PLANT ANIMAL INTERACTIONS

Pollination niche overlap between a parasitic plant and its host

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Abstract Niche theory predicts that species which share resources should evolve strategies to minimise competition for those resources, or the less competitive species would be extirpated. Some plant species are constrained to co-occur, for example parasitic plants and their hosts, and may overlap in their pollination niche if they flower at the same time and attract the same pollinators. Using field observations and experiments between 1996 and 2006, we tested a series of hypotheses regarding pollination niche overlap between a specialist parasitic plant *Orobanche elatior* (Orobanchaceae) and its host *Centaurea scabiosa* (Asteraceae). These species flower more or less at the same time, with some year-to-year variation. The host is pollinated by a diverse range of insects, which vary in their effectiveness, whilst the parasite is pollinated by a single species of bumblebee, *Bombus pascuorum*, which is also an effective pollinator of the host plant. The two species therefore have partially overlapping pollination niches. These niches are not finely subdivided by differential pollen placement, or by diurnal segregation of the niches. We therefore found no evidence of character displacement within the pollination niches of these species, possibly because pollinators are not a limiting resource for these plants. Direct observation of pollinator movements, coupled with experimental manipulations of host plant inflorescence density, showed that *Bombus pascuorum* only rarely moves between inflorescences of the host and the parasite and therefore the presence of one plant is unlikely to be facilitating pollination in the other. This is the first detailed examination of pollination niche overlap in a plant parasite system and we suggest avenues for future research in relation to pollination and other shared interactions between parasitic plants and their hosts.

Keywords *Bombus · Centaurea · Orobanche ·*
Facilitation · Mutualism

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Introduction

Niche theory predicts that organisms which compete for the same limiting resources should either evolve strategies to reduce the level of niche overlap ("character displacement" broadly defined) or not coexist sympatrically (MacArthur and Levins 1964, 1967; Silvertown 2004). This character displacement–extirpation dichotomy has been an important element within the development of ecological theory and has been tested in a range of organisms, usually at the community scale and with mixed results (see Table 7.1 in Chase and Leibold 2003). Discussions and field tests of niche similarity and species coexistence have not generally considered examples where species are constrained in their distributions to live in close sympatry,

due to their specialized ecologies. For example, some plant species are ecologically constrained to co-occur, such as narrow habitat specialists, and host-specific epiphytes or parasitic plants. These situations provide an ideal test of niche theory: if constrained species share limited resources, extirpation caused by their overlapping niches is not an option and character displacement of some kind must occur.

Studies of niche breadth and overlap in plant communities have tended to focus on the physiology and growth form of plants as the main determinants of niche structure and species coexistence (e.g. Tofts and Silvertown 2000; Silvertown et al. 2001; Chase and Leibold 2003; Silvertown 2004 and references therein). However, the large majority of plants require biotic pollen vectors to ensure that they can sexually reproduce and these pollinators are typically a limiting resource in most communities (Bierzychudek 1981; Burd 1994) though this may be offset to some extent by the ability of many angiosperms to self pollinate (Larson and Barrett 2000). The "pollination niche", i.e. flowering time, identity of pollinators, pollen and stigma presentation schedules, etc., is therefore an important aspect of plant niche structure which can potentially determine the likelihood of species coexistence, community assembly structure and character displacement (Robertson 1895; Heithaus 1974; Parrish and Bazzaz 1979; Rathcke 1988; Armbruster 1995; Stone et al. 1998; Hansen et al. 2000; Ollerton et al. 2003). Pollination niche overlap between species occurs when they flower at the same time and utilize the same pollinators. If pollination services are considered a resource, this can theoretically result in lower fitness of competing species via reduced seed set and pollen dispersal, providing the necessary conditions for either local extirpation or evolutionary shifts in flowering time or other floral traits, in order to attract different pollinators (Robertson 1895; Heithaus 1974; Parrish and Bazzaz 1979; Armbruster 1995; Ollerton et al. 2003). The evidence for such evolutionary changes within plant assemblages remains ambiguous, with limited examples in which there is evidence of a shift in pollination niche via character displacement or ecological sorting (Rathcke 1988; Stone et al. 1998; Armbruster et al. 1994; Kay and Schemske 2003).

In this paper we present the first study in which the interactions of a parasitic plant, its host, and their mutual pollinators are revealed, from the perspective of pollination niche overlap. The system we have studied is the rare European holoparasite *Orobanche elatior* Sutton (knapweed broomrape, Orobanchaceae) and its main host plant, *Centaurea scabiosa* L. (common knapweed, Asteraceae). If niche theory is correct,

and if pollinators are a limiting resource, plants which are forced into co-existence should not share a pollination niche—they should flower at different times of the year, place their pollen on different parts of the bodies of shared pollinators, and/or not require the services of the same pollinators. Previous work has shown that *C. scabiosa* is a self-incompatible, insect-pollinated species (Lack 1982c). Flowers of *O. elatior* are capable of autogamy via style bending, but fruit set is less assured than if flowers are visited by pollinators (autogamous versus open pollinated fruit set (mean $\pm$ SE, $54.9 \pm 9.9\%$ vs. $95.4 \pm 3.3\%$; $t = -3.6$, $P = 0.006$, unpublished data). In both species, the presence of relatively large nectar rewards and regular pollinator visits points to them being predominantly outcrossing species.

Using this system we developed and tested a series of hypotheses relating to pollination niche theory and the assumption that pollination systems evolve under a community-level regime of competition for pollinators, and that such competition would provide strong selection for minimising pollination niche overlap:

Hypothesis 1
The parasite *O. elatior* and its host *C. scabiosa* should not share pollinators, i.e. fundamental segregation of the pollination niche.

Hypothesis 2
If the host and parasite do share pollinators (hypothesis 1 is falsified) then the two species should not overlap in their flowering times, i.e. seasonal segregation of the pollination niche.

