

Pollination Success of the Corsican *Helicodiceros muscivorus* (Araceae)

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ABSTRACT

The pollination success of the dead horse arum, *Helicodiceros muscivorus*, was studied in one Corsican population. This aroid species is pollinated by deception, attracting blowflies by mimicking the floral volatiles emitted by mammal cadavers. The reproductive individuals were taller and larger than non-reproductive ones, indicating that the plant vigor and thus the available amount of resources is an important factor in the production of an inflorescence. The reproductive success of the dead horse arum increased with the size of the inflorescence, as judged by a positive linear correlation between the appendix length and the total number of flies trapped within the floral chamber. Larger inflorescences had a longer appendix and thus a better probability to attract and dupe pollinating flies. The absence of correlation between floral sex-ratio and the spadix size indicated that there was no expression of the size-advantage model in *H. muscivorus* apparent in some other Araceae. The most probable explanation is that pollination efficiency is high because of low diversity and high abundance of pollinating insects.

KEY WORDS

Dead horse arum, deceit pollination, plant vigor, floral trait correlations, Calliphoridae, Diptera.

INTRODUCTION

The dead horse arum *Helicodiceros muscivorus* (L.f.) Engl. is a member of the Araceae with a distribution limited to Corsica, Sardinia, and the Balearic Islands in the western Mediterranean Ocean (Boyce, 1994; Fridlender, 2000). Its pollination is achieved by deception. The inflorescence mimics dead mammals, producing heat and emitting a putrid smell that attracts necrophilous insects (Knuth, 1909; Stensmyr et al., 2002; Angioy et al., 2004). *H. muscivorus* is mainly pollinated by blowflies (Knuth, 1909; Stensmyr et al., 2002; Seymour et al., 2003a). Arcangeli (1890) recorded from a single inflorescence 371 flies (mainly *Lucilia* (*Somomyia*) and *Calliphora* species), but only seven beetles; in another inflorescence he collected 385 flies, 107 of which were *Lucilia caesar* (Arcangeli, 1883; Knuth, 1909). More recently, inflorescences of *H. muscivorus* were documented to mainly trap *Calliphora vicina* and *Lucilia caesar* on Sardinia (Stensmyr et al., 2002) and *Calliphora vomitoria*, *C. vicina* and *Lucilia regalis* on Corsica (Seymour et al., 2003a). The inflorescence is protogynous, attracting insects into a floral chamber where they deliver pollen to receptive female flowers during the early morning. They remain in the floral chamber overnight (Fig. 1). Early the next morning, female flowers are no longer receptive and the male flowers

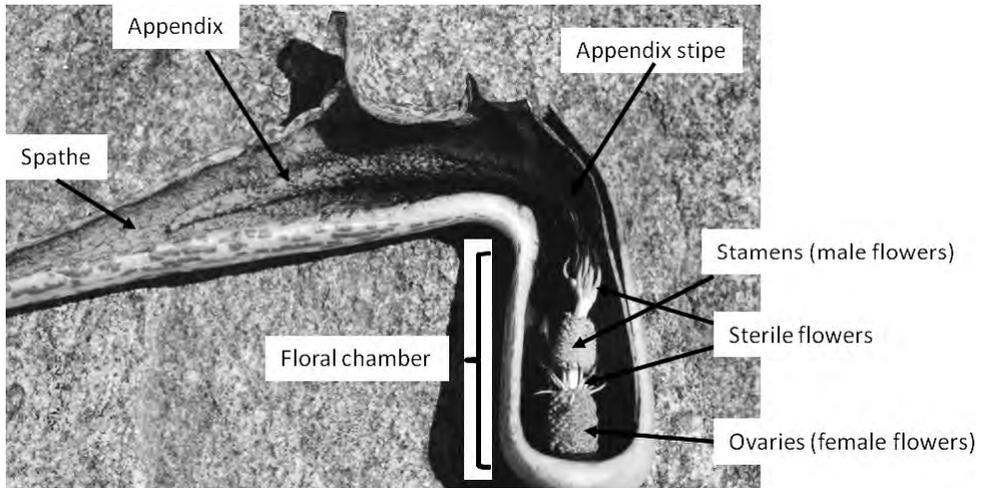


Fig. 1. Lateral view of an inflorescence of the dead horse arum showing its different parts (the spathe has been half removed). The spadix is composed of the appendix, the appendix stipe, the male and female zones and the sterile flowers. The inflorescence is naturally bent to 90° which allows flies to land and crawl along a horizontal spathe surface and enter the vertical floral chamber.

