BIOTROPICA 36(1): 118–122 2004

SHORT COMMUNICATIONS

Seed Predation on Brazil Nuts (*Bertholletia excelsa*) by Macaws (Psittacidae) in Madre de Dios, Peru[1]

ABSTRACT

We investigated the impact of seed predation by large macaws (*Ara* spp.) on Brazil nut, the seed of *Bertholletia excelsa* (Lecythidaceae). Counts of macaw-damaged fruit below 50 focal trees in a Peruvian Brazil nut harvesting concession indicated that macaws destroyed about 10 percent of the concession's crop. We compared this impact to other sources of variation in profits from harvesting and suggest methods to compensate harvesters while encouraging them to conserve macaws in their concessions.

RESUMEN

Se investigó el impacto causado por guacamayos (*Ara* spp.) en la depredación de semillas de castaña (*Bertholletia excelsa*: Lecythidaceae) en un rodal castañero en el Perú. En una muestra de 50 árboles se contó el número de frutos afectados por guacamayos encontrados en el suelo, y los resultados indican que alrededor del 10 porciento de la producción total del área de aprovechamiento ha sido eliminada por acción de guacamayos. Se comparó este impacto con otras causas de variabilidad en la rentabilidad de la cosecha, presentándose recomendaciones para compensar a los castañeros por la pérdida de producción, proporcionando incentivos para la conservación de guacamayos en sus áreas de aprovechamiento.

Key words: Ara; Bertholletia excelsa; *Brazil nut; Lecythidaceae; macaw; moist tropical forest; Peru; Psittacidae; seed predation.*

Pre-dispersal seed predation is common in tropical forests and can result in high levels of seed mortality (Peres 1991). Parrots are important pre-dispersal seed predators, but few studies have quantified the damage they cause to seed crops (Galetti & Rodrigues 1992). In this study, we report the impact of pre-dispersal seed predation by macaws (*Ara* spp.) on a forest emergent, the Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl.: Lecythidaceae).

The seed of *B. excelsa* (known in English as the Brazil nut) is one of the most economically important non-timber forest products (NTFP) in the Amazon (Mori 1992), with Peru exporting $4.8 million worth of Brazil nuts in 2000. All Peruvian Brazil nuts originate from the Madre de Dios department, where forests rich in individuals of *B. excelsa* cover *ca* 30 percent of the land area and *ca* 4500 families (*ca* 30% of the total population in the department) receive economic benefits from Brazil nut harvesting and primary processing. The Brazil nut is the only "nut" (it is a seed rather than a nut; Mori & Prance 1990) on the international market that is harvested exclusively from natural forests (Arana *et al.* 2002). Harvesting is thought to have little impact on the species composition and structure of the forest (Zuidema & Boot 2002). Thus, by supporting rain forest peoples and regional economies, Brazil nut harvesting can promote forest conservation (Clay 1997).

Through a combination of habitat loss and exploitation for the pet trade, macaws have declined from much of their former range and are of conservation concern in their remaining sites (Beissinger & Bucher 1992). Clay licks along Amazonian riverbanks attract large congregations of macaws, adding value to them as a resource for ecotourism, which may be an alternative to more destructive uses of the rain forest (Munn 1992). Harvesters, however, perceive macaws as having a major negative impact on their Brazil nut crop and may in some cases seek to eliminate them as pests (Ortiz 1995). To find a solution to the conflict between harvesters and macaws, it is first necessary to quantify the impact of macaws on the Brazil nut crop.

This study was conducted in primary moist tropical forest in a Brazil nut concession (923 ha) straddling the boundary between the Tambopata National Reserve and the Bahuaja Sonene National

[1] Received 7 April 2003; revision accepted 14 November 2003.

Park in Madre de Dios, southeastern Peru (12°39′03″S, 68°55′40″W; see Cornejo & Ortiz 2001 for a description of the site). The concession contains 621 *B. excelsa* individuals with reproductive potential, giving a density of 0.67 reproductive trees per ha, although not all trees are productive each year. No hunting of macaws is believed to occur in the concession or those areas surrounding it.

