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Looking out for birds

Nectar and pollen of the invasive century plant *Agave americana* as a food resource for endemic birds

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Capsule Flowers of an invasive plant species are more visited by native birds than flowers of ornithophilous endemic plants.

Aims To describe the bird guild and its behaviour visiting the century plant *Agave americana* in an insular environment and to determine which factors are affecting visitation rates.

Methods We noted number and species of birds visiting inflorescences on Tenerife, Canary Islands. We used multimodel inference of generalized linear models to analyse the factors affecting the number of visits and the visitor species richness.

Results Eighty-one per cent of inflorescences were visited by eight native bird species. All species fed on nectar and only the Atlantic Canary fed also on pollen. Foraging behaviour varied among species. Visitation rate increased with density and diversity of birds and flower characteristics and decreased through the day. The number of species visiting the inflorescences increased with diversity and density of birds in the surroundings and decreased through the day.

Conclusion The native bird community uses the invasive century plant as a feeding resource at a higher rate than it uses endemic ornithophilous plants. This could have negative effects for the pollination of endemic plants, but positive effects for birds.

The negative impact of introduced species is one of the major causes of biodiversity loss, especially in island ecosystems (Sax & Gaines 2008, Walsh et al. 2012). Despite the growing evidence of the negative impact of biological invasions on wildlife conservation, the underlying mechanisms of these impacts are understudied (Levine et al. 2003). Introduced species can act as competitors or predators of native biota (Blackburn et al. 2004), disrupting local pollination and seed-dispersal plant–animal mutualistic interactions (Traveset & Richardson 2006), and therefore affecting community structure and stability (Pyšek et al. 2012). Potential commensalism with native species by exotic species is frequently overlooked (Reichard et al. 2001, Corlett 2005, French et al. 2005). In fact, facilitative interactions between invasive and native species can occur in a wide range of habitats, have cascading effects across trophic levels, re-structure communities, and lead to evolutionary changes (Rodríguez 2006).

The Canary Islands constitutes one of the hottest spots for biodiversity in the world (Myers et al. 2000), holding a remarkably rich 40% endemic flora (~570 endemic species) (Santos-Guerra 2001). With a dense human population (~280 inhabitants/km²; ISTAC 2012), approximately 20% of the endemic plant species are threatened by multiple human activities including overgrazing by introduced animals, interspecific hybridization with garden plants, habitat lost by urban development or competition with introduced plant species (Francisco-Ortega et al. 2000). Out of 700 introduced plant species recorded in the Canary archipelago (Arechavaleta et al. 2010), 50 species are considered highly invasive (Sanz-Elorza et al. 2005). Although some of these invasive plants are widespread in insular ecosystems (Sanz-Elorza et al.

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2004), no quantitative studies have been carried out on their particular breeding biology in the Canary Islands. Besides the potential competition for space, these introduced plants could be disrupting the pollination of endemic plants, because they can share habitats, flowering seasons and pollinators (Traveset & Richardson 2006). However, introduced plants can also bring positive effects to the ecosystem by providing feeding resources for native threatened fauna (Schlaepfer *et al.* 2010).

Despite several Canarian endemic plants showing flowers with traits of bird pollination (the so-called ornithophilous syndrome), no specialist nectar-feeding birds live on the archipelago (Valido *et al.* 2004, Ollerton *et al.* 2009). Opportunistic birds can visit several native bird-flowers (Valido *et al.* 2004, Rodríguez-Rodríguez & Valido 2008, 2011, Ortega-Olivencia *et al.* 2012) as well as other non-native (cultivated or introduced) plants to obtain nectar (Vogel *et al.* 1984, Trujillo 1992, Martín & Lorenzo 2001, Rodríguez *et al.* 2014). In Europe a total of 46 bird species have been recorded visiting the flowers of 95 plant species (both exotic and native). Although the ecological importance of bird-flower visitation is still unknown, nectar and pollen seem to be important food resources for tits (*Cyanistes*) and warblers (*Sylvia* and *Phylloscopus*) during winter and spring (da Silva *et al.* 2014).

The century plant *Agave americana* is considered invasive in the Mediterranean basin and Macaronesian islands causing diversity impoverishment by competing with the native flora (Badano & Pugnaire 2004). It was introduced from Central America into the Canary Islands probably during the XVI century, and it is now widespread on most of the islands. It produces a large inflorescence and abundant nectar, which attract animals to feed on them. In this study, we investigated the consumption of nectar and pollen of the century plant by native birds to evaluate its current role as competitor or commensal species in the Canarian ecosystems. The main goals of this study were: (i) to describe basic floral traits related to bird pollination of the century plant in the Canary Islands; (ii) to quantitatively describe the bird community feeding on century plant flowers; (iii) to describe the foraging behaviour, including agonistic aggressions, of the visiting birds; (iv) to assess temporal and habitat relationships of the bird visitation pattern; (v) so to discuss the differences in bird community and visitation rates of this introduced plant in relation to other endemic plant species with ornithophilous traits.

METHODS

Study area and species

The Canary Islands lie in the Atlantic Ocean, about 100 km west of north-west African coast. We monitored plants on Tenerife, the largest and the highest island (2034 km^2 and up to 3718 m a.s.l.). The vegetation and landscape are influenced by north-easterly humid winds, diverse altitude and orientation. Humidity and diversity in vegetation structure increase with north-east orientation and altitude (see Del Arco *et al.* 2006, for further details).

