The allometry of fluctuating asymmetry in southern African plants: flowers and leaves

MICHAEL D. JENNIONS

A.B.R.G., Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS*

Several studies of fluctuating asymmetry (FA) in animals show that secondary sexual characters used in signalling have a negative relationship between size and asymmetry. Larger sexual traits are presumably more costly to produce, which should lead to greater developmental stress and corresponding increases in asymmetry. In the absence of among individual variation in the ability to handle these costs, the relationship between size and asymmetry should thus be positive. A negative relationship therefore suggests that expression of these traits is condition-dependent. In plants, flowers act as signals for pollinators and may show similar trends to animal signals. Leaves which are uninvolved in signalling should not. Møller & Eriksson (1994) found that 89% of species (*n* = 16 of 18) with insect-pollinated flowers showed a negative relationship between petal size and asymmetry, while 79% of species (*n* = 15 of 19) showed a positive relationship between leaf size and asymmetry. I carried out a similar study of 18 plant species. The average relationship between petal size and asymmetry did not differ significantly from zero in those species showing measurable FA in flowers (*n* = 12). The relationship was significantly negative in one species, and significantly positive between size and asymmetry for leaves and flowers. Levels of not show a significant positive relationship between size and asymmetry (*n* = 7). There was no significant difference in the slopes of the relationship between size and asymmetry for leaves and flowers. Levels of floral asymmetry for species with FA were significantly repeatable on individual plants in 33% (*n* = 4 of 12) of species, but leaf asymmetry was not significantly repeatable in any species. It is argued that condition-dependence of traits need not result in a negative relationship between size and asymmetry.

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ADDITIONAL KEY WORDS: — condition-dependence – fluctuating asymmetry – sexual selection.

CONTENTS

*Present address: Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Ancon, Republic of Panamá. (Email: stri02.gamboa.gam128@ic.si.edu)

INTRODUCTION

Sexual selection in plants is a field of growing interest (Wilson, 1990). Sophisticated mechanisms of post-pollination mate choice such as selective seed abortion (Marshall & Ellstrand, 1988) and female-mediated differential growth of pollen tubes (Snow & Spira, 1991) have been documented. The strongest selective force on hermaphroditic flowers, however, appears to be for the male function of dispersing pollen (Bell, 1985). Variation in flower morphology is related to the amount or rate of pollen transfer in several species (Gori, 1989; Campbell, 1989; Devlin, Clegg & Ellstrand, 1992). Floral features known to affect pollination include flower colour, size and scent. Less attention though, has been paid to understanding why pollinators respond to variation in these cues. Do these cues simply exploit sensory biases in pollinators, as is likely to be the case in bee-mimicking orchids (Møller & Eriksson, 1994) and the carrion-like scent of some fly-pollinated *Rafflesia* (Mat Salleh, 1991)? Or do the cues provide honest information about the rewards flowers offer to pollinators? Although there is good evidence that gross changes in flower coloration can signal presence or absence of pollinator rewards (Weiss, 1991), there is less evidence for continuous variation in floral traits, such as colour or size, being positively related to pollinator rewards. It has been suggested that studies of fluctuating asymmetries may be able to address this question (Møller, 1995; Møller & Eriksson, 1995).

Fluctuating asymmetries (FA) are small, random deviations from perfect bilateral symmetry which are random with respect to side and normally distributed in a population (Ludwig, 1932). These asymmetries arise as a result of developmental disruptions caused by genetic and environmental stress (reviewed by Van Valen, 1962; Palmer & Strobeck, 1986; Leary & Allendorf, 1989; Watson & Thornhill 1994) and there is evidence that levels of asymmetry are heritable (Thornhill & Sauer, 1992). Møller (1990) suggested that because secondary sexual characters such as ornaments and weapons are costly to produce their asymmetry may be a reliable measure of physiological stress during development and could be used by mates, competitors and predators as a cue of quality. High quality individuals in terms of resistance to developmental stress should be more symmetric. There is evidence from numerous animal species that levels of asymmetry are correlated with various components of fitness. Symmetric males appear to have advantages in terms of mating success (Thornhill 1992a; Harvey & Walsh, 1993; Liggett, Harvey & Manning, 1993; Arcese 1994; Møller 1994; but see Oakes & Barnard, 1994; Ryan *et al.*, 1995), fighting success (Thornhill 1992b) and longevity (Thornhill, 1992c; Møller, 1994; but see Packer & Pusey, 1993).

Studies of FA in plants have shown similar environmental causes of asymmetry to those found for animals. Asymmetry in the leaves of several species increases with proximity to potential stresses such as chemical factories and electrical transmission lines (reviewed in Freeman, Graham & Emlen, 1993). In brown algae (*Fucus furcatus latifrons*) branch length asymmetry increases with higher pollution levels (Tracy *et al.*,

cited in Freeman *et al.*, 1993). Sakai & Shimamoto (1965) showed that one measure of developmental stability, measured as the within flower variance in stamen length, differed among varieties of tobacco (*Nicotiana tabacum*). Similar results were reported by Paxman (1956) who examined varieties of *Nicotiana rustica* and showed heritable additive variation in developmental stability. There is also evidence that levels of flower asymmetry are correlated with a component of fitness, namely rate of pollen transfer. Møller (1995) and Møller & Eriksson (1995) found that symmetric flowers were visited more often by insects than were asymmetric flowers in 100% of species ($n = 10$), and in six species the difference in symmetry between visited and non-visited flowers was statistically significant.

