Importance of intraspecific variation in the pollination and seed dispersal functions of a double mutualist animal species

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Abstract

Although most plants depend on different animals for pollination and seed dispersal, sometimes the same animal species provides both functions, being thus involved in what has been termed a ‘double mutualism’. Very little is known on the effectiveness of such species as both pollinators and seed dispersers, and even less on the intraspecific level differences at the contribution of an animal mutualist to plant fitness. In this study, we focused on the interaction between a Mediterranean shrub *Cneorum tricoccon* (Rutaceae) and the Balearic lizard *Podarcis lilfordi* (Lacertidae) in order to assess: 1) the role of this lizard as a legitimate pollinator of the plant (previously thought to be exclusively insect-pollinated), and 2) the intraspecific variation in the use of flowers and fruits by lizard individuals, comparing males, females and juveniles. We further evaluated whether lizards show different fruit size selection depending on sex and age, with potential consequences for seed germination. Lizards visited more flowers and selected more hermaphrodite flowers than insects did, leading to relative increases in both fruit and seed set. Interestingly, female and juvenile lizards were the main flower visitors, whereas males were the main fruit consumers. Males selected the largest fruits (bearing the largest seeds) though this did not increase seed germination, which was only ca 15%. We concluded that *P. lilfordi* acts as a legitimate pollinator of *C. tricoccon* and, thus, confirm that this system constitutes a new case of double mutualism, especially common in island compared to mainland systems. Moreover, our findings show a large variation among conspecific individuals in their role as either pollinators or seed dispersers, with potential implications for plant reproductive success. Our study, therefore, highlights the importance of evaluating plant–animal interactions at the intraspecific level, and calls for more in-depth studies on the consequences of such intraspecific variation.

Keywords: *Cneorum tricoccon*, double mutualism, island ecosystems, Lacertidae, saurochory, saurophily

Introduction

Pollination and seed dispersal are two important processes for plant reproductive success (Neuschulz et al. 2016), which very often involve animals that pollinate and disperse the seeds when they visit the flowers and consume the fruits, respectively (Ollerton et al. 2011, Farwig and Berens 2012). Most animal-pollinated and -dispersed plants depend on different taxa for each function (Herrera and Pellmyr 2002). However, there are cases in which the same animal species provides pollination and seed dispersal services to the same plant species, a phenomenon called ‘double mutualism’ (Hansen and Müller 2009a). In a recent review, Fuster et al. (2019), reported ca. 300 potential cases of double mutualisms. However, little information still exists about them, mainly regarding the effectiveness of such mutualists in their double functions (Kelly et al. 2004, Hansen and Müller 2009a, Gomes et al. 2014, Olesen et al. 2018, Fuster and Traveset 2019). In some systems, as it has been documented for the Galápagos islands, double mutualisms may even belong to the core of the pollination-seed dispersal network (Olesen et al. 2018), i.e., double mutualist species are highly connected with other double mutualists, thus the two ecosystems functions operate as one functional unit. Islands, where double mutualisms are more frequently reported (Fuster et al. 2019), are ecosystems more prone to species extinctions due to frequent invasion by introduced species (Sax and Gaines 2008, Traveset et al. 2013). Such extinctions can cause disruptions of these prevalent mutualistic relationships and have dramatic consequences for the functioning of communities or ecosystems (*e.g.* Hansen and Müller 2009b, Bissessur et al. 2017). Hence, it is important, on the one hand, to detect such double mutualistic interactions and, on the other, to study the pollination and seed dispersal effectiveness of the partners involved (Schupp et al. 2017). The latter is indeed key information to know the dependency between the mutualist partners, and thus to predict how a disruption of one or both processes could affect such species.

Generally, effectiveness of pollinators and seed dispersers is measured at the species level, disregarding potential differences among conspecific individuals. However, a number of studies have shown inter-individual differences in their contribution to different components of effectiveness, e.g. different flower visitation rates or different pollination efficiency in their visits (Nyhagen et al. 2001, Rodríguez-Rodríguez et al. 2013, Fuster and Traveset 2019). Specialization and different preferences across conspecific insect individuals have also been found in pollen-transport networks (Tur et al. 2014). Similarly, intraspecific variation in animal seed-dispersers affects the seed dispersal process (reviewed in Zwolak 2018), influencing the size and number of flowers, fruits and seeds that can be handled, the distance that pollen or seeds are transported, and/or the habitats where seeds are deposited (e.g. González-Varo and Traveset 2016, Pérez-Méndez et al. 2018). Moreover, determining intraspecific variation both in animal mutualists and plants is important for the understanding of the mutualistic relationships (Snell et al. 2019 and references therein). Studies performed at the species level might mask the real function of intraspecific subgroups, as they may play different roles in the mutualism. However, there are yet few studies focused at assessing such roles (but see Rodríguez-Rodríguez et al. 2013, Tur et al. 2014, Pérez-Méndez et al. 2018, Zwolak 2018, Fuster and Traveset 2019).