release pollen, which coats the insects before their escape and attraction to another inflorescence (Seymour et al., 2003a). Historically, *H. muscivorus* has been erroneously thought to be carnivorous, because dead insects are commonly found at the bottom of the floral chamber (Knuth, 1909; Fridlender, 2000), but it is highly doubtful that they provide nutrition to the plant. *Helicodiceros muscivorus* is thermogenic as are many species in the Araceae (Gibernau et al., 2005). Its thermogenic pattern has been already studied (Seymour et al., 2003a) and can be summarized as follows. On one hand, the exposed appendix exhibits one strong temperature increase in the morning, which is important in insect attraction since heat enhances scent production and modifies the pollinators' behavior (Angioy et al., 2004). On the other hand, the male flowers in the floral chamber are also highly thermogenic throughout the following night (Seymour et al., 2003a). However, the sluggish behavior and low thoracic temperatures of flies emerging from a floral chamber of *Helicodiceros muscivorus* suggest that male floral warming does not

enhance their activity just prior to their departure in the morning (Seymour et al., 2003a), in contrast to the benefits offered to beetles visiting other aroid species (Seymour & Schultze-Motel, 1999; Seymour et al., 2003b; Lamprecht et al., 2013).

It is well established that plant size is related to reproduction, small individuals in general being non-reproductive, while larger ones bear one or more reproductive structures (Guillon et al., 2006; Revel et al., 2012). This is also true in several geophytic Araceae species since the production of the first inflorescence depends on a minimum weight of the tuber (Prime, 1960; Méndez, 2001; Vitt et al., 2003). Moreover larger plants produce larger and/or more numerous inflorescences/flowers than smaller ones (Lloyd & Bawa, 1984). The size advantage model predicts that zoophilous species should invest proportionally more in the female function (which is more costly) than in male function, with an increase of plant size/vigor. This inflorescence feminization has been shown to exist in some *Arum* species (Gibernau & Albre, 2008; Revel et al., 2012), and not in others (Chartier & Gibernau, 2009) in accordance

to the size advantage model predictions (Revel et al., 2012). In some species of the genus *Arisaema*, a complete inflorescence feminization exists, called paradioecy, since small reproductive individuals produce inflorescence bearing only male flowers whereas the same individuals when larger produce inflorescence bearing only female flowers (Barriault et al., 2010).

A related question is how the pollination success and the probability of set seed are linked to floral size or number (Méndez, 2001; Revel et al., 2012). In general, it is supposed that bigger flowers/inflorescences are more attractive to pollinators, have a higher probability of pollination, and a larger seed set (Revel et al., 2012). In *Arum*, the results are equivocal; some species exhibit a positive relationship between the number of flowers (or the size of the inflorescence), the number of trapped insects, and the fruit set, while other species do not (Méndez, 2001; Gibernau & Albre, 2008; Chartier & Gibernau, 2009; Revel et al., 2012). Such different results appear to depend mainly on the abundance of the pollinating insects in the environment. When pollinators are very abundant, non-limiting, there is no relationship. Regardless of the size of the inflorescence, some insects are attracted and trapped, and pollination takes place, whereas when pollinators are rare and strong competition exists among inflorescences/flowers, natural selection should advantage the larger and more attractive ones (Albre & Gibernau, 2008; Chartier et al., 2009; Revel et al., 2012).

