Acta Zool. Mex. (n.s.) 73: 145-153 (1998)

ENDOTHERMY AND FLORAL UTILIZATION OF *CYCLOCEPHALA CAELESTIS* (COLEOPTERA: SCARABAEOIDEA; MELOLONTHIDAE): A CLOUD FOREST ENDEMIC BEETLE

Gregg DIERINGER [1], Pedro REYES-CASTILLO [2], Manuel LARA [3], Leticia CABRERA R.[1], and Larisa LOYA [3]

[1]Department of Biological Sciences, Western Illinois University, Macomb, IL 61455, USA
[2]Instituto de Ecología, A.C., Apartado Postal No. 63, Xalapa 91000, Veracruz, MEXICO
[3]Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas, Cd. Victoria, Tamaulipas, MEXICO

RESUMEN

Un estudio sobre la ecología de la polinización de *Magnolia tamaulipana* y su polinizador, *Cyclocephala caelestis*, fue realizado en la Reserva de la Biósfera El Cielo, Tamaulipas, durante la primavera de 1996. *Cyclocephala caelestis* visitó las flores de *M. tamaulipana* con mayor frecuencia después de las 21:00 horas, siendo los machos más abundantes que las hembras. Citamos por primera vez dentro del género, la endotermia y regulación de la temperatura torácica en *C. caelestis*. El promedio de la temperatura torácica fue de 26.8°C ± SE = 0.3 con un exceso de 4.7°C ± SE = 0.3 sobre la temperatura ambiental. Los machos y hembras no se diferenciaron en su temperatura torácica media. En el interior de las flores, los escarabajos regularon su temperatura torácica, independientemente de las temperaturas ambiental y floral, y fueron observados apareándose y alimentándose de los pétalos. La endotermia quiza sea importante para realizar estas actividades de apareamiento y alimentación, las cuales las realizan durante la noche cuando disminuye la temperatura. Se piensa que el tejido de los pétalos contiene aceites etéreos en los que se disuelven ésteres quirales que son responsables del aroma floral y la atracción de las especies de *Cyclocephala*. Los tejidos de pétalos y sépalos contienen altas cantidades de carbohidratos y proteínas, sin embargo los pétalos presentan cuatro veces menos fibra, lo que probablemente explique el porque *Cyclocephala*, los prefiere como alimento.
Palabras Clave: *Cyclocephala*, *Magnolia*, polinización, endotermia, regulación de la temperatura.

ABSTRACT

A study of the pollination ecology of *Magnolia tamaulipana* and its specialized pollinator, *Cyclocephala caelestis* was conducted at the El Cielo Biosphere Reserve, Tamaulipas during the late spring of 1996. *Cyclocephala caelestis* visited flowers of *M. tamaulipana* most frequently after 2100 with males being more abundant than females. We report for the first time within the genus, endothermy and thoracic temperature regulation for *C. caelestis*. Thoracic temperature averaged 26.8°C ± SE = 0.3 with an excess temperature of 4.7°C ± SE = 0.3. Males and females did not differ in mean thoracic temperature. While within the flowers, beetles regulated their thoracic temperature independently of ambient and floral temperatures and were observed mating and feeding on petal tissue. Endothermy is probably important for mating and feeding activities which occur at night during cool temperatures. Petal tissue is thought to contain ethereal oils within which are dissolved chiral esters that are responsible for floral odor and the attraction of *Cyclocephala* species. Petal and sepal tissue both contain high amounts of carbohydrate and protein, but petals contain 4x less fiber, which probably accounts for its preference as a food tissue by *Cyclocephala*.
Key Words: *Cyclocephala*, *Magnolia*, pollination ecology, endothermy, thoracic temperature regulation.

INTRODUCTION

The dynastine scarab beetles of the genus *Cyclocephala* are very diverse, comprising over 250 species distributed primarily in the neotropics, with some endemic species occurring in temperate zones of North and South America. Information on the biology of this genus is available for less than 10% of these species (Ratcliffe, 1991) although they are known to have a close relationship with plants as pollinators with an estimated 900 neotropical plant species relying on *Cyclocephala* pollination (Schatz, 1990). Studies on *Cyclocephala* pollination have frequently focused on the thermogenic properties of the flowers they visit (Prance and Arias, 1975; Young, 1986; Gottsberger, 1989).

