

Noncorrelated evolution between herbivore- and pollinator-linked features in *Aristolochia chilensis* (Aristolochiaceae)

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The effect of mutualists (i.e. pollinators) and antagonists (i.e. herbivores) can have non-additive effects on plant fitness. This is often interpreted as evidence for correlated evolution on a suite of traits leading to an increase and decrease of the interaction of plants with mutualists and antagonists, respectively. This situation has been found to prevail in plants that have large floral and fruit displays but are not limited by pollinators for seed set. We suggest the alternative hypothesis, where plants limited by pollinators for seed set (e.g. deceit-pollinated plants) exhibit additive effects of pollinators and herbivores on fitness (i.e. noncorrelated evolution). Using a 2×2 factorial design, we tested this hypothesis by solely and simultaneously evaluating the effects of pollinators and the single herbivore, *Battus polydamas archidamas*, on female reproductive success of *Aristolochia chilensis*. Plants exposed to herbivores presented 2.6-fold greater herbivory than plants that excluded them. In addition, plants exposed to pollinators showed strong limitation by pollinators for seed set compared with other plants of the genus *Aristolochia*. However, only pollinators had a significant effect on fruit and seed set because plants that excluded them did not set fruits or seeds. Furthermore, herbivores and pollinators exerted additive effects on fruit and seed production. Collectively, these results indicate that herbivore- and pollinator-linked traits in *A. chilensis* exhibit non-correlated evolution. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 239–245.

ADDITIONAL KEYWORDS: additivity – correlated evolution – fitness.

INTRODUCTION

Plants may face numerous selective pressures elicited by different kinds of animals, mostly mutualists (i.e. pollinators) and antagonists (i.e. herbivores), which may influence their ecological and evolutionary responses (Zamora, 2000; Herrera & Pellmyr, 2002). However, empirical evaluations assessing the combined and isolated effects of these suites of animals are rather scarce (but see Herrera, 2000; Ehrlén, Käck & Ågren, 2002; Herrera *et al.*, 2002; Gómez, 2005). Non-additivity of effects on plant fitness triggered by mutualists and antagonists can be interpreted as evidence for correlated evolution on a suite of traits tending to increase and decrease the interaction of plants

with their mutualists and antagonists, respectively (*sensu* Herrera, 2000; Herrera *et al.*, 2002; Gómez, 2005). This is particularly important because correlational selection may be a mechanism for the functional integration of one trait with another, most likely promoting genetic integration (Lande, 1980; Brodie, 1992).

Herrera (2000) and Herrera *et al.* (2002) proposed a herbivore-dependent selection pressure led by pollinators based on the non-additive effects elicited by mutualists and antagonists on seed production and seedling recruitment in the perennial herbs *Paeonia broteroi* and *Helleborus foetidus*, respectively. The same authors claimed that their findings should be particularly frequent if herbivores prey on plants bearing large floral and fruit displays (i.e. plants also preferred by pollinators). Similar conclusions were arrived at by Gómez (2005) for *Erysimum*

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mediohispanicum, and by Valdivia & Niemeyer (2005) for *Alstroemeria umbellata*. However, as far as we are aware, no studies have shown that plants facing limitations by pollinators for seed production exhibit additive effects of pollinators and herbivores on reproductive success.

The pipevines of the genus *Aristolochia* are broadly distributed across temperate and mainly tropical regions around the world (Huber, 1993). Detailed studies on the pollination biology of the genus are rather scarce (but see Hall & Brown, 1993; Sakai, 2002; Burgess *et al.*, 2004), and evaluations on herbivory have been mainly performed from the herbivore rather than the plant perspective (Papaj *et al.*, 1992; Klitzke & Brown, 2000; Sime, Feeny & Haribal, 2000; Fordyce & Agrawal, 2001; Fordyce, 2001). We evaluated the selective pressures jointly exerted by herbivores and pollinators on the female reproductive success of *Aristolochia chilensis* Bridges ex Lindl. (Aristolochiaceae), a pipevine that is almost exclusively preyed by the black swallowtail butterfly, *Battus polydamas archidamas* Boisduval (Papilionidae), and is deceit-pollinated by insects and hence most likely pollinator-limited for seed set (Pellmyr, 2002). We predict that, if *A. chilensis* is limited by pollinators for seed production, then an additive effect of herbivores and pollinators on the female reproductive success is indeed to be expected, even if it is intensively preyed by its herbivores (*sensu* Herrera, 2000; Herrera *et al.*, 2002). By contrast, if *A. chilensis* is not pollinator-limited, non-additive effects are expected.

