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SYNTHESIS

The Developmental Instability—Sexual Selection Hypothesis: A General Evaluation and Case Study

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Abstract Developmental instability results from small, random perturbations to developmental processes of individual traits. Phenotypic outcomes of developmental instability include fluctuating asymmetry (FA, subtle deviations from perfect bilateral symmetry) and phenodeviance (minor morphological abnormalities). A great deal of research over the past 18 years has focused on the role of developmental instability in sexual selection. A driving force behind this research has been the developmental instability-sexual selection hypothesis, which posits that symmetry and lack of phenodeviance in secondary sexual traits are assessed by mates and rivals because they provide a reliable cue of individual genetic quality. The present article tests this hypothesis by evaluating its five main predictions using published results: expressions of developmental instability in secondary sexual traits should be (1) negatively correlated with mating success; (2) directly assessed by mates and sexual rivals; (3) heritable; (4) condition-dependent; and (5) negatively correlated with ornament size. The first two predictions receive considerable, though not ubiquitous, support from a range of animal species. However, FA in secondary sexual traits is generally not significantly heritable, indicating that FA is unlikely to reveal genetic quality that can be transmitted to offspring. Similarly, there is little evidence to support the predictions that FA is condition dependent, and that it is negatively phenotypically or genetically correlated with sexual trait size. Based on an evaluation of the evidence overall, it is concluded that this hypothesis is unlikely to be viable; it appears unlikely that mate choice for symmetry evolves by "good genes" sexual selection. Hypotheses that do not require asymmetry and phenodeviance to reveal heritable genetic quality may explain observed links between FA/phenodeviance and mating success. Results of a case study of *Drosophila bipectinata* are summarized, which reinforce this general conclusion. It is suggested that non-additive genetic variation arising from an interaction between trait-specific developmental genes and genetic background may drive sexual selection for reducing developmental instability in some cases. Levels of developmental instability variation in a population may need to surpass a critical threshold for sexual selection to operate, possibly explaining some of the pronounced heterogeneity in the effect of developmental instability on sexual selection reported in the literature.

Keywords Developmental instability · *Drosophila bipectinata* · Fluctuating asymmetry · Genetic quality · Mate choice · Mate competition · Phenodeviance · Sexual selection

Introduction

Developmental instability results from small, random perturbations to the developmental trajectory of individual traits (Waddington 1957). These perturbations, which arise from the stochastic nature of molecular and cellular processes (McAdams and Arkin 1999; Klingenberg 2003), compromise developmental precision. Thus, developmental instability may be understood as the outcome of an organism's failure to execute a developmental program (i.e., to achieve its "target phenotype", *sensu* Nijhout and Davidowitz 2003) prescribed by its particular genotype under a defined set of environmental conditions (Waddington 1957; Zakharov 1992; Willmore and Hallgrímsson 2005).

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Both fluctuating asymmetry (FA, subtle deviations from perfect symmetry in bilaterally symmetrical traits) and phenodeviance (minor morphological abnormalities) are phenotypic outcomes of developmental instability (for a more detailed explication of these measures, see the next section). A core idea of developmental instability studies is that these outcomes cannot readily be compensated post-developmentally, so that they provide indices, albeit imprecise ones, of how well an organism was able to cope with its developmental environment. As a consequence, symmetry and lack of phenodeviance are expected to reflect the ability of an organism to express high fitness in its particular environment (Møller 1990; Polak and Trivers 1994; Watson and Thornhill 1994). This expectation has generated a great deal of interest in the role of developmental instability in sexual selection because it suggested that symmetry might provide a cue of overall health and vigor in social interactions (Møller 1990; Ridley 1992; Møller and Pomiankowski 1993; Polak and Trivers 1994; Watson and Thornhill 1994; Polak 1997b; Møller and Thornhill 1998; Tomkins and Kotiaho 2001; Tomkins and Simmons 2003).

Borgia (1985) showed in the satin bower bird, *Ptilonorhynchus violaceus*, that symmetrical bowers were more attractive to females than asymmetrical bowers, and Markow (1987) first linked morphological symmetry to mating success: male *Drosophila melanogaster* mating in the laboratory were reported to be more symmetrical in sternopleural bristle number than single males. Møller (1990, 1992a) and Møller and Pomiankowski (1993) formulated a general and provocative hypothesis for the role of developmental instability in sexual selection built on the proposition that asymmetry reveals individual genetic quality, which ignited a great deal of research (Møller and Thornhill 1998; Tomkins and Simmons 2003; Van Dongen 2006). This hypothesis is evaluated here.

The developmental instability-sexual selection hypothesis states that individuals use FA and phenodeviance in secondary sexual traits as cues of the relative genetic quality of potential mates and sexual rivals. Thus, both intra- and intersexual competition are components of this hypothesis. In mate choice a preference for symmetry evolves as a function of indirect benefits females receive in the form of genetic factors that enhance offspring fitness (viability). Therefore, the developmental instability-sexual selection hypothesis as it relates to intersexual selection is a "good genes" argument (Andersson 1994; Kokko et al. 2006). In the context of intrasexual selection, assessment of developmental instability in weapons and status badges occurs because well-formed and symmetrical structures reveal superior body condition, vigor, overall health, and thus, effectiveness in combat. Assessment of developmental instability in the traits of rivals evolves because assessment reduces the costs of conflict by helping to settle disputes prior to potentially costly, escalated fighting (Møller and Pomiankowski 1993). Asymmetry and phenodeviance may also inflict a purely mechanical disadvantage in sexual competition, but this class of mechanisms does not require assessment of quality by conspecifics, and it is not further addressed here.

