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ORIGINAL ARTICLE

Reproduction of the West Mediterranean endemic *Arum pictum* (Araceae) on Corsica

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Abstract Pollination in the genus *Arum* appears to be in general a complex deceptive pollination process. The genus *Arum* is composed of 28 species, all belonging to the subgenus *Arum*, except *A. pictum*, the only species of the subgenus *Gymnomesium*, which is basal and sister to all other *Arum* species. The aim of this paper is to document the pollination ecology of the insular *Arum pictum*, the only *Arum* species to flower in autumn, on the island of Corsica (France). The anthesis cycle of *A. pictum* occurs during the day, attracting sphaerocerid flies and staphylinid beetles early in the morning and late in the afternoon of the first day. The pollen is released from the anthers early in the morning of the second day before the departure of the insects. Its thermogenic cycle matches the anthesis cycle with an original and unique, bimodal temperature pattern of the appendix (morning and afternoon), contrary to the unimodal pattern found in all other studied *Arum* species. Data from reproductive success and seed sets suggest that sexual reproduction in this species is limited by pollen (e.g. attracting lured insects) rather than by resources. The biology of this Western Mediterranean species appears to be different from other Western European *Arum* and close to some Eastern Mediterranean species. Further studies are needed to establish whether *Arum pictum* represents some ancestral stage or whether its peculiar biological traits are adapted to its insular distribution.

Keywords Floral volatiles · Ocimene · Insect pollination · Reproductive success · Sphaeroceridae · Thermogenesis

Introduction

Most cases of plant–pollinator interactions are mutualisms that benefit both partners (Proctor et al. 1996), but many antagonistic pollination systems exist, in which only the plant benefits as pollination is achieved by deception (Proctor et al. 1996; Renner 2006). Deceptive flowers exploit pollinators by signalling the presence of a reward without providing it. There are different ways to deceive a pollinator, corresponding to diverse types of reward mimics (Jersakova et al. 2006). Except the orchids, one of the families richest in rewardless flowers is the Araceae (Renner 2006). Pollination in the genus *Arum* (Araceae) has been recently reviewed (Gibernau et al. 2004) and appears to be a complex deceptive pollination process. Pollinators are attracted by a warm and odoriferous inflorescence, which mimics their brood site odour (Bermadinger-Stabentheiner and Stabentheiner 1995; Kite 1995; Kite et al. 1998). Attracted insects (mainly flies and beetles) fall or go down into a floral chamber. Lured insects are trapped within the floral chamber when stigmas are

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receptive, and pollination eventually occurs if the insects carry pollen grains. The upper part of the floral chamber is closed by horizontal hairs (i.e. modified sterile male flowers), thus once inside, insects cannot escape. The next day, the inflorescence starts its male phase, and the pollen is released and falls onto the insects. At the same time, the hairs wither, allowing the pollen-loaded insects to escape. The only known exception to this deceptive pollination system in the genus *Arum* is *A. creticum*, which is pollinated by a mining bee collecting pollen (Diaz and Kite 2006). Most studies published to date have documented species from southeastern Europe and the Middle East (Knoll 1926; Kullenberg 1953; Braverman and Koach 1982; Drummond and Hammond 1991, 1993). For Western Europe, pollination ecology is mainly known for *A. maculatum* (Prime 1960; Beck 1983; Lack and Diaz 1991; Ollerton and Diaz 1999; Diaz and Kite 2002) and *A. italicum* (Arcangeli 1883; Prime 1960; Méndez and Obeso 1992; Diaz and Kite 2002; Albre et al. 2003; Albre and Gibernau 2008). It appears from these studies that Eastern Mediterranean *Arum* species are mainly pollinated by dung flies and carrion beetles, whereas Western *Arum* attract mainly Nematocera flies (Psychodidae, Chironomidae, Ceratopogonidae). Interestingly, there is one mention of pollinating insects of *Arum pictum*. One inflorescence in culture at the Botanical Garden of Pisa captured 95 coprophilous insects, of which 86 were sphaerocerid flies, *Borborus* (*Copromyza*) *equinus* (Arcangeli 1886), suggesting pollinators related to those of the Eastern Mediterranean *Arum* species.

