

# Sex-ratio variation among *Arisaema* species with different patterns of gender diphasy

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## Abstract

*Arisaema* species exhibit gender diphasy, or sex change, where individual plants produce either male, monoecious or female inflorescences depending on their size. Three basic sex-change patterns have been described in *Arisaema*. Type I species change between male and monoecious phases, type II species change between male, monoecious and female phases, while type III species change between male and female phases. Theoretical models suggest that sex ratios should be biased toward males, the sex with the lowest cost of reproduction. The goal of this study was to examine sex-ratio variation among *Arisaema* species that differ in sex-change patterns. Data from an extensive literature review, consisting of all available studies reporting *Arisaema* sex ratios, were combined with data from extensive field surveys of *Arisaema dracontium* and *Arisaema triphyllum* in southern Indiana, USA. This data set contains nearly 30 000 plants from 12 species. All species conformed to either the type I or type III pattern of sex change. There was little evidence for a distinct type II pattern of sex change, given that plants with monoecious inflorescences were rare relative to plants with pistillate inflorescences. The mean sex ratio in type I species (79.9% male) was significantly greater than in type III species (63.7% male). The data are consistent with the prediction that type I species are likely to have greater costs associated with female reproduction. We suggest that all *Arisaema* species have similar patterns of floral development, but differ in their ontogenetic patterns for male and female flowering.

*Keywords:* *Arisaema*, cost of reproduction, gender diphasy, sex change, sex ratio.

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## Introduction

Sex-allocation research explores how natural selection alters the allocation of resources to male and female reproduction. Sex-ratio evolution and evolution of sex-determination systems comprise two complementary sex-allocation research programs (Bull 1981, 1983; Charnov 1982; Karlin & Lessard 1986). Sex-ratio evolution research investigates the evolutionary pressures acting on the ratio of male and female individuals in a population. In contrast, sex-determination research examines the mechanisms by which genetic factors govern male and female gamete production among individuals of a population or species. Population sex ratios are the predomi-

nant selective pressure acting on sex-determination systems (Bull 1983).

Sex-ratio evolution is presumed to select for sex-determination mechanisms that allow an equilibrium between gender-specific costs and fitness to be maintained (Karlin & Lessard 1986; Bull & Charnov 1988). Environmental sex determination (ESD) allows adaptive sex-ratio variation when male and female fitness fluctuates asymmetrically with environmental conditions (Charnov & Bull 1977). Sex-ratio variation in sex-changing plant populations has largely been attributed to environmental factors such as temperature, soil moisture, light levels, and so on (Freeman *et al.* 1980; Charnov 1982; Lovett-Doust & Cavers 1982a; Bierzychudek 1984; Schlessman 1988; Zimmerman 1991; Korpelainen 1998). Natural selection is predicted to select for male-biased populations when male fitness is less dependent upon environmental conditions than female fitness, and when

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the population is in a poor environment (Bull 1981; Bulmer & Bull 1982; Bull & Charnov 1988). Under better environmental conditions, the sex ratio is expected to become more female-biased because females will be relatively more fit compared to males (Bull 1981). The sex ratio presumably reflects the relative cost of male, compared to female, reproduction (Charnov 1982).

Empirical studies have demonstrated that *Arisaema* individuals express asexual, male and female phenotypes with increasing plant size. Male-phase plants produce an inflorescence of staminate flowers only in all gender-diphasic *Arisaema*, but species differ in the floral composition of the female-phase inflorescence. Hotta (1971) described three patterns of sex expression in *Arisaema*. One group of species produces a monoecious inflorescence containing both staminate and pistillate flowers during the functionally female phase. A second group of species produces a monoecious and then a pistillate inflorescence with increasing size during the functionally female phase. A third group of species changes directly from staminate to pistillate inflorescences with increasing plant size. Hotta (1971) noted that occasional monoecious inflorescences occurred in the latter group, but were rather abnormal. The frequency of pistillate female-phase plants within populations may differ among these gender-expression types (Clay 1993).

Cladistic analysis suggests that the genus *Arisaema* is monophyletic and that the staminate to monoecious sex-change pattern is the ancestral form of sex change (Hotta 1971; Murata 1984). The different gender expression patterns are presumably derived from this ancestral pattern of gender determination (Richardson 1999). Characterizing sex-ratio variation among populations of *Arisaema* species may provide insight into the selective pressures leading to evolutionary changes in sex-changing patterns. *Arisaema* is a model system for examining sex-ratio variation because it is the most species-rich gender-diphasic genus, exhibiting the greatest variation in gender-expression patterns, and it having the greatest number of reported sex ratios in natural populations (Hotta 1971; Freeman *et al.* 1980; Lloyd & Bawa 1984; Schlessman 1988; Clay 1993). The purpose of the present study is to characterize sex-ratio variation within and among *Arisaema* species with different patterns of sex change by analyzing a large database compiled from the published literature and field observations.