MATERIAL AND METHODS

NATURAL HISTORY AND STUDY SITE

The pipevine, *A. chilensis*, is a creeping perennial herb with a foul-smelling purplish blossom, which grows in semiarid regions of Chile from 27°S to 34°S, and from sea level to 1500 m a.s.l. It is a deceit-pollinated, protogynous plant bearing nonrewarding flowers that are visited by several insect species during the pistillate and staminate phases. Flowering and fruiting occur from August to December. Fruits are dehiscent nuts, 3–4 cm long, bearing black seeds, 4–4.5 mm long. Its leaves are 3–10 cm in diameter (Ruiz, 2001). Although no information is available with respect to flower visitors and pollinators, the leaves are almost exclusively eaten by *B. p. archidamas* caterpillars, even though it is possible to find other insects, such as aphids, albeit very infrequently (C. Valdivia, pers. observ.). Caterpillars develop exclusively on *A. chilensis* and then pupate in suspension from nearby branches or rocks (Peña & Ugarte, 1996). The distribution range of *B. p. archidamas* is approximately the same as that of *A. chilensis* (Peña & Ugarte, 1996).

Fieldwork was carried out from July to December 2004 at Cuesta Lo Prado in the coastal range of central Chile (33°28'S, 70°55'W), in a Mediterranean region characterized by dry summers and rainfall mainly in the autumn and winter (Hajek & Di Castri, 1975).

CORRELATED EVOLUTION ASSESSMENT

To determine a possible pathway for correlated evolution on herbivore- and pollinator-linked traits, we conducted an experiment with a 2 × 2 factorial design following Herrera (2000) by excluding solely and simultaneously herbivores (*B. p. archidamas* caterpillars) and pollinators. In brief, this methodological approach, rather than modifying a specific set of traits, allowed for a statistical dissection of plant fitness following the experimental exclusions. Thus, herbivore exclusions mimicked an ancestral situation in which plants presented a suite of traits that allowed them to escape from herbivores (or show resistance to them), which in turn produced an increased fitness of plants. On the other hand, pollinator exclusions mimicked an ancestral situation whereby plants exhibited a suite of traits that reduced the optimal mutualistic relationship between plants and pollinators, which in turn led to a decreased fitness of plants. Therefore, this artificial array allows the dissection of the isolated effects of herbivores and pollinators, as well as the combined actions of both. Furthermore, it allows for the detection of non-additive effects of herbivores and pollinators, which is the obligate condition for the occurrence of correlated evolution on traits related to them (for methodological details, see Herrera, 2000; Herrera *et al.*, 2002).

Given that *B. p. archidamas* has a wing-span of 7.5–10.5 cm (Peña & Ugarte, 1996), herbivores were excluded by enclosing plants with wire-net cages, 0.3 m high (~1 cm mesh) anchored in the ground and covering a surface of 1.5 × 1.5 m, thus ensuring that no butterfly would oviposit on the plants. Plants in the population studied were not infested by caterpillars at the beginning of the experiment; furthermore, caterpillars were never found in plants that were excluded from butterfly visits. Given that all floral visitors presented body sizes below 1 cm, it is likely that no pollinator was excluded from plants excluded to herbivores. On the other hand, because plants produced flowers which opened sequentially, they were individually enclosed each month at the bud stage with a tulle-mesh bag for preventing pollinator access, albeit allowing access of butterflies to leaves. Both treatment levels were factorially combined to conform the following four combinations: (1) control plants (i.e. exposed to herbivores and pollinators); (2) herbivore treatment (i.e. only exposed to pollinators); (3) polli-

nator treatment (i.e. only exposed to herbivores); and (4) simultaneous herbivore and pollinator treatment (i.e. excluded to both herbivores and pollinators).