While pollination by deception (e.g., mimicking carrion) and thermogenesis have been well documented, the reproductive success of *Helicodiceros muscivorus* has been poorly studied. On a survey of seven populations, ranging from 4 to 300 individuals, Fridlender (2000) observed that the proportion of flowering individuals varied from 17 to 75% ($46 \pm 24\%$) and the fructification rate from 33 to 85% ($60 \pm 21\%$). He noted that flowering individuals tended to be taller and that larger individuals produced larger infructescences (Fridlender, 2000). We here present data on

the reproductive success in one population of *Helicodiceros muscivorus* on Corsica. The main objective is to study the relationships between plant vigor or size and the pollination success in this deceptive pollinated aroid species. More precisely we ask: i) Are the size and number of inflorescences produced by *H. muscivorus* related to plant vigor or size? ii) Is the pollination success related to inflorescence size and/or plant vigor? iii) Is the availability of pollinators limited in the studied populations?

MATERIAL AND METHODS

Studied Population

Helicodiceros muscivorus was studied at Caporalino, 10 km South of Ponte Leccia, central Corsica. The plants were located on a steep rocky slope above the railway tracks, as described by Fridlender (2000), and were studied between 22 April and 6 May 2002.

Plant Survey and Measures

A total of 286 plants were marked and labeled as reproductive or not. Plant height and leaf length were measured on 220 of them. Plant height was estimated by measuring the vertical distance between the soil and the highest limb base (since blades are deeply pedatifid and some lobes can be more or less erect). Leaf length was estimated by measuring the length of the median lobe from the tip to petiole.

In addition, 86 reproductive individuals were measured and surveyed to see if they matured with an infructescence. Of these, plant height and leaf length were measured on 75 individuals and spathe length and height on 85 individuals to quantitatively compare reproductive individuals.

Linear correlation analyses among vegetative and floral traits were performed on 80 individuals.

Reproductive traits were measured or counted on 38 inflorescences, including spathe and spadix size, floral zones sizes (male, female and appendix), numbers of male and female flowers (Fig. 1).

Table 1. Comparison of some vegetative traits (plant height, leaf length and number of leaves) between non-reproductive (N = 139) and reproductive plants (N = 81) of *Heliconia muscivora*. SD: standard deviation. All traits were statistically different (see text).

	Non-reproductive plants mean \pm SD (range)	Reproductive plants mean \pm SD (range)
Plant height (cm)	35.9 \pm 10.8 (14–71)	43.1 \pm 13.3 (24–78)
Leaf length (cm)	18.1 \pm 4.1 (9.5–32)	20.9 \pm 4.2 (11.7–34)
Number of leaves	3.3 \pm .89 (1–5)	4.4 \pm .91 (3–6)

The floral sex ratio or maleness was calculated as the number of male flowers/ (number of male flowers + number of female flowers). Thus it equals 1 when the inflorescence is totally male and zero when it is totally female.

Insect Visitors

The number and species of insect visitors were surveyed in the early morning, before the insects from the previous day were released from the floral chamber. When insects were present, the appendix length was measured and the insects were collected, fixed in 70% alcohol and later identified. A linear correlation between the number of trapped insects and the appendix length was performed after log-transformation.

Statistical analyses were performed with the statistical software Past 2.17 (Hammer et al., 2001).

RESULTS

Non-reproductive versus Reproductive

Reproductive dead horse arums produce a solitary inflorescence appearing at the end of the foliage-producing growth phase. Out of 286 plants marked, 90 had an inflorescence, thus 31% of the individuals were reproductive. Reproductive individuals were significantly taller ($F_{1,218} = 16.44$, $p = 7 \times 10^{-5}$) with longer leaves ($F_{1,218} = 12.4$, $p = 5.2 \times 10^{-4}$) and a greater number of leaves ($F_{1,218} = 60.4$, $p < 1 \times 10^{-5}$) than non-reproductive ones (Table 1). The proportion of reproductive plants increased with the number of leaves per plant; none

of the one- or two-leaf plants was reproductive, half of the four-leaf plants were reproductive and all the six-leaf plants had inflorescences (Fig. 2).

