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IS INCREASED RESISTANCE TO PARASITISM AT THE ORIGIN OF POLYGYNY IN A MEXICAN POPULATION OF THE ANT *ECTATOMMA TUBERCULATUM* (HYMENOPTERA: FORMICIDAE)?GABRIELA PÉREZ-LACHAUD¹, JORGE E. VALENZUELA² AND JEAN-PAUL LACHAUD^{1,3*}¹El Colegio de la Frontera Sur, Dpto Entomología Tropical, Avenida Centenario Km 5.5, Chetumal 77014, Quintana Roo, Mexico²Instituto de Ecología, A.C., Dpto Entomología, Km 2.5 Antigua Carretera a Coatepec n°351, Xalapa 91070, Veracruz, Mexico³Centre de Recherches sur la Cognition Animale, CNRS-UMR 5169, Université de Toulouse UPS, 118 route de Narbonne, 31062 Toulouse Cedex 09, France

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ABSTRACT

The Neotropical ant *Ectatomma tuberculatum* (Olivier) shows a polymorphic social organization with strictly monogynous or facultative polygynous populations along its distribution range. The causative factors of these variations in social organization are unknown but biotic and abiotic environmental factors might explain the differences. In particular, recent studies have suggested that parasites and parasitoids could have an impact on host colony phenotype. Here, we report on eucharitid wasps and mermithid nematodes that attack the only known Mexican polygynous population of *E. tuberculatum* in Veracruz, Mexico. The results were compared with those previously obtained from a monogynous population in Chiapas, Mexico; the aim being to investigate environmental influences on colony social organization. The rather similar prevalence of parasitism between the 2 populations suggests that the hypothesis of an increased resistance to parasites and parasitoids as one of the factors responsible for the emergence of polygyny in *E. tuberculatum* populations does not apply. More likely, other kinds of environmental stress or constraints facilitate the development of polygyny, such as nest site limitations, risks of dispersal and/or high rates of predation.

Key Words: ectatommine ants, prevalence of parasitism, social structure, facultative polygyny, nest site limitation, Mexico

RESUMEN

La hormiga neotropical *Ectatomma tuberculatum* (Olivier) presenta una organización social polimorfa, con poblaciones estrictamente monogínicas o bien, poligínicas facultativas a lo largo de su rango de distribución. Los factores responsables de estas variaciones en su organización social se desconocen, pero factores ambientales bióticos y abióticos podrían explicar estas diferencias. En particular, estudios recientes sugieren que parásitos y parasitoides pudieran afectar el fenotipo de las colonias hospederas. Aquí reportamos sobre avispa eucharitidas y nemátodos mermitidos que atacan a la única población poligínica de *E. tuberculatum* conocida para México, en Veracruz. Se comparan estos resultados con los que se obtuvieron anteriormente de una población monogínica de Chiapas (México), con el objetivo de analizar las influencias ambientales sobre la organización social de las colonias. La prevalencia de parasitismo bastante similar entre ambas poblaciones sugiere que la hipótesis de una mayor resistencia a parásitos y parasitoides como uno de los factores responsables de la aparición de la poliginia en *E. tuberculatum* no es válida. Parece más probable que otras clases de estrés o limitantes ambientales estén implicadas, tales como limitación en sitios de nidificación, riesgos de dispersión o altas tasas de depredación.

Translation provided by the authors.

The importance of environmental pressure in shaping both species socioecology and community structure is a growing point of interest in recent studies on social insects in general (Oldroyd

& Beekman 2009; Wilson et al. 2009; Korb & Foster 2010), and ants in particular (Sorvary & Hakkarainen 2004; Robson & Kohout 2007; Linksvayer & Janssen 2009; McGlynn 2010).

Variation in social organization (the number of individuals in a social group, their behavioral and genetic relationships, and the way in which reproduction is partitioned among them) has been regarded as the product of diverse extrinsic and intrinsic selection pressures related both to local ecological factors and to competitive and cooperative interactions among group members (Ross & Keller 1995; Smith et al. 2008). By comparison with the numerous studies focused on behavioral and genetic mechanisms (see for example: Keller 1993; Chan et al. 1999; Clark et al. 2006; Goodisman et al. 2008; Gotzek & Ross 2008; Haag-Liautard et al. 2009; Suni & Gordon 2010), little attention has been paid to biotic environmental factors such as predation, competition, parasitism, or disease. However, such environmental factors are known to be important in structuring ant communities and populations. Predation by army ants on other ant species, for example, is thought to be a major factor affecting leaf litter community structure and life-history traits of ant colonies in the neotropics (Kaspari & O'Donnell 2003; O'Donnell et al. 2007), while high densities of predators such as larval ant lions (Gotelli 1996) or lizards (Huang et al. 2008) can strongly alter ground-foraging ant assemblages. Furthermore, various studies have shown that attacks by parasitoid phorid flies (Feener 2000; Philpott et al. 2009), eucharitid wasps (Lachaud & Pérez-Lachaud 2009; Pérez-Lachaud et al. 2010), or pathogens (Keller 1995a; Schmid-Hempel 1998; Naug & Camazine 2002) represent another important potential source of disturbance that can affect the composition and dynamics of ant communities as well as colony phenotype.

