorado Island (BCI), Panama, for a total of 15 months during 1974 and 1975. This island is located in Gatun Lake, part of the Panama Canal, and is a biological reserve operated by the Smithsonian Tropical Research Institute. Approximately 1500 ha in area, the island is covered with a semi-deciduous moist lowland forest with distinct dry and wet seasons. The flora, fauna, and climate of BCI have been studied since 1923 and are well documented (e.g. Croat 1978, Windsor 1990, Leigh *et al*. 1996).

Field. During the 15-month period, daily observations were made throughout the island involving both the producers and consumers of dung, with supporting laboratory observations and experiments. In the field, 100-m trailside strip censuses of leaf-perching beetles were conducted monthly at several locations to obtain species profiles of perching behavior and a measure of population characteristics. Baited pitfall trapping and bare-ground baiting with dung and carrion were also employed on a monthly basis. Occasional specific experiments and observations were also conducted involving particular beetle species. The timed observations documented in Table 1 were obtained on BCI from naturally occurring

howler monkey (*Alouatta palliata*) feces on a total of 10 days during the wet season period of 21 September–10 October 1975. Daytime temperature values were obtained from the instruments maintained by the island research staff (summarized in Windsor 1990).

Laboratory. During a 12-day period during September–October 1975, a series of four experiments was conducted in the open-air laboratory on BCI. These experiments matched various densities of *Csep* with another diurnal ball roller, *Canthon angustatus* Harold (= *Cang*). This species is smaller (6.5-8.0 mm) than *Csep* (8.5–12.0 mm), but is the numerically dominant diurnal dung beetle on BCI (Young 1978, Howden & Young 1981). These competition experiments were conducted in the presence of howler monkey dung and the subsequent number and size of dung balls each species possessed was recorded. The container was a 15 x 15 cm glass container with rounded corners, 20 cm in height with soil to a depth of 2 cm and a screen lid. Beetles were captured mornings in the field at howler monkey dung and held in the lab in darkened containers (to reduce activity) for several hours until the day's experiment began at 11:00 h, when air temperature was about 27°C. An amount of fresh howler monkey dung ca. equal to the amount contained in the dung balls of 4 *Cang* and 4 *Csep* was placed on soil in the center of the container (diameter of pile 3 cm). In the first three experiments (#s 1,2,3), single individuals of *Cang* were placed first in the container, then five minutes later single individuals of *Csep* were added. After 10 more minutes, the number of dung balls possessed by each beetle and its diameter was recorded. In the final experiment (#4), the sequence of adding each species was reversed, with *Csep* added first.

Laboratory observations of interactions between *Csep* and six other scarabaeine dung beetle species during this same period were conducted within a terrarium (122 x 30 cm) exposed to ambient daytime temperatures. Three species were large diurnal "butters", pushing with their head chucks of dung that they had cut from a dung pile, and were at least twice as heavy as *Csep* (Young, 1978). Those species and their lengths were: *Phanaeus pyrois* Bates (14–17 mm), *P. beltianus* Bates (14–18 mm), and *Sulcophanaeus cupricollis* (Newinson)(18–20 mm) (Howden & Young 1981). Five individuals of each species were separately placed in the terrarium with an amount of fresh howler monkey dung equivalent to the size of one *Csep* ball. After 10 minutes, a single *Csep* was added and the results of any interaction between the two individuals was noted after an additional 20 minutes. Three other smaller butter species were also examined with the same procedure: *Canthidium haroldi* Preudhomme (8–10 mm), *C. elegantulum* Balthasar (5–7 mm), and *C. aurifex* Bates (3–5 mm) (Howden & Young 1981).

RESULTS

Field observations. Based on many hours of field observations, the following composite picture of typical interactions at a common dung resource involving *Csep* can be presented.

During the early wet season (May–June), *Csep* arrives at 09:00 h at a fresh deposit of howler monkey dung and either: **1a** – if there are few or no other dung beetles on the dung, *Csep* flies directly to the dung, or **1b** – if there are many dung beetles already on the dung, *Csep* either: **1ba** – lands on the dung, **1bb** – lands on the ground ca. 30 cm from the dung, or **1bc** – flies to plant adjacent to the dung and alights on leaf 1 m above ground and in the sun.