Reproductive Success

Out of 86 reproductive individuals surveyed, 57 (66%) matured an infructescence. There were no statistical differences for the vegetative traits such as plant height ($F_{1,73} = 1.97$, $p = .16$), leaf length ($F_{1,73} = 1.89$, $p = .17$) or number of leaves ($F_{1,73} = .80$, $p = .37$) between and successful and non-successful reproduction (Table 2). On the contrary, reproductively successful plants had significantly taller ($F_{1,111} = 148.6$, $p < 1 \times 10^{-5}$) and longer ($F_{1,111} = 115.3$, $p < 1 \times 10^{-5}$) spathes (Table 2). In fact when considering the spathe length, inflorescences with spathes shorter than 12 cm had no reproductive success, whereas spathes longer than 20 cm were highly successful (Fig. 3). Apparently the probability of reproductive success changed around spathes of 16 cm (Fig. 3).

Floral Traits

Floral reproductive traits of *Heliconia muscivora* are presented Table 3. In summary, the single appendix represented 52% of the spadix total length, the two fertile zones represented 13% (6% for the male zone and 7% for the female zone), and the rest (about 35%) represented the sterile parts (appendix stipe, sterile zones above and below the stamens; Fig. 1). In terms of number of flowers, male flowers were on average

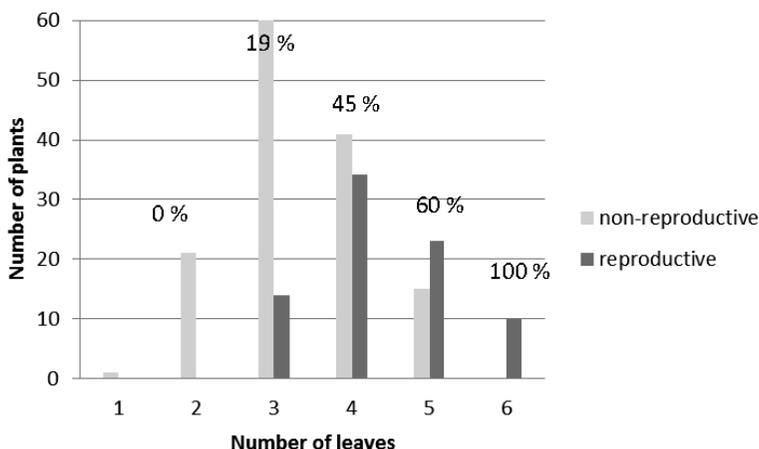


Fig. 2. Number of reproductive and non-reproductive plants in each class of leaf number and percentage of reproductive plants for each leaf class.

1.7 times more numerous than female flowers, leading to maleness of the floral sex ratio of the inflorescence of 62% (Table 3). The number of ovules per ovary was on average equal to 4.5 (Table 3). The fact that the fertile (male and female) zones (Fig. 4) as well as the number of male and female flowers (Fig. 5) increased at the same rate (same slopes) with an increase of the spadix size indicated that there was no bias in terms of resource allocation to the male or female function in relation to an increase of the vigor. This result was also confirmed by the absence of correlation between the spadix size and the floral sex ratio ($R^2 = 5 \times 10^{-4}$; $F_{1,45} = .022$; $p = .88$).

Insect Visitors

Insects from 21 inflorescences were collected and identified. They all were Diptera ($N = 355$), of which 291 (82%) were Calliphoridae and 64 (18%) were Fanniidae. Among the Calliphoridae, 73% belonged to two species of *Calliphora*: 172 *C. vomitoria* (15% of which were males) and 40 *C. vicina* (13% males); whereas the other 27% were only females of *Lucilia* species: 64 *L. regalis*, five *L. bufonivora*, and ten other *Lucilia* sp. The fanniid flies were also only females of the genus *Fannia* (54 *Fannia* sp, eight *Fannia pallitibia*), and two undetermined specimens. The