Studies by Endress (1984) have shown that *Elleschodes* beetles (Curculionidae) preferentially consume staminodia of *Eupomatia laurina* (Eupomatiaceae) which are also sticky and contain ethereal oils, within which volatile oils are dissolved. These oils produce the potent fragrance that attract *Elleschodes* beetles (Bergström *et al.*, 1991). *Magnolia* (Magnoliaceae) is also known to possess ethereal oils (Cronquist, 1981). Recent studies on tropical *Magnolia* have shown a type of specialization not found in temperate Magnolias involving floral thermogenicity and pollination by *Cyclocephala* beetles (Dieringer and Espinosa S., 1994; Dieringer and Delgado, 1994; Dieringer *et al.*, unpubl.). So far, two species of Mexican *Magnolia* have been studied, *M. schiedeana* and *M. tamaulipana*. Both possess petals that are very sticky to touch with the odor of the flower retained on the fingers after touching. We believe the increase in heat production by *Magnolia* flowers causes the emission of floral odors which specifically attract *Cyclocephala* (Raskin *et al.*, 1987; Robacker *et al.*, 1988; Schatz, 1990).

As in *Magnolia*, flowers pollinated by *Cyclocephala* frequently form a floral chamber within which the beetles stay. It has been suggested that the floral chamber functions as an adaption to retain heat during the cool evening hours. Given that the *Magnolia* flowers are thermogenic, this seems a reasonable hypothesis if *Cyclocephala* are not endothermic. However, a number of scarab beetles have been reported to exhibit endothermy (Bartholomew and Casey, 1977; Chappell, 1984; Heinrich and McClain, 1986; Morgan, 1987), but as yet not *Cyclocephala*. *Cyclocephala* species are active primarily during evening hours when temperatures are cool. We therefore suspected that *C. caelestis* might also be endothermic and that the floral chamber of *Magnolia* plays little or no role in heat conservation. It is for the above reasons we chose to continue our studies on *Magnolia tamaulipana* Schlecht, which is pollinated by *Cyclocephala caelestis* Delgado and Ratcliffe.

Our objectives for this study were to document visitation and behavior of *C. caelestis* adults on flowers *M. tamaulipana*; record observed sex ratios; determine thoracic temperatures; and estimate the relationship between thoracic, ambient, and flower temperatures.

MATERIALS AND METHODS

Cyclocephala caelestis is a small dynastine scarab beetle (mean length of 15mm and a width of 7cm) endemic to the El Cielo Biosphere Reserve, Tamaulipas, Mexico (Ratcliffe and Delgado-Castillo, 1990). Populations occur in cloud forest at altitudes of 1080-1400m. Local climate has a mean annual temperature of 13.8°C and annual precipitation ranging from 2000-3000mm with a rainy season occurring from May through October (Puig and Bracho, 1987).

The study site was located around the Canindo field station of the El Cielo Biosphere Reserve. Trees were found growing from Rancho Viejo to the ejido San José (elevation 1400m), a distance of approximately 2 km. Observations were made over 8 days from 22 May to 29 May between 1000 to 2230. Specimens of *C. caelestis* collected during this study were deposited in the Entomological Collection (IEXA) of the Instituto de Ecología, A. C., Xalapa, Veracruz.

Studies by Dieringer *et al.* (unpubl.) have shown that *C. caelestis* is a principal pollinator of *Magnolia tamaulipana*. Populations of *Magnolia tamaulipana* is also endemic to cloud forest with populations typically occurring between 800-1400m in altitude (Vázquez-G., 1994). The flowers are perfect and nectarless, although stigmas possess a drop of liquid that appears nectar-like. The flowers begin to open in the evening around 1800, are protogynous, and produce a strong fruity fragrance. The outer petals are initially held erect along with the inner petals, forming a chamber. The following day the outer petals begin to unfold, but the inner petals remain erect. The third day, the outer petals have unfolded and the inner petals have also begun to unfold. After opening, flowers remain female until around 0600-0700 when stigmas become brown, but anthers do not dehisce until around 1000-1100. The flower's life-span varies considerably, ranging from 12 to 24 hours after which the entire flower senesces and begins to turn brown.