Hypothesis 3
If the host and the parasite share pollinators and flower at the same time (hypotheses 1 and 2 falsified) the two species should differ in their sites of pollen placement, i.e. positional segregation of the pollination niche.

Hypothesis 4
If hypotheses 1, 2 and 3 are falsified (the host and the parasite share pollinators, flower at the same time and do not differ in their sites of pollen placement) there should be a difference in timing of pollinator activity on the plants during the day, i.e. diurnal segregation of the pollination niche.

Hypothesis 5
If the host and the parasite do share pollinators, an alternative to the competition hypothesis is that the presence of the larger, showier floral display of the host plant facilitates pollination in the parasite.

Facilitation is a non-trophic, positive interaction whereby one or both plant species benefit from the presence of each other, increasing the average individual fitness of at least one of the species through resource sharing (Callaway and Walker 1997; Kawanabe et al. 1993; Holmgren et al.1997). It may be considered a

special case of diffuse commensalism or mutualism and has also been termed the "magnet species" effect (Johnson et al. 2003).

To test these hypotheses we collected field data and performed manipulative experiments over a period of 11 years (1996–2006) in populations of *O. elatior* and *C. scabiosa* within Northamptonshire, UK.

Materials and methods

Study species and field sites

Orobanche elatior Sutton (the tall or knapweed broomrape, Orobanchaceae) is a holoparasite, which mainly infects *Centaurea scabiosa* L. (greater knapweed, Asteraceae), rarely other *Centaurea* spp., Asteraceae species, or *Thalictrum* spp. (Kreutz 1995). Generally considered rare, but sometimes locally frequent, its global distribution spans western and central Europe, southern Scandinavia, the northern Mediterranean region, to central Asia and northern India (Kreutz 1995). In Britain the species is "...rare but widespread..." (Clapham et al. 1987) and is restricted to grasslands overlying calcareous rock strata. The life cycle of *O. elatior* infecting *C. scabiosa* is typical of the genus, as outlined by Kreutz (1995). Minute, dust-like seeds are dispersed in late summer; they enter the soil and germinate in response to the proximity of host roots. The seedling attaches itself to a host root and taps into the host's vascular system. There then follows a period of growth (a few months to several years depending upon the species) during which the parasite develops as a tuber. Flowering is probably governed by resource levels within the tuber. The elongated (20–70 cm) inflorescence of zygomorphic flowers emerges from the ground, the flowers open acropetally and pollination (autogamy or exogamy) occurs. Following fruit maturation the inflorescence dries quickly and the seeds are dispersed. The parasite may die (as is the case for *O. elatior*) or sometimes survives to reproduce in subsequent years.

C. scabiosa is a tall (30–80 cm), erect, perennial herbaceous species, which is found in many parts of Britain on roadsides and dry grasslands, particularly on calcareous soils. The global distribution of this species is very similar to that of *O. elatior*, though it is found further west in Europe than the parasite, including Spain and Ireland (Flora Europea online: http://www.rbg-web2.rbge.org.uk/FE/fe.html). The composite flower head (capitulum) is 3–6 cm in diameter and is thistle-like, with a ring of long sterile outer florets.

The flowers of *O. elatior* are variably yellow to yellow-reddish-brown in colour, while the inflorescences of C. *scabiosa* are typical composite blooms, purple-red in colour. Nectar is known to be secreted by both species (Clapham et al. 1987; Lack 1982b). The limited data available for *O. elatior* suggests that both it and its host are pollinated primarily by *Bombus* spp. (Bumblebees, Hymenoptera: Apidae) (Jones 1989, 1991; Lack 1982c).

The county of Northamptonshire (UK) hosts several populations of *O. elatior*, the largest of which exists on the Scrub Field Local Nature Reserve in Northampton (Ordnance Survey grid reference SP 765639). This population of *O. elatior* was used as the primary site for data collection, although observations of pollinators were also made in other populations, as described in the Results.

Censusing flowering phenologies

In early June 1996, prior to flowering of the host plants and the emergence of *O. elatior* inflorescences, a total of 101 individual plants of *C. scabiosa* were randomly selected, tagged and numbered using red electrical insulation tape (see Ollerton and Dafni 2005). The tagged host plants were monitored 3 times a week (Monday, Wednesday and Friday) for number of open and un-withered inflorescences and for the presence of fresh broomrape inflorescences nearby. Monitoring of the host and parasite took place until flowering had ceased. This pattern of flowering plant census of the host and parasite was repeated with some modifications (including weekly rather than tri-weekly censuses) in 1997, 2000, 2004, 2005 and 2006. For the sake of brevity only the flowering data for 1996, 1997 and 2000 are presented; these are representative of the flowering times in the other years, except where noted in the Results.

In order to establish any potential effect of parasitism on inflorescence production and flowering time of the host plants, in 1996, 2000, 2004, 2005 and 2006 we separately censused parasitized and non-parasitized *C. scabiosa* individuals. Parasite inflorescences were assumed to be attached to the nearest *C. scabiosa* plant, though in most cases the inflorescences actually grew within the foliage of the host plant, suggesting that the root system of the host is not generally extensive or that the parasites selectively attach themselves to the thicker roots in close proximity to the crown of the host.

Floral biology and nectar secretion

Patterns of nectar secretion were assessed in 1996, 1997, 2000 and 2004 for *O. elatior* and 1996 and 2000 for *C. scabiosa*. Nectar volumes were determined using

glass microcapilliary pipettes and sugar concentrations (as sucrose equivalents) were estimated using a Bellingham and Stanley sugar refractometer [see Dafni et al. (2005) or Kearns and Inouye (1993) for details of these techniques].

Flower opening times of *O. elatior* were assessed by tagging individual late-stage flower buds and monitoring their progress during daylight hours. The number of ovules per ovary was assessed by subdividing immature ovaries and counting the ovules under a dissecting microscope.