If **1a,** *Csep* proceeds to cut out dung, pack it into a ball, and roll the ball away (**2a**).
If **1ba**, *Csep* attempts to either cut and pack a ball or take a ball away from another beetle (**2 b**).
If **1bb**, *Csep* waits for a beetle to roll a dung ball in its direction, then attempts to take it away from the resident beetle (**2c**).
If **1bc**, *Csep* remains in sun for at least several minutes, then flies down to the dung pile and attempts to cut out and pack a ball amongst the other competing beetles (**2d**).
If **2a**, *Csep* may have to defend its ball, perhaps successfully, from another *Csep* waiting nearby.
If **2b**, *Csep* is usually unsuccessful in obtaining a dung ball, and eventually leaves (**3a**).
If **2c**, *Csep* is successful in obtaining balls from other *Csep* and from other smaller ball-rollers except *Cang* (**3b**).
If **2d**, *Csep* is successful in obtaining balls from all other beetles (**3c**).
If **3a**, *Csep* may return to leaf surface in sun, or depart the area.
If **3b**, *Csep* loses some or all of its ball to one or more smaller but quicker *Cang* (**4a**).

TABLE 1. Behavior of *Canthon septemmaculatus* at food sites on Barro Colorado Island, Panama.

Time (hrs)*	Mean temp. °C at midpoint of observ. period	No. on leaf surfaces	No. on ground	No. pirating dung	No. obtaining dung from central site	Percent pirating**
0900-1100	24°	18	12	9	5	9/14 = 64
1100-1300	27°	19	21	7	18	7/25 = 28
1300-1500	29°	17	40	2	40	2/42 = 5
Totals		54	73	18	63	18/81 = 22

* Data collected during non-rainy periods on 10 days (data combined) during a 20-day period, September–October 1975.
** Based on successful obtainers of dung.

If **3c**, *Csep* with its ball must run the gauntlet of other beetles waiting around the dung pile (**4b**).
If **4a,** *Csep* may return to leaf surface in sun, or depart the area.
If **4b**, *Csep* may lose some or all of its ball to one or more smaller but quicker *Cang* or to freshly arrived *Csep*.

This sequence of events is altered when the howler monkey dung becomes available later in the day than ca. 12:00 h (Table 1). *Csep* in the afternoon does not perch on leaves exclusively in the sun and probably flies directly onto the dung resource, does not wait on the ground nearby to capture passing beetles with balls, and is usually successful in defending a ball from both other *Csep* and *Cang*.

During the late wet season (September - October) a different situation exists; *Csep* switches to consuming mostly carrion when it is available (Young 1978), and although it occasionally occurs perching on leaf surfaces near carrion, it does not attempt to pirate balls in areas adjacent to the carrion source. One result of this food shift is the avoidance of *Cang*, which is a very successful specialist throughout the year on howler monkey dung. When carrion is not available *Csep* is forced to compete at dung sources, with the results depicted above if the dung is from howler monkeys. When the dung is produced by some other vertebrate, *Csep* is much more successful in obtaining dung.

A closer examination of the characteristics of the dung balls that *Csep* and other species prepare indicates some of the difficulty that this species has in obtaining dung (Table 2). *Csep* typically ignores balls possessed by *Canthon lamprimus* Bates (= *Clam*), probably because the balls are so small that it would require six or more *Clam* balls to equal one *Csep* ball. Two balls of *Cang*, however, would approximate one *Csep* ball. The ball that *Csep* could thus create by pirating is usually about 25% smaller than the ball that *Csep* could create from the original dung source, but is usually sufficient for *Csep* to move away with the composite ball (Table 2).

Occasionally an individual of a large dung beetle species that is a butter of chunks of dung, rather than a roller of balls, will appear at the same howler monkey dung source as *Csep*. These diurnal species include *Phanaeus pyrois*, *P. beltianus*, and *Sulcophanaeus cupricollis* (Howden & Young 1981). Individuals of these species are all at least 14 mm in length and at least twice as heavy as *Csep* (Young 1978). *Csep* can easily take the chunk away from any of these individuals, in cool or warm situations, pack it into a ball, and roll it away from the dispossessed beetle. The same is true for the smaller butter species, such as the three *Canthidium* species.

Laboratory competition experiments. Table 3 indicates the problems individuals of *Csep* have competing with the most abundant diurnal dung beetle on BCI. When *Cang* arrives first at a howler monkey dung site, which is usually the case, only when there are few *Cang* and plenty of dung is *Csep* able to create and retain normal-sized dung balls (Experiment #1). When *Csep* arrives after *Cang* and is outnumbered, *Csep* success rate and size of dung ball is diminished (Experiment #2), usually to zero (Experiment #3). On the rare occasions when *Csep* arrives first, and *Cang* is late and in low numbers, *Csep* is able to achieve some success in creating and retaining dung balls (Experiment #4).

