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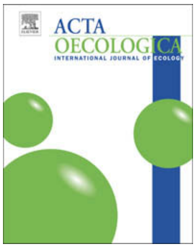

Original article

The town Crepis and the country Crepis: How does fragmentation affect a plant–pollinator interaction?

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ABSTRACT

In fragmented habitats, one cause of the decrease of plant diversity and abundance is the disruption of plant–animal interactions, and in particular plant–pollinator interactions. Since habitat fragmentation acts both on pollinator behaviour and plant reproduction, its consequences for the stability of such interactions are complex. An extreme case of habitat fragmentation occurs in urbanised areas where suitable habitat (in the present study small patches around ornamental trees) is embedded in a highly unsuitable environment (concrete matrix). Based on simple experiments, we ask whether pollinators can adapt their foraging behaviour in response to the amount of available resources (flowers) in the fragments and their isolation, as predicted by the optimal foraging theory. To do so we analysed the effect of fragmentation on the behaviour of pollinators visiting *Crepis sancta* (L.) Bornm. (Asteraceae), which forms large populations in the countryside and patchy populations in urban environments. More precisely we studied pollinator visitation rates, capitulum visit durations, capitulum search durations and capitulum size choice. Pollinators chose larger capitula in both types of populations and their foraging behaviour differed between the two population types in three ways: (1) pollinator visits were lower in urban fragmented populations, perhaps due to the lower accessibility of urban patches; (2) capitulum visit durations were longer in urban fragmented populations, a possible compensation of energy lost during flights among patches; and (3) capitulum search durations where longer in urban fragmented populations, which may represent an increase in capitulum prospecting effort. We discuss the possible impacts of such differences for plant population functioning in the two types of populations.

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1. Introduction

Species' responses to habitat fragmentation *sensu lato* can be complex because this mechanism can involve a reduction of total area of habitat, a decrease of the size of the fragments, an increase of their isolation and/or a change in their spatial arrangement (Saunders et al., 1991; Haila, 2002; Fahrig, 2003). In fragmented areas, plant diversity and abundance can decrease

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as a result of specific threats imposed by small population size, which can lead to lower performance and population dynamics in fragments. Individuals can thus suffer from demographic, environmental and genetic stochasticities (Matthies et al., 2004; Willi et al., 2005). The consequences of the latter can be particularly severe and may involve a range of different processes, e.g. the loss of auto-compatibility alleles due to genetic drift, increased inbreeding, and genetic erosion (Lande, 1988; Menges, 1991; Ellstrand and Elam, 1993; Young et al., 1996). However, the effects of fragmentation can also be indirect, through the disruption of plant–animal interaction, and particularly of plant–pollinator interactions (Kearns et al., 1998; Harris and Johnson, 2004; Aguilar et al., 2006; Biesmeijer et al., 2006; Fontaine et al., 2006). Considering the importance of pollinators in the reproduction of angiosperms and in agronomy, studying their response to fragmentation is particularly of concern (Kearns et al., 1998; Harris and Johnson, 2004, Steffan-Dewenter et al., 2005).

Fragmentation can affect pollinator communities in different ways. First, they can be affected both by the lack of suitable habitat and the fragmentation of their resources (McIntyre and Hostetler, 2001; Cane et al., 2006), which can in turn affect plant performance (Ward and Johnson, 2005). Second, as predicted by the optimal foraging theory (Charnov, 1976; Stephen and Krebs, 1986), pollinators may adapt their foraging behaviour depending on the amount of available resources and their spatial arrangement. In a fragmented context, pollinators can thus change their foraging behaviour (Goverde et al., 2002) to maintain their energetic gain depending on plant reward in fragments and flight distance among fragments. Moreover, pollinator abundance can decrease due to the lower attractiveness of isolated fragments or to the small population size or density of flowering plants (Steffan-Dewenter and Tscharntke, 1999; Goverde et al., 2002; Cheptou and Avendano, 2006). The change of pollinator behaviour can lead to pollen limitation and reduced seed set, and/or to a limitation of gene flow among fragments (Menges, 1991; Groom, 2001; Ward and Johnson, 2005). Since pollinators can drive the evolution of floral traits (reviewed in Kingsolver et al., 2001; see also Totland, 2001; Perez-Barrales et al., 2007), variation in pollinator behaviour between fragmented and continuous populations could thus select for different floral traits among them.