I first describe the phenotypic manifestations of developmental instability, FA and phenodeviance, the would-be targets of sexual selection. I then provide an overview and evaluation of this developmental instability-sexual selection hypothesis focusing on animals. To this end, I elaborate on each of five predictions of this hypothesis, and summarize the essential evidence for each, making use of key quantitative reviews of the literature that have recently been published. Although the five predictions I evaluate are not an exhaustive list of all the elements of the hypothesis the reader might encounter in the literature, this list does nevertheless contain the crucial predictions that have received the most attention. From consideration of our current state of knowledge in these five areas, I draw a general conclusion about the viability of the developmental instability-sexual selection hypothesis.

Finally, I summarize our own work with *Drosophila bipectinata* as it relates to the developmental instability-sexual selection hypothesis (Polak et al. 2004; Polak and Starmer 2005; Polak and Taylor 2007). Our field and laboratory studies of mainland and island populations have discovered pronounced variation in the strength of sexual selection for reducing developmental instability in a secondary sexual trait, the male sex comb, and they provide an opportunity for a relatively comprehensive test of the developmental instability-sexual selection hypothesis within a single species.

Measures of Developmental Instability

Fluctuating Asymmetry

At the level of the individual, several measures of developmental instability are recognized (Zakharov 1992; Graham et al. 1993). By far the most common measure is fluctuating asymmetry (FA), the subtle deviations from perfect symmetry in otherwise symmetrical bilateral traits (Ludwig 1932; Van Valen 1962). Barring somatic mutation and recombination, both components of a bilaterally symmetrical trait share an identical genetic background, so that departure from perfect symmetry is seen as a product of developmental instability. Asymmetry in a given trait is calculated as the difference between the value of the trait on the right side of the body minus that on the left (Van Valen 1962; Palmer and Strobeck 1986). FA is distinguished from other forms of bilateral asymmetry, namely directional asymmetry and antisymmetry, by the position and shape of the frequency distribution of signed right-minus-left trait values in a sample of individuals. It is appropriate to refer to a trait as exhibiting FA if the mean of this distribution is not significantly different from zero, and if the shape of the distribution is either normal or leptokurtotic (Van Dongen 2006). In contrast, directional asymmetry refers to the case where the mean of signed differences differs significantly from zero, and antisymmetry when the mean is zero but the distribution tends significantly toward platykurtosis or bimodality (Palmer and Strobeck 1986).

Fluctuating asymmetry values across traits within individuals may be combined to obtain a composite FA index, thus arguably yielding a more sensitive measure of individual developmental instability, and of individual quality (Leung et al. 2000; Gangestad et al. 2001). Such an approach to gauging quality assumes the existence of a genome-wide (global) buffering capacity (i.e., a hypothetical mechanism(s) that would modulate developmental noise throughout the organism and across developmental stages) (Gangestad and Thornhill 2003). Recent thinking suggests that organism-wide buffering may loosely be a product of the genes contributing to general health and body condition (Mitton 1993a; Thornhill and Gangestad 1999; Polak et al. 2003; Rhodes and Simmons 2007).

Developmental *stability*, on the other hand, is the result of corrective mechanisms that dampen the effects of perturbations on the development of a phenotype (Waddington 1957; Zakharov 1992); developmental instability and developmental stability, therefore, are flip sides of the same coin (Klingenberg 2003). Importantly, the existence of mechanisms that buffer development are emphasized in the definition of developmental stability (Waddington 1957; Klingenberg 2003; Hamdoun and Epel 2007; Willmore et al. 2007), permitting the existence of heritable variation for developmental stability, the fuel of evolution by natural selection. Some traits vary predictably in their degree of buffering. For example, functional traits exhibit reduced FA compared to less functional traits (e.g., wings of migratory versus nonmigratory birds, Balmford et al. 1993; and see Møller and Höglund 1991, Fenster and Galloway 1997), so we can conclude that selection has favored developmental stability more strongly in some traits than others, producing the variation in trait-specific buffering that we see today. Such patterns force the conclusion that developmental stability, and hence developmental instability, possess evolutionary potential.

Phenodeviance

Developmental instability is also measured as the incidence of phenodeviance, defined as minor phenotypic abnormalities in a particular trait occurring at low frequency in the population (Rasmuson 1960; Zakharov 1992; Jones 2006). Lerner (1954) coined the term “phenodeviant”, and understood morphological abnormalities as arising from properties of the genome, although environmental stresses on the developing organism are likewise recognized to induce abnormalities diagnostic of developmental instability (Hoyme 1993). West-Eberhard (2003) refers to developmental abnormalities as “low-frequency discrete phenotypes”, and attributes significant evolutionary potential to them (and see Rutherford and Lindquist 1998). Fenster and Galloway (1997) describe how the “release” of variation as phenodeviants because of breakdown of developmental stability might facilitate a population shift to a higher adaptive peak.