The genus *Arum* is composed of 28 species, all belonging to the subgenus *Arum* except *A. pictum*, the only species of the subgenus *Gymnomesium*, which appears to be basal and sister to all other *Arum* species (Boyce 2006; Mansion et al. 2008). Thus *A. pictum* appears to be a unique taxon within the genus *Arum*. This species presents some distinguishing characters such as (1) autumn flowering (versus spring for all other species) and (2) leaves produced after or at the same time as inflorescences (versus before, for all other species; Boyce 2006). Such flowering strategy is well known in Mediterranean plant communities (Thompson 2005). However, the only information available regarding its pollination ecology and reproductive system is from one plant cultivated at the Botanical Garden of Pisa (Arcangeli 1886). *A. pictum* is endemic to West Mediterranean islands: Corsica, Sardinia and Balearic Islands. It is known that island colonisation has often induced floral and reproductive changes for the colonising individuals. Among the main factors implicated in such changes can be: a new pollinating fauna, geographical isolation, small populations, few founders (low diversity) or a different community (Thompson 2005; Micheneau et al. 2008; Mortensen et al. 2008; Pereira 2008; Ricklefs and Bermingham 2008; Givnish et al. 2009; Ollerton et al. 2009). It is noteworthy that the only non-deceptive *Arum* species is *A. creticum*, an insular species endemic to Crete (Boyce 2006; Diaz and Kite 2006).

The aim of this paper is to document the pollination ecology of *Arum pictum* on the island of Corsica (France) in order to measure whether insularity has led to floral and biological modifications/adaptations as for *A. creticum*. First, we measured vegetative and floral traits in relation to reproductive effort (number of flowers and ovules) and success (number of seeds). Secondly, we quantified the reproductive and pollination system in relation to the attracted insects. Thirdly, we recorded the floral odours and the thermogenic pattern of inflorescences during anthesis.

Materials and methods

Study population and sampling

A natural population of *Arum pictum* L. fil. was studied at the rear of the beach at Sagone (Corsica, France). The plants were growing on sandy or rocky hillsides. The study was conducted at four periods: October 5–16, 2001, the first week of January 2002, March 12–18, 2002 and October 11–17, 2002. Complementary measurements on thermogenesis were obtained from four plants in cultivation at the University Paul Sabatier of Toulouse (France) in autumn 2003, 2004 and 2005.

Vegetative and reproductive morphology

Two hundred sixty-three individuals were randomly marked from different parts of the population and mapped. For each individual studied, the phenological and sexual stages were recorded. The number of leaves and inflorescences were counted; plant and spathe heights and leaf sizes of the upper surface (i.e. limb length and width) were measured. Leaves were approximated as a triangle with respect to their upper surface.

Moreover, 75 inflorescences were harvested in order to measure the different parts of the spadix, fertile male and female zones and appendix length. Finally, the number of male (stamens) and female (ovaries) flowers per inflorescence, the number of ovules and size (height, width) of one female flower per inflorescence were also calculated. The relationships between these characters were studied using linear regressions (SYSTAT 11 2004).

Reproductive and pollination system

The reproductive system of *A. pictum* was studied by performing two experiments. First, we tested spontaneous selfing and/or apomixis by bagging, prior to opening, 20 inflorescences with organdie bags. Second, using a small paintbrush, we hand-pollinated 15 receptive inflorescences with fresh pollen harvested from male-phase inflorescences located several metres away. Fruit set was calculated for these two treatments as well as for naturally pollinated inflorescences ($N = 245$). Finally, the numbers of berries and seeds were counted on all mature infructescences from the two experiments and on 47 open-pollinated infructescences.

Insect visitors

The insects trapped in 44 inflorescences at the male stage were collected and preserved in alcohol (75%). Each was identified and the sex ratios [female/(female + male)] of the most abundant species (*Coproica* and *Spelobia* spp.) were calculated. A few insects from different taxa were caught alive, then killed with ethylacetate in order to compare their pollen loads.

Thermogenesis

Thermogenesis in *A. pictum* was studied by measuring the temperatures of six inflorescences belonging to different plants in the field and four inflorescences in cultivation at the University Paul Sabatier of Toulouse (France). Every 10 min, temperatures were recorded in the three different zones of the spadix (appendix, male and female flowers) and of the ambient air, with four probes connected to two Digi-Sense® DualLogR® thermocouple thermometers. The two probes of one thermometer were inserted less than 5 mm deep into the male and female zones. One probe of the second thermometer was inserted into the middle of the appendix, whereas the second was used to record the ambient air temperature near the studied inflorescence.