An extreme case of habitat fragmentation is urbanised areas, where suitable habitat is embedded in a very unsuitable environment (concrete matrix). In this study, we analysed the effect of fragmentation on pollination process using a Mediterranean ruderal species *Crepis sancta* (L.) Bornm. (Asteraceae). This species forms large populations in the countryside which contrast with small "patchy" populations in urban environments. The aim of this study was to quantify how urban fragmentation affects plant–pollinator interactions by comparing pollinator behaviour in urban populations (small patches of suitable habitats around ornamental trees regularly spaced along the street pavement) with that in large continuous populations of *C. sancta* in countryside in the same region. In urban populations, we predict, according to the optimal foraging theory, that pollinators compensate energy lost in the flights among the patches and the rarity of the resource. First, resources should be better exploited at the capitulum level, which can translate into an increase of capitulum visit durations. Second, resources should be better exploited at the patch level (exploitation of the maximum of available capitula), which can translate either into an increase of capitulum search duration within patches or, if pollinators are more attracted by the largest capitula that are expected to be more rewarding, into a relaxation in capitulum size choice. By comparing urban and countryside populations, we thus assessed whether fragmentation causes differences in: (1) pollinator visitation rates; (2) capitulum visit and search durations; and (3) capitulum choice.

2. Materials and methods

2.1. *Study species*

Crepis sancta (L.) Bornm. (Asteraceae) is an herbaceous annual growing in disturbed habitats (vineyards, wastelands) or in young successional stages of abandoned fields of the Mediterranean region. Germination occurs in autumn after the onset of rain and rosettes grow in winter. *Crepis sancta* is one of the earliest flowering species in the study region, and produces 1–90 capitula per plant from February to April. This species can form large population of several thousands of individuals blooming synchronously during 6–8 weeks. Pollination is strictly entomophilous and generalist honeybees (*Apis mellifera*) are by far the most frequent pollinators but other hymenopterans can be observed. The inflorescence is composed of several dozens of florets each producing small amounts of nectar. *Crepis sancta* is a self-incopatible highly outcrossing species, albeit with low and variable levels of selfing (Cheptou et al., 2002). Two types of achenes are produced: a small number of peripheral achenes (3–10 per capitulum) without a pappus and numerous central achenes (70–100 per capitulum) with a pappus (Imbert et al., 1996).

2.2. *Study sites*

We studied large continuous populations (several thousands of individuals) that occur in the countryside and highly fragmented populations that can be found in urbanised areas. We selected sites in southern France: two large continuous populations in abandoned old fields, near Saint Mathieu-de-Tréviers (03° 51′ 36″ E, 43° 45′ 10″ N and 03° 51′ 44″ E, 43° 45′ 10″ N, 100 m a.s.l.) 20 km north of Montpellier, and two urban populations in Montpellier at Jacques Cartier avenue (03° 53′ 35″ E, 43° 36′ 25″ N, 60 m a.s.l.) and Henry Marès avenue (03° 51′ 21″ E, 43° 37′ 14″ N, 60 m a.s.l.). Urban populations grow in small suitable habitats (1–2 m^2) around ornamental trees regularly spaced (each 6–10 m) along the street pavement (hereafter called 'patches'). Due to the absence of management by public authorities, patches are colonised by early succession plant species (95 species identified in 2005, dominated by *Stellaria media* L., *Crepis sancta* (L.) Bornm, *Sonchus oleraceus* L., *Poa annua* L. and *Senecio vulgaris* L., F. Beilhe, unpublished). Each patch constitutes a deme with small population size (0–40 *C. sancta* individuals).

2.3. Experiment design

Pollinator surveys were done in 2006 and 2007, both in country and in urban populations. All were run over during sunny and warm days without wind and over a short period during the day (from 11:00 to 15:00 h) corresponding to the maximal activity period of pollinators and to the opening period of *C. sancta* capitula.