The century plant was introduced to the Canary Islands for several uses: as an ornamental plant, to obtain pharmacological products or fibres to make ropes or construction materials, as forage for domestic animals or fencing to delimitate property boundaries (Salas & Cáceres 2003). It is a monocarpic perennial plant, requiring around ten years to mature and producing a large panicule inflorescence (up to 9 m height), that has a central stalk with 15–34 composite umbels with yellow flowers in the upper half (Sanz-Elorza *et al.* 2004). Individual flowers gradually change from a staminate (male) to pistillate (female) state over a 4–6-day period (Slauson 2001). The flowering season in the Canary Islands spreads mainly from July to September depending on local climatic conditions (pers. obs.). Although data regarding the pollination biology of paniculate agaves are limited (e.g. nothing for the Canary Islands introduced populations), they have been assumed to be 'bat flowers' (Howell & Roth 1981). However, diurnal and other nocturnal visitors could be more important pollinators than previously thought due to the scarcity of precise studies in many species (Ortiz-Crespo 1974, Slauson 2001). Its seed production and germination percentage are low (Escobar-Guzmán *et al.* 2008), and it can bud asexually from adventitious shots to form new rosettes (Sanz-Elorza *et al.* 2004).

At least seven resident bird species from three families (Fam. Sylviidae: Canary Islands Chiffchaff *Phylloscopus canariensis*, Sardinian Warbler *Sylvia melanocephala*, Blackcap *Sylvia atricapilla* and Spectacled Warbler *Sylvia conspicillata*; Fam. Paridae: African Blue Tit *Cyanistes teneriffae*; Fam. Fringillidae: Atlantic Canary *Serinus canaria* and Common Chaffinch *Fringilla coelebs*) have been mentioned in the literature obtaining nectar from native bird-flower plants (Vogel *et al.* 1984, Valido *et al.* 2004, Rodríguez-Rodríguez & Valido 2008, 2011, Ortega-Olivencia *et al.* 2012). Other species could be potential nectar feeders because

they consume fruits and plant material, such as, for example, the endemics Bolle's *Columba bollii* and White-tailed Laurel *Columba junoniae* pigeons, Blackbird *Turdus merula*, Common Raven *Corvus corax*, European Robin *Erithacus rubecula* or Spanish Sparrow *Passer hispaniolensis* (Martín & Lorenzo 2001, Rodríguez *et al.* 2014). Some evidence such as feeding behaviour, pollen traces on the head, and the presence of pollen and sugar remains in droppings of European warblers *Sylvia* spp. suggest that the main target on flowers is nectar rather than pollen (Schwilch *et al.* 2001, Cecere *et al.* 2011, da Silva *et al.* 2014). No evidence for Canarian birds feeding on pollen exists (Valido *et al.* 2004).

Floral traits and plant characteristics

We examined basic floral traits of 73 century plants distributed along the altitudinal gradient (100–1000 m a.s.l.; Table 1). We also measured inflorescence panicule duration, flower size and sugar concentration. The nectar sugar concentration was measured using a hand refractometer and concentration was expressed as w/w% sucrose equivalents. Each of the monitored plants (where bird observations were made; $n = 77$) and its surroundings were described using 17 variables (see Table 2).

Bird visitation and foraging behaviour

To make observations for the study of bird visitation and foraging behaviour, we selected 77 plants (56 in July–September 2011 and 21 in July–August 2012) with inflorescences at different stages of ripeness, distributed throughout the altitudinal range from 120 to 1100 m and that could be monitored easily (presence of a good

vantage point, whenever possible with vegetation cover to hide the observer yet with good visibility). Observations were conducted with binoculars for a two-hour period (154 hours of effective census) from a vantage point situated more than 20 m from the plants. Some plants ($n = 8$) situated in a few sites (laurel forest and pastures) suitable to the localized endemic pigeons or ravens were observed from more than 150 m using a spotting scope. We noted the number and the species of birds visiting the inflorescences during the two-hour period.

As bird community in the area could be influencing visitation rates, a 10 min census of the birds heard or seen was carried out within the two-hour period. Censuses were conducted using a standardized protocol based on a point count at the observation point. We calculated density as birds/10 ha using the formula given in Bibby *et al.* (2000), the richness as the number of bird species, and diversity using the Shannon Diversity Index (Krebs 1999), taking into account the bird species that visited *A. americana* flowers.

A subsample of focal individuals was used for the study of foraging behaviour. We noted the species, sex (if possible), age (if possible), duration in seconds, number of composite umbels visited, the foraging technique used and if agonistic aggressions occurred. Because we could not identify birds individually (they were not ringed), some birds may have been observed several times. The proportion of repeatedly observed individual birds must be low because: (a) we conducted observations on 55 plants distributed throughout Tenerife; (b) an average of 8.3 birds and 1.8 species were observed per plant; (c) some species were sexed and aged (adult versus juvenile). As foraging techniques are related to the possibility of effective pollination, they were categorized in four different types based on previous studies (Martínez del Rio & Eguiarte 1987). These foraging techniques differed with the place where the birds obtained nectar or pollen from: perched on the flowers; perched on the branches; from the air by hovering in a 'hummingbird' fashion; perched upside down in a typical tit style (see Fig. 1). Because of bird behaviour during visits and the structure of inflorescence (height and lack of vegetation shield for birds), we are confident that small insectivorous birds were visiting the flowers to feed on nectar or pollen, although some of them may have picked up small invertebrates occasionally.

Table 1. Quantitative characterization of floral traits of a total of 73 century plants *Agave americana* from Tenerife Island during July–September 2011–2012. Sample size is different because not all variables were recorded in all plants.

Flower trait	Mean±sd	Range	n
Inflorescence panicule duration (days)	32 ± 12	16–68	61
Corolla length (mm)	16.0 ± 1.8	12–21	47
Corolla wide (mm)	11.1 ± 1.0	9–13	50
Corolla-stigma distance (mm)	45.4 ± 14.4	20–67	46
Corolla-anther distance (mm)	57.7 ± 4.9	49–67	42
Sugar concentration (%)	15.3 ± 1.4	13–17	9

Table 2. Variables employed to describe the inflorescences of century plant *Agave americana* from Tenerife Island where bird observations were made during July–September 2011–2012. Variables used in the multimodel inference after checking for collinearity, i.e. with variance inflate factors lower than 2.5, are in bold. VIF1 and VIF2 correspond to the variance inflate factors for the number of bird visits and visitor species richness full models, respectively.

