Journal of Insect Behavior, Vol. 9, No. 3, 1996

The Egg Capitulum of a Neotropical Walkingstick, *Calynda bicuspis*, Induces Aboveground Egg Dispersal by the Ponerine Ant, *Ectatomma ruidum*

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Accepted May 5, 1995; revised July 15, 1995

Field observations of a walkingstick, Calynda bicuspis, *reveal that its eggs are rapidly discovered and transported by the ponerine ant,* Ectatomma ruidum *during both dry and wet seasons in Costa Rica. The importance of the egg capitulum in inducing ant transport was established by presenting eggs from which the capitulum had been removed or sealed. Untreated eggs, including those initially taken into nests, were moved approximately 1 m and dropped on the surface of the ground, unlike the eggs of several Old World walkingstick species which ants bury. High rates of oviposition following the termination of prolonged copulatory periods appear to lead to the clumping of eggs, perhaps increasing their susceptibility to a specialist egg-parasitoid,* Amisega *sp. (Chrysididae, Amiseginae).*

KEY WORDS: oviposition; dispersal; *Calynda bicuspis*; walkingstick; Phasmidae; ants; Ponerinae; *Ectatomma ruidum*.

INTRODUCTION

Ovipositing females of many walkingstick species (Orthoptera; Phasmatidae) drop or flip their eggs to the ground where they closely resemble the seeds of many plants (Hinton, 1981; Hughes and Westoby, 1992a). Recent studies suggest that the resemblance between phasmid eggs and seeds represents evolu-

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tionary convergence brought about by ant dispersal or myrmechory. Compton and Ware (1991) in South African "fynbos" heath vegetation and Hughes and Westoby (1992a) in New South Wales, Australia, observed that ants rapidly discover and transport eggs of native phasmid species into their subterranean nests. The presence of the capitulum, a swollen, detachable extension of the opercular plate, was critical in attracting these services. Ants removed and consumed the capitulum within their nests without affecting egg viability. Cached eggs may receive protection from fire and hymenopteran egg-parasitoids. Thus, the capitulum served the same function as an "elaiosome," the oil-rich structure found on the tip of some seeds which promotes dispersal and burial (Beattie, 1985; Horvitz and Beattie, 1980; Hughes and Westoby, 1992b; 1992c).

Little is known about the dispersal adaptations of Neotropical walkingsticks, yet New World species in the subfamilies Heteronemiinae and Phibalosomatinae have well developed egg capitula (Clark, 1976a,b, 1979). In this study we show that capitulum-bearing eggs of the large, Central American walkingstick, *Calynda bicuspis* Stål (Heteronemiinae), are quickly and consistently discovered and transported by the ponerine ant, *Ectatomma ruidum* Roger, but are ignored if the capitulum is removed or coated. Observations of caged *C. bicuspis* females revealed that they oviposit intensely for brief periods following prolonged copulations, thereby promoting egg clumping and possible susceptibility to hymenopteran parasitoids. While walkingstick egg capitula function similarly to attract ants in the New and Old World Tropics, the dispersal services of the ants involved may be quite dissimilar in the two regions.

METHODS

The Insects

The walkingstick, *Calynda bicuspis*, described from a specimen collected in Chiriqui Province, Panama (Brunner von Wattenwyl, 1908), is abundant in the Pacific lowlands of Guanacaste Province, Costa Rica. Adult body length varies from 11 to 17 cm in females and 7 to 11 cm in males. A trough-shaped oviscape on the eighth sternite of females extends 1 to 2 cm beyond the end of the abdomen. This structure helps to hold recently extruded eggs and eventually to flip them forcefully past the dorsum. The terminalia of males includes a pair of rigid, sickle-shaped claspers under muscular control that are closed around the abdomen of a female as mating begins.

