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Sexual mass allocation in species with inflorescences as pollination units: a comparison between *Arum italicum* and *Arisaema* (Araceae)[1]

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Sex allocation models predict that cosexuality is stabilized by high allocation to attractive structures in pollen-limited species or by high allocation to shared structures that contribute to both genders. High investment in unilateral fixed costs favor the evolution of dioecy or gender change. With these predictions in mind, I studied sexual mass allocation at flowering in the monoecious *Arum italicum* (Araceae) and compared it with information available for its sex labile relative *Arisaema dracontium.* In *A. italicum,* 68% of biomass was allocated to structures believed to be involved in pollinator attraction and capture. This allocation pattern contrasts with that of *Arisaema dracontium,* in which 70% of biomass was allocated to scape, considered to be a unilateral fixed cost. The importance of attractive structures in *A. italicum* was further supported by a disproportionate increased allocation, in larger inflorescences, to the appendix (an attractive structure) compared to fertile flowers. In addition, an increase in inflorescence mass involved a disproportionate increase in mass allocation to male, rather than female, flowers. This pattern also contrasts with a size-related gender change from male to female in *Arisaema* species. These findings were consistent with sex allocation model predictions and shed light on the evolution of sex lability in *Arisaema* species.

Key words: accessory structures; allometry; Araceae; *Arisaema*; *Arum italicum*; sexual allocation; sexual lability.

An extreme form of gender modification, i.e., sexual lability, occurs in several species of *Arisaema* (Araceae) (Lovett Doust and Cavers, 1982b; Kinoshita, 1986; Clay, 1993). This gender change is reversible, not simply directional, and related to changes in plant size (Lovett Doust and Cavers, 1982b; Bierzychudek, 1984b; Kinoshita, 1986; Clay, 1993). Individual plant gender changes from pure male, when small, to monoecious [*A. dracontium* (L.) Schott.] or pure female [*A. ringens* (Thunb.) Schott.], when large. In *A. japonicum* Bl., *A. serratum* (Thunb.) Schott., and *A. triphyllum* (L.) Schott., middle-sized monoecious individuals may also be present. These changes have been usually interpreted in the framework of the size-advantage model (Policansky, 1981; Schlessman, 1988; see, however, Freeman, Harper, and Charnov, 1980, and Freeman et al., 1997). The size-advantage model (Ghiselin, 1969) postulates a sex change when an increase in body size is related to differential abilities to produce or sire offspring. For entomophilous plant species, as the ones considered here, the size-advantage model predicts a female-biased gender expression with increased size (Klinkhamer, de Jong, and Metz, 1997), because of the disproportionate benefit of increased resources for seed production compared to male fitness. Aside from plant size, other factors such as defoliation and reproductive history (Bierzychudek, 1984b) or environmental quality (Lovett Doust and Cavers, 1982b) can also be involved in gender change.

A significant element of sexual allocation theory in plants has focused on resource allocation to different flower structures (Charlesworth and Charlesworth, 1987; Charlesworth and Morgan, 1991). Those models have been used to predict under which conditions dioecy can evolve. In general, cosexuality is stabilized by high allocation to attractive structures (under pollen-limited seed production) or high allocation to shared structures that contribute to both genders (Charlesworth and Charlesworth, 1987; Charlesworth and Morgan, 1991). Disproportionate increases in fitness gain through one gender function (Charlesworth and Morgan, 1991) or high investment in unilateral fixed costs (sensu Lloyd, 1984) favor the evolution of dioecy (Charlesworth and Morgan, 1991) or gender change (Frank, 1987). In *Arisaema* (Lovett Doust and Cavers, 1982b; Clay, 1993) individuals produce just one inflorescence, which is the pollination unit (Fægri and van der Pijl, 1979). Therefore, the study of sexual allocation at an inflorescence level in the Araceae could shed light on the evolution of sexual lability. To my knowledge, this has been done just for *A. dracontium* (Lovett Doust and Cavers, 1982a). The structure receiving almost 70% mass allocation was the scape, considered to be a unilateral fixed cost (Lovett Doust and Cavers, 1982a; Kakehashi and Harada, 1987). Allocation to attractive structures, i.e., spadix and spathe, ranged between 12 and 17% (Lovett Doust and Cavers, 1982a). How this allocation pattern relates to gender lability requires a comparison with related, cosexual species. Here I do this by quantifying mass allocation to different inflorescence structures in *Arum italicum* Miller, a monoecious relative of *Arisaema* (Grayum, 1990).