Abbreviation	Description	Source	VIF1	VIF2
Plants				
UMBELS	Number of composite umbels	Field	1.6	1.7
IMMATURE	Proportion of composite umbels with immature flowers	Field	4698.2	5203.1
MATURE-flowers	Proportion of composite umbels with mature flowers	Field	1.5	1.5
SENESCENT-flowers	Proportion of composite umbels with senescent flowers	Field	1.4	1.3
HEIGHT	Height in metres of the inflorescence stalk	Field	1.8	1.6
Habitat				
HOUR	Time when observations were conducted	Field	1.4	1.4
SLOPE	Degree of slope measured from the highest and the lowest points in a circle of 30 m around the plant	GIS	1.5	1.5
ALTITUDE	Metres above the sea level at the base of the plant	GIS	1.6	1.5
NPLANTS	Number of flowering plants of *A. americana* in a 100 m radius from the studied plant	Field	1.4	1.5
INSECTS	Mean number of flying insects (Lepidoptera, Diptera and Hymenoptera) around the composite umbels counted four times during the two sample hours	Field	1.3	1.3
%FOREST	Percentage of land cover by forest in a 150 m radius from the plant	GIS[a]	2.2	1.9
%SHRUBS	Percentage of land cover by shrubland in a 150 m radius from the plant	GIS[a]	1.9	1.9
%GRASS	Percentage of land cover by grassland in a 150 m radius from the plant	GIS[a]	1.4	1.5
%OTHERS	Percentage of land cover by other vegetation types or human use in a 150 m radius from the plant	GIS[a]	32.8	52.7
Bird community				
Bird_DENSITY	Density of birds that potentially could visit *A. americana* flowers	Field[b]	1.6	1.7
Bird_RICHNESS	Number of species of birds that potentially could visit *A. americana* flowers	Field[b]	13.6	11.9
Bird_DIVERSITY	Shannon Diversity Index calculated using the birds that potentially could visit *A. americana* flowers	Field[b]	2.4	2.2

[a]Calculated using information given by Del Arco *et al.* (2006).
[b]See methods section for further details.

Data analysis

Interspecific differences in foraging behaviour (visit time, number of foraging techniques and number of umbels visited) were tested by Kruskal–Wallis tests. We used multimodel inference of generalized linear models (GLMs) to analyse the factors affecting the number of visits and the visitor species richness (Burnham & Anderson 2002). GLMs were modelled with negative binomial (number of visits) or Poisson (species richness) error distributions, depending on the overdispersion of count data, and log link functions. Prior to the multimodel inference modelling, we checked the collinearity among the 17 potential explanatory variables and, finally, selected 14 variables with variance inflation factors lower than 2.5 (see Table 2, Zuur *et al.* 2010).

Multimodel inference allowed the identification of the best possible models based on corrected Akaike's information criterion (AICc) and to rank all independent variables according to their influence on the two response variables (Burnham & Anderson 2002). The candidate models in the final selection, i.e. models within two AICc units from the best model, and their Akaike weight of evidence (w_i) were used to estimate averaged regression coefficients (Bartoń 2013). Thus, the explanatory variables were ranked by importance, i.e. sum of their w over all competing models (the closest to 1, the highest importance).

Models were fitted in R (version 2.15.2; R Core Team 2012) using the glm and glm.nb functions. We used the package MuMIn for some procedures of the multimodel inference method (Bartoń 2013) and variance inflation factors were determined using the function vif of the R-package car (Fox & Weisberg 2011).

RESULTS

Floral traits and plant characteristics

Mean height of the inflorescence panicule of century plant in Tenerife was 7 m ± 1.2 (± sd, range 4.1–9.0, $n = 77$), and contained 24.2 ± 4.4 umbels (mean ± sd, range 15–34, $n = 77$). They contained mature flowers

Figure 1. Foraging techniques of bird species visiting century plant *Agave americana* inflorescences on Tenerife Island (A = Common Chaffinch *Fringilla coelebs* perched on branches, B = Common Raven *Corvus corax* perched on flowers, C = African Blue Tit *Cyanistes teneriffae* perched upside down, D = Canary Islands Chiffchaff *Phylloscopus canariensis* feeding from the air, E = Goldcrest *Regulus regulus* perched on flowers (note the nectar in the bill tip in the inserted picture), F = Atlantic Canary *Serinus canaria* eating pollen perched on flowers) (see the main text for details on foraging techniques).

for 16–68 days, which produce very dilute nectar, i.e. around 15% of sugar concentration (Table 1). On average, forest, shrubs and grass covered 4%, 49% and 6% of land in a 150 m radius from studied plants, respectively.

Visitation rate and bird community

Sixty-three (81.1%) out of the 77 plants were visited at least by one bird species, feeding on nectar and/or pollen. The mean visitation rate of the inflorescences

Table 3. Number and descriptive parameters of the bird community visiting century plant *Agave americana* inflorescences on Tenerife during July–September 2011–2012.