## Materials and methods

### Study system

*Arisaema* comprises approximately 150 species divided into 12 sections based on cytological and morphological characters (Murata 1991; Watanabe *et al.* 1998). The

species are distributed throughout the temperate and subtropical regions of Africa, India, East and Middle Asia, with a few occurring in North America and Mexico (Murata 1984). The center of *Arisaema* diversity is Southeast Asia, with the majority of species occurring in China and Japan (Li 1980). Cladistic analyses by Murata (1984, 1990a, 1990b, 1991, 1995) and Watanabe *et al.* (1998) provide the basis for all subgeneric species classifications.

All species of the genus *Arisaema* are gender-diphasic, except two subspecies of *Arisaema flavum* from the section Dochafa, which are reportedly monoecious (Murata 1990b). Gender-diphasy is a highly derived condition within the Araceae (Grayum 1990) and is found in less than 0.01% of known plant genera (Lloyd & Bawa 1984).

Gender-diphasic sex expression is characterized by the sequential expression of asexual, male and female genders in a plant, with increasing resource levels and plant size. A single shoot is produced from an underground storage organ and the next shoot is preformed in the current growing season (Kinoshita 1986). Plant size can increase or decrease between growing seasons, with correlated changes in gender. Size change of the underground storage organ is positively correlated with the above-ground shoot size and gender (Maekawa 1924; Treiber 1980). Some *Arisaema* individuals have been projected to live up to 50 years (Bierzuchudek 1982).

### Data collection

*Arisaema* sex-ratio data were compiled from published reports and field surveys (see Richardson 1999 for details of surveys). Individuals that produce pistillate flowers were classified as female because the production of pistillate flowers qualitatively discriminates them from males, which produce only staminate flowers (Lloyd & Bawa 1984). Following standard practice (Charnov 1982), sex ratio is defined as the percentage of male plants within the population of reproductive plants (Appendix I contains the exact gender composition of each observation). For each sex-ratio observation, we recorded the species, location, year, sample size, numbers of male, monoecious and female plants, and source of the report (Appendix I). Sex-ratio data were categorized by two methods for analysis because sex-ratio reports varied from a single observation of a population in one year to observations of the same population over multiple years. The data were analyzed by population, where the mean sex ratio over one or more years was calculated for a population, and by observation, where each year's observation of a population was analyzed independently. For example, a single population census contributed one sex-ratio value to both the population and observation

data sets. In contrast, censuses of a population for three consecutive years contributed three sex ratios to the observation data set and one mean sex ratio to the population data set. Organizing data by populations and by observations provided the most liberal and conservative estimates of sex-ratio variation, respectively, in an attempt to account for differences in sampling techniques among studies.

We classified species into sex-change categories upon the relative frequency of monoecious and pistillate female-phase plants within and among the populations. Most species may have the ability to change between asexual, male, monoecious and female phenotypes (Maekawa 1924; Hotta 1971; Lovett Doust & Cavers 1982a; Kinoshita 1986; Clay 1993). Species with predominately monoecious female-phase inflorescences were classified as type I. Species with approximately equal proportions of monoecious and pistillate female-phases within populations, or species that display nearly equal proportions of populations that vary in the predominate female-phase morph, were classified as type II. Species with populations containing a large majority of pistillate females were classified as type III.

#### Data analysis

All data analyses were conducted using SAS version 6.06, and PROC GLM for unbalanced data sets was used to test whether there was a significant difference in the mean sex ratio between sex-change patterns. Levene's test (Levene 1960) was used to test for a difference in the variance of sex ratios between type I and type III sex-change patterns. To test for significant male or female biases in the mean sex ratio of each sex-change pattern,  $\chi^2$  tests were used. Fisher's exact test was used to test for differences in the

frequency of female-biased populations among sex-expression types.

## Results

### Phylogenetic distribution

Three of the 12 *Arisaema* sections were represented among 12 species with published sex-ratio data (Table 1). The ancestral *Arisaema* sections, *Tortuosa* and *Fimbriata* (Murata 1984; 1990a), contained both types I and III sex-change patterns while the more derived section *Pedatisecta*, which includes Jack-in-the-Pulpit (*Arisaema triphyllum*), were all type III. The lack of data from the remaining sections limit phylogenetic conclusions concerning the distribution of sex-change patterns and emphasize the need for additional sex-ratio data from more sections of the genus.

### Sex-change patterns

An extensive literature search combined with field surveys in southern Indiana produced a data set encompassing 12 *Arisaema* species, 81 populations, 143 observations and approximately 30 000 plants [the sample sizes of *Arisaema urashima* populations were not reported (Takasu 1987)] (Appendix I). The majority of the data came from the North American species *Arisaema dracontium* and *Arisaema triphyllum*, with approximately half of the total populations and observations coming from the latter species. Except for the single population of *Arisaema filiforme*, the type I species data set consisted of *A. dracontium* sex ratios. Moreover, *A. triphyllum* comprised 38 out of 52 (73%) of the type III population sex ratios with nine other *Arisaema* species totaling 14 populations. No *Arisaema* species could be interpreted as exhibiting a

**Table 1** *Arisaema* species included in this study organized by sections within the genus. The number of observations are equal to the number of populations unless otherwise noted.