The thick, woody, capsular fruits of *B. excelsa* contain 10–25 seeds, which have a bony coat, or testa. The fruits are considered to be functionally indehiscent—the seeds are not released at maturity—as the operculum falls inward and the opercular opening is narrower than the large seeds within (Peres *et al.* 1997). These defenses make seed predation upon *B. excelsa* very difficult (Mori & Prance 1990). Three species of large macaw were recorded in the study area (Red-and-green, *Ara chloroptera*; Scarlet, *A. macao*; and Blue-and-yellow, *A. ararauna*) and appeared to be the exclusive pre-dispersal seed predators of *B. excelsa* (Trivedi, pers. obs.). In February 2000, macaws began to feed on the immature *B. excelsa* fruits. Predation then peaked in April and May, after the period of fruit abortion but before the exocarps had hardened (F. Cornejo, pers. obs.). Macaws consumed a portion of each fruit before dropping the remainder to the ground. Once a week between April and July 2000, fallen fruit and fruit fragments were counted below 50 *B. excelsa* located in *ca* 100 ha in the middle of the concession. Damaged fruit decayed slowly on the forest floor and nearly all fruit attacked before the start of the study were judged to have been collected in the first week's count. As a comparison with the main study area, macaw-damaged fruit below trees in two other parts of the concession were counted at a single census. Thirty trees in an unharvested area 3 km to the south were sampled in the second week of the study and 18 trees 2 km to the north were sampled in the third week. Observations of the 50 focal trees showed that macaw foraging on *B. excelsa* continued at very low levels after the four-month study ended, but not enough to affect the overall results. Between February and April 2001, after the mature fruit had fallen, harvesters searched the ground and counted the final fruit production of each tree.

A total of 1249 macaw-damaged fruit were collected beneath the 50 sample trees, giving an average of 25 (SD = 35.1) fruit per tree. The rate of predation varied spatially, as has been commonly found in studies of pre-dispersal seed predation (Crawley 1985). There was great variation in the rate of predation among the 50 focal trees (variance: mean ratio = 49.3): a few trees received heavy predation levels while most were more lightly affected. The comparative surveys found that trees in the middle and north of the concession received similar overall predation rates (focal trees: median = 12 fruit, interquartile range = 6–23, $N = 50$; northern sample: median = 11, interquartile range = 5.5–23.3, $N = 18$; Mann–Whitney test: $U = 448.5$, NS), while trees in the unharvested portion in the south lost fewer fruit than those in the middle of the concession (focal trees: median = 10, interquartile range = 3–20, $N = 50$; southern sample: median = 2, interquartile range = 1–5.3, $N = 30$; Mann–Whitney: $U = 416.5$, $P = 0.001$).

Including fruit damaged by macaws, the 50 focal trees produced an average of 256.3 fruit (SD = 186.7, range = 19–954) and crop size varied substantially among trees (variance: mean ratio = 136.1). The number of fruit removed by macaws was not correlated with individual tree crop size (Pearson's correlation: $r = 0.127$, N = 50, NS) and so the proportional loss to a tree was inversely related to its crop size ($r = -0.471$, $N = 50$, $P = 0.001$; Fig. 1); consequently, predation was inversely density-dependent. The 50 trees lost a total of 9.8 percent of their crop to macaws. This was similar to the impact of parrots on two Neotropical lowland rain forest canopy tree species: 8 percent by Blue-headed Parrots (*Pionus menstruus*) on *Albizia* sp. (Galetti & Rodrigues 1992) and 6 percent by *Amazona* spp. on *Tetragastris panamensis* (Howe 1980). Also, this almost equaled the total impact of three parrot species on the canopy tree *Sterculia apetala* in Costa Rican tropical deciduous forest (Janzen 1972). Similar levels of crop damage by large-bodied primates such as woolly monkeys (*Lagothrix lagotricha cana*) on immature Brazil nut fruits have also been observed in Central Amazonia (C. A. Peres, pers. comm.); however, the impact was much less than the near complete loss caused by brown capuchin monkeys (*Cebus apella*) feeding on another species of emergent tree in the Lecythidaceae, *Cariniana micrantha* (Peres 1991).

Although there was spatial variation in macaw foraging—highlighting the need for studies in a larger sample of concessions—the results from this study indicated that macaws removed *ca* 10 percent of the concession's crop. Similar levels of damage to agricultural crops by birds can be sufficient to prompt concerns for farmers' income (Dolbeer *et al.* 1995, Tourenq *et al.* 2001). Brazil nuts are an extractive rather than an agricultural crop, however, and several factors limit the revenues generated. Crop size is

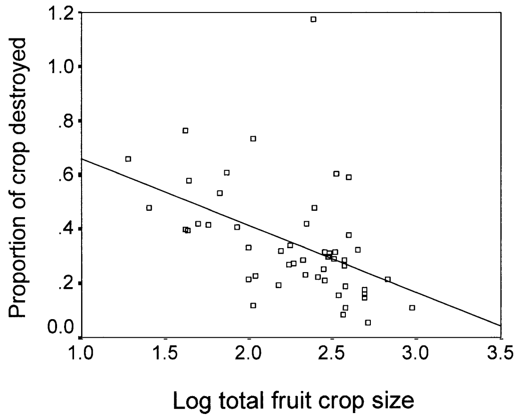

FIGURE 1. Relationship between fruit crop production and proportional crop loss through macaw predation in *Bertholletia excelsa* for 50 focal trees (adjusted $R^2 = 0.206$, $P = 0.001$, $y = 0.906 - 0.247x$). Total crop sizes were $\log_{10}$ transformed; a modified Freeman–Tukey arcsine transformation was used for proportional crop losses (Zar 1996).

