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FLUCTUATING ASYMMETRY AND VARIATION IN THE SIZE OF COURTSHIP FOOD GIFTS IN DECORATED CRICKETS

Fluctuating asymmetry (FA) describes small random deviations from perfect symmetry in any one character of a bilaterally symmetrical organism (Ludwig 1932). An individual's FA in a quantitative character is affected by the environmental stress the individual experiences during its development, as well as the ability of its genome to maintain organized development in the face of this stress (see reviews in Palmer and Strobeck 1986; Parsons 1990; Livshits and Kobylanskiy 1991). An increasing number of studies have attempted to relate FA to mechanisms of sexual selection, particularly the process of mate choice (Markow 1987; Møller 1990, 1992a, 1992b, 1992c; Manning and Hartley 1991; Møller and Höglund 1991; Markow and Ricker 1992; Thornhill 1992a, 1992b, 1992c; Liggett et al. 1993). Because secondary sexual characters often exhibit more variation in FA than other morphological characters (Møller and Höglund 1991; Møller 1992a), such traits could, in theory, be used by females to obtain additional information about their mates' overall genetic quality (Møller 1990, 1992a, 1992b, 1992c; Møller and Höglund 1991; Møller and Pomiankowski 1993).

Species in which males provide material benefits to females at mating appear especially well suited to examining the relationship between FA and mate preference. A male's ability to secure the resources needed for such investments should be related to his overall genetic quality and hence be reflected in his bodily symmetry. In scorpion flies, for example, the ability of males to produce salivary secretions that are used to induce females to mate is negatively correlated with male FA (Thornhill and Sauer 1992). Because female scorpion flies typically select males on the basis of gift quality (Thornhill 1976a, 1981, 1984), such could lead to a bias in favor of males with low FA. Recently, Thornhill (1992b) has also demonstrated that females can select males of low FA based on the pheromones produced by such males.

More commonly, male-produced courtship food gifts involve accessory-gland products that are transferred as adjuncts to ejaculates (Thornhill 1976b; Quinn and Sakaluk 1986; Sakaluk 1986a; Parker and Simmons 1989); the relationship of FA to investment in such gifts has not previously been examined. In the decorated cricket, *Gryllodes sigillatus* (Orthoptera: Gryllidae), males synthesize a two-part spermatophore consisting of a small sperm-containing vessel, the ampulla, surrounded by a larger gelatinous mass, the spermatophylax, that is consumed by the female after mating (Sakaluk 1984, 1987). After copulation, the spermatophore remains outside the female's body, attached to her genital opening. Typically, the female dismounts the male immediately after spermatophore transfer and

removes the spermatophylax, which easily detaches from the ampulla (Sakaluk 1984, 1987). The ampulla remains attached to the female, and its contents are emptied into the female reproductive tract while the female feeds on the spermatophylax. Usually within a few minutes of fully consuming the spermatophylax, the female removes and consumes the ampulla. The size of the spermatophylax is a good predictor of male insemination success, because larger spermatophylaxes take longer to be consumed and lead to longer ampulla attachment durations, which hence allows more sperm to enter the female's spermatheca (Sakaluk 1984, 1985). The amount of sperm transferred is vital to male fitness, because a male's fertilization success, relative to that of a female's other mates, is contingent in part on the numerical abundance of his sperm (Sakaluk 1986b).

The cost to male *G. sigillatus* of synthesizing a more elaborate spermatophore is reflected in male refractory periods that are about an order of magnitude longer than those of species whose spermatophores do not include a spermatophylax (Sakaluk 1985). Given that the synthesis of food gifts is costly, we would predict that the degree of FA in male *G. sigillatus* should be negatively correlated with the size of the spermatophylax, because only the better-adapted males should be able to secure the resources needed to produce the largest food gifts. This would result in a cryptic female preference (Thornhill 1983) of more symmetrical males, because these males would have both the highest insemination and fertilization success. Here we examine the relationship between male FA and investment in courtship food gifts and provide preliminary estimates of the additive genetic variation underlying male FA.

METHODS

Measurements were made on the forewings of males that had been preserved from an earlier study on the heritability of food gift size in *Gryllodes sigillatus* (Sakaluk and Smith 1988). In this study, parental males and females were collected as late-instar nymphs from a field site in southern Arizona, and each male paired for life with a single virgin female. Thirty-one pairs produced offspring, from which 50–60 offspring each were reared in 19-L buckets, repositioned several times a week to avoid systematic errors caused by environmental differences between families. Once adult, individual male offspring were maintained in separate cages under environmental conditions identical to those of their sires.

