

**COMPLEX IMPLICATIONS AROUND A SIMPLE TRAIT: ECOLOGICAL
CONTEXT DETERMINES THE FECUNDITY EFFECTS OF COROLLA
MARCESCENCE¹**

CARLOS M. HERRERA²

Department of Evolutionary Ecology, Estación Biológica de Doñana, CSIC, Avenida Américo Vespucio s/n 41092 Sevilla, Spain

- *Premise of the Study:* Post-anthesis functionality of persistent perianth parts has rarely been investigated, but available evidence suggests that perianth persistence may not always have an adaptive value. Given the high occurrence of the trait, that it may sometimes be maladaptive is an intriguing possibility and deserves exploration. This paper tests the hypothesis that the fitness value of corolla persistence after anthesis depends on ecological context, specifically the abundance of fruit predators and pollinators.
- *Methods:* The study was conducted on *Narcissus longispathus*, a species in which corolla marcescence is apparently maladaptive because withered corollas provide a shelter for fruit-predatory lepidopteran larvae. By experimentally manipulating corolla persistence, presence of fruit predators, and pollination, I tested whether variation in ecological scenario led to concomitant variation in the sign and magnitude of the effects of corolla marcescence on fecundity.
- *Key Results:* Persistent corollas were detrimental to fecundity when plants were exposed to larvae, but not when larvae were excluded. Pollination and herbivory had nonadditive effects on the fecundity consequences of corolla marcescence, the strongest detrimental effects of corolla persistence occurring for the “exposed to larvae + supplementary pollination” treatment combination.
- *Conclusions:* The hypothesis that ecological context is a major determinant of the fitness value of corolla marcescence was supported. In *N. longispathus*, corolla marcescence will be a maladaptive trait in situations in which pollinators and fruit predators are simultaneously abundant, but will be a neutral character in the absence of fruit predators, irrespective of pollinator service.

Key words: corolla marcescence; ecological context; fruit predation; *Narcissus longispathus*; nonadditive effects; pollen limitation; *Trigonophora flammea*.

In many flowering plants, parts of the perianth persist beyond the completion of anthesis. The protracted presence of structures whose function is to contribute to the success of flowers suggests that, after anthesis, they may be co-opted for novel functions unrelated to pollination. In some instances, the post-anthesis functionality of the perianth is quite apparent, as in species in which spiny or plumose calices aid in seed dispersal (van der Pijl, 1982). In other cases, however, the postfloral function of persistent perianth is far less obvious. Consider, for example, the inflated calyx syndrome of certain Solanaceae (Hu and Saedler, 2007) or the withered corollas that remain attached to the developing fruits of many plants (“marcescent corollas”; Little and Jones, 1980). The postanthesis functionality of persistent perianth parts has rarely been investigated, and the few studies conducted thus far have mostly focused on the function of the calyx (Yonemori et al., 1995; Nakano et al., 1997; Sisterson and Gould, 1999; Salopek-Sondi et al., 2000, 2002; Herrera, 2005); a recent study of mine (Herrera, 2010) is apparently the

first to investigate the functionality of marcescent corollas. These studies have not always confirmed an immediate utility or presumable adaptive value of persistent perianth parts. In some cases, persistent calices have beneficial effects by contributing photosynthates to developing fruits and seeds (Salopek-Sondi et al., 2000, 2002; Herrera, 2005), but in others the calyx appears to confer protection from parasitoids to the herbivorous larvae that feed on the enclosed fruit, a function that can hardly be interpreted as enhancing plant fitness (Sisterson and Gould, 1999). I have reported similarly contrasting results: persistent corollas had beneficial effects on fecundity in one species but were detrimental in another (Herrera, 2010). The evidence available, albeit limited, suggests that perianth persistence may sometimes confer detrimental effects on plant fitness. Given the widespread occurrence of perianth persistence across angiosperms, that the trait may be maladaptive in some of the taxa in which it occurs is an intriguing possibility and deserves further study.

