

POGONOMYRMEX MAYR HARVESTER ANTS (HYMENOPTERA: FORMICIDAE): AN ADDITIONAL COST ASSOCIATED WITH DUNG BEETLE, *CANTHON IMITATOR* BROWN (COLEOPTERA: SCARABAEIDAE), REPRODUCTION?

MARTIN J. WHITING
Transvaal Museum
P.O. Box 413, Pretoria 0001
South Africa¹

AND

WILLIAM GODWIN
Department of Entomology
Texas A&M University
College Station, TX 77840, U.S.A.

Abstract

Harvester ants, *Pogonomyrmex barbatus* (F. Smith), exerted an energetic cost on the dung beetle *Canthon imitator* Brown through behavioural interference, by causing brood ball abandonment. This was verified experimentally in eight independent trials. Significantly more *C. imitator* (87.5%) abandoned brood balls after encountering *P. barbatus* on ant mounds. No fatalities were recorded from trials although harvester ants were observed to sting and bite dung beetles. Five transects revealed a mean of 10.8 ± 1.11 (range: 9-15) ant mounds/200 m. For a total of 54 ant mounds, brood balls occurred at a mean of 1.3 ± 0.31 (range: 0-13)/mound. Compared to random points, brood balls occurred significantly more often on ant mounds (48% of mounds contained brood balls).

Historically, most reproductive studies have considered energetic costs largely in terms of female allocation to developing eggs or young (e.g., Semlitsch and Gibbons 1978; Brodie and Ducey 1989; Ford and Seigel 1989; Bradshaw *et al.* 1991). Reproductive behavior (e.g. courtship, mate searching, mate choice, parental care, and territory defence) can also be costly, although many animals offset these costs behaviourally (Brodie 1989; Schwarzkopf and Shine 1992; Godin and Briggs 1996). In dung beetles classified as rollers, reproduction involves location of a dung source and construction of a brood ball, followed by rolling and burying of the ball (Cambefort and Hanski 1991). This often occurs in the presence of highly competitive conspecifics (usually males) that fight to take over completed brood balls from one another (Hanski and Cambefort 1991). Therefore, the entire process may be costly, more so if it has to be repeated because the completed brood ball was lost prior to burying.

Preliminary observations of *Canthon imitator* Brown dung beetles in south Texas suggested that many individuals were losing possession of brood balls while traversing *Pogonomyrmex barbatus* (F. Smith) harvester ant mounds. The purpose of this study was to (1) test the response of dung beetles rolling balls

to encounters with harvester ants on the colony mound; and (2) determine if the presence of abandoned brood balls on ant mounds was nonrandom.

Canthon Hoffmannsegg is a new world genus of small to medium-sized dung beetles comprising 148 species, most of which feed on dung, although a few are carrion specialists (Gill 1991). In the *Canthonini*, construction of a brood ball is initiated by the "active" partner (most often the male), and may serve as a sexual display for the "passive" partner. The brood ball may be rolled by both sexes, although in some species the male rolls the brood ball with the female attached. *Canthon imitator* is often locally abundant and quick to locate a dung patch (Type I of Hanski 1991).

Pogonomyrmex barbatus is a common resident of the southern United States, extending to southern Mexico (Cole 1968). Harvester ants forage for seeds, often competing with other granivores (Brown and Davidson 1977), but are also known to feed on animal remains, particularly insect parts (Hölldobler and Wilson 1990). Colony densities may be high (Gordon 1991; Whiting *et al.* 1993), and colonies may live for 15-20 years (Gordon 1991). More detailed information on the biology of *P. barbatus* is available in Gordon and Kulig (1996).

Materials and Methods

Field work was conducted on King Ranch National Guard Training Area, adjacent to Kingsville, Kleberg County, Texas, U.S.A., during September 1993. The vegetation consisted of grassland interspersed with mesquite trees, prickly pear, and assorted woody shrubs.

To test the response of harvester ants to dung beetles rolling brood balls, eight trials were conducted in which a dung beetle with a brood ball was placed on the edge of an ant mound, and steered across the mound. Each beetle was tested only once. The reactions of both beetles and ants were recorded. Differences between beetles abandoning brood balls versus those retaining possession was assessed using a chi-square test.

To determine if the presence of abandoned brood balls on harvester ant mounds was nonrandom, we set up five 200 m transects. Transects were established in areas of moderate vegetation density possessing a suitable number of ant mounds, using a compass and 100 m tape. Ant mounds were surveyed in a 10 m area on each side of the 200 m transect, and the number of abandoned brood balls within a 1 m radius of the colony entrance was scored. Only active ant mounds were considered. Every 10 m we randomly selected a point and counted the number of brood balls within a 1 m radius of that point. (All random points were off ant mounds.) To ensure randomness, one investigator closed his eyes while the other investigator rotated himself; after a period of about 15 s the "blind" investigator touched the "rotator" and a marker was thrown over the "rotator's" left shoulder. A few days prior to the study, heavy rains had degraded the shape of abandoned dung balls. This provided an effective natural control for time, such that only complete dung balls a few days old were counted. Differences in the number of dung balls found on ant mounds compared to random points was assessed using a chi-square test. Means are presented ± 1 SE. Differences are considered significant at $\alpha < 0.05$.