Family/species/subspecies	Number of visits (%)	Plant visited (%)	Foraging behaviour			
			Time (sec)/visit Mean±sd (range)	No. of techniques/visit Mean±sd (Max.)	No. of umbels/visit Mean±sd (Max.)	*n*
SYLVIIDAE						
Canary Islands Chiffchaff *Phylloscopus canariensis*	1729 (59.2)	61.0	18.8 ± 31.2 (1–240)	1.5 ± 0.6 (4)	1.9 ± 1.4 (8)	219
Blackcap *Sylvia atricapilla*	46 (1.6)	13.0	27.1 ± 24.3 (6–93)	1.29 ± 0.6 (3)	1.5 ± 0.7 (3)	17
Sardinian Warbler *Sylvia melanocephala*	30 (1.0)	11.7	28.1 ± 26.5 (5–122)	1.33 ± 0.5 (2)	2.7 ± 1.8 (8)	21
Goldcrest *Regulus regulus teneriffae*	9 (0.3)	1.3	5.5 ± 3.0 (1–10)	1.0 (1)	1.3 ± 0.8 (3)	6
PARIDAE						
African Blue Tit *Cyanistes teneriffae teneriffae*	436 (14.9)	44.2	23.2 ± 20.9 (1–99)	1.2 ± 0.5 (2)	1.3 ± 0.7 (5)	104
CORVIDAE						
Common Raven *Corvus corax canariensis*	3 (0.1)	1.3	167.5 ± 153.4 (59–276)	2.0 ± 0 (2)	1.5 ± 0.7 (2)	2
FRINGILLIDAE						
Atlantic Canary *Serinus canaria*	668 (22.7)	57.1	47.1 ± 46.9 (2–257)	1.2 ± 0.4 (2)	1.5 ± 0.9 (5)	83
Common Chaffinch *Fringilla coelebs canariensis*	1 (< 0.1)	1.3	38	1.0 (1)	1.0 (1)	1
TOTAL	2922 (100)		26.1 ± 36.1	1.3 ± 0.6		453
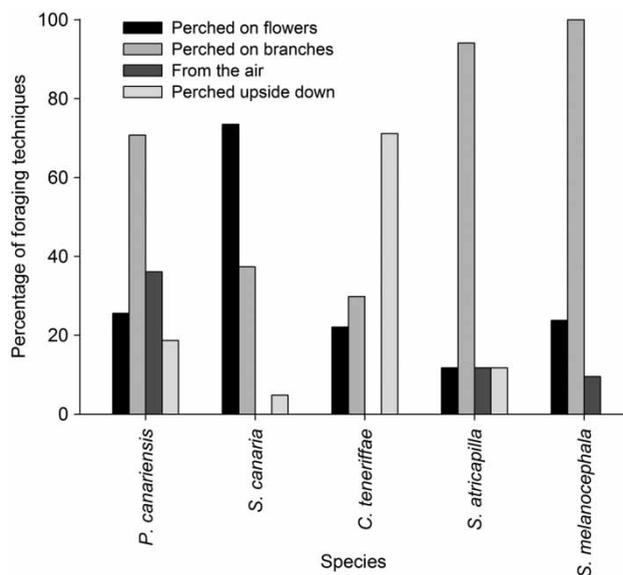
Figure 2. Percentage of foraging techniques used by the five most frequent bird species visiting century plant *Agave americana* inflorescences on Tenerife Island (see the main text and Fig. 1 for further details on foraging techniques).

was 19.0 ± 24.8 (range = 0–195) visits/hour. A total of eight bird species belonging to four families were observed visiting plants (Table 3). All the species,

including the Goldcrest *Regulus regulus*, were feeding on nectar, and only the Canary also on pollen. The most frequent species visiting the plants was the Canary Islands Chiffchaff with 59.2% of the total visits distributed in 61% of the studied plants, followed by the Atlantic Canary (22.7% of visits and 57% of plants) and the African Blue Tit (14.9% of visits and 44% of plants) (Table 3).

Foraging behaviour

All species were detected feeding on nectar directly from floral receptacles or directly from the surface of the plant (usually some nectar drops were available just outside of the flowers). The only species feeding on pollen was the Atlantic Canary (36% of visits) biting directly off the anthers, especially immature ones (see Fig. 1F).

All species used the foraging technique of perching on a branch for feeding on nectar, and only the Canary Islands Chiffchaff and the Blackcap used the four foraging techniques (Fig. 2). The foraging behaviour of the three most frequent bird species (Canary Islands Chiffchaff, Atlantic Canary and African Blue Tit) differed in the time spent visiting, the number of inflorescences visited and the number of different foraging techniques used per visit (Kruskal–Wallis tests:

Table 4. Multimodel inference results for number of bird visits to century plant *Agave americana* inflorescences on Tenerife. Importance (weight of evidence), averaged coefficient estimates and confidence intervals (95% CI) of explanatory variables are given. Variables are sorted by importance according to the weight of evidence and the significant averaged coefficients (i.e. confidence intervals not including the 0). See Table 2 for variable description.

Variables	Importance	Averaged estimate	Adjusted se	Lower CI	Upper CI
Intercept		2.673	1.519	−0.303	5.650
Bird_DENSITY	1.00	0.018	0.006	0.006	0.030
Bird_DIVERSITY	1.00	0.951	0.275	0.411	1.491
SENESCENT-flowers	1.00	1.822	0.775	0.303	3.341
HOUR	0.93	−2.127	0.934	−3.958	−0.296
HEIGHT	0.85	−0.416	0.164	−0.737	−0.095
UMBELS	0.77	0.085	0.040	0.007	0.162
INSECTS	0.37	−0.037	0.023	−0.082	0.007
%SHRUBS	0.32	−0.012	0.008	−0.028	0.003
MATURE-flowers	0.16	−2.292	1.970	−6.153	1.568
%FOREST	0.07	0.019	0.022	−0.025	0.062

Table 5. Multimodel inference results for visitor species richness of birds to century plant *Agave americana* inflorescences on Tenerife. Importance (weight of evidence), averaged coefficient estimates and confidence intervals (95% CI) of explanatory variables are given. Variables are sorted by importance according to the weight of evidence and the significant averaged coefficients (i.e. confidence intervals not including the 0). See Table 2 for variable description.