Flower visitors and pollen loads

In 1996, 1997, 2000, 2004, 2005 and 2006 observations were made of flower visitors to the parasite *O. elatior*. In 1996 and 2000 this included detailed study of rates of flower visitation at different times of the day. In 1996, 2005 and 2006, data on flower visitors to the host *C. scabiosa* were also collected over the course of the flowering period [this species had previously been well studied by Lack (1982a, b, c)]. The flower visitation data were used to calculate values for niche breadth and overlap for the two species (see statistical analyses below)

In 1996 a representative sample of flower visitors to the two species was captured and anaesthetized using ether. Samples of pollen were taken from four body areas (face, dorsal, and front and back ventral surfaces) using 5 mm × 5 mm squares of Sellotape Invisible Delux adhesive tape. The squares were pressed against the insect's body using fine forceps, and then mounted on glass microscope slides. In the laboratory these slides were checked for numbers of *C. scabiosa* and *O. elatior* pollen grains. On a technical note, it was found that viewing the slides glass-side-up gave much the better view of the pollen. Most of the insects were released unharmed, apart from a small number of specimens retained for identification purposes.

Facilitation experiment

In order to test the hypothesis that the presence of the host's floral display could facilitate pollinator visits to the parasite, during 2000, the number of host inflorescences (capitulae) adjacent to broomrape inflorescences were experimentally manipulated. Single parasite inflorescences were randomly allocated to one of five treatments, in which either 0, 1, 10, 20 or 50 ex situ host capitulae were arranged around the parasite. The capitulae, attached to their stems, were maintained in water-filled containers. Four replicates were set up per treatment and the experiment was run over

6 days, with observations occurring between 0600 and 1815 hours on all days except two, when observations were made between 1215 and 1815 hours. Each replicate was monitored for a 15-min period and the number of pollinator visits to each broomrape inflorescence counted. The total number of observation periods per treatment varied from nine to 11 for full days of observation and from four to six for afternoon sampling period, for a total range of 49–52 per treatment.

Statistical analyses

All statistical analyses were performed using SPSS 8.0 for Windows (1997; SPSS, Chicago, Ill.). Averages are presented as mean ± SE. Values for pollination niche breadth of both plant species and niche overlap between the two species were calculated following the approach of Levins (1968) and Pianka (1973) as presented in Waite (2000), using the data for proportions of pollinators in 1996, 2005 and 2006. This takes into account both the number of pollinator species and their relative abundance as flower visitors to these plant species.

Results

In the Scrub Field Local Nature Reserve in 1996, 1997 and 2000 the flowering times of the parasite *O. elatior* overlapped with that of the host *C. scabiosa* (Fig. 1). In 2004, 2005 and 2006 there was only partial overlap of the parasite and the host, with *O. elatior* flowering 1–2 weeks earlier than *C. scabiosa* (data not presented). In all years, the flowering of the parasite occurred during the early to mid period of host flowering and was much briefer than that of the host. The parasite affected the numbers of host capitulae in some years but not in others. In 1996 the mean (median) number of capitulae per plant was 13.6 (4.0) for parasitized versus 15.2 (11.0) for non-parasitized plants (Mann–Whitney $U_{24,50} = 467$, $P = 0.124$). In 2000 the mean (median) number of capitulae per plant was 4.0 (2.5) for parasitized versus 26.7 (17.0) for non-parasitized plants (Mann–Whitney $U_{32,62} = 149.5$, $P < 0.0001$). The effect of the parasite on the flowering date of parasitized versus unparasitized plants was also variable between years. The peak flowering date of parasitized plants in 1996 was only a couple of days later than that of non-parasitized plants; however, in 2000 the peak date of flowering was 21 days later for the parasitized plants (Fig. 1). Similar patterns were observed in 2004, 2005 and 2006, where parasitized plants began to flower 1–2 weeks later than unparasitized individuals
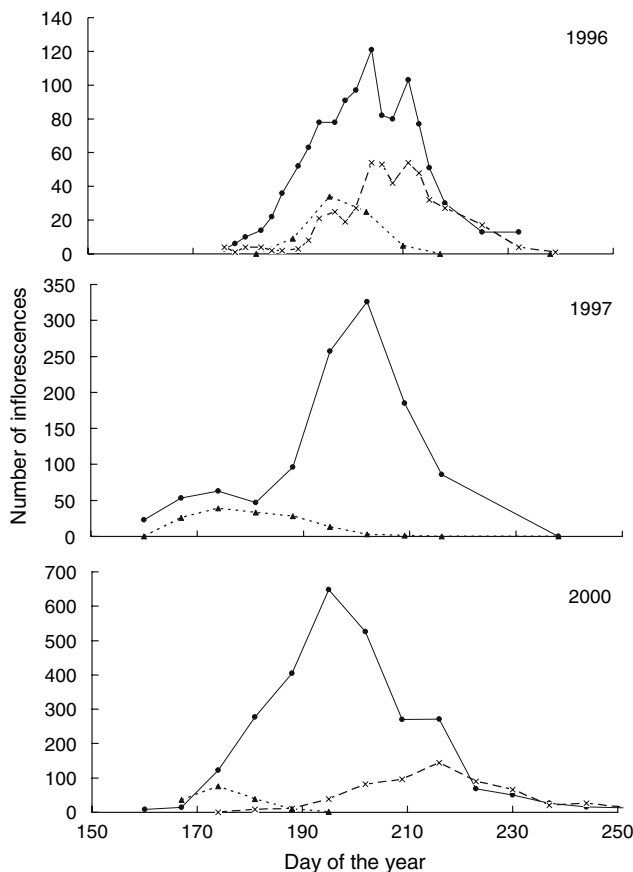
Fig. 1 Flowering phenologies of unparasitized host (*filled circle*), parasitized host (*cross*) and parasite (*filled triangle*) in 1996, 1997 and 2000

Fig. 2 Relationship between mean visitation rate of insects to *Centaurea* inflorescences (*filled circle*) and *Orobanche* flowers (*open triangle*) and the amount of pollen carried by insects (pollen load) in 1996. Error bars have been omitted to aid interpretation

(data not shown). Thus parasitism by *O. elatior* may have a negative effect on both inflorescence production and on the flowering time of *C. scabiosa*, although this effect is larger in some years than in others, perhaps because of climatic differences between years, e.g. average temperature or water availability.