2.3.1. *Pollinator surveys: visitation rate, pollination route and capitulum choice*

In order to examine whether capitulum visit durations and capitulum search durations differ between the two population types, the pollinator route was followed in both population types in 5–21 April 2006 (hereafter 'duration experiment'). In this experiment, all observations were performed on the honeybee *Apis mellifera*, the most active pollinator. For each individual, a top was recorded on minidisk each time it lands on or takes off a *C. sancta* capitulum, and durations (s) were calculated with Audacity 1.3 Beta® software.

We examined whether pollinators choose *C. sancta* capitula depending on their size (diameter in mm), i.e. whether the size of chosen capitula was higher than the size of non-visited ones. We carried-out 30-min pollinator surveys in urban patches (03/13/07–04/04/07, $n = 27$ surveys) and in 2 m^2 quadrats haphazardly located in large populations (02/27/07–03/12/07, $n = 24$ surveys) (hereafter 'diameter experiment'). Differences in survey periods were due to phenological gap between the two population types. Diameter of all *C. sancta* capitula in the patches or in the quadrats were measured, and visited and non-visited capitula were recorded for each individual pollinator. Additionally, the experiment allowed comparing the number of pollinator visits and the number of visited capitula between the two population types.

To determine whether capitulum size choice was done at a local scale (i.e. among the closeness capitula), we used the duration experiment, where every visited capitula was marked with a coloured adhesive tape in order to find again them easily and measure their diameter and the diameter of the five closest non-visited *C. sancta* capitula. Finally, to test whether capitula sizes were linked to their maturity, we estimated maturity visually (1 = few mature florets, 2 = intermediate number of mature florets, 3 = nearly all or all florets were mature).

2.3.2. *Experimental manipulation: capitulum choice at local and coarser scales*

In order to detect whether the choice of capitula depending on their size was done at a the scale of a group of capitula, we compared visitation rates in pairs of quadrats (0.8 ∗ 0.8 m, 1 m away) in which we experimentally manipulated capitulum diameter in a large population of the experimental CEFE-CNRS gardens in Montpellier (hereafter 'choice experiment'). This experiment involved selectively cutting either large or small capitula in such a way that the final number of capitula was the same in the two quadrats. Three 1-h surveys were done (5, 9 and 26 March 2007): we counted the number of pollinators entering in each quadrat and for each one the number of visited *C. sancta* capitula.

2.4. Data analyses

Statistical analyses were performed using Statistica 7.0 and R, and we give in the text the mean ± SE of non-transformed data. Non-parametric tests were used when there were violations of assumptions of parametric tests, even after appropriate transformations.

Differences in capitulum visit durations or capitulum search durations between urban populations and country populations (duration experiment) were assessed with *t*-tests after logarithmic transformation that homogenised variances.

To examine whether pollinators choose capitula depending on their size in quadrats and patches of the two population types (diameter experiment) and whether this relation differed between populations, we used a mixed generalised linear model (glmer function in lme4 package, R) with a Binomial function link (model: visitation = population type + capitulum diameter - + population type × capitulum diameter), with population type as a fixed effect and capitulum diameter varying randomly between quadrats. Due to the too low number of visited quadrats, the two studied populations in each population type were pooled. To reach sufficient sample sizes, only patches and quadrat in which at least nine capitula were visited or not by a pollinator were used (urban populations $n = 3$; country populations $n = 11$).

To examine whether pollinators choose capitula depending on their size at a fine scale, differences in capitulum diameter between visited capitula and at the most the five closest capitula (duration experiment) were assessed by ranking them depending of their size (except capitula already visited). Thus, if a visited capitulum was larger than the closest capitula, its rank was assigned as 1. For each visited capitulum, a random distribution of ranks was generated and the mean rank of visited capitula was compared to the mean rank of the random distribution with a Wilcoxon rank sum test in each population type. Capitulum ranks were compared between population types.

