THE ROYAL SOCIETY

Fluctuating paradigm

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A prominent paradigm in evolutionary biology over the last ten years has been the role of fluctuating asymmetry in sexual selection. Fluctuating asymmetry in bilaterally paired traits, and in particular sexual traits, has been proposed to be a reliable indicator of individual quality and the focus of selection through sexual competition and attractiveness. We surveyed the literature on fluctuating asymmetry and sexual selection and found a marked chronological decline in the proportion of studies supporting the paradigm through the 1990s. Our data are supported by an independent meta-analysis of the literature. The data conform with the notion of a scientific revolution in which the early phase of a paradigm change is characterized by a publication bias, a less critical approach to research, or both. The patterns we observe in the fluctuating asymmetry literature suggest caution in drawing general conclusions from meta-analyses conducted before revolutions have settled.

Keywords: fluctuating asymmetry; paradigm shift; scientific revolutions

1. INTRODUCTION

Scientific research generally follows a steady progression during which empirical evidence is gathered to evaluate current theoretical ideas. From time to time, scientific disciplines experience what Kuhn (1970) described as revolutions, when new paradigms are raised that promise to explain phenomena that have long appeared paradoxical. One recently advanced paradigm in evolutionary biology is the role of fluctuating asymmetry in sexual selection (Ridley 1992). Fluctuating asymmetry is proposed to reflect the underlying developmental stability of an organism and thus provide a reliable indicator of genetic quality (Møller 1993; Møller & Pomiankowski 1993). Levels of fluctuating asymmetry are proposed to be exaggerated in secondary sexual traits; males of high genetic quality are thought to produce large and symmetrical secondary sexual traits that increase competitive success and provide females with reliable indicators of potential indirect benefits of mate choice.

A role for fluctuating asymmetry in sexual selection was first proposed in 1990 (Møller 1990) and has since become increasingly controversial (Hoekstra 1997). Here we provide quantitative evidence from studies of the role of fluctuating asymmetry in sexual selection that conform with Kuhn's notions of scientific revolutions. More importantly, our observations send a general warning to the scientific community concerning the way in which we respond to current and popular ideas.

2. METHODS

We examined all studies of sexual selection in relation to fluctuating asymmetry in sexual and non-sexual traits, published since 1990. Support for the fluctuating asymmetry paradigm was recognized if asymmetrical males were unsuccessful in competition and/or were unsuccessful in acquiring mates, or if sexual traits could signal male quality via a negative relationship between trait size and asymmetry. Human faces were treated as sexual traits because they are attractive to members of the opposite sex. To avoid any possible subjectivity, we included all studies of asymmetry and sexual selection in our analysis. We also noted whether studies had examined the repeatability of measured asymmetries. Fluctuating asymmetry has statistical properties identical to measurement error; both are normally distributed about a mean of zero. Thus, it is essential to show that the variance in asymmetry observed between individuals is greater than the variance due to measurement error, and, ideally, to partition out measurement error in comparisons between groups of individuals identified as successful and unsuccessful in reproductive competition (Merilä & Björklund 1995). All studies that have examined natural variation in asymmetry were classified as appropriately using repeatability analysis on the conservative basis of confirming significantly greater between-subject than within-subject variance in measured asymmetry. Repeatability analysis is not necessary for experimental manipulations of asymmetry. A complete list of studies and their categorization can be found in electronic Appendix A at www.pubs.royalsoc.ac.uk/publish/pro_bs/rpb1419.htm.

In analysing multiple data sets there is a risk of pseudoreplication. If, for example, one species is studied several different times with the same outcome, it could weight the result in a given direction. We chose studies as our unit of analysis because we were concerned with how the results of studies of fluctuating asymmetry have changed with time. We conducted logistic regression analysis, scoring studies as supporting or not supporting the paradigm and examining the effect of year of publication. Multiple studies of the same species that were published in the same year were entered as a single datum. There are no cases in which the outcomes of such studies differed. Multiple studies of the same species were considered independent if they were performed in different years, because we were interested in whether support for the hypothesis changed across years.