It has been suggested that a negative relationship between size and asymmetry is evidence that a trait is a condition-dependent indicator of quality (Møller & Höglund, 1991; but see Balmford, Jones & Thomas, 1993; Arcese, 1994). Larger secondary sexual characters are often more costly to produce or maintain (Møller 1989; Evans & Thomas, 1992; Backwell *et al.*, 1995) and asymmetry increases with developmental stress. Therefore, unless individuals producing larger ornaments are in better condition, asymmetry should increase with ornament size (Møller & Pomiankowski, 1993). Møller & Eriksson (1994) recently used this prediction to test whether flower size is a condition-dependent indicator of quality. They found a significant ($P < 0.05$) negative relationship between petal size and asymmetry in 50% of species ($n = 9$ of 18) with insect-pollinated flowers, indicating that larger flowers are produced by plants that suffer lower costs at the time of production than plants producing smaller flowers. Their results suggest that flower size is generally condition-dependent in the European species studied. In support of this claim, Møller & Eriksson (1995) have also presented evidence for a positive relationship between flower symmetry and the standing crop of nectar in 100% of species ($n = 6$). In two species, the relationship was statistically significant. In contrast with flowers, Møller & Eriksson (1994) found that asymmetry increases with leaf size. This suggests that larger leaves are more costly to produce, but that investment in leaves is not condition-dependent.

In animals secondary sexual characters tend to show greater levels of asymmetry than non-sexual morphological traits (Møller & Höglund, 1991; Møller, 1992; but see Barnard 1994; Tompkins & Simmons, 1995). This trend has been attributed to greater directional selection on sexual traits through female choice or male-male competition, leading to selection for new mutations and decreased developmental canalization (Clarke & McKenzie 1987; Møller & Pomiankowski, 1993). However, it should be noted that directional selection on sexually selected traits does not occur at equilibrium where sexual selection for elaboration and natural selection are equal and opposite in magnitude (Balmford & Read, 1991; Thomas 1993).

Here I present data collected from plants examining: (1) levels of fluctuating asymmetry in flowers and leaves. If there is strong directional selection on flower size due to pollinator preferences, then levels of asymmetry may be greater in flowers than in leaves due to decreased developmental canalization (Møller & Pomiankowski 1993); (2) the repeatability of absolute asymmetry in flowers and leaves on individual plants. If asymmetry in flowers and leaves reflects specific qualities of plants then it should be significantly repeatable on individual plants; (3) the allometric relationship between size and asymmetry in flowers and leaves. If flowers are condition-dependent, then it is generally argued that there should be a negative relationship between size and asymmetry. In contrast, Møller & Eriksson (1994) suggest that a

significant positive relationship should arise between leaf size and absolute asymmetry due to directional selection for larger leaves combined with high phenotypic plasticity and reduced developmental canalization; (4) the relationship between absolute asymmetry of flowers and leaves on individual plants. If asymmetry in these traits is mainly due to variation among plants in their ability to withstand developmental stress, then there should be a significant positive correlation between the asymmetry of the two traits.

METHODS

I measured asymmetry in the flowers and leaves of 18 hermaphroditic species from 15 families in July–August 1993 and September 1994 in South Africa from sites around Cape Town (33° 55'S, 18° 22'E), Hermanus (34° 27'S, 19° 12'E) and Springbok (29° 42'S, 17° 54'E). The species measured were: *Albuca cooperi* (Liliaceae), *Chasmanthe floribunda* (Iridaceae), *Chrysanthemoides monilifera* (Asteraceae), *Cyanella orchidiformis* (Tecophilaeaceae), *Cyphia volubilis* (Campanulaceae), *Heliophila africana* (Brassicaceae), *Lapeirousia arenicola* (Iridaceae), *Lebeckia sericea* (Fabaceae), *Microloma calycinum* (Asclepiadaceae), *Nemesia versicolor* (Scrophulariaceae), *Nemesia sp* (Scrophulariaceae), *Oxalis purpurea* (Oxalidaceae), *Pelargonium fruticosum* (Geraniaceae), *Polygala myrtifolia* (Polygalaceae), *Solanum burchellii* (Solanaceae), *Strelitzia reginae* (Strelitziaceae), *Tecomaria capensis* (Bignoniaceae) and *Wahlenbergia annularis* (Campanulaceae).

I measured the length of paired left and right petals for 11 species with bilaterally symmetric flowers. When there was a choice of paired petals, I chose the larger pair to increase measurement accuracy. For radially symmetric flowers, I measured two petals that were opposite one another in species with four petals (*H. africana, O. purpurea*); or all petals in *A. cooperi, M. calycinum, S. burchellii* and *W. annularis*; because of the large number of petals in *C. monolifera* I measured the two petals that were visually assessed as being the longest and shortest (see Møller & Eriksson, 1994). I always chose fully opened, undamaged flowers. I measured the maximum width of the left and right half of the leaf from the centre of the mid-vein to the leaf margin. In *C. floribunda* and *S. reginae* I measured maximum leaf width at a fixed point (respectively 5 cm and 30 cm from the leaf tip) as an index of asymmetry. In *P. fruticosum, O. purpurea* and *C. volubilis* I measured the length of paired leaf parts from the plant stem to their apices. Exclusion of the leaves of these three species from the analyses does not change the significance of my results. That these leaf measurements were of developmentally paired traits is indicated by the result that, with the exception of *C. volubilis*, they all showed FA (mean signed asymmetry of zero and normally distributed). In most cases the leaf immediately below each measured flower was used. If this leaf was damaged, or if it was impossible to associate a flower with a specific leaf (e.g. *S. reginae*), the nearest suitable leaf was picked haphazardly.