To examine whether pollinators choose capitula depending on their size at a the scale of a group of large or small sized capitula, we compared the number of pollinator visits and the total number of visited capitula between manipulated quadrats for each survey date (choice experiment) with χ^2 tests. A random nested ANOVA was used to compare the numbers of visited capitula by each pollinator (after square root transformation that homogenised variances, model: number of visited capitula = survey date + quadrat type (survey date)).

Relations between pollinator visits (number of pollinator visits or number of visited capitula in the quadrats) and *C. sancta* resource (number of capitula, mean capitulum diameter per quadrat) were examined with Spearman correlations (diameter experiment, country population data). In order to detect whether capitulum diameter depended on their maturity, diameters were compared among capitula differing by their maturity level with Kruskall–Wallis ANOVA (duration experiment).

3. Results

In the duration experiment, we followed pollination routes of 22 honeybees (*A. mellifera*) in country populations and of three honeybees in urban populations (due to the scarcity of pollinators in this habitat). However, the number of visited capitula by route was substantial (9–127). Capitulum visit duration was longer in urban populations (9.16 ± 1.32 s) than in country populations (4.41 ± 0.15 s) ($t_{1007} = 4.19$, $p < 0.001$). Capitulum search duration was longer in urban populations (2.79 ± 0.38 s) than in country populations (1.42 ± 0.04 s) ($t_{981} = 5.26$, $p < 0.001$), even when search durations corresponding to the way between two patches in urban populations were not taken in account (2.35 ± 0.30 s) ($t_{978} = 4.13$, $p < 0.001$).

In the diameter experiment, 18/24 quadrats were visited by at least one pollinator in country populations (49 pollinator visits), and only three patches on 32 were visited in urban populations (seven pollinator visits) (Fig. 1). *Apis mellifera* was the pollinator observed in country populations, whereas in urban patches we observed some undetermined small hymenopterans (57% of the observations). At the quadrat and patch levels, pollinators chose larger capitula: in each population type, visited capitula had a significantly higher diameter (country populations: 2.14 ± 0.03, urban populations: 2.18 ± 0.04) than non-visited capitula (country populations: 2.02 ± 0.03, urban populations: 2.00 ± 0.05, $z = 2.774$, $p < 0.01$, Fig. 2), and the interaction between population type and capitula diameter was not significant ($z = -1.386$, $p > 0.05$). In the duration experiment, the mean size rank of the visited capitula among the closest capitula was more frequently 1 (64.6% of the case in country populations, 47.2% in urban populations). The chosen capitulum was in general larger than the closest non-visited capitulum. The mean rank of the random distribution (country populations = 2.3, urban populations = 2.5) is significantly different from mean rank of the visited capitula (country populations = 1.6, urban populations = 1.9) (country populations: $p < 0.001$; urban populations: $p = 0.007$). Capitulum ranks do not differ between population types ($U = 1954$, $p < 0.05$).

In the choice experiment, pollinators did not choose groups of *C. sancta* with large capitulum size vs. groups with small capitulum size (Table 1). First, the number of pollinators visiting capitula did not differ between the two types of manipulated quadrats for the three survey dates ($\chi^2_2 = 0.03$; $p = 0.983$), neither did the number of visited capitula ($\chi^2_2 = 1.42$; $p = 0.493$). Moreover, the number of visited capitula by pollinator visit did not differ between the two types of manipulated quadrats ($F_{5,88} = 1.31$, $p = 0.268$; survey date effect: $F_{2,6.1} = 4.79$, $p = 0.056$; quadrat type (survey date) effect: $F_{3,88} = 0.47$, $p = 0.704$). In this experiment, all the observed pollinators were *A. mellifera* individuals.