Floral volatiles

Volatile compounds emitted by an inflorescence were collected by adsorption–desorption (headspace) technique with a Porapak®Q collection trap. Three open inflorescences were sampled in the field on October 12, 13 and 14, 2002 during 2 h in the morning (between 08:00 hours and 10:00 hours). Samples were desorbed with 5 ml dichloromethane. Gas chromatography–mass spectrometry (GC–MS) analysis was performed with a Finnigan Trace 2000 chromatograph directly coupled to a mass spectrometer quadrupole detector using an apolar capillary column Restek RTX-5MS (5% diphenyl, 95% dimethylpolysiloxane), 30 m × 0.25 mm, 0.25 µm film thickness. The ion source was operated in electron-impact mode (EI 70 eV) with the mass spectra scanned from m/z of 38 to 300. The temperature of the injection port was set at 250°C, and the helium flow constant at 1 ml/min. The oven temperature was programmed as follows: 50°C for 2 min, then 5°C/min up to 250°C, then 5 min at 250°C. Tentative compound identifications were performed according to the mass spectrum library and manual interpretations (Jean-Marie Bessière, pers. comm.).

Results

Vegetative and reproductive morphology

Arum pictum sprouted in autumn, the inflorescences appearing in October, before or with the leaves. Of the 263 *Arum*, 200 (76%) were mature individuals and produced a total of 232 inflorescences. A mature plant produced an average of 1.16 ± 0.54 inflorescences. Most of the mature individuals had one inflorescence (89.6%), some individuals produced two inflorescences (7%) and a few produced between three or five inflorescences (3.4%). Vegetative morphological traits are presented in Table 1. Plant height was correlated with leaf area and spadix length ($R^2 = 0.31$, $F_{1,176} = 94.4$, $P < 10^{-5}$ and $R^2 = 0.15$, $F_{1,66} = 11.4$, $P = 1.25 \times 10^{-3}$, respectively). A positive relationship was also found between the number of leaves and the inflorescence number ($R^2 = 0.43$, $F_{1,176} = 205$, $P < 10^{-5}$).

The mean sizes of the different parts of the inflorescences are shown in Table 1. The appendix appeared to be an important part of the inflorescence, as its length represented about half (31–62%) of the total spadix size (three-quarters when considering only the fertile zones). The female zone was about twice as long as the male zone. The numbers of both male and female flowers increased with spadix length (male flowers $y = 0.70x + 83.08$; $R^2 = 0.16$; $F_{1,54} = 10$, $P = 2.5 \times 10^{-3}$; female flowers $y = 0.68x + 32.3$; $R^2 = 0.17$; $F_{1,62} = 13.1$; $P = 6 \times 10^{-4}$), and the two slopes were not significantly different ($F_{1,54} = 0.01$; $P = 0.9$). Although the lengths of the two fertile zones were not positively correlated ($R^2 = 0.03$, $P = 0.16$), a positive relationship between the numbers of male and female flowers was found ($R^2 = 0.23$, $F_{1,61} = 18.6$, $P = 6 \times 10^{-5}$).

Reproductive system and fructification

An inflorescence contained on average 170 ± 39 (range 95–285) stamens (male flowers) and 114 ± 32 (range 52–183) ovaries, each containing about 5 ± 2 ovules (range 2–10). Consequently, an inflorescence was estimated to produce 628 ± 325 potential seeds. A positive relationship was found between the number of ovules per flower and the size

Table 1 Vegetative and reproductive morphological measures [mean ± standard deviation (SD)] of mature individuals of *Arum pictum* from Corsica

Vegetative measures			Reproductive measures		
Plant height (mm)	$N = 178$	154.1 ± 53	Spathe length (mm)	$N = 165$	156.4 ± 29
Number of leaves	$N = 200$	1.68 ± 1.4	Spadix length (mm)	$N = 91$	118.2 ± 21
Leaf length (mm)	$N = 155$	133.7 ± 31	Appendix length (mm)	$N = 74$	57.1 ± 15.4
Leaf width (mm)	$N = 155$	68 ± 15	Male zone (mm)	$N = 75$	5.1 ± 1.2
Surface of one leaf (mm^2)	$N = 155$	4,711 ± 2,002	Female zone (mm)	$N = 75$	11 ± 2
Total leaf surface (mm^2)	$N = 155$	9,350 ± 9,197	Stipe (mm)	$N = 74$	32.3 ± 5.4