We visited trees twice each day and examined as many flowers as could be reached with an 8-foot step ladder. Data recorded included the total number of *Cyclocephala* encountered, the sex of each beetle, activities of beetles while within flowers, sexual phase of the flower, flower temperature (T_f), ambient temperature (T_a), and beetle thoracic temperature (T_{th}). Temperatures were recorded using copper-constantan thermocouples (0.3 mm in diameter) connected to a portable, battery powered, digital thermometer (Omega Eng.) accurate to ± 0.01°C. Flower temperature was taken by placing the thermocouple wires into the androphore. Thoracic temperatures were obtained by taking beetles from flowers and inserting the thermocouple wire into the thorax within 5 seconds. Statistical guidelines follow those of Zar (1984).

RESULTS

The frequencies of male and female beetles recorded within flowers of *Magnolia tamaulipana* throughout the life-span of an average flower are presented in Table 1. A total of 188 *Cyclocephala* was observed. Both males and females show a similar pattern, being most abundant during the first evening when flowers were initially female. In general, flowers began to open around 1800 hours and continued opening throughout the night. Beetles were most abundant after 2100, averaging 2.1 beetles/flower. Males were more abundant than females at all but the first period of observation with a combined sex ratio of approximately 5:1.

Table 1

Frequency of *Cyclocephala caelestis* males and females within flowers of *Magnolia tamaulipana* across the life-span of an average flower as sampled across 8 days (22 May - 29 May).

Day	Time interval (75 min.)	$N_{flowers}$	No. males	No. females
1	1830-1944	8	0	1
1	1945-2059	25	20	2
1	2100-2214	62	113	15
2	1000-1114	44	5	4
2	1115-1259	40	9	5
2	1300-1414	17	8	6
2	1415-1559	13	0	0
3	1000-1114	4	0	0
Totals		213	155	33

While within the flower, beetles were observed to feed on petal tissue and at times the base of the anthers. The stigmas produced a nectar-like substance which the beetles may also have been consuming. The petal tissue seems to be of particular importance since only petals and not sepals were chosen. Males and females were also observed copulating within flowers. Of the 9 occasions that copulation was observed, 8 occurred after 2100 and one at 1130.

Thoracic temperatures of male and female *Cyclocephala caelestis* taken from flowers of *M. tamaulipana* had a mean of 27.0°C ± SE = 0.3, N = 35 and 26.1°C ± SE = 0.6, N = 12, respectively with excess thoracic temperatures (T_{th} - T_a) of 4.9°C ± SE = 0.3 and 4.1°C ± SE = 1.9, respectively. No significant difference in excess thoracic temperature was detected between male and female beetles ($t = 1.24$, $df = 45$, $P = 0.22$). Combining sexes, *C. caelestis* beetles possessed a mean thoracic temperature of 26.8°C ± SE = 0.3 (range 21.4-31.3°C) and a mean excess thoracic temperature of 4.7°C ± SE = 0.3.

The relationship between T_{th} and T_a is presented in figure 1A. The least-squares linear regression of T_{th} on T_a was significant ($F = 5.86$, $df = 1, 45$; $P = 0.02$) and had a slope significantly different from 1 ($t = 3.43$, $df = 45$, $P < 0.001$). Mean flower temperature was 23.8°C ± SE = 0.3, N = 47 with a mean excess flower temperature ($T_f - T_a$) of 2.7°C ± SE = 0.3. The relationship between T_{th} and T_f is presented in figure 1B. The least-squares linear regression of T_{th} on T_f was significant ($F = 5.64$, $df = 1, 45$; $P = 0.02$) and had a slope significantly different from 1 ($t = 5.30$, $df = 45$, $P < 0.001$). These data indicate that thoracic temperatures were independent of ambient and floral temperatures and suggest beetles are endothermic and regulate thoracic temperatures while within flowers.

