

RISKS AND COSTS OF INTERACTIONS BETWEEN PLANTS AND HUMMINGBIRDS

Carlos Lara

Laboratorio de Ecología del Comportamiento, Centro Tlaxcala de Biología de la Conducta
UAT-UNAM, Carretera Tlaxcala-Puebla Km 1.5, Colonia Xicohtencatl S/N C.P. 90070,
Tlaxcala, México. *E-mail*: laracar@garza.uatx.mx

Resumen. – **Riesgos y costos de las interacciones entre plantas y colibríes.** – Los colibríes pueden actuar como mutualistas transportando polen entre las flores que visitan, pero además pueden actuar como vectores de diversos organismos que pueden afectar la interacción con sus plantas. El transporte de estos antagonistas puede resultar en la transmisión de enfermedades, consumo de polen y disminución del néctar floral. De esta manera, la armonía aparente del mutualismo entre plantas y colibríes puede ser alterada por los organismos antagonistas. El presente trabajo pretende contribuir a esta inexplorada línea de investigación, la cual se enfoca en las implicaciones de especies de un tercer nivel sobre la interacción planta-colibrí.

Abstract. – Hummingbirds can act as mutualists by transporting pollen grains among flowers, but they may also act as vectors of several organisms which could affect the interaction with their plants. The transmission of such antagonists by hummingbirds searching for nectar rewards may end up in sexually transmitted diseases, pollen consumption and depletion of nectar rewards. Therefore, the supposedly harmonious, mutualistic interaction between plants and hummingbirds can be defeated by the transmission of antagonistic organisms along with pollen grains. The present paper is an attempt to contribute to this recent line of inquiry which focuses on the implications of third level species on the plant-hummingbird interaction. *Accepted 5 January 2004.*

Keys words: Antagonists, hummingbird-plant interaction, flower mites, fungal pathogens, nectar thieves.

INTRODUCTION

The use and abuse of plant-pollinator interactions by antagonistic organisms has been shown in an increasing number of studies (Roy 1993, Shykoff *et al.* 1996, Maloof & Inouye 2000, Irwin *et al.* 2001; Lara & Ornelas 2001a, 2003; Irwin & Maloof 2002, Leege & Wolfe 2002, Gómez 2003). Hummingbird-plant interaction is also at risk because nectar rewards and pollination services are usually “exploited” by species that do not provide a return benefit to either mutualist partner (Lara & Ornelas 2002b). The present paper is

an attempt to contribute to this recent line of inquiry, which focuses on the implications of third level species on the plant-hummingbird interaction. I will show some field and experimental evidence on the importance of antagonistic organisms on hummingbirds and their plants

THE RISKS AND COSTS

Hummingbirds can act as mutualists by transporting pollen grains among flowers (Feinsinger 1987, Stiles 1981), but they may also act as vectors by carrying several antagonistic

organisms (Colwell 1995, Lara & Ornelas 2001b). In this way, the role of hummingbirds is analogous to that they have as pollinators of plants (Colwell *et al.* 1974, McDade & Kinsman 1980, Navarro 1999, Ornelas 1994, Lara & Ornelas 2001a). The transmission of such antagonists by birds visiting flowers for nectar rewards may end up in sexually transmitted diseases (Jennersten 1983; Roy 1993, 1994), pollen consumption (Paciorek *et al.* 1995), and depletion of nectar rewards (Colwell 1995; Lara & Ornelas 2001b, 2002b). Therefore, the supposedly harmonious, mutualistic interaction between plants and hummingbirds can be defeated by the transmission of antagonistic organisms along with pollen grains.

Although nectar of hummingbird-pollinated flowers is regularly robbed by a variety of non-pollinating, “illegitimate” visitors such as bees, ants, passerine species, and hummingbirds (Colwell *et al.* 1974, McDade & Kinsman 1980, Roubick 1982, Ornelas 1994, Arizmendi *et al.* 1996, Traveset *et al.* 1998, Irwin & Brody 1999, Navarro 1999, Lara & Ornelas 2001a), the most common nectar robbers in many of these hummingbird flowers are the hummingbird flower mites (Lara & Ornelas 2001b, 2002b).

Hummingbird flower mites (Acari: Mesostigmata, Ascidae) feed on pollen and nectar from flowers of a great variety of plant species exclusively pollinated by hummingbirds (Colwell 1985, Dobkin 1987, Heyneman *et al.* 1991, Naskrecki & Colwell 1998). Although reported for 20 plant families including Heliconiaceae, Rubiaceae, Lobeliaceae, Gesneriaceae, and Ericaceae (Colwell 1985), flowers mites are absent in other plant families rich in hummingbird-pollinated species such as Labiateae, Convolvulaceae, Malvaceae, Onagraceae, and Acanthaceae.