affected by the level of fruit abortion, which may vary among trees and among years. Moreover, the size of a concession's crop varies substantially among years, perhaps as a result of alternate-year bearing in which trees deplete their accumulated reserves in good production years and take longer than a year to accumulate more (Rosengarten 1984). In addition to predation by macaws, the number of fruit available for collection from the forest floor may be further reduced by the primary dispersal agent of *B. excelsa*, the agouti (*Dasyprocta* sp.; Peres & Baider 1997, Zuidema & Boot 2002). A portion of the nuts collected is also wasted through spoilage or by being left in the forest. Most importantly, the market value of the Brazil nut in the nearest town, Puerto Maldonado, dropped by more than 50 percent in 2001, reflecting its highly variable value on the international commodities market. Thus, the impact of market forces on the value of the crop was potentially five-fold greater than that of macaws.

Given that the hunting of macaws is illegal, a number of institutional actions could help generate more income for harvesters and offset the impact of macaws (Clay 1997, Nelson *et al.* 2000). The main aspect of Brazil nut management within the control of the harvester is the efficiency of harvesting. Refining harvesting methods has been shown to reduce costs by a third (Arana *et al.* 2002). In addition to such measures, harvesters may be encouraged to view macaws as assets through the adoption of income-generating activities that implicitly or explicitly involve the conservation of macaws on their concessions. These may include ecotourism—as part of a diversified forest management system involving the extraction of other NTFPs (*e.g.,* the fruit of the aguaje palm, *Mauritia flexuosa*)—and "green-labeling" of Brazil nut products.

Macaws are a highly valuable resource to ecotourism and although they are typically scarce, it may be financially viable for tourists to view macaws in the wider forest beyond the clay licks, which are currently the foci of ecotourism operations (Munn 1992). Discreet macaw watching by tourists at macaw nests and heavily attacked *B. excelsa* in Brazil nut concessions may provide harvesters with additional revenue. There is a demand in consumer countries for certified "green" (Bennett 2000) and organic products and, sometimes, premium prices can be gained. It is, however, harder to obtain an organic or ethical premium for Brazil nuts than for coffee or cocoa/chocolate (Collinson *et al.* 2000). Assuming this difficulty can be overcome, "green" marketing strategies could be endorsed via Brazil nut forest certification, which is being initiated in some areas of Bolivia and Peru (Myers *et al.* 2000; V. Sequeira, pers. comm.). If the certification criteria included realistic wildlife conservation principles that could be appropriately monitored and assessed (Putz *et al.* 2000), then certification may provide a mechanism to increase harvest revenues while protecting wildlife such as macaws within Brazil nut extractive reserves.

Special thanks are extended to Proyecto Conservando Castañales (ACCA) for hosting this study and providing base data and logistical support. We are grateful for the input and support of C. Baider, C. Peres, and V. Sequeira and also for the invaluable field assistance of P. Maceda, P. Maceda, and V. Cuenca. J. McCathie, S. Mori, C. Peres, and V. Sequeira made helpful comments on earlier drafts of the manuscript. Funding for this study was provided by the UK Natural Environment Research Council and the School of Biological Sciences, University of East Anglia.

Arana, A., V. Sequeira, and J. Torres. 2002. Mejoramiento del sistema de cosecha de castaña (*Bertholletia excelsa*) en Madre de Dios y sus impactos en la economía del productor castañero. PCC/ACCA, Lima, Peru.

Beissinger, S. R., and E. H. Bucher. 1992. Sustainable harvesting of parrots for conservation. *In* S. R. Beissinger and N. F. R. Snyder (Eds.). New World parrots in crisis: Solutions from conservation biology, pp. 73–115. Smithsonian Institution Press, Washington, DC.

Bennett, E. L. 2000. Timber certification: Where is the voice of the biologist? Conserv. Biol. 14: 921–923.

Clay, J. W. 1997. Brazil nuts. The use of a keystone species for conservation and development. *In* C. H. Freese (Ed.). Harvesting wild species—Implications for biodiversity and conservation, pp. 246–282. Johns Hopkins University Press, Baltimore, Maryland.

Collinson, C., D. Burnett, and V. Agreda. 2000. Economic viability of Brazil nut trading in Peru, 2520. Natural Resources and Ethical Trade Programme, Natural Resources Institute, University of Greenwich, Kent, England.