TABLE 2. Size and weight characteristics of three species of Scarabaeinae and their obtained dung balls on Barro Colorado Island, Panama.

Species	Beetle* length (mm)	Beetle wet weight (g)	Ball** diameter (mm	Ball wet weight (g)
Canthon septemmaculatus (non-pirated)	8.5-12.0 (n = 25)	0.15 (n = 25)	14-20 (n = 20)	1.58 (n = 20)
Canthon septemmaculatus (pirated)	8.5-12.0 (n = 15)	0.15 (n = 15)	11-14 (n = 11)	1.21 (n = 11)
Canthon angustatus	6.5-8.0 (n = 25)	0.05 (n = 25)	9-12 (n = 20)	0.70 (n = 20)
Canthon lamprimus	5.5-7.0 (n = 12)	0.01 (n = 12)	5-8 (n = 8)	0.18 (n = 8)

* Measurements of males and females combined.
** Some balls had both male and female in possession.

Competition experiments with the three large species of "butter" dung beetles were supportive of the field observations. In each of the 15 exposures of a butter individual with a single *Csep*, the butter lost to *Csep* the chunk it initially possessed. Results of the competition experiments with the three smaller butter *Canthidium* species were mixed. The largest *Canthidium*, *C. haroldi*, in five exposures to *Csep* lost its chunk every time. Chunks that the two smaller *Canthidium* species created were apparently too small for the *Csep* to contest, as the *Csep* individual inspected and then left alone the chunk and its beetle.

DISCUSSION

Stealing, pirating, taking – terms that have been variously applied to behaviors associated with competition between animals. A more formal description of these actions can be presented by use of the term kleptoparasitism, which etymologically refers to the theft by one organism of any already procured resource from another organism (Iyengar 2008). For the purposes of this discussion, the term refers to the facultative direct interaction with a host possessing food. Among arthropods, this behavior has been described in social Hymenoptera, Diptera, Coleoptera, Hemiptera, Araneae, and Acarina (Iyengar 2008). Within the Coleoptera, members of the Staphylinidae (Seevers 1965), Silphidae (Trumbo 1994), and Scarabaeidae (Hammond 1976) are most frequently identified as kleptoparasites.

In the Scarabaeidae, two types of kleptoparasitism have been described: (1) small beetles entering dung balls of larger species while they are being made or after they have been abandoned, and (2) smaller species buried in a dung brood mass of larger

TABLE 3. Laboratory experiments matching various densities of *Canthon angustatus* and *Canthon septemmaculatus* in a closed container with howler monkey dung on Barro Colorado Island, Panama.

	#Cang	#Csep	#Cang w/balls	Size of balls (diam., mm)	#Csep w/balls	Size of balls (diam., mm)
Experiment #1 (day 1)	4	4	4	9-12	4	12-20
Experiment #2 (day 5)	12	4	12	7-8	1	8
Experiment #3 (day 10)	36	4	27	3-6	0	0
Experiment #4 (day 12)	12	4	12	6-9	2	7-10

Cang = *Canthon angustatus*
Csep = *Canthon septemmaculatus*

species (Hammond 1976, Martin-Piera & Lobo 1993, Davis & Huijbregts 2000). Within balls of *Canthon* and *Scarabaeus* may be species of (e.g.) *Onthophagus* or *Caccobius*; within buried brood masses of *Copris*, *Thorectes*, *Geotrupes*, *Onthophagus*, and *Phanaeus* may be smaller species of (e.g.) *Onthophagus* and *Aphodius* (Hammond 1976). None of the various reports of kleptoparasitism in dung beetles describe the active taking by one species of the dung ball or chunk possessed by another species.

Barro Colorado Island contains at least 55 species of scarabaeine beetles that occur at carrion, dung, and/or rotting fruit/fungi (Howden & Young 1981). Of the 28 species that are diurnal, and excluding the seven very rare species and the one species that is an exclusive carrion feeder, 20 species occur at dung. Of those 20 species, 13 roll or butt dung away from the dung site for eventual burial. In that group of 13 species, there are two that are among the most abundant on the island, a roller, *Canthon angustatus* (*Cang*), and a butter, *Canthidium aurifex*. In the group of seven roller species, the largest is the unusual species *Canthon septemmaculatus* (*Csep*). This species is distributed from Panama to Argentina, occurring in shrub-land, forest-pasture ecotomes, dry open forests, and in cleared areas within moist forests (Howden & Young 1981), indicating that it is more common in open habitats than in closed-canopy forests such as on BCI, and that it probably is better adapted thermally to those open habitats.

