

Relationship between floral tube length and nectar robbing in *Duranta erecta* L. (Verbenaceae)

LUIS NAVARRO^{1*} and RODRIGO MEDEL²

¹Departamento de Biología Vegetal, Facultad de Ciencias, Campus As Lagoas-Marcosende, Universidad de Vigo, 36200-Vigo, Spain

²Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

Received 26 May 2008; accepted for publication 2 June 2008

Although nectar robbing is a common phenomenon in plant species with tubular flowers or flowers with nectar spurs, the potential effect of this illegitimate interaction on plant reproductive success has not received the deserved attention. In the present study, we analysed the functional relationship between flower morphology and nectar robbing, and examined the reproductive consequences of the interaction in a population of *Duranta erecta* (Verbenaceae) on the island of Cuba. The results show that nectar robbing is conducted by the carpenter bees *Xylocopa cubaecola* and affects up to 44% of flowers in the studied population. However, not all the flowers have the same probability of being robbed. The chance of flowers being robbed increases with flower length and flower diameter. Moreover, nectar robbing significantly decreases the chance that flowers will set fruit. Also, the impact of nectar robbing on the probability of flowers to set fruits is dependent on the plant. We suggest that nectar robbing may represent an opposite selective force that balances the selection for longer corollas often imposed by pollinators specializing in visiting tubular flowers. Such a relationship with nectar robbers would have obvious implications for the evolution of tubular or closed flowers. This preliminary finding deserves further research in light of the ecological and evolutionary consequences of nectar robbing in tubular flowers. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 96, 392–398.

ADDITIONAL KEYWORDS: Cuba, evolution of flower length, phenotypic selection, robbery, *Xylocopa cubaecola*.

INTRODUCTION

The term nectar robbing is invoked when some floral visitors remove floral nectar by biting or piercing holes in flowers, circumventing the floral opening used by legitimate floral visitors (Inouye, 1980, 1983). Although nectar robbing is a common phenomenon in plant species with tubular flowers or flowers with nectar spurs (Maloof & Inouye, 2000), the potential effect of this illegitimate interaction on plant reproductive success has not yet received enough attention in the scientific literature. Recent evidence has shown that nectar robbing could have direct and indirect effects on plant fitness. For example, illegitimate visitors may decrease plant reproduction by directly damaging reproductive tissues (Maloof & Inouye, 2000;

Irwin, Brody & Waser, 2001) or indirectly through changes in the behaviour of legitimate pollinators (Irwin & Brody, 2000; González & Valdivia, 2005; Castro, Silveira & Navarro, 2008). Although nectar robbers act in most cases as plant antagonists for plant reproduction (Maloof & Inouye, 2000), they could also benefit plant fitness under some circumstances (Navarro, 2000). Consequently, changes in plant reproduction may occur in response to direct effects, to indirect effects, or to both.

Subsequent to studies by Darwin (1859, 1877), long floral tubes have been traditionally interpreted as a floral adaptation for pollination by long-tongued or long-billed pollinators. Several studies have shown that legitimate pollinators may select for long corollas (Fenster, 1991; Alexandersson & Johnson, 2002). However, the negative impact of robbing on plant fitness may translate into a selective force that

*Corresponding author. E-mail: lnavarro@uvigo.es

counter balances the selection for longer corollas imposed by specialist pollinators. Unfortunately, the relationship between flower morphology and the odds a flower will be robbed has been overlooked in the literature and, consequently, the role of nectar robbers as selective agents on flower morphology has not been evaluated in natural populations (Maloof & Inouye, 2000); but see also Lara & Ornelas (2001) and Urcelay, Morales & Chalcoff (2006).

The present study aimed to evaluate the functional relationship between flower morphology and nectar robbing, and examine the reproductive consequences of the interaction in a population of *Duranta erecta* (Verbenaceae) on the island of Cuba. Accordingly, we analysed the frequency of nectar robbing, as well as the effect of nectar robbing on individual and plant female fitness. We also estimated the probability of a flower being robbed as a function of flower morphology.