Adults and nymphs are active throughout the year, feeding on more than a dozen species of herbaceous and woody dry forest plants (Windsor and Massey, 1983). During the dry season (December through April) walkingsticks occur principally on swollen thorn acacias (*Acacia collinsii* and *A. cornigera*) occupied by the black, obligate, acacia ant, *Pseudomyrmex beltii*. During the wet season, walkingsticks are encountered principally on nonant plants, *Mimosa pigra* and *Indigofera* sp. (Leguminosae) and *Guazuma ulmifolia* (Sterculiaceae).

Ectatomma ruidum is a medium-sized ponerine ant widely distributed through the American tropics (Kugler and Brown, 1982). Nest densities are often high, varying between 0.18 and 0.61 per m^2 on Barro Colorado Island, Panama (Levings and Franks, 1982) and averaging 0.14 per m^2 at the La Selva Station in Costa Rica (Breed *et al.*, 1982). Foragers have the striking ability to acquire the chemical recognition labels of ants in neighboring *E. ruidum* colonies, thus facilitating rampant intercolony thievery of food items (Breed *et al.*, 1990).

The Study Site

Our study was conducted at the Palo Verde Field Station, 20 km SW of Bagaces, Guanacaste Province, Costa Rica. Seasonally deciduous, tropical dry forest occurs on limestone hills surrounded by lower areas of young successional forest, savannas, and a broad *Parkinsonia* swamp bordering the Tempisque River. Our study was restricted to the young successional vegetation occurring between the entrance road and the marsh, an area of high walkingstick density. Herbs and shrubs in the area were searched using a headlamp in the early evening (2100–2400).

Behavioral Observations

The first observations on the interaction between ants and walkingstick eggs were made during February 1992 (dry season). Trials were conducted during August 1992 (wet season) comparing the preferences of ants for normal eggs and eggs from which the capitulum was scraped from the opercular plate using an insect pin. Trials during January 1993 (dry season) compared normal eggs and those whose capitula were covered by a small quantity of water-based, fast-drying correction fluid (Mistake Out, Liquid Paper Corporation, Boston, MA). Control and treated eggs were presented simultaneously, separated by 1–2 cm, upon leaves pinned to the ground. Precautions taken to minimize the transfer of foreign substances to eggs included the use of forceps, rubber gloves, and frequently washed hands. Ant nests near depots used earlier in the same day were chosen for excavation. Soil from each nest excavated was collected and passed carefully through a 1-mm sieve. To determine the distance and direction eggs were initially transported, single eggs were placed on leaf depots located 2 cm from focal *E. ruidum* nest entrances in August 1992, January 1993, and June 1994. Once an egg was removed, transported, and dropped, a second egg was placed on the depot and so on.

Fresh field-collected females were held for several days within taffeta bags tied around live foliage of a preferred food plant to obtain eggs and to determine oviposition rates. Five other females were held for 18 days in separate screened rearing cages containing potted food plants. Mating, defined as the closure of male claspers around the female's abdomen, was recorded after single males were introduced into each of the cages on the fifth day. Females were monitored and eggs removed from each cage three to five times per day.

RESULTS

Egg Morphology

The egg of *C. bicuspis* measures 2 × 3.5 mm and weighs 7.0 mg (SD = 0.6 mg, $n = 57$). An open, dome-shaped capitulum is attached to the opercular plate which seals the anterior pole of the egg (Fig. 1a). The capitulum contains a translucent, spongy matrix protected by a tough, fibrous wall (Fig. 1b). The matrix is flexible when first deposited but becomes friable as the egg ages. An average capitulum weighs 0.09 mg, 1.1% of the egg weight. Despite a porous capitulum, eggs placed in water sink immediately.