In the diameter experiment, the number of pollinator per quadrat was not correlated with the number of capitula ($R_{sp} = 0.238$, $p = 0.241$) or with capitulum diameter ($R_{sp} = 0.017$, $p = 0.945$). The number of visited capitula per quadrat or patch was correlated with the number of capitula ($R_{sp} = 0.677$, $p = 0.002$) but not with capitulum diameter ($R_{sp} = 0.256$, $p = 0.306$). In urban population, the number of capitula per patches was higher (41.8 ± 3.0, $n = 24$) than in quadrats of country population (26.7 ± 1.7, $n = 32$) (Mann–Whitney *U*-test = 597.0, $p < 0.001$) and capitulum diameter was smaller (1.99 ± 0.01, $n = 1338$) than in country population (2.10 ± 0.01, $n = 640$) (Mann–Whitney *U*-test = 488,797.0, $p < 0.001$). In duration experiment, capitulum diameter was higher in higher levels of capitulum maturity (country populations $H = 20.50$, $p < 0.001$, urban populations $H = 14.49$, $p < 0.001$), e.g. in country populations, the diameter of capitula is 15.8 ± 1.13 mm in maturity class 1, 19.7 ± 0.30 mm in class 2 and 20.9 ± 0.32 mm in class 3 (Fig. 3).

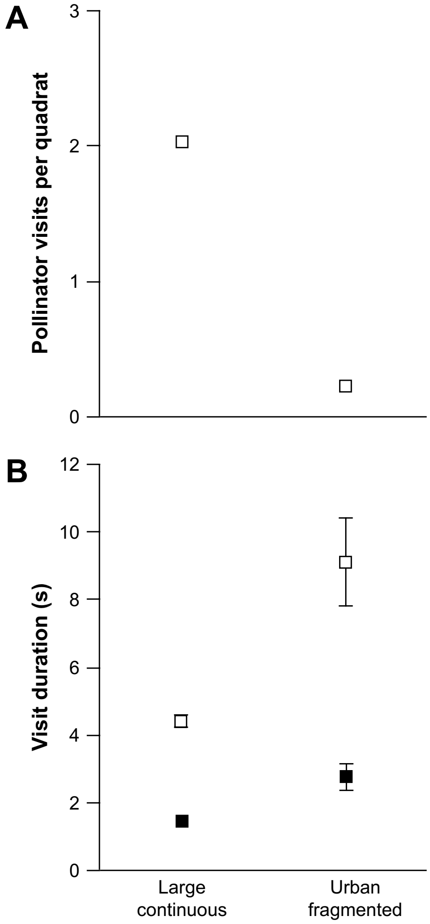

Fig. 1 – Pollinator behaviour between urban fragmented and large continuous populations. (A) Number of pollinator visits in patches and quadrats per survey (diameter experiment). (B) Capitula search (filled squares) and visit (empty squares) durations (duration experiment)

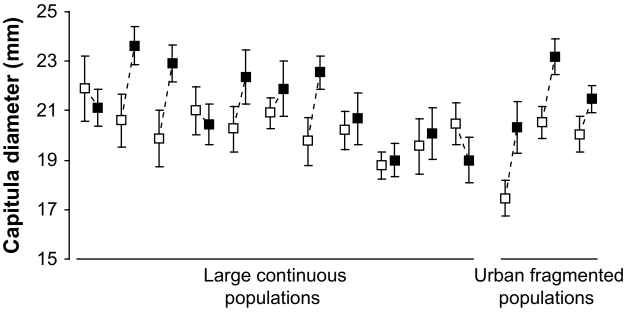

Fig. 2 – Comparison between size of visited and non-visited capitula. Mean diameter (±SE) of visited (filled squares) and non-visited capitula (empty squares) within each patch or quadrat (symbolised by a dashed line) in urban fragmented populations and large continuous populations (diameter experiment).

Table 1 – Descriptive statistics of the choice experiment. Values are mean ± SE

	Quadrat type	Date		
		03/05/07	03/09/07	03/26/07
Quadrat mean capitulum diameter (cm)	Small capitula	1.9 ± 0.04	2.02 ± 0.03	1.82 ± 0.03
	Large capitula	2.43 ± 0.03	2.51 ± 0.03	2.19 ± 0.04
Pollinator visit number	Small capitula	8	28	10
	Large capitula	9	29	10
Visited capitulum number	Small capitula	62	135	44
	Large capitula	70	121	48
Number of visited capita per pollinator	Small capitula	8.75 ± 2.72	4.17 ± 0.49	4.8 ± 1.25
	Large capitula	6.89 ± 3.02	4.82 ± 0.7	4.4 ± 0.88