Leaves were approximated as a triangle with respect to their upper surface (mm^2). Total upper leaf surfaces were estimated for each individual by multiplying the number of leaves by the mean upper leaf surface. Data recorded in October 2001

of the female flower zone ($R^2 = 0.21$, $F_{1,53} = 13.7$, $P = 5.1 \times 10^{-4}$) or the spadix length ($R^2 = 0.38$, $F_{1,48} = 29$, $P = 2.1 \times 10^{-6}$).

In natural conditions, about one-third of the inflorescences of *A. pictum* (31%) produced infructescences (Table 2), bearing on average 63 mature fruits (range 13–126). Each fruit or berry contained about three developed seeds, which represented a mean of about 183 seeds per infructescence. Thus, natural pollination resulted in maturation of about 55% of potential berries and 29% of potential seeds per infructescence. As all bagged inflorescences did not mature, spontaneous selfing or apomixis is unlikely to occur in *Arum pictum*. On the other hand, 14 out of 15 (93.3%) of the hand-pollinated inflorescences set fruit (Table 2). Natural and hand-pollinated fructification rates were statistically different ($\chi^2_1 = 8.4$, $P = 0.004$), even though the number of hand-pollinated inflorescences was limited.

A significantly higher number of berries developed from hand-pollinated inflorescences than from open-pollinated inflorescences (Table 2). On the other hand, the number of developed berries (fruits) was not significantly correlated with plant size, leaf area or spathe length. The total number of seeds produced was significantly higher in hand-pollinated inflorescences than in open-pollinated inflorescences (Table 2). The total number of seeds per inflorescence was positively correlated with the number of developed berries ($R^2 = 0.82$, $F_{1,49} = 218.1$, $P < 10^{-3}$) but was not significantly correlated with plant size, leaf area or spathe length. A significantly higher number of berries developed from hand-pollinated inflorescences than from open-pollinated inflorescences ($F_{1,59} = 6.63$; $P = 0.013$; Table 2). The total number of seeds produced and the mean number of seeds per fruit were also significantly higher in hand-pollinated inflorescences than in open-pollinated inflorescences ($F_{1,59} = 5.43$; $P = 0.023$ and $F_{1,4149} = 28.30$; $P < 10^{-3}$, respectively; Table 2). A positive linear regression was found between the mean number of seeds per infructescence and the number of developed berries ($R^2 = 0.43$, $F_{1,49} = 37.57$, $P < 10^{-3}$), but not with plant size, leaf area or spathe length.

Insect visitors

Flies were the most abundant visitors, representing about 52.5% of the insects attracted to the inflorescences of *A. pictum*. Sphaeroceridae flies, some Sciaridae and Scatopsidae represented the main trapped Diptera. The most frequent and abundant species of Sphaeroceridae were *Coproica hirticula*, *Coproica ferruginata* and *Spelobia bifrons* (Table 3). Staphylinidae (Coleoptera) and Braconidae (Hymenoptera) were also well represented (Table 3). Of inflorescences at anthesis, 70% ($N = 91$) trapped insects. An inflorescence trapped an average of 5.5 ± 4.5 insects (range 1–22). The sex ratio of the attracted *Coproica* and *Spelobia* was strongly female biased, being 70–78% depending on the species.

Table 2 Percentage of infructescence produced out of *N* inflorescences, mean ± SD numbers of berries and total seed per infructescence, and mean number of seeds per berry

	N	Infructescence set (%)	Developed berries	Seeds per infructescence	Seeds per berry
Self-pollination	20	0	–	–	–
Hand-pollination	15	93.3	86.1 ± 34.8	274.4 ± 144.48	3.2 ± 1.4
Natural conditions	245	31	62.7 ± 28.2	183 ± 124.10	2.9 ± 1.5

Data recorded in October 2001

Table 3 Total number and percentage of the different insect taxa visiting 53 *Arum pictum* inflorescences in Sagone