Oviposition and Developmental Period

Median oviposition rates for 12 solitary females ranged from 0.25 to 0.38 egg per h. Individual oviposition rates were positively correlated with female body length ($r = 0.66$, $P < 0.01$, $n = 12$). Five other *C. bicuspis* females held in separate cages for 4 days deposited from 0.2 to 1.2 eggs per h (Fig. 2). When males were added to each cage, matings immediately ensued. Copulation intervals over the next 13 days ranged from 20 to 62 h (avg. = 35.9 h; SD = 11.4 h; $n = 19$); intercopulation intervals ranged from 6 to 54 h (avg. = 32.9 h; SD = 13.3 h; $n = 14$). Oviposition occurred in all but one observation period within each of the 14 intercopulation intervals. Peak oviposition rates, ranging among females from 2.4 to 5.0 eggs per h, occurred immediately after the cessation of mating. Females failed to oviposit in at least one observation period in each of the 19 copulations. Recently mated females dropped eggs to the floor of rearing cages where their distributions were highly clumped.

The developmental period for eggs varied within broods from 70 to 150 days.

Egg Transport

Four fresh *C. bicuspis* eggs and a ballast stone were placed in 10-cm petri dishes each located beneath 1 of 12 *A. collinsii* trees. When visited 8 h later (0730 h), some eggs were missing from all dishes, and overall, 44 of 48 eggs had disappeared.

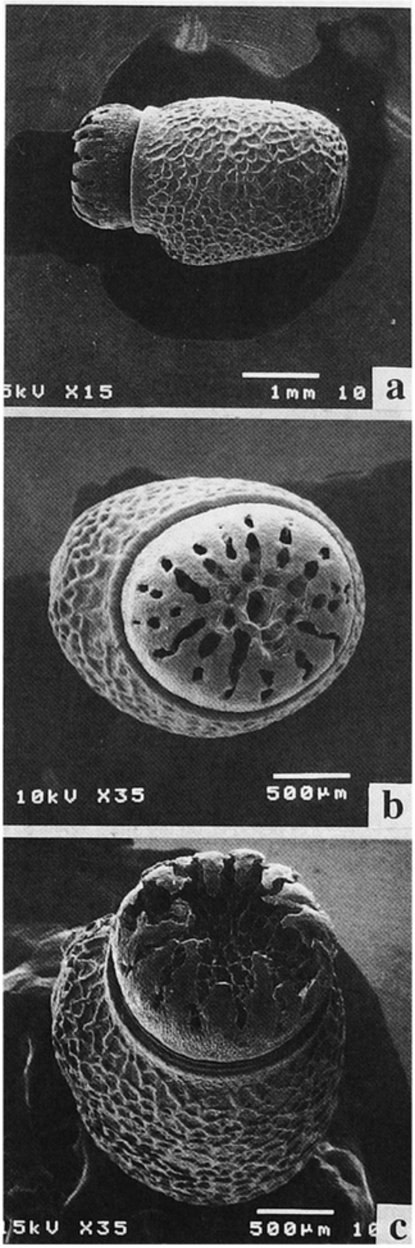

Fig. 1. (a) Scanning electron micrograph of a *Calynda bicuspis* egg showing the size and fibrous nature of the exterior wall of the capitulum. (b) End view of the capitulum showing the porous nature of the capitulum matrix. (c) End view of an egg whose capitulum matrix was largely removed during its residence in an *Ectatomma ruidum* nest.

