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Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis

Received: 16 December 1996 / Accepted after revision: 5 May 1997

Abstract Recent theoretical arguments have claimed that negative relationships between the size and symmetry of secondary sexual traits are indicative of honest signalling of male quality. The patterns of fluctuating asymmetry in beetle horns have been proposed to support the honest signalling hypothesis. Here we examine three assumptions of the hypothesis, (1) that traits are costly to produce; (2) the levels of fluctuating asymmetry are indicative of stress imposed during development; and (3) that males with larger traits should have more symmetrical traits, using the horned beetle, *Onthophagus taurus*. Experimental manipulations of brood mass were used to manipulate horn size and asymmetry. The development of horns was found to be environmentally determined and costly in terms of delayed development and increased risk of pre-adult mortality. Decreasing resource availability increased relative horn asymmetry. However, horn height was positively related to absolute horn asymmetry. While the results do support the hypothesis that sexual selection on secondary sexual traits should increase levels of fluctuating asymmetry, they provide no support for the notion that the patterns of asymmetry honestly signal male quality. Horns are used in disputes between males and may be indicative of male parental investment. Thus, we conclude that while horn size may be an indication of male quality, the patterns of fluctuating asymmetry are not.

Key words Fluctuating asymmetry · Beetle horns · *Onthophagus taurus* · Sexual selection · Honest signalling

Introduction

Møller (1993a) argued that strong directional sexual selection should act against genetic modifiers that canalise development, so increasing the levels of developmental instability that are manifest as fluctuating asymmetry (FA). FA is characterised by random deviations from perfect symmetry in bilaterally paired traits (Palmer and Strobeck 1986; Parsons 1990a, b). Thus, sexually selected traits, such as ornaments or weapons, should exhibit higher levels of FA than functional morphological traits such as legs or wings (Møller and Höglund 1991; Møller 1992a; Møller and Pomiankowski 1993). Moreover, since FA is an epigenetic measure of developmental stability, an individual's FA may be indicative of its underlying genetic quality (Møller 1993a). Thus females could use the levels of FA in male secondary sexual traits as an indicator of male quality during mating decisions (Møller 1993b) and males could use the levels of FA in weapons to resolve disputes (Møller 1992a). Møller (1993a) argued that honest signalling of male quality could be maintained where secondary sexual traits are costly to produce. Individuals of high genetic quality should be buffered against the costs of producing elaborate secondary sexual traits, while individuals of low quality should not. Thus, high-quality individuals should be able to produce both large and symmetrical traits while individuals of low quality produce small and asymmetrical traits. Recent analyses of the patterns of fluctuating asymmetry have therefore looked for negative associations between trait size and symmetry that might be indicative of honest signalling. Comparative studies of beetle horns and bird spurs (Møller 1992a), feather ornaments (Møller and Höglund 1991) and primate canine teeth (Manning and Chamberlain 1993) provide support for the hypothesis, while studies of the tails of long-tailed birds (Balmford et al. 1993) and the forceps of earwigs (Tomkins and Simmons 1995) fail to support the hypothesis.

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The problem with comparative studies is that they may be confounded by sampling bias (Swaddle et al. 1994; Simmons et al. 1995). Typically, comparative studies rely on museum collections that can be derived from a variety of different populations. Differences in environmental conditions can cause reductions in both trait size and symmetry so that combined data from different populations may reveal a negative association between trait size and symmetry that is not present within populations (Simmons et al. 1995). In the context of sexual selection, it is the differential ability of individuals within a given environment to maintain trait size and symmetry that is proposed to reliably signal quality. Within population studies of secondary sexual traits have failed to find negative relationships between trait size and symmetry (Oakes and Barnard 1994; Evans et al. 1995; Mateos and Carranza 1996; Møller et al. 1996; Allen and Simmons 1996; Tomkins and Simmons 1996; Hunt 1996).