		Total number	%	No. of inflorescences	Insects per inflorescence
	Coproica hirticula	67	23.1	33	2.03 ± 1.5
	Coproica ferruginata	25	8.6	19	1.3 ± 0.6
Sphaeroceridae	*Spelobia bifrons*	23	7.9	17	1.4 ± 0.8
	Coproica hirtula	3	1	1	–
	Leptocera nigra	1	0.3	1	–
	Cypsela spp.	6	2	4	–
	Sphaerocera spp.	11	3.8	9	–
Sciaridae		10	3.4	8	–
Scatopsidae		7	2.4	6	–
Braconidae		30	10.3	18	1.6 ± 1.1
Staphylinidae		65	22.4	22	2.8 ± 3.2
Other		43	14.8	30	–

Number of inflorescences containing a given insect taxa (out of 53). The sum is higher than 53, as an inflorescence may trap insects from different taxa. The number of insects per inflorescence (mean ± SD) was calculated based on the number of inflorescences containing this taxa. Data recorded in October 2001

Pollen counts showed that sphaerocerid flies regularly (5 out of 8) carry small amounts of pollen (5–20 pollen grains), but further data are necessary to quantify pollinator efficiencies precisely. The two braconid specimens observed had no pollen, and only 1 staphylinid out of 17 was carrying some pollen (fewer than five grains). Of insects remaining in the inflorescences on the second and third day (i.e. after the flowering cycle), 80% were Braconidae and Staphylinidae.

Thermogenesis

The appendix and the male flowers appeared to be responsible for heat production in inflorescences of *Arum pictum*.

The first temperature rise, caused by the male flowers, was recorded the night before the opening of the spathe between 23:30 hours and 01:00 hours (Fig. 1a). The temperature of the flowers reached a maximum of 24–26°C at 02:00–03:00 hours, which is 6–8.5°C warmer than ambient air (Fig. 1b), and was maintained around this temperature for 6–8 h (until 10:30–12:30 hours). The appendix started heating up about the same time as the male flowers were at maximum temperature, and finally reached 27–29°C between 05:45 hours and 07:00 hours, when the spathe began to unfold (Fig. 1a). The appendix reached a maximum temperature difference of 10–13.9°C above ambient air, which was about 17–18°C at this time (Fig. 1b). Around 07:20 hours, the spathe was wide open and male flower temperature declined, followed by appendix temperature, to reach ambient temperature at around 12:00 hours.

A second thermogenic phase began at the end of this first day of flowering: the appendix started heating up at about 15:20–16:00 hours, while the male flowers started heating up around 17:00–19:20 hours (Fig. 1a). Appendix temperature quickly reached a "plateau" around 27–30°C between 18:00 hours and 22:20 hours (6.5–10°C above ambient air). After 18:00–19:00 hours, it decreased gradually until reaching ambient level, at 03:00–06:00 hours on the morning of the second day of flowering (Fig. 1a). Male flower temperature increased more slowly, and reached a "plateau" around 21–23°C (5.5–8°C above ambient air) from 00:00–02:00 hours to 08:30–09:30 hours on the morning of the second day. The temperature then declined, returning to ambient level. Concerning female flowers, no notable temperature increase was recorded. The temperature records at the University Paul Sabatier at room temperature showed the same overall pattern and confirmed the bimodal temperature pattern of the appendix (Fig. 1c).

Floral volatiles

Arum pictum is characterised by a dung odour close to horse/donkey dung, described as pungent (Boyce 1993). Several bad smelling compounds were identified from the floral odour of *A. pictum*, and differences among individuals in the floral volatile profiles were found (Table 4). Individuals 1 and 2 had similar scent profiles, dominated by the monoterpene ocimene and related derivatives (dihydroocimene). In addition, other molecules, most related to dung, were present, such as skatole, indole and benzyl alcohol. Individual 3 appeared to be different, with different monoterpenes (alpha-pinene or camphene) and absence of the ocimene family, higher concentrations of dung molecules (skatole, indole or benzyl alcohol) and presence of trimethoxybenzene and delta-cadinene.