The social structure of an ant species is related, *inter alia*, to the number of reproductive queens in mature colonies. True polygyny - the occurrence of several reproducing queens per colony—is particularly common in ants (Pamilo 1991; Keller 1995b), queen number being variable among colonies of the same species and even of the same population (Chapuisat et al. 2004). Several authors have discussed the evolution of polygyny as an ecologically flexible trait driven by environmental factors (Hölldobler & Wilson 1977; Nonacs 1988; Keller 1995b). Different hypotheses have been generated to account for variation in queen number including competition, nest site limitation, food availability, risks of dispersal, and inter- and intraspecific social parasitism (Keller 1995b; Gardner et al. 2007; McGlynn 2010). Polygyny and/or multiple mating (polyandry) are thought to be beneficial to the colony by increasing resistance to parasites and pathogens due to an enhancement in the genetic diversity of the workers (Schmid-Hempel 1994, 1998; Hughes et al. 2008). More specifically, genetically diverse host populations are

predicted to have lower levels of infection or parasitism prevalence, but studies addressing this issue are scant (Hughes & Boomsma 2004; Gardner et al. 2007; Reber et al. 2008), and the results are not always consistent (see Castella et al. 2010).

Ectatomma tuberculatum (Olivier) (Hymenoptera: Formicidae: Ectatomminae) is a Neotropical ground-nesting, predatory ant that occurs in both wet forest and dry forest habitats from Mexico to northern Argentina, and from sea level to about 1500 m in altitude (Weber 1946; Brown 1958; Valenzuela et al. 1995; Quiroz-Robledo & Valenzuela-González 2007). This species, regarded as a potential biocontrol agent in different agroecosystems (Cook 1904a, b; Weber 1946; Lachaud et al. 1996; Ibarra-Núñez et al. 2001), is ecologically dominant in coffee and cocoa plantations in Chiapas, Mexico (Schatz & Lachaud 2008), and in the arboreal ant mosaic of cocoa plantations in Brazil (Majer et al. 1994). Colony structure and social organization of *E. tuberculatum* populations seem to vary according to as yet unidentified regional causative factors. For example, the population at Rosario Izapa, in the Soconusco region of Chiapas, Mexico, is characterized by the presence of a single, large queen per colony, well-differentiated from the workers (Pérez-Lachaud et al. 2010); from 253 nests of *E. tuberculatum* collected from the whole Soconusco region over 16 yr, only 3 were digynous and one contained 4 non-functional, mermithised dealate females (Lachaud, unpublished data). At that site, nest population ranged from 22 to 1849 adults (mean colony size = 515, $n = 104$, Lachaud & Pérez-Lachaud, unpublished data), and nest density was estimated at between 600 and 1500 nests/ha (Schatz & Lachaud 2008). In contrast, facultative polygyny (colonies coexisting as monogynous or polygynous in the same population) is characteristic of populations in Brazil (Hora et al. 2005b), but also in a population found at Apazapan, Veracruz, Mexico (Hora et al. 2001, 2005a), where nest population ranged from 6 to 429 adults (mean colony size = 106, $n = 29$, recalculated from Hora et al. 2001).

Because of the clearly established differences between the 2 Mexican *E. tuberculatum* populations studied so far (Chiapas and Veracruz), some doubts emerged concerning species identification. However, the results of current genetic polymorphism analyses using specific microsatellite loci (see Poteaux et al. 2003) confirmed that both populations belong to the same species and only differ by a reduced number of nucleotide base pairs (Nettel et al., unpublished data). Different selective environmental pressures have been put forward to explain the observed differences in social organization (Hora et al. 2005b; Zinck et al. 2007, 2008), including differences in genetic diversity

and resistance to parasitism (Pérez-Lachaud et al. 2010). Though the 2 above-mentioned populations have been the object of extensive studies, no comparative study has been made concerning the diversity of parasites attacking them.

Here we report on 2 groups of parasites, eucharitid wasps and mermithid nematodes, which attack the polygynous *E. tuberculatum* population of Apazapan, Veracruz, with the aim of adding information on the ecology of this species in order to better understand the mechanisms underlying facultative polygyny.

MATERIALS AND METHODS

Study Site

The study site was located at Apazapan, Veracruz, Mexico (19°19'38"N; 96°43'21"W, 300 m above sea level); nests were collected at the same site (referred to as Apz 1, see Hora et al. 2005a) where both polygynous and monogynous *E. tuberculatum* colonies infested by *Ectatomma parasiticum* Feitosa & Fresneau had been previously collected by Hora et al. (2001). This site is a remnant of tropical dry forest and has an irregular orography. Surrounding natural vegetation is characteristic of lowland deciduous scrub (Castillo 1995). The climate of the region is warm, subhumid, with heavy rains during the summer months and at the beginning of autumn, and sparse rains during winter. The annual average temperature is 25.5°C with an average annual total rainfall of 1250 mm. The Rendzina type soil (dark, grayish-brown, humus-rich, shallow soil over limestone that has calcareous topsoil) supports a semi-deciduous tropical rain forest characterized by the presence of *Cecropia peltata* L., *C. obtusifolia* Bertol. (Cecropiaceae), *Heliocarpus pallidus* Rose, *H. mexicanus* (Turcz.) (Tiliaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Mimosaceae), and groves of evergreen oaks, *Quercus peduncularis* Née, *Q. polymorpha* Schltdl. & Cham., and *Q. oleoides* Schltdl. & Cham. (Fagaceae) (Mora-Aguilar & Montes de Oca 2009).