MATERIAL AND METHODS

Duranta erecta L. (Verbenaceae) is a morphologically variable and polymorphic perennial shrub or tree up to 6 m tall that has a wide distribution in forests of Tropical-subtropical America including the Antilles. It has been synonymized similar to *Duranta repens*, although the accepted name is *D. erecta* (Mendez, 2003). The flowers are open for one day (mean \pm SD = 1.3 ± 0.5 days; D. Rojas, pers. comm.). They are displayed in terminal racemes and are pentamerous and hermaphroditic with a violet to pale blue tubular corolla, approximately 10 mm long (mean \pm SD = 10.6 ± 2.2 mm). The style and anthers are included in the corolla tube (5.9 ± 0.3 for style length and 4.9 ± 0.4 mm for anther length; D. Rojas, pers. comm.) and the nectar is accumulated in the bottom portion of the narrow corolla tube (Fig. 1). The small diameter of the corolla tube prevents visitors with body diameter > 2 mm from gaining free and legitimate access to nectar. Similarly, although the tube length is highly variable in this species (range = 5–15 mm), floral visitors with proboscis length < 9 –10 mm are incapable of collecting nectar legitimately. Pollen and nectar rewards are offered to insect visitors, and effective pollinator visitation is necessary to set fruit. The species is xenogamous, with geitonogamous crosses setting fruits. Autogamous crosses do not set fruits (Reddy & Reddi, 1996). The fruits are yellow drupes of approximately 7–11 mm and they are completely included in the accrescent calyx when ripe (Fig. 1E). In the study site, the flowers are visited mainly by *Apis mellifera*, which forage for pollen, and the stingless bee *Melipona beecheii* (L. Navarro, pers. observ.) (Fig. 1A). Robbing is performed by *Xylocopa cubaecola* (Díaz

and Sanchez 1998) with proboscis length in the range 5.5–6.2 mm (A. Vale, D. Rojas & L. Navarro, pers. comm.)

The study was conducted during July 2006 in the valley of Viñales National Park, which is located in the Sierra de los Órganos range, in the province of Pinar del Río on the island of Cuba. The area is characterized by limestone karst peaks, oak (*Quercus oleoides*), and pine forest of *Pinus caribaea* and *Pinus tropicalis*. *Duranta erecta* in the area is located in small and isolated populations. The population selected for the study was located in the municipality of Viñales on the island of Cuba and corresponds to a dense population of approximately 20 plants.

Because robbers make a visible incision at the base of the corolla tube and the calyx, nectar robbing was easily recorded by examination of flowers or fruits. Because the accrescent calyx persists in the fruit, the scar of the incision made by nectar robbers permits easy determination of whether the former flower had been robbed or not (Fig. 1F, G). Thus, to estimate the incidence of nectar robbing and to investigate its possible effects on fruit set, we examined 484 old flowers randomly chosen on 11 plants, approximately 2 weeks after flowering (when calyx incisions due to nectar robbers were still clearly visible) and recorded whether or not each flower had set fruit.

Moreover, because the floral tube length is so variable and, in some cases, is within the range of the proboscis length of *X. cubaecola*, we assessed whether floral tube length and diameter at the opening of the tube influenced the chance of a flower being robbed. To this end, we selected ten flowering plants and measured corolla tube length and diameter in 60 flowers (six flowers on each of ten plants). Measured flowers were chosen at the basis of racemes to eliminate architectural effects; nevertheless, preliminary observations indicate that there is no variation in floral length at the intraplant level there is but at the interplant level (D. Rojas & L. Navarro, unpubl. data). The floral tube length was measured from the basis of the tube, where the nectaries are located, to the tube mouth. All measures were performed using a digital caliper to the nearest 0.1 mm. Moreover, we recorded both scar of any incision made by nectar robbers and the presence or absence of flower damage attributable to nectar robbing in each measured flower. To this end, we analysed both the pistil and stamens, looking for any kind of damage.