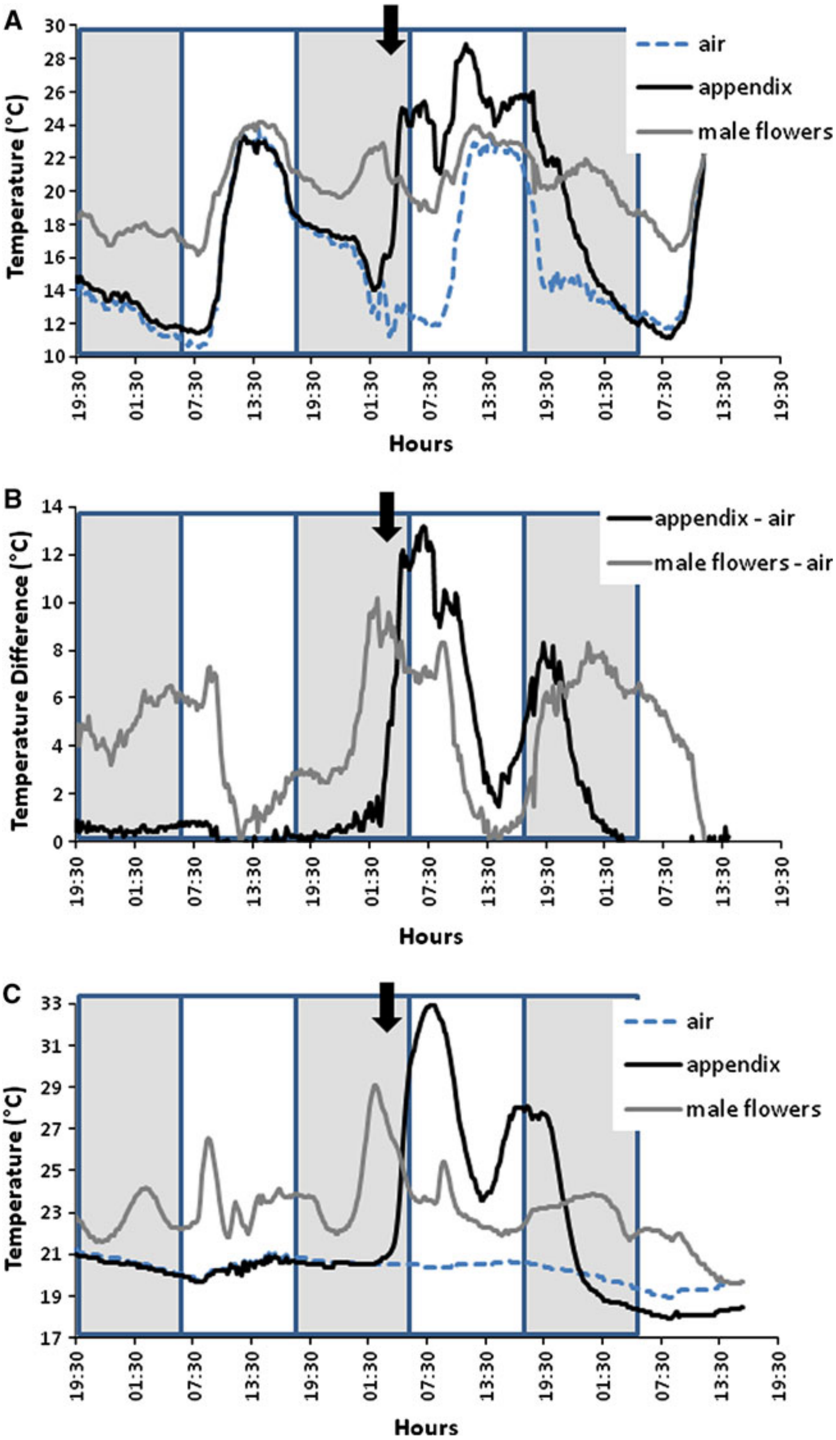

Fig. 1 Temperatures of the appendix and male flowers of *Arum pictum* during three days: the day prior to the spathe unfolding, the female phase day, and the male phase day. The *grey boxes* show the night period and the *black arrows* mark the spathe opening. **a** Temperatures of the appendix (*black line*), the male flowers (*grey line*) and ambient air (*dotted line*) recorded from one inflorescence of *Arum pictum* in the field on Corsica. **b** Temperature differences between the appendix and ambient air (*black line*) and the male flowers and ambient air (*grey line*) in the field on Corsica. **c** Temperatures of the appendix (*black line*), the male flowers (*grey line*) and ambient air (*dotted line*) recorded from one inflorescence of *Arum pictum* in culture in a room at the University of Paul Sabatier, Toulouse (France). Note that ambient temperature is fairly constant