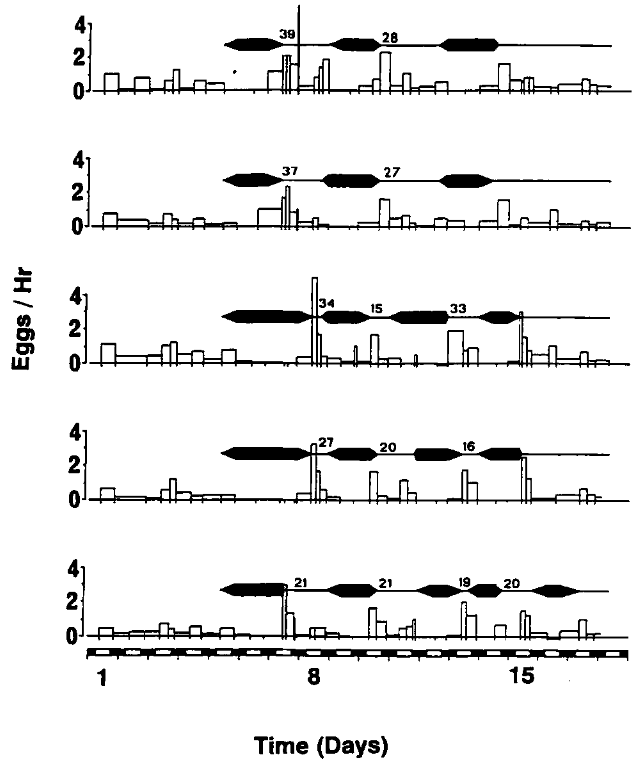

Fig. 2. The oviposition rates of five *Calynda bicuspis* females recorded at irregular intervals over 18 days. One male was introduced into each cage on the fifth day. Copulation intervals are indicated by the expanded portions of the lines floating above the bars. The number of eggs oviposited during intercopulation intervals is indicated.

We next placed four eggs in each of three dishes spaced several meters apart and began continuous observations. *E. ruidum* foragers approached two of the stations within the first minutes of observation. Within the next 5 min clusters of three to six *E. ruidum* accumulated at each depot where individuals nuzzled the open end of the capitula (Fig. 3a). Eggs were grasped in the mandibles near the capitulum, with the ants sometimes falling over while contracting the gaster as though to sting (or mark) the surface. Then, with mandibles clasped around the collar of the egg beneath the opercular plate (Fig. 3b), eggs were lifted from the substrate and carried away (Fig. 3c) on relatively straight trajectories. All eggs were removed by *E. ruidum* foragers within 2 h. Other terrestrial invertebrates were observed to nudge or, in the case of very minute ants, to feed at the open end of the capitulum. These species seldom moved the egg

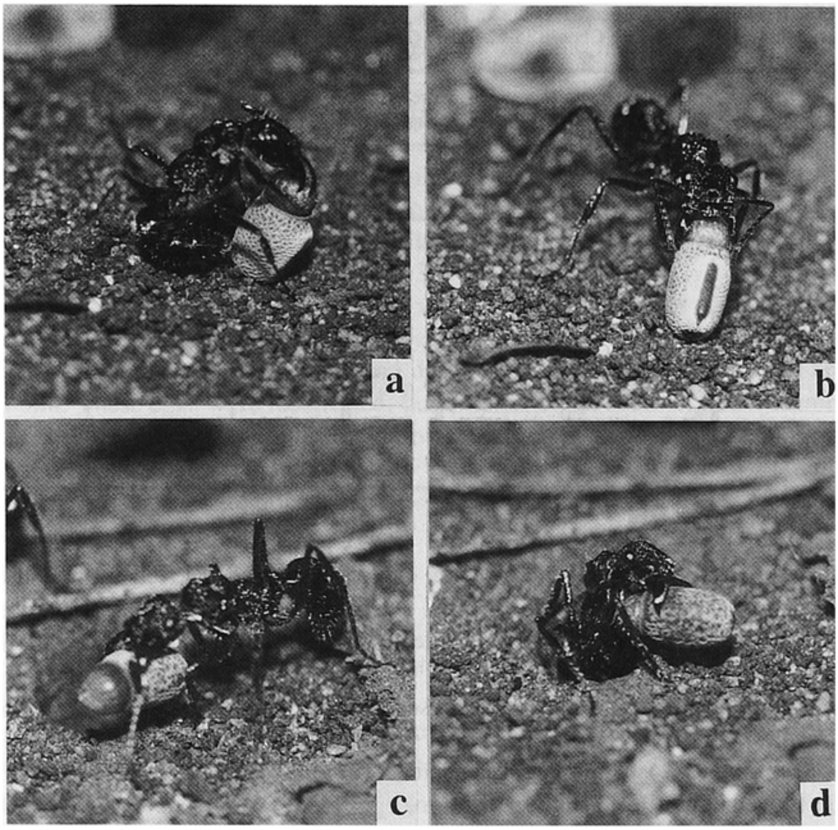

Fig. 3. (a) *Ectatomma ruidum* forager shortly after discovering an egg, treating the egg as a prey item by holding it by the capitulum while doubling the gaster and possibly attempting to sting (or mark) the egg surface. (b) The same worker, now preparing to lift the egg from the substrate by the collar beneath the operculum. (c) A forager carrying the egg. (d) A forager taking an egg into its nest entrance.