Cornejo, F. H., y E. Ortiz. 2001. La regeneración natural de castaña (*Bertholletia excelsa* Humb. & Bonpl.) y sus implicancias para su manejo en la Reserva Nacional de Tambopata al sudeste de Perú. *En* L. O. Rodriguez (Ed.). El Manu y otras experiencias de investigación y manejo de bosques neotropicales, pp. 83–90. Pro-Manu, Peru.

Crawley, M. J. 1985. Seed predators and plant population dynamics. *In* M. Fenner (Ed.). Seed ecology, pp. 157–191. Chapman and Hall, London, England.

Dolbeer, R. A., P. P. Woronecki, and T. W. Seamans. 1995. Ranking and evaluation of field corn hybrids for resistance to blackbird damage. Crop Prot. 14: 399–403.

Galetti, M., and M. Rodrigues. 1992. Comparative seed predation on fruit by parrots in Brazil. Biotropica 24: 222–224.

Howe, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. Ecology 6: 944–959.

Janzen, D. H. 1972. Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. Ecology 53: 350–361.

Mori, S. A. 1992. The Brazil nut industry—Past, present and future. *In* M. Plotkin and L. Famolare (Eds.). Sustainable harvesting and marketing of rainforest products, pp. 241–251. Island Press, Washington, DC.

———, and G. T. Prance. 1990. Taxonomy, ecology, and economic botany of the Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.: Lecythidaceae). Adv. Econ. Bot. 8: 130–150.

Munn, C. A. 1992. Macaw biology and ecotourism or "When a bird in the bush is worth two in the hand". *In* S. R. Beissinger and N. F. R. Snyder (Eds.). New World parrots in crisis: Solutions from conservation biology, pp. 47–72. Smithsonian Institution Press, Washington, DC.

Myers, G. P., A. C. Newton, and O. Melgarejo. 2000. The influence of canopy gap size on natural regeneration of Brazil nut (*Bertholletia excelsa*) in Bolivia. For. Ecol. Manage. 127: 119–128.

Nelson, V., M. Galvez, and M. Blowfield. 2000. Social impact of ethical and conventional Brazil nut trading on forest-dependent people in Peru, rep. no. 2501. Natural Resources and Ethical Trade Programme, Natural Resources Institute, University of Greenwich, Kent, England.

Ortiz, E. G. 1995. Survival in a nutshell. Americas 47: 6–17.

Peres, C. A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in Central Amazonia. Biotropica 23: 262–270.

———, and C. Baider. 1997. Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in southeastern Amazonia. J. Trop. Ecol. 13: 595–616.

———, L. C. Schiesari, and C. Baider. 1997. Vertebrate predation of Brazil-nuts (*Bertholletia excelsa*, Lecythidaceae), an agouti-dispersed Amazonian seed crop: A test of the escape hypothesis. J. Trop. Ecol. 13: 69–79.

Putz, F. E., D. P. Dykstra, and R. Heinrich. 2000. Why poor logging practices persist in the tropics. Conserv. Biol. 14: 951–956.

Rosengarten, F., Jr. 1984. The book of edible nuts. Walker, New York, New York.

Tourenq, C., S. Aulagnier, L. Durieux, S. Lek, F. Mesleard, A. Johnson, and J. L. Martin. 2001. Identifying rice fields at risk from damage by the Greater Flamingo. J. Appl. Ecol. 38: 170–179.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice–Hall, Upper Saddle River, New Jersey.

Zuidema, P. A. and R. G. A. Boot. 2002. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: Impact of seed extraction on recruitment and population dynamics. J. Trop. Ecol. 18: 1–31.

Mandar R. Trivedi[2]

School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, England

Fernando H. Cornejo

Asociación para la Conservación de la Cuenca Amazónica (A.C.C.A.), Calle Cusco 499, Puerto Maldonado, Perú

and

Andrew R. Watkinson

Schools of Biological and Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, England

[2] Corresponding author. Current address: Environmental Change Institute, School of Geography and the Environment, University of Oxford, 1A Mansfield Road, Oxford, OX1 3SZ, England; e-mail: mandar.trivedi@eci.ox.ac.uk

BIOTROPICA 36(1): 122–126 2004

Myrmecophagy in Mycetophiloidea (Diptera): Note on a Keroplatidae from Africa[1,2]

ABSTRACT

Information on an undescribed keroplatid fly (tribe Orfeliini) from Cameroon is presented. Its myrmecophagous larvae live in hollow stems of an understory myrmecophytic tree. Data on the biology of this fly and its interaction with one of the plant's strictly associated ant species *Cataulacus mckeyi* (Myrmicinae) showed that the number of keroplatid larvae per tree was not limited by occupation competition with the ant. Through predation on workers, keroplatid larvae may have a sizeable impact on colonies of *C. mckeyi*.