All measurements were made to the nearest 0.1 mm using dial callipers. I measured the petals and leaves of at least ten individuals per species twice, and then calculated repeatability (intra-class correlation coefficients; Zar, 1984). These repeated measurements of trait size and absolute asymmetry from the same leaf or flower are presented in Appendix 1. If measurements were not significantly repeatable I excluded them from statistical tests.

Absolute symmetry is defined as the unsigned difference between the left and right

trait values. I accepted traits as showing fluctuating asymmetry (FA) if there was no significant deviation of the signed asymmetries from a mean of zero (one-sample t-tests), and they were normally distributed (Lilliefors tests). Because of multiple testing, I used the sequential Bonferroni correction for table-wide probabilities (Rice, 1989). Separate Bonferroni corrections were made for tests of normality and tests of mean value. Any species in which the corrected P-value was less than 0.10 was regarded as failing to show fluctuating asymmetry for the trait in question.

To control for trait size, I also calculated relative asymmetry for each flower or leaf as absolute asymmetry divided by mean trait size (Palmer & Strobeck, 1986). Across species, the allometric relationship between log-transformed absolute asymmetry and log-transformed mean trait size showed isometry (H_O ß = 1: leaves, 0.865 ± 0.183, $t = -0.738$, d.f. = 10, $P > 0.20$; flowers, 0.832 ± 0.235,, $t = -0.715$, d.f. = 16, $P > 0.20$). Hence, relative asymmetry was a suitable control for trait size (Tompkins & Simmons, 1995).

I have treated species from different families as independent points for statistical testing. Strictly speaking this procedure is incorrect, although there is no evidence that the allometric relationships studied are phylogenetically constrained. If they were, then standardized regression coefficients of petal asymmetry on mean length should be significantly repeatable within families. Using my data and that of Møller and Eriksson (1994) I found this was not the case for seven families. The estimate of repeatability was almost zero ($r = -0.037$, d.f. = 6,9, $F = 0.921$, $P = 0.52$). Despite the lack of repeatability, I only used one species per family in statistical tests. In the one statistic where more than one species per family could be used, the range of values resulting from the use of different family representatives is shown.

Methods to determine the allometric relationship between size and asymmetry are controversial (Evans & Hatchwell, 1993; Sullivan, Robertson & Aebsicher, 1993; Cuthill, Swaddle & Witter, 1993). Here I use the most common approach, namely to relate absolute asymmetry to mean character size (Palmer & Strobeck, 1986). I used Spearman correlation coefficients rather than a parametric technique because the value of signed asymmetry is normally distributed, hence absolute asymmetry cannot be normally distributed. I used only one flower or leaf per plant when calculating relationships. Two analyses involving different measures of 'asymmetry' were performed for radially symmetric flowers. First, absolute asymmetry was measured as the longest minus the shortest petal. This approach allowed for a direct comparison of my results with those of Møller and Eriksson (1994). Second, I determined the within-flower variance in petal size, and this was then used as a measure of developmental instability (Freeman et al., 1993).

I used one-sample t-tests to test the null hypothesis that mean Spearman correlation coefficients did not differ from zero. Matched-pairs and two sample t-tests were used to check for significant differences between coefficients for flowers and leaves. Correlation coefficients were transformed using the Fisher z-transformation (Zar, 1984: 310). Variability in leaf and petal size was described using the coefficient of variation (CV). Repeatability of traits on an individual were estimated from a one-way analysis of variance (Zar, 1984). Differences in individual repeatability for petal and leaf size, CV for leaf and petal size and relative and absolute asymmetry between flowers and leaves were all tested using matched-pair or two-sample t-tests and sign tests. Relative asymmetry was first log-transformed. All tests are two-tailed unless otherwise stated. The minimum detectable difference of statistical tests when power

was set at 90% was calculated using methods from Zar (1984). Data were analysed using the SYSTAT statistical package.

Fluctuating asymmetry

Tests for normality and a mean left-right difference of zero indicating which traits showed FA are presented in Appendix 2. Traits which failed to show FA were flowers in *L. arenicola, C. orchidiformis, C. volubilis* and *Nemesia sp.*; and leaves in *C. monilifera, C. orchidiformis, C. volubilis, Nemesia sp.* and *W. annularis*. I took a conservative approach and also excluded leaves from *H. africana* from the category of traits showing FA because the original *P*-value for deviation from a normal distribution was less than 0.01 (although not significant at the 10% level with a sequential Bonferroni correction).

Trait size and asymmetry

Summary statistics for size and asymmetry are presented in Table 1. There was considerable intra-specific variation in size for both flowers and leaves, but leaves showed greater variability than flowers (Sign test of coefficients of variation, $P = 0.003$, $n = 12$). My measure of leaf size was smaller than that for flowers (Sign test, $P < 0.01$, $n = 12$). In the seven species where both flowers and leaves showed FA, relative asymmetry did not differ significantly between leaves and flowers (matched *t*-test, $t = 1.346$, d. f. $= 6$, $P = 0.227$). However, comparing the mean relative asymmetry of leaves and flowers showing FA for all species where data was available, there was a marginally significant difference with leaves showed greater relative asymmetry (Two-sample *t*-test, d. f. $= 19$, $t = 2.013$, $P = 0.053$; leaf $= 0.089 \pm 0.014$ SE; flower 0.059 ± 0.009 SE).

