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Pollination in the Early-purple Orchid

Mike Gasson

My interest in Early-purple Orchid pollination began some three years ago as a by-product of monitoring herbivore impacts. The largest remaining area of ancient woodland in Norfolk is Foxley Wood, which has existed as a managed habitat since the times of the Domesday Book. Whilst maintaining the woodland rides in Foxley back in the late winter of 2009/2010, I realised the extent to which emergent rosettes and flower buds of *Orchis mascula* are consumed by herbivores (Figure 1). Deer are the main culprits, with the Reeves Muntjac the prime offender. With the support of



Fig. 1: Heavy browse on emergent *Orchis mascula* rosette and spike (top) and survival of remnant flowers all of which set fruit (bottom).

Photos by Mike Gasson

Norfolk Wildlife Trust, I started a monitoring project that was intended to clarify the impact of deer on the wood's orchid populations using a variety of exclusion experiments and a total mapping of the *O. mascula* population over three seasons (Figure 2). The major conclusion was that whilst heavy browse weakened the plants, it did not extend to the opened flower spikes with even extensively damaged plants still able to set fruit on what was left by the deer. My suspicion is that the well documented "tom cat" odour associated with the flowers of *O. mascula* acts as a deterrent to would be "browsers". This is in marked contrast to the wood's Greater Butterfly-orchids, whose nectar-rich flowers appear to be selectively browsed by deer – but that is another story!

I was especially concerned to establish the impact of browse on the recruitment of new Early-purple Orchid plants and monitored fruit set frequencies at a series of stations throughout the wood. Figure 2 summarizes data from the 2010 season. Before starting this study, I had the impression that *O. mascula* pollination was relatively inefficient, being the expectation for an allogamous orchid species that relied on food deception to attract its pollinators. I was aware of the pioneering work of Darwin (1877) and