C. scabiosa was visited by a wide range of day-flying Hymenoptera and Lepidoptera (Fig. 2). Hoverflies (Diptera: Syrphidae) were also occasional visitors but were not recorded during formal visitation censuses. Overall visitation rates of the taxa varied widely, with that of the most frequent visitor (*Bombus lapidarius* workers) 1.7 times greater than the next most frequent visitor (male *B. lapidarius*) and 61 times greater than the least frequent visitor (various Lepidoptera spp.). There was also a great deal of variation in the amount of pollen carried by the various taxa, with 2 orders of magnitude difference in total pollen load between the first and last ranked taxa, female *B. lapidarius* and Lepidoptera spp., respectively (Fig. 2). All of these taxa contact the stigmas of flowers of *C. scabiosa* when foraging on inflorescences and can be considered to be pollinators.
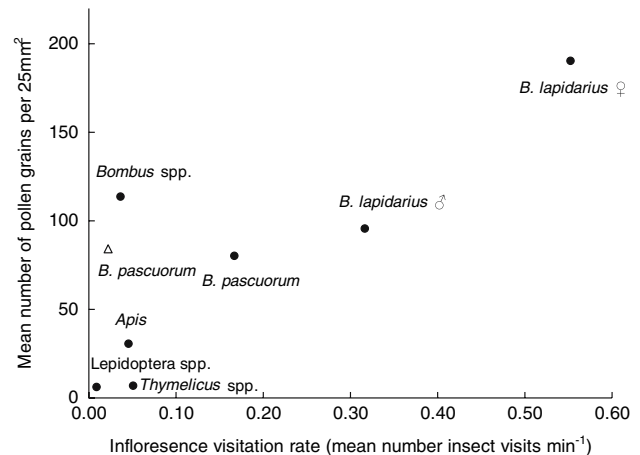
The observed rate of flower visitation by each of these taxa was strongly positively correlated with their mean pollen loads (Pearson's $r = 0.83$, $df = 6$, $P = 0.02$, see Fig. 2). This might be expected if a higher visitation rate resulted in a greater accumulation of pollen on the insects' bodies.

The pollinator spectrum of *O. elatior* was restricted to a single species of bumblebee, *Bombus pascuorum*, which contacts the anthers and stigma of flowers with its head and body. On very rare occasions, other *Bombus* species were seen briefly visiting *O. elatior*, as was a single individual of a social wasp, *Vespula* sp. (Hymenoptera: Vespidae) and on two occasions unidentified hoverflies (Diptera: Syrphidae). However, these must be considered at best to be extremely rare pollinators of the parasite, and more probably individuals who were simply investigating *O. elatior* as a possible source of nectar. *B. pascuorum* was consistently observed to be the only pollinator of *O. elatior* at the Scrub Field in 1996, 1997, 2000, 2004, 2005 and 2006. In 2000, two hundred hours of observations at this site, plus observations of *O. elatior* populations at nature reserves at Barnack, Collyweston and Twywell (all within 75 km of the Scrub Field) confirmed *B. pascuorum* as the sole pollinator. The relationship between *O. elatior* and its pollinator seems to be temporally and geographically stable, at least within the East Midlands of England. This may be due to the deep corolla tube of *O. elatior* (13.7 ± 1.8 mm, $n = 51$ flowers) which means that nectar is accessible only to long-tongued insects. In contrast, the flower tube of *C. scabiosa* is quite short (4.3 ± 0.7 mm, $n = 89$ flowers), thus allowing a wider range of insects to forage.

The host and the parasite do not differ in their placement of pollen on *B. pascuorum*, the pollinator which they share in common. The average numbers of pollen

grains of *Orobanche* versus *Centaurea* on the different parts of the bumblebees' bodies were: dorsal = 6.0 (±8.3) versus 2.4 (±6.8); face = 5.8 (±9.3) versus 21.4 (±35.6); front ventral = 32.8 (±37.3) versus 20.0 (±25.7); rear ventral = 20.5 (±28.2) versus 56.2 (±135.0). These data were analysed using a univariate general linear model (GLM) with number of pollen grains as the dependent variable and pollen identity (host or parasite) and position of pollen on the insect's body as fixed factors. The overall GLM was non-significant ($F = 1.3$, $P = 0.28$) as was, crucially, the interaction between pollen identity and position on the body ($F = 1.0$, $P = 0.39$).

Both *C. scabiosa* and *O. elatior* produce nectar as a reward to visiting insects. The average volume of nectar per flower was much smaller for *C. scabiosa* than *O. elatior*, for example 0.2 ± 0.04 μl (1996) and 0.5 ± 0.3 μl (2000) in the host versus 5.9 ± 3.3 μl (1996) and 1.4 ± 0.9 μl (2000) in the parasite. This difference between the species is unsurprising given the much smaller size of the flowers of *C. scabiosa* compared to *O. elatior*. However, the capitulae of *C. scabiosa* func-

tion as single flowers and typically contain about 50 fertile florets (mean = 49.3 ± 19; $n = 44$ capitulae). Multiplying this value by the average nectar volume per floret suggests that capitulae of *C. scabiosa* contain between 4 and 16 times the typical per-flower nectar volume of *O. elatior*.

The nectar of the host plant is usually more concentrated than that of the parasite: in *C. scabiosa*, percent sugar concentration ranged from 37.3 ± 17.5% (1996) to 42.9 ± 6.6% (2000), compared to typical values of 12.1 ± 4.3% (1996) to 23.5 ± 4.5% (2000) in *O. elatior*.

