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Original article

Flower size and longevity influence florivory in the large-flowered shrub *Cistus ladanifer*

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ABSTRACT

Plants with larger and longer-lived flowers receive more pollinator visits and increase reproductive success, though may also suffer more from antagonistic interactions with animals. Florivores can reduce fruit and seed production, so selection on flower size, floral longevity and/or number of flowers may thus be determined by the relative effects of both pollinators and florivores. In this study flowers of *Cistus ladanifer*, a large-flowered Mediterranean shrub, were monitored to evaluate the effects of flower size, floral longevity and number of flowers on levels of florivory in four populations. Number of flowers was variable but did not differ among populations. Both flower size and floral longevity of *C. ladanifer* showed broad variation and significantly differed among populations. Overall, 7% of flowers suffered attack by florivores, which were mainly ants picking the stamens and beetles consuming petals and pollen. Within-populations, larger and longer-lived flowers tended to be affected by florivores more frequently. The low overall incidence of florivores and its lack of between-population variation suggest that florivory may not influence intraspecific variation of these floral traits. However, moderate florivory levels on the largest and longest-lived flowers open the possibility of exerting selection towards smaller and shorter-lived flowers in some of the populations studied.

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1. Introduction

Attractiveness to pollinators plays a decisive role in the reproductive ecology of entomophilous plants. The importance of the number of displayed flowers for pollinator visitation rates and fruit production has been broadly reported (Brody and Mitchell, 1997; Thompson, 2001; Harder and Johnson, 2005). Larger flowers have also been associated with higher pollinator attraction and, as a result, an increase in cross-pollination and reproductive success (Galen, 1989; Kudoh and Whigham, 1998; Arista and Ortiz, 2007). In the same way, floral longevity (the length of time that flowers remain open and functional) involves both a greater amount of pollen removal, and higher amount and quality of pollen deposition, on the flower (Primack, 1985; Ashman and Schoen, 1994, 1996). As a consequence, longer-lived flowers may also increase reproductive success.

Despite its benefits, floral attractiveness can also be related with greater plant–animal antagonist interactions. For example, floral herbivores (i.e. florivores) cause damage to open flowers, including damage to bracts, sepals, petals, androecium and/or gynoecium (McCall and Irwin, 2006). Thus, florivores may reduce fruit and seed

production by degrading the attractive properties of flowers for pollinator service or by direct consumption of viable gametes (Schemske and Horvitz, 1988; Krupnick et al., 1999; Irwin, 2006; Cardel and Koptur, 2010). In this way, florivores can exert negative selective pressures on the same floral traits positively selected for pollinators (Galen, 1999; Irwin et al., 2001; Irwin, 2006). There is evidence that florivory increases with increasing components of plant attractiveness to pollinators such as the number of flowers displayed and flower size (Galen, 1999; Mosleh Arany et al., 2009). Longer floral longevity should also increase the risk of florivory, as documented for other antagonistic interactions (e.g., fungal infection: Shykoff et al., 1996; Kaltz and Shykoff, 2001). However, the effects of floral longevity on the incidence of florivory seem to have been only scarcely studied and are not even mentioned in reviews of non-pollinator influences on floral traits (Strauss and Whittall, 2006).

The strength of agents of selection can vary geographically and lead to contrasting selective pressures at different locations (Thompson, 1982, 2005). Several studies have reported that individuals in those populations with a higher incidence of florivores display fewer, smaller flowers (Galen, 1999; Mosleh Arany et al., 2009). Thus, documenting spatial variation in incidence of florivory is important to understand differences in floral display related traits among populations.

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Table 1

Location and ecological data of study populations of *C. ladanifer*. Column of climate shows the annual mean rainfall (mm) and the annual mean temperature (°C) (Ninyerola et al., 2005, $N = 20$ yr).