Here, we studied a potential plant-lizard double mutualism, examining both pollination and seed dispersal services provided by lizards at the intraspecific level. We focused on the interaction between an endemic Mediterranean shrub (*Cneorum tricoccon* L., Rutaceae) and a Balearic endemic lizard (*Podarcis lilfordi* L., Lacertidae). Lizards, especially in island ecosystems, have been shown to play an important role as pollinators and seed dispersers of a wide range of plant species (Traveset and Sáez 1997, Olesen and Valido 2003, Olesen and Valido 2004, Traveset and Riera 2005, Valido and Olesen 2007, Rodríguez-Rodríguez et al. 2013, Gomes et al. 2014, 2016,

Celedón-Neghme et al. 2016, Nogales et al. 2017, Valido and Olesen 2019), and also as double mutualists (Fuster et al. 2019). Specifically, *P. lilfordi* visits flowers and consumes fruits of several plants (Pérez-Mellado and Traveset 1999, Pérez-Mellado et al. 2000), acting both as legitimate pollinator (e.g. Traveset and Sáez 1997, Celedón-Neghme et al. 2016) and legitimate seed disperser (e.g. Rodríguez-Pérez et al. 2012, Celedón-Neghme et al. 2013, Neghme et al. 2017). Previous studies showed that *P. lilfordi* visits the flowers of *C. tricocon*, considered entomophilous until now (Traveset 1995a), and that it also consumes the fruits and disperses the seeds (Traveset 1995b). However, the lizard role in the pollination of this plant and in some aspects of its seed dispersal remained unknown. Therefore, we firstly aimed at determining whether *P. lilfordi* constitutes a legitimate pollinator of *C. tricocon*, comparing its effectiveness with that of insects, in terms of fruit and seed set and germinability. Secondly, we wanted to determine whether there is intraspecific variation in the use of either flowers or fruits by male, female or juvenile lizards, specifically assessing potential differences among these groups in the quantitative component of both pollination and seed dispersal. Finally, we evaluated the size of seeds excreted by lizards in order to test if any differential selection for seed size exist, testing also this potential selection at plant germination level.

Material and Methods

Study area and species

We conducted the study at Sa Dragonera Natural Park (39° 35' N, 2° 19' E), an islet of 288 ha located ca. 800 m off the western coast of Mallorca Island, Balearic Islands (Mediterranean Sea). The islet has a Mediterranean climate and our study area has a vegetation dominated by shrubs of *C. tricocon* and *Pistacia lentiscus*, and where *Ephedra fragilis*, *Olea europaea*, *Phillyrea angustifolia*, *Pinus halepensis* and

Rosmarinus officinalis are also common. The islet has no carnivores that can prey upon lizards, and thus there is a high density of *P. lilfordi* (Pérez-Mellado et al. 2008).

Cneorum tricocon L. (Rutaceae), a western Mediterranean endemic, is a relict species from the Tertiary, which evolved under tropical conditions (Raven 1973). It is present in the Balearic Islands, and some remnant populations are found in the southern Iberian Peninsula and south-western France, as well as in some localities in the western coast of Italy. This shrub is approximately 1 m tall, and is an andromonoecious species, *i.e.* with hermaphrodite and male flowers in the same individual. Flowers are yellow ca. 7 mm long and 2 mm wide, with usually three carpels and stamens, occasionally two or four. Hermaphrodite flowers have a pistil slightly longer than the stamens; these stamens are longer in the male ones (Traveset 1995a). The plant is self-compatible and known to be insect-pollinated (Traveset, 1995a). However, *Podarcis lilfordi* L., an endemic Balearic lizard species from the Gymnesic Islands (Mallorca, Menorca, Cabrera and surrounding islets) has also been seen visiting the flowers in some islets (Fig. 1). The flowering period of *C. tricocon* lasts from October to June, with a maximum intensity during March and April. Ripe fruits are red with three cocci (with one seed inside each). They are present from April to July, and those that are not consumed can remain on the plant for more than a year. Its current native seed dispersers in the Balearics are exclusively the two endemics lizards (*P. lilfordi* and *P. pityusensis*, Fig. 1), although alien carnivores such as pine martens and genets – introduced in some of the larger Balearic Islands– also consume and disperse the seeds (Traveset 1995b), the former quite effectively and replacing lizards to some extent where these do not longer exist (Celedón-Neghme et al. 2013).