Mites have a commensalistic relationship with hummingbirds by hitching rides from

flower to flower in the nostrils of the hummingbirds, without any harm or benefit for the latter (phoresy; Proctor & Owens 2000). This statement is based on the collection of flower mites from the nasal turbinates of mainly long-billed hummingbirds (*Threnetes*, *Glaucis*, *Phaethornis*, *Campylopterus*, *Chlorestes*, *Amazilia*, *Eugenes*, *Lampornis*; Baken & Yunker 1963, Fain *et al.* 1977, Hyland *et al.* 1978). Most of these hummingbirds have nostrils completely exposed (Ridgway 1911), so the mites can easily hide in.

Some surveys have documented that nectar consumption by mites reduces the availability of nectar to hummingbirds up to 50% (Colwell 1995; Lara & Ornelas 2001b, 2002b). This affects the hummingbird foraging patterns and might indirectly affect the pollen transmission (Lara & Ornelas 2002a). The role of these mites as competitors for nectar doubtless represents a far more costly negative interaction, from the point of view hummingbird energetics, than the mites’ exploitation of the birds for transport (Colwell 2000). It has been shown that this energetic effect can have substantial ecological consequences (Miller & Travis 1996). Maloof & Inouye (2000) have summarized the possible behavioral changes in pollinators that would be caused by nectar reduction by floral antagonists such as nectar robbers. In short, these behavioral changes in pollinators include flight distance, number of flowers visited, and time spent on each flower. Yet, the generality of these results has not been explored thoroughly.

Animal-pollinated plants in natural populations are often subject to a multitude of herbivores and pathogens, facing the dilemma that the more pollinators they attract, the more likely they are to be attacked or infected (Ornelas *et al.* in prep.). Antagonistic organisms can interfere with plant reproduction by interfering with pollination through (1) flower

destruction that can lead pollinators to change of plant moreover without any previous flower visited and (2) the damage to important floral structures such as anthers, stigmas and ovaries, that can reduce the amount of pollen received by flowers and can lead to improper development of seeds.

It has been shown that some fungal pathogens can use and abuse of pollinators to ferry gametes between plants as a way to promote fungal sexual reproduction, and/or use their host's pollinators to transfer infectious spores to a new host (Jennersten 1983, Batra & Batra 1985, Alexander & Maltby 1990, Batra 1991, Roy 1996). Also, fungal pathogens that infect the reproductive structures of plants can reduce their seed production (Alexander 1987; Roy 1994, 1996; Marr 1997, Carlsson-Granér *et al.* 1998, Pfunder & Roy 2000, Collin *et al.* 2002). This phenomenon has been widely studied on fungal diseases transmitted by insects (Jennersten 1988, Bultman & White 1988, Batra 1991). However vertebrate-pollinated plants are also at risk.

Hummingbird-flowers are attractive to a variety of pollinating and non-pollinating visitors which have the capacity to transport a variety of fungal spores, and therefore to increase the probability of infection. The anther smut fungus *Fusarium moniliforme* (Sched.) Snyder & Ansen (Deuteromycota: Section *Liseola*) infects the flowers of *Moussonia deppeana* (Schlecht. & Cham.) Hanst. (Gesneriaceae), a protandrous, hummingbird-pollinated perennial shrub (Lara & Ornelas 2003). *Fusarium* appears to modify the *Moussonia* flowering phenology and to increase the allocation of resources to pollinator attraction and reward. Increased floral displays enhance visitation by its pollinator, the Amethyst-throated Hummingbird (*Lampornis amethystinus*), which is an effective vector of *Fusarium* spores, thus increasing the dissemination of this fungal disease (Lara & Ornelas 2003).

Although this is the first record about hummingbirds acting as disease vectors, it appears that anther smuts are commonly present on natural plant populations and use hummingbirds for their dissemination.

The exploitation of plant-hummingbird mutualism by fungi is still unexplored. However it offers interesting parallels and contrasts with other pollinator-disease transmission systems such as the production of healthy and diseased flowers on systemically infected plants. Likewise, hummingbird-transmitted diseases can be a good model for examining potential relationships such as energy allocation to pollinator attraction, the nectar production schedules after infection by fungi (Lara & Ornelas 2003), and the nectar thievery by flower mites (Lara & Ornelas 2001, 2002a).

These results suggests that hummingbird preference might affect the dynamics of disease transmission and the outcomes of plant-hummingbird mutualistic interactions.

GENERAL CONCLUSION

Little attention has been paid as to whether an antagonistic organism relates to selection pressures on the hummingbird-plant interaction. Although antagonists can affect in several ways the interaction, important aspects such as the reduction in attractiveness can reduce hummingbird visitation and influence disease transmission. Nectar rob and flower infection in hummingbird-plants may entail an energy cost, and could lead to a reduction in seed production by plants under natural conditions.