Sampling Method for Eucharitid Wasps

Eucharitidae (Hymenoptera: Chalcidoidea) are specific, specialized ectoparasitoids of ant brood, with a highly modified life cycle (Clausen 1941; Heraty 1994). Adults emerge inside the host nest, mating occurs outside, females lay eggs into or on plant tissue, and the very mobile first-instar larvae (planidia) are presumed to attach to foraging ant workers (or to intermediate hosts) for passive phoretic transport to the ant nest (Clausen 1940; Heraty 2000). The planidia actively seek the suitable developmental host stage (Clausen 1940, 1941; Heraty 1994; personal ob-

servation) and further development takes place on the newly transformed ant pupae (Clausen 1940; Pérez-Lachaud et al. 2006b).

Nine nests of *Ectatomma tuberculatum* were thoroughly excavated on 21 Sep and 23 Sep 2010 and taken to the laboratory. The presence or absence of alate and dealate females in each nest was noted, as well as the number of males, workers, cocoons (pupae), larvae, and the presence of eggs. Cocoons were isolated in plastic containers topped with wire mesh and kept at room temperature ($28 \pm 2^\circ\text{C}$ and $75 \pm 5\%$ relative humidity) for about one week to wait for parasitoid emergence. Then the identity, number, and sex of emerging adult wasps were recorded. After this period, all the cocoons were dissected under a stereomicroscope (Nikon, 75x), and both the number and stage of development of parasitoids (planidia, late larvae, pupae and pharate adults) were recorded. Larvae were also inspected, and the presence of round melanized scars (evidence of the previous attachment of a planidium), and both the number and location of planidia, if present, were recorded.

Sampling Method for Mermithid Nematodes

No complete life cycle of any mermithid parasite of Neotropical ants is known; but in a manner similar to the European mermithid *Pheromermis villosa* Kaiser that parasitizes sexuals of *Lasius flavus* (Fab.) and *L. niger* (L.) (Kaiser 1986), they are thought to have an indirect life cycle; i.e., the ant—which corresponds to the developmental host—becomes infected by eating paratenic hosts containing infective stages of the mermithid. Infection of the ant occurs in the larval stage in that the mermithid juvenile enters the body cavity of the ant larva and initiates development. Known mermithids infecting *Ectatomma* species (Wheeler 1930; Weber 1946; Poinar et al. 2006) are carried into the adult stage of the ant. Upon emergence from the ant, the post-parasitic juvenile enters an aquatic or moist habitat to mature, mate, and oviposit (Poinar et al. 2006).

Adult workers parasitized by mermithids were recognized from the morphological modifications of the ants brought about by the parasites and were maintained in the laboratory. Post-parasitic juveniles emerged from worker ants, and were maintained in water until the mermithids molted to the adult stage 3 wk later. Identification of the mermithid nematodes was performed by George Poinar, Jr. (Oregon State University, USA).

Voucher specimens of ants and parasitoids were deposited in the Arthropod collection of ECOSUR at Chetumal, Quintana Roo, Mexico. Mermithids were deposited in the collection of the USDA Nematode Laboratory, Beltsville, Maryland.

RESULTS

Nest Architecture

Ectatomma tuberculatum nests at Apazapan were characterized by a loose architecture. The entrance of the nest exhibiting the characteristic external chimney gallery, made of rough plant fibers and soil particles, was located at the base of a tree and could run vertically up to a height of 60-90 cm (2 to 3 ft) (Wheeler 1924). However at Apazapan there was no central vertical gallery with several horizontal chambers spreading from it, as is typical for nests in Chiapas and Brazil (Cook 1904a; Valenzuela et al. 1995; Hora et al. 2005b). Instead, the main gallery just under the entrance, followed the roots of the supporting tree, skirted round large and medium sized stones, and was extended backwards almost horizontally following the slope of site. By contrast with the 3 to 6—and sometimes up to 10—chambers (empty spaces whose soil and ceiling were compacted with debris and cocoon remains) found in nests in Chiapas (Lachaud, unpublished data), no chambers were observed in the nests in Apazapan. Workers and brood were found scattered in hollow cavities formed behind stones or between roots and stones, and loosely dispersed in the soil. Finally, while *E. tuberculatum* nests collected in Chiapas reached depths of up to 2 m (Valenzuela et al. 1995), nests at Apazapan hardly reached 0.60 m.