Section	Species	Populations	Observations
Section <i>Fimbriata</i>	<i>Arisaema barbatum</i>	1	
	<i>Arisaema filiforme</i>	1	
Section <i>Pedatisecta</i>	<i>Arisaema angustatum</i>	1	
	<i>Arisaema iyoanum</i>	1	
	<i>Arisaema japonicum</i>	3	
	<i>Arisaema ringens</i>	1	
	<i>Arisaema serratum</i>	1	7
	<i>Arisaema sikokianum</i>	1	
	<i>Arisaema triphyllum</i>	38	73
	<i>Arisaema yamatense</i>	1	
Section <i>Tortuosa</i>	<i>Arisaema dracontium</i>	28	48
	<i>Arisaema urashima</i>	4	

type II sex-change pattern (approximately equal proportions of monoecious and pistillate inflorescences), so only types I and III sex-change pattern classes could be compared.

One plant with a pistillate inflorescence was reported out of 6449 *A. dracontium* plants scored for gender (Appendix I). Similarly, two out of 108 *A. filiforme* plants had a pistillate inflorescence versus 31 with a monoecious inflorescence. Therefore, both type I species had purely pistillate female-phase plants, but they were extremely rare. Similarly, six out of nine type III species had plants with monoecious inflorescences, but they were rare relative to plants with pistillate inflorescences. Pistillate, female-phase individuals were more numerous than monoecious, female phase plants in 51 out of 52 populations and 91 out of 94 observations. Most data on type III species were from *A. triphyllum*. In this species, most populations were reported to contain female-phase plants with monoecious inflorescences. In one population (S27), the majority of female-phase plants had a monoecious inflorescence (see Appendix I). In total, these data indicate considerable variation in gender expression within the type I and type III patterns.

#### Sex ratio

Both sex-change patterns had significantly male-biased sex ratios. The type I species had a 79.9% mean population sex ratio compared to a 63.7% mean population sex ratio in type III species ( $F=20.04$ ; d.f.=81;  $P<0.0001$ ) (Table 2). The range of population sex ratios of types I and III species were similar, ranging from 34% to 100% in type I species versus 20% to 90% in type III species (Fig. 1a). Three all-male populations (ON7, IN1 and IN3) were reported from the type I species, *A. dracontium*, while

none were reported from any type III species. Levene's test indicated that there was no statistical difference between the variance in sex ratios between sex-change patterns (11.9 vs 13.2;  $F=0.22$ ; d.f.=81;  $P=0.54$ ).

The type I Asian species *A. filiforme* sex ratio was comparable to those reported from North American *A. dracontium*. Similarly, there was no significant difference between the mean sex ratio of the Asian and North American type III species, 68.6% versus 69.4%, respectively ( $F=0.93$ ; d.f.=51;  $P=0.84$ ).

Male-biased population sex ratios occurred more frequently than female-biased ones among both sex-expression types (type I:  $\chi^2=21.5$ ,  $P=0.0001$ ,  $n=29$ ; type III:  $\chi^2=27.7$ ,  $P=0.001$ ,  $n=52$ ). There was no significant difference in the frequency of female-biased populations among sex-expression types ( $\chi^2=1.47$ ;  $P=0.22$ ;  $n=81$ ), although female-biased populations occurred in type III species at over twice the frequency of type I species, (17% to 6.9%, respectively; Fig. 1a).