Table 2. Comparison of some vegetative (plant height, leaf length and number of leaves) and reproductive (spathe height and length) traits between successful ($N = 27$) and non-successful ($N = 29$) reproductive plants of *Helicodiceros muscivorus*. SD: standard deviation. Statistical difference: NS: non-significant, *: $p < 10^{-5}$.**

	Reproductive failure mean \pm SD (range)	Reproductive success mean \pm SD (range)	Statistical difference
Plant height (cm)	38.4 \pm 8.4 (21–54)	42.4 \pm 13.5 (22–80)	NS
Leaf length (cm)	19.1 \pm 3.6 (11.7–28)	20.2 \pm 3.6 (12.6–28)	NS
Number of leaves	4.1 \pm .74 (3–6)	4.3 \pm .92 (3–6)	NS
Spathe height (cm)	5.7 \pm 2 (3–9.5)	9.3 \pm 1.2 (7–12.5)	***
Spathe length (cm)	12.1 \pm 3.6 (6.7–20)	20 \pm 3.8 (14–32)	***

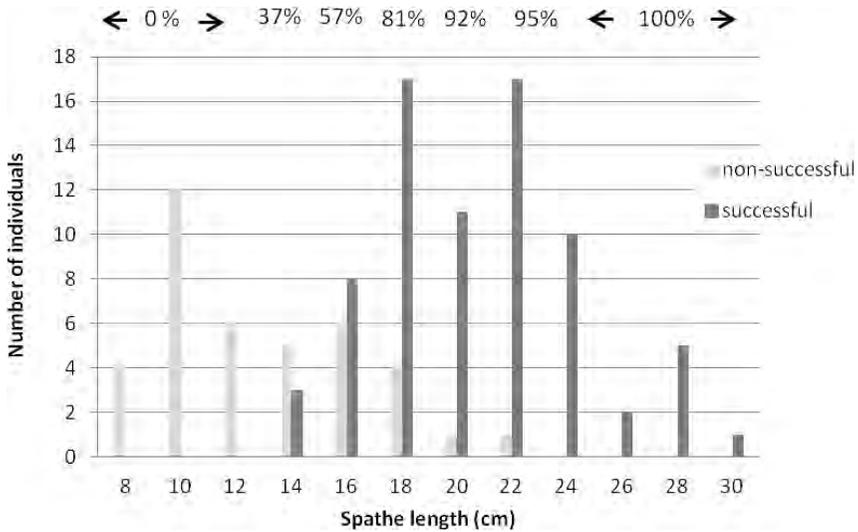


Fig. 3. Number of successful and non-successful plants in each class of spathe length (cm) and percentage of successful reproductive plants for each spathe class.

number of trapped flies per inflorescence was relatively high with a global average (mean \pm SD): 16.9 ± 18.8 (range: 2–84). When considering the most abundant species separately, the average numbers of trapped flies per inflorescence were: *Calliphora vomitoria* (9.1 ± 12.6 ; range: 0–54), *C. vicina* (3.3 ± 3.4 ; range: 0–13), *Lucilia regalis* (3.4 ± 4.5 ; range: 0–20), and *Fannia* sp (4.2 ± 4.1 ; range: 0–15). A positive linear correlation also occurred between the appendix length and the total number of flies trapped within the floral chamber ($R^2 = .28$; $F_{1,20} = 7.31$; $p = .013$).

DISCUSSION

Plant Size and Reproductive Status

This study shows that the reproductive status was linked to the size of the plant,

which we equate to plant vigor. But since we studied vegetative traits, a clear minimum size (threshold) was not found as it has been shown for the weight of the tuber in *Arum* or corm in *Arisaema* (Prime, 1960; Méndez, 2001; Vitt et al., 2003), probably because these vegetative traits are determined by many factors (resources, developmental, physiological, environmental) and not linearly linked to plant vigor, contrary to the tuber or corm weight which represents the resource for developing the individual. In terms of number of leaves, the probability of being reproductive increased with a higher number of leaves and half of individuals with four leaves were reproductive (Fig. 2). A similar trend occurred with plant height and leaf length (Table 1). In summary, reproductive indi-