The host and the parasite appeared to differ in their daily pattern of pollinator visits, with *Centaurea* pollinators predominantly visiting in the mid afternoon followed by a second peak towards early evening, and *Orobanche* pollinators visiting early in the morning and then peaking in their visitation during the late afternoon (Fig. 3). However, there was no statistically significant difference between these patterns (see Fig. 3). Likewise there was no significant difference between the species in the pattern of diurnal nectar production, which was relatively constant during the day (Fig. 3).

Fig. 3 Diurnal patterns of pollinator visitation and nectar production for the host (*Centaurea*) and the parasite (*Orobanche*) in 1996 and 2000 (visitation data are not available for *Centaurea* in 2000). Note that the *y*-axis scales for visitation rates differ due to variations in insect activity on inflorescences between species and between years. *Bars* show SEs. There is no statistically significant difference between the two species with regard to the patterns of pollinator visitation in 1996 (two-sample Kolmogorov–Smirnov test on the proportional accumulated data $z = 0.58$, $P = 0.89$) or the patterns of nectar production in 1996 (two-sample Kolmogorov–Smirnov test on the proportional accumulated data $z = 0.316$, $P = 1.00$) or 2000 (two-sample Kolmogorov-Smirnov test on the proportional accumulated data $z = 0.25$, $P = 1.00$)
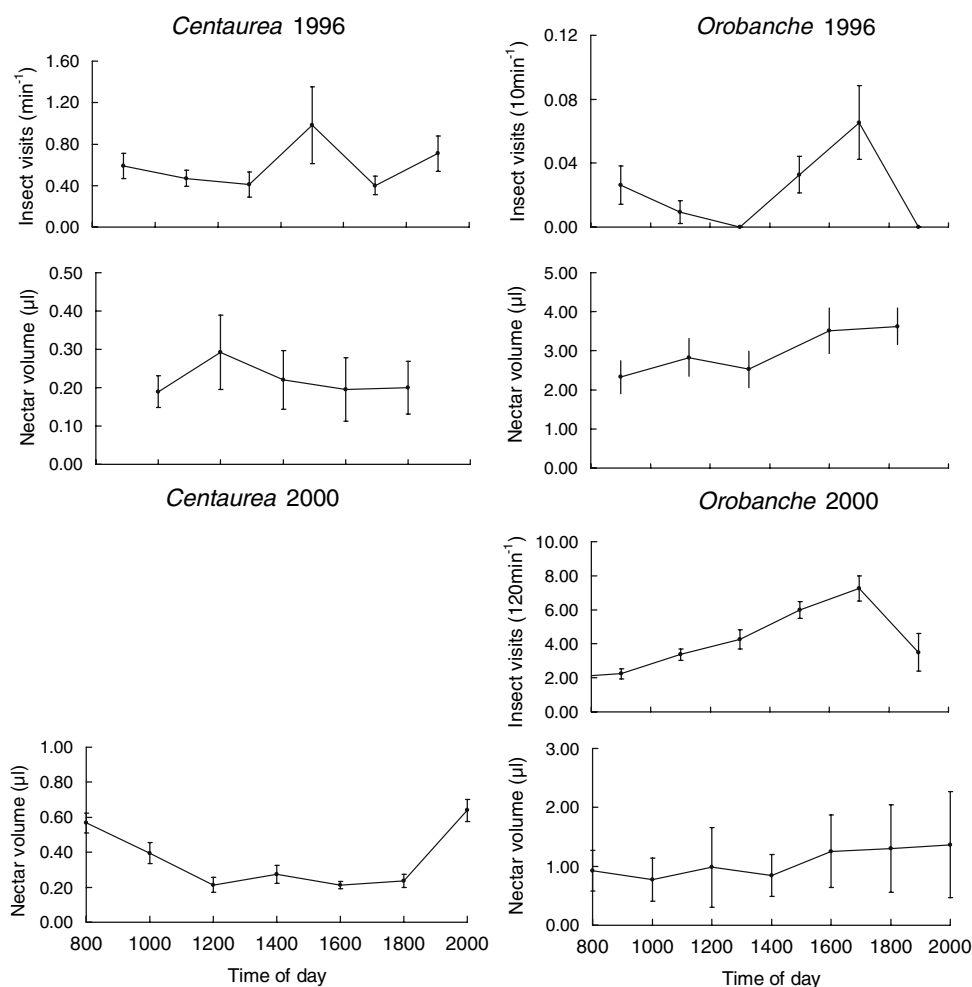
The pollination niche breadth of *O. elatior* was consistent between the 3 years for which it was calculated (Table 1, note that Levins' measure of niche breadth begins at zero, implying that there is a single pollinator for that species). The niche breadth of *C. scabiosa* was more variable, increasing by over 50% between 1996 and 2005, and 70% between 1996 and 2006. The diversity of pollinators was in fact slightly less in 2005 and 2006 (*Apis mellifera* was not recorded) but there was a greater evenness of pollinator abundance, accounting for the increase. Pollination niche overlap between the two species was very variable between 1996 and 2005 (increasing by a factor of 2.6) but much less so between 2005 and 2006. This increase in overlap was due to the greater importance of *Bombus pascuorum* as a pollinator for *Centaurea scabiosa* in 2005 and 2006 compared to 1996 (Table 1).

In 1996, we spent 432 plant-minutes observing pollinator movements to and from individual plants of *C. scabiosa*, during which 852 plant-minutes of *O. elatior* observations were also made. On only one occasion was an individual of *B. pascuorum* seen to move from *C. scabiosa* to *O. elatior*, despite relatively high visitation rates of this bee to the host plant (Fig. 2). This low rate of movement of pollinators between host and parasite is confirmed by the low levels of *C. scabiosa* pollen found on individual *B. pascuorum* which were

captured foraging on *O. elatior* (mean number of pollen grains = 10.7 ± 14.0; $n = 13$ bees). In contrast, host plant pollen loads carried by *B. pascuorum* foraging on *C. scabiosa* were 80.7 ± 70.3 ($n = 10$ bees), whilst parasite pollen loads of *B. pascuorum* foraging on *O. elatior* were 84.4 ± 158.2 ($n = 13$ bees).