DISCUSSION

The data presented indicate that *Cyclocephala caelestis* preferentially visited flowers of *Magnolia tamaulipana* at night after 2100 hours. In doing so, they were most frequently encountered in female-phase flowers during the early evening hours. Males were more abundant than females during this time period. This is in contrast to *Magnolia schiedeana*, a Mexican cloud forest species, that is pollinated by *Cyclocephala jalapensis* (Dieringer and Espinosa S., 1994). Flowers of *M. schiedeana* open early in the morning, around 0500 to 0700 hours. Consequently, *C. jalapensis* is observed more frequently early in the day and, for this species, females are more common than males.

Cyclocephala caelestis clearly possesses an elevated thoracic temperature indicative of endothermy. Although beetles were undoubtedly receiving heat from the thermogenic flowers, the regression of T_{th} on T_f had a slope significantly different from 1 suggesting regulation of thoracic temperature independent of floral temperature. Endothermy is fairly common among large-bodied beetles such as the Scarabaeidae (Morgan and Bartholomew, 1982; Chappell, 1984; Heinrich and McClain, 1986; Morgan, 1987). The relationship between T_{th} and T_a had a slope significantly different from 1 indicating that *C. caelestis* was regulating its thoracic temperature independent of ambient temperature while within flowers. Therefore, it is unlikely that the floral chamber of thermogenic *Magnolia* flowers functions to retain heat for visiting *Cyclocephala*.

Other scarab beetles such as large dynastine beetles *(Megasoma elephas)* and flower scarabs (Melolonthidae: Cetoniinae) regulate their thoracic temperature while in flight (Morgan and Bartholomew, 1982; Heinrich and McClain, 1986). However, flower scarabs (subfamily Cetoniinae) do not maintain an elevated thoracic temperature once they land on a flower even though they pursue the same kinds of activities, mating and feeding, as does *C. caelestis* (Heinrich and McClain, 1986).