There are two major assumptions made in comparative analyses of FA and the honest signalling hypothesis. In general, honest signalling models of sexual selection assume that secondary sexual traits are costly to produce, yet there are currently very few empirical demonstrations of the costs associated with trait development (Halliday 1987; Partridge and Endler 1987; Balmford et al. 1993; Arnqvist 1994). Moreover, comparative studies of patterns of FA are correlational only and make the assumption that the levels of FA observed are indicators of the individuals inability to cope with stress imposed during its development. Although stress is known to influence the levels of FA (Parsons 1990b) rarely have the effects of stress on the patterns of FA in sexual and non-sexual traits been compared (Møller 1992b).

In his comparative study, Møller (1992a) found that in general there was a negative relationship between horn height and FA across eight species of horned beetles, including one species of onthophagine, *Onthophagus mnischechi*. However, although we found that horns were more asymmetric than naturally selected morphological traits, we failed to find negative relationships between horn height and asymmetry within *O. taurus* or *Bubas bison* (Hunt and Simmons submitted). Here we report an experimental manipulation of horn height and asymmetry in *O. taurus*, in which we examine both the costs of trait expression and the influence of stress on trait size and patterns of asymmetry.

Methods

Experimental manipulations

One factor that has been shown to increase FA is reduced nutrition during development (Sciulli et al. 1979; Kieser et al. 1986; Parsons 1990a; Nilsson 1994). The brood mass in scarabaeines constitutes both a food source and an external environment for developing larvae. Manipulations of brood mass size have been shown to influence the phenotypic expression of horns in *O. acuminatus* (Emlen 1994a, b). Therefore, by manipulating the brood mass, stress can be

placed on the developing larvae which should result in altered expression of traits and levels of FA.

Five males and five females were randomly placed into 22.5 × 22.5 × 16 cm square containers. The animals in each container were provided with 1 litre of cow dung and permitted to mate for a 10-day period. In order to standardise dung quality across the experiment, all dung samples to be used were fully homogenised before being allocated to containers. Each of the containers was sealed with a single layer of fine nylon meshing and a single layer of black plastic. Both layers were secured with heavy duty elastic bands. After the 10-day mating period the sand in each of the containers was sifted using mechanical sieves (0.5 cm² grid mesh) which enabled the brood masses to be collected.

Brood masses that were produced from these matings had all excess sand removed from their exterior using a dissecting probe and were gently opened to ensure they contained developing larvae. Only brood masses containing newly emerged first instar larvae (> 5 mm in length) were used in experiments to ensure that the majority of their development would occur within the parameters of the experiment. Brood masses containing newly emerged larvae were then weighed and sorted into the following seven weight categories: < 2 g, 2–2.5 g, 2.5–3 g, 3–3.5 g, 3.5–4 g, 4–4.5 g and > 4.5 g. The brood masses were then randomly selected from these categories, reweighed and then manipulated sequentially according to one of four treatments. This ensured an even spread of brood mass sizes were tested within each of the treatments. The first treatment (dung addition) involved adding 1.03 g (1 SD of the mean brood mass of 4.32 g) of dung to the posterior region of the brood mass (i.e. the pole not containing the egg chamber). The flat side of a scalpel blade was used to compress the dung and ensure that it was tightly adhered to the brood mass. Dung used in additions was the same homogeneous mixture that was provided to the mating adults. The second treatment (dung removal) involved cutting 1.03 g of dung from the posterior region of the brood mass using a sharp scalpel blade. In both treatments manipulation was directed at the posterior region of the brood mass since larvae are known to actively feed downwards through this area (Halfiter and Edmonds 1982). The third treatment (manipulated control) tested the likelihood that the physical removal of dung may have added to the stress levels experienced in the removal treatments. It involved an identical procedure to the dung removal treatment except that the removed quantity of dung was then replaced to the site of removal. The final treatment (unmanipulated control) served as a control in which the brood masses were not manipulated. In each of the first two treatments 125 brood masses were processed, while only 88 and 89 brood masses were in the third and fourth treatments, respectively.