Although most populations contain a variety of minor morphological abnormalities, by definition, such abnormalities occur at low frequency in the population, and so typically will be less sensitive and empirically useful than FA (which is ubiquitous) as a measure of developmental instability (Zakharov 1992; Møller and Swaddle 1997). Major aberrations indeed often are extremely rare, such as the grotesque head anomalies occurring at a frequency of 0.02% among males of the anvil-headed fly *Zygothrica dispar* (Grimaldi 1987). Jones (2006) notes that a defining feature of minor abnormalities is that they occur at a frequency of 4% or less in the general population, although this figure may rise considerably in natural or captive populations experiencing genetic or environmental stresses (Leary et al. 1984; Ribnik and Hoyme 1989). For example, goldfish (*Carassius auratus*) collected from a polluted pond in the Ukraine had an 11% rate of phenodeviance (as jaw abnormalities) compared to 0% in a sample from a nearby unpolluted site (Graham et al. 1993).

If phenodeviance reflects developmental instability, then phenodeviant categories should exhibit relatively higher average FA compared to nonphenodeviant categories. Leary et al. (1984) compared FA levels between trout with and without morphological abnormalities. As predicted, the frequency of asymmetric characters was significantly lower in trout without deformities compared to trout with one abnormality or multiple abnormalities. Similar results are reported for dental asymmetry and morphological abnormalities in humans (Bailit et al. 1970), and for sex comb traits in *Drosophila bipectinata* (Polak and Taylor 2007).

Phenodeviance has been deployed very rarely in studies of sexual selection (e.g., Møller 1993a); only one recent study has revealed a role for phenodeviance, demonstrably linked to developmental instability, in sexual selection (Polak and Taylor 2007; and see *A case study*, below). More emphasis should be placed on phenodeviance in sexual selection studies, to expedite tests of the role of developmental instability in sexual selection, and to help validate the use of FA as an index of developmental instability. The degree to which FA reliably reflects developmental instability is still debated in part because the relative importance of environmental and post-developmental (e.g., behavioral lateralization) as sources of FA variation is poorly understood (Nijhout and Davidowitz 2003; Van Dongen 2006).

The Developmental Instability-Sexual Selection Hypothesis

The developmental instability-sexual selection hypothesis makes at least five testable predictions. Expressions of developmental instability in secondary sexual traits should be (1) negatively correlated with mating success; (2) directly assessed by mates and sexual rivals; (3) heritable; (4) condition-dependent; and (5) negatively correlated with ornament size. Each prediction is evaluated in turn below.

Developmental Instability Should be Negatively Correlated with Mating Success

If developmental instability is important for sexual selection by mediating either mate selection or intrasexual competition, differences in FA and phenodeviance among individuals should be negatively correlated with measures of reproductive success. Testing for such correlations is a commonplace endeavor in the field (Møller and Thornhill 1998; Tomkins and Simmons 2003), and indeed, may be an only recourse to researchers when manipulative experiments are impractical.

However, uncovering a negative correlation between developmental instability and any one or more estimates of reproductive success does not in itself demonstrate that developmental instability is the target of sexual selection (Swaddle 2003). This is because a correlation between developmental instability and reproductive success may arise incidentally as a consequence of a variety of underlying "third party" mechanisms. For example, FA and phenodeviance may become negatively associated with components of reproductive success as an incidental outcome of unstable individuals being of poor overall health, itself causing them to be smaller and less vigorous in courtship and physical contests, or less able to produce high-quality ejaculates. Links to underlying health parameters are likely to explain why mating success correlates with "cryptic" FA or phenodeviance, cryptic in the sense that they are unobservable by mates and competitors, occurring in traits such as sternopleural bristles in *Drosophila* or finger ridge patterns in humans. Markow and Gottesman (1993) suggest that cryptic FA in human finger ridge counts may predict sexual performance because finger asymmetry reveals developmental instability in the central nervous system (CNS). Such linkage may explain why cryptic FAs across a range of body traits predict complex behavioral phenotypes, such as dancing ability (Brown et al. 2005). Martin and López (2000) found asymmetry in pheromone producing structures (femoral pores) in rock lizards, *Lacerta monticola*, and showed that females preferentially associated with males with low FA in femoral pores. The proportion of some chemical compounds varies with both pore number and FA (López et al. 2006), suggesting that the preference for low FA males is mediated by olfactory cues of relative health.

When developmental instability increases with loss of heterozygosity, which has been documented in some studies but which is not a general phenomenon (Vøllestad et al. 1999; Alibert and Auffray 2003), individuals with high developmental instability may suffer reduced mating success because of compromised physiological efficiency (Mitton 1993b), or because of elevated homozygosity in the genome overall or at specific sets of loci involved, for example, in immune function (Thornhill and Møller 1997; Charlesworth and Charlesworth 1999). Genetic pleiotropy may also be a cause of incidental associations (McKenzie and O'Farrell 1993). In humans, finger FA and various measures of ejaculate quality, including sperm number and sperm swimming speed, are negatively correlated perhaps as a result of pleiotropic effects of specific *Hox* genes (Manning et al. 1998).