In 2000, systematic observations of *B. pascuorum* movements showed that under natural conditions the majority of inter-plant movements were intraspecific (Table 2a). Less than 12% of movements were between parasite and host or vice versa. Almost 70% of the observed movements in the control period were from parasite to parasite, possibly due to the longer residence times of visitors to capitulae of *C. scabiosa* (18.6 ± 13.4 s) compared to visits to *O. elatior* flowers (0.3 ± 0.2 s). This in turn is probably governed by the greater overall nectar reward available in a *C. scabiosa* capitulum (see above). Following the instigation of the experiment in which density of host capitulae was artificially increased, the proportion of parasite-to-parasite movements dropped by almost 60%, whilst the proportion of all other classes of movement increased (Table 2a). In particular, the incidence of movement from parasite to host increased by a factor of 2.6. However, manipulation of the density of host capitulae around parasite inflorescences largely did not affect the rate of visitation of *B. pascuorum* to *O. elatior*

Table 1 Percentage of visits observed by the different pollinators, and calculations of pollination niche breadth and niche overlap[a], for the host (*Centaurea scabiosa*) and parasite (*Orobanche elatior*) in 1996, 2005 and 2006

	C. scabiosa 1996	*O. elatior* 1996	*C. scabiosa* 2005	*O. elatior* 2005	*C. scabiosa* 2006	*O. elatior* 2006
Bombus lapidarius	73.7	0.0	45.8	0.0	28.8	0.0
Bombus pascuorum	14.2	100.0	28.8	100.0	28.8	100.0
Bombus spp.	3.1	0.0	16.1	0.0	29.7	0.0
Apis mellifera	3.9	0.0	0.0	0.0	0.0	0.0
Lepidoptera	5.0	0.0	9.3	0.0	20.3	0.0
Niche breadth	0.43	0.00	0.67	0.00	0.71	0.00
Niche overlap	0.19	0.19	0.50	0.50	0.53	0.53

[a] Note that niche overlap is a symmetrical measure and therefore is identical for the two species in each year

Table 2 Percentages of bumblebee movements between host and parasite during the control and experimental observation periods in 2000. *G*-test on raw data: $G = 9.2$, $P < 0.05$. Percentages do not sum to 100 as movements from host or parasite to other species accounted for a small fraction of movements. Results of experiment manipulating densities of host capitulae around parasite inflorescences. One-way ANOVA: $F_{4,26} = 22$, $P = 0.09$

Direction of *B. pascuorum* movement

	Host to parasite	Host to host	Parasite to host	Parasite to parasite
Control period	11.8	2.9	8.8	67.6
Treatment period	16.1	10.8	22.6	39.8

Number of host capitulae adjacent to the parasite

	0	1	10	20	50
Mean number of *B. pascuorum* visits to *O. elatior* per 15 min $\pm$ SE	2.5 ± 0.7	5.0 ± 1.4	5.1 ± 0.9	4.8 ± 1.4	3.4 ± 0.6

(Table 2b); there appeared to be a slight negative effect when there was zero host capitulae, although this was statistically significant only at $P = 0.10$. These results may appear to contradict the bee movement data, but they make sense if bee activity on parasite inflorescences is kept constant by intraspecific competition for nectar or aggression between conspecifics. In summary, manipulating the density of host capitulae adjacent to parasite inflorescences altered the behaviour of *Bombus pascuorum*, making it more likely to move between the two species, but did not affect the overall rates of visitation to parasite inflorescences.

Discussion

There is significant pollination niche overlap in the *Centaurea–Orobanche* host–parasite system: the two species share an important pollinator and, crucially, overlap to some extent in their flowering times. Formal niche breadth statistics have rarely been calculated in pollination studies, but to put these results into context, a study of the pollination niches of nine species of asclepiad (Apocynaceae subfamily Asclepiadoideae) in South Africa by Ollerton et al. (2003) calculated niche breadths ranging from 0.00 (a single pollinator) to 0.65. The host and the parasite, with niche breadths of 0.43–0.71 and 0.00, respectively (Table 1), therefore span the full breadth of specialized–generalized pollination systems encountered in a South African grassland plant assemblage. Niche overlap between generalist–specialist pairs of asclepiad species (equivalent to the *Centaurea–Orobanche* situation) ranged from 0.06 to 0.26, which is comparable to that found in the present study in 1996 (niche overlap = 0.19), but far less than in 2005 and 2006 (niche overlap = 0.50 and 0.53, respectively), see Table 1. The pollination niche of the parasite therefore overlaps wholly with that of the host plant in terms of utilising a highly specific pollinator, though from the host's perspective the overlap is only partial.

Using these results we can therefore test the hypotheses set out in the Introduction.

Hypothesis 1

The parasite *O. elatior* and its host *C. scabiosa* do not share pollinators, i.e. fundamental segregation of the pollination niche.

This hypothesis is rejected as the host plant *C. scabiosa* and the parasite *O. elatior* significantly overlap in their use of pollinators: an important pollinator of the host (*B. pascuorum*) was the sole pollinator of the

parasite (Fig. 2). It is unlikely that the rather generalized pollination system of *C. scabiosa* has evolved as a response to competition with *O. elatior* for pollinators because: (1) *O. elatior* is rather rare and most populations of *C. scabiosa* are not parasitized, but are visited by a similarly wide range of pollinators (Lack 1976, 1982c); (2) other species of *Centaurea* which are not parasitised by *O. elatior* also have generalized pollination systems (e.g. Harrod and Taylor 1995; Agrawal et al. 2000; Hirsch et al. 2003), including the often sympatric *C. nigra* with which *C. scabiosa* also shares pollinators (Lack 1982a, b, c).

Hypothesis 2

The two species should not overlap in their flowering times, i.e. seasonal segregation of the pollination niche.