RÉSUMÉ

Nous présentons des informations sur une espèce non-décrite de Keroplatidae (tribu Orfeliini), au Cameroun. Les larves myrmécophages se développent dans les tiges creuses d'une myrmécophyte de sous-bois. Des données sur la biologie de cette espèce et son interaction avec l'une des fourmis-hôtes de cette plante, *Cataulacus mckeyi*, montrent que le nombre de larves par arbre n'est pas limité par la compétition pour l'occupation avec la fourmi. En prédatant les ouvrières, ces larves ont un impact potentiellement important sur les colonies de *C. mckeyi*.

Key words: Africa; Cataulacus mckeyi; *Keroplatidae;* Leonardoxa africana; *myrmecophagy; Orfeliini; tropical rain forest.*

LEONARDOXA AFRICANA (BAILL.) AUBRÉV. SUBSP. *AFRICANA* (CAESALPINIOIDEAE) is an understory tree in coastal rain forest of Cameroon (Central Africa). This myrmecophyte is strictly associated with two ant species, the formicine *Petalomyrmex phylax* Snelling and the myrmicine *Cataulacus mckeyi* Snelling (McKey 1984, 2000). Plants provide food and nesting sites to *P. phylax*, which effectively protects the young leaves against insect herbivores (Gaume *et al.* 1997). This mutualistic interaction is often parasitized by *C. mckeyi*, which uses the host plant but does not protect young leaves (Gaume & McKey 1999). To understand the factors allowing persistence of the parasitic ant in this system, I have attempted to characterize all potential mortality factors responsible for the limited life span of *C. mckeyi* colonies (Debout 2003). In addition to physical disturbances of host individuals, several biological factors such as the frequent presence of myrmecophagous dipteran larvae inside the domatia (swollen stems) of *L. a. africana* may play a role. These larvae were identified by L. Matile of the Muséum National d'Histoire

[1] Received 20 February 2003; revision accepted 22 November 2003.

[2] This paper is dedicated to the late L. Matile (†2001). His irreplaceable knowledge of the Keroplatidae is sorely missed.

Naturelle (MHNH; Paris, France) as belonging to the tribe Orfeliini of the subfamily Keroplatinae (family Keroplatidae, superfamily Mycetophiloidea).

Before Matile's (1990) monograph, Keroplatidae, like many dipteran families, was poorly known from all points of view (morphology, systematics, phylogeny, and biogeography). The superfamily Mycetophiloidea is comprised of relatively small gnats (4–8 mm), which are brown or black with small yellow spots and are generally known as "fungus gnats." Their two principal diagnostic characteristics are a bent thorax and long coxa. Seven families are included: Ditomyiidae, Diadocidiidae, Keroplatidae, Bolitophilidae, Mycetophilidae, Lygistorrhinidae, and Sciaridae. Generally, larvae of Mycetophiloidea are associated with fungal carpophores, in which they spin a web under the hymenium to gather spores or feed on carpophore tissues. Some exceptions to these habits are known, particularly in the Keroplatidae and the Mycetophilidae. In these families, several species have predatory larvae, which kill their prey using oxalic acid produced by salivary glands and deposited as droplets on the web. In temperate regions, adults of Mycetophilidae can be found in humid and shady places (*e.g.,* hollow trees, riverbanks, and caves). In the tropics, they principally inhabit forests and woodlands, and adults of some species can be very abundant and widespread during the rainy season; however, data on biology and ecology of Mycetophiloidea are scarce (Matile 1990).

The family Keroplatidae, comprised of three subfamilies (Arachnocampinae, Macrocerinae, and Keroplatinae), is cosmopolitan but very poorly known. About 800 species in 80 genera have been described, but numerous species await naming (and surely more await discovery). This is particularly true for the tribe Orfeliini (Keroplatinae), about which almost nothing is known. None of the known larvae of Keroplatidae develop inside mushrooms, and all spin a web that functions either to trap spores or to capture small living animal prey. All known larvae of the tribe Orfeliini are carnivorous and prey preferentially on ants (L. Matile, pers. comm.). Keroplatidae are known from all over the world (*e.g.,* Central America [Panama; Aiello & Jolivet 1996], Australasia [New Zealand; Pugsley 1983], Sri Lanka [Chandler & Matile 1998, Krombein *et al.* 1999], Japan [Uesugi 2002], and Europe [Chandler & Gatt 2000, Menzel & Ziegler 2001]). Several European surveys suggest that the North African fungus gnat fauna may share most of its species with the Mediterranean fauna but little is known beyond that. No data appear to exist about fungus gnats in tropical Africa (references in Chandler & Gatt 2000).