Colony Composition

From the 9 nests collected, 6 had only workers and brood, and only 3 contained dealate females: one with 1 dealate female, 1 with 2 dealate females and 1 with at least 7 dealate females and several alate females at the moment of collection. However, the following day, when the latter nest was cleaned and individuals were counted, most of the winged alate females had lost their wings leading to a total of 18 dealate females and 3 alate females (Table 1). No small size females, belonging to the social parasite species *Ectatomma parasiticum*, which resembled *E. tuberculatum* females in all morphological characteristics but size, were found. Worker numbers ranged from 7 to 150 at the moment of collection (72.3 ± 13.5 , mean \pm SEM). Five out of the 9 nests collected had cocoons and only 3 had a few larvae.

Eucharitid Parasitism

Only 2 of the *E. tuberculatum* nests were parasitized by eucharitid wasps, which accounted for a global nest parasitism of 22.2%. From a total of 57 cocoons collected from 5 nests, 15 were parasitized, i.e., the global prevalence of parasitism of cocoons was 26.3% (Table 1). Three larvae, 6 pupae

TABLE 1. CHARACTERISTICS AND COMPOSITION OF *ECTATOMMA TUBERCULATUM* NESTS FROM APAZAPAN, VERACRUZ, PREVALENCE OF EUCHARITID PARASITISM AMONG ANT BROOD, AND MEAN NUMBER OF ADULT EUCHARITIDS AND MERMITHERGATES IN PARASITIZED NESTS.

Collecting date	Dealate females	Alate females	Workers	Pupae	Larvae	Eggs presence	Parasitized pupae (%)	Parasitized larvae (%)	Eucharitid adults	Mermithized workers
21/09/2010	0	0	61	0	0	—	—	—	—	0
21/09/2010	0	0	50	5	0	—	—	—	0	0
21/09/2010	18	3	150	3	1	1 (20%)	0	0	0	6
21/09/2010	0	0	7	0	0	—	—	—	—	0
23/09/2010	0	0	47	0	0	—	—	—	—	0
23/09/2010	1	0	64	0	0	—	—	—	—	0
23/09/2010	0	0	71	4	4	0	0	0	0	0
23/09/2010	2	0	100	3	0	0	0	—	0	0
23/09/2010	0	0	101	42	4	14 (33.3%)	1 (25%)	7	0	0

and 7 adult eucharitids were retrieved: 6 adults belonged to *Isomerula coronata* (Westwood) (2 females, 4 males) and one was a *Dilocantha lachaudii* Heraty male. One case of superparasitism was identified. In fact, most of the cocoons (42/57) belonged to the same nest from which 14 were parasitized by eucharitids accounting for a prevalence of parasitism of cocoons of 33.3% for that nest. Furthermore, from a total of 9 larvae collected from 3 nests only 1 larva was parasitized (i.e., a global prevalence of parasitism of larvae of 11.1%), and bore a planidium attached to the left maxilla.

Mermithid Parasitism

Six workers, all belonging to the largest polygynous nest collected, had enlarged gasters and all were found to be mermithized. One of the workers died before mermithid emergence but 5 post-parasitic juvenile mermithids emerged from the other workers, causing their death. Of these, 2 adults were retrieved and were killed in hot water at 50°C and then placed in fixative (5% formalin). Both specimens were juvenile females identified as belonging to the genus *Meximermis* Poinar, Lachaud, Castillo & Infante and, most probably, to the same species, *M. ectatommi* Poinar, Lachaud, Castillo & Infante as that parasitizing *E. ruidum* Roger in Chiapas (see Poinar et al. 2006). However, in the absence of males and mature females, species identification could not be certified.

DISCUSSION

Apart from some scarce myrmecophiles found very occasionally within their nest, such as a gas-tropod, a small diploped (Meropoda), a lepis-matid or Nicoletiidae thysanuran, a worm infesting the refuse dumps, and a Histeridae beetle (Cook 1905; Pérez-Lachaud & Lachaud, unpublished data), colonies of *E. tuberculatum* are mainly parasitized by eucharitid parasitoid wasps and mermithid nematodes. Parasitism of *E. tuberculatum* by the eucharitid wasp *I. coronata* was known only from an earlier report on a Guatemalan population (Cook 1905). More recent studies in Chiapas, Mexico (Lachaud et al. 1998; Pérez-Lachaud et al. 2006a, 2010) confirmed parasitism by *I. coronata* and additionally reported 2 other eucharitid parasitoids attacking this ant host, belonging to 2 different genera, *D. lachaudii* and an undescribed, uncommon species of *Kapala*. Regarding nematode parasitism, originally reported for *E. tuberculatum* populations from Panama and Trinidad and, perhaps, from Costa Rica (Emery 1890; Wheeler 1930), it has also been observed in at least 16 out of 253 nests collected from the Soconusco population (Lachaud, unpublished data). On the other hand, the facultatively

polygynous population of Apazapan is the only one where the social ant parasite *E. parasiticum* is known to occur (Hora et al. 2001, 2005a; Feitosa et al. 2008), but neither eucharitid nor mermithid parasitism had ever been reported for it before.