Repeatability of traits on individual plants

On individual plants, flower size was significantly repeatable in 10–12 of 15 species (66-80%), and leaf size in 5–6 of 10 species (50-60%) (Table 2) (range due to use of different family representatives). Leaf size tended to show greater repeatability than flower size, and the difference was marginally significant (matched *t*-test, $t = 2.095$, d. f. $= 10$, $P = 0.063$). On individual plants leaf absolute asymmetry was not significantly repeatable in any of 11 species, and mean repeatability for absolute asymmetry did not differ significantly from zero for species with leaves with measurable FA (mean $\pm$ SE $= 0.012 \pm 0.057$; one-sample *t*-test, $t = 0.197$, d. f. $= 5$, $P = 0.85$). Flower absolute asymmetry was significantly repeatable on individual plants in 4 of 12 species with FA (33%) (Table 2). The mean repeatability of absolute asymmetry was significantly greater than zero in species with flowers showing FA (mean $\pm$ SE $= 0.116 \pm 0.039$; one-sample *t*-test, $t = 2.974$, d. f. $= 11$, $P = 0.013$).

TABLE 1. Size and fluctuating asymmetry in floral and leaf traits (Mean ± SE). Relative asymmetry is absolute asymmetry/mean size. Asymmetry that was not fluctuating (either because of directionality, or non-normality) is indicated by an asterisk

Species	Petal size (mm)	Leaf size (mm)	Absolute petal asymmetry (mm)	Absolute leaf asymmetry (mm)	Relative petal asymmetry	Relative leaf asymmetry	n
Albuca cooperi	16.85 (0.20)	–	0.93 (0.05)	–	0.047 (0.003)	–	55
Chasmanthe floribunda	14.11 (0.22)	6.49 (0.18)	0.39 (0.04)	0.92 (0.11)	0.028 (0.003)	0.142 (0.017)	50
Chrysanthemoides monilifera	14.30 (0.28)	8.94 (0.34)	1.42 (0.14)	0.64 (0.14)*	0.107 (0.013)	0.075 (0.015)	50
Cynella orchidiformis	11.67 (0.16)	–	0.38 (0.08)*	–	0.031 (0.005)	–	54
Cyphia volubilis	12.17 (0.19)	8.09 (0.36)	0.25 (0.05)*	0.40 (0.06)*	0.020 (0.004)	0.050 (0.006)	45
Heliophila africana	14.48 (0.22)	6.95 (0.36)	0.70 (0.10)	0.50 (0.10)*	0.048 (0.007)	0.068 (0.010)	37
Lapeirousia arenicola	11.15 (0.14)	–	0.28 (0.03)*	–	0.025 (0.003)	–	57
Lebeckia sericea	9.38 (0.15)	–	0.31 (0.04)	–	0.033 (0.004)	–	51
Microloma calycinum	12.98 (0.34)	–	1.51 (0.10)	–	0.119 (0.008)	–	52
Nemesia versicolor	7.20 (0.13)	–	0.25 (0.03)	–	0.035 (0.004)	–	65
Nemesia sp	11.51 (0.11)	3.70 (0.15)	0.26 (0.03)*	0.23 (0.03)*	0.022 (0.003)	0.064 (0.006)	78
Oxalis purpurea	10.23 (0.21)	11.53 (0.27)	1.25 (0.13)	0.41 (0.04)	0.128 (0.014)	0.038 (0.004)	63
Pelargonium fruticosum	9.74 (0.31)	8.02 (0.38)	0.40 (0.07)	1.14 (0.17)	0.041 (0.006)	0.139 (0.021)	25
Polygala myrtifolia	12.90 (0.15)	6.11 (0.22)	0.40 (0.06)	0.37 (0.04)	0.031 (0.005)	0.064 (0.007)	26
Solanum burchellii	10.35 (0.13)	6.00 (0.24)	0.93 (0.06)	0.54 (0.06)	0.090 (0.006)	0.088 (0.009)	50
Strelitzia reginae	128.40 (1.27)	62.90 (2.73)	3.26 (0.25)	5.00 (0.45)	0.026 (0.002)	0.083 (0.007)	74
Tecomaria capensis	13.96 (0.39)	7.86 (0.34)	0.56 (0.11)	0.55 (0.09)	0.040 (0.008)	0.072 (0.011)	29
Wahlenbergia annularis	15.18 (0.26)	3.05 (0.15)	0.86 (0.09)	0.47 (0.20)*	0.056 (0.005)	0.115 (0.021)	80

TABLE 2 Repeatability of floral and leaf traits on individual plants based on the measurement of two or more flowers or leaves per plant (F-statistic). traits are excluded either because they were not measurable, or because my measurements were not significantly repeatable. Degrees of freedom are from a one-way ANOVA from which repeatability was calculated