Negative associations have been found between FA and a range of correlates of reproductive success, including sexual attractiveness (Møller 1992a; Thornhill 1992a; Gong and Gibson 1996; Sheridan and Pomiankowski 1997; Simmons et al. 2004; Brown et al. 2005), female reproductive rate (Forkman and Corr 1996), competitive ability (Thornhill 1992b; Møller and Zamora-Muñoz 1997; Bateman 2000), copulation probability and/or rate (Møller and Zamora-Muñoz 1997; Carchini et al. 2000; Santos 2001; Cooley 2004; Koshio et al. 2007), mating speed (Radesäter and Halldórsdóttir 1993; Polak and Stillabower 2004), ejaculate quality (Manning et al. 1998; Roldan et al. 1998; Farmer and Barnard 2000; Gomendio et al. 2000; Firman et al. 2003), competitive fertilization success (Otronen 1998), courtship gift quality (Thornhill 1992b), and estimated lifetime breeding success (Harvey and Walsh 1993; Kruuk et al. 2003).

In contrast, there exists a large literature demonstrating no detectable associations between FA and a diversity of reproductive traits (Eggert and Sakaluk 1994; Birkhead and Fletcher 1995; Markow et al. 1996; Brown 1997; Polak 1997a; Dufour and Weatherhead 1998; Jennions 1998b; Van Dongen et al. 1999; Gonçalves et al. 2002; Hosken et al. 2003; Cooley 2004; Ketola et al. 2007). In some cases reverse associations have even been found. In male red flour beetles, *Tribolium castaneum*, asymmetry in male courtship behavior (leg rubbing frequency) was *positively* correlated with male paternity share, perhaps because of interaction between male behavior and matching anatomical asymmetry in the female reproductive tract (Fedina and Lewis 2006).

Thus, FA is significantly negatively associated with differential mating success in many species, and this effect has been detected across a taxonomic range of animals. However, the literature is strongly heterogeneous, with the predicted negative correlations between FA and components of reproductive success being species and trait specific, and subject to publication bias (Thornhill and Møller 1998; Palmer 1999; Simmons et al. 1999; Tomkins and Simmons 2003; Møller et al. 2005). Nevertheless, the significant negative correlations between FA and mating success that do exist lend support to the developmental instability-sexual selection hypothesis.

Developmental Instability Should be Assessed by Mates and Rivals

For tests of this prediction to be conclusive, they must utilize an experimental approach where asymmetry is manipulated independently of other potential causes of differential reproduction. To most meaningfully gauge adaptive processes in nature, the phenotypic manipulation should be within the range of values of wild populations (Swaddle 2000; Uetz and Taylor 2003). It is shown below that manipulative studies have altered levels of asymmetry in either artificial ornaments, morphological traits of live males, or realistic models of males.

Direct assessment of FA or phenodeviance may in theory occur by way of several channels of communication, *viz*: visual, tactile, vibratory, auditory and olfactory (Møller and Swaddle 1997; Uetz and Taylor 2003). The majority of empirical studies have focused on the visual assessment of FA in sexually and nonsexually selected traits (Swaddle 2000; Swaddle 2003). In most nonsexually selected traits, however, the degree of asymmetry in a population is less than 1–2% of trait size (Møller and Höglund 1991; Swaddle 1999a; Swaddle 2000), cautioning that morphological asymmetries in such traits may be below the limit of visual detectability by conspecifics (Swaddle 2000; Uetz and Taylor 2003). Swaddle (1999b), for example, has shown that European starlings (*Sturnus vulgaris*) could not detect length asymmetries in projected images of the magnitude they would normally encounter in the wild (but see Swaddle and Johnson 2007), and warned against merely assuming that visual assessment of asymmetry by conspecifics can occur in a given system. Morphological asymmetries may often fall below the threshold of detectability for individuals, meaning that in many cases relative symmetry cannot function as a direct cue in assessment (Gangestad and Thornhill 2003). Thus, visual assessment of asymmetry per se in morphological traits is probably rare because of physiological limits to perceptual sensitivities, and costs (e.g., as lost time and fecundity) constraining the evolution of asymmetry assessment by females.

Evolutionary costs of assessment, however, may be relaxed in the case of secondary sexual traits. One reason is that the degree of FA and phenodeviance expressed in sexual traits may be relatively large, up to 10 times that observed in homologous traits in females and nonsexually selected traits in males (Møller and Höglund 1991; Møller 1992c; Swaddle 1999a), although not all secondary sexual traits exhibit this pattern (Balmford et al. 1993; Manning and Chamberlain 1993; Tomkins and Simmons 1995). Thus, the degree of asymmetry in secondary sexual traits may often be obvious enough to be detected directly and quickly (Swaddle 1999a), and so with mitigated cost. Such assessment may occur on the basis of developmental instability expressed not only in secondary sexual traits presented to females (e.g., Møller 1992a; Morris and Casey 1998; Morris et al. 2006), but also in weapons and status badges used in combat and other mutual assessment contexts (e.g., Malyon and Healy 1994; Polak and Trivers 1994; Swaddle and Witter 1995; Polak 1997b).

Developmental instability in secondary sexual traits may also be facilitated because many morphological secondary sexual traits are presented such that their right and left counterparts are positioned next to each other and can be viewed simultaneously, thus making departures from symmetry readily apparent (Jenkins 1982; Møller and Pomiankowski 1993), as in human facial features (Rhodes and Simmons 2007) and tail length in barn swallows (Møller 1992a).