Study sites	Altitude (m)	Climate	Substrate	Vegetation cover
Monte Valdelatas (40.32°N, 3.41°W)	720	Dry 520 mm, 14 °C	Clay and sand	Dehesa with <i>Quercus ilex</i> and <i>Pinus pinea</i> interspersed in a shrub matrix
La Pedriza (40.44°N, 3.52°W)	940	Subhumid 771 mm, 12 °C	Clay and sand	Patchy scrubland with <i>Q. ilex</i> among boulders and rocks
Vista Real (40.44°N, 3.57°W)	1120	Subhumid 820 mm, 11 °C	Granite and sand	Patchy scrubland with <i>Juniperus oxycedrus</i> among boulders and rocks
Puerto de Canencia (40.50°N, 3.46°W)	1300	Subhumid 865 mm, 9 °C	Granite and sand	Dispersed wooded slope with <i>Pinus sylvestris</i> and <i>Quercus pyrenaica</i>

In this study, we evaluate the effect of three floral attractiveness-related traits (flower size, floral longevity and number of flowers displayed) on incidence of florivory in four populations of *Cistus ladanifer*. We address the following specific questions: (1) Does florivory increase with flower size, floral longevity and number of flowers? (2) Does florivory vary among populations? Given the potential relationship between floral attractiveness and florivory incidence, we expect florivory to be higher both on larger and on longer-lived flowers within-populations, as well as on flowers of showier plants that produce more flowers.

2. Materials and methods

2.1. Species and study area

C. ladanifer (Cistaceae) is a shrub 100–250 cm tall that inhabits acid and dry soils in warm open areas of the western Mediterranean. The flowering period spans March to June and each plant produces white flowers of approximately 7–10 cm in diameter, often exhibiting dark coloured spots at their bases. The flowers are the largest in the family with an average of more than 150 anthers and 1000 ovules, are self-incompatible and secrete some nectar (Herrera, 1992). The pollinators are mainly bees, beetles and flies (Talavera et al., 1993). A predispersal seed predator, the larva of the moth *Cleonymia yvanii* (Noctuidae), attacks very young fruits, where it spends part or all its pre-imaginal development (Serrano et al., 2001; Delgado et al., 2007). Flowers last at least 1 day, with individual plants showing some plasticity for this trait (A.L. Teixido, M. Méndez and F. Valladares, unpublished results).

The study was conducted from March to June of 2009 in a south–north altitudinal gradient from 720 to 1300 m a.s.l. in Madrid province, central Spain (39.53°–41.09° N, 3.03°–4.34° W). A total of four populations were chosen to study florivory (Table 1). All populations had similar orientation (south), slope (0–10°) and tree canopy cover (0–10%).

2.2. Floral traits and florivory incidence

At each population, 10 similarly-sized plants (1.03 ± 0.37 m³, Kruskal–Wallis test, $\chi^2 = 1.432$, $P = 0.698$, $N = 40$) were randomly selected and tagged before the beginning of the flowering in a plot

Table 2

Mean \pm SD flower size (cm), floral longevity (d) and number of flowers of *C. ladanifer*, and florivory incidence (%) on flowers at each population.

Population	Flower size	Floral longevity	Number of flowers	Florivory incidence
Monte Valdelatas	7.00 \pm 1.13	1.38 \pm 0.56	17.31 \pm 8.26	9.77
La Pedriza	8.02 \pm 0.74	1.92 \pm 0.70	19.93 \pm 9.08	9.70
Vista Real	8.12 \pm 0.81	1.21 \pm 0.41	18.57 \pm 11.30	3.68
Puerto de Canencia	8.60 \pm 0.79	1.23 \pm 0.48	19.40 \pm 8.71	4.77
Total	7.95 \pm 0.86	1.44 \pm 0.62	18.82 \pm 10.08	6.94

of 20 \times 20 m. For each plant, presence or absence of a spot on its flowers was recorded. In other species, dark petal spots have been shown to act as visual signals for insect pollinators (Johnson and Midgley, 1997; Van Kleunen et al., 2007; Thomas et al., 2009). Hence, spots might also be visual signals to florivores. During the flowering peak (when all individuals produced more than 10 flowers per day), 63–74 flowers were haphazardly selected and tagged per plant, for a total sample size of 645 flowers in Monte Valdelatas, 701 in La Pedriza, 706 in Vista Real and 671 in Puerto de Canencia (total $N = 2723$). On each plant, the number of open flowers was counted each day. In addition, 5–10 randomly selected flowers were monitored daily to assess floral longevity (number of days open). Flower diameter (cm) was also measured every day that they remained open and then averaged.

Florivory was considered as any type of damage to open flowers (see Introduction). Hence, we included animals that consumed pollen and/or picked the stamens, as well as full flower loss by eating the pedicel. Thus, these animal–flower interactions did not allow effective pollination (Inouye, 1980; McCall and Irwin, 2006). We limited our study of florivory to open flowers, so floral bud attack was not considered. Florivory was scored shortly before floral senescence, usually in the afternoon or the evening.