Received 4 December 1998 *Accepted* 16 December 1998

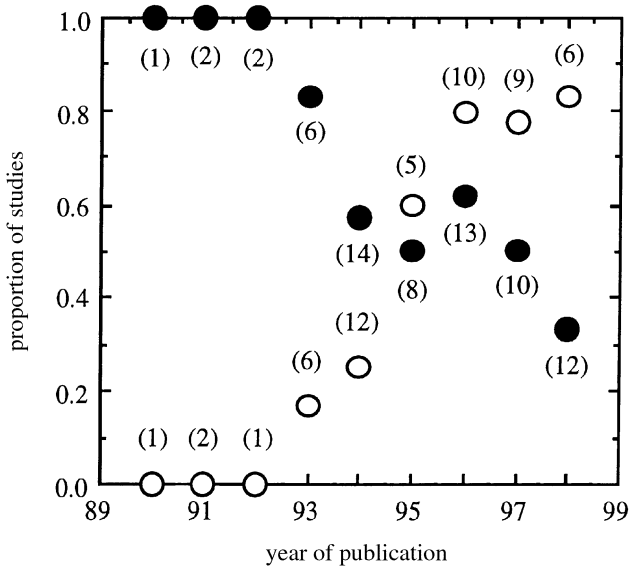

Figure 1. Proportion of studies of fluctuating asymmetry in secondary sexual traits that support its role in sexual selection (solid symbols), plotted against the year of publication. Numbers of studies are given in parentheses. The proportion of studies in which repeatability analysis was performed where necessary are plotted as open symbols. A complete list of references and their categorization can be found in electronic Appendix A.

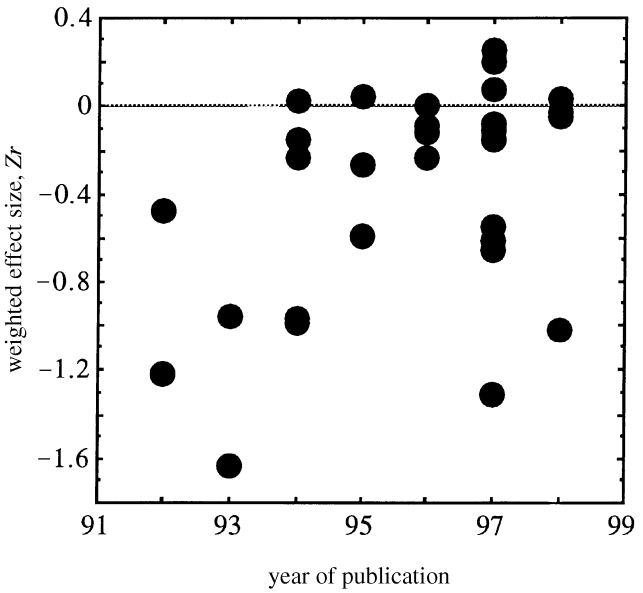

Figure 2. Weighted effect sizes for studies of fluctuating asymmetry in secondary sexual traits and sexual selection, plotted against year of publication. A negative effect size occurs when fluctuating asymmetry in sexual traits reduce male reproductive success (data calculated from table 1 of Møller & Thornhill (1998)). There is a continuing shift towards zero effect with year of publication.