Variables	Importance	Averaged estimate	Adjusted se	Lower CI	Upper CI
Intercept		0.326	0.552	−0.756	1.409
Bird_DIVERSITY	1.00	0.434	0.167	0.107	0.760
HOUR	0.94	−1.219	0.554	−2.305	−0.132
Bird_DENSITY	0.79	0.005	0.003	−0.001	0.011
NPLANTS	0.32	0.017	0.013	−0.009	0.043
%FOREST	0.23	−0.016	0.013	−0.041	0.009
ALTITUDE	0.08	0.000	0.000	−0.001	0.000
INSECTS	0.07	−0.009	0.013	−0.034	0.017
%GRASS	0.06	0.007	0.012	−0.016	0.030
HEIGHT	0.06	−0.043	0.072	−0.184	0.098

$x^2 = 50.1$, df = 2, $P < 0.001$; $x^2 = 12.0$, df = 2, $P = 0.003$; $x^2 = 27.3$, df = 2, $P < 0.001$, respectively; Table 3).

We recorded only 11 agonistic interactions during the 453 monitored visits (African Blue Tit over Canary, $n = 1$; Chiffchaff over Chiffchaff, $n = 2$; Chiffchaff over Canary, $n = 1$; Canary over Canary, $n = 5$; Canary over Chiffchaff, $n = 1$ and Sardinian Warbler over Sardinian Warbler, $n = 1$).

Bird visitation pattern

The number of visits to inflorescences was positively related to the density and diversity of birds present in the surroundings (Bird_DENSITY and Bird_DIVERSITY), the maturity of the inflorescence (SENESCENT-flowers) and the number of umbels (UMBELS); and negatively related to the time of day (HOUR) and inflorescence height (HEIGHT) (Table 4). The remaining variables had lower importance (Table 4). The number of bird species visiting the inflorescences (richness) increased with the diversity and density of birds in the surroundings (Bird_DIVERSITY and Bird_DENSITY), and decreased with time of day (HOUR), while the remaining variables had lower importance (Table 5).

DISCUSSION

The visitation rate (19.0 ± 24.8 birds per hour) and number of species were considerably higher than those previously recorded for the Canary Islands endemic ornithophilous plants, which never exceed the five visits per hour and five bird species (see Table 6). The fact that the century plants studied were distributed in a great variety of habitats from 120 to 1000 m of

Table 6. Visitation rates (visits/hour/plant) and percentage of plants visited (in brackets) by native birds to endemic and exotic plant species on Tenerife and Gran Canaria Islands.

| Bird species | Endemic | | | | Exotic |
	Isoplexis canariensis	*Canarina canariensis*	*Echium wildpretii*	*Scrophularia calliantha*	*Agave americana*
Phylloscopus canariensis	0.6 (84.3)	0.05 (9.0)	0.56 (–)	0.1 (–)	11.23 (61.0)
Sylvia melanocephala	0.02 (3.4)	–	–	0.01 (–)[a]	0.19 (11.7)
Sylvia atricapilla	–	–	–	–	0.30 (13.0)
Regulus regulus	–	–	–	–	0.06 (1.3)
Cyanistes teneriffae	0.04 (4.0)	0.04 (2.0)	–	0.01 (–)	2.83 (44.2)
Corvus corax	–	–	–	–	0.02 (1.3)
Fringilla coelebs	<0.01 (0.1)	–	–	–	0.01 (1.3)
Serinus canaria	0.01 (1.8)	–	2.94 (–)	–	4.34 (57.1)
Study details:					
No. of bird visitor species	5	2	2	4	8
No. of plants	50	227[b]	20	120[c]	77
No. of hours	725	77.5	–	33.8	154
Nectar sucrose content (%)	< 33	12–16	6–29	9–45[c]	13–17
Bloom season	Spring–Summer	Winter–Spring	Summer	Spring	Summer
Island	Tenerife	Tenerife	Tenerife	Gran Canaria	Tenerife
Habitat	Laurel forest	Laurel forest	High mountain shrub	Pine wood-thermophilous forest-laurel forest	Coastal shrub-thermophilous forest-laurel forest
Source	Rodríguez-Rodríguez & Valido (2008)	Rodríguez-Rodríguez & Valido (2011)	Valido *et al.* (2002)	Ortega-Olivencia *et al.* (2012)	Present study

[a]Include both *Sylvia melanocephala* and *S. atricapilla*.
[b]Study based on flower observations.
[c]A. Ortega-Olivencia pers. comm.

altitude, in contrast to native species that are usually restricted to one habitat (or at least where studies has been conducted) could explain the differences observed. Nectar composition could also be influencing the observed high visitation rate. One of the defining characteristics of bird pollinated flowers is that they produce copious and dilute nectar (usually 20–25%), and several hypotheses have been proposed to account this phenomenon related to more efficient extraction, to discourage bees or the water requirements of birds (Nicolson *et al.* 2007, Johnson & Nicolson, 2008, Cecere *et al.* 2011). In the Canary Islands water availability for birds is in general low, especially in the summer months, when the century plant flowers. Its dilute nectar (~15%; see Table 1) corresponds to the lowest range for ornithophilous species (Table 6) and could be aimed to meet the water requirements of birds (Nicolson *et al.* 2007). Furthermore, inflorescence duration and the amount of resources provided (note that inflorescences can be ripe for more than 30 days; see Table 1) may also explain the high visitation rates. In fact, the number of visits was positively related to the maturity and size of inflorescences (see below).