2.3. Statistical analysis

We tested the effects of population (fixed factor), plant within population (random factor), plant size, presence of spot and floral longevity (fixed factors) on presence of florivores by fitting Generalized Linear Mixed Models (GLMMs). Both flower size and number of flowers were also included as covariates. We assumed a binomial error distribution with a logit canonical link function. We used the restricted maximum likelihood (REML) and, because our data were unbalanced, we used Satterthwaite's method to determine the approximate denominator degrees of freedom. Due

Table 3

Generalized linear mixed model for presence of florivores on *C. ladanifer* (2723 flowers from 40 plants in 4 populations). Analyses were based on one GLMM with binomial error with logit canonical link function using REML estimation. Random effects were tested with Wald Z-tests and fixed effects with Type III F-tests. Significant P -values are marked in bold.

Effect	df	Estimate \pm SD	Test value	P
<i>Random</i>				
Plant (Population)	–	0.27 \pm 0.14	2.00	0.116
<i>Fixed</i>				
Population	1, 3	–3.62 \pm 2.05	1.80	0.146
Plant size	1, 28.4	–0.25 \pm 0.21	1.44	0.239
Spot	1, 29.4	0.29 \pm 0.27	1.16	0.290
Floral longevity	1, 2681	0.99 \pm 0.27	45.16	<0.001
Flower size	1, 1045	0.12 \pm 0.21	13.83	<0.001
Number of flowers	1, 1663	–0.07 \pm 0.04	0.64	0.422
Floral longevity \times population	3, 952	–0.39 \pm 0.34	0.87	0.458
Flower size \times population	3, 433	0.57 \pm 0.26	1.12	0.183
Number of flowers \times population	3, 1222	0.13 \pm 0.05	2.05	0.101

Table 4
Logistic regressions for the effects of flower size on presence of florivores for each of populations of *C. ladanifer*. Significant *P*-values are marked in bold.

Population	R ²	β ± SD	df	N	P
Monte Valdelatas	0.26	0.56 ± 0.12	1	645	<0.001
La Pedriza	0.15	0.48 ± 0.18	1	701	0.013
Vista Real	0.18	0.65 ± 0.27	1	706	0.016
Puerto de Canencia	0.01	0.16 ± 0.23	1	671	0.477

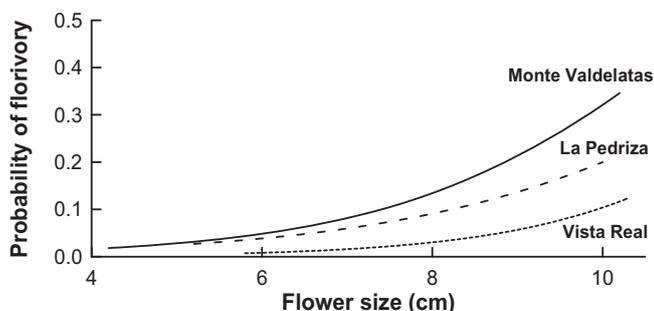


Fig. 1. Logistic adjustments showing the increased probability of florivory with increases in flower size, in the three populations of *C. ladanifer* where the relationship between flower size and florivory were significant (Table 4).

to the complexity of the model structure and the relatively large number of potential explanatory variables, we only considered the interaction between floral longevity and population, flower size and population and number of flowers and population. All the computations were performed using the GLIMMIX Macro of SAS (SAS Statistical Package, 1990; SAS Institute, Cary, NC, USA).

Due to the limitations of GLIMMIX to carry out *a posteriori* tests, two additional analyses were carried out to further explore the exact relationship of both flower size and floral longevity with florivory. Firstly, we correlated flower size with florivory by means of logistic regressions for each population. Secondly, we used contingency tables to test whether florivores disproportionately occurred on flowers of greater longevity at each population. Contingency tables were analysed using the G-test (Sokal and Rohlf, 1995). For population 3, flowers lasting 2 and 3 days were pooled in order to avoid empty cells (Sokal and Rohlf, 1995). These two analyses were performed with SPSS 15.0 (SPSS Inc., Chicago, Illinois, USA).