Brood balls were then buried in individual sealed 9 × 9 × 7 cm containers filled with moist sand and were maintained in a constant temperature room on a 26 °C (11 h) dark and 29 °C (13 h) light cycle. Containers were placed randomly on vertical shelving and soil moisture level was tested every 2 days. At the end of each week, a few brood masses from each treatment were randomly selected, opened gently and the developmental stage assessed. From the time pupation was first observed containers were checked daily for emerged beetles. The percentage survivorship, and developmental period were noted in each of the treatments. In those cases where the larvae died during development, brood masses were opened at the conclusion of experiments to determine the possible cause of death.

Measurement of FA

All animals were measured on emergence. We determined the height of the left and right sides of the paired head horns of males and the lengths of the left and right elytra of both males and females. Pronotum width was taken as an independent measure of male and female body size. FA was calculated as the left minus right measure of horn height and elytra length. All FA measurements were made twice. Measurement error was estimated for the level of FA in bilateral traits following method 1 of Merilä and Björklund (1995). Measurement error in the signed values of FA

was lowest for horns (horn height 5.9%; male elytra 17.7%; female elytra 20.1%) and there was significantly greater variance between individuals than between repeated measures of the same individual (horns $F = 241.0$; male elytra $F = 234.7$; female elytra $F = 45.7$; all $df 19, 40$, $P < 0.001$). The mean of our two measures of FA were used for subsequent analyses. Traits were accepted as showing true FA; the mean signed asymmetries did not differ from zero (horns $t = 0.423$, $n = 149$, NS; male elytra, $t = -0.701$, $n = 149$, NS; female elytra, $t = -0.129$, $n = 100$, NS) and were not significantly skewed (horns, $g1 = 0.321$, $t = 1.63$, NS; male elytra, $g1 = -0.062$, $t = 0.314$, NS; female elytra, $g1 = 0.017$, $t = 0.070$, NS). Asymmetries were leptokurtic in distribution (horns, $g2 = 3.195$, $t = 8.09$; male elytra, $g2 = 1.316$, $t = 3.333$; female elytra, $g2 = 1.807$, $t = 3.778$; all $P < 0.001$). Leptokurtosis in the adult population is expected to arise through selection operating against asymmetric individuals during the course of development (Naugler and Leech 1994; Ueno 1994). In contrast, skewness or platykurtosis is likely to reflect a developmental bias generating directional and antisymmetry, respectively (Palmer and Strobeck 1986). Unless otherwise stated, all FA data were analysed using non-parametric statistics and values given are corrected for ties in the data (Swaddle et al. 1994). All data not involving FA were analysed using log-transformed data to ensure normality and homoscedasticity (Zar 1984).

Results

Effect of manipulations on development

The weight of experimentally manipulated brood masses differed significantly between the manipulation treatments ($F_{(3,231)} = 214.87$, $P < 0.0001$) (Table 1). Brood mass weight in the dung removal treatment was significantly lower, and brood mass weight in the dung addition treatment was significantly higher, than the controls.

For both males and females, beetles emerging from the dung addition treatment were significantly larger and beetles emerging from the dung removal treatment were significantly smaller than from the controls (males: $F_{(3,107)} = 14.47$; females: $F_{(3,117)} = 16.15$; $P < 0.0001$) (Table 1). Male horn size differed significantly between the treatments ($F_{(3,107)} = 9.86$, $P < 0.0001$) (Table 1). Horn size in the dung addition treatment was signifi-

cantly greater and horn size in the dung removal treatment was significantly smaller than in controls. Across treatments there was a sigmoidal relationship between pronotum width and horn height (Fig. 1). This sigmoidal relationship is characteristic of the genus *Onthophagus* where males exhibit dimorphisms in body plan (Emlen 1996; Hunt 1996); males switch at a critical body size from the minor "hornless" morph to the major "horned" morph. Thus, when dung was added to the brood mass, developing larvae tended to utilise the additional dung and develop into majors, while removing dung restricted larval development so that only minors were produced (see Emlen 1994a for a similar result with *O. acuminatus*).