3. RESULTS AND DISCUSSION

We found a pronounced change in the fluctuating asymmetry data since 1990 (figure 1). The proportion of studies supporting a role of fluctuating asymmetry in sexual selection has declined steadily from 100% in the early 1990s to its current value of 36%. The negative relation is most prominent in sexual traits (log-likelihood $=84.86$, $\chi^2=6.21$, 1 d.f., $p=0.013$, $b=-0.34\pm0.1$) but is also present in non-sexual traits (log-likelihood $=32.01$, $\chi^2=2.61$, 1 d.f., $p=0.106$, $b=-0.37\pm0.24$). A recent meta-analysis (Møller & Thornhill 1998) reported a significant general effect of fluctuating asymmetry on sexual selection. We used the methods of Møller & Thornhill (1998) to calculate the weighted effect size with studies as units of analysis (Zr) from their tabulated effect sizes (r) (table 1 in Møller & Thornhill (1998)). We included only those studies included by Møller & Thornhill, and assigned unpublished studies to the year 1998. In their study, there was a significant positive relation between effect size and year of publication for sexual traits ($F_{1,32}=7.20$, $p=0.012$) but not for non-sexual traits ($F_{1,30}=0.24$, $p=0.63$); the median weighted effect size for sexual traits decreased from -0.691 in 1992, to -0.128 in 1997 (the negative sign reflects the negative effect fluctuating asymmetry has on reproductive success; see figure 2). Thus, independent meta-analysis supports our observation in figure 1.

Kuhn (1970) noted that after a paradigm shift there is an increasing professionalization when normal science leads to precision in observation and theory, through the development of skills and concepts specific to the paradigm. Our survey revealed a change in practice in fluctuating asymmetry studies; an increasing proportion of studies used repeatability analyses that correctly distinguish true fluctuating asymmetry from measurement error (Palmer 1994; Swaddle *et al.* 1994; Björklund & Merilä 1997) (for sexual traits, log likelihood $=52.74$, $\chi^2=20.71$, 1 d.f., $p=0.000$, $b=0.82\pm0.23$, figure 1; for non-sexual traits, log-likelihood $=28.72$, $\chi^2=4.93$, 1 d.f., $p=0.026$, $b=0.53\pm0.26$). Moreover, studies using repeatability analyses are less likely to support a role of fluctuating asymmetry in sexual selection; for sexual traits, 19 out of 25 studies without repeatability support the paradigm compared with 11 out of 28 studies with repeatability (Fisher's exact test, $p=0.012$). The corresponding figures for non-sexual traits are 11 out of 15 and 6 out of 16 ($p=0.073$).

Recent studies of the heritability of secondary sexual traits suggest that research in this related area is also in the early phase of a Kuhnian revolution, in which current popular ideas are seized upon with less critical examination (Alatalo *et al.* 1997). Following the publication of theoretical models that suggest ways in which genetic variance in fitness traits can be maintained, estimates of the heritability of such traits have increased in magnitude, while sample sizes have decreased. Tregenza & Wedell (1997) suggest that one factor contributing to this chronological change could be taxonomic bias; increasing numbers of heritability studies are being performed on birds where large sample sizes are difficult to obtain. We examined the distribution of fluctuating asymmetry studies involving insects, mammals, birds, fish or lizards, and flowers, across year of publication and found no significant heterogeneity ($\chi^2=38.08$, 1 d.f., $p=0.21$) that could explain the trends observed in figures 1 and 2.

Our analyses, and those of Alatalo *et al.* (1997) provide quantitative evidence of the need for publishing decisions

to be based on appropriateness of study methods and statistical analyses rather than rejection of the null hypothesis. Furthermore, they raise the issue of how we evaluate scientific literature. Meta-analysis is a useful tool to examine the generality of biological phenomena (Arnqvist & Wooster 1995). However, given the trends observed in the fluctuating asymmetry literature, care must be taken in choosing which studies are included in analyses. Perhaps more importantly, analyses aimed at assessing the generality of recently advanced paradigms should wait until revolutions have settled (e.g. see Hamilton & Poulin 1997). The chronological changes that we and Alatalo *et al*. (1997) observe, show how our evaluation of the scientific literature can be biased by the initial enthusiasm for new ideas. Our aim here is not to claim that fluctuating asymmetry has no role to play in sexual selection, although our analysis does question its generality. If scientific revolutions arise in response to an accumulation of anomalies (Kuhn 1970), we should expect yet another paradigm shift in the study of sexual selection.

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An electronic appendix to this paper appears at www.pubs.royalsoc.ac.uk/publish/pro_bs/rpb1419.htm