For each treatment, 15 plants were selected and monitored from July to December 2004. In these plants, herbivory was monthly recorded by using the herbivory index (HI) developed by Dirzo & Domínguez (1995). One-hundred randomly chosen leaves per plant were checked monthly by registering the degree of foliar surface disappearance triggered both by herbivores and by damage due to senescence. A distinction between these two factors could not be obtained. Each leaf was assigned to one of the following six categories (0, 1, 2, 3, 4, or 5) depending on whether 0%, 1–6%, 7–12%, 13–25%, 26–50%, or 51–100%, respectively, of foliar surface was absent. The HI per plant was determined by the equation:

$$HI = \sum_{i=0}^5 x_i n / N$$

where n is the frequency of observations, x_i is the damage category, and N is the total number of observations. A single per-plant estimate of HI was monthly obtained and assessed through a repeated measures analysis of variance (ANOVA).

When the reproductive season was over, fruits with their respective seeds were collected to determine the reproductive success of plants after experiencing the four treatments. Because fruit and seed production did not meet the normality assumption even after applying appropriate transformations (analyses not shown but assessed through a Kolmogorov–Smirnov test), correlational selection was evaluated by ran-

domizing the original values 10 000 times (Manly, 1997; Herrera, 2000). Furthermore, to estimate the power ($1 - \beta$) of the ANOVA used to detect correlational selection, a power test for the interaction effect was applied *sensu* Kirk (1982).

RESULTS

HERBIVORY AND POLLINATION

Overall, only herbivores had significant effects on foliar removal of *A. chilensis* throughout the time assessed (Table 1). At the end of the reproductive season, plants with pollinators excluded presented 2.6-fold more foliar surface removal in the presence of herbivores than in their absence ($P < 0.001$). Similarly, plants with pollinators included presented 2.7-fold more foliar surface removal in the presence of herbivores than in their absence ($P < 0.001$). The highest herbivore abundance, in terms of the number of larvae per plant, occurred in November (Fig. 1A). However, plants presented the highest foliar surface removal in December, most likely due to the senescence of leaves (Fig. 1B).

Flowers of *A. chilensis* were visited by five orders of insects as well as by some species of acari. Sexually mature flowers presented more than 90% of all floral visitors, with the main floral visitors being colepterans, which were mainly found at the staminate stage of flowers (Table 2). The only floral visitor observed carrying pollen from *A. chilensis* was the Asillidae *Tillobroma* sp., which represents all dipterans found inside the flowers.

Table 1. Summary of repeated measures analysis of variance testing the effects of herbivores and pollinators on foliar removal of *Aristolochia chilensis*

Source	d.f.	MS	F
Within-subjects			
Herbivores	1	57.631	61.447*
Pollinators	1	0.006	0.007
Herbivores × Pollinators	1	0.004	0.004
Error	56	52.521	
Between-subjects			
Time	3	98.108	161.886*
Time × Herbivores	3	24.093	39.750*
Time × Pollinators	3	0.111	0.184
Time × Herbivores × Pollinators	3	0.013	0.022
Error	168	33.942	

Pollinators were maintained in the analyses to discard the eventual effects of pollinator exclusion on the feeding behaviour of *Battus polydamas archidamas*, and hence on foliar surface removal.

* $P < 0.001$.

d.f., degrees of freedom.