The developmental period for males differed significantly between the treatments ($F_{(3,107)} = 8.108$, $P < 0.0001$) (Table 1). Males took significantly less time to develop in the dung removal treatment (i.e. emerged

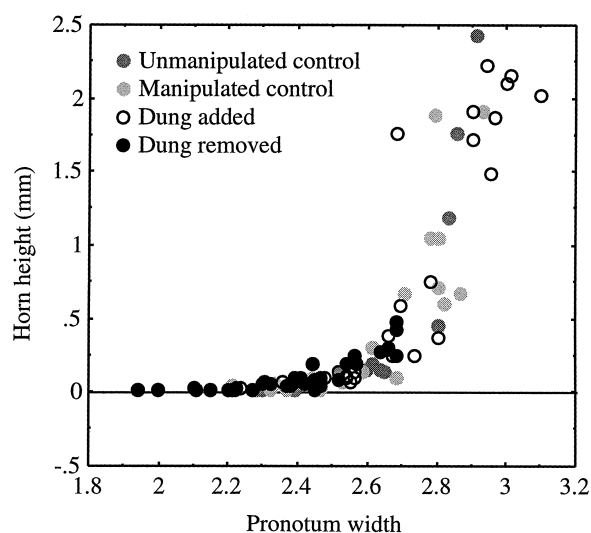


Fig. 1 Relationship between horn height and pronotum width for males emerging from brood masses in the four experimental treatments

Table 1 Morphological and life history parameters of male and female *Onthophagus taurus* emerging from manipulated brood masses. Values are given as mean \pm SE. Different letters indicate significant differences between the treatments at $P < 0.05$ (AFA absolute fluctuating asymmetry)

Parameters	Unmanipulated control	Manipulated control	Dung added	Dung removed
Male				
Pronotum width (mm)	2.57 \pm 0.05 ^b	2.55 \pm 0.05 ^b	2.71 \pm 0.04 ^c	2.38 \pm 0.03 ^a
Horn height (mm)	0.41 \pm 0.14 ^b	0.41 \pm 0.12 ^b	0.82 \pm 0.17 ^c	0.11 \pm 0.02 ^a
Time to emergence (days)	36.6 \pm 0.37 ^b	36.7 \pm 0.33 ^b	37.5 \pm 0.18 ^c	35.6 \pm 0.28 ^a
AFA horns	0.014 \pm 0.005 ^a	0.015 \pm 0.004 ^a	0.029 \pm 0.008 ^a	0.011 \pm 0.003 ^a
AFA elytra	0.003 \pm 0.001 ^a	0.004 \pm 0.001 ^a	0.004 \pm 0.007 ^a	0.008 \pm 0.001 ^b
<i>n</i>	20	24	26	41
Female				
Pronotum width (mm)	2.66 \pm 0.05 ^b	2.65 \pm 0.05 ^b	2.81 \pm 0.04 ^c	2.41 \pm 0.03 ^a
Time to emergence (days)	35.3 \pm 0.59 ^b	35.9 \pm 0.37 ^b	36.6 \pm 0.35 ^b	36.0 \pm 0.29 ^b
AFA elytra	0.005 \pm 0.005 ^a	0.01 \pm 0.005 ^a	0.004 \pm 0.001 ^a	0.008 \pm 0.001 ^a
<i>n</i>	32	29	23	37
Survivorship (%)	58.4	60.2	39.2	62.4
Brood mass weight (g)	2.51 \pm 0.06 ^b	2.44 \pm 0.06 ^b	3.39 \pm 0.07 ^c	1.40 \pm 0.05 ^a

sooner) and significantly longer to develop in the dung addition treatment than in controls. The time taken for females to develop did not differ significantly between the treatments ($F_{(3,117)} = 1.288, P = 0.282$).