Visual censuses of flower visitors and fruit consumers

In order to analyze the quantity component of pollination effectiveness, we censused flowers visitors during periods of 15 – 20 min, randomly distributed from 8:00

h to 18:00 h. These censuses were conducted from early April to early May (covering the flowering peak of the species) on a total of 42 different individuals, i.e. focal plants (22 in 2015 and 20 in 2016), accumulating a total of ≈ 49 h and 60 h in 2015 and 2016, respectively. Each individual was observed 1 h minimum and ca. 4 h maximum, and individuals were separated at least 3 m from each other. We also carried out a total of 10 h of nocturnal censuses during 5 days, from 21:00 to 24:00, but no visitors were observed, which suggests that the plant is pollinated only during the day, at least in this islet. In every census, we recorded (1) the number of insects and lizards visiting the plant, (2) the number and type of flowers visited (hermaphrodite or male), (3) the time that each animal spent on the plant, as well as (4) the total number of open (available) flowers on the plant. We visually distinguished and classified lizards as juvenile, female and male. Adults are distinguishable from juveniles by their larger body size, and the two sexes are also easy to distinguish as males have larger and more robust bodies and heads than females (Salvador 2009). In this work, we considered as quantity component of pollination effectiveness (QNC) the hermaphrodite flowers visit rate, because these are the flowers that will develop fruits and seeds. We quantified nectar standing crop in the different flower types by collecting and measuring the volume of nectar with microcapillaries. Data were obtained from a total of 19 plants (8 in 2015 and 11 in 2016), in different days (3 plants per day), and from 3 – 8 flowers per plant (measuring a total of 65 hermaphrodite and 72 male flowers). We also measured nectar sugar concentration with a handheld refractometer (Bellingham & Stanley, Tunbridge Wells, Kent, UK). Measures were made between 9:00 – 11:00 h, in flowers bagged the night before, and thus not previously visited by any animal.

During the seed dispersal phase, when fruits were mature, we performed additional censuses of lizard visits to plants, specifically during June of 2016, recording fruit consumption. We again distinguished among males, females and juveniles. These

censuses were performed on the same 20 individuals used for flower visitor censuses in 2016, accumulating a total of ≈ 32 h. Observation followed the same scheme of 15 – 20 min from 8:00 h to 18:00 h. In every census we recorded the number of fruits consumed by each individual lizard as well as the number of ripe fruits present on the plant.

Pollinator exclusion experiment and breeding system

Towards the end of March 2015 and 2016, we set up an exclusion experiment to assess the contribution of insects and lizards to plant pollination success. In a total of 16 plants (10 in 2015 and 6 in 2016), we excluded lizards by means of a plastic fence around the plant across which they could not climb (Fig. S1). Another group of 16 individuals (10 in 2015 and 6 in 2016) were used as controls, i.e. they were opened to all pollinators. In every individual plant, we tagged and emasculated 10 – 15 hermaphrodite flowers prior to anthesis.

Another group of 14 individual plants (6 in 2015 and 8 in 2016) were used to assess the breeding system of the plant in this islet. In every plant, we tagged and used 3–5 hermaphrodite flowers for the following treatments: 1) *control* (flowers were left intact and open to all pollinators), 2) *geitonogamy* (previously emasculated flowers were hand-pollinated with pollen from flowers of the same individual), and 3) *xenogamy* (emasculated flowers were hand-pollinated with pollen from flowers of another individual located at least 10 m away). In the geitonogamy and xenogamy treatments, we used two sub-treatments (with 3–5 flowers of the same plant, keeping the same number of flowers in each sub-treatment as in the control), pollinating the flowers with pollen from either male or hermaphrodite flowers. After emasculation and previous anthesis, the flowers were kept bagged with cloth bags to avoid animal visits as well as to exclude arrival of pollen transported by wind (although there is no evidence of anemogamy in this plant species; Traveset 1995a), until the stigma was receptive to be hand-pollinated. We assumed that stigma was receptive when its shape and size was

visually equal to that of open flowers. After hand-pollinating them, the flowers were bagged again. Once the flowers of all the experiments developed into fruits, including the controls, they were kept bagged to avoid their loss before collection.