STATISTICAL ANALYSIS

We regressed flower length and flower diameter on the chance of flowers being robbed. We fitted a logistic model in a generalized linear model (GLM) using link-logit to estimate the logistic regression

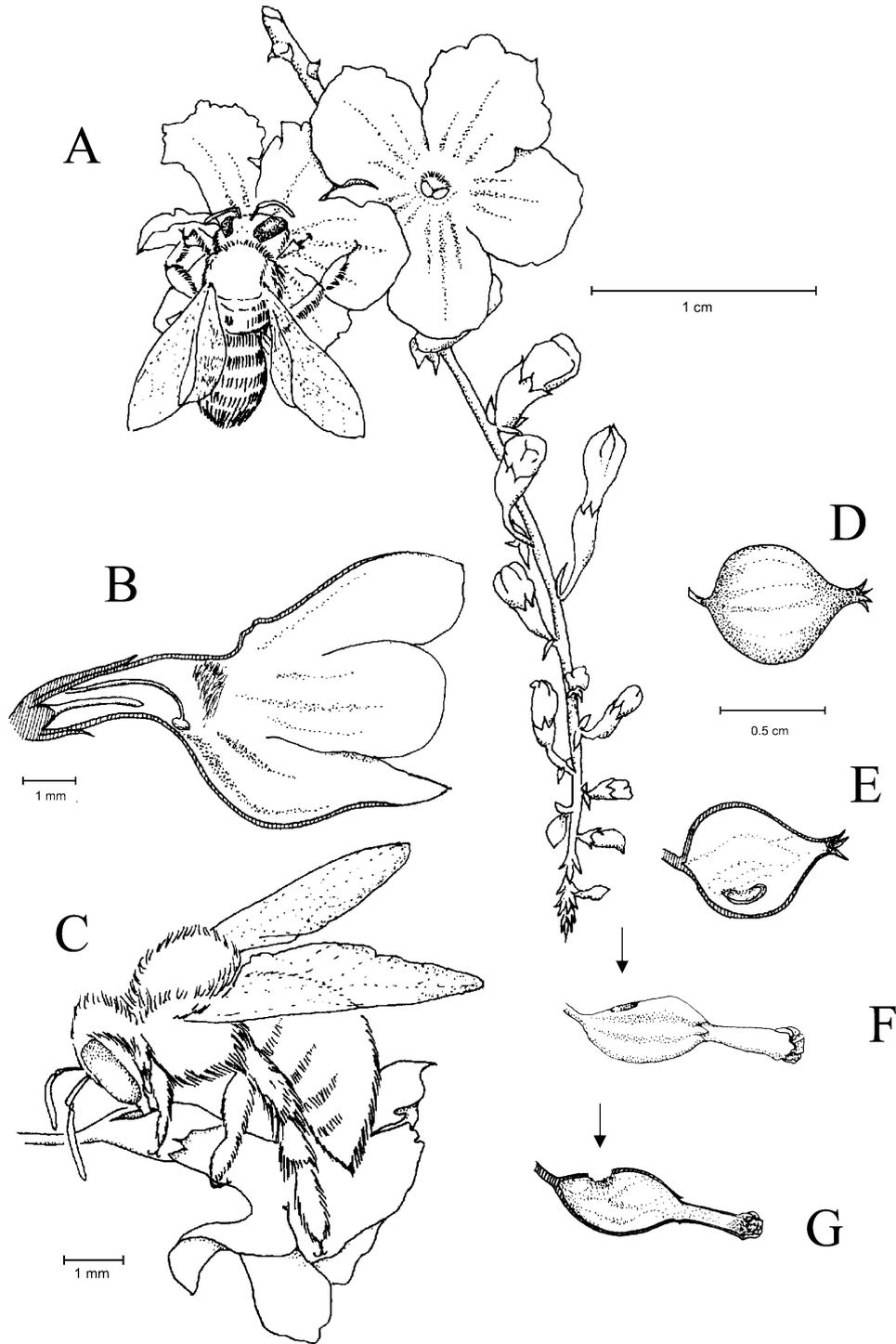


Figure 1. *Duranta erecta*. A, inflorescence with an individual of *Melipona beecheii* visiting a flower legitimately. B, detail of an open flower showing disposition of sexual organs inside the corolla. C, individual of *Xylocopa cubaecola* making a hole in the calyx. D, detail of the drupaceous fruit. E, cross section of a fruit with the persistent calyx. F, detail of a wilted flower previously robbed. G, cross section, approximately 2 weeks after flowering. Because the acrescent calyx (B, E, G, ruled line) persists in the wilted flower or in the initial fruit, the scar of the incision made by nectar robbers (arrow) permits to an easy determination of whether the former flower had been robbed or not.