There was significant heterogeneity in survival across treatments ($\chi^2 = 16.65, df3, P < 0.001$; Table 1). Larval survivorship was highest in the dung removal treatment and lowest in the dung addition treatment. Observations of brood masses at the conclusion of experiments indicated that the majority of deaths were the result of attack by soil nematodes and that animals in the dung removal treatment were less likely to have been infested than animals in the dung addition treatment (dung removal 19%, dung addition 45%, unmanipulated control 56%, manipulated controls 40%; $\chi^2 = 13.54, df3, P < 0.001$). Where nematode attack was noted it occurred primarily between late pupation and the hardening of the teneral adult's exoskeleton.

Patterns of FA

There were significant positive relationships between absolute FA and horn height, and flat relationships between elytra length and FA, within all four experimental treatments (Table 2). The levels of absolute FA in horns were not significantly influenced by brood mass manipulation ($H_{\text{corr}} = 4.09, n = 111, P = 0.25$). However, to control for the allometric relationships between horn height and FA, levels of horn FA between the treatments were compared using analysis of covariance (Zar 1984). The rate of increase in absolute FA with horn size differed significantly between the treatments

Table 2 Patterns of fluctuating asymmetry (FA) in the horns and elytra of male *O. taurus* and in the elytra of female *O. taurus* within each of the experimental treatments

Treatments	Spearman rank correlation	<i>n</i>
Males		
Dung removal		
Horn height	0.675**	41
Elytra length	-0.005	41
Dung addition		
Horn height	0.558**	25
Elytra length	0.099	25
Unmanipulated control		
Horn height	0.595**	20
Elytra length	0.010	20
Manipulated control		
Horn height	0.789**	24
Elytra length	-0.145	24
Females		
Dung removal	-0.098	37
Dung addition	-0.342	23
Unmanipulated control	-0.248	32
Manipulated control	-0.062	29

** $P < 0.001$

($F_{(3,103)} = 4.417, P < 0.003$) (Table 3). Tukey test revealed that the rate of increase was significantly greater in the dung removal treatment than in controls while the rate of increase did not significantly differ between the dung addition and control treatments. Therefore, for a given increase in horn height, males in the dung removal treatment had relatively greater increases in FA.

The degree of absolute FA in the elytra of males differed significantly between the treatments ($H_{\text{corr}} = 7.885, n = 111, P = 0.048$) (Table 1). Absolute FA in elytra was significantly greater in the dung removal treatment than in all other treatments, while the dung addition and control treatments did not differ. Absolute FA in the elytra of females did not differ between the treatments ($H_{\text{corr}} = 4.981, n = 121, P = 0.173$).

Discussion

Our experimental manipulation of horn expression in *O. taurus* provides empirical evidence of a cost of horn production. Individuals provided with extra dung utilised additional resources to increase both body size and horn height. Thus, horn expression in *O. taurus* has a large environmental component, as demonstrated in *O. acuminatus* by Emlen (1994a). Increased investment in horns had the effect of increasing male developmental period. With the addition of dung, both males and females increased their body size by some 8% compared with controls but it was only males that had an increased developmental period. These data therefore suggest that longer developmental periods are required for the production of larger horns and not for increased body size. Delayed development is likely to increase the risk of pre-adult mortality, especially when there is predation pressure (Meats 1971). We did find decreased survival in our dung addition treatment where males were producing horns. One source of mortality in our experiment was through predation by soil nematodes. We do not know how prevalent nematode infestations are under natural situations, and it may be that the levels of predation in our laboratory cultures were higher than would naturally occur in the field. Nevertheless, our observation that longer developmental periods were associated with elevated levels of nematode predation are of heristic value since they show how the development of horns can incur costs for males that should act against

Table 3 Allometric slopes for $\log(1 + x)$ absolute FA on $\log(1 + x)$ mean horn size within each of the experimental treatments