Although nest sample size at Apazapan was relatively small, it is worth noting that the same multi-species system of parasitoids and parasites attacked *E. tuberculatum* colonies both in Veracruz and in Chiapas, whatever the social structure (monogyny or facultative polygyny) of their populations. Both populations hosted a mermithid parasite, presumably the same species in both cases; though the specimens from Chiapas have not yet been identified. Moreover, the polygynous population from Veracruz, hosted the same predominant eucharitid parasitoid species, *D. lachaudii* and *I. coronata*, as the monogynous population from Chiapas (Pérez-Lachaud et al. 2010). In Apazapan most of the individual parasitoids belonged to *I. coronata*, while *D. lachaudii* prevailed as the main parasitoid of *E. tuberculatum* in the Rosario Izapa population. However, populations of both eucharitid species in Chiapas appeared to vary inversely in frequency, with predominance of one or the other species during the year (Pérez-Lachaud et al. 2010), and such patterns could also occur at Apazapan; but a larger sample, distributed along the year, is needed to verify this trend.

Nest collection at Apazapan was performed over too short a period to allow extrapolation of the real annual prevalence of parasitism at the scale of the population. However, the value of 26.3% obtained for the global prevalence of eucharitid parasitism for cocoons from the 9 nests collected at the end of Sep was fully compatible with that recorded in Chiapas during the same period of the year and with a similar sample size for the monthly collected nests: 27.1% for Oct 2004 ($n = 8$) and 14.4% for Sep 2005 ($n = 10$) (see Table 1 in Pérez-Lachaud et al. 2010). These results suggest that the prevalence of parasitism was rather similar between both populations and, therefore, that the hypothesis of increased resistance to parasites and parasitoids as one of the factors responsible for polygyny emergence in *E. tuberculatum* populations is not supported. This conclusion seems to be given further weight by 2 apparently adaptive biological traits related to parasitism, which make unnecessary the emergence of polygyny, i.e., i) the apparent potential of *E. tuberculatum*, at least for the Rosario Izapa population (Pérez-Lachaud et al. 2010), to modulate the impact of eucharitids on the colonies through differences in the seasonal timing of eucharitid main attack and sexual brood production by ants, and ii) the polydomy that seems to characterize this species (García-Pérez et al. 1991; Hora et al. 2005b) and that would reduce the probability of

any given colony having its whole brood parasitized (Pérez-Lachaud et al. 2010).

Variation in morphological, behavioral, physiological and life history traits is thought to enable an individual (or a colony in the case of social insects) to maximize its reproductive success under a wide range of conditions, and thus cope better with variable ecological constraints (Foitzik et al. 2010). The causes of the facultative polygyny found at Apazapan or in Brazil thus seem to have originated from environmental stress or constraints other than parasitism. Nest site limitation, risks of dispersal, and/or high rates of predation that could be linked (see Bourke 1999; Kaspari & O'Donnell 2003; Linksvayer & Janssen 2009) to the lower colony sizes recorded for polygynous populations (Brazil: Hora et al. 2005b; Apazapan: Hora et al. 2001 and these results) could be promising candidate explanations. An important difference between Chiapas and Veracruz sites is the type and structure of the soil, which seemingly determined the structure of the nests at both sites. At Apazapan, our observations indicate that the number of trees available as nest supports is more than enough, but digging difficulties due to the very rocky soil of the site could be a much more limiting factor for foundresses. In such conditions, the founding of a new colony by dispersed females would be extremely risky and, as suggested by Keller (1995b), could favor the selection of young mated queens seeking adoption into established colonies (secondary polygyny), or readoption in their mother colony, as apparently occurs in the Brazilian population (Zinck et al. 2007). Further studies detailing the soil characteristics in the different sites and their consequences on both nest structure and colony foundation possibilities, along with within colony genetic diversity studies would help reach a better understanding of the environmental pressures controlling the emergence of polygyny in *E. tuberculatum* and the socioecology of this species.