more than a few millimeters, and in no case were they able to remove an egg from a petri dish.

Effect of Removing and Coating the Capitulum

The role of the capitulum in attracting ants was investigated by comparing the probability of removal of entire eggs and eggs from which the capitulum had been removed. Entire and altered eggs were presented in pairs in a series of trials at five depots, each located approximately 1.5 m from the center of *Mimosa pigra* plants. Each depot was observed continuously between 0800 and

Table I. The Dispersal Agent, Preference for Eggs With (+) and Without (−) a Capitulum, and Destination of the First Egg Chosen in 62 Trials Conducted at Depots Near 11 *E. ruidum* Colonies

	Dispersal agent		Preference capitulum		Destination		
Depot	*E. ruidum*	Other species	+	−	Nest	Discarded	Lost
1, 3, 6	4	0	4	0	2	1	1
4	4	0	3	1	3	1	0
9	5	0	5	0	2	3	0
7	4	1	5	0	3	0	2
5	6	1	6	1	4	0	3
8	7	1	8	0	6	0	2
2	8	0	5	3	7	1	0
10	8	0	8	0	1	7	0
11	13	0	13	0	3	10	0
62	59	3	57	5	31	23	8

1100 h. A trial was concluded when an egg was removed. Eleven entire and no altered eggs were removed (binomial probability ≤0.001). Six eggs were removed by *E. ruidum* foragers, while five eggs were removed without the observer noting the agent of removal.

Intact and altered eggs were presented in a second series at 11 depots located 0.5 m from focal *E. ruidum* colonies. *Ectatomma ruidum* foragers removed 59 (95%) of the eggs presented (Table I). Intact eggs were the first eggs moved in 57 (92%) trials. Thirty-one eggs (55%) were taken into *E. ruidum* nest entrances (Fig. 3d), while 23 (45%) were taken away from the depot and dropped. Proportions of eggs taken into, rather than away from, nests differed among trials ($\chi^2 = 21.5$, df = 4, $P < 0.001$) (Table I). On two occasions discarded eggs were picked up and moved a second time by foragers before again being dropped.

A third experiment controlling for shape and weight of experimental eggs was conducted. Eggs with the capitulum painted, eggs with the posterior pole painted, and untreated eggs were presented in each of 27 trials at 14 depots located 5 cm from different *E. ruidum* nest entrances. Capitulum-painted eggs were the last remaining eggs in 24 trials ($\chi^2 = 17.7$, df = 2, $P < 0.001$). Slight differences in the order of removal of posterior-pole painted eggs and untreated eggs were not significant ($\chi^2 = 0.73$, df = 1, $p = 0.39$).

Attraction to Eggs of Different Ages

The attractiveness of *C. bicuspis* eggs oviposited during the previous 12 h was compared to that of eggs oviposited 48 to 72 h earlier. Pairs of "new" and "old" eggs were presented sequentially at a depot 5 cm from the entrance of a single *E. ruidum* nest entrance. Seventeen pairs were presented between 0755 and 1030, with each presentation taking place after the fate of both eggs of the previous pair had been determined.

"New" eggs were more vigorously nudged and mandibulated in all trials and were grasped in the mandibles and moved from the depot before "old" eggs in 13 of 17 trials (binomial probability = 0.025). "New" eggs were taken into the focal nest in 14 trials and immediately discarded away from the nest in 3 trials. "Old" eggs were treated similarly, with 10 taken into the nest and 7 discarded away from the nest ($\chi^2 = 0.39$, df = 1, $P > 0.5$).