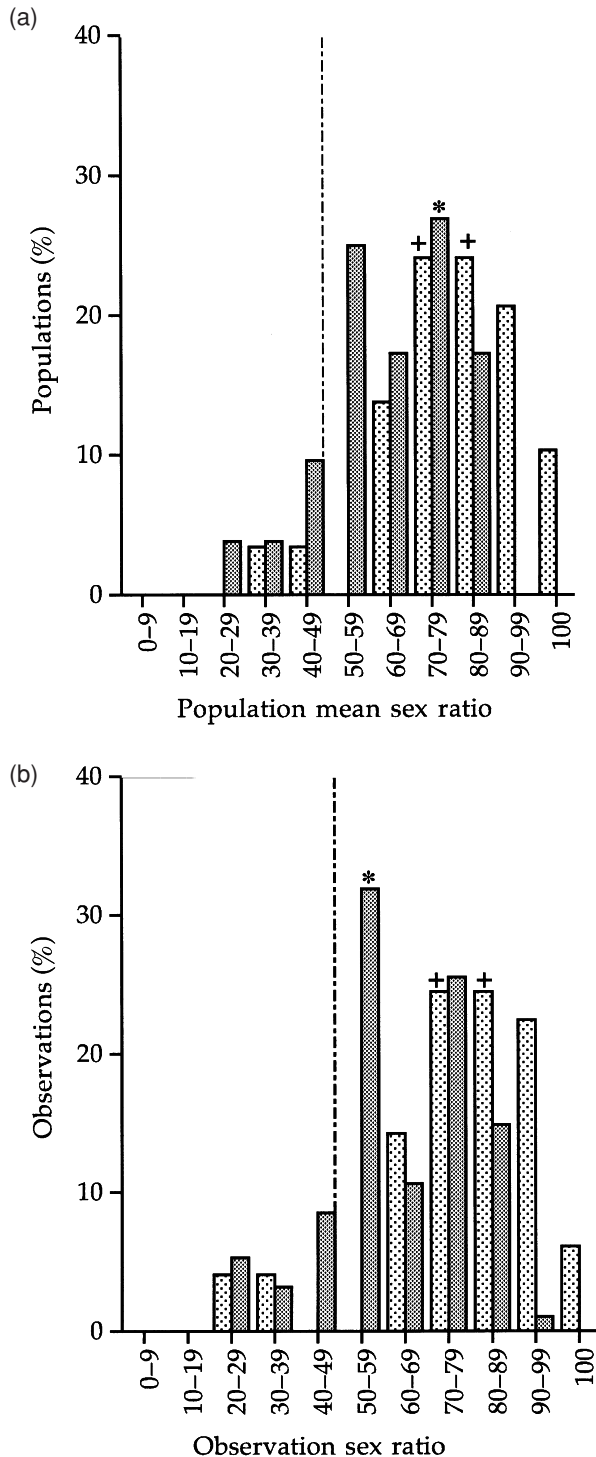
Many populations displayed substantial sex-ratio variation over time. Twenty out of 81 populations exhibited sex-ratio shifts of over 10% between years (Appendix I). This variation may reflect limited sampling of different plants from year to year, but may also reflect changes in survival and sex-change patterns within populations (Richardson 1999). Among type III species, populations varied in the frequency of female-phase plants with pistillate inflorescences over time, but tended to maintain fairly constant frequencies of female-phase plants with monoecious inflorescences.

The results of the statistical analyses of the sex-ratio observation data set were quantitatively similar to the results of the population sex-ratio analyses. Mean sex ratio and sex-ratio distribution for observations versus populations were similar (Fig. 1b; Table 2). Type I species

**Table 2** Sex ratios of type I and type III species by population and observation, including *Arisaema dracontium* and *Arisaema triphyllum*

	Number	No. plants	Male (%)	Monoecious (%)	Female (%)
By population					
Type I	29	6 557	80.0	20.0	0.07
<i>Arisaema dracontium</i>	28	6 449	80.4	19.6	0.07
Type III	52	23 367	63.7	5.1	31.2
<i>Arisaema triphyllum</i>	38	20 357	61.8	6.9	31.3
Total	81	29 924	69.5	10.2	20.3
By observation					
Type I	49	6 557	78.3	21.7	0.08
<i>A. dracontium</i>	48	6 449	78.5	21.5	0.04
Type III	94	23 367	62.8	6.5	31.9
<i>A. triphyllum</i>	74	20 357	62.0	8.0	31.4
Total	143	29 924	68.1	13.3	21.7

had a significantly lower mean sex ratio than type III species ( $F=28.9$ ;  $d.f.=141$ ;  $P<0.0001$ ), but there was no difference between sex-change patterns in the range of sex ratios or in the proportion of female-biased observations.



## Discussion

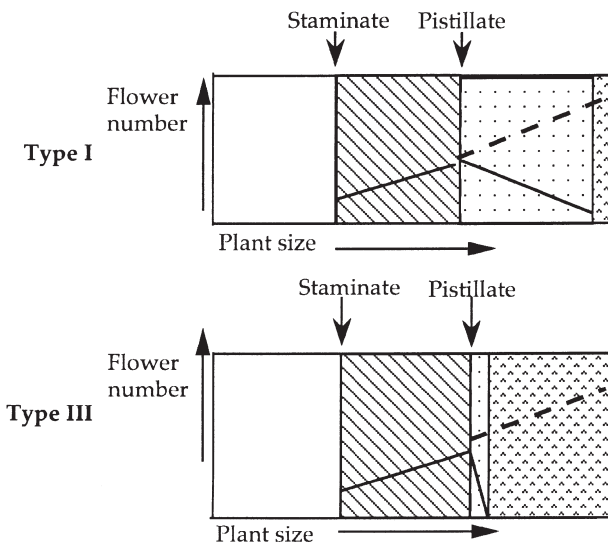
The data reviewed here did not provide clear evidence supporting a type II sex-change pattern, and revealed that sex-expression classifications are not concise descriptors of gender variation in a species. Monoecious females were found in all type I populations, but three out of 6557 female-phase plants had purely pistillate inflorescences. Among type III species, both monoecious and pistillate female-phase plants occurred in the majority of populations, but pistillate plants predominated in 51 out of 52 populations. The occurrence of monoecious females in most type III populations suggests that type I and type III species comprise a gradient of sex-expression forms where monoecious female-phase plants predominate at one extreme and pistillate female-phase plants predominate at the other extreme. However, there are no sex-ratio data available from most species in the genus, and there have been few long-term observations on species other than *A. triphyllum*. The high frequency of monoecious plants in Treiber's (1980) *A. triphyllum* observations from populations S27 and P5 indicate that the type II sex-change pattern may exist at the population level. Demographic studies of sex change in these populations could determine if the predominance of monoecious females reflects short-term fluctuations in a normal type III gender-expression pattern or evolutionary divergence towards a type II gender-expression pattern.