Two mutually nonexclusive hypotheses can be advanced to explain instances of apparently maladaptive perianth persistence, which for convenience can be termed the “developmental constraint” and “ecological context” hypotheses. Under the developmental constraint hypothesis, postanthesis persistence of perianth parts is the consequence of abscission being limited or impeded by some physiological and/or anatomical characteristics of the floral verticils involved, such as the lack of an abscission layer. The observations that postanthesis petal abscission tends to be a phylogenetically conserved trait (van Doorn, 2001) and that corolla marcescence is sometimes used

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²Author for correspondence (e-mail: herrera@ebd.csic.es)

as a diagnostic character to discriminate among taxonomic entities above the species level (e.g., Watson, 1964; Panero et al., 1999; Gillespie and Kron, 2010), are consistent with this hypothesis. Under the ecological context hypothesis, the adaptive value of perianth persistence is variable and depends on relevant features of the ecological scenario. For example, marcescent corollas that protect developing seeds from invertebrate seed predators might appear as neutral or maladaptive when such predators are absent (Herrera, 2010). Conversely, marcescent corollas that seems maladaptive because they provide a shelter for invertebrate herbivores might be neutral, or even enhance fitness, when herbivores are absent. In these examples, variation among conspecific populations in the abundance of fruit or seed predators would lead to shifts in the fitness consequences of corolla marcescence along the hypothesized adaptive–neutral–maladaptive continuum.

Here, I present the results of an experimental test of the ecological context hypothesis for explaining an instance of apparently maladaptive corolla marcescence. The study was conducted on a natural population of the wild daffodil *Narcissus longispathus*, a species whose withered, persistent corollas provide a shelter for fruit-predatory lepidopteran larvae (*Trigonophora flammea*) after anthesis. By experimentally manipulating corolla persistence and the presence of fruit predators according to a factorial design, it was possible to test for variation of the fecundity effects of corolla marcescence in ecological scenarios that differed in the abundance of fruit predators. An increasing number of studies have shown that, within plant populations, variation in the impact of postanthesis seed and fruit predators on fecundity depends on prior pollination service. These herbivores may preferentially select fruits that originated from flowers that had enjoyed improved pollinator service, leading to nonadditive effects of herbivory and pollination on fecundity (Herrera, 2000; Herrera et al., 2002; Cariveau et al., 2004; Gómez, 2005). Through this indirect mechanism, the fitness value of corolla marcescence could eventually become contingent not only on the presence of fruit predators, but also on the pollinating environment via the latter's influence on fruit predation risk. To broaden the ecological space over which the ecological context hypothesis was tested, pollination intensity was incorporated as another factor in the experimental design of the present study. In addition to revealing the complexities around a simple yet underexplored plant trait, the results will also contribute to the broader issue of the significance of ecological context as a determinant of the fitness value of plant reproductive features (Ashman and Morgan, 2004; Ashman, 2006; Alonso and Herrera, 2008) and, more generally, illustrate the importance of considering ecological context when interpreting the results of manipulative field experiments.

MATERIALS AND METHODS

Natural history of study organisms—*Narcissus longispathus* Pugsley (Amaryllidaceae) is a perennial herb endemic to southeastern Spain. Leaves and floral scapes start to emerge from underground bulbs in late February. Each bulb produces one scape, which generally bears a single hermaphroditic, long-lived flower (mean duration = 16 d) with a pale yellow, tubular perianth about 45 mm long and 25 mm wide at its opening (Fig. 1A). Flowering occurs from late February to late April, a period characterized by cool, rainy weather with frequent snowfalls that often limits the activity of the main pollinators (solitary bees). Flowers are self-compatible, but spontaneous selfing occurs infrequently (<2% of flowers within pollinator exclusions set fruit). After flowering, the large corolla withers and remains firmly attached to the developing ovary (Fig. 1B) until it is shed in early June, shortly before fruit dehiscence and seed release.

Details on the pollination ecology, mating system, and population genetics of *N. longispathus* can be found in Herrera (1995), Barrett et al. (2004), Medrano et al. (2005), and Medrano and Herrera (2008).

Flowers and developing fruits of *N. longispathus* are often eaten by larvae of *Trigonophora flammea* (Lepidoptera, Noctuidae). The small (4–6 mm long), young larva climbs the floral scape shortly after anthesis and feeds on parts of the corolla and, less often, the anthers. After floral withering, the larva stays inside the shriveled corolla, feeding first on the remains of the style and stamens and then, after boring into the ovary near the base of the style, on the developing seeds. Larvae continue feeding on developing fruits until pupation in late May, shortly before fruit ripening. Most or all seeds in a damaged fruit may eventually be destroyed. The foraging behavior of *T. flammea* larvae varies with age (Alonso and Herrera, 1996). Up to the 4th instar the larvae stay permanently inside the corollas or fruits, feeding on the same plant for many days. After entering the 5th instar, the 15–20 mm-long larvae remain in the litter beneath the plants during the daytime, and climb to the developing fruit every night to feed. They do not usually feed on the same fruit on consecutive nights, and I never observed more than one *T. flammea* larva at a time per flower or fruit, or the larvae of other lepidopteran species.