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REFERENCES CITED

- BOURKE, A. F. G. 1999. Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* 12: 245-257.
- BROWN, JR., W. L. 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). *Bull. Mus. Comp. Zool., Harvard* 118: 173-362.
- CASTELLA, G., CHRISTE, P., AND CHAPUISAT, M. 2010. Covariation between colony social structure and immune defences of workers in the ant *Formica selysi*. *Insectes Sociaux* 57: 233-238.
- CASTILLO, C. G. 1995. Ecología del paisaje del municipio de Jalcomulco, Veracruz. MSc. thesis, Facultad de Ciencias, UNAM, Mexico, 192 pp.
- CHAN, G. L., HINGLE, A., AND BOURKE, A. F. G. 1999. Sex allocation in a facultatively polygynous ant: between-population and between-colony variation. *Behav. Ecol.* 10: 409-421.
- CHAPUISAT, M., BOCHERENS, S., AND ROSSET, H. 2004. Variable queen number in ant colonies: no impact on queen turnover, inbreeding, and population genetic differentiation in the ant *Formica selysi*. *Evolution* 58: 1064-1072.
- CLARK, R. M., ANDERSON, K. E., GADAU, J., AND FEWEL, J. H. 2006. Behavioral regulation of genetic caste determination in a *Pogonomyrmex* population with dependent lineages. *Ecology* 87: 2201-2206.
- CLAUSEN, C. P. 1940. The oviposition habits of the Eucharidae (Hymenoptera). *J. Wash. Acad. Sci* 30: 504-516.
- CLAUSEN, C. P. 1941. The habits of Eucharidae. *Psyche* 48: 57-69.
- COOK, O. F. 1904a. Notes on the habits of the Kelep, or Guatemalan cotton-boll-weevil ant. *U.S.D.A. Bulletin* # 49, 15 pp.
- COOK, O. F. 1904b. An enemy of the cotton-boll-weevil. *Science* 19: 862-864.
- COOK, O. F. 1905. The social organization and breeding habits of the cotton protecting Kelep of Guatemala. *U.S.D.A. Technical Series* No. 10, pp. 1-55.
- EMERY, C. 1890. Studi sulle Formiche della Fauna Neotropica. I. Formiche di Costa Rica. *Bull. Soc. Ent. Ital.* 22: 38-80.
- FEENER, JR., D. H. 2000. Is the assembly of ant communities mediated by parasitoids? *Oikos* 90: 79-88.
- FEITOSA, R. M., HORA R. R., DELABIE, J. H. C., VALENZUELA, J., AND FRESNEAU, D. 2008. A new social parasite in the ant genus *Ectatomma* F. Smith (Hymenoptera, Formicidae, Ectatomminae). *Zootaxa* 1713: 47-52.
- FOITZIK, S., KURECK, I. M., RÜGER, M. H., AND METZLER, D. 2010. Alternative reproductive tactics and the impact of local competition on sex ratios in the ant *Hypoponera opacior*. *Behav. Ecol. Sociobiol.* 64: 1641-1654.
- GARCÍA-PÉREZ, J. A., PEÑA-SÁNCHEZ, R., CAMARGO-HUIQUI, P., AND CHAMPALBERT, A. 1991. Rutas de forrajeo utilizadas por *Ectatomma tuberculatum* O. (Hymenoptera: Ponerinae) en una plantación de cacao en el Soconusco, Chiapas México. *Folia Entomol. Mexicana* 82: 161-171.
- GARDNER, M. G., SCHÖNROGGE, K., ELMES, G. W., AND THOMAS, J. A. 2007. Increased genetic diversity as a defence against parasites is undermined by social parasites: *Microdon mutabilis* hoverflies infesting *Formica lemni* ant colonies. *Proc. R. Soc. B* 274: 103-110.
- GOODISMAN, M. A. D., KOVACS, J. L., AND HUNT, B. G. 2008. Functional genetics and genomics in ants (Hymenoptera: Formicidae): The interplay of genes and social life. *Myrmecol. News* 11: 107-117.
- GOTELLI, N. J. 1996. Ant community structure: effects of predatory ant lions. *Ecology* 77: 630-638.
- GOTZEK, D., AND ROSS, K. G. 2008. Experimental conversion of colony social organization in fire ants (*So-*