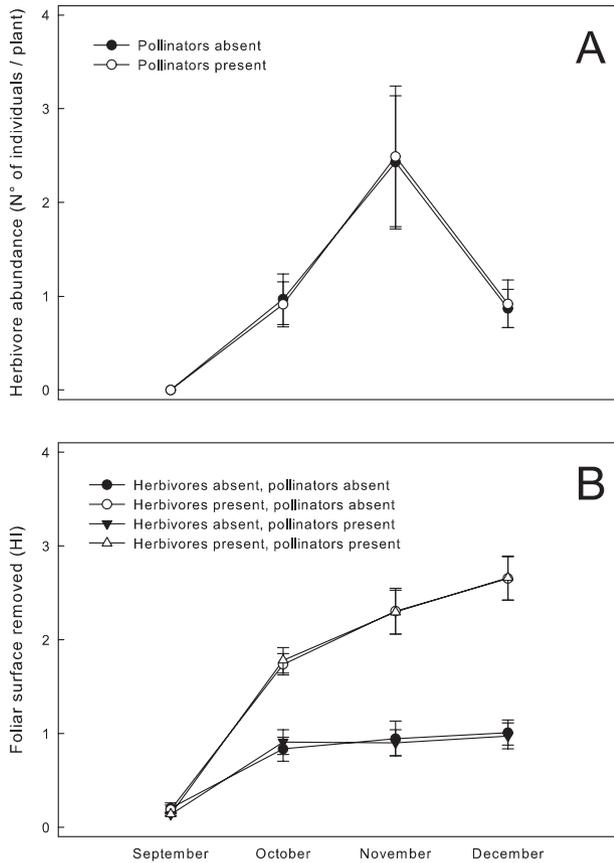


Figure 1. A, abundance of larvae of *Battus polydamas archidamas* per plant. B, disappearance of foliar surface in plants of *Aristolochia chilensis* exposed to larvae of *B. p. archidamas*. HI, herbivory index.

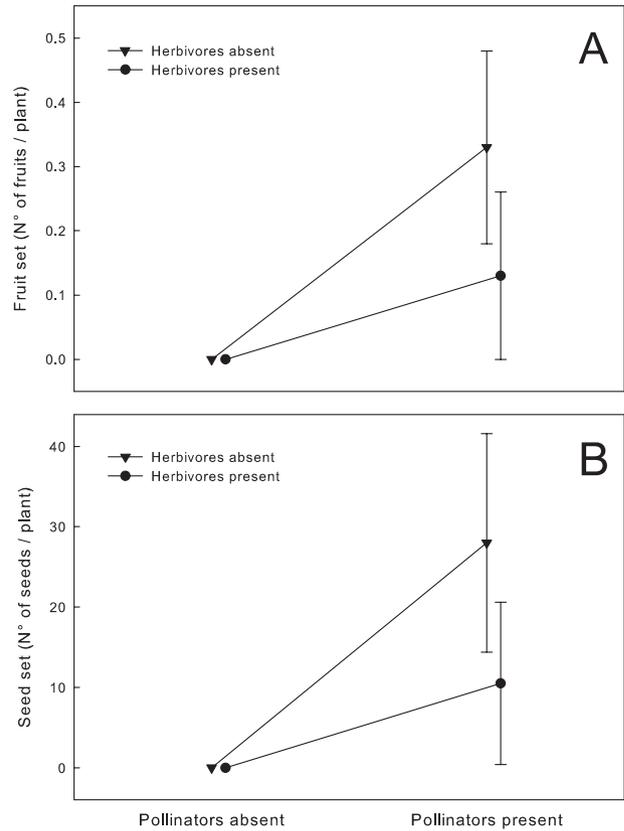


Figure 2. Mean number (standard error) of fruit (A) and seeds (B) per plant of *Aristolochia chilensis* exposed to, and excluded from, herbivores and pollinators. For clarity, the x-axis has been slightly displaced for the herbivore treatments.

Table 2. Abundance of floral visitors (individuals per 30 flowers) of *Aristolochia chilensis* at different ripeness stages

Floral visitors	Pistillate flowers	Staminate flowers	Senescent flowers	Total
Hymenoptera	3 (8.5)	2 (5.7)	0 (0.0)	5 (14.3)
Orthoptera	0 (0.0)	1 (2.9)	0 (0.0)	1 (2.9)
Coleoptera	2 (5.7)	11 (31.4)	0 (0.0)	13 (37.1)
Hemiptera	2 (5.7)	6 (17.1)	1 (2.9)	9 (25.7)
Diptera	3 (8.5)	0 (0.0)	2 (5.7)	5 (14.3)
Acari	2 (5.7)	0 (0.0)	0 (0.0)	2 (5.7)
Total	12 (34.3)	20 (57.1)	3 (8.6)	35 (100.0)

Data are N (%).