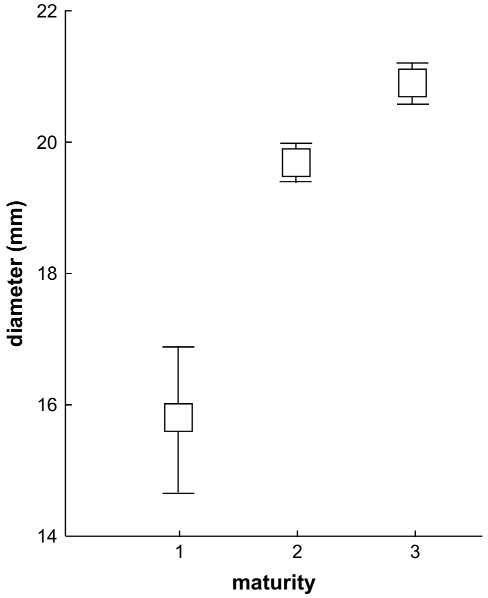

Fig. 3 – Relationship between capitulum size and maturity. Mean diameter (±SE) of capitula depending on their maturity class (duration experiment): 1 = few mature florets, 2 = intermediate number of mature florets, 3 = nearly all or all florets were mature.

4. Discussion

In urban populations, we predicted that the energy consumed during foraging flights among patches and the low reward due to small *C. sancta* population size can be avoided by pollinators (they do not forage in these patches). This may compensated by an increase of resource foraging in patches through an increase of capitulum visit duration or an increase of the number of visited capitula (Zimmerman, 1982; Goverde et al., 2002); a systematic search (Goulson, 1999) that could cause a relaxation of the need to choose the most rewarding capitula. In our study, pollinators chose *C. sancta* capitula depending on their size in both types of populations. However their foraging behaviour differed between the two population types, which can lead to direct consequences in reproductive biology and evolution of floral traits of *C. sancta*.

4.1. *Pollinator behaviour in large continuous vs. urban fragmented populations*

Pollinator visits were higher in quadrats of country populations (49 visits for 24 quadrat surveys, diameter experiment) than in quadrat of urban populations (seven visits for 32 quadrat surveys, diameter experiment). This may reflect differences in pollinator abundance between urban and rural areas, as a result of a limitation of nesting sites or resource availability (McIntyre and Hostetler, 2001; Cane et al., 2006) and generalised anthropic effects (Biesmeijer et al., 2006). However, urban continuous populations located in the proximity of urban fragmented populations showed a large number of pollinators (Andrieu E., pers. obs. and Table 1). These differences in visitation rates may thus be a consequence of the lower accessibility of urban patches: crowded streets, walls and buildings can be an obstacle for pollinators (Bhattacharya et al., 2003). Finally, whereas the number of capitula was higher in patches of urban populations, their diameter was smaller, meaning that their attractiveness could be lower.

The main result of this study and the most marked difference in pollinator behaviour is that, as predicted by the optimal foraging theory (Charnov, 1976; Stephen and Krebs, 1986), capitulum visit duration was longer in urban populations (9.16 ± 1.32 s) than in country populations (4.41 ± 0.15 s) (Fig. 1). As pollinators rarely co-occur in our quadrats (Andrieu E., pers. obs), this cannot be due to a higher interference by other pollinators in country populations, which has been shown to cause ~12% of pollinator departures in *Cirsium purpuratum* (Ohashi and Yahara, 2002). We suggest this twofold difference in visit duration expresses a compensation of energy lost to find patches. As patch localisation is highly predictable in urban context, this latter corresponds mainly to flight distance among patches. In the case of patchy resources with long travel time, optimal foraging theory predicts that pollinators increase the ratio of visited flowers (systematic search) (Goulson, 1999). The longer search durations in urban populations (2.79 ± 0.38 s) compared to country populations (1.42 ± 0.04 s), even when flights among patches were not taken into account (2.35 ± 0.30 s) (Fig. 1), and despite the fact that capitula are closer in urban patches than in quadrats of country populations, could be considered as an increase of capitulum prospecting effort, and is thus consistent with this prediction. Longer search durations have also been shown to be linked to the presence of landmarks (Plowright and Galen, 1985) which is the case here: country populations are in large open areas whereas urban patches are surrounded by ornamental trees and buildings. Moreover longer search durations can be observed in less rewarding areas (Waddington, 1980; Giurfa, 1996) as in urban populations were capitula are smaller and *C. sancta* rarer.