Two hours after the above trials were initiated, a worker ant exited the focal nest with a marked egg which it carried 20 cm and dropped. Another 10 eggs were brought to the surface and dropped away from the nest in the next 90 min. These eggs were recollected, but unfortunately, their original treatment was not recorded. After a lull in foraging activity between 1100 and 1500, they were presented beside additional "new" eggs near the same colony entrance. In each of eight presentations, "new" eggs were selected first and taken immediately into the nest, while "recycled" eggs were eventually transported away from the nest and dropped.

Six presentations of "new" and "recycled" eggs were performed later in the same day at a second nest. "New" eggs were moved first in each of the trials, however, unlike the previous trials, both classes of eggs were taken away and dropped.

The capitula of all eggs taken into nests and later brought to the surface, when observed with a stereomicroscope, were found to have been irregularly opened and the matrix largely removed (Fig. 1c).

Attractiveness of Eggs Relative to Other Objects

We simultaneously presented *E. ruidum* foragers with a choice among an intact phasmid egg, a crushed *Pseudomyrmex* worker, and a dry phasmid feculum. Items were presented on a depot 5 cm from the entrance of a single colony. A presentation was terminated after 20 min or after two of the objects were removed.

While walkingstick feculae were largely ignored, crushed ants were the first object removed in 17 trials (81%) and the second object in four trials (Table II). Crushed ants were taken into the focal nest in 18 trials and into neighboring *E. ruidum* nests in three trials. Eggs were the first object removed in four trials, but the second object selected in 16 trials. Eggs were taken into nest entrances in three of the first four presentations, but in the following 14 trials, they were moved away from the focal nest and dropped. On three occasions, *E. ruidum* foragers carried discarded eggs another 1–2 m before dropping them on the ground. Indeed, as the day progressed it was common to see ants moving eggs in all directions across the observation area.

Table II. The Order of Removal and Destination of Phasmid Eggs, Crushed *Pseudomyrmex* Workers, and Dried Phasmid Feculae Presented Simultaneously at Depots Near a Single *Ectatomma* Colony

	Eggs	Crushed ants	Feculae
Order of removal			
First	4	17	0
Second	16	4	1
Not removed	0	0	19
Destination			
Focal nest	3	18	0
Other nest	0	3	0
Discarded	15	0	1
Not moved	2	0	21
Lost	2	1	0

Distances and Directions of Egg Movement

The mean distance 30 eggs were transported away from a single depot in August 1992 was 1.1 m (SD = 0.1 m). This movement did not entirely rid the distribution of clumping as one-third of the eggs were dropped very close together 1 m north of the depot (Fig. 4a). The other eggs were dispersed over the 4 × 4-m plot. During January 1993, the mean distance 17 eggs were transported was 1.6 m (SD = 0.8 m). During June 1994 the mean distance 28 eggs were transported was 0.75 m (SD = 0.4 m). Although the distances moved were less than in the preceding series, the resulting distribution (Fig. 4b) lacked clumping. Additionally, there were no *E. ruidum* nests within the plot, while at least three were present in the former.

The Content of *Ectatomma* Nests

Nine *E. ruidum* nests were excavated during August 1992 to determine if *Calynda* eggs were cached within. Vertical nest tubes, often topped by small tumuli, descended approximately 15–25 cm before reaching the first, horizontal, pancake-shape gallery. Two deeper galleries were found in several of the larger nests. The contents of each gallery, primarily ant eggs, larvae, and pupae, were aspirated into vials. The surrounding soil was removed and passed through a 1-mm sieve. The number of adult ants recovered from these colonies varied between 14 and 73; pupae, 0 and 80; and larvae, 0 to 92. No phasmid eggs or egg fragments were found either among the aspirated nest contents or in the sieved soil.