Study area and methods—The study was conducted during February through June, 1988–1990, on a large *N. longispathus* population located at 1160 m elevation in Fuente del Perro, near the village of Vadillo-Castril, in the Parque Natural de Cazorla-Segura-Las Villas (Jaén province, southeastern Spain). Each study year, scapes bearing flower buds, each presumably corresponding to a different plant, were individually marked at the beginning of the flowering season ($n = 241, 190,$ and 271 in 1988, 1989, and 1990, respectively) and then inspected every 7–15 d until fruits ripened in early June. On each occasion, the occurrence of damage by *T. flammea* larvae was recorded for each flower or fruit. Fruits were collected shortly before ripening, and the number of mature seeds were counted and weighted. In 1989 and 1990, presence of *T. flammea* larvae in flowers or fruits during inspections was also recorded. To evaluate pollen limitation, a subsample of marked flowers ($n = 176, 53,$ and 105 in 1988, 1989, and 1990, respectively) was subjected every year to additional pollination by rubbing a newly dehiscid anther from a different flower (≥ 5 m away) against the stigma. The rest of the flowers ($n = 65, 137,$ and 166 in 1988, 1989, and 1990, respectively) were exposed to natural pollination and served as the control.

The hypothesized effect of corolla marcescence on reproductive performance via its effect on fruit predation by larvae, and its possible interaction with pollination, were tested on the plants marked in 1989 ($n = 190$) by means of a fully crossed factorial experiment involving three two-level factors (capitalized to avoid ambiguity): Corolla Persistence (control vs. corolla removed after flowering, $n = 115$ and 75 flowers, respectively), Pollination Intensity (control vs. supplementary pollination, $n = 137$ and 53 flowers, respectively), and Fruit Predation (control vs. larvae excluded, $n = 115$ and 75 flowers, respectively). Marked flowers (each corresponding to a different plant) were randomly assigned to one of the eight treatment-level combinations. Corolla Persistence was modified by removing the corolla in a subset of marked flowers shortly after flower withering, while the rest were left unmanipulated (i.e., the dry corolla remained attached to the developing fruit as in Fig. 1B). Pollination Intensity was modified by adding supplementary pollen to some flowers while leaving others exposed to natural pollination, as described above. Finally, variation in Fruit Predation was achieved by coating the central portion of some scapes with Rat-Stop (a persistent glue similar to the well-known brand Tangle-foot), which prevented larvae from accessing them, while other scapes were left untreated. The Rat-Stop application was done immediately after corolla withering, so any treatment effect will reflect the magnitude of cumulative larval predation on fruits during the entire ≈ 2 -mo period of fruit development.

Data analysis—Statistical analyses were performed with the SAS package. When response variables were proportions (e.g., probability of flowers setting fruit, frequency of fruit damage), they were modeled as binomial processes using logits, and the significance of factor effects was tested using the GLMIX procedure (SAS Institute, 2006). For continuous response variables (e.g., seed number, seed mass), factor effects were tested by fitting appropriate linear models to the data using the MIXED procedure and restricted maximum-likelihood estimation. The LSMEANS statement was used to obtain model-adjusted least-squares means of response variables for different treatment combinations and their standard errors and confidence intervals (CI), and these are the values given in the Results. All means are reported ± 1 SE. The SLICE option of the LSMEANS statement was used for testing the significance of “simple main effects”, that is, the effects of a given factor at different treatment



Fig. 1. (A) Flower and (B) developing fruit of *Narcissus longispathus*, the latter showing the persistent corolla characteristic of the species. The fruit was photographed in late April, about midway between the end of anthesis and fruit ripening.

levels, or treatment-level combinations, of the other factors (for details see, e.g., Pedhazur, 1982:362–365; Schabenberger et al., 2000).