Like in other native bird-flower plants (Vogel *et al.* 1984, Valido *et al.* 2004, Rodríguez-Rodríguez & Valido 2008, 2011; Table 6), the most frequent species using the century plant flowers were the Canary Islands Chiffchaff, the Atlantic Canary and the African Blue Tit. Although it is known that nectar is included in the diet for some of these species (see review in da Silva *et al.* 2014), the insular syndrome may be also affecting their choice. The low species richness on islands may lead to increased densities of individual species, so intraspecific competition increases, resulting in a wider niche breadth (Olesen & Valido 2004). In fact, the majority of the species in our study show a high density and wide distribution range from the coast to high elevations, occupying a great variety of habitats (Martín & Lorenzo 2001).

The observations of the Goldcrest *R. regulus* and the Common Raven feeding on the century plant nectar were novel, as well as the pollen consumption by the Atlantic Canary, which probably constitutes one of the few cases of a native Palearctic bird feeding on this resource.

All species of goldcrests and kinglets are almost exclusively insectivorous, preying on small arthropods with soft cuticles, such as springtails, aphids and spiders (see review in Del Hoyo *et al.* 2006). Only occasional records on plant material as food have been reported for some species such as *Regulus regulus*, *Regulus ignicapillus* and *Regulus calendula* (Bardin 1987, Jordano 1987, Del Hoyo *et al.* 2006). In our study, we observed (and photographed; Fig. 1E) at least two individuals of Goldcrest feeding on nectar in one century plant inflorescence situated in the proximities of a well-developed laurel forest, the typical habitat of the species in the Canaries. These feeding records of nectar of century plant flowers (present study), together with observations made on other cultivated species (pers. obs.), suggest that the Goldcrest could occasionally feed on endemic bird-flowers.

During the last few years, Common Ravens feeding on nectar of the century plant have been observed in the Teno massif, north-west Tenerife (Rodríguez *et al.* 2014), where the bulk of its threatened population (less than 20 pairs) still survive (Siverio *et al.* 2010). Canarian population diet has been studied based on pellet analysis, reporting food items with hard structures, e.g. bones, elytra or seeds (Nogales & Hernández 1994). This highlights the importance of using direct observations to study foraging ecology because nectar feeding could pass unnoticed using pellet analysis (Sakai *et al.* 1986). The low visitation rate observed could be a direct consequence of their low abundance and threatened status on Tenerife (Siverio *et al.* 2010) or because nectar is not energetically viable as a food source. Thus, the potential role of century plant as a trophic resource deserves more studies and should be taken into account in the management and conservation of this regionally threatened species since availability of other resources, such as carcases of domestic livestock, have decreased during the last decades (Siverio *et al.* 2010).

Pollen can contain over 60% of protein depending on the plant species, and usually a large amount of nitrogen. Its relative importance as a source of protein to vertebrates is controversial due to the presence of a strong coat highly resistant to degradation by digestive enzymes (Roulston & Cane 2000, Gartrell & Jones 2001). We observed a high proportion of Canaries feeding on pollen (36%, Fig. 1F) which contrasts with the mostly anecdotal records of birds feeding on pollen in the Western Palearctic (Bardin 1987). Whether the contribution of pollen to the diet of Canaries is significant needs further study.

According to their behaviour and their way of obtaining nectar, the majority of bird species visiting the century plant flowers cannot be considered as true pollinators for it, given that many of them may not transport pollen (Herrera & Pellmyr 2002). The best foraging technique in favour of pollen transport is perching on flowers because bird bellies are usually in direct contact with anthers and stigmas (see Fig. 1). Two species, the Common Raven and Atlantic Canary, are the more likely candidates to be true pollinators, i.e. able to transport pollen grains from anthers to stigmas of the century plant because of their main foraging techniques (Fig. 2). However, only the Atlantic Canary is a common and widespread bird on the island, and so it alone may play an important role in plant reproduction.

According to our models, the visitation rate and number of species visiting inflorescences were related to the density and the diversity of birds in the surroundings of the plants. Thus, a higher number of visits and species visited the inflorescences in areas with higher density and diversity of birds. This reasonable result is even more evident if we consider that birds did not defend the inflorescences (note that only 11 agonistic interactions were observed during 453 monitored visits) as occurs in other bird species visiting flowers of other agave species (see Martínez del Rio & Eguiarte 1987). Higher visitation rates and richness during the morning were probably related to patterns of bird activity, but also with the competition with insects that are more active during the midday with higher temperatures. In this sense, introduced honeybees *Apis mellifera* and other insects compete with native birds for nectar of Canarian endemic plant species, such as *Echium wildpretii* and *Navaea phoenicea* (Valido *et al.* 2002, pers. obs.), or of other species worldwide (e.g. Hansen *et al.* 2002, Whelan *et al.* 2009). Other factors such as age and size of the inflorescence regulated the visitation rates. Older (higher SENESCENT), larger (higher UMBELS) and shorter (lower HEIGHT) inflorescences were more frequently attended than younger, smaller and higher ones. This may perhaps be related to experience, visibility and accessibility. Thus it is possible that (1) older inflorescences have had more time to attract

birds than younger ones, because birds learn the location of a long-lasting source of food; (2) larger inflorescences provide a higher amount of nectar and they are more visible and (3) shorter inflorescences permit access in a safer way than higher inflorescences because they are closer in proximity to vegetation cover that might act as a refuge (see Herrera & Pellmyr 2002).

Understanding biological invasions by integrating facilitative interactions has important implications for management, eradication and restoration of invaded ecosystems (Rodríguez 2006). Although further research is needed to evaluate the nutritional significance of nectar to birds (e.g. Martínez del Rio *et al.* 2001, Brown *et al.* 2010, Symes *et al.* 2011), and to understand the avian role in the pollination of the century plant, our study shows a clear case of a facilitative interaction between an invasive plant and native birds. The higher visitation rates of the century plant in comparison with endemic plants suggest that birds may obtain a presumably important feeding resource during the harder conditions of late summer.