Survey performed on 30 flowers at each stage, each from a different plant. Flowers at the bud stage did not present floral visitors.

CORRELATED EVOLUTION ASSESSMENT

From the herbivore perspective, no significant difference in seed and fruit set was observed when pollinators were either absent or present in plants exposed to

herbivores (Tukey’s HSD test: $P = 0.80$ for fruit set; $P = 0.83$ for seed set; Fig. 2). Similarly, when herbivores were excluded, seed and fruit set were not reduced by the absence of pollinators ($P = 0.12$ for fruit set; $P = 0.20$ for seed set; Fig. 2).

Table 3. Summary of analysis of variance testing the effects of herbivores and pollinators on fruits and seeds per plant on *Aristolochia chilensis*

Source	d.f.	MS	F
Fruits per plant:			
Herbivores	1	0.150	0.926
Pollinators	1	0.817	5.044*
Herbivores × Pollinators	1	0.150	0.926
Error	56	0.162	
Seeds per plant:			
Herbivores	1	756.2	0.657
Pollinators	1	4628.8	4.023*
Herbivores × Pollinators	1	756.2	0.657
Error	56	1150.5	

Analyses were performed by randomizing the original data set 10 000 times.

* $P < 0.05$.

d.f., degrees of freedom.

From the pollinator perspective, plants excluded from pollinators did not set fruits or seeds regardless of whether they were exposed to herbivores or not ($P = 1.00$ for fruit and seed sets; Fig. 2), whereas neither fruit nor seed sets were reduced by herbivores in the presence of pollinators ($P = 0.53$ for fruit set; $P = 0.66$ for seed set; Fig. 2).

However, taking into account the whole effect of herbivores and pollinators, only pollinators had a significant impact on the female reproductive success of *A. chilensis* (Table 3). Furthermore, there was no statistical interaction between herbivores and pollinators (i.e. there was an additive effect on fitness; Table 3). The power of the interaction was $0.10 < 1 - \beta < 0.20$ for both fruit and seed sets, therefore indicating that a much larger population size is required to disclose a significant interaction between herbivores and pollinators.

DISCUSSION

According to Herrera *et al.* (2002) and Gómez (2005), non-additivity in the effect of pollinators and herbivores is expected to be frequent in systems where herbivores cause copious flower and fruit losses due in part to large floral and fruit crops attracting more herbivores. However, although our results showed that *B. p. archidamas* herbivory had a significant effect on foliar removal on *A. chilensis*, there was no effect on fruit and seed production. This result is surprising because previous evidence highlights the importance of herbivores of the *Battus* genus in modulating the reproductive success of *Aristolochia* plants. Rausher & Feeny (1980) reported a negative effect of *Battus phile-*

nor on the reproductive success of *Aristolochia reticulata* regardless of whether it grows at low or high density. This negative effect was even more intense when interspecific competition for limiting resources occurred (Fowler & Rausher, 1985).

Although herbivores did not affect the fitness of *A. chilensis*, pollinators did have a significant effect on reproductive success by increasing seed set. This result is in agreement with other species of the *Aristolochia* genus, which have been shown to be pollinator-limited for seed set (Sakai, 2002). Furthermore, the number of floral visitors was very low in *A. chilensis* compared with the tropical plant *Aristolochia grandiflora* because the latter presented as many as hundreds of insects inside the flowers at different stages of maturity (Burgess *et al.*, 2004). In *A. grandiflora*, 454 insects excluding larvae per flower were found at the pistillate stage (Burgess *et al.*, 2004), in contrast with 0.4 insects per flower found at the same stage of *A. chilensis*. Certainly, the very low number of floral visitors to *A. chilensis*, particularly of the Asillidae *Tillobroma* sp., which was the only insect observed carrying pollen, accounted for the very low amounts of fruits and seeds produced by plants exposed to pollinators.