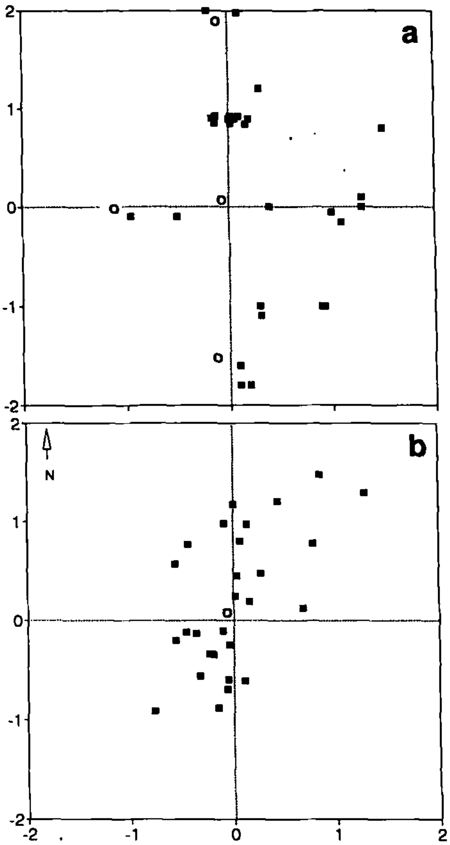

Fig. 4. The dispersal pattern of *Calynda bicuspis* eggs carried away from depots located at the very center of each 4 × 4-m plot. Nest entrances within the plots are indicated by open circles.

Observation of an Egg-Parasitoid

Perhaps the most important observation in this study was made when one or two small wasps were observed attacking eggs presented at a single depot in the trials comparing normal and capitulum-less eggs at roughly 0900 in the open grassland at the west end of the airstrip (August 1992). In one of several interactions observed, a wasp spent several seconds straddling an egg, possibly preparing the egg for oviposition, before dragging the egg from the leaf surface. The wasp was captured and subsequently identified as *Amisega* sp. (Chrysididae).

DISCUSSION

We demonstrated that the attractiveness and likelihood of immediate transport by ants were substantially reduced when the egg capitulum was removed or covered by paint. However, eggs which attracted ants were not subsequently treated the same way by ants of different colonies. Some ants immediately transported eggs away and discarded them, while other ants carried eggs into the nest where the capitulum matrix was removed. After 1–2 h these eggs were returned to the surface, carried away, and dropped. Although eggs without a capitulum matrix were initially less attractive than unaltered eggs, most eventually were carried away and discarded. Regardless of treatment received, eggs were transported and left on the ground surface. These results contrast with the dispersal of "elaiosome"-bearing eggs of the South African walkingstick, *Bacillus? coccyx* (Compton and Ware, 1991) and the Australian walkingstick, *Ctenomorpha chronus* (Hughes and Westoby, 1992a). In these species ants find and transport eggs into their nests where they remain until hatching. Although some of the eggs of *C. bicuspis* initially go into the nest, our observations indicate that they soon are brought back out, transported away and left on the ground. Further, excavations indicated that eggs are not cached for long periods within nests.

Ectatomma ruidum workers discarded eggs at average distance ranging from 0.75 to 1.6 m in a variety of directions. Thus, in some cases eggs were dropped within or near the home-range boundaries of adjacent colonies. Observations of secondary transport were numerous enough to lead us to suspect that many eggs are transported even farther. Further, thief ants from adjacent colonies infiltrate, remove food, and transport these items into neighboring colonies (Breed *et al.*, 1990, 1992). Thus, when eggs were presented very near a particular colony entrance, thieves within that colony immediately transported eggs into the entrance of a neighboring colony. Thieves within that colony could then carry eggs to other colonies, and so on, enhancing the likelihood that *C. bicuspis* eggs are dispersed distances considerably greater than we measured after the first removal.