Similarly, behavioral displays involving alternating left–right stereotypic movements and sequences of movements, which likewise could accentuate asymmetry or abnormal CNS phenotypes, making them easier to detect (Møller and Swaddle 1997; Uetz and Taylor 2003). In the nereid fly, *Glyphidops* sp., males alternately rub their right and left tarsi with jittery movements on the eyes and sides of the prothorax of the female during mounting (Eberhard 1996, p. 74; and see Edvardsson and Arnqvist 2000); symmetry in some components of these movements could be favored in sexual selection, perhaps by enhancing fertilization success. This possibility was examined in a study of *Tribolium castaneum* beetles, but leg rubbing symmetry did not enhance male paternity share (Fedina and Lewis 2006). Very little is known about the thresholds of detection of asymmetry through sensory modalities other than vision, and this is a fruitful area for future research.

Several manipulative experiments have revealed a direct role of asymmetry in the visual assessment of conspecifics.

Several studies have demonstrated such an effect using artificial ornaments. The earliest work on this topic involved zebra finches, *Taeniopygia guttata* (Swaddle and Cuthill 1994a; Bennett et al. 1996). Females were presented with males adorned with different combinations of colored leg bands. Females spent more time in front of males adorned with the symmetrical patterns, as opposed to asymmetric or cross-asymmetric patterns (Swaddle and Cuthill 1994a; but see Jennions 1998a), and increased their reproductive output in response to symmetrically banded males (Swaddle 1996). A preference for leg band symmetry has also been demonstrated in bluethroats, *Luscinia s. svecica* (Fiske and Amundsen 1997). But the preference for leg band asymmetry in either species does not demonstrate a preference for FA, as the leg band represents a novel, nonmorphological trait whose asymmetry levels are manipulated in an extreme manner, outside the range of natural variation. The responsiveness of these species to symmetry in arbitrary artificial ornaments may have originated in contexts other than sexual selection, such as for food item recognition.

Researchers have altered asymmetry experimentally within the natural range of variation in secondary sexual traits of males, and have shown that asymmetric treatments are less attractive to females than their symmetrical counterparts. Such effects have been demonstrated for tail length in barn swallows, *Hirundo rustica* (Møller 1992a, 1993b), chest plumage in zebra finches, *Taenopigia gutata* (Swaddle and Cuthill 1994b), vertical bar number in swordtail fishes, *Xiphophorus cortezi* (Morris 1998; Morris and Casey 1998), and human facial features, *Homo sapiens* (Grammer and Thornhill 1994; Perrett et al. 1999; Simmons et al. 2004; and see discussions in Tomkins and Simmons 2003; Rhodes and Simmons 2007). Schlüter et al. (1998) manipulated degree of asymmetry in the number of vertical bars in realistic silicon models of male sailfin mollies (*Poecilia latipinna*), and demonstrated a female preference for symmetrical bars; the preference also occurred for symmetry among living males. Uetz and Smith (1999) used video image manipulation to experimentally alter asymmetry in the conspicuous tufts on the forelegs of male wolf spiders, *Schizocosa ocreata*, and in video playback trials showed that female spiders exhibited reduced receptivity to asymmetrical males. Mazzi et al. (2003) independently manipulated the length and relative asymmetry of the pelvic spines of computer-animated three-spined sticklebacks, *Gasterosteus aculeatus*, and showed that females spent more time orienting toward the symmetrical male model, regardless of spine length.

Thus, manipulative experiments in which either live males, playbacks of live males, or models were experimentally altered, have demonstrated a preference for symmetry. No study has yet demonstrated a direct role for phenodeviance arising from developmental instability in mate assessment.

In contrast, experimental manipulations of secondary sexual traits have failed to demonstrate a preference for symmetry in other animals. These experiments have involved the manipulation of the forceps of earwigs, *Forficula auricularia* (Tomkins and Simmons 1998), and the wattles, ear lappets and hackle feathers of the neck in male red junglefowl, *Gallus gallus* (Ligon et al. 1998). In intrasexual competition, asymmetry in the number of chest spots was unrelated to dominance status in female starlings, *Sturnus vulgaris* (Swaddle and Witter 1995), and manipulated tail or wing patch asymmetry did not influence outcomes of aggressive behavior among male barn swallows *Hirundo rustica* (Møller 1992a, 1993b) or chaffinches, *Fringilla coelebs* (Jablonski and Matyjasiak 1997), respectively.

Thus, although a preference for symmetry per se in mate "choice" (quotes because this term is used broadly) has been demonstrated, it is not a general phenomenon. This in itself does not falsify the present prediction, as the presence of heterogeneity across species applies to many phenomena in biology, such as the effect of secondary sexual trait size on sexual selection (Andersson 1994). Moreover, a preference for *asymmetry* has even been reported in some cases (Oakes and Barnard 1994; but see Brookes and Pomiankowski 1994). Morris et al. (2006) demonstrated a female age-dependent preference for manipulated asymmetry in the pigmented vertical body bars of video animations of males in two closely related species of *Xiphophorus* fishes. But the asymmetrical male treatment in this experiment had a larger number of bars on one side of the body than the symmetric treatment, so the apparent preference for asymmetry may reflect a preference for greater trait size (and see Gross et al. 2007). No study has yet revealed a role for FA or phenodeviance in assessment in intrasexual competition.