3. Results

3.1. Flower size, floral longevity and number of flowers

Flower size ranged between 4.2 and 10.8 cm and significantly differed among populations ($F_{3, 2720} = 385.21, P < 0.001$). Longevity of individual flowers ranged from 1 to 5 days, but mean floral longevity (\pm SD) of the species was 1.44 ± 0.62 d and significantly differed among populations (Wald Z-test, $Z = 2.01, P = 0.022$). Number of flowers ranged between 10 and 63 flowers per plant and

did not significantly differ among populations ($F_{1, 3} = 0.25, P = 0.859$), but did differ among plants within-populations ($F_{3, 35} = 41.89, P < 0.001$). Table 2 shows mean flower size, mean floral longevity and mean number of flowers in each population.

3.2. Florivory incidence

Overall, 189 flowers (ca. 7%) had some type of florivory (Table 2). The main florivores were several ant species picking stamens and beetles consuming petals and pollen. The incidence of florivory on *C. ladanifer* flowers did not differ among populations (Table 3). The incidence of florivory was significantly influenced by flower size and floral longevity (Table 3). Effects of flower size on florivory were significantly positive in three populations (Table 4) and were higher than 30% in Monte Valdelatas (Fig. 1). In addition, there was a significant positive effect of floral longevity on the proportion of damaged flowers, ranging from approximately 3% in 1 day flowers to 67% in 5 day flowers (Table 5).

4. Discussion

Both flower size and longevity positively influenced florivory incidence in *C. ladanifer*. The effect of flower size on the probability of damage by florivores is relatively well documented (Galen, 1999; Galen and Cuba, 2001; Lara and Ornelas, 2001). In contrast, our finding of increased florivory on longer-lived flowers is novel. Previously, higher floral longevity has been related only to increased risk of anther smut infection (Shykoff et al., 1996; Kaltz and Shykoff, 2001). Thus, floral longevity seems to have been understudied in relation to plant–animal antagonistic interactions and deserves further research.

Contrary to our expectations, number of flowers did not affect florivory. This is surprising, because florivore incidence has been previously associated with reduction in the number of flowers displayed (Krupnick et al., 1999; Mosleh Arany et al., 2009; Penet et al., 2009), as well as with other plant–animal antagonistic interactions, such as higher incidence of predispersal seed predators (Hainsworth et al., 1984; English-Loeb and Karban, 1992; Kudoh and Whigham, 1998) and herbivores (Ehrlén, 1997; Strauss and Whittall, 2006; Sandring et al., 2007). In our case, the dominant florivores (ants and beetles) may use cues other than number of flowers to locate their food plants.

The relevance of florivores as agents of natural selection is dependent, among other factors, on their overall incidence. Studies on florivory have reported moderate to high incidences (e.g., 75% in Galen, 1999; see however Breadmore and Kirk, 1998; Malo et al., 2001). Our maximum values of damaged flowers reported (approximately 10%) along with the absence of significant differences of florivory incidence among populations would suggest at best a mild selective influence of florivores on *C. ladanifer*. As a comparison, the incidence of predispersal seed predation of *C. ladanifer* in the same area was greater than 40% (Delgado et al., 2007). However, temporal variation should be considered since

Table 5
Proportions of damaged flowers by florivores for each floral longevity of each of populations of *C. ladanifer*. Sample size is in brackets. Likelihood ratio is the value of the G-statistic for testing that flowers with florivores are distributed randomly with respect to floral longevity. Significant *P*-values are marked in bold.

Population	Floral longevity (d)					df	Likelihood ratio (G)	P
	1	2	3	4	5			
Monte Valdelatas	0.075 (425)	0.108 (195)	0.308 (26)	–	–	2	11.561	0.003
La Pedriza	0.033 (182)	0.075 (414)	0.250 (84)	0.429 (14)	0.666 (3)	4	46.210	<0.001
Vista Real	0.027 (561)	0.069 (145)	–	–	–	1	5.119	0.024
Puerto de Canencia	0.038 (532)	0.074 (121)	0.111 (18)	–	–	2	4.061	0.131

annual variation in the influence of florivores has occasionally been documented (Galen and Cuba, 2001; Kawagoe and Kudoh, 2010).