Species	Petal size	Leaf size	Petal asymmetry	Leaf asymmetry	Degrees of freedom
Albuca cooperi	0.69 (5.70)***	–	0.15 (1.36)	–	41,45
Chasmanthe floribunda	0.93 (26.05)***	–	0.30 (1.86)*	–	49,50
Chrysanthemoides monilifera	0.37 (2.16)***	0.18 (1.45)	0.19 (1.46)	0.07 (1.16)	49,50
Cynella orchidiformis	0.81 (14.00)***	–	-0.18 (0.53)	–	21,46
Cyphia volubilis	0.57 (4.09)***	0.70 (6.34)***	-0.11 (0.78)	-0.15 (0.70)	14,20
Heliophila africana	0.24 (2.86)***	0.19 (2.32)***	0.15 (2.05)***	-0.01 (0.95)	33,163
Lapeirousia arenicola	0.53 (3.62)***	–	0.11 (1.27)	–	32,43
Lebeckia sericea	0.92 (24.98)***	–	0.16 (1.38)	–	48,49
Microloma calycinum	0.81 (20.20)***	–	0.23 (2.31)*	–	16,48
Nemesia versicolor	0.32 (2.29)*	–	–	–	18,34
Nemesia sp	0.30 (1.96)	0.83 (12.36)***	0.58 (4.02)**	0.23 (1.66)	17,23
Oxalis purpurea	0.06 (1.14)	0.65 (5.46)***	0.13 (0.73)	-0.23 (0.55)	26,37
Pelargonium fruticosum	0.10 (1.47)	0.09 (1.46)	-0.08 (0.63)	-0.01 (0.95)	20,75
Polygala myrtifolia	0.00 (1.46)	0.73 (18.53)***	-0.10 (0.41)	-0.03 (0.79)	12,74
Solanum burchellii	0.49 (5.16)***	0.56 (6.53)***	0.17 (1.90)*	0.06 (1.29)	16,58
Strelitzia reginae	0.64 (5.87)***	0.66 (6.47)	-0.20 (0.53)	0.15 (1.49)	15,26
Tecomaria capensis	0.04 (1.20)	0.07 (1.25)	0.09 (1.43)	0.13 (1.67)	19,71
Wahlenbergia annularis	0.26 (1.77)	0.37 (2.28)	–	0.29 (1.86)	16,20; 7,9a

a. degrees of freedom for petals and leaves respectively.
*P<0.05, **P<0.01, ***P<0.001.

Allometry of asymmetry

The mean Spearman correlation coefficient between absolute asymmetry and mean petal size for species showing floral FA did not differ significantly from zero (mean ± SE = 0.024 ± 0.053, one-sample t-test, $t = 0.45$, d. f. = 11, $P = 0.66$) (Table 3). The correlation was significantly negative in only one of 12 species, *P. purpurea*. A second analysis used the within flower variance in petal size as the measure of flower asymmetry for radially symmetric flowers also showed that the mean correlation was not significantly different from zero (mean ± SE = 0.085 ± 0.050, one-sample t-test, $t = 1.80$, d. f. = 9, $P = 0.11$). The correlation was not significantly negative in any of 10 species, and was significantly positive for *W. annularis*.

The mean correlation coefficient between absolute asymmetry and mean leaf size for species showing FA did not differ significantly from zero (mean ± SE = 0.126 ± 0.102, one-sample $t = 1.25$, $P = 0.26$). The correlation was significantly positive in two species, *S. burchelli* and *S. reginae*. In six of seven species the correlation was more positive for leaves than flowers. However, there was no significant difference between the correlation coefficients of species with both leaves and flowers showing FA (Matched t-test, $t = 1.265$, d. f. = 6, $P = 0.23$) This was also true if the sample size was increased by using all correlations from all species for traits showing FA (two-sample t-test, d.f. = 17, $t = 0.91$, $P = 0.39$) (Table 3).

TABLE 3. Size and asymmetry relationship. Spearman correlation coefficients for the relationship between absolute asymmetry and mean size. One leaf and flower per plant. Only traits showing FA where measurement of absolute asymmetry was significantly repeatable are shown

| Species | Between absolute asymmetry and mean size | | Between leaf and petal asymmetry |
	Petal (Petal[a])	Leaf	
Albuca cooperi	−0.084 (-0.096)	–	–
Chasmanthe floribunda	0.024	0.161	−0.088
Chrysanthemoides monilifera	−0.156	–	–
Heliophila africana	0.164	–	–
Lebeckia sericea	0.229	–	–
Microloma calycinum	0.223 (0.239)	–	–
Oxalis purpurea	−0.337**	−0.179	−0.056
Pelargonium fruticosum	0.228	0.430	0.081
Polygala myrtifolia	0.157	−0.274	−0.058
Solanum burchellii	−0.129 (−0.132)	0.396**	0.194
Strelitzia reginae	−0.08	0.265*	−0.099
Tecomaria capensis	0.053	0.085	−0.003
Wahlenbergia annularis	– (0.224*)		
Mean	0.024 (0.085)	0.126	−0.004
t-test	0.46 (1.80)	1.233	0.103
P-value	0.655 (0.11)	0.264	0.920
n	12 (10)	7	7

*$P<0.05$,**$P<0.01$.
[a]Values in parenthesis are the correlation between within-flower variance in petal size and mean petal size. Summary statistics in parenthesis are for this correlation for radially symmetric flowers and the correlation between absolute asymmetry and mean size for bilaterally symmetric flowers. *Chrysanthemoides monilifera, Heliophila africana* and *Oxalis purpurea* were excluded, because within-flower variance in petal size could not be calculated, as not all petal were measured.

Relationship between leaf and flower asymmetry

If asymmetries accurately reflect the interaction between individual quality and environmental stress, there should be a positive correlation between asymmetry in different traits. However, the mean Spearman correlation between absolute asymmetry in flowers and leaves on individual plants in species showing FA in both did not differ significantly from zero (mean $\pm$ SE = –0.004 $\pm$ 0.04, one-sample *t*-test, $t = 0.095$, d. f. = 6, $P = 0.93$) (Table 3). Correlations between leaf and petal asymmetry on individual plants did not differ significantly from zero in any of the species.