The occurrence of monoecious female-phase plants in most type III populations, and all type I populations, is consistent with the hypothesis that type I is the ancestral form of sex change for *Arisaema*. This highlights the importance of the monoecious phase in the evolution of sex change from non-sex-changing, monoecious ancestors in the family Araceae (Hotta 1971). Sex-changing *Arisaema* suggest that a critical step in the evolution of gender diphasy is developmental lability in the production of staminate and/or pistillate flowers on a single inflorescence. Hotta (1971) noted that pistillate inflorescences frequently bear rudimentary, non-functional staminate flowers above the pistillate flowers. We have also observed occasional staminate inflorescences with undeveloped pistillate flowers at the base. The existence of

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**Fig. 1** Type I and type III population sex ratio distributions. (a) Sex ratio distribution of type I ( $n=29$ ) and type III ( $n=52$ ) populations. To the left of the vertical dotted line are female-biased populations. The modal sex ratio classes for type I and type III sex change patterns are indicated by the symbols + and \*, respectively. (b) Sex ratio distribution of type I ( $n=49$ ) and type III ( $n=94$ ) observations. To the left of the vertical dotted line are female-biased populations. The modal sex ratio classes for type I and type III sex change patterns are indicated by the symbols + and \*, respectively.

these aberrant inflorescences suggest that all individuals have a latent ability to produce monoecious inflorescences. Evolution of the ability to suppress pistillate flower production may have allowed all sex-changing *Arisaema* species to become reproductive at a smaller size and at lower resource levels. The type III sex-change pattern results from the truncation of the monoecious phase by early cessation of staminate flower production, leading to a fully pistillate state at an earlier developmental period, smaller sizes and younger ages than in the type I sex-change pattern (Fig. 2).

Testing the hypothesis of variable developmental timing of flower production requires empirically characterizing ontogenetic divergence of staminate and pistillate floral production among species with different sex-expression types (Richardson 1999). However, there is not an adequate sample of the species or intrageneric sections within the genus to make phylogenetic inferences concerning the origin and evolutionary lability of sex-change patterns within *Arisaema* at present.



**Fig. 2** Hypothesized *Arisaema* sex change patterns (floral initiation thresholds by gender/inflorescence composition). The alternative patterns of sex change in *Arisaema* are represented as a function of plant size ( $x$ -axis) and floral production ( $y$ -axis). (□) Asexual/no flowers; (▨) male/staminate; (▩) female/monoecious; (⊞) female/fully pistillate; (—) staminate floral production; (---) pistillate floral production. Sex change types I and III are distinguished by their frequencies of monoecious and pistillate female-phase plants within a population. Type I species can produce fully pistillate inflorescences but individuals that reach such large sizes are rare. Type III species have a small intermediate size range where monoecious inflorescences are produced. In both type I and type III sex change patterns, staminate flower number declines with increasing plant size in monoecious female-phase plants. Model follows Clay (1993).

### Sex ratio and the cost of reproduction

The predominance of male-biased sex ratios in *Arisaema* supports the prediction that unequal sex ratios occur when male and female reproductive costs vary asymmetrically with environmental conditions (e.g., Bull 1981; Charnov 1982; Bull & Charnov 1988). Male reproduction in *Arisaema* is presumed to be limited by pollinator availability, whereas female reproduction is thought to be limited by resources for fruit and seed production (Bierzychudek 1982, 1984; Lovett-Doust & Cavers 1982a; Lloyd & Bawa 1984; Kinoshita 1987). The cost of reproduction in females is expected to covary with the environmental conditions more than the cost of reproduction in males, due to greater resource allocation to female function (Lovett-Doust & Cavers 1982a). *Arisaema* individuals consistently apportion more biomass to female function than to male function because female inflorescences are larger than male inflorescences, and females have the additional resource investment of seed production. Female reproductive cost is expected to become relatively greater under conditions of resource limitation. Male-biased populations may result from sex-ratio selection to equilibrate male and female reproductive costs within populations (Bull & Charnov 1988).

Sex-ratio comparisons that further suggest that female reproduction is likely to be more costly for type I species is the occurrence of all-male populations, which were not reported in type III species. Likewise, the two-fold higher frequency of female-biased populations in type III versus type I species is consistent with a greater cost of female reproduction in type I species.