REFERENCES

Arechavaleta, M., Rodríguez, S., Zurita, N. & García, A. (eds) 2010. *Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009*. Gobierno de Canarias, S/C de Tenerife.

Badano, E.I. & Pugnaire, F.I. 2004. Invasion of *Agave* species (Agavaceae) in south-east Spain: invader demographic parameters and impacts on native species. *Divers. Distrib.* **10:** 493–500.

Bardin, A.V. 1987. [Tree sap nectar, and pollen as a food source for tits and Goldcrests during early spring.] *Russ. J. Zool.* **66:** 789–790 (in Russian).

Bartoń, K. 2013. MuMIn: Multi-model inference, R package, version 1.9.0.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. 2000. *Birds Census Techniques*, 2nd edn. Academic Press, London.

Blackburn, T.M., Cassey, T., Duncan, R.P., Evans, K.L. & Gaston, K.J. 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* **305:** 1955–1958.

Brown, M., Downs, C.T. & Johnson, S.D. 2010. Sugar preferences and digestive efficiency in an opportunistic avian nectarivore, the Dark-capped Bulbul *Pycnonotus tricolor. J. Ornithol.* **151:** 637–643.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.

Cecere, J., Spina, F., Jenni-Eiermann, S. & Boitani, L. 2011. Nectar: an energy drink used by European songbirds during spring migration. *J. Ornithol.* **152:** 923–931.

Corlett, R.T. 2005. Interactions between birds, fruit bats and exotic plants in urban Hong Kong, South China. *Urban Ecosyst.* **8:** 275–283.

Del Arco, M., Wildpret, W., Pérez, P.L., Rodríguez, O., Acebes, J.R., García, A., Martín, V.E., Reyes, J.A., Salas, M., Díaz, M.A., Bermejo, J.A., González, R., Cabrera, M.V. & García, S. 2006. *Mapa de Vegetación de Canarias*. GRAFCAN, Santa Cruz de Tenerife.

Del Hoyo, J., Elliot, A. & Christie, D.A. (eds) 2006. *Handbook of the Birds of the World. Vol. 11*. Lynx Edicions, Bellaterra.

Escobar-Guzmán, R.E., Zamudio Hernández, F., Gil Vega, K. & Simpson, J. 2008. Seed production and gametophyte formation in *Agave tequilana* and *Agave americana. Botany* **86:** 1343–1353.

Fox, J., & Weisberg, S. 2011. *Multivariate Linear Models in R*, 2nd edn. Sage Publications, Thousand Oaks, CA.

Francisco-Ortega, J., Santos-Guerra, A., Kim, S.-C. & Crawford, D.J. 2000. Plant genetic diversity in the Canary Islands: a conservation perspective. *Am. J. Bot.* **87:** 909–919.

French, K., Major, R. & Hely, K. 2005. Use of native and exotic garden plants by suburban nectarivorous birds. *Biol. Conserv.* **121:** 545–559.

Gartrell, B.D. & Jones, S.M. 2001. *Eucalyptus* pollen grain emptying by two Australian nectarivorous psittacines. *J. Avian Biol.* **32:** 224–230.

Hansen, D.M., Olesen, J.M. & Jones, C.G. 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? *J. Biogeogr.* **29:** 721–734.

Herrera, C.M. & Pellmyr, O. (eds) 2002. *Plant-Animal Interactions: An Evolutionary Approach*. Blackwell Science, Oxford.

Howell, D.J. & Roth, B.S. 1981. Sexual reproduction in *Agaves*: the benefits of bats; the cost of semelparous advertising. *Ecology* **62:** 1–7.

ISTAC. 2012. *Instituto Canario de Estadística*. Gobierno de Canarias. Available at: http://www.gobiernodecanarias.org/istac/temas_estadisticos/demografia/poblacion/cifraspadronales/ (accessed 17 July 2013).

Johnson, S.D. & Nicolson, S.W. 2008. Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biol. Lett.* **4:** 49–52.

Jordano, P. 1987. Notas sobre la dieta no-insectívora de algunos Muscicapidae. *Ardeola* **34:** 89–98.

Krebs, C.J. 1999. *Ecological Methodology*. Addison Wesley Longman, Menlo Park, CA.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B* **270:** 775–781.

Martín, A. & Lorenzo, J.A. 2001. *Aves del Archipiélago Canario*. Francisco Lemus editor, La Laguna.

Martínez del Rio, C. & Eguiarte, L.E. 1987. Bird visitation to *Agave salmiana*: comparison among hummingbirds and perching birds. *Condor* **89:** 357–363.

Martínez del Rio, C., Schondube, J.E., McWhorter, T.J. & Herrera, L.G. 2001. Intake responses in nectar feeding birds: digestive and metabolic causes, osmoregulatory consequences, and coevolutionary effects. *Am. Zool.* **41:** 902–915.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403:** 853–858.

Nicolson, S.W., Nepi, M. & Pacini, E. 2007. *Nectaries and Nectar.* Springer, Dordrecht.

Nogales, M. & Hernández, E.C. 1994. Interinsular variations in the spring and summer diet of the Raven *Corvus corax* in the Canary Islands. *Ibis* **136:** 441–447.

Olesen, J.M. & Valido, A. 2004. Lizards and birds as generalized pollinators and seed dispersers of island plants. In Fernández-Palacios, J.M. & Morici, C. (eds) *Ecología Insular/Island Ecology*, 229–249. Asociación Española de Ecología Terrestre (AEET)-Cabildo de La Palma, S/C de La Palma.

Ollerton, J., Cranmer, L., Stelzer, R.J., Sullivan, S. & Chittka, L. 2009. Bird pollination of Canary Islands endemic plants. *Naturwissenschaften* **96:** 221–232.