Recently, Møller et al. (2005) reported a highly significant overall meta-analytic effect size (r) of -0.308 ± 0.029 (s.e.) describing the general role of FA in sexual selection. Tomkins and Simmons (2003) reported a considerably smaller effect size of -0.156 ± 0.03, having restricted their calculations to studies that had conducted adequate repeatability analyses of FA data when appropriate (Palmer and Strobeck 2003). This value is equivalent to FA explaining 2.4% of the variation in sexual selection outcomes (arising from both mate choice and intrasexual competition). Breakdown of this effect revealed that experimental studies involving secondary sexual traits wherein asymmetry was manipulated, yielded a two-fold greater effect size compared to observational studies, confirming the enhanced sensitivity of manipulative studies in detecting significant effects (Tomkins and Simmons

2003, and see Møller and Thornhill 1998; Møller et al. 2005). When Tomkins and Simmons (2003) purged their data set of significant outliers, a procedure that eliminated heterogeneity in their data set but which was perhaps unnecessarily stringent, their overall effect fell prey to the "file drawer" threat. This outcome warns of the possibility that a number of unpublished studies might exist in researchers' file drawers that could render the overall effect of FA on sexual selection statistically insignificant.

In sum, the developmental instability is not a panacea to variation in reproductive success arising from competition for mates. As a result, early enthusiasm for a general role of FA in sexual selection (Møller 1990; Ridley 1992; Møller and Pomiankowski 1993; Polak and Trivers 1994; Watson and Thornhill 1994) has been tempered (Houle 1998; Simmons et al. 1999; Tomkins and Kotiaho 2001; Gangestad and Thornhill 2003; Tomkins and Simmons 2003). A distillation of nearly two decades of research does yield the conclusion that asymmetry per se is important in sexual selection in *some* vertebrate and invertebrate species. Understanding the causes of this heterogeneity is a next significant challenge to researchers in the field.

Expressions of Developmental Instability Should be Heritable

That FA has a heritable genetic basis is a crucial prediction of developmental instability-sexual selection hypothesis because in the absence of such, FA is unlikely to be associated with genetic fitness benefits through which a preference for symmetry via indirect selection could evolve (Lande 1981; Kirkpatrick and Barton 1997; Fuller and Houle 2003; Kokko et al. 2003).

Heritability estimates for FA (h^2_{FA}) are generally small and insignificant for individual traits, though significant estimates have been reported in some nonsecondary sexual traits, including bristles (Scheiner et al. 1991) and wings (Santos 2002) in *Drosophila*, and a secondary sexual trait (outer-most tail feathers) in barn swallows, *Hirundo rustica* (Møller 1994). Estimates of average h^2_{FA} across studies judged to be relatively reliable as a result of their control of potential confounds such as maternal/paternal and common environmental effects, consistently fall below 5%: 0.025 (Whitlock and Fowler 1997); 0.041 (Gangestad and Thornhill 1999); 0.035 (Van Dongen and Lens 2000); 0.046 (Van Dongen 2000), and the magnitudes of these values are in accord with the earliest available estimates (Mather 1953; Reeve 1960).

In a recent review of h^2_{FA} estimates, Fuller and Houle (2003, p. 165) report a mean value of 0.026 (SE, 0.015) across 21 studies of both animals ($N = 19$) and plants ($N = 2$). This mean estimate is close to significant ($P = 0.092$), but it may be biased upwards because some studies that went into its calculation (Corruccini and Potter 1981; Arnqvist and Thornhill 1998; Pechenkina et al. 2000) rounded negative h^2_{FA} estimates to zero (Fuller and Houle 2003). Of these 21 studies, only four report h^2_{FA} estimates for sexually selected traits, all of which are nonsignificant. The traits are genital morphology in water striders (Arnqvist and Thornhill 1998), fore-tibia length in dung flies (Blanckenhorn et al. 1998), forceps length in earwigs (Tomkins and Simmons 1999), and eyestalks in stalk-eyed flies (Bjorksten et al. 2000). One exception is a value of 0.72 ($P < 0.05$) reported by Arnqvist and Thornhill (1998) for FA in a component of genital morphology of the water strider *Gerris incognitos*, although this value is likely an overestimate judging from the much smaller estimate of the broad-sense heritability for this trait. Recently, Blanckenhorn and Hosken (2003) confirmed the lack of heritability for tibia length FA in dung flies, Kruuk et al. (2003) reported non-significant heritability for FA in antler traits of red deer (*Cervus elaphus*), and Ketola et al. (2007) reported zero heritability for FA in a courtship song-producing structure (the harp) in male decorated crickets (*Gryllodes sigillatus*), despite significant heritability for both trait size and body condition in *Gryllodes*.

It is recognized that FA is only weakly correlated with underlying developmental instability, such that any asymmetry in a given trait will be a poor predictor of underlying developmental stability (Whitlock 1996; Houle 2000). Thus, even in the presence of significant genetic variation underlying developmental instability in the population, h^2_{FA} will likely still be very small and statistically insignificant. In fact, it has been shown that enormous sample sizes (>5,000) in FA studies are required to gain precise estimates of the heritability of developmental instability (h^2_{DI}), a standard achieved by none of the above studies concerning h^2_{FA} in secondary sexual traits (Van Dongen 2007). When these h^2_{FA} estimates are considered in the context of the "standard model" relating FA to developmental instability (Whitlock 1996; Whitlock 1998), which obtains h^2_{DI} by way of a mathematical transformation, h^2_{DI} may in some cases be substantial, with estimates reaching 0.55 (Gangestad and Thornhill 1999; but see Van Dongen and Lens 2000; Fuller and Houle 2003).