Discussion

The main pollinators of *Arum pictum* are sphaerocerid flies and staphylinid beetles. No psychodid flies were captured by *A. pictum* inflorescences, whereas *Psychoda* species are present on Corsica (Vaillant 1978) and known to be the main pollinators of *Arum* species in West Europe (Lack and Diaz 1991; Drummond and Hammond 1993; Gibernau et al. 2004). Most of the *Coproica* (Sphaeroceridae) captured by *A. pictum* inflorescences are females (more than 70%). This phenomenon was previously recorded in *A. italicum* (99.8% of the *Psychoda*) and in *A. maculatum* (100% of the *P. phalaenoides*) (see review in Gibernau et al. 2004). Thus, the fragrance emitted by the appendix at the beginning of the flowering female phase may have sex-specific properties: some compounds would attract

Table 4 Composition (%) of floral volatiles from three inflorescences sampled during the morning

	Inflorescence 1	Inflorescence 2	Inflorescence 3
Anisaldehyde	–	–	0.6
Trimethoxybenzene	–	–	7.4
Benzyl alcohol	4.6	2.8	19.7
Delta-cadinene	–	–	13.3
Camphene	–	–	7.5
Alpha-copaene	–	–	1
Germacrene D	–	–	7.8
6-Methylheptenone	0.5	0.6	–
Indole	2.4	1.6	12.1
Linalool	–	–	–
Gamma-muurolene	–	–	1
Dihydroocimene	34	4.6	–
Ocimene	52	87.2	–
Alpha-pinene	–	–	15
Methyl salicylate	–	0.3	–
Skatole	2.2	0.8	13
2-Undecanone	–	0.5	–
Total	95.7	98.4	98.4

Coproica females and repel the males, or this biased sex ratio represents the biological cycle, with only females being attracted to the oviposition sites. Sphaerocerid flies (*Coproica*, *Spelobia*) and Staphylinid beetles (Staphylinidae) are typical pollinators in *Arum dioscoridis*, *A. orientale* and *A. nigrum* (Knoll 1926; Drummond and Hammond 1991). Pollen counts showed that sphaerocerid flies occasionally carried some pollen, but further data are necessary to quantify pollinator efficiencies precisely.

The flowering cycle is the classic 24 h process in *Arum* (see "Introduction") but mainly characterised by a time shift from dusk to dawn (see below). The pollination system of *Arum pictum* displays original features with respect to other Western *Arum* species, though the pollination ecology of the Western *A. pictum* is similar to that of many Eastern Mediterranean *Arum* species, attracting mainly dung flies (Sphaeroceridae) and beetles (Staphylinidae). The staphylinids are unlikely to be the major pollinators, since less than 6% carried some pollen; despite their abundance, the most probable pollinators would be Sphaeroceridae flies. Thus the pollination ecology of *Arum pictum* appears to be very different from Western *Arum* species, which attract mainly midge flies. Another major difference from Western *Arum* species is the shift to anthesis during day time. Most of the studied *Arum* species are pollinated at dusk and in the evening. Day pollination is known to exist in *Arum creticum*, another insular species but pollinated by bees on Crete (Diaz and Kite 2006), *A. dioscoridis* whose spathes open early in the morning (before 08:30 hours) and emit a strong dung-like smell throughout the rest of the first day (Drummond and Hammond 1991) in cultivation in England, and *A. nigrum* (Knoll 1926) in Croatia. The pollination strategy in *Arum pictum* is based on oviposition site dupery and, like in many other Eastern Mediterranean *Arum* species, floral volatiles such as skatole, indole or benzyl alcohol have been identified in cow dung smell (Kite 1995).