RESULTS

Pollination deficit—Seed production by *N. longispathus* flowers was consistently pollen-limited at the study locale during the course of the study. Considering only flowers and fruits that were not damaged by larvae, supplementary pollination significantly enhanced both the probability of individual flowers setting fruit (hereafter “fruit set”; estimated as the proportion of flowers in a given treatment that set fruit) and the mean number and mass of seeds per fruit (Table 1). Pollen limitation occurred consistently across years, as denoted by statistical nonsignificance of all the treatment \times year interaction effects

(Table 1). For all years combined, fruit set was increased from 77.6% in flowers exposed to natural pollination to 86.5% in flowers with extra pollen added. Furthermore, for all years combined, additional pollination increased the mean number of seeds per undamaged fruit from 16.8 ± 1.2 to 21.8 ± 1.4 , and the mass of seeds per fruit from 154 ± 11 mg to 202 ± 13 mg.

Fruit predation by *Trigonophora larvae*—Fruit-feeding by *T. flammae* larvae had considerable impact on the reproduction of *N. longispathus*. Fruit damage was frequent, and damaged fruits ripened far fewer seeds than undamaged ones. Frequency of damage to developing fruits varied among years, but it was high in all cases: 27.0% in 1988, 41.7% in 1989, and 35.8% in 1990. Fruit predation by the larvae reduced the mean number of mature seeds produced per fruit by 50–75%, from 11.5 ± 1.1 to 5.3 ± 1.9 seeds/fruit in 1988 ($F_{1,173} = 7.67$, $P = 0.006$), from 22.1 ± 1.3

TABLE 1. Significance of effects of Pollination Intensity (supplementary pollination vs. control), study year (1988, 1989, and 1990), and their interaction, on components of seed production in *Narcissus longispathus*. Only undamaged flowers and fruits were included in these analyses. Statistically significant *P* values are in bold.

Dependent variable	Effect	df	χ^2 or <i>F</i>	<i>P</i>
Fruit set ^a	Pollination Intensity (P)	1	11.01	0.0009
	Year (Y)	2	16.85	0.0002
	P × Y	2	2.91	0.23
Number of seeds per fruit ^b	Pollination Intensity	1, 365	11.91	0.0006
	Year	2, 365	28.58	<0.0001
	P × Y	1, 365	1.54	0.21
Seed mass per fruit ^b	Pollination Intensity	1, 359	11.65	0.0007
	Year	2, 359	24.28	<0.0001
	P × Y	1, 359	1.29	0.28

^a Probability of individual flowers eventually maturing a fruit, modeled as a binomial process. Significance of effects tested by fitting a logistic regression model.

^b Significance of effects tested by fitting a linear model. Seed number and seed mass log-transformed for the analyses.

to 11.0 ± 2.1 seeds/fruit in 1989 ($F_{1,188} = 19.95, P < 0.0001$), and from 24.2 ± 1.6 to 5.3 ± 1.9 seeds/fruit in 1990 ($F_{1,180} = 57.17, P < 0.0001$).

The incidence of *T. flammaea* on developing fruits was contingent on pollination regime. The mean estimated probability of fruit damage (pfd) was significantly higher ($F_{1,621} = 4.25, P = 0.039$) among developing fruits from flowers that had received supplementary pollination (pfd = 0.381, 95% CI = 0.313–0.454) than among those from naturally pollinated flowers (pfd = 0.283, 95% CI = 0.227–0.347; data for the 3 yr combined). This effect, however, might be confounded with fruit set, since flowers that receive supplementary pollination set fruit more often than naturally pollinated ones and, thus, one would expect a higher incidence of damage among fruits that originated from hand-pollinated flowers. To account for this possibility, one additional analysis was conducted using only data for flowers that eventually matured at least one seed. In this subsample, the mean estimated probability of fruit damage was also significantly higher ($F_{1,266} = 3.96, P = 0.047$) among fruits from flowers that received supplementary pollination (pfd = 0.307, 95% CI = 0.224–0.403) than among those from naturally pollinated flowers (pfd = 0.157, 95% CI = 0.082–0.281; data for the 3 yr combined). Thus, the higher incidence of fruit predators on fruits from pollen-supplemented flowers was not an artifact of their higher fruit set.