Males and their spermatophores were weighed using a Mettler H54AR analytical balance accurate to 0.01 mg. Spermatophores were obtained by carefully pulling on the spermatophylax portion visible in the male's spermatophoric pouch (Alexander and Otte 1967); when handled in this manner, the spermatophylax separated easily from the ampulla. Spermatophores were first air-dried for 24 h, then dried to constant weight in a drying oven for 0.5 h at 58°C just before the final weighing.

Parental males were preserved within 24 h of their death in vials containing 70% ethanol. Some of the sires ($n = 10$) were cannibalized by their mates after they had died, which thereby precluded their preservation. In the present study,

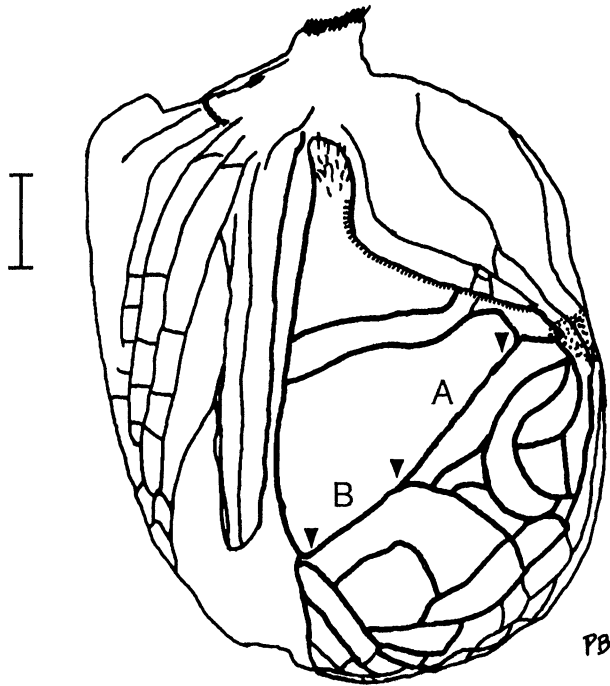


FIG. 1.—Ventral surface of the right tegmen of *Gryllodes sigillatus* showing the location of measurements for fluctuating asymmetry. Scale bar = 1 mm.

measurements were made on the 21 remaining sires and the 183 sons produced by these males. Offspring were killed and preserved 10 d after their adult molt. Although the cuticle of crickets and other insects continues to thicken beyond the adult molt (Zuk 1987), body size is fixed at this time (Chapman 1982) such that the age at which males were preserved is not likely to have had an effect on the size of the characters measured. Body mass, however, can change during an adult's lifetime, but this effect was minimized by measuring male body mass at the same adult age (10 d) in sires and offspring.

From each male, the right and left tegmina were removed, turned ventral side up, and mounted on microscope slides in Hoyer's medium. Measurements were made at $250\times$ magnification using a Wild M5 stereomicroscope equipped with a drawing tube. We measured the distances between the junctions of distinct wing veins for wing measurements A and B (see fig. 1). As an additional measure, we counted the number of file teeth on each tegmen using an Olympus BH-2 microscope with Nomarsky optics. All data were analyzed using the procedures of the Statistical Analysis System for personal computers (SAS 1988).

TABLE 1
ASYMMETRY OF THREE TEGMINAL CHARACTERS IN MALE *GRYLLODES SIGILLATUS*

CHARACTER	GENERATION (<i>n</i>)	ASYMMETRY (RIGHT MINUS LEFT VALUE)			<i>t</i> -TEST	
		Range	Mean	SE	<i>t</i>	<i>P</i>
Number of teeth in stridulatory file	P (21)	-5 to +9	1.05	.82	1.276	.217
	F1 (176)	-19 to +12	-.05	.33	-.156	.876
Wing measure A (mm)	P (21)	-.05 to +.15	.069	.013	5.259	.0001
	F1 (173)	-.50 to +.50	.028	.009	3.216	.0016
Wing measure B (mm)	P (21)	-.10 to +.15	.006	.012	.466	.647
	F1 (179)	-.50 to +.40	.007	.009	.797	.426

NOTE.—Student's *t*-tests were used to detect any deviation from a mean of zero.

RESULTS

Measures of Fluctuating Asymmetry

We first determined whether wing measurements exhibited fluctuating asymmetry according to the criteria of Palmer and Strobeck (1986). The asymmetry in the number of teeth in the stridulatory files, as well as in wing measurement B, fluctuated around a mean of zero, whereas wing measurement A was found to be consistently larger on right wings than on left wings in both parental and filial males (table 1). The asymmetry pattern in wing measure A does not, therefore, fulfill the criteria for fluctuating asymmetry, and this character was omitted from further analyses.