Another important factor in determining the selective relevance of florivores is the extent to which damage is greater on larger or longer-lived flowers. For flower size, florivory probabilities of approximately 18%–35% on largest flowers (Fig. 1) open the possibility of relevant selective pressures towards smaller flowers in Monte Valdelatas and La Pedriza. For floral longevity, florivory incidences of 25% to –67% on flowers lasting three or more days may also open these same possibilities towards short-lived flowers at those two populations (Table 5). Nevertheless, formal phenotypic selection analysis, and verification that flower longevity is a genetically controlled trait, would be needed to confirm these possibilities.

In conclusion, our results support the notion that some floral traits associated with attractiveness to pollinators are also attractive to different types of florivores. Both larger and longer-lived flowers suffered higher incidence of florivory within populations of *C. ladanifer*. The low overall incidence of florivores and its lack of between-population variation suggest that these florivory patterns may not influence intraspecific variation of these floral traits. However, moderate florivory levels on the largest and longest-lived flowers open the possibility of exerting a relevant selective pressure towards smaller and shorter-lived flowers in some of our study populations.

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References

- Arista, M., Ortiz, P.L., 2007. Differential gender selection on floral size: an experimental approach using *Cistus salvifolius*. *J. Ecol.* 95, 973–982.
- Ashman, T.-L., Schoen, D.J., 1994. How long should flowers live? *Nature* 371, 788–791.
- Ashman, T.L., Schoen, D.J., 1996. Floral longevity: fitness consequences and resource costs. In: Lloyd, D.G., Barrett, S.C.H. (Eds.), *Floral Biology: Studies on Floral Evolution in Animal-pollinated Plants*. Chapman and Hall, New York, pp. 112–139.
- Breadmore, K.N., Kirk, W.D.J., 1998. Factors affecting floral herbivory in a limestone grassland. *Acta Oecol.* 19, 501–506.
- Brody, A.K., Mitchell, R.J., 1997. Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed production in the hummingbird-pollinated plant *Ipomopsis aggregata*. *Oecologia* 110, 86–93.
- Cardel, Y.J., Koptur, S., 2010. Effects of florivory on the pollination of flowers: an experimental study with a perennial plant. *Int. J. Plant Sci.* 171, 283–292.
- Delgado, J.A., Serrano, J.M., López, F., Acosta, F.J., 2007. Seed predation heterogeneity in the loculate fruits of a Mediterranean bushy plant. *J. Nat. Hist.* 41, 1853–1861.
- Ehrlén, J., 1997. Risk of grazing and flower number in a perennial plant. *Oikos* 80, 428–434.
- English-Loeb, G.M., Karban, R., 1992. Consequences of variation in flowering phenology for seed head herbivory and reproductive success in *Erigeron glaucus* (Compositae). *Oecologia* 89, 588–595.
- Galen, C., 1989. Measuring pollinator-mediated selection on morphometric floral traits: bumblebees and the alpine sky pilot, *Polemonium viscosum*. *Evolution* 43, 882–890.
- Galen, C., 1999. Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. *Bioscience* 49, 631–640.
- 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.
- Hainsworth, F.R., Wolf, L.L., Mercier, T., 1984. Pollination and pre-dispersal seed predation: net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata*. *Oecologia* 63, 405–409.
- Harder, L.D., Johnson, S.D., 2005. Adaptive plasticity of floral display size in animal-pollinated plants. *Proc. R. Soc. Lond., B., Biol. Sci.* 272, 2651–2657.
- Herrera, J., 1992. Flower variation and breeding systems in the Cistaceae. *Plant Syst. Evol.* 179, 245–255.
- Inouye, D.W., 1980. The terminology of floral larceny. *Ecology* 61, 1251–1253.
- Irwin, R.E., Brody, A.K., Waser, N.M., 2001. The impact of floral larceny on individuals, populations and communities. *Oecologia* 129, 161–168.