Larva-bearing corollas and fruit predation—In both 1989 and 1990, the presence of a young *T. flammaea* larva inside the corolla of an open or withered flower on at least one occasion was significantly associated with increased probability of subsequent damage to the fruit that eventually developed from that flower. The frequency of damage to fruits originating from flowers where larvae had and had not been observed were, respectively, 60.6% and 34.1% in 1989, and 66.7% and 32.8% in 1990 ($P = 0.012$ and 0.0015 for 1989 and 1990, respectively; two-tailed Fisher’s exact probability tests). Furthermore, flowers where larvae had been observed at least once eventually produced about half as many seeds as those where larvae were never seen (1989: 10.3 ± 2.9 vs. 19.8 ± 1.8 seeds/flower; $F_{1,113} = 7.56, P = 0.007$; 1990: 8.4 ± 4.1 vs. 17.3 ± 1.5 seeds/flower; $F_{1,180} = 4.15, P = 0.04$). These results demonstrate that the early

presence of young larvae inside open flowers or withered corollas was a major determinant of subsequent predation on the developing fruits as the season progressed.

Corolla persistence, fruit predation, and pollination—The factorial experiment conducted in 1989 was analyzed by fitting a model including the three main effects (Pollination Intensity, Fruit Predation, Corolla Persistence) and all two- and three-way interactions, with the number of seeds produced per flower (log-transformed) as the response variable. The Fruit Predation and Corolla Persistence main effects were statistically significant (Table 2). Artificial removal of the corolla increased seed production from 18.4 ± 2.8 to 24.1 ± 3.0 seeds/flower, and post-floral exclusion of lepidopteran larvae likewise increased seed production from 19.1 ± 2.9 to 23.5 ± 3.0 seeds/flower. Nevertheless, the two-way interaction between these factors was statistically significant (Table 2), which prompts consideration of the simple main effects involved (Fig. 2). Corolla removal had a highly significant, positive effect on seed production when developing fruits were exposed to larvae ($F_{1,163} = 9.50, P = 0.0024$), but it was inconsequential when larvae were artificially excluded ($F_{1,163} < 0.01, P = 0.96$). Furthermore, larval exclusion significantly enhanced seed production for flowers that retained the persistent corolla (control), but had no effect in flowers that had their corollas removed (Fig. 2). These results, in addition to demonstrating nonadditivity of the effects of pollination and fruit predation on seed production, also clearly denote a detrimental role of the persistent corolla via increased fruit predation.

The three-way interaction was nearly significant (Table 2), which suggested that one or more two-way interactions were not consistent across levels of the other factor. One of these possibilities is illustrated in Fig. 3. Consideration of two-way simple main effects revealed that the Corolla Persistence × Pollination Intensity interaction was statistically significant for flowers exposed to larvae (Fig. 3, top row; $F_{3,163} = 3.32, P = 0.021$), but not for those where larvae had been excluded (Fig. 3, bottom row; $F_{3,163} = 0.78, P = 0.51$). The relationship between seed production and Corolla Persistence depended on the treatment-level combination of Fruit Predation and Pollination Intensity. Persistent corollas were detrimental to seed production when developing fruits were exposed to larvae (Fig. 3, top row), but not when larvae were excluded (Fig. 3, bottom row). Furthermore, within the first group, the magnitude of the negative effect on fecundity of persistent corollas was most severe for the “supplementary pollination + exposed to larvae” treatment combination (Fig. 3, top right panel).

TABLE 2. Significance of effects of Corolla Persistence (corolla removed after flowering vs. control), Pollination Intensity (supplementary pollination vs. control), Fruit Predation (larval herbivores excluded after flowering vs. control), and their two- and three-way interactions, on the number of seeds matured per flower (log-transformed). Statistically significant and near-significant *P* values are in bold.