DISCUSSION

Several of the results presented here are in agreement with the findings of Møller & Eriksson (1994): (1) there was greater size variation in leaves than petals; (2) petal and leaf size were often repeatable on individual plants, (3) no significant correlation existed between absolute asymmetry in leaves and flowers on individual plants. A full discussion of the implication of these results can be found in Møller & Eriksson (1994). My results differ slightly in that (1) I documented that absolute asymmetry of flowers (but not leaves) was, on average, significantly repeatable on individual plants; (2) there was only a marginally significant trend for relative asymmetry to be greater in leaves than flowers; (3) Leaf size showed a weak trend towards greater repeatability on individual plants than did flower size.

The most obvious difference between our studies, however, concerned the relationship between trait size and asymmetry. I found no relationship between trait size and absolute asymmetry in flowers. The mean correlation was almost zero using the same method of analysis for radially symmetric flowers as Møller & Eriksson (1994). The mean correlation was even more positive when the correlation between mean size and variance in petal size was used for the radially symmetric species. If the probability of Type II error is set at 0.10, these one-sample *t*-tests should detect samples where Irl $\geq$ 0.18 or Irl $\geq$ 0.19 respectively with a power of 90%. Given the strength of the relationship recorded by Møller & Eriksson (1994) we might reasonably expect mean correlation coefficients of this magnitude. Møller (1995) found that $r^2 = 0.98$ for the regression of petal asymmetry on mean length based on average values from 10 sites for *Epilobium angustifolium*. In contrast to the results presented here, Møller & Eriksson (1994) found negative relationships between size and asymmetry in flowers for 16 of 18 species, nine of which were significant. Using this proportion of species with negative correlations ($P = 0.89$) as the null hypothesis, my results differ significantly (Binomial test, $P < 0.001$). I also found only one species with a significant negative correlation (and one significant positive correlation using variance in petal size as the measure of developmental instability).

In my study there was no relationship between size and asymmetry in leaves. If the probability of Type II error is set at 0.10, this test should detect a sample where the mean Irl $\geq$ 0.39 with a power of 90%. Møller & Eriksson (1994) found a positive relationship between leaf asymmetry and mean size in 15 of 19 species. Using this proportion of species with positive correlations as the null hypothesis, my results did not differ significantly from theirs (Binomial test, $P > 0.20$). Given this, the results of

the two studies can be pooled, in which case the combined evidence does suggest that leaf asymmetry increases with leaf size ($n = 20$ of 26 species).

Finally, there was no significant difference in the correlation between mean size and absolute asymmetry for leave and flowers. For the unpaired t-test comparing the mean correlations for flowers and leaves if one uses the observed variance in the data to estimate the minimum detectable difference between two such samples it is 0.122. Again, this magnitude of difference between flowers and leaves would seem reasonable based on the results of Møller & Eriksson (1994).

Similar conflicting results as to the relationship between size and asymmetry in birds' tails have been reported by Møller & Höglund (1991) and Balmford *et al.* (1993). I can think of three possible explanations why my results differ from those of Møller & Eriksson (1994). First, 15 of the 18 insect-pollinated species studied by Møller & Eriksson (1994) had radially symmetric flowers. In my study, there were six species with bilaterally symmetric flowers showing FA. Five of these six species had positive correlation coefficients, while four of six species with radially symmetric flowers had negative correlation coefficients between absolute asymmetry and mean size. Conclusions may therefore differ when bilateral and radially symmetric flowers are investigated. Second, my study sites may have been in places where there is reduced pollinator selection for floral symmetry. Cape Town and Hermanus are extremely windy. This may make it very difficult for pollinators to assess floral symmetry, thereby reducing selection on flowers for symmetry. It may be worthwhile for plants to invest in flower size even if this is at the expense of increased floral asymmetry. The importance of pollinator preferences for symmetry in determining the allometry of FA could be tested by examining FA in species where pollinators are nocturnal and probably use non-visual cues, for example, bat or moth pollinated flowers (Anonymous reviewer, pers. comm.). In Namaqualand flowering occurs after the first rains in a 'desert bloom'. There may be greater selection for flower production than for flower symmetry because of the limited period over which pollination can occur. In addition, given the extremely high density of plants, there may be little cost to insects of visiting flowers with lower pollinator rewards because of the short inter-plant distances. This explanation is open to future testing by comparing the allometry of symmetry between areas with flowering seasons of varying duration. Third, although Møller & Eriksson (1994) do not mention the method used to measure traits, Møller & Eriksson (1995) used an ocular micrometer. This should lead to considerably more accurate measurements of asymmetry than those from the use of dial callipers which I used in my study.

Condition-dependence and the relationship between size and symmetry

Several workers have argued that condition-dependent ornaments should show a negative relationship between size and asymmetry (Møller & Höglund, 1991; Møller & Pomiankowski, 1993). This argument appears to be based on two points. First, when signals are costly, individuals that are in better condition will be able to invest more heavily in these characters because they pay smaller costs per unit increase in size. This is the basis of the handicap principle (Grafen, 1990). Møller & Pomiankowski (1993) suggest this implies that those "that develop the most extravagant secondary sexual characters suffer less from developmental stress… resulting in a negative correlation of asymmetry with size". Second, they suggest that

there are direct costs to asymmetry, including natural selection against asymmetry (Møller, 1991; Balmford & Thomas, 1992; Balmford *et al.*, 1993) and sexual selection for symmetric traits (Møller, 1992; Swaddle & Cuthill 1994). So high quality individuals should be able to ensure that they produce both larger and more symmetric signals.