A variety of different measures have been used in the study of FA (Palmer and Strobeck 1986). To find the best measure for a given character, it is necessary to determine whether FA is correlated with character size; if it is, a relative measure of FA should be used. In our sample, the degree of absolute asymmetry in the number of teeth on the stridulatory files was correlated with the size of the character (i.e., the mean number of teeth in a file) in both parental ($r = 0.51$, $P = .018$) and filial males ($r = 0.20$, $P = .007$). Therefore, we used a relative measure of FA (numerical difference between right and left value, divided by the mean character size: $|R - L| \cdot 2/[R + L]$; Palmer and Strobeck 1986) in analyses involving this character. In wing measure B, the degree of asymmetry was not dependent on the mean size of the character (parental: $r = 0.03$, $P = .90$; filial: $r = 0.08$, $P = .27$). Thus we used an absolute measure of FA (the numerical difference between right and left value: $R - L$; Palmer and Strobeck 1986) in analyses involving wing measure B. The relative asymmetry of file tooth number and the absolute asymmetry of wing measure B were not significantly correlated in either generation (sires: $n = 21$, $r = 0.38$, $P = .09$; sons: $n = 176$, $r = 0.01$, $P = .90$).

Additive Genetic Variation of Fluctuating Asymmetry

As a first attempt to measure additive genetic variation in FA, we determined the intrafamily correlation of both wing characters. For the FA of file tooth num-

ber, an ANOVA showed no significant differences between families ($n_{\text{sons}} = 176$, $n_{\text{families}} = 21$, $F = 0.90$, $P = .59$), whereas there were significant differences between families in the FA of wing measure B ($n_{\text{sons}} = 179$, $n_{\text{families}} = 21$, $F = 174$, $P = .032$). The intrafamily correlation for wing measure B was, however, very low, which indicates that other sources of variation influence FA much more strongly than additive genetic variation (r_i , the coefficient of intraclass correlation, was 0.08, which indicates that only 8% of the observed variation was due to differences between families). Having found significant differences between families in the FA of wing measure B, we estimated narrow-sense heritability from a son-on-sire regression ($h^2 = 2 \cdot b$; Falconer 1963). The heritability estimate for the FA of wing measure B, corrected for differences in family size, was not significantly different from zero ($h^2 = -0.0218$; SE = 0.2056, $P = .92$). Thus we conclude that neither wing character exhibits significant additive genetic variation in its FA.

Fluctuating Asymmetry and Spermatophore Size

Spermatophylax mass was correlated with male body mass in both sires ($n = 19$, $r = 0.64$, $P = .003$) and sons ($n = 183$, $r = 0.63$, $P = .0001$), but FA was not significantly correlated with male body mass for either file tooth number (sires: $r = 0.26$, $P = .28$; sons: $r = 0.01$, $P = .89$) or wing measure B (sires: $r = 0.03$, $P = .89$; sons: $r = 0.09$, $P = .25$). Hence, the relationship between FA and spermatophylax size was assessed using a partial correlation analysis, partialing out the influence of male body mass. There was no significant correlation between the mass of the spermatophylax and FA for either file tooth number (sires: $r_{\text{partial}} = 0.03$, $P = .90$; sons: $r_{\text{partial}} = -0.05$, $P = .53$) or wing measure B (sires: $r_{\text{partial}} = 0.23$, $P = .35$; sons: $r_{\text{partial}} = -0.03$, $P = .71$).

DISCUSSION

Fluctuating asymmetry was found in only two of the three characters we measured. The third character, wing measurement A, was consistently larger on the right than on the left tegmen of experimental animals. A directional asymmetry of this sort could indicate an evolutionary retrogression of the left tegmen, which has been described for a number of other cricket species (Masaki et al. 1987). In most cricket species, including *Gryllodes sigillatus*, the right tegmen is folded over the left, so that singing activity involves the plectrum on the left tegmen and the file on the right. However, neither the number of teeth on the stridulatory file nor wing measure B exhibited any directional asymmetry. Thus, if there is any retrogression of the left tegmen, it clearly does not involve these characters.