Effect	$F_{1,163}$	<i>P</i>
Corolla Persistence (C)	4.47	0.036
Pollination Intensity (P)	0.69	0.41
Fruit Predation (FP)	11.81	0.007
C × P	0.01	0.96
C × FP	4.05	0.045
P × FP	0.01	0.96
C × P × FP	3.29	0.071

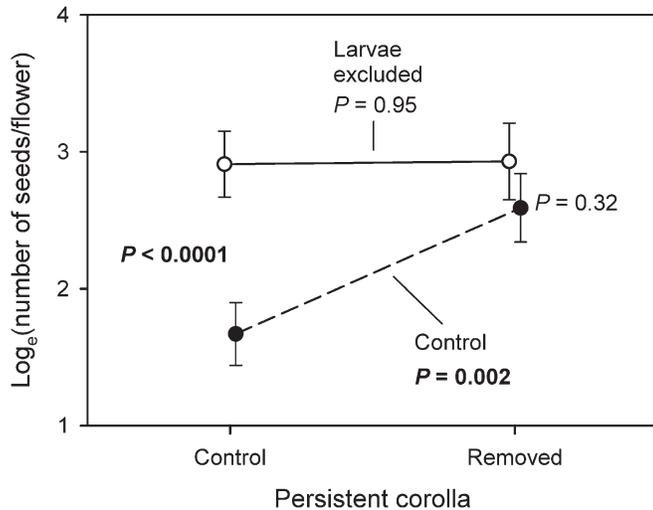


Fig. 2. Interaction graph for the two-way interaction effect of Corolla Persistence and Fruit Predation on seed production by *Narcissus longispathus* flowers, with the two levels of Pollination Intensity combined. Dots are model-adjusted, least-squares cell means, and vertical segments extend over ± 1 SE. P values shown correspond to tests of significance for the four simple main effects involved.

DISCUSSION

Ecological context—loosely defined as the composition and abundance of organisms and resources with which a species interacts—varies in time and space, and such variation may influence both the outcome of interspecific interactions and the shape of selection functions on traits (Thompson, 1988; Ashman and Morgan, 2004; Ashman, 2006; Herrera et al., 2006). By experimentally mimicking a variety of ecological scenarios that differ in herbivory and pollination levels, the present study has shown that the fecundity effects of corolla marcescence are strongly context-dependent in *N. longispathus*, a finding that supports the ecological context hypothesis for the persistence of that apparently maladaptive trait in this species. Results for the subset of plants with unmanipulated corollas also provided evidence that pollination service and fruit predation can have nonadditive effects on seed production, an aspect that remains relatively unexplored despite its potential ecological and evolutionary significance (Strauss and Irwin, 2004).

Nonadditive effects of pollination and fruit predation—When acting sequentially, pollination and herbivory (including fruit and seed predation) may influence each other through indirect effects, leading to nonadditive effects on fecundity (Strauss and Irwin, 2004; Pohl et al., 2006). In the situation studied more often, in which herbivory is the antecedent and pollination the subsequent interaction, it has been suggested that indirect effects of herbivory on pollination should be most likely when (1) seed production is pollen-limited, given that additional pollen will only improve seed production in a pollen-limited plant, and (2) pollinators are able to discriminate between character states of plastic floral or plant characters susceptible to modification by the effects of herbivory (Mothershead and Marquis, 2000). A similar prediction has been advanced for the less-studied situation in which pollination is the antecedent and herbivory the subsequent interaction (Herrera et al., 2002). In this case, indirect effects of pollination on herbivory should be particularly

frequent when seed production is pollen-limited, fruit-feeding herbivores cause extensive fruit losses, and they are preferentially attracted to plants that have more numerous or better (e.g., larger, with more seeds) fruits because they had been favored by pollinators. This prediction is supported by previous investigations using factorial experimental designs (Herrera, 2000; Herrera et al., 2002; Gómez, 2005; but see Valdivia and Niemeyer, 2007), and also by the results of this study on *N. longispathus*. In the study population, seed production was pollen-limited, the probability of larval damage was highest for fruits originating from flowers that received supplementary hand-pollination and, as predicted, the factorial experiment revealed nonadditivity of pollination and herbivory on seed production.

Among *N. longispathus* plants that retained the withered corolla through fruit development (i.e., the natural condition), pollination and fruit predation had nonadditive effects on seed production. Plants that received supplementary pollination experienced proportionally greater losses to fruit predators than those exposed to natural pollination, which eventually offset any seed-production advantage derived from increased pollination. This effect arose from the greater incidence of larvae on fruits from flowers that received extra pollination. The proximate mechanism underlying pollination-dependent fruit-predation risk cannot be ascertained at present, although it is probably related to the foraging behavior of larvae. The latter may discriminate among available fruits and favor those that originated from hand-pollinated flowers or, if unable to discriminate *a priori* among fruit types, may stay longer and feed more thoroughly on fruits from supplementary pollination in response to their greater seed content.