Hummingbirds and their plants seem to respond to antagonistic organisms in a subtle and complex way. When antagonists affect traits relevant to the pollination system, the potential selection imposed by pollinators might be altered by direct or indirect influence of antagonists (Ornelas *et al.* in prep.). Future

studies are needed to explore the implications of third level species on plant-hummingbird interactions.

ACKNOWLEDGMENTS

Thanks to Citlalli Castillo, Armando Martínez, Clementina González, Leonor Jiménez, and Mariano Ordano for assistance in the field. I greatly appreciated the comments on earlier drafts of this manuscript by Anaid Diaz, Patricia González and Raúl Ortíz Pulido. I am also indebted to Francisco Ornelas for his inspiration.

REFERENCES

- Alexander, H. M. 1987. Pollination limitation in a population of *Silene alba* infected by the anther-smut fungus, *Ustilago violacea*. *J. Ecol.* 75: 771–780.
- Alexander, H. M., & A. Maltby. 1990. Anther-smut infection of *Silene alba* caused by *Ustilago violacea*: factors determining fungal reproduction. *Oecologia* 84: 249–253.
- Arizmendi, M. C., C. A. Domínguez, & R. Dirzo. 1996. The role of an avian nectar robber and of hummingbird pollinators on the reproduction of two plant species. *Funct. Ecol.* 10: 119–127.
- Baker, E. W., & C. E. Yunker. 1964. New blattisociid mites (Acarina: Mesostigmata) recovered from Neotropical flowers and hummingbird's nares. *Ann. Entomol. Soc. Am.* 57: 103–126.
- Batra, S. W. T. 1991. Floral mimicry and insects as vectors of conidia. Pp. 93–97 in Batra, L. R. (ed.). *World species of Monilinia (fungi): their ecology, biosystematics and control*. J. Cramer, Berlin, Germany.
- Batra, L. R., & S. W. T. Batra. 1985. Floral mimicry induced by mummy-berry fungus exploits host's pollinators as vectors. *Science* 228: 1011–1013.
- Bultman, T. L., & J. F. White. 1988. "Pollination" of a fungus by a fly. *Oecologia* 73: 317–319.
- Carlsson-Granér, U., T. Elmqvist, J. Ågren, H. Gardfjell, & P. Ingvarsson. 1998. Floral sex ratios and seed set in dioecious *Silene dioica*. *J. Ecol.* 86: 79–91.
- Collin, C. L., P. S. Pennings, C. Rueffler, A. Widmer, & J. A. Shykoff. 2002. Natural enemies and sex: how seed predators and pathogens contribute to sex-differential reproductive success in a gynodioecious plant. *Oecologia* 131: 94–102.
- Colwell, R. K., B. J. Betts, P. Bunnell, F. L. Carpenter, & P. Feinsinger. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flower-piercer *Diglossa plumbea*, and its evolutionary implications. *Condor* 76: 447–452.
- Colwell, R. K. 1985. Stowaways on the hummingbird express. *Nat. Hist.* 94: 56–63.
- Colwell, R. K. 1995. Effects of nectar consumption by the hummingbird flower mite *Proctolaelaps kirmsei* on nectar availability in *Hamelia patens*. *Biotropica* 27: 206–217.
- Colwell, R. K. 2000. Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. *Am. Nat.* 156: 495–510.
- Dobkin, D. S. 1987. Synchronous flowers abscission in plants pollinated by hermit hummingbirds and the evolution of one-day flowers. *Biotropica* 19: 90–93.
- Fain, A., K. E. Hyland, & H. G. Aitken. 1977. Flower mites of the family Ascidae phoretic in nasal cavities of birds (Acarina: Mesostigmata). *Acta Zool. Pathol. Antverp.* 69: 99–154.
- Feinsinger, P. 1987. Approaches to nectarivore-plant interactions in the New World. *Rev. Chil. Hist. Nat.* 60: 285–319.
- Gómez, J. M. 2003. Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum medeolobispanicum*: consequences for plant specialization. *Am. Nat.* 162: 242–256.
- Heyneman, A. J., R. K. Colwell, S. Nacem, D. S. Dobkin, & B. Hallet. 1991. Host plant discrimination: experiments with hummingbird flower mites. Pp. 455–485 in Price, P. W., T. M. Lewinsohn, G. W. Fernandes, & W. W. Benson (eds.). *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley and Sons, New York, New York.
- Hyland, K. E., A. Fain, & A. S. Moorhouse. 1978.