The thermogenic pattern was synchronised with the pollination process and occurred during the early morning and at the end of the afternoon. Such a pattern contrasts with species heating during the first evening or night after the spathe has opened in *A. italicum*, *A. maculatum*, *A. rupicola* and *A. jacquemontii*. On the other hand, heat produced during the early morning until midday was reported in *A. dioscoridis*, *A. creticum* and *A. palaestinum* (review in Gibernau et al. 2004; Seymour et al. 2009). Another variable parameter is the intensity of heat production. The difference in temperature between the spadix and ambient air can be high (15–20°C) as in *A. italicum*, *A. maculatum*, *A. rupicola* and *A. jacquemontii*, medium (9–10°C) as in *A. dioscoridis*, low (3°C) as in *A. palaestinum* and *A. creticum*, or null as in *A. hygrophilum* (review in Gibernau et al. 2004; Seymour et al. 2009). From this review, the pollination ecology of *A. pictum* appears to be close to *A. dioscoridis*. However this latter species has not been properly studied, so no further comparison is possible (Drummond and Hammond 1991). In general the appendix produces one massive temperature increase in *Arum* (Bermadinger-Stabentheiner and Stabentheiner 1995; Albre et al. 2003; Seymour et al. 2009) or related genera (Seymour and Schultze-Motel 1999; Seymour et al. 2003). In this paper, we have documented for the first time one species, *Arum pictum*, whose appendix is able to increase its temperature, stop heating and then re-start the thermogenic process, leading to the production of two temperature increases within the same day in a manner similar to fertile male flowers (Fig. 1b, c; Albre et al. 2003; Seymour et al. 2009). This double temperature increase may be related to two insect attraction periods, during the early morning and the end of the afternoon, perhaps to maximise the chance of attracting potential pollinators (70% of the inflorescences visited). Nevertheless, data on fructification showed that the reproductive success of *A. pictum* was pollen limited (see next paragraph). Further studies are needed to understand the cause and role of this new thermogenic pattern of the appendix.

All the bagged inflorescences of *A. pictum* aborted without setting any fruit, whereas 31% of control inflorescences set fruit in natural conditions. Thus, spontaneous selfing or apomixis is unlikely to occur in *A. pictum*, as also reported for *A. italicum* (Albre et al. 2003) and *A. maculatum* (Lack and Diaz 1991). Of the hand-pollinated inflorescences, 14 out of 15 set fruit: this rate appears to be higher than the proportions observed in the unmanipulated inflorescences, probably because of pollen limitation as shown in *A. italicum* (Albre and Gibernau 2008). Such pollen limitation could explain the high rate of non-maturing infructescences in non-predated plants (69%), as this is frequent in Araceae species: 49.7% for *Arum italicum* (Albre and Gibernau 2008), 50% for *Dieffenbachia longispatha*, 87% for *Symplocarpus renifolius* (Young 1986; Uemura et al. 1993) and 22.3–92.2% for *Arum maculatum*, according to the population (Ollerton and Diaz 1999).

The relationship found between the number of developed fruits and the mean number of seeds per fruit appears to depend more on pollination efficiency than on plant vigour or size: the attracted insects deposit the pollen they carry on the stigmas, resulting in fruit and seed development. The more numerous the pollen-loaded insects, the more pollen grains they deposit on each stigma. Hence large plants have large appendices; they tend to attract more pollinators, thus increasing their potential seed production (Méndez and Obeso 1992). Similarly, natural and hand-pollinated fructification rates were statistically different. Significantly higher numbers of berries and seeds developed from hand-pollinated inflorescences than from open-pollinated inflorescences. On the other hand, the number of developed berries (fruits) or seeds was not correlated with plant size, leaf area or spathe length. All these results suggest that reproductive success is pollen rather than resource limited, certainly in terms of success of attracting and deceiving pollinators.

In conclusion, *Arum pictum* appears to be a very distinctive taxon. First, the pollinators (sphaerocerid flies) and the anthesis cycle (day pollination) of this Western Mediterranean species appear to be similar to Eastern Mediterranean species. Second, this species is also characterized by a major shift in its flowering season to the autumn. The reproduction of *A. pictum* thus represents a unique combination of floral and phenological characters among *Arum* species but is similar to some other Mediterranean taxa (Thompson 2005). Since this is the only species in the subgenus *Gymnomesium* and basal to other *Arum* species, it is not easy to determine whether its characters represent some ancestral stage or have evolved as insular adaptations (Boyce 2006; Mansion et al. 2008). A comparative study with the related genus *Biarum* which has both spring- and autumn-flowering species (Boyce 2008) could provide new insights into this question.

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