We showed that mating and ovipositional behavior of *C. bicuspis* promotes underdispersion of eggs. Solitary females tend to produce and flip an egg every 3 to 6 h throughout the day and night. However, the small males which ride on the backs of mature females have relatively large and strong claspers which grip and appear to slow or even stop oviposition for substantial periods by collapsing the terminal segments. When males eventually relax their grip, oviposition of 20–30 eggs within a few hours is not unusual.

Because abdomens of *C. bicuspis* are often heavy and distended with eggs following extended mating sessions, egg flipping by solitary females may not occur at all or may occur less efficiently. Males standing over and attempting to reclasp females may additionally impede egg flipping. Under these conditions the ubiquitous workers of *E. ruidum* may rapidly disperse clumped distributions of recently oviposited phasmid eggs.

Additional aspects of *C. bicuspis* biology, all in need of further study, may promote initial underdispersion of eggs. If females utilize the same food plant on successive evenings, as our observations suggest, then oviposition will be concentrated around the bases of food plants. Further, if females use the same daytime perches oviposition will tend to be concentrated in those areas.

While advantages dispersed eggs may receive remain to be demonstrated for *C. bicuspis*, our observation of a wasp attacking eggs at a depot on the ground provides a putative selective agent. The subfamily Amesiginae of the Chrysididae (Cuckoo wasps) are specialist walkingstick egg parasitoids occurring in all zoogeographical regions except Antarctica (Kimsey and Bohart, 1990). Other than fungi and a eupelmid wasp on Fiji, the Amiseginae and their sister group, the Loboscelidiinae, are the only known mortality factor for walkingstick eggs (Bedford, 1978; Krombein, 1957, 1960, 1983). Parasitization rates by Amiseginae as high as 65% have been reported for Australian walkingstick eggs (Campbell, 1960, 1961). Numerous malaise trap samples collected from the nearby Santa Rosa National Park contained Amiseginae, indicating that this egg-parasitoid may not be rare (personal communication, P. Hanson). If *Amisega* sp. is a density-responsive egg-parasitoid, then better-dispersed walkingstick eggs may have lower rates of predation than clumped eggs.

The property of the capitulum matrix which attracts *E. ruidum* is unknown. Perhaps, as suggested by Hughes and Westoby (1992a), the compound will be similar to the diglygeride attractant in some plant elaiosomes (Brew *et al.*, 1989). The rapid assembly of *E. ruidum* workers near phasmid eggs and the tendency of the attractive properties to diminish over a few days suggest that the substance is volatile and is present in small quantities. The possibility exists that both the dispersal agent and the parasitoid utilize the same short-lived cue emanating from the capitulum. If true, then the speed of discovery and transport by ants becomes critical for egg survival. Additionally, ant removal of the capitulum matrix could substantially lower the chance that an egg will be discovered by a parasitoid. Chances of surviving the long developmental time (72–150 days) may not be much different than chances of evading parasitoids in the 3 to 5 days following oviposition.

Finally, *C. bicuspis* eggs must be highly susceptible to the dry season fires which today plague Central America. However, fire may have been far less common in Central America in the past. Sediment cores taken from lakes in the pacific lowlands of Central Panama indicate that dry forests have burned extensively only during the past 11,000 years, the period of human residence in the area (Piperno *et al.*, 1990). The apparent rarity or absence of burning prior to this date may explain why *C. bicuspis* eggs are not stored underground as are Old World phasmid eggs. Alternatively, we could be observing the incipient stages of selection for underground storage and nymphal survival. Among issues related by this introductory study, it will be interesting to determine how susceptible early instar nymphs are to *Ectatomma* predation.

ACKNOWLEDGMENTS

We thank P. Hanson for identifying *Amisega*, A. Aiello and W. Eberhard for reviewing an early draft, and students in the OTS Fundamentals in Tropical Biology courses for assistance in data collection. We appreciate the hospitality of the Costa Rican Park Service personnel and applaud their efforts to protect a part of this threatened ecosystem. The Organization for Tropical Studies, Inc., and the Smithsonian Tropical Research Institute provided logistical and financial support.

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