coefficients on a flower basis. The significance of logistic coefficients was estimated directly from t -values. To evaluate whether plants differ in the chance of being robbed and setting fruit (1 = presence of fruit; 0 = absence of fruit), we performed a GLM regression using a binomial error, with plants and robbing as predictor variables (1 = robbed; 0 = not robbed). All analyses were performed in S-Plus 7.0 (Tibco).

RESULTS

Forty-four percent of flowers in the studied population were robbed by *X. cubaecola*. After landing on top of the horizontal flower tube, carpenter bee grasps the corolla with its legs to prevent itself against falling over. Next, it perforates the flower using the hard tip of its tongue, creating a split near the base of the tube through which it sucks nectar before flying away. The scars left by the carpenter bees are easily distinguishable from those of other nectar robbers in Cuba, such as some species of hummingbirds. During this process, the body of the carpenter bee does not contact the sexual organs which are enclosed in the floral tube. Although *X. cubaecola* could promote self-pollination whereas shake flowers (Graves, 1982; Navarro, Guitián & Ayensa, 2008), the herkogamy of sexual structures linked to the not production of fruits under autogamy, prevent any positive effect.

There were differences between robbed and non-robbed flowers both in flower tube length (mean \pm SE, 9.83 ± 0.97 mm for non-robbed versus 11.25 ± 1.03 mm for robbed flowers, $N = 60$, $P < 0.001$) and tube diameter (1.83 ± 0.21 mm for non-robbed versus 1.97 ± 0.23 mm, $N = 60$, $P = 0.004$). Moreover, there were differences in flower length for the whole of the analysed plants ($F_{9,50} = 3.14$, $P < 0.005$ for flower tube length and $F_{9,50} = 2.53$, $P < 0.05$ for tube diameter). Logistic regression analyses revealed that the chance of flowers being robbed increased with flower length (logistic regression coefficient $b \pm$ SE, 1.31 ± 0.34 , $N = 60$, $P < 0.001$) and flower diameter ($b \pm$ SE, 3.61 ± 1.33 , $N = 60$, $P = 0.009$) (Fig. 2). The analysis of robbed flowers also showed that nectar robbers did not inflict any damage to the reproductive organs ($N = 60$).

Results from GLM analysis revealed that the chance of flowers producing fruits was dependent on the plant involved (coefficient \pm SE, -0.23 ± 0.07 , $P = 0.006$). Similarly, robbing decreased the chance of flowers setting fruit (coefficient \pm SE, -4.77 ± 0.62 , $P < 0.001$). Finally, the interaction of plant \times robbery was significant (coefficient \pm SE, 0.27 ± 0.08 , $P < 0.001$), indicating that the impact of robbery on the probability of a flower setting fruit was dependent on the plant factor (Fig. 3).