Most sexual allocation models consider the division of a fixed amount of resources between floral structures (Lloyd, 1984; Charlesworth and Charlesworth, 1987). However, inflorescence size is variable in *Arisaema* (both within and between morphs; Lovett Doust and Cavers, 1982a; Kinoshita, 1986)

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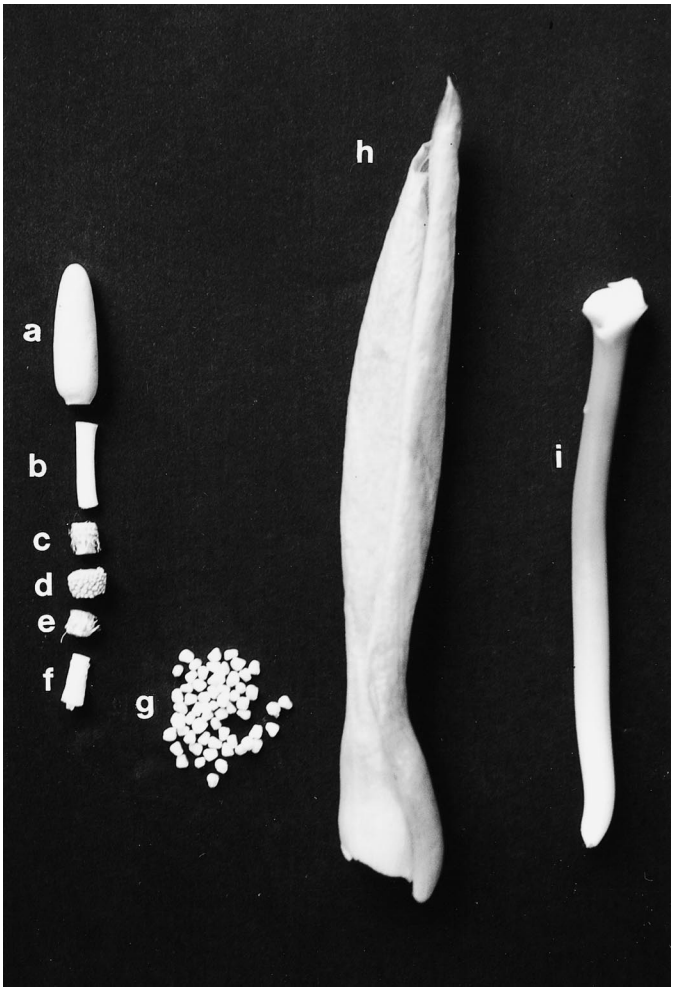

Fig. 1. An inflorescence of *Arum italicum* close to anthesis, showing the different fractions considered in the present study: (a) appendix, (b) stipe, (c) staminodes, (d) androecium, (e) pistillodes, (f) axis supporting female flowers, (g) gynoecium, (h) spathe, (i) scape. All structures are in their natural, vertical position. Fractions (f) and (i) were pooled for analysis. Arrangement of fractions corresponds to natural position in the inflorescence, excepting that the gynoecium has been detached from its supporting axis, spathe should cover all structures in the left side of the picture, and scape should hold all structures situated at its left.

and in *Arum italicum* (Méndez, 1998). This variation, partially explained by plant size (Ewing and Klein, 1982; Bierzychudek, 1984a; Méndez, 1998), has potentially important consequences. The size of the appendix, an attractive structure, is directly related to inflorescence size as is male and female flower number (Ewing and Klein, 1982; Clay, 1993; Méndez, 1998). Changes in inflorescence size can therefore affect fitness gain curves separately through each gender function. For example, the number of insects trapped in the inflorescence of *Arum italicum* increased with increasing appendix length (Méndez and Obeso, 1992). Therefore, resource-dependent gender expression could be linked to allometric variation in proportional allocation to different inflorescence fractions. In plants producing just one (*Arisaema*) or a few (*Arum*; mostly 1–3) inflorescences, this could be an important way of adjusting gender to the available resource level.