Large capitula are expected to be more rewarding in pollen and/or nectar. In the glasshouse, large capitula do not have more florets (estimated by seed number) than small capitula (48 individuals from five populations, $R_{sp} = 0.08$, $p = 0.558$, unpublished), but we do not know whether they contain more resources per floret than small ones. However in our study, capitulum diameter is linked to its maturity, i.e. to its number of mature florets, both in country and urban populations (Fig. 3), thus large capitula are probably more rewarding. Other studies have found a relation between pollinator visits and flower size or flower display size (Conner and Rush, 1996; Thompson, 2001; Elle and Carney, 2003): we found here that pollinators tend to visit the largest capitula. In our study, pollinators discriminate between large and small capitula (Fig. 2) at a small scale (among the closest capitula) but not between groups of rewarding (i.e. large) and not rewarding (i.e. small) capitula (choice experiment). This is consistent with the fact that honeybees visit flowers nearby (Levin and Kerster, 1969; Waddington, 1980); the number of visited capitula in a quadrat was correlated with the total number of capitula in the quadrat. Finally, capitulum size choice was not relaxed in urban populations. The scarcity of the resource or the energy lost during flights among patches did not lead to a systematic search of capitula since large capitula are preferred in both population types.

4.2. *Expected effects on plant reproduction*

We have shown that pollinator visitation rate in urban fragmented population was lower compared to large continuous population, which can have two possible consequences on *C. sancta* population functioning. First, it can cause a reduced male and female fecundity, *C. sancta* being a highly auto-incompatible species. This is supported by the Allee effect detected in urban pollination of *C. sancta*: the number of pollinator visits and seed set are correlated to plant density (Cheptou and Avendano, 2006). Second, the low visitation rate could lead to a lower genetic variability within progeny, as a consequence of the low number of pollen donors. This is consistent with progeny array analyses (Cheptou et al., 2002; Cheptou and Avendano, 2006), which showed that the number of fathers per progeny within capitula was 1 in urban populations, whereas it reached 1.6–6.25 in country populations. However, in the male point of view, it also results in a lower competition among pollen grains. In *C. sancta*, capitulum diameter has a probable genetic basis (diameters differ among populations in common garden, Cheptou P.-O., unpublished data), the choice for larger capitula could cause a selective pressure on this trait if it leads to variation in plant fitness. However we did not detect such variations of capitula size choice in this study.

The longer capitulum visitation durations in urban populations, coupled with the pollinator preference for visiting capitula nearby, could lead to a higher geitonogamy. Additionally, as *C. sancta* possesses a self-incompatibility system and its selfing rate in urban population is higher than in country populations (Cheptou and Avendano, 2006), geitonogamy could severely decrease both male and female fitness. However, these longer visitation durations can also lead to a higher amount of pollen collected by pollinators and thus a better pollen export.

5. Conclusion

Our study thus demonstrates clear differences in pollinator behaviour between country and urban *C. sancta* populations, particularly a lower visitation rate and longer capitulum visit duration in urban populations. Through these modifications in plant–pollinator interactions, urbanisation can thus lead to lower plant fecundity, and possibly reduced fitness, which needs now to be explored. The study of selection patterns of floral traits, particularly capitulum size and floret number and size, will also be necessary to examine the consequences of pollinator behaviour on plant trait evolution. Since dispersal ability is likely to drive selection for capitula size in our study species (Cheptou et al., 2008) it could act as a conflicting selection pressure (Mothershead and Marquis, 2000; Cariveau et al., 2004; Celedon-Neghme et al., 2007) on floral traits, an issue that now awaits attention.

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