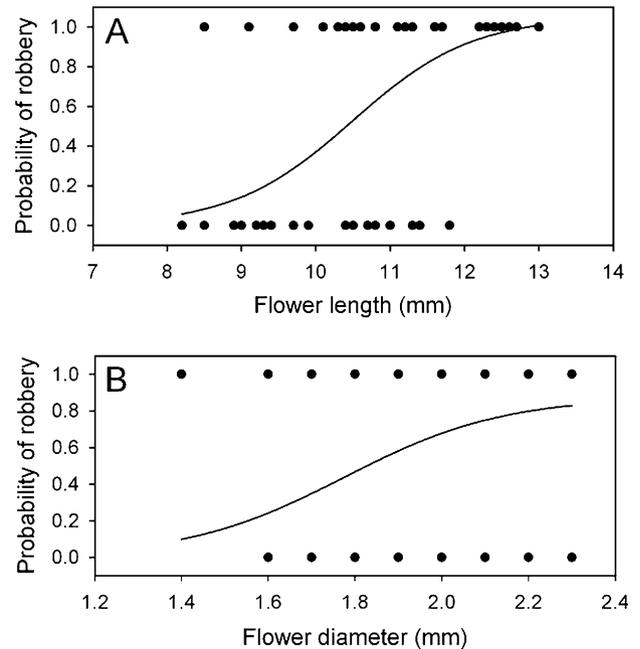


Figure 2. Logistic regression of flower length (A) and flower diameter (B) on the chance of robbery shown by flowers of *Duranta erecta* ($N = 60$ in the two cases). Lines represent the fit of a sigmoid equation of three parameters of the form $a/[1 + \exp(-(x - x_0)/b)]$ to data.

DISCUSSION

The flowers of *D. erecta* suffer nectar robbing by carpenter bees (*X. cubaecola*) in Cuba. Díaz and Sanchez (1998) and Díaz and Vale (2001) showed that *X. cubaecola* legitimately visit and pollinate some species of plants in Cuba, although they also serve as nectar robbers of some tubular flowers. Carpenter bees have long been described as nectar robbers of tubular flowers (Faegri and van der Pijl, 1979; Navarro, Guitián & Guitián, 1993; Scott, Buchmann & O'Rourke, 1993; Delaplane, 1995; Sampson & Cane, 2000). A similar interaction to that described in the present study has recently been reported by Schlindwein *et al.* (2003) in Rio Grande do Sul (Brazil). In their study, however, a different carpenter bee (*Xylocopa nigrocincta*) acted as the thief of nectar from *D. erecta*.

Although the study of nectar robbing has grown rapidly in the last two decades, the importance of robbing for plant fitness is only now becoming apparent. Nectar robbers, accessing nectar 'illegitimately', could affect the plant fitness (Maloof & Inouye, 2000). Although, in some instances, this effect could be positive for female fitness (Navarro, 2000), overall, it has negative consequences for female reproductive success (Irwin *et al.*, 2001). Moreover, that effect may be contingent on the identity of robbers, the pollinator

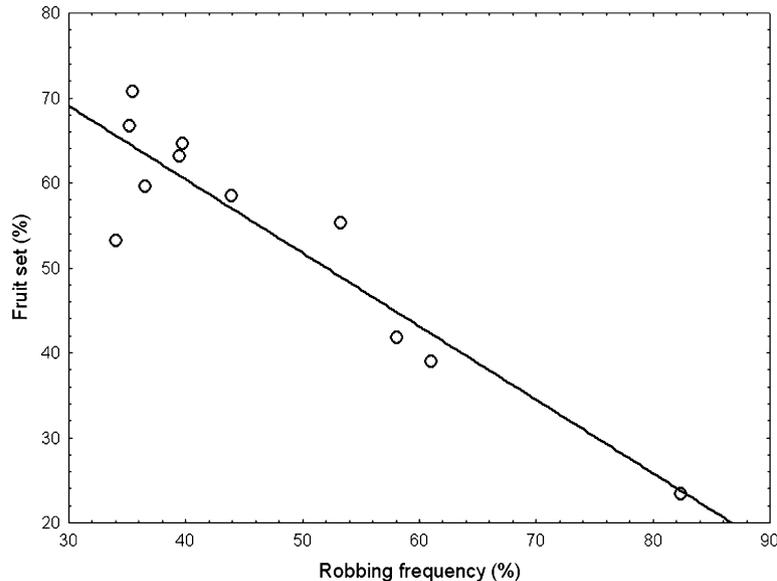


Figure 3. Scatterplot of the fruit set at the plant level as a function of the robbing percentage for each plant (black dots) and fitted linear model (line).