- lenopsis invicta*): worker genotype manipulation in the absence of queen effects. *J. Insect Behav.* 21: 337-350.
- HAAG-LIAUTARD, C., VITIKAINEN, E., KELLER, L., AND SUNDSTRÖM, L. 2009. Fitness and the level of homozygosity in a social insect. *J. Evol. Biol.* 22: 134-142.
- HERATY, J. M. 1994. Classification and evolution of the Oraseminae in the Old World, including revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae). *Life Sciences Contributions*, Royal Ontario Museum 157: 1-176.
- Heraty, J. M. 2000. Phylogenetic relationships of ORASEMINAE (Hymenoptera: Eucharitidae). *Ann. Entomol. Soc. Am.* 93: 374-390.
- HÖLLDOBLER, B., AND WILSON, E. O. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64: 8-15.
- HORA, R. R., DOUMS, C., POTEAUX, C., FÉNERON, R., VALENZUELA, J., HEINZE, J., AND FRESNEAU, D. 2005a. Small queens in the ant *Ectatomma tuberculatum*: a new case of social parasitism. *Behav. Ecol. Sociobiol.* 59: 285-292.
- HORA, R. R., FÉNERON, R., VALENZUELA, J., FAVILA, M. E., AND FRESNEAU, D. 2001. Queen-size dimorphism in the ant *Ectatomma tuberculatum* (Hymenoptera: Formicidae: Ponerinae). *Sociobiology* 38: 407-420.
- HORA, R. R., VILELA, E., FÉNERON, R., PEZON, A., FRESNEAU, D., AND DELABIE, J. 2005b. Facultative polygyny in *Ectatomma tuberculatum* (Formicidae, Ectatomminae). *Insectes Sociaux* 52: 194-200.
- HUANG, S. C., NORVAL, G., AND TSO, I. M. 2008. Predation by an exotic lizard, *Anolis sagrei*, alters the ant community structure in betelnut palm plantations in southern Taiwan. *Ecol. Entomol.* 33: 569-576.
- HUGHES, W. O. H., AND BOOMSMA, J. J. 2004. Genetic diversity and disease resistance in leaf-cutting ant societies. *Evolution* 58: 1251-1260.
- HUGHES, W. O. H., RATNIEKS, F. L. W., AND OLDROYD, B. P. 2008. Multiple paternity or multiple queens: two routes to greater intracolony genetic diversity in the eusocial Hymenoptera. *J. Evol. Biol.* 21: 1090-1095.
- IBARRA-NÚÑEZ, G., GARCÍA, J. A., LÓPEZ, J. A., AND LACHAUD, J.-P. 2001. Prey analysis in the diet of some ponerine ants (Hymenoptera: Formicidae) and web-building spiders (Araneae) in coffee plantations in Chiapas, Mexico. *Sociobiol.* 37: 723-755.
- KAISER, H. 1986. Über Wechselbeziehungen zwischen Nematoden (Mermithidae) und Ameisen. *Zool. Anzeig.* 217: 156-177.
- KASPARI, M., AND O'DONNELL, S. 2003. High rates of army ant raids in the Neotropics and implications for ant colony and community structure. *Evol. Ecol. Res.* 5: 933-939.
- KELLER, L. 1993. The assessment of reproductive success of queens in ants and other social insects. *Oikos* 67: 177-180.
- KELLER, L. 1995a. Parasites, worker polymorphism, and queen number in social insects. *Am. Nat.* 145: 842-847.
- KELLER, L. 1995b. Social life: the paradox of multiple-queen colonies. *Trends Ecol. Evol.* 10: 355-360.
- KORB, J., AND FOSTER, K. R. 2010. Ecological competition favours cooperation in termite societies. *Ecol. Letters* 13: 754-760.
- LACHAUD, J.-P., LÓPEZ-MÉNDEZ, J. A., SCHATZ, B., DE CARLI, P., AND BEUGNON, G. 1996. Comparaison de l'impact de prédation de deux ponérines du genre *Ectatomma* dans un agro-écosystème néotropical. *Actes Coll. Ins. Soc.* 10: 67-74.
- LACHAUD, J.-P., AND PÉREZ-LACHAUD, G. 2009. Impact of natural parasitism by two eucharitid wasps on a potential biocontrol agent ant in southeastern Mexico. *Biol. Control* 48: 92-99.
- LACHAUD, J.-P., PÉREZ-LACHAUD, G., AND HERATY, J. M. 1998. Parasites associated with the ponerine ant *Ectatomma tuberculatum* (Hymenoptera: Formicidae): first host record for the genus *Dilocantha* (Hymenoptera: Eucharitidae). *Florida Entomol.* 81: 570-574.
- LINKSVAYER, T. A., AND JANSSEN, M. A. 2009. Traits underlying the capacity of ant colonies to adapt to disturbance and stress regimes. *Syst. Res.* 26: 315-329.
- MAJER, J. D., DELABIE, J. H. C., AND SMITH, M. R. B. 1994. Arboreal ant community patterns in Brazilian cocoa farms. *Biotropica* 26: 73-83.
- MCGLYNN, T. P. 2010. Polygyny in thief ants responds to competition and nest limitation but not food resources. *Insect. Soc.* 57: 23-28.
- MORA-AGUILAR, E. F., AND MONTES DE OCA, E. 2009. Escarabajos necrófagos (Coleoptera : Scarabaeidae y Trogidae) de la región central baja de Veracruz, México. *Acta Zool. Mexicana* (n.s.) 25: 569-588.
- NAUG, D., AND CAMAZINE, S. 2002. The role of colony organization on pathogen transmission in social insects. *J. Theor. Biol.* 215: 427-439.
- NONACS, P. 1988. Queen number in colonies of social Hymenoptera as a kin-selected adaptation. *Evolution* 42: 566-580.
- O'DONNELL, S., LATTKE, J., POWELL, S., AND KASPARI, M. 2007. Army ants in four forests: geographic variation in raid rates and species composition. *J. Anim. Ecol.* 76: 580-589.
- OLDROYD, B. P., AND BEEKMAN, M. 2009. Intergenerational reproductive parasitism in a stingless bee. *Mol. Ecol.* 18: 3958-3960.
- PAMILO, P. 1991. Evolution of colony characteristics in social insects. II. Number of reproductive individuals. *Am. Nat.* 138: 412-433.
- PAMILO, P., AND ROSENGREN, R. 1984. Evolution of nesting strategies of ants: genetic evidence from different population types of *Formica* ants. *Biol. J. Linn. Soc.* 21: 331-348.
- PÉREZ-LACHAUD, G., LÓPEZ-MÉNDEZ, J. A., AND LACHAUD, J.-P. 2006a. Eucharitid parasitism of the Neotropical ant *Ectatomma tuberculatum*: Parasitoid co-occurrence, seasonal variation, and multiparasitism. *Biotropica* 38: 574-576.
- PÉREZ-LACHAUD, G., HERATY, J. M., CARMICHAEL, A., AND LACHAUD, J.-P. 2006b. Biology and behavior of *Kapala* (Hymenoptera: Eucharitidae) attacking *Ectatomma*, *Gnamptogenys* and *Pachycondyla* (Formicidae: Ectatomminae and Ponerinae) in Chiapas, Mexico. *Ann. Entomol. Soc. Am.* 99: 567-576.
- PÉREZ-LACHAUD, G., LÓPEZ-MÉNDEZ, J. A., BEUGNON, G., WINTERTON, P., AND LACHAUD, J.-P. 2010. High prevalence but relatively low impact of two eucharitid parasitoids attacking the Neotropical ant *Ectatomma tuberculatum* (Olivier). *Biol. Control* 52: 131-139.
- PHILPOTT, S. M., PERFECTO, I., VANDERMEER, J., AND UNO, S. 2009. Spatial scale and density dependence in a host parasitoid system: an arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid. *Environ. Entomol.* 38: 790-796.