Even given this probable adaptation to such habitats, *Csep* is fairly common on BCI, and is the only species of Scarabaeinae seen to routinely steal/pirate/take dung balls/chunks from other species in the immediate vicinity of the resource. This usually occurs when *Csep* first arrives in the area of a food source. If other beetles are already there and no "moving" food is available, or if unsuccessful in a fight for a food item, *Csep* may then move onto the main food source. Further observations and experiments, however, have shown that this pirating behavior was not that easily defined.

Why does Canthon septemmaculatus *pirate dung from conspecifics and other species?*

1. Perching on leaf surfaces above the ground is a common activity for diurnal dung beetles, as at least 15 species on BCI can be found sometime during the day on leaves (Young 1984b).

2. Waiting for a dung ball to come along on the ground is the strategy sometimes used by single males and females of this and other *Canthon* species to obtain a ball and a mate. Thus sitting on the periphery of activity at the food source may not be unusual.

3. If the ball that comes along is controlled by a conspecific, depending on the size of the beetle the waiting *Csep* individual may either fight for possession of the ball or let the ball and beetle pass.

4. If the approaching ball is possessed by a nonconspecific, the possessor is probably much smaller than *Csep*, whereupon *Csep* may just take over and keep it. The ball would probably be too small for eventual use, so *Csep* may just sit with it and wait for another to come along, adding the two balls together and then rolling the composite ball away. If the approaching beetle is not a roller but is butting a chunk of dung, *Csep* can easily take the chunk away, pack it into a ball, and either wait for more or leave the area.

5. Ambient temperature may act as an on/off switch. If the ambient temperature is high enough to permit rapid action, *Csep* may immediately upon arrival move onto the dung pile and compete with conspecifics and other species. If the temperature is too low for fast action, *Csep* may merely sit on the periphery and wait for a ball to roll by, ignoring balls occupied by conspecifics of the same or larger size but attempting to take over balls of smaller-sized conspecifics and other species.

6. *Csep* may increase its potential rate of action upon arrival by perching on a leaf in the sun for a period to increase its body temperature before attempting to compete on the dung source. The role of elevated body temperature in dung beetles as it relates to successful activity at a dung source has been documented at elephant dung in Africa (Bartholomew & Heinrich 1978, Heinrich & Bartholomew 1979). As indicated previously for *Csep* (Young, 1984a), considerable internal temperature gain can be obtained by perching on a sunlit leaf, both from radiant energy from the sun and by radiation flux from the leaf substrate.

7. *Csep* has virtually no chance of creating and retaining a normal-sized dung ball from a howler monkey dung pile if many *Cang* have arrived before *Csep*. So *Csep* waits at the periphery of the site for a beetle to come by rolling a ball. If the roller is a smaller conspecific, the waiting *Csep* has a good

chance of obtaining the dung ball. If the roller is a *Cang*, the chances of success are lower, but still possible.

8. Laboratory competition experiments between *Csep* and *Cang* demonstrated that *Cang* moves faster than *Csep* at daytime shade ambient temperature, consistently outcompeting *Csep* at a dung pile and at contested dung balls (Table 3). *Csep* usually can not take a dung ball away from *Cang*, because *Cang* would continually position itself so as to be between the ball and *Csep*. The converse was not true: *Csep* could not retain an intact ball, because *Cang* would cut from under *Csep* a piece of the larger ball and roll the resultant smaller ball away, leaving *Csep* with a reduced-size ball. If a 2nd and then 3rd *Cang* arrived, each would take a portion of the *Csep* ball, finally leaving *Csep* with such a small piece that it would eventually abandon it. The scenario in the field was somewhat different, however. If *Csep* perched on a leaf in the sun before interacting with *Cang*, the beetle was well able to either take a ball away from *Cang*, or defend a ball it already possessed. In other words, at presumed high internal body temperatures, *Csep* is the most successful diurnal fighter at a resource site, obtaining dung from any size of individual of any species.