Length (cm)	Mean \pm SD	Number of	Mean \pm SD
Spadix	21.7 ± 4.4	Female flowers	159 ± 26
Female zone	$1.4 \pm .4$	Male flowers	266 ± 58
Male zone	$1.2 \pm .3$	Ovules per ovary	4.5 ± 1
Appendix	11.7 ± 3.2	Floral Sex ratio	$0.62 \pm .04$

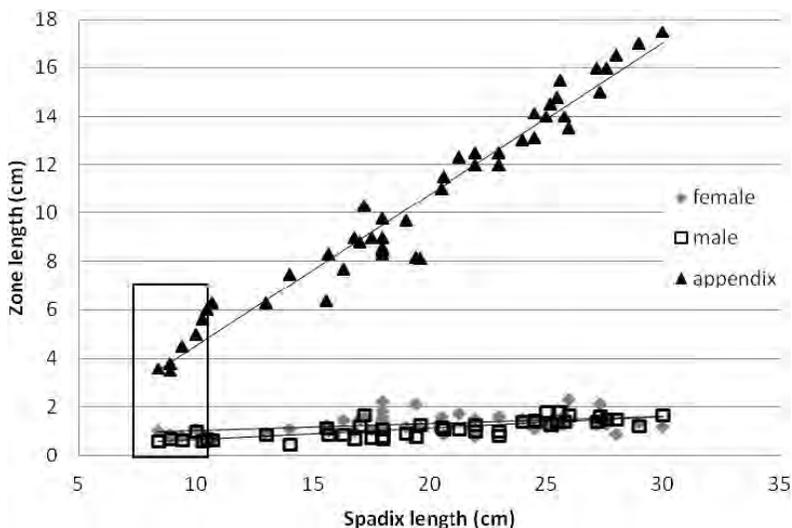


Fig. 4. Linear relations between the spadix length and the length of different spadix zones (appendix, male flower and female flowers). Due to the autocorrelation between the data the linear regressions are obligatory but we are interested in the values of the slopes and their differences. The square on the left of the graph represents non-successful reproductive inflorescences. The length of the appendix increases faster ($y = 0,6254x - 1,7583$; $R^2 = 0,955$) with an increase of the spadix size than the fertile (male or female) zones ($F_{1,45} = 81,3$, $p < 10^{-5}$). On the other hand, the slopes for the male ($y = 0,0468x + 0,1954$; $R^2 = 0,619$) and female ($y = 0,0284x + 0,7462$; $R^2 = 0,195$) zones are not statistically different ($F_{1,45} = 3,217$, $p = .079$).

viduals were larger than non-reproductive ones, as has been noted for *Arum cylindraceum* (Fridlender, 2000). It is well known that plant vigor is related to reproduction, with small individuals being non-reproductive in contrast to larger ones (Guillon et al., 2006; Revel et al., 2012).

Reproductive Success

In the studied population, about 1/3 of the individuals were reproductive, and 2/3 of the reproductive individuals successfully reproduced (i.e., maturing infructescences). This fructification rate is quite high for Araceae. It has been documented to vary between 13% and 50% in *Symplocarpus renifolius* or *Dieffenbachia longispatha* (Young, 1986; Uemura et al., 1993), between 8 and 78% in *Arum maculatum* and *A. italicum* (Ollerton & Diaz, 1999; Méndez & Diaz, 2001) and between 33 and 85% in

A. cylindraceum (Fridlender, 2000). Contrary to the reproductive status, the reproductive success was not linked to vegetative traits such as plant or leaf size, or leaf number; but rather to the inflorescence size (Table 2). Larger inflorescences were more likely to be pollinated and develop infructescences than smaller ones; there was a positive linear correlation between the appendix length and the total number of flies trapped within the floral chamber. Again, a clear minimum size threshold was not found, but a critical size was determined, since about half of the inflorescences of a length greater than 16 cm developed successfully to infructescences. This probability strongly diminished below this size and strongly increased for larger spathes (Fig. 3). Such a relationship between plant vigor and reproductive success is well known (Lloyd & Bawa, 1984; Guillon et al., 2006; Revel et al., 2012).