The two species overlap appreciably in their flowering phenology, though the host does flower for a longer period and the exact timings are variable between years (Fig. 1). This hypothesis is clearly falsified and there is no evidence for seasonal segregation of the pollination niche. It is tempting to speculate that the parasite's suppression of host capitulae production, and the negative effect on flowering time, might be adaptive for *O. elatior* (and mediated by hormonal effects?), in that it could reduce competition between the parasite and its host plant. We believe that this is unlikely for two reasons: (1) the annual variability of the effect on host flowering suggests that the parasite has little control over it; and (2) our facilitation experiment has shown that there is no advantage to the parasite in suppressing its host's capitulum production as host inflorescence density does not affect pollination visitation rates to the parasite.

Hypothesis 3

The two species should differ in their sites of pollen placement, i.e. positional segregation of the pollination niche.

Analysis of the position of pollen on the insects' bodies showed that there were no significant differences in pollen placement; therefore this hypothesis can be rejected.

Hypothesis 4

There should be a difference in timing of pollinator activity on the plants during the day, i.e. diurnal segregation of the pollination niche.

The observations that we made regarding daily patterns of insect activity in relation to nectar

production do not support this hypothesis (Fig. 3). Though there appeared to be a difference in timing of peak visitation to the two species, this was not statistically significant. We therefore cannot confirm the suggestion by Stone et al. (1998) that diurnal segregation of the pollination niche may be an important, but neglected, means by which competition for pollinators can be reduced in taxa which use the same pollen vectors.

Hypothesis 5

The larger, showier floral display of the host plant facilitates pollination in the parasite.

The nectar of the host species is of greater quantity and quality than that of the parasite and is accessible to the pollinators for less energy expenditure than is involved in flying between flowers on an *Orobanche* inflorescence. This probably contributes to the much greater attractiveness of *C. scabiosa* to insect visitors and the longer residence times of insects on the flower heads of the host. However, during the surveys of 1996 and 2000, the majority of *B. pascuorum* movements were intraspecific (Table 2a). The low frequency of between-species movements was not in itself surprising because *Bombus* spp., in common with most pollinators, exhibit flower constancy during foraging runs and tend to visit sequences of the same plant species (Heinrich 1976; Chittka et al. 1997), whilst the rare movements from host to parasite may be examples of "minoring" sensu Heinrich (1979). Similarly, Johnson et al. (2003) showed experimentally that interspecific movements by bumblebees between nectar-producing and rewardless species were more likely to occur if the flowers of the two species were the same colour, which is not the case in the *Centaurea–Orobanche* system. Experimental manipulation to increase the number of host capitulae surrounding a parasite was expected to increase bee foraging activity on the parasite by attracting more bees to the vicinity, but this proved not to be the case (Table 2b). We can therefore reject this hypothesis—there is no evidence that direct facilitation is occurring, though we cannot rule out the possibility that indirect facilitation is important, i.e. the more abundant host species plays a dominant role in sustaining the population of *B. pascuorum*, which also advantages the parasite.

In summary, significant pollination niche overlap appears to be maintained in this host–parasite system without it having resulted in character displacement of flowering time, pollinator identity, pollen placement, or diurnal pollinator segregation. This is in line with at least one previous study, which also found no evidence of character displacement, despite significant niche overlap (Ollerton et al. 2003). A major assumption of hypotheses 1–4 is that seed production in *C. scabiosa* and *O. elatior* is pollen limited, and that pollinators therefore represent a resource for which the plants compete. We have no direct evidence of pollen limitation in either of these species, and this is a significant limitation of our study. Average seed set in this *Centaurea* population was rather low in 1996 (mean ± SE = 26.1 ± 2.8%, n = 43 inflorescences, unpublished data). However, previous studies of other populations of *C. scabiosa* in the UK (Lack 1982c) and in Scandinavia (Ehlers 1999) suggest that the species is generally not pollen limited, and that individuals receive sufficient visits by major pollinators to maximise seed set to match resources. Data from pollinator observations in the Scrub Field population in 1996 showed that inflorescences have a high rate of visitation from insects carrying significant densities of pollen (Fig. 2), which would not be expected in a pollen-limited species. Visitation rates to *O. elatior* are lower than for its host (Fig. 2), but fruit set in open-pollinated inflorescences of the parasite is usually >95% (see Introduction), so the parasite also may not be pollen limited. Although the evidence is circumstantial, it could explain why our study has found no support for any of our hypotheses 1–4, despite pollination niche overlap between the two species. If both the parasite and the host are receiving enough pollinator visits, and adequate pollen is reaching stigmas, then there would be no natural selection for either species to adapt to different pollinators (hypothesis 1), to have evolved to minimise flowering time overlap (hypothesis 2), to place pollen on different parts of the bodies of their pollinators (hypothesis 3), or to evolve a diurnally segregated pollination niche (hypothesis 4). Our cautious conclusion is therefore that significant overlap in the pollination niche can be maintained between species within a community in the absence of pollen limitation. However, we note that the degree of pollen limitation can be geographically and temporally variable for a species (e.g. Vanhoenacker et al. 2006) and so a more thorough study of pollen limitation within the *Centaurea–Orobanche* system, in different years and across populations, would be required to fully assess this conclusion.

The interaction between *B. pascuorum* and the flowers of *O. elatior* is ecologically specialized from the plant's perspective and seems to be a function of the relatively long tongue of this bumble bee, and the fact that it is a less discriminating forager than other long-tongued bees (Prŷs-Jones and Corbet 1991; Goulson 2003). The relationship between *O. elatior* and its pollinator appears to be stable over moderate temporal and

spatial scales, at least in the portion of its range that we surveyed. This is unusual as many Northern Hemisphere studies have documented spatio-temporal variation in pollinator identity (reviewed by Ollerton 1996 and Waser et al. 1996; Waser and Ollerton 2006), though see Johnson and Steiner (2000, 2003) for an alternative, Southern Hemisphere perspective. The relationship demonstrates a feature of pollination biology that seems to be quite widespread—plants specializing on a single pollinator tend to utilize common, widespread pollinators. Within a plant assemblage this can result in a nested pattern of plant–pollinator interactions in which specialized plants interact mainly with generalist pollinators and specialist pollinators interact mainly with generalized plants (Bascompte et al. 2003; Dupont et al. 2003; Ollerton et al. 2003; Vázquez and Aizen 2006; Jordano et al. 2006). Specialist–specialist interactions are exceedingly rare and may have been removed from communities due to the "ecological filtering" effect of natural climate change and other perturbations (Ollerton et al. 2003).