The fruits of all exclusion and breeding system treatments were collected once ripened in order to assess fruit and seed set, measure seed weight and conduct a germination experiment. Plant size was obtained from all individuals. This variable was measured as plant volume, considering the plant as a cylinder and thus we recorded its height and width.

Seed measures and germination experiment

All fruits and seeds resulting from all treatments were weighted. In order to test if lizards might exert any type of seed size selection and the possible consequences of this on seed germination, we also collected seeds from ca. 250 lizard scats (which contained between 1 – 3 seeds), in the same study area and both years. We measured them (to the nearest 0.1 mm) and tested their germination rate. We set up a germination experiment in a greenhouse at the IMEDEA institute. On October of 2015 and 2016, we sowed 70-100 seeds of each treatment (lizard exclusion and control) and 50 seeds of each of the five treatments of the breeding system experiment (geitonogamy with pollen from male flowers “GM” and from hermaphrodite flowers “GH”; xenogamy with pollen from male flowers “XM” and from hermaphrodite “XH”; and control “Cbr”). We randomly selected a similar number of seeds of each individual plant. Lastly, we planted 100 seeds haphazardly chosen from those extracted from the lizard scats. Seeds were sown in germination trays, only one seed per cell (cell dimensions: 4 x 4 x 4.4 cm), previously filled with universal substrate and watered every 2–3 days. Apex emergence (germination hereafter) from the two seed blocks (2015 and 2016) was recorded every 2–3 days during 18 months (including two autumn seasons, i.e. two mass germination events).

Data analysis

Nectar volume from different flowers type (males and hermaphrodites) was analyzed by means of a t-test. The visitation rate to hermaphrodite flowers (number of hermaphrodite flowers contacted $\times h^{-1}$, i.e. the quantity component of pollination effectiveness) was analyzed with generalized linear mixed models (GLMMs) fitting data to a gamma error distribution and using pollinator (insects vs lizards) as fixed effect (see Fig. 1). In order to control for floral display, which might influence pollinator attraction, we included the total number of flowers per plant as offset; census ID was nested within individual plant and included as random effect (i.e. each census conducted in each individual plant). We also tested for differences in the quantity component among different lizard age/sex subgroups (i.e. juveniles, adult females, and adult males) running a GLMM with the same structure than the previous model, but only including lizards visits. Finally, differences in flower selection (male vs hermaphrodite) between lizards and insects, i.e. the proportion of flowers of each type contacted (flowers contacted $\times$ flowers available $^{-1}$) per visit, were assessed by means of another GLMM fitting data to a gamma error distribution, including pollinator, flower type and their interaction as fixed effects, and census ID nested within individual plant as random effect.

Differences in fruit consumption (fruits consumed $\times h^{-1}$), i.e. quantity component of seed dispersal effectiveness, among different lizard subgroups were tested with another GLMM with gamma error distribution, using lizard subgroup as fixed effect, census ID nested within individual plant as random effect, and this time including the total number of fruits per plant as offset in order to control for fruit display.

To test for differences in fruit and seed set among treatments (both in the exclusion and the breeding system experiment), we used GLMMs fitting data to a binomial error distribution in the case of fruit set, and to a negative binomial

distribution in the case of seed set, in order to deal with overdispersion (see Fig. 1). We included treatment (control and lizard excluded in the case of exclusion experiment; and Cbr, GM, GH, XM and XH treatments, previously defined for the breeding system experiment) and plant size as predictors, and individual plant as a random effect.

The correlation between fruit and seed weight was explored by means of a GLMM fitting data to a gamma error distribution, including fruit weight as fixed effect and plant ID as random effect. We used data from fruits and seeds only from control plants of the breeding system experiment, thus from non-emasculated (and not altered) flowers. Although individual variation was already considered in the previous GLMM, which considered plant ID as random factor, we further explored if such variability indeed exists in seed weight; for this, we used plant ID as fixed effect. The effect of treatment on seed weight was analyzed by means of GLMM fitting data to a gamma error distribution, including the same fixed and random effects as in the previous model. The potential selection on seed size exerted by lizards was tested by comparing the weight of the lizard-dispersed seeds with that of control seeds (gathered from the open-pollinated, non-emasculated flowers); a GLM fitting data to a gamma error distribution was performed, including as fixed effects: treatment (dispersed seeds vs control), year (to know whether the potential selection was year-dependent), and their interaction.