To test this possibility, I explored the variation in proportional resource allocation to different structures in *A. italicum* inflorescences differing in size. My question was: given an increase in the amount of resources allocated to an inflorescence, will all the structures get a similar proportional increase in allocation or will some of them receive a disproportionate investment? I hypothesize that disproportionate increases in allocation to specific structures with increased inflorescence size result from adaptive plasticity and can reveal which structures are more important for fitness. Several allometric changes in allocation with inflorescence size could be tested. I focused upon the following comparisons, chosen *a priori*: (1) androecium vs. gynoecium and (2) fertile flowers vs. appendix. Comparison 1 tests changes in allocation to male vs. female function with an increase in resources. Comparison 2 tests the relative change in allocation to the most obvious attractive structure (Boyce, 1993) vs. sexual structures.

TABLE 1. Mass allocation (in grams) to primary and accessory structures in inflorescences near anthesis (N = 20) of *Arum italicum*. The proposed function of each structure is indicated.

Structure	Function[a]	Mass allocation (g) Mean	SD	%
Primary structures				
Androecium	M	0.0935	0.0470	4.0
Gynoecium	F	0.0859	0.0285	3.7
Accessory structures				
Spathe	T, P	0.81	0.31	35.1
Appendix	A	0.67	0.41	29.0
Stipe	S	0.0312	0.0132	1.4
Staminodes	T	0.0365	0.0135	1.6
Pistillodes	T?	0.0332	0.0136	1.4
Scape	S, P	0.55	0.25	23.8
Total		2.31	0.96	100.0

[a] A = attraction, F = female, M = male, P = photosynthesis, S = support, T = trap.

MATERIALS AND METHODS

Plant species—*Arum italicum* is a herbaceous, perennial geophyte mainly distributed in southern Europe, although reaching the British islands and the Black Sea (Boyce, 1993). In the study area (province of Asturias, northwest Spain), it is common in riparian forests, hedgerows, roadsides, and other shaded, disturbed, lowland habitats.

Being highly integrated structures (Méndez, 1998: Fig. 1) from the morphological and functional point of view, inflorescences are the pollination units (Fægri and van der Pijl, 1979). Flowers are unisexual, very simple, and arranged on the lower portion of a linear axis called the spadix. Aside from unisexual whorls of fertile flowers (Fig. 1), two groups of bristle-like sterile flowers are present: pistillodes (sterile female flowers) and staminodes (sterile male flowers) (Fig. 1). The upper portion of the spadix consists of a stipe (Fig. 1) sustaining a sterile club-like appendix (Fig. 1). A large, green bract (the spathe; Fig. 1) surrounds the inflorescence axis. The inflorescence is borne on a green scape (Fig. 1), connected to an underground tuber. For further description of both flowers and inflorescences in *Arum*, see Boyce (1993).

The inflorescence attracts and deceives small Diptera (Boyce, 1993), with the help of heat and odor production by the starch-rich, sterile appendix (Lance, 1972). Attracted insects get trapped in a chamber that the lower portion of the spathe forms around the flowers. According to the usual description of pollination in the genus *Arum* (Fægri and van der Pijl, 1979; Boyce, 1993), the appendix is an attractive structure; the spathe and staminodes form the trap. The importance of the appendix and the spathe for pollination has been analyzed by Lack and Díaz (1991) and Méndez and Obeso (1992). However, the exact contribution made to pollination by other structures of *Arum* inflorescence, e.g., pistillodes, is unknown. Likely functions are proposed in Table 1.