Perhaps, the most revealing result of our study was that *A. chilensis* showed an additive effect of herbivores and pollinators on seed production, indicating that the selection pressures exerted by herbivores and pollinators are not correlated. Although this result might be considered a statistical artefact due to the low power of the interaction in the ANOVA, it is worthwhile highlighting that we worked with nearly all plants growing in the study site, and therefore a lack of statistical significance can be attributable to weak selection rather than an insufficient sample size (for a general example of natural selection, and sample and population sizes, see Medel, Botto-Mahan & Kalin-Arroyo, 2003). Consequently, it may be confidently proposed that plant features linked to herbivores and pollinators were not selected correlatedly by both types of plant animal-interactors.

The additive effect of herbivores and pollinators on seed production is contrary to other reports showing that pollinators and herbivores usually exert their selective pressures in a more complex ecological scenario, where herbivores may modulate or even cancel the effects of pollinators (Herrera, 2000; Ehrlén *et al.*, 2002; Herrera *et al.*, 2002; Gómez, 2005; Valdivia & Niemeyer, 2005). The results of the present study may be explained by the fact that plants producing very few seeds, as a result of a decreased pollination service, may reinvest resources from vegetative tissues towards effectively pollinated flowers to insure reproductive success (Zimmerman & Pyke, 1988). Because deceit-pollinated plants such as *A. chilensis* are

restricted for seed production by pollinator activity rather than by environmental resources (Primack & Stacy, 1998; Johnson *et al.*, 2003), there may be very few physiological restrictions that impair reallocations of resources within plants under herbivory.

The present study indicates that plants limited by pollinators for seed production may face the additive effects of mutualists and antagonists on reproductive success. This finding is in accordance with studies by Herrera *et al.* (2002) and Gómez (2005) who predicted the generality of non-additive effects (i.e. correlated evolution) exerted by different suites of animals on plants having large flower and fruit displays, but under high pollinator presence. Therefore, it is worthwhile noting that the evolution of herbivore- and pollinator-linked traits exhibited by *A. chilensis* may be representative of other plants exhibiting a high pollinator-limitation for seed set, even though they may be under selection by herbivores.