Energy consumption and competition. Due to typically high levels of competition at a dung food site, losing a food ball to a "pirate" could be very costly. To expend considerable energy detecting and moving to the resource, making a ball, defending it against conspecifics and others while moving it away from the resource site, and then to lose it to another beetle, forces the loser to expend further energy to obtain another food ball. Those individuals with high rates of energy consumption and/or limited energy stores thus have a problem. They either must avoid situations where they could fight and lose possession of a resource, or have a technique for obtaining some amount of resource at most attempts. Both *Csep* and *Cang*, as potential pirate victims with relatively limited energy stores (Young 1978), represent both possibilities. *Cang* employs the strategy of attempting to be quicker, faster, and more aggressive than any other species at howler monkey dung. Individuals arrive early, cut out a piece of dung and pack it fast, rolling it quickly away, in the process aggressively butting out of the way any beetle of any size that is obstructive, expending considerable energy but being consistently successful. Conversely, *Csep* only participates in the scramble competition on a dung source when it is sufficiently "warmed up" to be successful. At other times it waits at the periphery of the resource and attempts to pirate a dung ball, expending very little time and energy in the attempt but achieving some success. The facultative kleptoparastism of *Csep* may be a function of ambient temperature and internal body temperature, representing the typical ectothermic activity pattern of warming up in the morning from an external heat source, in combination with difficulties competing against *Cang*.

ACKNOWLEDGMENTS

Research on Barro Colorado Island during 1974 was supported by the Environmental Sciences Program and the National Zoological Park, Smithsonian Institution, and during 1975 by the Harris Foundation of New York, a Smithsonian Pre-doctoral Fellowship, and the Dept. of Zoology, University of Maryland College Park. Development of this topic was aided by discussions with G. Bernon, T.L. Erwin, H.F. Howden, and D.H. Morse.

REFERENCES

Andresen, E. 2005. Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. Biotropica 37: 291–300.

Bartholomew, G.A., & B. Heinrich. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. Journal of Experimental Biology 73: 65–83.

Croat, T.R. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California.

Davis, A.J., & H. Huijbregts. 2000. Apparent kleptoparasitic behaviour among Bornean rainforest dung beetles (Coleoptera: Scarabaeidae). Coleopterists Bulletin 54: 88–89.

Hammond, P.M. 1976. Kleptoparasitic behaviour of *Onthophagus suturalis* Peringuey (Coleoptera: Scarabaeidae) and other dung beetles. Coleopterists Bulletin 30: 245–249.

Heinrich, B., & G.A. Bartholomew. 1979. Roles of endothermy and size in inter- and intraspecific competition for elephant dung in an African dung beetle, *Scarabaeus laevistriatus*. Physiological Zoology 56: 563–567.

Horgan, F.G. 2007. Dung beetles in pasture landscapes of Central America: proliferation of synanthropogenic species and decline of forest specialists. Biodiversity & Conservation 16: 2149–2165.

Howden, H.F., & O.P. Young. 1981. Panamanian Scarabaeinae: taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). Contributions of the American Entomological Institute 18: 1–204.

Iyengar, E.V. 2008. Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. Biological Journal of the Linnean Society 93: 745–762.

Larsen, T.H., Lopera, A., & A. Forsyth. 2008. Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. Conservation Biology 22: 1288–1298.

Leigh, E.G. Jr., Rand, A.S., & D.M. Windsor (eds.). 1996. The ecology of a tropical forest: seasonal rhythms and long-term changes, 2nd ed. Smithsonian Institution Press, Washington, DC.

Martin-Piera, F., & J.M. Lobo. 1993. New data and observations on kleptoparasitic behaviour in dung beetles from temperate regions (Coleoptera: Scarabaeoidea). Acta Zoologica Mexicana 57: 15–18.

Seevers, C.H. 1965. The systematics, evolution, and zoogeography of staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). Fieldiana (Zoology) 47: 137–351.

Trumbo, S.T. 1994. Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. Oikos 69: 241–249.

Windsor, D.M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Contributions to the Earth Sciences 29: 1–145.

Young, O.P. 1978. Resource partitioning in a neotropical necrophagous scarab guild. Ph.D. Thesis, Univ. Maryland, College Park. 228 pp.

Young, O.P. 1984a. Perching of neotropical dung beetles on leaf surfaces: an example of behavioral thermoregulation? Biotropica 16: 324–327.

Young, O.P. 1984b. Perching behavior in a neotropical forest dung beetle community. Proceedings of the XVII International Congress of Entomology 1984: 337.