Ecological context and corolla marcescence—In *N. longispathus*, the marcescent corolla probably provides protection to the young larvae of *T. flammea*, as found in other species (Sisterson and Gould, 1999), but this can only be conjectured at present. Regardless of the possible benefits to fruit predators, corolla marcescence was consequential for seed production in *N. longispathus*, and the sign and magnitude of the effect depended on herbivory and pollination treatment-level combinations, as predicted by the ecological context hypothesis (see also Herrera, 2010). Persistent corollas were detrimental when scapes were exposed to larvae, but not when larvae were excluded. In addition, among plants exposed to larvae, the magnitude of the detrimental effect was greater among those that received extra pollen. Strong, statistically significant detrimental effects of corolla persistence occurred only for the “supplementary pollination + exposed to larvae” treatment combination. The effect of corolla persistence was also detrimental, although not statistically significant, for the combination “natural pollination + larvae excluded”. These seem among the first results demonstrating that the fecundity effects of a simple plant trait, and thus presumably its fitness value, may depend on the combination of pollination and fruit-predation levels.

Factorial experiments testing for the effect of different interactors on the fitness consequences of a given plant trait may be unfeasible in the field or lead to biologically unrealistic treatment-level combinations. In the present study, however, the factorial design involving Pollination Intensity and Fruit Predation generated reasonably realistic treatment-level combinations. Exclusion of lepidopteran larvae mimics the conditions that prevail in high-elevation *N. longispathus* populations where fruit-feeding lepidopteran larvae very rarely occur (C. M. Herrera, personal observation), whereas the additional pollination treatment imitates