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REFERENCES

- Brodie ED. 1992.** Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* **46**: 1284–1298.
- Burgess KS, Singfield J, Meléndez D, Kevan PJ. 2004.** Pollination biology of *Aristolochia grandiflora* (Aristolochiaceae) in Veracruz, Mexico. *Annals of the Missouri Botanical Garden* **91**: 346–356.
- Dirzo R, Domínguez C. 1995.** Plant–herbivore interactions in Mesoamerican tropical dry forests. In: Bullock S, Mooney S, Medina E, eds. *Seasonally dry tropical forests*. Cambridge, MA: Cambridge University Press, 304–345.
- Ehrlén J, Käck S, Ågren J. 2002.** Pollen limitation, seed predation and scape length in *Primula farinosa*. *Oikos* **97**: 45–51.
- Fordyce JA. 2001.** The lethal plant defense paradox remains: inducible host-plant aristolochic acids and the growth and defense of the pipevine swallowtail. *Entomologia Experimentalis et Applicata* **100**: 339–346.
- Fordyce JA, Agrawal AA. 2001.** The role of plant trichomes and caterpillar group size on growth and defence of the pipevine swallowtail *Battus philenor*. *Journal of Animal Ecology* **70**: 997–1005.
- Fowler NL, Rausher MD. 1985.** Joint effects of competitors and herbivores on growth and reproduction in *Aristolochia reticulata*. *Ecology* **66**: 1580–1587.
- Gómez JM. 2005.** Non-additive effects of herbivores and pollinators on *Erysimum mediohispanicum* (Cruciferae) fitness. *Oecologia* **143**: 412–418.
- Hajek E, Di Castri F. 1975.** *Bioclimatología de Chile*. Santiago: Dirección de Investigación, Universidad Católica de Chile.
- Hall DW, Brown BV. 1993.** Pollination of *Aristolochia littoralis* (Aristolochiales: Aristolochiaceae) by males of *Megaselia* spp. (Diptera: Phoridae). *Annals of the Entomological Society of America* **86**: 609–613.
- Herrera CM. 2000.** Measuring the effects of pollinators and herbivores: evidence for non-additivity in a perennial herb. *Ecology* **81**: 2170–2176.
- Herrera CM, Medrano M, Rey PJ, Sánchez-Lafuente AM, García MB, Guitián J, Manzaneda AJ. 2002.** Interactions of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualisms- and antagonisms-related traits. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 16823–16828.
- Herrera CM, Pellmyr O. 2002.** *Plant–animal interactions. An evolutionary approach*. Oxford: Blackwell Publishing.
- Huber H. 1993.** Aristolochiaceae. In: Kubitzki K, ed. *The families and genera of vascular plants*, Vol. 2. Berlin: Springer-Verlag, 129–137.
- Johnson SD, Peter CI, Nilsson A, Ågren J. 2003.** Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* **84**: 2919–2927.
- Kirk RE. 1982.** *Experimental design: procedures for the behavioral sciences*. Monterrey, CA: Brooks/Cole.
- Klitzke CF, Brown Jr KS. 2000.** The occurrence of aristolochic acids in neotropical trochilid swallowtails (Lepidoptera: Papilionidae). *Chemoecology* **10**: 99–102.
- Lande R. 1980.** The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* **94**: 203–215.
- Manly BFJ. 1997.** *Randomization, bootstrap, and monte carlo methods in biology*. London: Chapman & Hall.
- Medel R, Botto-Mahan C, Kalin-Arroyo M. 2003.** Pollinator-mediated selection on the nectar guide phenotype in the Andean monkey flower, *Mimulus luteus*. *Ecology* **84**: 1721–1732.
- Papaj DR, Feeny P, Sachdevgupta K, Rosenberry L. 1992.** D-(+)-Pinitol, an ovoposition stimulant for the pipevine swallowtail butterfly, *Battus philenor*. *Journal of Chemical Ecology* **18**: 799–815.
- Pellmyr O. 2002.** Pollination by animals. In: Herrera CO, Pellmyr O, eds. *Plant–animal interactions. An evolutionary approach*. Oxford: Blackwell Publishing, 157–184.
- Peña LE, Ugarte AJ. 1996.** *Las Mariposas de Chile*. Santiago: Editorial Universitaria.
- Primack R, Stacy E. 1998.** Costs of reproduction in the pink lady's slipper orchid (*Cypripedium acaule*); an eleven year experimental study. *American Journal of Botany* **85**: 1672–1679.
- Rausher MD, Feeny P. 1980.** Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* **61**: 905–917.
- Ruiz E. 2001.** *Aristolochiaceae*. In: Marticorena M, Rodríguez

- R, eds. *Flora de Chile*, Vol. 2. Concepción: Universidad de Concepción, 33–34.
- Sakai S. 2002.** *Aristolochia* spp. (Aristolochiaceae) pollinated by flies breeding on decomposing flowers in Panama. *American Journal of Botany* **89**: 527–534.
- Sime KR, Feeny P, Haribal MM. 2000.** Sequestration of aristolochic acids by the pipevine swallowtail, *Battus philenor* (L.): evidence and ecological implications. *Chemoecology* **10**: 169–178.
- Valdivia CE, Niemeyer HM. 2005.** Reduced maternal fecundity of the high-Andean perennial herb *Alstroemeria umbellata* (Alstroemeriaceae) by aphid herbivory. *New Zealand Journal of Ecology* **29**: 321–324.
- Zamora R. 2000.** Functional equivalence in plant–animal interactions: ecological and evolutionary consequences. *Oikos* **88**: 442–447.
- Zimmerman M, Pyke GH. 1988.** Reproduction in *Polemonium*: assessing the factors limiting seed set. *American Naturalist* **131**: 723–738.