I suggest that neither of these factors precludes a condition-dependent trait showing a flat or even positive relationship between size and asymmetry because both the relative costs and benefits of increased size and symmetry must be considered. For example, in a male bird the mating benefits gained from increased investment in tail length through female choice of long-tailed males may outweigh the costs of reduced survivorship arising from flight costs associated with increased asymmetry. For certain functions relating tail length to mating success, high quality males may invest in tail length to the extent that they suffering greater developmental costs than lower quality, small-tailed males, resulting in greater asymmetry for high quality, long-tailed males. This line of reasoning is supported by Grafen (1990) who demonstrated mathematically that at a signalling equilibrium the highest quality males need not possess the greatest survivorship. If the benefits of increased ornamentation compensate for reduced longevity there need not be a positive relationship between male quality, as indicated by tail length, and survivorship. Given that one cost of asymmetry in birds is reduced flight manoeuvrability (Møller 1991) which could lead to reduced survivorship, Grafen's model clearly shows that under certain conditions asymmetry may increase with tail length, even if tail length is an honest signal of male quality.

It may be argued, however, that when female choice (or pollinator preferences) select for both greater signal size and symmetry there should be a positive relationship between the two. That is, high quality males should produce 'better' signals in terms of both the cues of size and symmetry. However, Reynolds (1993) has recently provided experimental evidence to show that sexually selected traits may show negative or positive correlations depending on the interaction between costs and benefits. There is some empirical support for the claim that condition-dependence does not always lead to a negative relationship between size and asymmetry. Brookes & Caithness (1995) found no relationship between total amount of orange coloration and asymmetry in amount of coloration on either side of the body in guppies (*Poecilla reticulata*), although orange coloration is known to be condition-dependent (Kodric-Brown, 1989). In oribi (*Ourebia ourebi*) horn symmetry predicts male harem size (and is therefore likely to indicate male quality), but symmetric horns were not longer than asymmetric ones (Arcese 1994). I suggest that while a negative relationship *is* evidence for condition-dependence, the reverse argument does not hold. Thus the hypothesis that flower size is condition-dependent can not be rejected using data on the allometry of asymmetry.

Repeatability of asymmetry

The absence of a within-plant correlation between leaf and petal asymmetry (as reported here) has been used to suggest that the quality properties reflected by asymmetry in flowers is specific (Møller & Eriksson, 1994). Sakai and Shimamoto (1965) also found no correlation between indices of floral and leaf developmental stability in tobacco plants, while there was a positive correlation between indices of

stability for stamen and pistil length. It has therefore been suggested that different sets of genes control floral and foliage traits (Freeman *et al.*, 1993). However, many studies of FA report no correlation between asymmetry in different traits, even when these traits develop at the same time, and are uninvolved in signalling (Palmer & Strobeck, 1986). It is therefore difficult to assess how important the lack of a correlation between petal and leaf asymmetry really is.

Interestingly, I also found that, absolute flower asymmetry was significantly repeatable on individual plants in three species. This suggest that flower asymmetry may give some indication on the condition of the plant during flower production. If plant condition during flower production (as indicated by floral asymmetry) is also correlated with pollinator rewards then it may pay pollinators to pay attention to variation in floral asymmetry (Møller & Eriksson, 1995). Møller & Eriksson (1994) did not generally find significant within plant repeatability of petal asymmetry. The difference in our results may be attributable to the fact that many of the species I studied only flower for a short period reducing environmental variation experienced during production of flowers on the same plant.

Conclusion

Aspects of flower morphology are selected through pollinator preferences which predominantly effects the flower's male function of distributing pollen (Bell, 1985). Flowers that accurately signal the rewards they offer to pollinators may therefore be at a selective advantage. Features of flowers that have been shown to be important to pollinators include flower size (Bell, 1985), colour (Stanton *et al.*, 1989; Weiss, 1991) and scent. However, not all flowers provide honest signals. For example, sensory traps such as female bee mimicry in orchids provide no benefits for visiting males but are probably maintained because 'cheating' only occurs at a low level (Dawkins & Guilford, 1991).

My study was on species with flowers where measurements of asymmetry were possible, and where deviations from symmetry were most easily detectable (bilaterally symmetric, or radially symmetric with few petals). In many species it would be an almost impossible task for a human to assess asymmetry visually. In general the time costs of assessing symmetry would appear to be greater than those associated with size assessment. Despite these potential inhibiting costs, it has recently been shown that insect pollinators preferentially visit more symmetric flowers (Møller & Eriksson, 1995). This preference may be related to the greater nectar content of more symmetric flowers. A pollinator preference for symmetric flowers may explain my finding that flowers tend to show lower relative asymmetry than leaves. It has been argued that directional selection leads to higher levels of asymmetry due to decreased developmental canalization and selection for new mutants (Møller & Pomiankowski, 1993). One might thus predict that flowers should show higher levels of asymmetry than leaves. However, the natural selection costs of asymmetry in leaves are likely to be low compared to those for non-sexual traits in animals, where asymmetry will often affect locomotion (Thomas, 1993). Thus pollinator selection for symmetric flowers may lead to lower levels of asymmetry in flowers compared to leaves.