Finally, different tests were carried out with seed germination data (see Fig. 1). First, we compared germinability (% of germinated seeds) among the exclusion treatments (control vs lizard-exclusion). Second, we compared the five different treatments from the breeding system experiment (Cbr, GM, GH, XM and GH). Both tests were performed using GLMMs, including individual plant as random effect. And third, a GLM tested for differences between the two controls (both emasculated and non-emasculated) and lizard-dispersed seeds. The three sets of models were performed

considering a binomial error distribution and using treatment, seed weight, and their interaction as fixed effects.

All analyses were performed with the R software (version 3.3.3.; R Development Core Team 2017). GLMs and GLMMs with gamma and binomial distributions were fitted with “glm” and “glmer” functions, respectively, and with the “glmer.nb” function in the case of negative binomial distribution (package lme4; Bates et al. 2015). The Akaike information criterion corrected for small sample sizes (AICc; Zuur et al. 2009) was used in all models to select the best ones (i.e. those with lowest AICc values). This model selection was done using the “dredge” function in the “MuMIn” package (Barton 2016). Models with $\Delta\text{AICc} \leq 2$ were considered to be equivalent.

Results

A total of 142 lizard and 187 insect visits were recorded on the flowers of *C. tricocon*. The number of hermaphrodite flowers visited by lizards, i.e. the lizard quantity component of pollination effectiveness (QNC) was threefold the number visited by insects ($\chi^2 = 13.95$, $df = 1$, $P < 0.001$; Fig. 2a). Although similar number of female, juvenile and male lizards visited the plants (50, 43 and 49 lizards respectively), the number of hermaphrodite flowers visited varied significantly among these lizard subgroups ($\chi^2 = 16.95$, $df = 2$, $P < 0.001$; Table S1). Females and juveniles were the most frequent visitors (Fig. 2b). Lizards were not interested in the stamens or pollen but searched for nectar at the bottom of flowers. In addition, lizards and insects showed different flower preferences ($\chi^2 = 6.14$, $df = 1$, $P = 0.013$). While insects preferred male over hermaphrodite flowers, lizards visited similar proportions of both flower types, but selected more hermaphrodites than insects (Fig. 2c). Hermaphrodite flowers produced 1.72 times higher amounts of nectar than male flowers ($t = 4.76$, $df = 32.24$, $P < 0.001$;

T-test; Fig. 2d). Sugar concentration of such nectar was higher than 50% in both flower types; unfortunately, a more precise estimate could not be taken in the field.

Both, fruit and seed set were consistently higher in open-pollinated plants than in lizard-excluded ones in all models (see Table S1 and Fig. 3ab), indicating that lizards do contribute significantly to pollination. In the breeding system experiment, fruit and seed production did not differ among treatments (Cbr, GM, GH, XM, XH), and thus the selected models did not include this variable (Table S1). Plant size showed a positive effect on fruit set, i.e. larger individuals set more fruits proportionally to the number of flowers than smaller ones (Table S1 and Fig. S2).

During the fruiting period, lizards were the only fruit consumers and, again, differences between lizard subgroups were found. A total of 19 records of females, 1 of juvenile, and 27 of males visiting the plants were registered. Male lizards showed higher fruit consumption rate than either females or juveniles ($\chi^2 = 10.79$, $df = 2$, $P = 0.005$; Fig. 3c).

Strong differences were observed among individual plants in seed weight ($\chi^2 = 111.5$, $df = 6$, $P < 0.001$), although this variable did not differ between control and the lizard-exclusion treatment, thus treatment was not considered as predictor variable in the selected models (Table S1). Seed weight was found to be positively associated to fruit weight ($\chi^2 = 155.2$, $df = 1$, $P < 0.001$); it was also affected by plant size, both in the exclusion and the breeding system experiments (Table S1; Fig. S3ab). Some differences in seed weight were detected when comparing treatments in the breeding system experiment, although only in 2015: XM seeds were significantly lighter (30.89 ± 1.19 mg, $N = 63$) than either control (35.00 ± 1.81 mg) or GM seeds (34.42 ± 1.78 mg) ($Z = 3.19$, $P = 0.013$; $Z = 2.98$, $P = 0.024$; respectively). An interaction effect between treatment and year was thus found when comparing the weight of control seeds (not emasculate) and lizard-dispersed seeds ($\chi^2 = 7.62$, $df = 1$, $P = 0.006$; Table S1). Seeds

dispersed by lizards were heavier than control seeds in 2015 ($Z = 4.75$, $P < 0.001$; Fig. 3d) but not in 2016 ($Z = 0.89$, $P = 0.809$). Moreover, control seeds were heavier in 2016 than in 2015 ($Z = 2.94$, $P = 0.017$).