Myrmecophagous keroplatids are known from Central America (Aiello & Jolivet 1996) and Sri Lanka (Chandler & Matile 1998, Krombein *et al.* 1999). Larvae are found in domatia of the myrmecophytes (*e.g., Humboldtia laurifolia* Vahl [Leguminosae: Caesalpinioideae] and *Besleria formicaria* Nowicke [Gesneriaceae]) hosting colonies of ants. Larvae spin a strand of silk that runs the length of the domatium. Larvae are primarily myrmecophagous, but may also feed on dead animal matter or on insects other than ants present in the domatia. Larvae capture live prey using their silk strand (Aiello & Jolivet 1996). The impact of these predators on growth and survival of incipient ant colonies may be especially high, since as many as 50 ant heads can be found in one keroplatid-occupied domatium of *H. laurifolia* (Chandler & Matile 1998). Two oviposition strategies are known in myrmecophagous keroplatids: female flies sometimes oviposit on the inner wall of the chosen domatium close to the entrance hole and in other cases, female flies "shoot" eggs through the entrance holes (Kovac & Matile cited in Chandler & Matile 1998).

This paper is the first report of a myrmecophagous Keroplatidae in Africa. They thus occur in three tropical continents, and although reports are few and scattered, may be widespread. The fly I studied is a frequent occupant of *L. a. africana* domatia. Despite repeated efforts, I was unable to rear this fragile fly. As species determination requires examining male genitalia, identification of this fly, or its description as a new species, is not yet possible. Samples of larvae of the species investigated in this study have been deposited in the insect voucher collections at the MNHN (Paris, France) and the American Museum of Natural History (New York, New York).

To estimate the frequency and distribution of this keroplatid fly, I examined occupants of domatia in *L. a. africana* trees. The distribution of *L. a. africana* is patchy and a patch ("population") is often comprised of between 100 and 500 trees. Each tree is occupied by a single nest of a single ant species. The two ants associated with *L. a. africana* occur at different frequencies and differ essentially in colony size, longevity, and proportion of domatia they occupy. On average, 75 percent of available trees are occupied by *P. phylax*, while frequency of occupancy by *C. mckeyi* varies from 0 to 30 percent of trees

(A. Daleck, pers. comm.). Colony size of *P. phylax* can reach up to 10,000 workers, whereas a colony of *C. mckeyi* is comprised of up to only hundreds of individuals (Gaume 1998).

This study was carried out principally in a population of *L. a. africana* (named BOU) located in rain forest near the village of N'kolobondé (3°13′N, 10°15′E; 150 m elev.), Littoral Province, Cameroon. In the study area, a 2500 m^2 quadrat (a 50 × 50 m area divided into 5 × 5 m grids) was laid out in the population and all trees were censused and mapped. A total of 277 *L. a. africana* trees were located in the study area. The mean local density was 0.15 trees per m^2. Of all the trees, 68 percent were occupied by *P. phylax*, 16 percent were unoccupied, and 14 percent were occupied by *C. mckeyi*. Occupants of the remaining 2 percent could not be assessed because their crowns were too high to examine.

I also studied the frequency and abundance of keroplatids in *Leonardoxa* trees for six other different plant populations taken from an 85 km long transect. I focused on the presence of keroplatids in trees occupied by *C. mckeyi*. I collected 76 nests of *C. mckeyi* by complete dissection of the host tree. Occupants of domatia in a tree constitute a "nest," and a single colony occupies one to several "nests" (*i.e.,* individual trees; Debout *et al.* 2003). All domatia occupants were counted and preserved in 95 percent ethanol.

In the system we studied, keroplatid larvae were found in domatia of trees occupied by *C. mckeyi* and those occupied by *P. phylax*. Larvae are elongate with translucent brownish heads (Fig. 1A), and their length may attain that of the occupied domatium (3–4 cm). Each larva is solitary, resting alone on a strand of silk that is connected by perpendicular silk threads to the walls of the domatium. Larval development requires more than three weeks, and larvae are often parasitized by undetermined hymenopteran parasitoids, as was also noted by Aiello and Jolivet (1996). Preliminary tests on their myrmecophagy showed no preferences of larvae for one or the other of the two ant species that inhabit domatia of *L. a. africana* (G. Debout, pers. obs.). When an ant is caught in the silk web, the larva spins a silk cocoon around it and then eats the ant from the inside, leaving the cuticle intact (Fig. 1B). In the study site BOU, 75 percent of all trees occupied by *C. mckeyi* contained at least one keroplatid larva.