However, the developmental instability-sexual selection hypothesis states that assessment occurs on the basis of FA and phenodeviance, of course because it cannot occur directly for developmental instability. Thus, heritability estimates pertaining specifically to FA and phenodeviance are what count for the evaluation of the potential for the evolution of assessment of these traits by good genes sexual selection. Thus, when taken together, the evidence, though still limited, indicates that there is very little additive genetic variation for FA in secondary sexual traits. Perhaps nonadditive genetic effects (dominance and epistasis) are more important features in the genetic control of FA and phenodeviance (Leamy 1997; Van Dongen and Lens 2000; Leamy and Klingenberg 2005; Van Dongen and Talloen 2007). The question of the relative contributions of these different genetic effects to FA and phenodeviance in secondary sexual traits is unresolved.

Developmental Instability in Sexual Traits Should be Condition Dependent

Condition may be defined as the quantity of limiting resources an organism has available for allocation to competing fitness-related traits (Tomkins et al. 2004). The buildup of condition is expected to be influenced by developmental, physiological and behavioral traits, and thus to be under polygenic control (Andersson 1982; Rowe and Houle 1996; Kirkpatrick and Barton 1997). Because developmentally unstable individuals are expected to be less well adapted to their environment (i.e., to be of poor genetic quality), a negative relationship between developmental instability and condition is expected, revealed as elevated FA in secondary sexual traits because of the heightened condition dependence of such traits (Møller and Pomiankowski 1993; Andersson 1994; Tomkins and Simmons 2003).

There is empirical evidence to show that the relative size of many secondary sexual traits among males is condition dependent (Andersson 1994; Johnstone 1995; Veiga and Puerta 1996; Griffith et al. 1999; Hill 2000; Kotiaho 2000; Badyaev and Duckworth 2003; Cotton et al. 2004a; Polak and Starmer 2005; but see Cotton et al. 2004b). In contrast, there is relatively little evidence to suggest that developmental instability in secondary sexual traits is also condition dependent. Correlational studies attempting to link body condition and developmental instability are relatively common, but these have produced conflicting findings. For example, Solberg and Sæther (1993) found that FA in antlers correlated negatively with body mass and condition within age categories of moose, *Alces alces*, sampled over a 25-year period in central Norway, suggesting that antler FA does reveal genetic quality in *Alces*. Blanckenhorn et al. (1998) found a negative correlation between FA and body levels of lipids and glucose among field-caught dung flies, *Scathophaga stercoraria*, a finding consistent with that of Swaddle (1997) who showed that relatively symmetrical flies enjoyed superior foraging success. In contrast, FA in male song producing structures in decorated crickets (*Gryllodes sigillatus*) (Ketola et al. 2007) and in male horn length in mountain goats (*Oreamnos americanus*) (Côté and Festa-Bianchet 2001) showed a lack of significant associations with body condition. Causation in correlational studies in any event is generally not possible to assign. For example, significant negative correlations between body condition and FA in field samples are not strong evidence of causal linkage between condition and developmental instability, for one because differential exposure among individuals to stressful environments during development cannot easily be excluded as a possible mechanism for correlations among traits.

What hinders a strong evaluation of the present prediction is scarcity of available experimental studies, and the diversity of ways in which condition is estimated by different researchers. The most popular experimental approach has been to study FA responses to varying level of stress, such as nutrient availability, parasitism and temperature. Even here, results of experiments must be interpreted with caution, as relatively elevated mortality of developmental unstable phenotypes under highest stress (Møller 1997) may mask any real effects of stress treatment on FA and phenodeviance.

Møller (1992b) found that in barn swallows, *Hirundo rustica*, FA in the outermost tail feathers of males, a secondary sexual trait, increased with experimentally elevated ectoparasite burden. Folstad et al. (1996) showed that antler FA decreased, independently of trait size, in response to antihelminthic treatment of naturally infected reindeer (*Rangifer tarandus*). However, treatment did not affect body condition, suggesting that FA does not reveal body condition in *Rangifer*. David et al. (1998) examined responses of size and FA to nutrient limitation in eyestalks, wing width and wing length, in the Malaysian stalkeyed fly, *Cyrtodiopsis dalmanni*. Males of this species have more greatly exaggerated eyestalks than females, and females exhibit a preference for males with the widest eyespans (Wilkinson and Reillo 1994). In another population, none of the FA traits of *C. dalmanni* responded significantly to nutrient limitation, despite the fact that eyespan in males was dramatically reduced, and was more sensitive to the stress treatment than eyespan in females and other nonsecondary sexual traits (and see Bjorksten et al. 2001 for a similar lack of FA response to heat shock). Hasson and Rossler (2002) tested for FA response to nutritive stress in supra fronto orbital bristles in male medflies (*Ceratitis capitata*), these bristles being a dimorphic secondary sexual trait in which symmetry is favored by sexual selection in at least one population (Hunt et al. 1998). No significant effect of stress on FA was detected, despite a significant decrease in adult body size.

In a survey of eight *experimental* studies addressing condition dependence of FA in secondary sexual traits published prior to 2001, Tomkins and Simmons (2003) report a nonsignificant weighted overall effect size of 0.008 (s.e., 0.04), although this value may be biased downward because of differential mortality across developmental instability classes (Møller 1997). Of seven studies that compared condition dependence of FA for secondary sexual traits and nonsecondary sexual traits, none revealed that FA in sexual traits was more sensitive to stress than nonsecondary sexual traits. Thus, there is little support for the prediction that secondary sexual trait FA is generally condition dependent, or that secondary sexual traits are more revealing of condition than ordinary, nonsecondary sexual traits (Tomkins and Simmons 2003). However, only a few species have been studied in this regard, and fewer still have examined condition dependence of FA in traits where FA is a demonstrated target of sexual selection (Møller and Cuervo 2003).