TABLE 2. Slope of allometric relationships between inflorescence structures of *A. italicum* ($N = 20$ in all comparisons). Percentage of variance explained by the regression ($P < 0.001$ in all comparisons) and results of the t test performed to test departure of isometry (slope = 1) are also indicated.

Comparison[a]	Slope ± 1 SE	R^2	t	P
Gynoecium vs. androecium	0.508 ± 0.109	0.55	−4.514	<0.001
Appendix vs. fertile flowers	1.900 ± 0.243	0.77	3.704	<0.001

[a] Variables were $\log_{10}$ transformed for analysis.

Study site and variables measured—Biomass allocation to different inflorescence structures was studied in a hedgerow population located at El Cristo, Oviedo (43°20′ N, 5°53′ W; 300 m above sea level). Twenty inflorescences, belonging to different single-inflorescenced plants, were collected between 28 March and 8 April 1995. To insure full development of structures, inflorescences were chosen that were within 3 d of anthesis. The following structures were considered: androecium and gynoecium (primary structures; Table 1, Fig. 1), and spathe, scape, appendix, stipe, staminodes, and pistillodes (accessory structures; Table 1, Fig. 1). This partition allows direct comparison with the data of Lovett Doust and Cavers (1982a). For staminodes, pistillodes, and androecium, the spongy axis to which flowers are attached was included in the respective fractions (Fig. 1). This could overestimate mass allocated to sterile flowers but it made a small contribution to androecium mass. For the gynoecium, however, female flowers were considered independently from the axis to which they are attached (Fig. 1); this axis is a continuation of the scape fraction, with which it was pooled. Structures were ovendried at 60°C for a week and weighed to the nearest 0.01 g (spathe, scape, and appendix) or 0.0001 g (remaining structures). Biomass was chosen as allocation currency because it can be considered as an integral measure of allocation (Bazzaz and Ackerly, 1992) and to make data comparable with those of Lovett Doust and Cavers (1982a). Notwithstanding, it must be kept in mind that using nitrogen or other limiting nutrient as currency could reveal contrasting patterns with respect to those based on biomass allocation (e.g., Ashman and Baker, 1992).

Statistical analyses—Differences in average mass allocation to androecium and gynoecium within inflorescences were tested by means of a t test for paired samples. Normality of the difference among pairs of values was previously tested (Zar, 1999).

The study of allometric variation in biomass allocation to different structures within an inflorescence remains problematic. ANCOVAs based on regression of pairs of variables against total inflorescence mass are flawed because of autocorrelation problems. Direct regression of pairs of variables against each other, a common practice in allometry studies (LaBarbera, 1989), is preferable (see Koelewijn and Hunscheid, 2000, for a similar approach). This approach was possible due to the high correlation between each structure mass and total inflorescence mass ($r \geq 0.72$; $P \leq 0.0003$). Prior to regression, pairs of variables were $\log_{10}$ transformed. If allocation remains unchanged with increased inflorescence size, the expected slope of the regression line on log-transformed values is 1, indicating isometry. Departures from this expected isometric slope value indicate preferential allocation to one of the structures compared. Departures from a slope value of 1 were tested by means of a t test (Sokal and Rohlf, 1981). Reduced major axis regression (Green, 1999) produced similar results and will not be presented here.

RESULTS

In inflorescences close to anthesis, >90% of inflorescence biomass was allocated to accessory structures, mainly to those involved in pollinator attraction and capture (Table 1). Almost 60% of biomass were allocated to green, potentially photosynthetic structures (Table 1). No significant difference was found between biomass allocated to androecium or gynoecium ($t_{19} = 1.13$, $P = 0.273$; Table 1).

The slope of the allometric relationship between gynoecium and androecium was significantly lower than 1 (Table 2), i.e., an increase in inflorescence mass involved a disproportionate allocation to androecium vs. gynoecium. The slope of the allometric relationship between appendix and fertile flowers was significantly greater than 1 (Table 2), indicating a disproportionate allocation to the appendix in larger inflorescences.