assemblage, and the reproductive biology of the plant (Irwin *et al.*, 2001). In this case, nectar robbing by *X. cubaecola* appears to be responsible of a detrimental effect by decreasing the probability of fruit set of *Duranta erecta*. The lower probability of flowers to set fruit in robbed plants has been attributed to both direct effects on plants, as, for example, by damaging floral reproductive structures (Galen, 1983; Traveset, Willson & Sabag, 1998; Zhang *et al.*, 2007), or to indirect effects. In this latter instance, the robbery could modify the direct plant-pollinator relationship through at least three mechanisms: (1) affecting the flight behaviour of legitimate pollinators between plant visits; (2) decreasing the overall legitimate pollinator visitation rate to plants; and (3) affecting the percentage of flowers probed per plant (Zimmerman & Cook, 1985; Irwin & Brody, 1998, 1999; Maloof, 2001; Castro *et al.*, 2008).

In this case, nectar robbers did not inflict any damage to the sexual structures of *D. erecta*. Although during the study long-tongued social bees (*M. beecheii*) were observed visiting flowers of *D. erecta* for nectar, any indirect effect as mentioned above, could be responsible for decreasing fruit set. Castro *et al.* (2008) showed that robbed flowers in the narrow endemic *Polygala vayredae* were less visited by legitimate pollinators as a consequence of its lower nectar reward. A similar behaviour of *Melipona* bees in the case of *D. erecta* would explain our results. A more detailed study of the effect of nectar robbing on legitimate pollinator behaviour is needed.

On an individual basis, our results also show that plants with a higher proportion of robbed flowers had

a reduced proportion of fruit set. Similarly, González & Valdivia (2005) showed that inflorescences of *Puya coerulea* with a high proportion of robbed flowers had a reduced probability of being visited by the legitimate pollinator *Patagona gigas*, which in turn, decreased the probability that undamaged flowers in the same inflorescences will be visited.

Galen & Cuba (2001) showed that larger flowers of the alpine skypilot, *Polemonium viscosum*, were on a selective disadvantage compared to smaller flowers because they were more frequently visited by nectar-robbing ants. Similarly, in *P. vayredae*, Castro *et al.* (2008) showed the preference of robbers for specific floral traits such as nectar production, which is positively correlated with corolla tube length. Nectar robbers in this species preferably visit the highest nectar-producing flowers, conditioning negatively its reproductive success. Ornelas *et al.* (2007) and Gómez *et al.* (2008) have recently shown that there is a correlated evolution between nectar production and corolla tube length. These authors propose that this correlation occurs because flowers with longer corollas will be able to hold more nectar or to have larger nectaries. The present study has shown that, in *D. erecta*, the probability of being robbed is positively related to corolla length and diameter. Possibly, these floral traits are related to floral rewards, although more detailed studies are needed. Taking into account the fact that robbed flowers have a lower probability of setting fruit, and assuming that smaller flowers, which are less robbed, will be visited by legitimate pollinators, this could suggest a selective pressure by robbers to decrease flower tube length in *D. erecta*.

Pollinators have long been identified as selective agents driving flower specialization, and the depth of flowers is one of the flower characters most extensively studied. However, the selective impact of nectar robbing on flower morphology has mostly been ignored (Maloo & Inouye, 2000). This omission is unfortunate because nectar robbing appears to be responsible of the wide between-population variation in corolla length shown by some species (Waser, 1979; Roubik, Holbrook & Parra, 1985). As recently suggested by Lara & Ornelas (2001) after carrying out experiments with artificial flowers, and having been demonstrated by Urcelay *et al.* (2006) in natural populations of *Campsidium valdivianum*, nectar robbing may represent an opposite selective force that balances the selection for longer corollas often imposed by specialist pollinators.

In the present study, the fitness gains of being adapted to long-tongued visitors will possibly be counteracted by fitness loss as a consequence of the preference of nectar robbers for longer flowers. Adaptation to lower corolla sizes in this species would require little loss, or even gains, in the fitness contribution respect to higher corolla sizes. Thus, this case can represent another example of striking specialization for the less effective visitor (Aigner, 2001).