In this study, we have demonstrated for the first time that a parasitic plant and its host overlap in their pollination niches. The only published precedent for our study is that of Gomez (1994) who documented the effect of parasitic *Cuscuta epithymum* (Cuscutaceae) on one of its hosts, *Hormathophylla spinosa* (Brassicaceae). Although Gomez's study was not undertaken from the perspective of pollination niche overlap, he did note that the pollinators of *C. epithymum* that he observed are usually also pollinators of *H. spinosa*, and that the pollination spectrum of *C. epithymum* may be affected by the particular host plant that this generalist parasitizes. Clearly we would like to know how commonly parasites and hosts share pollinators, and a survey of published studies suggests that parasites and hosts may frequently utilise the same functional group of pollinations (sensu Fenster et al. 2004). For example, the hemiparasites *Rhinanthus serotinus* and *Euphrasia* spp. are often pollinated by bumblebees (*Bombus* spp.), as are the *Trifolium* spp., which sometimes host them (Knuth 1909; Kwak 1978; Svensson and Carlsson 2004; Hellstrom et al. 2004; Carvell et al. 2006). *Pedicularis* spp. and their host Fabaceae can also be bumblebee pollinated (Knuth 1909; Macior 1973, 1975, 1983; Laverty 1992; Sun et al. 2005; Hong and Li 2005) and large bees, which pollinate *Agalinis auriculata* may also pollinate host Asteraceae (Molano-Flores et al. 2003; Mulvaney et al. 2004). Finally, New Zealand Loranthaceae are frequently bird pollinated (Ladley et al. 1997) as are some tree species which could potentially host these mistletoes (Anderson 2003). Plant–pollinator interactions can be geographi-

cally variable and therefore such examples, whilst they are suggestive, would require further study of sympatric populations of parasite and host. Other parasite–host combinations probably do not share pollinators; for example most African Loranthaceae are thought to be bird pollinated (Polhill and Wiens 1998; Watson 2001) whereas host trees such as *Acacia* spp. are more frequently insect pollinated (Stone et al. 2003). In Rafflesiaceae, all species studied to date are pollinated by saprophilic flies (e.g. Beaman et al. 1988, Bänziger and Pape 2004). Whilst nothing is known about the pollinators of their host *Tetrastigma* vines, they are likely to be small Hymenoptera (the flowers are sweetly scented and wholly unlike those of the parasites); although the flowering times of host and parasite may overlap, there is considerable spatial separation between them, the host flowering in the rainforest canopy, and the parasite flowering on the forest floor (H. Bänziger, personal communication). A number of mistletoes flower in the winter and their flowering period does not overlap with that of their host, for example the genus *Tristerix* (Medel et al. 2002; Aizen 2003) and the European species of *Viscum* (Knuth 1909; Stace 1991; Aparicio et al. 1995). Mistletoes have been considered a keystone resource in the communities they inhabit, due partly to their extended and seasonal flowering phenologies (Watson 2001). Is the unusual timing of flowering an adaptation to prevent competition for pollinators with their larger tree hosts?

In addition to competing for pollinators, host plants may affect the interactions of parasites or hemiparasites and their pollinators in relatively subtle ways, for example by making them more or less attractive to pollinators. Research by Adler (2003) showed that compared to plants parasitizing grasses, *Castilleja indivisa* individuals parasitizing leguminous hosts had larger floral displays and therefore attracted more pollinators. This may be a widespread phenomenon as other studies have documented greater flower production in particular host–parasite combinations (e.g. Matthies 1998). Shared mutualistic interactions between parasitic plants and their hosts include not just pollination: seed dispersal of host *Juniperus monosperma* by birds was shown to be increased by the presence of fruit of the mistletoe *Phoradendron juniperinum* (van Ommeren and Whitham 2002), and likewise facilitation of avian seed dispersal was demonstrated between host *Cecropia schreberiana* and the mistletoe *Phoradendron hexastichum* (Carlo and Aukema 2005). Related to this, Herrera (1988) found that the hemiparasite *Osyris quadripartita* is co-dispersed with other endozoochorous shrubs in bird faeces, in direct proportion to the frequency with which it uses those shrubs as

hosts. An assortment of further interactions between parasitic plants and other organisms may also be affected by host identity. The palatability of parasites for herbivores has been shown to be significantly affected by the transfer of secondary compounds from host to parasite in *Castilleja* spp. (Marvier 1996; Adler 2000, 2002) and in *Rhinanthus serotinus*, where the defensive alkaloids actually originate from the endophytic fungus infecting the host grass (Lehtonen et al. 2005). However, no such effect was found between *Melampyrum arvense* and a range of hosts (Schadler et al. 2005). Additionally, it has been suggested that Australian mistletoes possessing leaves which mimic the leaves of their host trees have reduced herbivory, but the evidence to support this is ambiguous (Canyon and Hill 1997). Belowground interactions between host plants and other organisms can also be affected; for example parasitic plant infection was shown to reduce mycorrhizal fungal colonization of roots in the grass *Lolium perenne* (Davies and Graves 1998). The relative importance of facilitation or suppression of third-party interactions is yet to be determined for most host–parasite systems: we are only beginning to unravel the complexity of such multi-species relationships, and to identify their general patterns across taxa and communities, providing abundant opportunities for future research.

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