Treatment	Slope \pm SE	Intercept	<i>n</i>
Dung removal	0.118 \pm 0.018**	-0.001	41
Dung addition	0.051 \pm 0.009**	0.001	26
Unmanipulated control	0.051 \pm 0.007**	-0.001	20
Manipulated control	0.053 \pm 0.004**	-0.000	24

** $P < 0.0001$

horn expression. Arnqvist (1994) similarly showed that development of the notal organ in male water striders, *Gerris odontogaster*, was costly in terms of increased moult duration and a concomitant increased risk of cannibalism. Our data suggest that ontogenetic constraints on the production of complex secondary sexual morphologies may not be restricted to hemimetabolous insects (Arnqvist 1994).

Our manipulations also affected the levels of FA in the predicted direction; limiting the availability of resources during development had the effect of increasing absolute FA in the elytra of males and increasing relative FA in horn height. Female FA was unaffected by brood mass manipulation. While not strong, these effects support the notion that levels of FA can be indicative of developmental instability arising from stress experienced during ontogeny (Parsons 1990b; Møller 1993a). However, the patterns of FA fail to support the honest signalling hypothesis. We found that across treatments there was a general tendency for the addition of resources to result in an increase in the levels of absolute FA in horn height. Within treatments there were strong positive, rather than negative relationships between horn height and FA. Thus, increased investment in horn expression appears to result in elevated levels of FA, a pattern also seen in field collected samples (Hunt 1996). The positive relationship between horn height and FA lends further support to the notion that horns are costly to produce, since males that invest in horn production exhibit greater developmental instability. Under the honest signalling hypothesis for FA, those individuals that produce larger traits are proposed to be of superior quality so that they also produce more symmetrical traits (Møller 1993a; Møller and Pomiankowski 1993). Clearly our results directly contradict this prediction and do not support the comparative analysis of beetle horns by Møller (1992a).

We conclude that the patterns of FA in the horns of *O. taurus*, are not indicative of male quality. Nevertheless, horns do appear to be subject to strong sexual selection, given the obvious costs entailed in their production, the strong positive relationship between horn height and FA, and the fact that they exhibit greater levels of FA than other morphological traits (Møller 1992a; Hunt 1996). For both *O. acuminatus* and *O. taurus*, larger males are able to produce relatively longer horns (Emlen 1994a; Hunt 1996; this study) suggesting that horn size is an indication of male quality. The horns of beetles have been shown to confer a selective advantage on males when competing over access to females (Eberhard 1979, 1982; Otte and Stayman 1979; Brown et al. 1985; Brown and Bartalon 1986). In *O. acuminatus*, males with larger horns have a competitive advantage over males with smaller horns (Emlen 1994b). Females may also use horns as arbitrary signals of male intention to invest parentally. The morphological dimorphisms in male Onthophaginae are associated with behavioral differences between males in terms of their contributions to brood ball production; in both

O. binodis and *O. taurus*, horned males help females provision brood masses while hornless males do not (Cook 1988; Cook 1990; Hunt 1996; see also Halfter and Edmonds 1982). Females obtain direct benefits from mating with horned males because male brood ball provisioning increases female fecundity (Cook 1988). An integral part of courtship behavior in the horned males of *O. binodis* is an “upward jerk” of the head and pronotum during which the horn would be displayed to the female (Cook 1990). This display is performed while head on to the female and is utilised less frequently by hornless males (Cook 1990). Grafen (1990) showed how costly male ornaments and female preferences for them could evolve so that the intensity of female preference increases directly with ornament size as a result of fecundity benefits (see also Heywood 1989; Hoelzer 1989; Price et al. 1993). Thus, horn size may be a signal of male quality that can be used by males for resolving aggressive interactions and females during mating decisions.

Acknowledgements We thank David Cook, Ian Dadour for advice and practical support in rearing beetles, and Douglas Emlen and Dale Roberts for comments on the manuscript in an earlier form. L.W.S was supported by an Australian Research Council Senior Research Fellowship.

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Communicated by P. Pamilo