The main aim of the present study was to show the existence of floral visitors others than pollinators, which are not well fitted to the specialized floral morphology of *D. erecta*, but are capable of robbing floral nectar concealed in the interior of floral tube. By doing this, floral visitors affect negatively the female fitness and this effect is more pronounced in flowers with long corollas. This phenomenon may represent a selective force that opposes to the selective advantage of long corollas in legitimate pollination. This preliminary finding deserves further research in the light of the ecological and evolutionary consequences of nectar robbing in tubular flowers.

ACKNOWLEDGEMENTS

The work was partially financed under grants from the AECI and CGL2006-13847-CO2-02 from the Spanish Ministerio de Ciencia y Tecnología and the FEDER funds from the European Union to L.N. The project CYTED 2003-XII-6, in which both authors are participating, financed the travel of authors to Isle of Cuba. The comments of Maria Bosch and three anonymous reviewers on a preliminary version substantially improved this manuscript. We also would like to thank Danny Rojas and Angel Vale who provided us valuable support with data on *X. cubaecola* proboscis length and the floral biology of this species.

REFERENCES

- Aigner PA. 2001.** Optimality modelling and fitness trade-offs: when should plants become pollinator specialists? *Oikos* **95**: 177–184.
- Alexandersson R, Johnson SD. 2002.** Pollinator-mediated selection on flower-tube length in a hawkmoth-pollinated *Gladiolus* (Iridaceae). *Proceedings of the Royal Society of London Series B Biological Sciences* **269**: 631–636.
- Castro S, Silveira P, Navarro L. 2008.** Floral traits variation, pollinator attraction and nectar robbers in *Polygala vayredae* (Polygalaceae). *Ecological Research* doi 10.1007/s11284-008-0481-5.
- Darwin C. 1859.** *On the origin of species*. London: J Murray.
- Darwin C. 1877.** *The different forms of flowers on plants of the same species*. London: J Murray.
- Delaplane KS. 1995.** Bee foragers and their pollen loads in South Georgia rabbiteye blueberry. *American Bee Journal* **135**: 825–826.
- Díaz AL, Sanchez U. 1998.** Feeding and nesting plants of *Xylocopa cubaecola* (Hymenoptera: Apidae). *Caribbean Journal of Science* **34**: 152–155.
- Díaz AL, Vale A. 2001.** Actividad polinizadora y aspectos conductuales de la abeja *Xylocopa cubaecola* Lucas (Hymenoptera: Apoidea) en condiciones naturales. *Fitosanidad* **5**: 25–30.
- Faegri K, Van Der Pijl L. 1979.** *The principles of pollination ecology*, 3rd edn. Oxford: Pergamon.
- Fenster CB. 1991.** Selection on floral morphology by hummingbirds. *Biotropica* **23**: 98–101.
- Galen C. 1983.** The effect of nectar-thieving ants on seedset in floral scent morphs of *Polemonium viscosum*. *Oikos* **41**: 245–249.
- Galen C, Cuba J. 2001.** Down the tube: pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. *Evolution* **55**: 1963–1971.
- Gómez JM, Bosch J, Perfectti F, Fernández JD, Abdelaziz M, Camacho JPM. 2008.** Association between floral traits and rewards in *Erysimum mediohispanicum* (Brassicaceae). *Annals of Botany* **101**: 1413–1420.
- González PL, Valdivia CE. 2005.** Direct and indirect effects of nectar robbing on the pollinating behaviour of *Patagona gigas* (Trochilidae). *Biotropica* **37**: 693–696.
- Graves GR. 1982.** Pollination of *Tristerix mistletoe* (Loranthaceae) by *Diglossa* (Aves, Thraupidae). *Biotropica* **14**: 316.
- Inouye DW. 1980.** The terminology of floral larceny. *Ecology* **61**: 1251–1253.
- Inouye DW. 1983.** The ecology of nectar robbing. In: Bentley B, Elias TS, eds. *The biology of nectaries*. New York, NY: Columbia University Press, 153–174.
- Irwin RE, Brody AK. 1998.** Nectar robbing in *Ipomopsis aggregata*: effects on pollinator behavior and plant fitness. *Oecologia* **116**: 519–527.
- Irwin RE, Brody AK. 1999.** Nectar-robbing bumblebees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* **80**: 1703–1712.
- Irwin RE, Brody AK. 2000.** Consequences of nectar robbing