Seed germination was rather low, being ca. 11% in control (not emasculated) seeds and 15% in lizard-dispersed seeds. No differences were found in germination between either the exclusion treatments or the breeding system treatments; likewise, no differences existed between control and lizard-dispersed seeds (Table S1).

Discussion

Our study confirms that *P. lilfordi* acts as a legitimate pollinator of *C. tricocon* and, thus, this system constitutes a new case of double mutualism (Fuster et al. 2019), as the lizard also disperses its seeds legitimately. This is actually the second case of this phenomenon reported from Europe, specifically from the Balearic Islands, showing the importance that some vertebrate species can have for some plants in the fragile island ecosystems (Bellard et al. 2017). Our results also highlight the importance of accounting for intraspecific variation in both functions –pollination and seed dispersal– of the double mutualism. Adult female and juvenile lizards were the main pollinators whereas adult males were the most important seed dispersers. Hence, there is a segregation of mutualistic function between lizard subgroups, underlining the importance of each subgroup to maintain both pollination and seed dispersal functions. To the best of our knowledge, this segregation of functions within the same animal species for the same plant species had never been reported, and we hypothesize that it could be more widespread than previously thought in other mutualistic interactions.

Lizard implication in the double mutualism

Although *C. tricocon* was considered an insect-pollinated plant (Traveset 1995a), we demonstrated that both insects and lizards act as legitimate pollinators.

Thus, the plant presents a mixed pollination system, similar to that described for other species, whereby both insects and vertebrates contribute to pollination success (*e.g.* Ortega-Olivencia et al. 2012, Gomes et al. 2014, Celedón-Neghme et al. 2016, Fuster and Traveset 2019). We indeed found that lizards in Dragonera Island were quantitatively more important than insects, as reported for another plant species in this island, *Ephedra fragilis* (Celedón-Neghme et al. 2016, Fuster and Traveset 2019), and in other systems (*e.g.* Traveset and Sáez 1997, Hansen et al. 2007, Gomes et al. 2014). Moreover, lizards preferred hermaphrodite over male flowers, possibly attracted by their higher nectar production (although the patterns of nectar secretion should be assessed more precisely in further studies), whereas insects visited higher proportions of male flowers. A previous study in New Zealand (Eifer 1995), specifically with the perennial herb *Phormium tenax*, already reported flower selection by geckos as a function of nectar production. A higher visitation of hermaphrodite flowers might in turn increase plant fruit crop, as these flowers are those developing into fruits. Although we cannot know the exact contribution of lizards to pollination quality, our results evidence a positive effect, increasing both fruit and seed set as compared to plants only pollinated by insects. The breeding system experiment indicated that either fruit or seed set did not depend upon pollen origin, i.e. on whether the pollen was from the same individual or a conspecific. Thus, the increase in fruit production in lizard-visited flowers was probably due to the higher frequency of flower visits compared to insects and also to the large number of pollen grains they probably deposit on the stigmas.

Seed weight may sometimes depend on pollinator identity (*e.g.* Celedón-Neghme et al. 2016), but this was not the case here. Both lizard and insect pollination produced seeds of similar weight. Likewise, seed germinability did not depend either on pollen origin or the pollinator agent implicated; hence, lizards and insects seem to

promote the production of seeds of similar quality, i.e. they are similarly efficient as pollinators of *C. tricocon*.