If FA in morphometric characters is a measure of the genetic quality of an individual or its adaptedness to current environmental conditions, one would expect it to exhibit little additive genetic variation, because selection for individuals with less FA should soon lead to fixation of the best-adapted genotypes (Fisher's fundamental theorem; Fisher 1930; Charlesworth 1987). Indeed, the majority of studies on various insects and vertebrates suggest that there is little or no additive genetic variation in the FA of single morphological characters

(Mason et al. 1967; Livshits and Kobylansky 1991; see also reviews in Palmer and Strobeck 1986; Livshits and Kobylansky 1989; Price et al. 1991); only a single study reported a highly significant heritability for the FA ($h^2 = 0.6$) of a single morphological character (Hagen 1973). Thornhill and Sauer (1992) also reported a very high heritability estimate ($h^2 = 1.1$) for the FA of wing size in a scorpion fly, but their results may have been confounded by a paternal nutritional effect.

Although the absence of significant additive genetic variation in FA in *G. sigillatus* is consistent with previous studies, our experimental design, along with that of many other studies, may not have been optimal for detecting such variation. Although males of the parental generation spent most of their preadult life in a natural environment, their offspring hatched and developed under laboratory conditions. It is likely that there are differences between conditions in the field and the artificial environment experienced in the laboratory, which may be important for the development of males. If FA is a measure of the goodness of fit of an individual's genotype to the current environmental conditions, changing the environment may well obscure additive genetic variation in FA by changing the conditions to which males are adapted.

We found no relationship between the degree of FA and the mass of the spermatophylax synthesized by male *G. sigillatus*. This result contrasts with the only other study of courtship feeding and FA in insects: Thornhill and Sauer (1992) found that field-collected male scorpion flies, unable to secrete a salivary mass as a courtship food gift, had a significantly higher FA than those males which could. What accounts for these conflicting results? If the lab environment in which *Grylloides* offspring were reared substantially diminished the environmental stress to which they were subjected, such would tend to extinguish any correlation between FA and gift size. However, it seems equally possible that other factors, such as increased larval competition resulting from high rearing densities, might actually augment any existing correlation. Moreover, *G. sigillatus* sires spent the majority of their development in the natural environment, yet still failed to show the expected correlation. Within-male variation in the mass of the spermatophylax size might also obscure any relationship between FA and gift size, but our measurements were made on the first or second spermatophores ever produced by males, and previous work has revealed that male *Grylloides* hold constant their investment in spermatophores across successive matings (Sakaluk and Smith 1988).

For most of the observed range in spermatophylax mass, males that produce the largest spermatophylaxes can be considered the best-adapted individuals because such males secure the highest fertilization success (Sakaluk 1984, 1985, 1986b). However, males that invest beyond the minimum spermatophylax mass required to ensure complete sperm transfer may reduce the concordance between gift size and FA in at least two ways. First, if consumption of the spermatophylax has no appreciable effect on female fitness, as appears to be the case in *G. sigillatus* (Will and Sakaluk, in press), males producing overlarge spermatophylaxes may bear a cost in the form of increased intercopulatory intervals and, ultimately, reduced mating opportunities. Second, when the operational sex ratio

is extremely female biased, sperm competition is probably less relevant to a male's reproductive success than his ability to mate frequently; in such a situation, selection may favor smaller food gifts than when the operational sex ratio is male biased. Both of these arguments, however, are predicated on a presumed trade-off between copulation frequency and spermatophore mass; to the best of our knowledge, no such trade-off has been documented for any species.

Finally, it may be that, despite arguments to the contrary (Møller 1990, 1992*a*, 1992*b*, 1992*c*; Møller and Höglund 1991; Thornhill 1992*a*, 1992*b*, 1992*c*; Thornhill and Sauer 1992), FA is not a reliable indicator of current adaptedness. Although a large number of studies have shown correlations of FA with various environmental and genetical factors during development (see reviews in Mitton and Grant 1984; Allendorf and Leary 1986; Palmer and Strobeck 1986; Parsons 1990), the mechanisms that underlie the observed correlations are poorly understood (Palmer and Strobeck 1986; Price et al. 1991; Clarke et al. 1992). One particularly troubling aspect is that many studies appear to find little concordance between FAs of different characters in the same individual (this note; Van Valen 1962; Mason et al. 1967; Markow and Ricker 1992; see also review in Palmer and Strobeck 1986); several authors have therefore questioned the use of FA to assess an individual's developmental stability (Van Valen 1962; Mason et al. 1967; Palmer and Strobeck 1986). Why does the covariance of FA with other fitness measures depend on which morphological characters are used to measure FA? One reason may be that the fitness consequences of bilateral symmetry differ from character to character. We suggest that only those characters whose symmetry, per se, directly influences fitness will be reliable indicators of the overall adaptedness of individuals; in contrast, even the best-adapted individuals may show high FA in characters whose symmetry has no bearing on fitness. Clearly, more basic research on the causes and effects of FA is needed to assess its validity as a fitness correlate and a measure of developmental stability.

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