- for realized male function in a hummingbird-pollinated plant. *Ecology* **81**: 2637–2643.
- Irwin RE, Brody AK, Waser NM. 2001.** The impact of floral larceny on individuals, populations, and communities. *Oecologia* **129**: 161–168.
- Lara C, Ornelas JF. 2001.** Preferential nectar robbing of flowers with long corollas: experimental studies of two hummingbird species visiting three plant species. *Oecologia* **128**: 263–273.
- Maloof JE. 2001.** The effects of a bumble bee nectar robber on plant reproductive success and pollinator behavior. *American Journal of Botany* **88**: 1960–1965.
- Maloof JE, Inouye DW. 2000.** Are nectar robbers cheaters or mutualists? *Ecology* **81**: 2651–2661.
- Mendez I. 2003.** Verbenaceae. In: Greuter W, Rankin R, eds. *Flora de la república de Cuba. Serie A Plantas vasculares*, Fascículo 7. Ruggell: Gantner Verlag KG.
- Navarro L. 2000.** Pollination ecology of *Anthyllis vulneraria* subsp. *vulgaris* (Fabaceae): nectar robbers as pollinators. *American Journal of Botany* **87**: 980–985.
- Navarro L, Guitián J, Guitián P. 1993.** Reproductive biology of *Petrocoptis grandiflora* Rothm (Caryophyllaceae), a species endemic to Northwest Iberian Peninsula. *Flora* **188**: 253–261.
- Navarro L, Guitián P, Ayensa G. 2008.** Pollination ecology of *Disterigma stereophyllum* (Ericaceae) in Southwestern Colombia. *Plant Biology* **10**: 512–518.
- Ornelas JF, Ordano M, de Nova AJ, Quintero ME, Garland T Jr. 2007.** Phylogenetic analysis of interspecific variation in nectar of hummingbird-visited plants. *Journal of Evolutionary Biology* **20**: 1904–1917.
- Reddy TB, Reddi CS. 1996.** Pollination ecology of *Duranta repens* (Verbenaceae). *Journal of the Bombay Natural History Society* **93**: 193–201.
- Roubik DW, Holbrook MN, Parra GV. 1985.** Roles of nectar robbers in reproduction of the tropical treelet *Quasia amara* (Simaroubaceae). *Oecologia* **66**: 161–167.
- Sampson B, Cane J. 2000.** Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *Journal of Economic Entomology* **93**: 1726–1731.
- Schlindwein C, Schlumpberger B, Wittmann D, Moure JS. 2003.** O gênero *Xylocopa* Latreille no Rio Grande do Sul, Brasil (Hymenoptera, Anthophoridae). *Revista Brasileira de Entomologia* **47**: 107–118.
- Scott PE, Buchmann SL, O'Rourke MK. 1993.** Evidence for mutualism between a flower-piercing carpenter bee and ocotillo: use of pollen and nectar by nesting bees. *Ecological Entomology* **18**: 234–240.
- Traveset A, Willson MF, Sabag C. 1998.** Effect of nectar-robbing birds on fruit set of *Fuchsia magellanica* in Tierra del Fuego: a disrupted mutualism. *Functional Ecology* **12**: 459–464.
- Urcelay C, Morales CL, Chalcoff VR. 2006.** Relationship between corolla length and floral larceny in the South American hummingbird-pollinated *Campsidium valdivianum* (Bignoniaceae). *Annales Botanici Fennici* **43**: 205–211.
- Waser NM. 1979.** Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). *Oecologia* **39**: 107–121.
- Zhang YW, Robert GW, Wang Y, Guo YH. 2007.** Nectar robbing of a carpenter bee and its effects on the reproductive fitness of *Glechoma longituba* (Lamiaceae). *Plant Ecology* **193**: 1–13.
- Zimmerman M, Cook S. 1985.** Pollinator foraging, experimental nectar-robbing and plant fitness in *Impatiens capensis*. *American Midland Naturalist* **113**: 84–91.