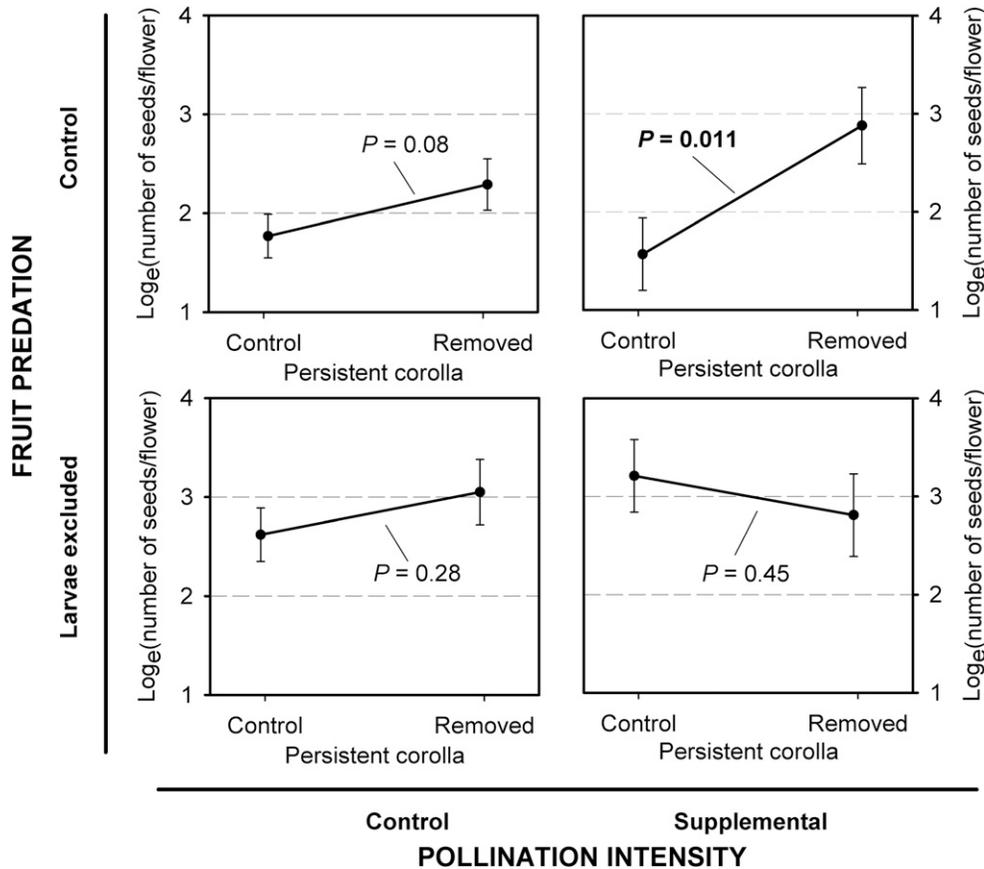


Fig. 3. One of the three possible representations of the three-way interaction effect of Pollination Intensity, Fruit Predation, and Corolla Persistence on seed production by *Narcissus longispatus* flowers. Dots are model-adjusted, least-squares cell means, and vertical segments extend over ± 1 SE. *P* values shown correspond to tests of significance for simple main effects involving fecundity comparisons between Pollination Intensity treatment levels.

conditions in certain south-facing, well-insolated populations where pollinators are abundant nearly every year and pollen is generally not limiting (Herrera, 1995: table 1). It can thus be assumed that the four treatment combinations of pollination and fruit-predation intensities occur naturally in one or another *N. longispatus* population. The results of my study can therefore be interpreted as implying that, in *N. longispatus*, corolla marcescence will appear as a maladaptive trait detrimental to fitness in lowland sites where pollinators and fruit predators are simultaneously abundant, but it will seem a neutral character unrelated to fitness in situations of absence of fruit predators such as highland localities, irrespective of variation in pollinator service.

Although the results of this study clearly support the ecological context hypothesis for explaining apparently maladaptive corolla marcescence in *N. longispatus*, the possible significance of the developmental constraint hypothesis should also be considered. Persistence of the corolla is an invariant character in *N. longispatus*; I have never observed any plant shedding the corolla shortly after flowering over many years of investigations in all known populations of this species (C. M. Herrera personal observation). Furthermore, constancy of the character applies also to other species in the genus *Narcissus* (e.g., *N. cuatrecasasi*, *N. hedraeanthus*, *N. bugei*), as well as to species in other genera within Amaryllidaceae that have marcescent corollas (e.g., *Crinum*, *Pancratium*, *Amaryllis*; C. M. Herrera personal observation). Constancy of this floral trait across a broad group of species that

otherwise exhibits exceptional floral diversity (Graham and Barrett, 2004) might reflect some anatomical constraint(s) limiting the evolution of nonmarcescent corollas.

Concluding remarks: organ marcescence in plants—The possible adaptive value of marcescence, the retention of dead plant organs that normally are shed, is poorly understood. Leaf marcescence is frequent in temperate deciduous trees and alpine plants, and limited experiments suggest that it can reduce the impact of herbivores and water and temperature stress on plants (Smith, 1979; Svendsen, 2001; but see Karban, 2007). Marcescent corollas occur in many flowering plant families, and corolla marcescence has been used as a diagnostic character to discriminate among taxonomic entities at the species level (e.g., Albert and Struwe, 1997) and above (e.g., Watson, 1964; Panero et al., 1999; Gillespie and Kron, 2010). The results presented here, along with those of Herrera (2010), show that marcescent corollas, like marcescent leaves, are sometimes functional structures with effects on plant fitness and should not be dismissed *a priori* as biologically irrelevant leftovers from past functions. Retaining dead, physiologically inert structures may under some circumstances be an effective means for plants to perform certain fitness-enhancing functions without incurring additional energy and nutrient costs, such as the protective role for developing seeds played by the marcescent corollas of the summer-flowering shrub *Lavandula latifolia* (Herrera, 2010). Costlessness might also favor the long-term persistence

over evolutionary time of predominantly neutral, leftover structures, even though in some particular ecological scenarios they might be occasionally exploited by antagonists, as illustrated here for the marcescent corollas of *N. longispathus* and also by Karban (2007) for *Quercus lobata*, where marcescent leaves increased attack by cynipid gall makers the following spring. I hypothesize that, in the long run, the fate of withered structures (i.e., shedding vs. marcescence) will depend on an interplay between the potential anatomical or physiological constraints limiting abscission and the predominant sign of the fitness effect of marcescence over a species' range of ecological scenarios. The simplicity of the experimental layout required to test for the fitness consequences of variation in marcescence should help to achieve a better understanding of the ecological and evolutionary correlates of this widespread but underexplored trait, while at the same time providing a workable study system for testing hypotheses on the relative roles of developmental constraints and ecological factors as determinants of plant traits.

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