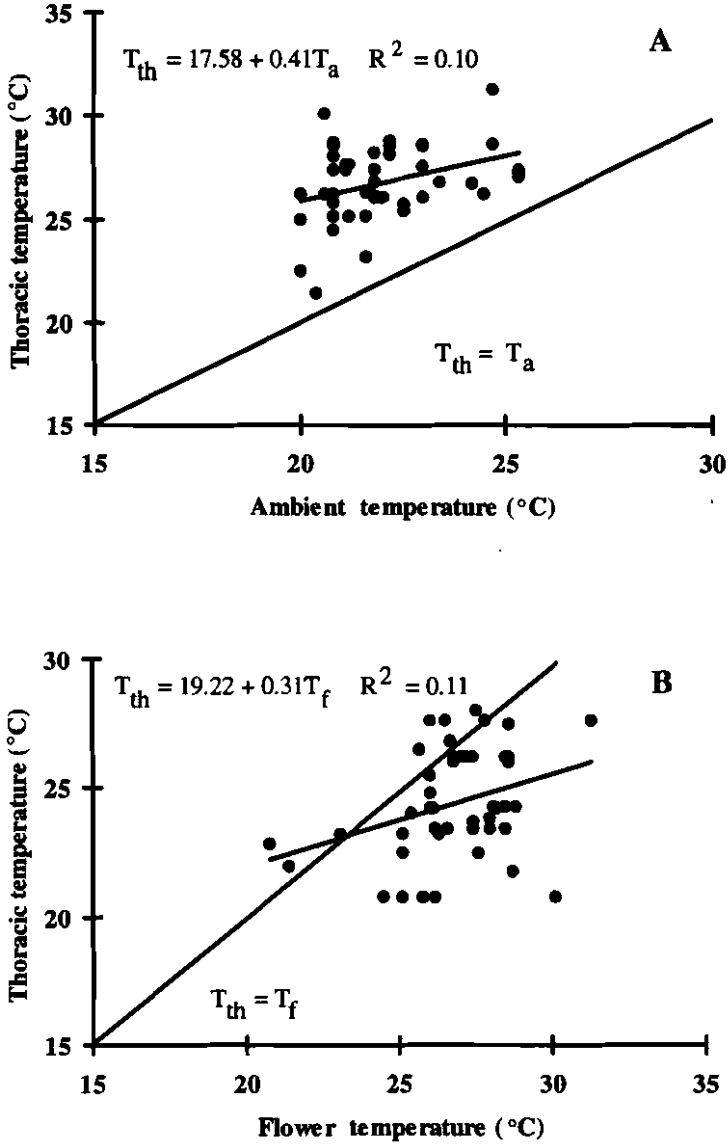


Figure 1

A. The relationship between thoracic temperature (T_{th}) and ambient temperature (T_a) for 47 individuals of Cyclocephala caelestis while visiting flowers of Magnolia tamaulipana in Mexico. The long solid line represents an isotherm where points would lie if thoracic temperature was equal to ambient temperature. B. The relationship between thoracic temperature (T_{th}) and flower temperature (T_f) for 47 individuals of Cyclocephala caelestis while visiting flowers of Magnolia tamaulipana in Mexico. The long solid line represents an isotherm where points would lie if thoracic temperature was equal to flower temperature.

Nevertheless, studies on the scarabs *Cotinus texana* (Chappell, 1984) and *Popillia japonica* (Oertli and Oertli, 1990) suggest regulation of thoracic temperature in the absence of locomotory activity. Studies on *P. japonica* which is of similar size to *C. caelestis*, show a similar relationship between T_{th} and T_a while at rest, possessing a slope of 0.736 (Oertli and Oertli, 1990) which does not statistically differ from that of *C. caelestis* ($t = 1.88$, $df = 45$; $0.1 < P > 0.05$). For *C. caelestis*, an elevated thoracic temperature may be important to maintain mating and feeding activities since these activities are performed at night under cool ambient temperatures.

The primary activities of *C. caelestis* within flowers were mating and feeding on petal tissue. Mating by dynastine scarabs has frequently been observed within flowers (Gibbs *et al.*, 1977; Beach, 1982; Young, 1986; Gottsberger, 1989). Feeding on petal tissue by dynastine scarab beetles has now been reported for *Talauma ovata* (Gibbs *et al.*, 1977), *Magnolia schiedeana* (Dieringer and Delgado, 1994; Dieringer and Espinosa, 1994), *M. tamaulipana*, and *Annona* spp. (Gottsberger, 1989).

A petal and sepal tissue analysis for *M. tamaulipana* indicated that both contain large and similar amounts of carbohydrates and protein (Dieringer *et al.*, unpubl.). However, petals possess approximately 2x the amount of lipids but 4x less fiber than sepals. The difference in lipid content presumably reflects presence of volatile oil containing ethereal oils in the petals. Floral thermogenicity is most likely an adaptation to volatilize these oils (presumably chiral esters) to produce the floral odor which attracts *C. caelestis*. It has even been suggested that, for *Cyclocephala*, floral odors function as sex pheromones since they tend to be species specific (Schatz, 1990). The lower fiber content probably explains *Cyclocephala*'s preference for petals over sepals since petal tissue would be much easier to digest than sepal tissue.

Within Mexico, *Magnolia* spp. are generally endemic to a narrow region and restricted to cloud forest. The *Cyclocephala* spp. visiting these Mexican *Magnolia* are also endemic and possess a very similar distribution. These overlapping distributions plus the data presented here suggest a highly coevolved relationship between Mexican *Magnolia* and pollinating *Cyclocephala* beetles and may be typical of most *Magnolia* in tropical forests.

ACKNOWLEDGEMENTS

This study was supported by Michaux grants awarded to GD and LRC by the American Philosophical Society. We thank the Instituto de Ecología y Alimentos for use of a field vehicle and numerous facilities which they provided. Leonardo Delgado of the Instituto de Ecología, A. C. confirmed the identification of *Cyclocephala caelestis*. Joe Coelho loaned us his digital thermometer. Joe Coelho, Beryl Simpson, John Neff, M.A. Morón, and an anonymous reviewer provided helpful criticism on an earlier draft of the manuscript.

LITERATURE CITED

Bartholomew, G.A. & T.M. Casey. 1977. Endothermy during terrestrial activity in large beetles. *Science* 195:882-883.

Beach, J.H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). *Amer. J. Bot.* 69:1074-1081.