DISCUSSION

Sexual mass allocation in Arum italicum and in Arisaema—*Accessory structures*—As in many outcrossing species (Cruden and Lyon, 1985), sexual mass allocation at flowering was biased towards accessory structures in *Arum italicum* (present study) and *Arisaema dracontium* (Lovett Doust and Cavers, 1982a). As proposed by Lloyd (1984) for species producing mostly a single inflorescence, there are large fixed costs in *A. italicum* and in *Arisaema dracontium.* These fixed costs include the scape, the spathe, and the appendix and are related to the complex inflorescence architecture and the pollination mechanism. Allocation patterns to accessory structures differed in both aroid species in a way consistent with the predictions of the models, as summarized in the introduction (Charlesworth and Charlesworth, 1987; Frank, 1987; Charlesworth and Morgan, 1991). Combined mass of spathe and appendix, the two structures most obviously related to pollinator attraction and capture, comprised >60% of total inflorescence mass in the monoecious *A. italicum.* By contrast, almost 70% mass allocation in the sex-labile *Arisaema dracontium* was to the scape (Lovett Doust and Cavers, 1982a), a unilateral fixed cost (Kakehashi and Harada, 1987).

The relationship between allocation to different inflorescence structures and fitness is unknown for *Arisaema.* Some information exists, however, for the relationship between absolute structure size and fitness in *A. italicum.* Méndez and Obeso (1992) showed that number of insects trapped in the inflorescences increased with increasing appendix length, which is related to appendix mass. Although it has been assumed that attractive structures in general mainly increase male fitness (Stanton, Snow, and Handel, 1986), a longer appendix was also related to increased fruit initiation (Méndez and Díaz, in press). In addition, correlation between the appendix length and functional gender from data in Méndez (1998) was not significant ($P = 0.455$), indicating that relative male and female success was not dependent on appendix length. Therefore, the disproportionate allocation to appendix with increasing inflorescence mass in *A. italicum* supports the idea that attractive structures are important for absolute fitness in this species and not a mere result of developmental or architectural constraints. Some evidence of the importance of accessory structures for fitness exists for other monoecious aroids. In *Dieffenbachia longispatha,* male and female reproductive success were positively related to inflorescence size, but not to male or female flower number (Young, 1990). In *Philodendron solimoesense,* the amount of floral visitors increased with an increasing length of the middle, sterile portion of the spadix (Gibernau et al., 1999).

The fitness benefit of increased allocation to attraction assumes pollen limitation (Charlesworth and Charlesworth, 1987). This has been shown for *Arum maculatum* (Ollerton and Díaz, 1999) but only indirect evidence exists for *A. italicum* (Méndez, 1998; Méndez and Díaz, in press). However, pollen limitation is present also in *Arisaema triphyllum* (Bierzychudek, 1981). In fact, Lloyd and Bawa (1984) argue that pollen limitation can limit male, but not female, fitness in *Arisaema* beyond a certain inflorescence size, but the hypothesis has not been tested. Information about the influence of appendix size on pollinator attraction and reproductive success is much needed for *Arisaema* species. The large interspecific variation present in appendix length in this genus (Vogel and Martens, 2000) should also be studied in the context of sexual lability and sexual allocation.

An alternative explanation for the contrasting allocation patterns in *A. italicum* and *Arisaema* is that costs, rather than benefits, are different. However, building costs of attractive structures seem to be higher in *Arum* than in *Arisaema. Arisaema* appendices are not thermogenic (Vogel and Martens, 2000) and lack the starchy storage tissue typical from *Arum* (Lance, 1972). Photosynthetic abilities of the spathe could be also lower in *Arisaema* than in *Arum* because of the presence of unpigmented stripes in the former, but this requires further investigation.