As a general rule, keroplatid larvae were frequent in trees occupied by the ant species *C. mckeyi*. Among the 76 collected nests, 71 percent (*i.e.,* 54 nests) harbored from 1 to 13 keroplatid larvae. This occupation rate is not trivial because for the 54 trees with keroplatids, the proportion of domatia occupied by these larvae averaged 11 percent of all domatia (*i.e.,* 3.9 ± 0.5 domatia). There was no correlation between size of the ant colony and the number of keroplatid larvae occupying its tree ($R^2 = 0.045$; $P = 0.07$), or between colony size and the ratio of domatia occupied by larvae to domatia occupied by ants ($R^2 = 0.064$; $P = 0.03$). This occupation frequency ratio was relatively constant (0.29 ± 0.07). I postulate that this high occupation rate may have a great impact on ant colonies if the daily predation rate by larvae is high.

On trees occupied by *C. mckeyi*, the number of larvae was correlated with the number of available empty domatia ($R^2 = 0.33$; $P < 0.001$). Nevertheless, when several keroplatid larvae were present on the same tree, they were dispersed over the entire tree (no aggregation of larvae), and many domatia remained unoccupied either by ants or by larvae. This paradox between the high frequency of keroplatids—the larvae were encountered in all *Leonardoxa* populations and were present in up to 75 percent of *Cataulacus*-occupied trees—and the low density of occupation per tree may be due to an avoidance behavior reflecting high intraspecific competition. If larvae reach densities at which significant intraspecific competition occurs, this would be a further clue that keroplatids may have a sizeable impact through predation on workers of *C. mckeyi* colonies. The low density of occupation per tree, however, could also be a strategy to avoid hymenopteran parasitoids (or could simply be the result of parasitoid attack).

Preliminary dissection data on 10 *P. phylax*-occupied trees suggested that keroplatids showed no preference for either ant species, as indicated by frequency of occupation. In the site BOU, 6 of the 10 *P. phylax*-occupied trees studied had 2–7 keroplatid larvae (*i.e.,* a 4 % occupation frequency of all domatia per tree) and the occupation ratio (keroplatid-occupied domatia to *P. phylax*-occupied domatia) was around one-third (0.30 ± 0.19), as in *C. mckeyi*-occupied trees. Indeed, when compared to the 12 *Cataulacus*-occupied trees dissected during the same field session at the same site, neither the mean proportion of all domatia occupied by keroplatid larvae (*t*-test; $P = 0.40$) nor the mean ratio of domatia occupied by larvae to domatia occupied by ants (*t*-test; $P = 0.97$) was significantly different in trees occupied by the two ants.

Further work to evaluate the impact of keroplatids on this system will require rearing enough larvae to obtain at least one male for species determination or description. Fungal infection appeared to be an

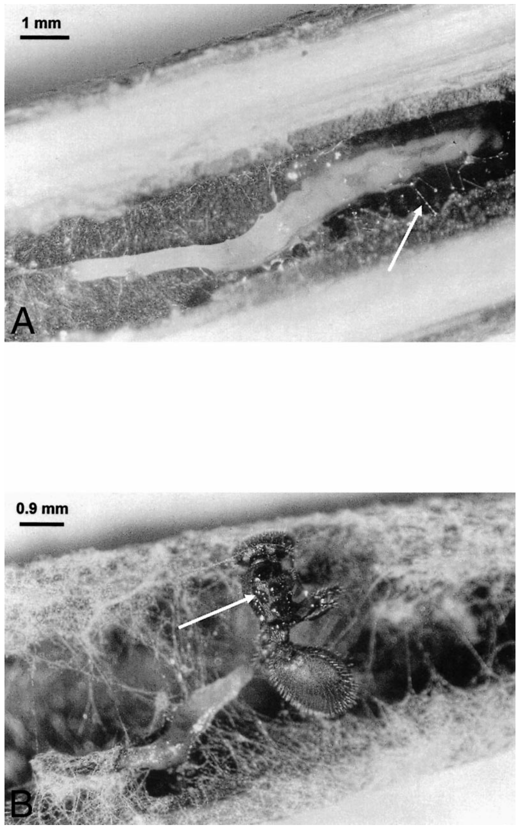

FIGURE 1A. An elongate larva of the undetermined keroplatid (subfamily Keroplatinae, tribe Orfeliini), on its strand of silk, inside a domatium of *Leonardoxa africana* subsp. *africana*. The perpendicular silk threads that connect the central web to the domatium walls can be seen (white arrow). B. A worker of *Cataulacus mckeyi* caught in the silk web product by the larva. The larva is spinning a silk cocoon around the ant. The white arrow shows droplets (probably of oxalic acid) on the dorsal surface of the alitrunk of the worker.