Bergström, G., I. Groth, O. Pellmyr, P.K. Endress, L.B. Thien, A. Hüberner & W. Francke. 1991. Chemical basis of a highly specific mutualism: chiral esters attract pollinating beetles in Eupomatiaceae. *Phytochemistry* 30:3221-3225.

Chappell, M.A. 1984. Thermoregulation and energetics of the green fig beetle (*Cotinus texana*) during flight and foraging behavior. *Phys. Zool.* 57:581-589.

Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants.* Columbia University Press, New York. 1262 pp.

Dieringer, G. & L. Delgado. 1994. Nôtes on the biology of *Cyclocephala jalapensis* (Coleoptera: Scarabaeidae): an endemic of eastern Mexico. *Southwest. Entmol.* 19:309-311.

Dieringer, G. & J.E. Espinosa S. 1994. Reproductive ecology of *Magnolia schiedeana* (Magnoliaceae), a threatened cloud forest tree species in Veracruz, Mexico. *Bull. Torrey Bot. Club* 121: 154-159.

Endress, P.K. 1984. The flowering process in the Eupomatiaceae (Magnoliales). *Bot. Jahrb. Syst.* 104:297-319.

Gibbs, P.E., J. Semir & N.D. da Cruz. 1977. Floral biology of *Talauma ovata* St. Hil. (Magnoliaceae). *Ciencia e Cultura* 29:1437-1441.

Gottsberger, G. 1989. Beetle pollination and flowering rhythm of *Annona* spp. (Annonaceae) in Brazil. *Pl. Syst. Evol.* 167:165-187.

Heinrich, B. & E. McClain. 1986. "Laziness" and hypothermia as a foraging strategy in flower scarabs (Coleoptera: Scarabaeidae). *Phys. Zool.* 59:273-282.

Morgan, K.R. 1987. Temperature regulation, energy metabolism and mate-searching in rain beetles (*Pleocoma* spp.), winter-active, endothermic scarabs (Coleoptera). *J. Exp. Biol.* 128:107-122.

Morgan, K.R. & G.A. Bartholomew. 1982. Homeothermic response to reduced ambient temperature in a scarab beetle. *Science* 216:1409-1410.

Oertli, J.J. & M. Oertli. 1990. Energetics and thermoregulation of *Popillia japonica* Newman (Scarabaeidae, Coleoptera) during flight and rest. *Phys. Zool.* 63:921-937.

Prance, G.T. & J.R. Arias. 1975. A study of the floral biology of *Victoria amazonica* (Poepp.) Sowerby (Nymphaeaceae). *Acta Amaz.* 5:109-139.

Puig, H. & R. Bracho (eds.). 1987. *El bosque mesofilo de montaña de Tamaulipas.* Instituto de Ecología, A.C., Mexico D.F. 186 pp.

Raskin, I., A. Ehmann, W.R. Melander & B.J.D. Meeuse. 1987. Salicylic acid: a natural inducer of heat production in *Arum* lilies. *Science* 237:1601-1602.

Ratcliffe, B.C. 1991. The scarab beetles of Nebraska. *Bull. Univ. Kansas State Mus.* 12:1-333.

Ratcliffe, B.C. & L. Delgado-Castillo. 1990. New species and notes of *Cyclocephala* from Mexico (Coleoptera: Scarabaeidae: Dynastinae). *Folia Entomol. Mex.* 80:41-57.

Robacker, D.C., B.J.D. Meeuse & E.H. Erickson. 1988. Floral aroma: how far will plants go to attract pollinators? *Bioscience* 38:390-398.

Schatz, G.E. 1990. Some aspects of pollination biology in Central American forests, *In:* K.S. Bawa and M. Hadley (eds.). *Reproductive ecology of tropical forest plants*. Parthenon Publishing Group Limited, Paris, France. pp. 69-84.

Young, H.J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *Amer. J. Bot.* 73:931-944.

Vázquez-G. J.A. 1994. *Magnolia* (Magnoliaceae) in Mexico and Central America: a synopsis. *Brittonia* 46:1-23.

Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice Hall, NJ. 718 pp.

Recibido: 25 de julio 1997
Aceptado: 21 de octubre 1997