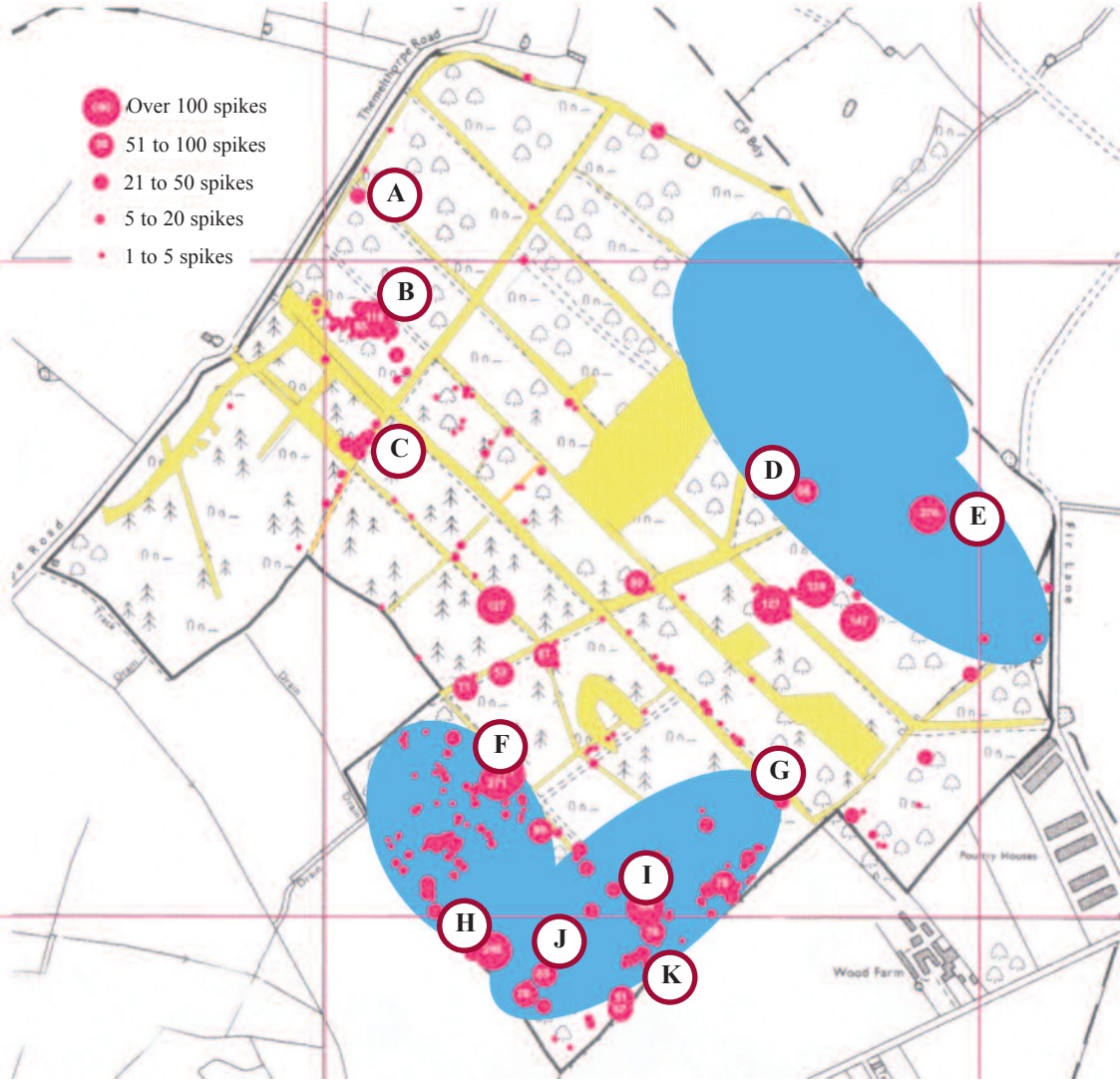


Fig. 2: Map of Foxley Wood showing the distribution of 5,508 flowering plants of *Orchis mascula* in the 2010 season. Solid red circles are GPS locations for groups of plants. Letters in brown rings are the locations where fruit set was measured later in the same season. The figures are percent fruit set followed in brackets by the total number of flowers counted at each location: A – 47% (102); B – 61% (265); C – 36% (111); D – 53.1% (96); E – 62% (293); F – 42% (442); G – 34% (103); H – 50% (272); I – 47% (112); J – 52% (304); K – 39% (117). The global fruit set for the entire wood is 49% (2,222). Blue underlays indicate the distribution of Bluebell (*Hyacinthoides non-scripta*) in the wood; an estimate of Bluebell fruit set was 62% (302). Bumblebee pollination (2010) and repeated white butterfly visits (2011) were observed in area B and a re-evaluation of fruit set in 2011 gave higher frequencies of 83% (414). Early Purple Orchid fruit set in other Norfolk woods were measured during 2010 with the following results: Honey-pot Wood 48% (208); Wayland Wood 34% (160); small wood near Loddon 37% (186).

Müller (1883) that first established the fundamentals of *Orchis* pollination, as well as the importance of naive bumblebee queens as the major pollinating insect. Also, the detailed work of Nilsson (1983) revealed low frequencies of seed set, as well as the observation that the lowest flowers on an orchid spike were pollinated preferentially. Much of this was reviewed recently by Jacquemyn *et al.* (2009). Hence, it was something of a surprise to find such high levels of fruit set in the Early-purple Orchids of Foxley Wood.

Most of the wood's Early-purple Orchids have an association with strong stands of Bluebell (*Hyacinthoides non-scripta*), leading to the thought that these rewarding companion flowers may play a key role in maintaining strong local concentrations of pollinating insects. Although both Darwin (1877) and Müller (1883) thought that insect visitors extracted a reward other than nectar from the spur lining, it is now generally accepted that no reward is offered and that *O. mascula* is a food deceptive orchid, as first proposed by Delpino (Müller, 1883). In Foxley Wood, bumblebees were frequently encountered on the Bluebells, although observing them as orchid visitors was a rare event. In part, this may be because it was not, at the time, the focus of monitoring. Also, others have found it difficult to record the pollination event: Darwin (1877) never did and Nilsson (1983) reports spending 30 hours to gain three observations of bumblebee visits to *O. mascula*. I made one casual observation of *Bombus terrestris* on *O. mascula* and its behaviour was completely consistent with previously published accounts. The bee spent only a short time on an individual plant, visiting a few of its flowers, before moving on to the base of another orchid's flower spike. Many different orchids were visited in this way. It is well established that *O. mascula* has evolved a finely tuned mechanism with caudicle bending time adapted to the time a pollinator typically spends on an individual plant. The result is that cross pollination is promoted.

Rather more frequent pollination events were recorded in an early study by Müller (1883) for a dense population of Early-purple Orchids on an especially favourable day for insect activity. Five pollination events were recorded in a few hours and, interestingly, potential pollinators were captured and checked for the presence of orchid pollinia. A return of 32 positives amongst 97 bumblebees suggests that the orchids had been visited regularly.

The part of Foxley Wood where my own pollination event was observed happened also to have one of the highest recorded fruit set rates (61%). However, there was a problem in that the site is relatively remote from the main concentrations of Bluebells in the wood (Figure 2). This rather dampened my belief in *Hyacinthoides non-scripta* as a key companion species that contributed to higher orchid fruit set by holding pollinators within the local habitat. In the 2011 season, a chance observation in this same area revived the idea with a twist. This particular part of the wood had



Fig. 3: Small White butterfly taking nectar from Bugle (*Ajuga reptans*)

Photo by Mike Gasson

been coppiced recently and whilst it lacks Bluebells it does contain a very strong population of Bugle (*Ajuga reptans*). On a sunny morning, whilst counting the flowering spikes of *O. mascula*, I watched for an hour or so as large numbers of white butterflies (Orange Tip *Anthocharis cardamines*, Small White *Pieris rapae* and Green-veined White *Pieris napi*) “nectared” on the Bugle plants (Figure 3). The interesting observation was that the butterflies repeatedly visited the orchid flowers, searching for nectar, switching between individual plants before returning to the more abundant Bugle.