- Irwin, R.E., 2006. The consequences of direct versus indirect species interactions to selection on traits: pollination and nectar robbing in *Ipomopsis aggregata*. *Am. Nat.* 167, 315–328.
- Johnson, S.D., Midgley, J.J., 1997. Fly pollination of *Gorteria diffusa* (Asteraceae), and a possible mimetic function for dark spots. *Am. J. Bot.* 84, 429–436.
- Kaltz, O., Shykoff, J.H., 2001. Male and female *Silene latifolia* plants differ in per-contact risk of infection by a sexually transmitted disease. *J. Ecol.* 89, 99–109.
- Kawagoe, T., Kudoh, H., 2010. Escape from floral herbivory by early flowering in *Arabidopsis halleri* subsp. *gemmifera*. *Oecologia* 164, 713–720.
- Krupnick, G.A., Weis, A.E., Campbell, D.R., 1999. The consequences of floral herbivory for pollinator service to *Isomeris arborea*. *Ecology* 80, 125–134.
- Kudoh, H., Whigham, D.F., 1998. The effect of petal size manipulation on pollinator/seed-predator mediated female reproductive success of *Hibiscus moscheutos*. *Oecologia* 117, 70–79.
- Lara, C., Ornelas, J.F., 2001. Preferential nectar robbing of flowers with long corollas: experimental studies of two hummingbird species visiting three plant species. *Oecologia* 128, 263–273.
- Malo, J.E., Leirana-Alcocer, J., Parra-Tabla, V., 2001. Population fragmentation, florivory, and the effects of flower morphology on the pollination success of *Myrmecophila tibicinis* (Orchidaceae). *Biotropica* 33, 529–534.
- McCall, A.C., Irwin, R.E., 2006. Florivory: the intersection of pollination and herbivory. *Ecol. Lett.* 9, 1351–1365.
- Mosleh Arany, A., de Jong, T.J., van der Meijden, E., 2009. Herbivory and local genetic differentiation in natural populations of *Arabidopsis thaliana* (Brassicaceae). *Plant Ecol.* 201, 651–659.
- Ninyerola, M., Pons, X., Roure, J.M., 2005. Atlas climático digital de la Península Ibérica. http://opengis.uab.es/wms/iberia/espanol/es_cartografia.htm accessed September 2009.
- Penet, L., Collin, C.L., Ashman, T.L., 2009. Florivory increases selfing: an experimental study in the wild strawberry, *Fragaria virginiana*. *Plant Biol.* 11, 38–45.
- Primack, R.B., 1985. Longevity of individual flowers. *Annu. Rev. Ecol. Syst.* 16, 15–37.
- Sandring, S., Riihimäki, M.A., Sovalainen, O., Ågren, J., 2007. Selection on flowering time and floral display in an alpine and a lowland population of *Arabidopsis lyrata*. *J. Evol. Biol.* 20, 558–567.
- Schemske, D.W., Horvitz, C., 1988. Plant-animal interactions and fruit production in a neotropical herb: a path analysis. *Ecology* 69, 1128–1137.
- Serrano, J.M., Delgado, J.A., López, F., Acosta, F.J., Fungairiño, S.G., 2001. Multiple infestation by seed predators: the effect of loculate fruits on intraspecific insect larval competition. *Acta Oecol.* 22, 1–8.
- Shykoff, J.A., Bucheli, E., Kaltz, O., 1996. Flower lifespan and disease risk. *Nature* 379, 779–780.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, third ed. W.H. Freeman and Co, New York.
- Strauss, S.Y., Whittall, J.B., 2006. Non-pollinator agents of selection on floral traits. In: Harder, L.D., Barrett, S.C.H. (Eds.), *Ecology and Evolution of Flowers*. Oxford University Press, Oxford, pp. 120–138.
- Talavera, S., Gibbs, P.E., Herrera, J., 1993. Reproductive biology of *Cistus ladanifer* (Cistaceae). *Plant Syst. Evol.* 186, 123–134.
- Thomas, M.M., Rudall, P.J., Ellis, A.G., Savolainen, V., Glover, B.J., 2009. Development of a complex floral trait: the pollinator attracting petal spots of the beetle daisy, *Gorteria diffusa* (Asteraceae). *Am. J. Bot.* 96, 2184–2196.
- Thompson, J.D., 1982. *Interaction and Coevolution*. John Wiley and Sons, New York.
- Thompson, J.D., 2001. How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia* 126, 386–394.
- Thompson, J.D., 2005. *The Geographic Mosaic of Evolution*. University of Chicago Press, Chicago.
- Van Kleunen, M., Nanni, I., Donaldson, J.S., Manning, J.C., 2007. The role of beetles marks and flower colour on visitation by monkey beetles (Hopliini) in the greater Cape floral region, South Africa. *Ann. Bot.* 100, 1483–1489.