Regarding the seed dispersal process, lizards are the main seed dispersers of this plant in Dragonera Island (Celedón-Neghme et al. 2013), although some seeds have been occasionally observed in gulls' regurgitations (Calviño-Cancela 2011). In the larger Balearic Islands, Mallorca and Menorca, alien carnivores (specifically, pine martens and genets) are the responsible of dispersing *C. tricocon* (Riera et al. 2002), even having influenced the distribution of this shrub in Mallorca (Rotllan-Puig and Traveset 2016). A closely related species to *C. tricocon*, *Neochamaelea pulverulenta* (Vent.) Erdtman, endemic to the Canary Islands, is also dispersed –in this case exclusively– by endemic lizards in the *Gallotia* genus (Valido and Nogales 1994, Pérez-Méndez et al. 2016). We found that lizards selected larger fruits (defecating thus larger seeds) although this showed to be not consistent in time, as we detected such selection in 2015 but not in 2016. Seeds were generally heavier the second year, what we attribute to better abiotic conditions (e.g. higher water availability; mean precipitation during fruiting period (April – July) was 68.1 mm in 2016 compared to 18.6 mm in 2015; source: AEMET). Thus, lizards could be exerting a selective pressure on seed size mostly on dry years, when seeds might be generally smaller. Similarly, in another study (Traveset et al. in press), *Podarcis* lizards were found to select larger fruits in populations with small fruits. Given that seed weight is usually associated to germination and survival probability (Norden et al. 2009, Kolodziejek 2017, Ruiz et al. 2017), lizards likely also enhance germination and seed survival probability by selecting larger seeds in seasons when small seeds are produced.

Intra-specific segregation in the mutualistic functions

Not all lizard individuals played the same or similar role in the two processes of the double mutualism. Females and juveniles invested more time searching for nectar,

and thus made frequent visits to the flowers of *C. tricocon*, being quantitatively more involved in pollination than males. This interesting finding is consistent with that of another study carried out in Mauritius with *Lomatophyllum tormentorii* and *Gastonia mauritiana* plants, whose flowers are more frequently visited by female than by male geckos (Nyhagen et al. 2001). Curiously, however, we found the opposite in *Ephedra fragilis* in the same Dragonera Island, i.e. adult males of *P. lilfordi* were the most important flower visitors of this plant whilst juvenile visits were very scarce (Fuster and Traveset 2019). In at least one other study, adults of *Phelsuma sundbergi* geckos were reported to displace smaller conspecifics from flowering plants (Cheke 1984). It may thus be a general pattern that individuals of the same animal species may show different flower visitation patterns (Smith et al. 2019). Whether one sex visits more flowers than the other is probably context-dependent and it is influenced by several factors, including energy requirement by each sex or stage during the particular flowering period, availability of other food sources or territoriality of the species. (e.g. Durtsche 2000, Fialho et al. 2000, Rodríguez et al. 2008, Mata et al. 2016)

Flower visitation rate related to the quantitative component of pollination effectiveness may, however, not be associated to the quality component (Calviño-Cancela and Martín-Herrero 2009) and, thus, both must be analyzed (Schupp et al. 2017). For instance, Rodríguez-Rodríguez et al. (2013) found that adult *Gallotia* lizards in the Canary Islands visited fewer flowers than juveniles, but the efficiency of the former in terms of viable seeds produced was higher. Moreover, our results highlight that both quantitative and qualitative components need to be considered also at the intraspecific level, to determine the contribution of each subgroup to pollination success. The same holds for the seed dispersal process; both components of seed dispersal effectiveness can be influenced by intraspecific variation in the animal dispersers (see review in Zwolak 2018). For instance, sexual dimorphism in body size

and morphology might influence the size range and the number of manipulated, or ingested, fruits and seeds. The sexual dimorphism present in the behavior and in the cognitive functioning might also affect the number of dispersed seeds, the dispersal distance and the type of habitats where seeds are deposited (Wenny and Levey 1998, Karubian and Durães 2009). However, very little information still exists on this aspect (Zwolak 2018). In the case of *C. tricocon*, male lizards were the main fruit consumers and subsequent seed dispersers. They are often aggressive when defending their territory; in fact, on several occasions, we observed males pushing away females and juveniles that tried to climb the plants where they were feeding. Larger individuals, with wider heads and mouths, are capable of ingesting larger sizes of fruits, which might affect seed germination for some species, though it does not seem to be the case of *C. tricocon*. Seeds excreted by large lizards might also germinate faster which could be advantageous under some circumstances, as reported by Pérez-Méndez et al. (2018). In our system, thus, lizard subgroups are involved in different ways in the pollination and seed dispersal processes: while females and juveniles are the main pollinators, males are the most important dispersers, but all of them contribute to plant fitness.

The causes of intraspecific segregation in the mutualistic functions and resource use may be diverse. One possibility is that while females and juveniles get sufficient energy from nectar, which is easily accessible to them, males are foraging for animal prey during the flowering season of *C. tricocon*. The larger size of males may limit their ability to manipulate flowers to access the nectar and pollen; moreover, climbing the plants might suppose a greater effort for males than for females and juveniles, given the higher weight. On the other hand, fruits may provide more energy than flower nectar, compensating the effort invested by males to obtain them. Resource segregation within a species has already been reported in lizard populations (Kaliontzopoulou et al. 2012, but see Santamaría et al. 2019) as well as in other animal groups (*e.g.* Leung et al.