Breeding experiments, manipulating environmental conditions and then monitoring flower and leaf size/symmetry and pollinator rewards may help to address the

general importance of symmetry in pollinator-plant interactions. The visual and neurological mechanisms by which insects could preferentially visit symmetric flowers also need urgent attention. Compound eyes generally have far lower resolution than those of humans, and it is unclear whether insects could rapidly detect small floral asymmetries. There is recent evidence from work by Lehrer *et al.* (1995) that bees have an innate preference for symmetric shapes compared to asymmetric ones. However, bees were offered a choice between symmetric and highly asymmetric shapes and this innate preference may not be able to account for preferential visitation when flowers differ by less than 1 mm in symmetry.

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APPENDIX 1

Repeatability of measurements, based on measuring the same flower or leaf twice (*F*-statistic). Degrees of freedom for leaf and petal size are 19.20 (except for *H. africana* for leaf and petal: 39.40). For leaf and petal asymmetry degrees of freedom are 9.10 (except for *P. fruticosum* for petals: 63.64: *H africana* for petal and leaf: 19.20)

Species	Mean petal size	Mean leaf size	Absolute petal asymmetry	Absolute leaf asymmetry
Albuca cooperi	0.99 (3247)***	–	0.85 (12.16)***	–
Chasmanthe floribunda	0.95 (42.1)***	0.98 (93.89)***	0.55 (3.4)*	0.92 (23.7)***
Chrysanthemoides monilifera	0.98 (108.7)***	0.99 (999.9)***	0.91 (21.3)***	0.97 (68.6)***
Cynella orchidiformis	0.96 (49.48)***	–	0.51 (3.09)*	–
Cyphia volubilis	0.99 (773.5)***	0.99 (999.9)***	0.79 (9.5)***	0.97 (69.2)***
Heliophila africana	0.97 (75.0)***	0.99 (602.1)***	0.93 (27.4)***	0.88 (15.9)***
Lapeirousia arenicola	0.99 (670.5)***	–	0.79 (8.92)***	–
Lebeckia sericea	0.98 (83.62)***	–	0.53 (3.25)***	–
Microloma calycinum	0.999 (1682)***	–	0.91 (22.3)***	–
Nemesia versicolor	0.99 (999.9)***	0.99 (296.4)***	0.92 (23.6)***	0.84 (19.7)***
Nemesia sp	0.98 (102.8)***	–	0.40 (2.36) ns	–
Oxalis purpurea	0.98 (86.8)***	0.99 (999.9)***	0.94 (33.6)***	0.62 (4.3)*
Pelargonium fruticosum	0.98 (118.3)***	0.96 (128.3)***	0.29 (1.8)**	0.80 (8.8)**
Polygala myrtifolia	0.99 (227.0)***	0.99 (999.9)***	0.79 (8.6)**	0.84 (11.5)**
Solanum burchellii	0.99 (162.1)***	0.99 (717.4)***	0.75 (7.11)***	0.96 (49.5)***
Strelitzia reginae	0.99 (173.5)***	0.99 (613.5)***	0.90 (19.2)***	0.92 (25.1)***
Tecomaria capensis	0.81 (9.7)***	0.99 (394.1)***	0.89 (17.5)***	0.89 (51.0)***
Wahlenbergia annularis	0.99 (1512)***	0.99 (8.84)***	0 (1.00) ns	0.80 (8.84)***

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

APPENDIX 2

Tests for normality (Lilliefors test) and for a mean of zero (one sample t-test). Probability values are corrected using the sequential Bonferroni correction procedure (independently for normality and mean value tests) so that initial $n = 23$. "Rad" indicates a radially symmetric trait

Species	Normality		Mean of Zero	
	Petal	Leaf	Petal	Leaf
Albuca cooperi	Rad	–	Rad	–
Chasmanthe floribunda	0.09 (0.30)	0.11 (0.12)	1.28 (0.21)	1.87 (0.07)
Chrysanthemoides monilifera	Rad	0.19 (<0.001)*	Rad	0.19 (<0.001)*
Cynella orchidiformis	0.17 (0.001)*	–	2.25 (0.28)	–
Cyphia volubilis	0.24 (<0.001)*	0.13 (0.06)	0.69 (0.49)	3.23 (0.002)*
Heliophila africana	Rad	0.17 (0.009)	Rad	0.99 (0.33)
Lapeirousia arenicola	0.11 (0.12)	–	3.62 (0.001)*	–
Lebeckia sericea	0.11 (0.14)	–	1.06 (0.30)	–
Microloma calycinum	Rad	–	Rad	–
Nemesia versicolor	0.11 (0.04)	–	1.26 (0.21)	–
Nemesia sp	0.53 (<0.001)*	0.13 (0.004)*	1.00 (0.32)	1.78 (0.08)
Oxalis purpurea	Rad	0.08 (0.36)	Rad	1.86 (0.068)
Pelargonium fruticosum	0.11 (0.65)	0.12 (0.45)	1.13 (0.27)	0.11 (0.91)
Polygala myrtifolia	0.08 (1.00)	0.19 (0.014)	0.73 (0.47)	1.08 (0.29)
Solanum burchellii	Rad	0.07 (0.91)	Rad	0.08 (0.93)
Strelitzia reginae	0.10 (0.069)	0.09 (0.19)	2.04 (0.045)	1.37 (0.18)
Tecomaria capensis	0.17 (0.032)	0.13 (0.26)	0.48 (0.63)	0.12 (0.90)
Wahlenbergia annularis	Rad	0.36 (<0.001)*	Rad	0.98 (0.33)

*$P<0.10$ with Sequential Bonferonni (corrected for set of statistical tests, i.e. Lilliefors or *t*-test).