important mortality factor in my rearing attempts. Use of antifungal solutions appears to enhance the probability of larval survival to adulthood (P. Jolivet, pers. comm.) and this should be incorporated in future attempts. Observations must be conducted on more *P. phylax*-occupied trees to determine if prevalence of keroplatids is equivalent to that on trees occupied by *C. mckeyi*. It will be of particular interest to more precisely define the impact of this predator on growth and survival of incipient ant colonies (regular predation may have an especially high impact on small colonies) or on foundresses attempting to establish a new colony. Dietary habits and preferences of this keroplatid must be studied by choice experiments. Finally, it must be determined whether ant workers can avoid domatia harboring a keroplatid larva or are attracted to investigate these domatia. With the addition of this first record from Africa, such flies appear to be widespread in tropical regions. They are likely to occur in many myrmecophytes. Abundant in the system I studied, they may have an important impact on numerous ant–plant symbioses. Unfortunately, they have been virtually ignored. This paper is offered in hope that it will encourage those studying other ant–plant systems to look a little more closely for these potentially important ant predators.

I thank the Ministry of Research, Science and Technology of the Republic of Cameroon for permission to carry out this study. The late Loïc Matile shared with me his knowledge of Keroplatidae. P. Jolivet is especially acknowledged for having put me in touch with L. Matile; D. McKey greatly improved the English. Both made valuable comments on the manuscript, as did J. T. Longino and an anonymous reviewer. Fieldwork was funded by grants from the Institut Français de la Biodiversité and the National Geographic Society's Committee for Research and Exploration. I am grateful to Big John for his hospitality in N'kolobondé, and to A. N. Ngomi for his help with collection of domatia.

Aiello, A., and P. Jolivet. 1996. Myrmecophily in Keroplatidae (Diptera: Sciaroidea). J. N.Y. Entomol. Soc. 104: 226–230.

Chandler, P., and P. Gatt. 2000. Fungus gnats (Diptera: Bolitophilidae, Keroplatidae and Mycetophilidae) from the Maltese islands. Stud. Dipterol. 7: 69–81.

Chandler, P. and L. Matile. 1998. A new species of *Platyceridion* Tollet (Diptera, Keroplatidae) with a larva predatory in ant infested internodes of *Humboldtia laurifolia* Vahl. Stud. Dipterol. 5: 163–173.

Debout G. 2003. Parasite et mutualisme de protection—Le cas de *Cataulacus mckeyi*, fourmi symbiotique de *Leonardoxa africana africana*. Ph.D. dissertation. Université Montpellier II, Montpellier, France.

———, E. Provost, M. Renucci, A. Tirard, B. Schatz, and D. McKey. 2003. Colony structure in a plant-ant: Behavioural, chemical and genetical study of polydomy in *Cataulacus mckeyi* (Myrmicinae). Oecologia 137: 195–204.

Gaume L. 1998. Mutualisme, parasitisme, et évolution des symbioses plantes-fourmis: le cas de Leonardoxa (Légumineuse) et de ses fourmis associées. PhD thesis, 200 pp., ENSAM-University of Montpellier 2, Montpellier.

———, and D. McKey. 1999. An ant–plant mutualism and its host-specific parasite: Activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. Oikos 84: 130–144.

———, ———, and M. C. Anstett. 1997. Benefits conferred by "timid" ants: Active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. Oecologia 112: 209–216.

Krombein, K. V., B. B. Norden, M. M. Rickson, and F. R. Rickson. 1999. Biodiversity of the domatia occupants (ants, wasps, bees and others) of the Sri Lankan myrmecophyte *Humboldtia laurifolia* Vahl (Fabaceae). Smithsonian Contributions to Zoology 603. Smithsonian Institution Press, Washington, DC.

Matile L. 1990. Recherche sur la systématique et l'évolution des Keroplatidae (Diptera: Mycetophiloidea). Mémoires du Muséum National d'Histoire Naturelle, série A (Zoologie), tome 148. Editions du Muséum National d'Histoire Naturelle, Paris, France.

McKey D. 1984. Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rain forest in Cameroon. Biotropica 16: 81–99.

———. 2000. *Leonardoxa africana* (Leguminosae: Caesalpinioideae): A complex of mostly allopatric subspecies. Adansonia 22: 71–109.

Menzel, F., and J. Ziegler. 2001. New records of Diptera from the Hohe Tauern National Park (Austria), including information on flower visiting and the description of two new black fungus gnat species (Sciaridae). Stud. Dipterol. 8: 355–409.

Pugsley, C. W. 1983. Literature review of the New Zealand glowworm *Arachnocampa luminosa* (Diptera: Keroplatidae), in the Glowworm Cave, Waitomo. J. R. Soc. N.Z. 14: 387–407.

Uesugi, K. 2002. Notes on the genus *Neoplatyura* of Japan including the description of three new species (Diptera: Keroplatidae). Stud. Dipterol. 9: 191–202.

Gabriel Debout

CEFE-CNRS
1919, route de Mende
34293 Montpellier cedex 5, France
E-mail: debout_gabriel@hotmail.com