A greater cost of female reproduction in many type I species may be a consequence of simultaneous allocation to both male and female function during the female phase. In type III species, all resources allocated to reproduction are invested in pistillate flowers and seeds, resulting in a lower reproductive cost per seed set. Lovett-Doust & Cavers (1992a, 1992b) reported that over 40% of female-phase plant biomass was allocated to reproduction at fruit maturity in *A. triphyllum* (type III) compared to less than 20% in *A. dracontium* (type I). Takasu (1987) also found that *A. urashima*, a type III species, allocated approximately 40% of female-phase plant biomass to reproduction. This difference in sex-allocation patterns among females may further account for the higher frequency of female-biased populations in type III species. Type III species may have a greater ability to respond to extreme environmental conditions through adaptive sex-ratio adjustment than type I species due to lower female reproductive costs.

Under poor resource conditions, populations are expected to become more male-biased, and tradeoffs among life-history traits become more pronounced

(Stearns 1993; Roff 1994). Type III species are expected to have diminished tradeoffs compared to type I species because female reproductive allocation is translated into seed production more efficiently. Type III species should have greater survival rates, greater growth rates and greater percentages of females remaining female from year to year compared to type I species. Thus, type III populations may persist and have lower sex ratios under environmental conditions unsuitable for type I species.

Our finding that *Arisaema* species with a predominantly monoecious female phase have consistently higher sex ratios than *Arisaema* species with a predominantly pistillate female phase may be true for other gender-diphasic species as well. The subtribe *Guraniinae* (Cucurbitaceae) and *Panax trifolium* (Araliaceae) are diphasic taxa that exhibit monoecious female phases and extremely male-biased sex ratios. *Guraniinae* sex ratios ranged from 73% to 94% (Condon 1984) while *Panax* sex ratios ranged from 77% to 89% (Schlessman 1991). However, there are no data from natural populations of other diphasic plant taxa outside of *Arisaema* that produce both monoecious and pistillate female phases for direct comparison.

#### *Phylogenetic distribution of sex-change patterns*

The species used in this study occurred in only three of 11 *Arisaema* sections documented in the literature. Furthermore, 75% of the species described in this study were from the section *Pedatisecta* (Murata 1995). Of these species, only North American *A. dracontium* and *A. triphyllum* have sex-ratio data from multiple populations and multiple years. Data from these North American species are important because each species represents a distinct pattern of sex expression found in the genus. There were no sex-ratio data providing evidence of species with a type II sex-change pattern, but clearly more data derived from Asian species are necessary to understand diversification of sex-expression patterns and to quantify sex-ratio variation among *Arisaema*. Asian *Arisaema* display greater morphological and ecological diversity than North American species (Murata 1984).

#### *Characterizing Arisaema sex expression patterns*

The frequency of monoecious inflorescences may be underestimated in many type III *Arisaema* species. The possibility of monoecious individuals was not even mentioned in many studies reviewed here. Monoecious female-phase plants often exhibit morphologies bearing a greater resemblance to fully pistillate females than to males. If plant gender is assigned without close examination of the actual floral composition, monoecious individuals may be overlooked or misclassified as pistillate, underestimating the frequency of monoecious female-

phase plants within populations. Moreover, when monoecious individuals occur at low frequencies, they could be overlooked due to sampling error. Monoecious *A. triphyllum* plants are reported in most, but not all, populations. It is unclear whether there is variation among populations in the production of monoecious female-phase plants, or variation in the assessment of the female phase among researchers. The ability to detect the presence of the different morphs may increase with the number of populations sampled. For example, Clay (1993) found only one fully pistillate individual in one of four populations of the type I species, *A. dracontium*. Furthermore, species characterizations based on herbarium sheets may not adequately represent the morphological variation within and among populations, or the temporal and developmental variation within an individual. *Arisaema flavum* was thought to be strictly monoecious from examination of a herbarium specimen, yet characterization of natural populations revealed geographic variation in sex-expression patterns (Murata 1990b). Similarly, the existence of gender-diphasy in the tribe *Guraniinae* (Cucurbitaceae) was not detected from herbarium sheets because they did not reflect the temporal gender variation within an individual (Condon & Gilbert 1982). Collectors may also discriminate against unusual gender morphs in favor of more typical forms. There is a need to examine multiple natural populations from different geographic regions to quantify the sex-expression patterns within and among populations and species.

In conclusion, sex-allocation research in *Arisaema* has documented basic ecological and life-history parameters such as plant-size distribution, the size asymmetry of male and female plants, sex ratios and morphological variation within and among natural populations. In this study we have shown that the sex-change pattern has an influence on sex ratio. These consistent differences in sex ratio may result from differences in the female cost of reproduction between sex-change patterns, and provide insights into the adaptive significance of a sex change. The two North American species of *Arisaema*, which make up the majority of the database, appear to be representative of the genus as a whole. However, the lack of sex-ratio data from a larger number of species and from long-term studies limits the ability to detect and quantify factors influencing sex-expression and sex-ratio variation.

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## Appendix I.