Data available for Japanese *Arisaema*s (Kinoshita, 1986) suggest that the slope of increase in scape mass with pseudostem diameter was higher in females than in males in three out of four species. As long as inflorescence mass is related to plant size (which is not reported by Kinoshita, 1986 but is known for other *Arisaema*; Bierzychudek, 1984a), this means that allocation to scape in females increases disproportionately with inflorescence size compared to males. Reanalysis of Kinoshita's data would clarify this point, which is consistent with high unilateral costs in *Arisaema.*

Primary structures—Méndez (1998) found no relationship between inflorescence or plant size and floral sex ratio in *A. italicum.* Male and female flower number were weakly related to both inflorescence and plant size (Méndez, 1998). Furthermore, male and female flower number increased at a similar rate with increases in inflorescence size (Méndez, 1998). However, the present study showed that an increase in inflorescence mass involved a disproportionately greater increase in mass allocation to male, compared to female, flowers. These differences between mass- and number-based phenotypic gender measures probably reflect that an increase in inflorescence size entails an increase in flower size, rather than in number. Similar weak relationships between flower number and plant size have been found for *Arisaema triphyllum* (Bierzychudek, 1984a) and *A. dracontium* (Clay, 1993).

An increase in male investment with inflorescence size is interesting for several reasons. First, it shows that average allocation to primary structures, usually reported in sexual allocation studies at a flower level (Cruden and Lyon, 1985), can give only a partial picture of gender allocation. This is also illustrated by the results of Koelewijn and Hunscheid (2000) in *Plantago coronopus.* An allometric change in the investment was also present, in this case the bias being towards female gender. Second, this change goes in the opposite direction than expected according to the size-advantage hypothesis (Klinkhamer, de Jong, and Metz, 1997) and with the pattern of change in *Arisaema dracontium* (Lovett Doust and Cavers, 1982a; Clay, 1993). This allometric change in phenotypic gender in *A. italicum* was not related to an increased functional maleness, however (correlation between spathe length and functional gender from data in Méndez [1998] was not significant).

Plant vs. flower level of analysis—The inflorescence level studied in this paper complements the traditional treatment of gender change considering whole plants. First, inflorescence size is related to plant size in *Arum italicum* (Méndez, 1998) and *Arisaema triphyllum* (Bierzychudek, 1984a). Second, patterns at both levels are consistent. This is especially true for *Arisaema*s, which produce a single inflorescence. Pattern of gender adjustment is slightly more complicated in *Arum italicum,* due to the ability to produce several inflorescences (Méndez, 1998). Despite this, in multi-inflorescenced plants, the last-produced (and smaller) inflorescence showed a female-biased floral ratio compared to the first and larger one (Méndez, 1998). This was considered to be independent of allometric effects (Méndez, 1998) but this claim needs to be reconsidered. Analysis of residuals of regressions against inflorescence size by means of paired *t* test in Méndez (1998: Table 4) are flawed. *t* tests compare means and the average of regression residuals is always zero, preventing such analysis. Tests in Méndez (1998) did not yield that conclusion due to inappropriate treatment of missing data. Thus, changes in inflorescence size are the most likely reason for changes in gender expression between inflorescences.

In conclusion, patterns of mass allocation to inflorescence structures in monoecious and sex-labile Araceae were consistent with model predictions. Generality of the trends found in this paper must be confirmed by the study of other species, the use of other allocation currencies, and the calculation of fitness gain curves for different inflorescence structures.

NOTE ADDED IN PROOF: There is a study of sex allocation at an inflorescence level in *Arisaema urashima* Hara (Takasu, 1987. *Plant Species Biology* 2: 29–56) I was not aware of. Biomass allocation to different inflorescence structures, as retrieved from Fig. 12, 2 Apr, in Takasu (1987), was as follows: 10–14.3% to primary structures, 52.9–38.6% to scape, 12.8–22.8% to appendix, 18.6–20% to spathe and 5.7–4.3% to spadix (in all fractions, data for female inflorescences precede those for male ones). Although less extreme that in *Arisaema dracontium,* allocation to scape in *Arisaema urashima* exceedes from that in *A. italicum,* while allocation to attractive structures is below 50%. Pooling the fraction ''spadix'' with either the scape or the attractive structures does not alter these conclusions. Consistency of Takasu's data with the pattern described in the present paper is remarkable because *Arisaema urashima* has a long, filamentous appendix which could have tilted the proportional allocation towards attractive structures.

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