- POINAR, JR., G., LACHAUD, J.-P., CASTILLO, A., AND INFANTE, F. 2006. Recent and fossil nematode parasites (Nematoda: Mermithidae) of Neotropical ants. *J. Invert. Pathol.* 91: 19-26.
- POTEAUX, C., HORA, R. R., VAUTRIN, D., FRESNEAU, D., AND SOLIGNAC, M. 2003. Isolation of polymorphic microsatellite loci in the ponerine ant *Ectatomma tuberculatum*. *Mol. Ecol. Notes* 3: 635-637.
- QUIROZ-ROBLEDO, L. N., AND VALENZUELA-GONZÁLEZ, J. 2007. Distribution of poneromorph ants (Hymenoptera: Formicidae) in the Mexican state of Morelos. *Florida Entomol.* 90: 609-615.
- REBER, A., CASTELLA, G., CHRISTE, P., AND CHAPUISAT, M. 2008. Experimentally increased group diversity improves disease resistance in an ant species. *Ecol. Letters* 11: 682-689.
- ROBSON, S. K. A., AND KOHOUT, R. J. 2007. A review of the nesting habits and socioecology of the ant genus *Polyrhachis* Fr. Smith. *Asian Myrmecol.* 1: 81-99.
- ROSS, K. G., AND KELLER, L. 1995. Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annu. Rev. Ecol. Syst.* 26: 631-656.
- SCHATZ, B., AND LACHAUD, J.-P. 2008. Effect of high nest density on spatial relationships in two dominant ectatommine ants. *Sociobiology* 51: 623-643.
- SCHMID-HEMPPEL, P. 1994. Infection and colony variability in social insects. *Phil. Trans. R. Soc. Lond. B* 346: 313-321.
- SCHMID-HEMPPEL, P. 1998. Parasites in social insects. Princeton University Press. Princeton, New Jersey, 409 pp.
- SMITH, C., ANDERSON, K., TILLBERG, C., GADAU, J., AND SUAREZ, A. 2008. Caste determination in a polymorphic social insect: nutritional, social, and genetic factors. *Am. Nat.* 172: 497-507.
- SORVARY, J., AND HAKKARAINEN, H. 2004. Habitat-related aggressive behaviour between neighbouring colonies of the polydomous wood ant *Formica aquilonia*. *Anim. Behav.* 67: 151-153.
- SUNI, S. S., AND GORDON, D. M. 2010. Fine-scale genetic structure and dispersal distance in the harvester ant *Pogonomyrmex barbatus*. *Heredity* 104: 168-173.
- VALENZUELA-GONZÁLEZ, J., LÓPEZ-MÉNDEZ, A., AND LACHAUD, J.-P. 1995. Activity patterns and foraging activity in nests of *Ectatomma tuberculatum* (Hymenoptera: Formicidae) in cacao plantations. *Southwest. Entomol.* 20: 507-515.
- WEBER, N. A. 1946. Two common ponerine ants of possible economic significance, *Ectatomma tuberculatum* (Olivier) and *E. ruidum* Roger. *Proc. Entomol. Soc. Washington* 48: 1-16.
- WHEELER, W. M. 1924. Courtship of the Calobatas. *J. Hered.* 15: 147-165.
- WHEELER, W. M. 1930. Two mermithergates of *Ectatomma*. *Psyche* 37: 48-54.
- WILSON, E. E., MULLEN, L. M., AND HOLWAY, D. A. 2009. Life history plasticity magnifies the ecological effects of a social wasp invasion. *Proc. Natl. Acad. Sci. USA* 106: 12809-12813.
- ZINCK, L., JAISSON, P., HORA, R. R., DENIS, D., POTEAUX, C., AND DOUMS, C. 2007. The role of breeding system on ant ecological dominance: genetic analysis of *Ectatomma tuberculatum*. *Behav. Ecol.* 18: 701-708.
- ZINCK, L., HORA, R. R., CHÂLINE, N., AND JAISSON, P. 2007. Low intraspecific aggression level in the polydomous and facultative polygynous ant *Ectatomma tuberculatum*. *Entomol. Exp. Appl.* 126: 211-216.