Ortega-Olivencia, A., Rodríguez-Riaño, T., Pérez-Bote, J.L., López, J., Mayo, C., Valtueña, F.J. & Navarro-Pérez, M. 2012. Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. *Ann. Bot.* **109:** 153–167.

Ortiz-Crespo, F.I. 1974. The giant hummingbird *Patagona gigas* in Ecuador. *Ibis* **116:** 347–359.

Pyšek, P, Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob. Change Biol.* **18:** 1725–1737.

R Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org/ (accessed 5 February 2013).

Reichard, S.H., Chalker-Scott, L. & Buchanan, S. 2001. Interactions among non-native plants and birds. In Marzluff, J.M., Bowman, R. & Donnelly, R. (eds) *Avian Ecology and Conservation in an Urbanizing World*, 179–224. Kluwer Academic, Boston.

Rodríguez, L.F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occurs. *Biol. Invasions* **8:** 927–939.

Rodríguez, B., Siverio, F., Siverio, M., Rodríguez, A. & Barone, R. 2014. *Los Vertebrados Terrestres de Teno. Catálogo ilustrado y comentado*. GOHNIC, Buenavista del Norte.

Rodríguez-Rodríguez, M.C. & Valido, A. 2008. Opportunistic nectar-feeding birds are effective pollinators of bird-flowers from Canary Islands: experimental evidence from *Isoplexis canariensis* (Scrophulariaceae). *Am. J. Bot.* **95:** 1408–1415.

Rodríguez-Rodríguez, M.C. & Valido, A. 2011. Consequences of plant-pollinator and floral-herbivore interactions on the reproductive success of the Canary Islands endemic *Canarina canariensis* (Campanulaceae). *Am. J. Bot.* **98:** 1465–1474.

Roulston, T.H. & Cane, J.H. 2000. Pollen nutritional content and digestibility for animals. *Plant Syst. Evol.* **222:** 187–209.

Sakai, H.F., Ralph, C.J. & Jenkins, C.D. 1986. Foraging ecology of the Hawaiian crow, an endangered generalist. *Condor* **88:** 211–219.

Salas, M. & Cáceres, M.T. 2003. Notas históricas y estudio de algunas plantas mesoamericanas en Canarias: piteras, tuneras y estramonios. *Vegueta* **7:** 255–263.

Santos-Guerra, A. 2001. Flora vascular nativa. In Fernández-Palacios, J.-M. & Martín-Esquivel, J.L. (eds) *Naturaleza de las Islas Canarias*, 185–192. Turquesa, Santa Cruz de Tenerife.

Sanz-Elorza, M., Dana Sánchez, E.D. & Sobrino Vesperinas, E. (eds) 2004. *Atlas de las Plantas Alóctonas Invasoras en España*. Dirección General para la Biodiversidad, Madrid.

Sanz-Elorza, M., Dana Sánchez, E.D. & Sobrino Vesperinas, E. 2005. Aproximación al listado de plantas vasculares alóctonas invasoras reales y potenciales en las islas Canarias. *Lazaroa* **26:** 55–66.

Sax, D.F. & Gaines, S.D. 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proc. Natl. Acad. Sci. U.S.A* **105:** 11490–11497.

Schlaepfer, M.A., Sax, D.F. & Olden, J.D. 2010. The potential conservation value of non-native species. *Conserv. Biol.* **25:** 428–437.

Schwilch, R., Mantovani, R., Spina, F. & Jenni, L. 2001. Nectar consumption of warblers after long-distance flights during spring migration. *Ibis* **143:** 24–32.

da Silva, L.P, Ramos, J.A., Olesen, J.M., Traveset, A. & Heleno, R.H. 2014. Flower visitation by birds in Europe. *Oikos* **123:** 1377–1383.

Siverio, M., González, E.I. & Siverio, F. 2010. Population size and status of Common Raven (*Corvus corax*) on the central-western islands of the Canarian archipelago. *Vieraea* **38:** 123–132.

Slauson, L.A. 2001. Insights on the pollination biology of *Agave* (Agavaceae). *Haseltonia* **8:** 10–23.

Symes, C.T., Mckechnie, A.E., Nicolson, S.W. & Woodborne, S.M. 2011. The nutritional significance of a winter-flowering succulent for opportunistic avian nectarivores. *Ibis* **153:** 110–121.

Traveset, A. & Richardson, D.M. 2006. Biological invasions as disruptors of plant-animal mutualisms. *Trends Ecol. Evol.* **21:** 208–216.

Trujillo, O. 1992. *Los Sílvidos en Gran Canaria*. Cabildo Insular de Gran Canaria, Las Palmas de Gran Canaria.

Valido, A., Dupont, Y.L. & Olesen, J.M. 2002. Native birds and insects, and introduced honey bees visiting *Echium wildpretii* (Boraginaceae) in the Canary Islands. *Acta Oecol.* **23:** 413–419.

Valido, A., Dupont, Y.L. & Olesen, J.M. 2004. Bird-flower interactions in the Macaronesian islands. *J. Biogeogr.* **31:** 1945–1953.

Vogel, S., Westerkamp, C., Thiel, B. & Gessner, K. 1984. Ornithophilie auf den Canarischen Inseln. *Plant Syst. Evol.* **146:** 225–248.

Walsh, J.C., Venter, O., Watson, J.E.M., Fuller, R.A., Blackburn, T. M. & Possingham, H.P. 2012. Exotic species richness and native species endemism increase the impact of exotic species on islands. *Global Ecol. Biogeogr.* **21:** 841–850.

Whelan, R.J., Ayre, D.J. & Beynon, F.M. 2009. The birds and the bees: pollinators behaviour and variation in the mating system of the rare shrub *Grevillea macleayana*. *Ann. Bot.* **103:** 1395–1401.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Meth. Ecol. Evol.* **1:** 3–14.