### *Arisaema* sex ratios by sex-change pattern and species

#### Type I

Species and site	Overall sex ratio (%male)	Year	N	Male (%)	Monoecious (%)	Female (%)	Reference
<i>Arisaema dracontium</i>							
ON1	86	1994	347	86	14	0	1
ON3	94	1993	44	93	7	0	1
ON4	83	1993	23	78	22	0	1
		1994	33	88	12	0	1
ON5	81.5	1993	4	80	20	0	1
		1994	6	83	17	0	1
ON 6	82	1994	124	82	18	0	1
		1995	123	82	18	0	1
ON 7	100	1995	20	100	0	0	1
OH1	78	1995	586	78	22	0	1
OH2	93	1995	27	93	7	0	1
OH3	66	1995	217	66	34	0	1
IN 1	100	1994	10	100	0	0	1
IN 2	94	1994	16	94	6	0	1
IN 3	100	1994	9	100	0	0	1
IN4	90	1994	42	90	10	0	1
IN 5	83	1994	6	83	17	0	1
IN 6	88	1994	53	88	12	0	1
Population 1	35	1985	49	35	65	0	2
		1986	62	34	66	0	2
Population 2	74	1985	53	70	30	0	2
		1986	54	78	22	0	2
Population 3	40	1985	62	40.4	58	1.6	2
Population 4	71	1986	59	71	29	0	2
Campus	74	1979	243	74	26	0	3
St. Thomas	75	1979	721	75	25	0	3
Goose Pond	66.7	1992	150	44	56	0	4
		1993	150	63	37	0	4
		1994	150	75	25	0	4
Griffy	85.4	1990	150	90	10	0	4
		1991	150	95	5	0	4
		1992	150	93	7	0	4
		1993	150	76	24	0	4
		1994	150	73	27	0	4
Grey's Swamp	73	1992	150	74	26	0	4
		1993	150	81	19	0	4
		1994	150	64	36	0	4
Hardin Ridge	69.7	1992	150	61	39	0	4
		1993	150	79	21	0	4
		1994	150	69	31	0	4
Twin Swamp	76	1992	150	63	37	0	4
		1993	150	84	16	0	4
		1994	150	81	19	0	4

Species and site	Overall sex ratio (%male)	Year	N	Male (%)	Monoecious (%)	Female (%)	Reference
Population 1	96	1920	108	91	9	0	5
		1921	693	81	19	0	5
Population 2	95.5	1920	45	95	5	0	5
		1921	28	96	4	0	5
<i>Arisaema filiforme</i>	69.4	1948	108	69.4	28.7	1.9	6
Type III							
<i>Arisaema angustatum</i>	52.4	1988	172	52.4	0	47.6	7*
<i>Arisaema barbatum</i>	80.6	1948	36	80.6	2.7	16.7	6
<i>Arisaema iyoanum</i>							
Omogo Vally	72.7	1986	117	72.7	0	27.3	8
<i>Arisaema japonicum</i>							
	73.5	1978	589	73.5	1.5	25	6
Ashiu Experimental Forest	72.5	1986	80	72.5	1.25	26.25	8
<i>Arisaema japonicum var. atropurpureum</i>	79.8	1988	124	79.8	0	20.2	7*
<i>Arisaema ringens</i>							
Mt. Godai	83.6	1986	373	83.6	0	16.4	8
<i>Arisaema serratum</i>							
Tajiri Shrine	29.7	1986	431	29.7	0.5	69.8	8
Tajiri Shrine	57.6	1981	118	58.5	0	41.5	9
		1982	134	61.2	0	38.8	9
		1983	133	53.4	0.8	45.8	9
		1984	171	56.7	1.2	42.1	9
		1985	184	58.2	0	41.8	9
		1986	189	57.7	0	42.3	9
<i>Arisaema sikokianum</i>							
Tosashimizu City	71.8%	1986	71	71.8	0	28.2	8
<i>Arisaema triphyllum</i>							
Fall Creek experimental plot	57.7	1977	123	61	0	39	10*
		1978	135	56	44	10	
		1979	127	56	44	10	
Fall Creek, Pine grove	57	1979	135	57	0	43	10
Brooktondale, experimental plot	76.3	1977	124	77	0	23	10
		1978	140	69	0	31	10
		1979	149	83	0	17	10
Brooktondale, trail head	64	1977	104	64	0	36	10
Warren Woods	52.5	1978	89	55	0	45	10
		1979	108	50	0	50	10
Monkey Run	60	1978	100	66	0	34	10
		1979	79	54	0	46	10
Shindagin Hollow	70	1979	100	70	0	30	10
Highland State Park	57.7	1990	567	57.7	3	39.3	11
Vermont Agricultural Station	35.5	1982	160	35.6	3.8	60.6	12
Campus	42	1978	483	36.9	12.2	50.9	12
		1979	1099	46.9	15	38.1	12
Komaka A	44.3	1979	599	45.1	13.2	41.7	13
Komaka A		1979	708	44.5	13.6	41.9	13
Fingal-Shedden A	50.5	1979	212	50.0	13.2	36.8	13
Fingal-Shedden B		1979	592	51.0	13.5	35.5	13
Huron	51	1978	507	50.8	10.7	38.5	13
		1979	1162	51.0	11	38	13
Fanhawe	58.3	1979	652	58.3	10.7	31	13
Lanbeth	60.2	1979	631	60.2	10.9	28.9	13
Byron	68	1978	484	59.6	9	31.4	13
		1979	676	76.3	7.5	16.2	13
Lebo	67.6	1979	213	67.6	13.3	19.3	13
Dingman	85.6	1978	505	84.0	3.8	12.2	13
		1979	634	87.2	5.2	7.6	13
Thorn Creek Preserve	77	1987	604	77	0	23	14*