- Ascidae associated with the nasal cavities of Mexican birds (Acarina: Mesostigmata). *N. Y. Entomol. Soc.* 86: 260–267.
- Irwin R. E., & A. K. Brody. 1999. Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* 80: 1703–1712.
- Irwin, R. E., & J. E., Maloof. 2002. Variation in nectar robbing over time, space and species. *Oecologia* 133: 525–533.
- Irwin, R. E., A. K. Brody, & N. M., Waser. 2001. The impact of floral larceny on individuals, populations, and communities. *Oecologia* 129: 161–168.
- Jennersten, O. 1983. Butterfly visitors as vectors of *Ustilago violaceae* spores between caryophyllaceous plants. *Oikos* 40: 125–130.
- Jennersten, O. 1988. Insect dispersal of fungal disease: effects of *Ustilago* infection on pollinator attraction in *Viscaria vulgaris*. *Oikos* 51: 163–170.
- Lara, C., & J. F. Ornelas. 2001a. Preferential nectar robbing of flowers with long corollas: experimental studies of two hummingbird species visiting three plant species. *Oecologia* 128: 263–273.
- Lara, C., & J. F. Ornelas. 2001b. Nectar “theft” by hummingbird flower mites and its consequences for seed set in *Moussonia deppeana*. *Funct. Ecol.* 15: 78–84.
- Lara, C., & J. F. Ornelas. 2002a. Effects of nectar theft by flower mites on hummingbird behavior and the reproductive success of their host plant, *Moussonia deppeana* (Gesneriaceae). *Oikos* 96: 470–480.
- Lara, C., & J. F. Ornelas. 2002b. Flower mites and nectar production in six hummingbird-pollinated plants with contrasting flower longevities. *Can. J. Bot.* 80: 1216–1229.
- Lara, C., & J. F. Ornelas. 2003. Hummingbirds as vectors of fungal spores in *Moussonia deppeana* (Gesneriaceae): taking advantage of a mutualism? *Am. J. Bot.* 90: 260–267.
- Leege, L. M., & L. M. Wolfe. 2002. Do floral herbivores respond to variation in flower characteristics in *Gelsemium sempervirens* (Loganiaceae), a distylous vine? *Am. J. Bot.* 89: 1270–1274.
- Maloof, J. E., & D. W. Inouye. 2000. Are nectar robbers cheaters or mutualists? *Ecology* 81: 2651–2661.
- Marr, D. L. 1997. Impact of a pollinator-transmitted disease on reproduction in healthy *Silene acaulis*. *Ecology* 78: 1471–1480.
- McDade, L. A., & S. Kinsman. 1980. The impact of floral parasitism in two Neotropical hummingbird-pollinated plant species. *Evolution* 34: 954–958.
- Miller, T. E., & J. Travis. 1996. The evolutionary role of indirect effects in communities. *Ecology* 77: 1329–1335.
- Naskrecki, P., & R. K. Colwell. 1998. Systematics and host plants affiliations of hummingbirds flower mites of the genera *Tropicoseius* Baker and Yunker and *Rhinoseius* Baker and Yunker (Acari: Mesostigmata: Ascidae). Thomas Say Publications in Entomology, Monographs, Entomological Society of America, Lanham, Maryland.
- Navarro, L. 1999. Pollination ecology and effect of nectar removal in *Macleania bullata* (Ericaceae). *Biotropica* 31: 618–625.
- Ornelas, J. F. 1994. Serrate tomia: an adaptation for nectar robbing in hummingbirds? *Auk* 111: 703–710.
- Paciorek, C. B., B. Moyer, R. Levin, & S. Halpern. 1995. Pollen consumption by the mite *Proctolaelaps kirmsei* and possible fitness effects on *Hamelia patens*. *Biotropica* 27: 258–262.
- Pfunder, M., & B. Roy. 2000. Pollinator-mediated interactions between a pathogenic fungus, *Uromyces pisi* (Pucciniaceae), and its host plant, *Euphorbia cyparissias* (Euphorbiaceae). *Am. J. Bot.* 87: 48–55.
- Proctor, H., & I. Owens. 2000. Mites and birds: diversity, parasitism and coevolution. *Trends Ecol. Evol.* 15: 358–364.
- Ridgway, R. 1911. *The Birds of North and Middle America*, part V. Smithsonian Institution Press, Washington, D.C.
- Roubik, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63: 354–360.
- Roy, B. 1993. Floral mimicry by a plant pathogen. *Nature* 362: 56–58.
- Roy, B. 1994. The use and abuse of pollinators by fungi. *Trends Ecol. Evol.* 9: 335–339.
- Shykoff, J. A., E. Bucheli, & O. Kaltz. 1996. Flower lifespan and disease risk. *Nature* 379: 779.

LARA

- Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution with particular reference to Central America. *Ann. Mo. Bot. Gard.* 68: 323–351.
- Traveset, A., M. F. Willson, & C. Sabag. 1998. Effect of nectar-robbing birds on fruit set of *Fuchsia magellanica* in Tierra del Fuego: a disrupted mutualism. *Funct. Ecol.* 12: 459–464.