Because of the flower and insect morphologies involved it is highly unlikely that butterflies are effective pollinators of *O. mascula* but it was very clear that the presence of Bugle as a rewarding companion species was responsible for the frequent butterfly visits to the orchid flowers. Doubtless the same would be true for effective pollinators such as bumblebee queens. It may be relevant that Jacquemyn *et al.* (2008) reported increased fruit set as a consequence of coppice management, although the highest Foxley fruit set in 2010 (62%) was from an area of mature woodland maintained as a non-intervention area.

Later in the same season, I again counted fruit set in this area. From 17 plants and 414 flowers the global fruit set was 83%, ranging from 55 to 100% for individual plants. Hence, overall these East Anglian Early-purple Orchids behave very differently from Swedish populations that have become the established norm in many accounts of Early-purple Orchid pollination. In my local orchids there is absolutely no suggestion that the lower flowers are pollinated preferentially and fruit set frequencies are vastly higher than those recorded in Sweden by Nilsson. For example, using data collated by Claessens & Kleynen (2011) the overall fruit set for Swedish *O. mascula* was 8% (for 29,388 flowers) with a range for individual populations of 3% to 15%. Another example of fruit set frequency comes from Dormont *et al.* (2010). Their study was concerned primarily with the evolution of colour polymorphism and they presented data to suggest that the presence of white morphs within a population of *O. mascula* had the effect of elevating fruit set frequencies in the normal purple morphs. What interests me is the fact that these relatively isolated orchid populations on a limestone plateau in southern France had generally low fruit set frequencies, the elevation reported amounting to a shift from 6% for an exclusively purple population to 27% for one with both purple and white morphs. Dormont *et al.* (2010) confirmed the positive influence of a colour variant by adding artificial

white lures to an exclusively purple population. Whilst this study and its interpretation are logical, it is totally trumped in frequency terms when a population such as that at Foxley generates fruit set twice as high as the elevated frequency cited by Dormont *et al.* (2010). Variant morphs are extremely rare within the Foxley Wood population of Early-purple Orchids. In 2010, only 3 pale morphs (2 pink and one near white) were found amongst 5,508 flowering plants.

In contrast, there are other reports of much higher fruit set in German populations of *O. mascula*. Again using the data collated by Claessens & Kleynen (2011), records from Germany have an overall fruit set frequency of 33% (for 5,316 flowers) with a range for individual populations from 7% to 68%. Also, I have checked fruit set frequencies at several other Norfolk woods finding broadly similar frequencies (Figure 2), although none as high as those for Foxley Wood.

From all of this information I have gained the impression that fruit set frequency varies markedly depending on the number of pollinating insects maintained in a particular habitat. Given relatively low numbers of pollinators the classic picture emerges with poor seed set and preferential pollination of the lower flowers on a spike. This pattern is typical of the populations studied by Nilsson (1983) and Dormont *et al.* (2010). But where larger numbers of pollinating insects are held within a local habitat much higher fruit set occurs and the oft-mentioned preferential pollination of the lower flowers is not apparent. In Foxley Wood, the major factor contributing to the retention of active pollinating insects appears to be the presence of large numbers of companion species that, unlike the Early Purple Orchid, do offer a nectar reward. The two best candidates for this role are Bluebell (*Hyacinthoides non-scripta*) and Bugle (*Ajuga reptans*). This is not an original concept but one that was first proposed by Thompson (1978) and studied in European orchids by Johnson and colleagues (e.g. Johnson *et al.*, 2003). It has been called “Magnet Species Effect” and as this name implies, it may function by increasing the local abundance of pollinators.

Looking at information on *O. mascula* pollination in recent general orchid texts reveals variation in the views of well-respected authors:

Foley & Clarke (2005) have “the Early Purple Orchid has a rather repugnant cat-like scent, but small insects are attracted to the flowers and very successfully effect pollination, shown by the resulting high quantity of seed that is set.”

Harrap & Harrap (2005) follow a detailed description of classic bee-promoted pollination biology with “Early Purple Orchid is self-compatible and is sometimes self-pollinated”. With respect to fruit set frequency they have “Seed set is variable, with the lowest, earliest-opening flowers most likely to be pollinated.”

Kretzschmar *et al.* (2007) have “The species is allogamous: this is confirmed by the percentage of flowers setting seed, which lies between 23% and 48%.”

Hence, there does seem room for more data gathering and further exploration of pollination in *O. mascula*. Now is a good time to check out flowering Early-purple Orchids for companion flowers and possible pollinators. It would be interesting to get records for fruit set frequency from UK populations in different habitats. I have placed a recording form on the HOS website and will happily collate any observations and information from members. Whilst not in quite the same class as the very successful spur-length study co-ordinated by Richard Bateman (Bateman & Sexton, 2009; Bateman *et al.*, 2012), there is an opportunity here to pool resources and maybe throw a little more light on what remains an imperfectly understood process.

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