Species and site	Overall sex ratio (%male)	Year	N	Male (%)	Monoecious (%)	Female (%)	Reference
Eastabrook Woods	55.9	1977–9	2038	63.3	Np	36.7	15 <sup>†</sup>
				44.8	Np	55.2	15
				59.5	Np	40.5	15
Creekside	22.3	1991	150	27	Np	73	4 <sup>§</sup>
		1992	150	22	Np	78	4 <sup>§</sup>
		1993	150	20	Np	80	4 <sup>§</sup>
		1994	150	20	Np	80	4 <sup>§</sup>
Lakeside	57	1992	150	58	Np	42	4 <sup>§</sup>
		1993	150	56	Np	44	4 <sup>§</sup>
		1994	150	57	Np	43	4 <sup>§</sup>
Southern Indiana	80.3	1992	150	85	Np	15	4 <sup>§</sup>
		1993	150	74	Np	26	4 <sup>§</sup>
		1994	150	82	Np	18	4 <sup>§</sup>
University of Delaware Campus	42.8	1977	Np	42.8	1.8	55.4	16 <sup>†</sup>
Pop. 1	89.4	1961	47	89.4	6.4	4.2	17
Pop. 2	74.3	1961	39	74.3	2.6	23.1	17
Pop. 3	42.4	1961	33	42.4	9.1	48.5	17
Pop. 1	60	1922	1209	60	13	27	5
Pop. 2	73	1922	310	73	4	23	5
Pop. 3	59	1922	39	59	7	34	5
Pop. 4	79	1922	150	79	10	11	5
Pop. 5	40	1922	166	40	22	38	5
T2	63.9	1976	278	56.1	8.6	35.3	18
		1977	174	59.2	6.9	33.9	18
		1978	267	76.4	7.9	15.7	18
T15	85.2	1976	192	82.2	5.3	12.5	18
		1977	234	89.8	3.4	6.8	18
		1978	236	83.0	8.1	8.9	18
S27	61.9	1976	59	59.3	10.2	30.5	18
		1977	60	68.3	16.7	15.0	18
		1978	54	59.2	9.3	31.5	18
S29	68.9	1976	146	73.3	16.4	10.3	18
		1977	146	82.2	8.2	9.6	18
P4	75.9	1976	143	76.9	5.6	17.5	18
		1977	131	72.5	11.5	16.0	18
		1978	124	78.2	7.3	14.5	18
P5	74.3	1976	64	75.0	9.4	15.6	18
		1977	80	73.8	15	11.2	18
		1978	97	74.2	10.3	15.5	18
Floodplain	51	1976	103	48.5	7.8	43.7	18
		1977	86	53.5	7.0	39.5	18
Slopes	81.2	1976	87	78.2	4.6	17.2	18
		1977	57	84.2	3.5	12.3	18
<i>Arisaema urashima</i>							
Esazaki	83.3	1981	Np	83.3	Np	16.7	19 <sup>§</sup>
Mihama	82.2	1983	Np	82.2	Np	17.8	19
Okinoshima	75.8	1981	Np	75.8	Np	24.2	19
Shirahama	79.8	1982	Np	79.8	Np	20.2	19
<i>Arisaema yamatense</i>							
Kibune Shrine	34.1	1986	88	34.1	1.1	64.8	8

Np, data not provided in the study; \*the presence of a monoecious sexual state not mentioned in the article; <sup>†</sup>Policansky (1981) does not report the temporal sequence of the population sex ratio but mentions that individuals with at male and female flowers at a frequency of at least 10% account for less than 1% of the individuals sampled. <sup>‡</sup>Monoecious individuals accounted for 3 out of 100 sampled female plants in a population with an approximate density of  $3.6 \pm 0.2$  sexual individuals per  $0.25 \text{ m}^2$  where  $1.5 \pm 0.1$  individuals were male and approximately  $2.0 \pm 0.1$  were female; <sup>§</sup>The presence of monoecious individuals are noted but not quantified in population sex ratios. Sources: 1. Boles (1996); 2. Clay (1993); 3. Lovett Doust and Cavers (1982a); 4. Richardson (unpubl. data); 5. Schaffner (1922); 6. Murata (1984); 7. Takasu (1988); 8. Kinoshita (1986); 9. Kinoshita (1987); 10. Beirzychudek (1982); 11. Cornett (unpubl. data); 12. Ewing and Klein (1982); 13. Lovett Doust and Cavers (1982b); 14. Parker (1987); 15. Policansky (1981); 16. Rust (1981); 17. Sakamoto (1961); 18. Treiber (1980); 19. Takasu (1987).