Results and Discussion

Significantly (87.5%; $\chi^2_1 = 4.5$, $P < 0.05$) more beetles abandoned their dung balls after either encountering ants or being attacked by them. In one

¹ also, Department of Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa, e-mail: whiting@tm.up.ac.za

trial, a beetle abandoned its ball after encountering only one ant. In another trial, an ant attached itself to the beetle by its mandibles, and simultaneously stung it. The beetle rolled its brood ball into thick grass, pausing in an attempt to free itself of the ant. After two hours the pair was collected and placed in a plastic bag; after eight hours the ant was still attached to the beetle. There were no beetle fatalities from encounters with harvester ants.

Harvester ants usually ignored abandoned brood balls, although at least a few individuals appeared to palpate them.

Ant mounds occurred at a mean of 10.8 ± 1.11 (range: 9–15)/200 m. A total of 54 ant mounds were counted on transects, of which 48% contained brood balls. For all ant mounds, brood balls occurred at a mean of 1.3 ± 0.31 (range: 0–13)/mound. Only one abandoned brood ball was found at 50 random points, which was significantly fewer than on ant mounds ($\chi^2_1 = 44.18$, $P < 0.0001$).

The frequency with which individual beetles lost their brood balls, and the specific energetic costs associated with the construction of dung balls was not evaluated. This study demonstrated that behavioural interference by the harvester ant *P. barbatus* has the potential to exert an energetic cost on *Canthon imitator* during reproduction. Harvester ants encountering dung beetles near the colony entrance are immediately aggressive, usually resulting in the beetle abandoning its dung ball. There appears to be no benefit to the ant colony, other than the removal of a potential "threat".

At our study area, harvester ant mound density was high. Presumably, the impact of harvester ants on dung beetles is a function of ant density, and will be site specific.

Acknowledgments

This study was financially supported by the Texas National Guard, through a contract with the Texas Parks and Wildlife Department (Texas Natural Heritage Program). Dave Diamond is thanked for allowing MJW time to perform the field work. P. W. Bateman is thanked for critically reading the manuscript. B. C. Ratcliffe graciously provided information on *Canthon* and commented on the manuscript.

Literature Cited

- Bradshaw, S. D., H. Saint Girons, and F. J. Bradshaw. 1991. Seasonal changes in material and energy balance associated with reproduction in the green lizard, *Lacerta viridis*, in western France. *Amphibia-Reptilia* 12:21–32.
- Brodie, E. D., III. 1989. Behavioral modification as a means of reducing the cost of reproduction. *American Naturalist* 134:225–238.
- Brodie, E. D., III., and P. K. Ducey. 1989. Allocation of reproductive investment in the redbelly snake *Storeria occipitomaculata*. *American Midland Naturalist* 122: 51–58.
- Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880–882.
- Cambefort, Y., and I. Hanski. 1991. Dung beetle population biology [pp. 36–50]. In: *Dung beetle ecology* (I. Hanski and Y. Cambefort, editors). Princeton University Press, New Jersey. xii+481 pp.
- Cole, A. C., Jr. 1968. *Pogonomyrmex* harvester ants: a study of the genus in North America. University of Tennessee Press, Knoxville. x+222.
- Ford, N. B., and R. A. Seigel. 1989. Phenotypic plasticity in reproductive traits: Evidence from a viviparous snake. *Ecology* 70:1768–1774.
- Gill, B. D. 1991. Dung beetles in tropical American forests [pp. 211–229]. In: *Dung*

- beetle ecology (I. Hanski and Y. Cambefort, editors). Princeton University Press, New Jersey. xii+481 pp.
- Godin, J. J., and S. E. Briggs. 1996. Female mate choice under predation risk in the guppy. *Animal Behaviour* 51:117–130.
- Gordon, D. M. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist* 138:379–411.
- Gordon, D. M., and A. W. Kulig. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* 77:2393–2409.
- Hanski, I. 1991. Epilogue [pp. 366–371]. In: *Dung beetle ecology* (I. Hanski and Y. Cambefort, editors). Princeton University Press, New Jersey. xii+481 pp.
- Hanski, I., and Y. Cambefort. 1991. Competition in dung beetles [pp. 305–329]. In: *Dung beetle ecology* (I. Hanski and Y. Cambefort, editors). Princeton University Press, New Jersey. xii+481 pp.
- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Belknap Press, Cambridge. xii+732 pp.
- Schwarzkopf, L., and R. Shine. 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behavioural Ecology and Sociobiology* 31:17–25.
- Semlitsch, R. D., and J. W. Gibbons. 1978. Reproductive allocation in the brown water snake, *Natrix taxipilota*. *Copeia* 1978:721–723.
- Whiting, M. J., J. R. Dixon, and R. C. Murray. 1993. Spatial distribution of a population of Texas horned lizards (*Phrynosoma cornutum*: Phrynosomatidae) relative to habitat and prey. *Southwestern Naturalist* 38:150–154.

(Received 24 March, 97; accepted 18 June 1997. Publication funded in part by the Patricia Vaurie bequest)