2012, Miranda et al. 2012, Wan et al. 2013, Mata et al. 2016). It has been hypothesized as a way to avoid intraspecific competition between different sexes or age groups (Barboza and Bowyer 2000, but see Main 2008). In areas with few food resources and high animal densities of some species, like those often found in islands, such segregation could perhaps be more likely. Intraspecific variation in the contribution to pollination or seed dispersal mutualisms is increasingly being reported in different systems (Rodríguez-Rodríguez et al. 2013, Tur et al. 2014, Fuster and Traveset 2019). Further studies considering such inter-individual differences may in fact help us to better understand the functioning of these ecological processes (González-Varo and Traveset 2016, Zwolak 2018, Smith et al. 2019).

In conclusion, the results of our study are twofold: on the one hand, we show that *P. lilfordi* acts as a legitimate and important pollinator of *C. tricocon*, and thus acts as a double mutualist of this plant, as it is also its main seed disperser. On the other hand, by focusing on the intraspecific level, we unveil a resource segregation in the double mutualism functions, as female and juvenile lizards are the main nectar consumers and pollinators whereas males are the main fruit consumers and seed dispersers. This intraspecific variation in the mutualistic functions is still little documented although we believe it could be more widespread than previously thought. Focusing on either the animal population or individual level may result in different mutualistic performance, potentially having important implications for plant fitness. At the population level, lizard population density might remain unchanged despite high variation at the individual or intraspecific group level in their density or behaviour regarding a specific mutualistic service, which could affect plant fitness. In our system, for instance, if lizard population density does not show changes but the number of males (mainly involved in seed dispersal process) is altered, seed dispersal success might decline accordingly. Focusing at the lizard population level, we would not predict such

decline. In another scenario, lizard population density could be altered but mostly due to changes in number of females rather than males; in this case seed dispersal success would be expected to be less affected than pollination success. However, considering that our plant-lizard system is a double mutualism, the consequences of such alterations in the lizard densities are a bit more complex to foresee. Thus, for instance, even if the number of males remains unaltered, plant fitness could still be affected as, pollination might decline due to the alteration of female or juvenile groups, resulting in less fruits to be dispersed. In short, the intraspecific variation and its implication is an important aspect of the mutualistic interactions. Such importance has already been underlined and discussed in the literature (Fortuna et al. 2008, Dupont et al. 2011, Gómez and Perfectti 2012, González-Varo and Traveset 2016, Zwolak 2018, Smith et al. 2019) and our study, therefore, provides empirical evidence for the claim that future studies on mutualistic interactions should address such variation and its consequences.

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Figure Legends

Figure 1. Diagram of the study components and models tested. In the fixed factor column ‘+’ means that both variables were used as fixed factors; and ‘x’ means that both variables and their interaction were used as fixed factors. Abbreviations: Cbr (control flowers not emasculated), GM and GH (geitonogamy pollination with male and hermaphrodite pollen, respectively), XM and XH (xenogamy pollination with male and hermaphrodite pollen, respectively), Cex (control flowers emasculated previous anthesis). Photo credits: F.Fuster (flower and pollination) and X. Rotllan-Puig (seed dispersal).

Figure 2. Hermaphrodite flowers visitation rate (flowers visited $\times$ h⁻¹) of insects and lizards (a) and of different lizard subgroups (b). Proportion of flowers contacted in every visit (flowers of each type contacted in every visit $\times$ flowers of each type available into the plant⁻¹) of insects and lizards (c). Nectar standing crop of hermaphrodite and male flowers (μ l $\times$ flower⁻¹) (d). Values show mean $\pm$ SE (standard error) in (a), (b) and (c). Different letters above the bars indicate significant differences (Tukey's post hoc tests, $P < 0.05$).

Figure 3. Fruit set (% flowers that made fruits) (a) and seed set (number of seeds x flower⁻¹) (b) resulting from the lizard exclusion experiment (plants open to pollination -control- and plants only pollinated by insects). Fruit consumption (fruits consumed x hour⁻¹) by different lizard subgroups (c). Values show mean $\pm$ SE (standard error). Seed weight of control (not emasculated flowers) and lizard-dispersed seeds in 2015 and 2016 (d). Different letters above the bars indicate significant differences (Tukey's post hoc tests, $P < 0.05$).