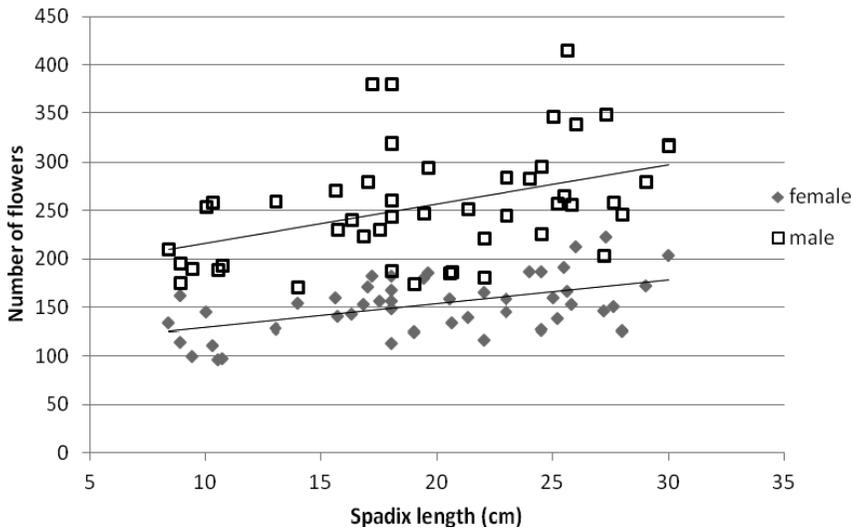


Fig. 5. Linear relationship between the spadix length (cm) and the number of female and male flowers in *Helicodiceros muscivorus*. The two slopes are not significantly different ($F_{1,45} = 1.216$, $p = .27$) indicating that both female and male number of flowers increase similarly with an increase of the spadix size ($Y = 3.285 X + 88.24$ (female) or 190.3 (male)).

Floral Traits

As in other species from the tribe Araceae, a significant proportion of the spadix size of *H. muscivorus* was allocated to the appendix (Fig. 1), in fact more than half the length (52%). The appendix size represented 34% of the total spadix length in *Arum maculatum* (Chartier & Gibernau, 2009), and 44% in *A. italicum* (Gibernau & Albre, 2008). Such high investment in the appendix has been found in *A. italicum*, *A. idaeum*, *A. creticum*, *A. concinatum*, and *Arisaema* in terms of relative (44–90%) weights among the spadix parts (Méndez, 2001; Seymour et al., 2009). Moreover, the appendix size increased proportionally more than the fertile zones in longer spadices (Fig. 4). The same result has been found in *A. maculatum* and *A. italicum* (Gibernau & Albre, 2008; Chartier & Gibernau, 2009). The appendix is crucial for pollinator attraction by producing heat and emitting the floral odors (Kite, 2000; Diaz & Kite, 2002; Albre et al., 2003), especially for these species which are obligatorily allogamous (Lack & Diaz, 1991; Albre & Gibernau, 2008; Chartier et al., 2013). Thus,

the more important investment made by the plant when more resources are available concerns the pollinator attraction function. In this study, a positive correlation was found between the appendix length and the total number of flies caught by the inflorescence within its floral chamber, as in *A. italicum* (Mendez & Obeso, 1992).

In terms of fertile zones, their relative size (13%) is smaller than in *A. maculatum* with 19% of the spadix length (Chartier & Gibernau, 2009) and in *A. italicum* with 23% (Gibernau & Albre, 2008). Moreover female and male zones had an equivalent size in *H. muscivorus*, with respectively 7 and 6% of the spadix length, contrary to *A. maculatum* and *A. italicum* in which the female zone is longer than the male one (12 vs. 7% in *A. maculatum* and 17 vs. 6% in *A. italicum*) (Gibernau & Albre, 2008; Chartier & Gibernau, 2009). The fact that the fertile (male and female) zones (Fig. 4) as well as the number of male and female flowers (Fig. 5) increased at the same rate (same slopes) with an increase of the spadix size indicated that there was no bias in terms of resource allocation to the male or female

function in relation to an increase of the vigor. This result was also confirmed by the absence of correlation between the spadix size and the floral sex ratio, indicating no significant feminization of the inflorescence with an increase in the total size. Hence *Helicodiceros muscivorus* does not follow the size advantage model. This inflorescence feminization has been shown to exist in some aroid species such *Arum italicum*, *A. cylindraceum* or *Arisaema triphyllum* (Gibernau & Albre, 2008; Barriault et al., 2010; Revel et al., 2012), but not in *Arum maculatum* (Chartier & Gibernau, 2009).

Insect Visitors

We found that the main pollinators in Corsica were Calliphoridae blowfly species as in previous studies in Sardinia (Stensmyr et al., 2002; Angioy et al., 2004), but the species were not the same. In Corsica the main pollinator of the dead horse arum was *Calliphora vomitoria* (60% of the trapped insects), but *Lucilia regalis* and *C. vicina* were not negligible, whereas in Sardinia *Calliphora vicina* and *Lucilia caesar* were the main pollinators (Stensmyr et al., 2002). We documented that flies from the genus *Fannia* (Fanniidae) were also attracted. A study of human cadaver fauna showed that there are up to eight different cohorts (named “escouades”) of insects according to the stage of degradation (Méglin, 1894). *Calliphora* flies are amongst the first cohort, *Lucilia* the second and *Fannia* the fourth (Méglin, 1894). Thus, the dead carcass floral odor attracts a diversity of necrophilous flies (Kite, 2000; Stensmyr et al., 2002). Moreover this floral odor presents a sex-specificity since a majority of female flies were attracted, 90% in this study and 78% in Sardinia (Stensmyr et al., 2002). Only a “few” males of *Calliphora* were attracted none of *Lucilia* and *Fannia*. While the inflorescences of the dead horse arum attract some male flies, real animal carcasses are apparently visited mainly by females intent on laying eggs (Stensmyr, 2002). Such differences may be explained by variations in the blend composition and

particularly the minor components of scent, but further studies are necessary to answer this question. Females are attracted to carcasses looking for oviposition and nutrition whereas males are rather floricolous; this sexual alimentary differentiation is also known for mosquitoes. Now it is possible that some mating takes place on or near the carcasses, thus explaining the presence of some trapped males.

In addition to the odor, Angioy et al. (2004) have shown that the heat from the appendix increases the probability of a blowfly entering the floral chamber. Thus the heat works in conjunction with the odor cues and fine-tunes the deceit, modifying the behavior of attracted blowflies, by mimicking the microbial fermentation and its associated temperature elevation of a dead carcass. Finally, the trap mechanism is not “absolute” like in *Arum* where attracted flies are trapped for 24 h within the floral chamber. In the dead horse arum, blowflies were observed coming in and out from the floral chamber, because there is no efficient physical barrier as in other *Arum* species.

In conclusion, the reproductive success increased with the size of the inflorescence. Larger inflorescences have larger appendices and thus higher probability to attract and dupe pollinating flies. The absence of correlation between floral sex-ratio and the spadix size indicates that there is no expression of the size-advantage model in *H. muscivorus*. The most probable explanations (Chartier & Gibernau, 2009; Revel et al., 2012) are that in *Helicodiceros muscivorus*: i) the attractiveness is high, as the floral odor is a very good mimic of the cadaver smell; ii) the pollinator diversity is low, with only a few blowfly species are attracted (2–4); and iii) the insects are very abundant, for example the floral chamber of the most visited inflorescence in this study contained 84 flies, and in Sardinia 100 visits/inflorescence/day is estimated (Angioy et al., 2004).

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