Developmental Instability Should be Negatively Correlated with Sexual Trait Size

A negative relationship between size and FA is expected because both secondary sexual trait size and developmental stability are thought to be a function of overall genetic quality (Møller 1990). This possible cause of negative size–FA scaling is referred to as the "quality heterogeneity" hypothesis (Polak and Starmer 2005). The predicted negative relationship between size and FA have been reported for traits subject to mate choice and intrasexual selection (Møller 1990, 1992c, 1993c, 1994; Møller and Höglund 1991; Manning and Chamberlain 1993; Schlüter et al. 1998; Koshio et al. 2007), and Møller and Cuervo (2003) provide data suggesting that the size–FA relationship becomes more negative as intensity of sexual selection for trait size increases across species.

This prediction, however, has encountered difficulty for at least two reasons. One is that negative relationships between FA and size of sexually selected traits do not always occur, even when trait size is apparently condition dependent (Møller 1992c; Balmford et al. 1993; Evans et al. 1995; Hunt and Simmons 1997; Arnqvist and Thornhill 1998; Blanckenhorn et al. 1998; Hunt and Simmons 1998; Tomkins and Simmons 1998; David et al. 1999; Kruuk et al. 2003; Bartos and Bahbouh 2006; Ketola et al. 2007). For example, in moose (*Alces alces*) antler size and antler point FA were *positively* correlated in all of four age classes examined in Norway, despite evidence that antler symmetry and size both appear to reveal enhanced body condition and possibly survivorship in this population (Solberg and Sæther 1993). Thus, the existence of negative size–FA correlations is not a general phenomenon.

A second source of difficulty is that at least two alternative hypotheses have been proposed to account for negative size–FA correlations, meaning that the existence of negative correlations, especially in heterogeneous samples from nature, cannot automatically be used to support the developmental instability-sexual selection hypothesis without careful consideration or follow-up investigation to understand how negative size–FA correlations are generated. One is that individuals producing the largest traits in the population are constrained for mechanical and/or aerodynamic reasons to produce symmetrical ornaments (Balmford et al. 1993; Evans 1993; Evans et al. 1995). According to this hypothesis, which so far lacks empirical support, the strength of natural selection for symmetry is an increasing function of trait size. This effect is a plausible mechanism for negative size–FA correlations when energetic costs of asymmetry increase with trait size (Evans 1993).

Alternatively, the "environmental heterogeneity" hypothesis (Polak and Starmer 2005) points to the role of heterogeneity in environmental stress as the source of negative size–FA correlations (Møller and Pomiankowski 1993; Swaddle et al. 1994; Simmons et al. 1995; Swaddle et al. 1995; Polak et al. 2004). Here, negative size–FA relationships are posited to arise purely from environmental effects; individuals developing in a high-stress environment produce traits that are small and relatively asymmetrical, while individuals developing under high quality conditions develop traits that are large and symmetrical (Simmons et al. 1995; Polak and Starmer 2005). The necessary conditions for this hypothesis to work are that stress damages both size and developmental stability (e.g., Parsons 1990, 1992). If these conditions are met, the relationship between trait size and FA is prone to be negative in the general population (i.e., pooled across environments) (Simmons et al. 1995; Polak and Starmer 2005).

Thus, the existence of negative size–FA correlations observed in natural populations, even for secondary sexual traits not subjected to natural selection for aerodynamic efficiency, clearly cannot automatically be used to support the notion that symmetry reveals genetic quality (Møller and Pomiankowski 1993). The apparent support that the quality heterogeneity hypothesis previously received from the existence of negative size–FA correlations (e.g., Møller and Höglund 1991; Møller 1992c; Manning and Chamberlain 1993) may to an extent be unjustified because many of these correlations were derived from heterogeneous field and museum samples. Different objections have been raised to using museum specimens in this context (Swaddle et al. 1994).

To minimize these confounding environmental effects, correlations preferably should be based on homogeneous samples of individuals with known developmental histories (Swaddle et al. 1994), such as from a single season or local habitat, or from the laboratory. Yet, even laboratory estimates of size–FA correlations involving secondary sexual traits do not exhibit the expected negative correlations (e.g., Arnqvist and Thornhill 1998; David et al. 1999; Hunt and Simmons 1997; Hunt et al. 1998; Ketola et al. 2007). Polak and Starmer (2005) argue that the strongest test of this prediction would come from negative *genetic* correlations between size and ornament FA. The only available estimates of this genetic parameter come from our studies of *Drosophila bipectinata*, and these estimates are *positive* (Polak et al. 2004; Polak and Taylor 2007), failing to support developmental instability-sexual selection hypothesis.

Is the Developmental Instability-Sexual Selection Hypothesis Viable?

Of the five predictions evaluated above, the first two, which link developmental instability and mating success, receive relatively strong support. There are numerous species for which a negative association between asymmetry of a secondary sexual trait and mating success (or correlate thereof) has been reported. We also have convincing experimental evidence that females favor symmetry in secondary sexual traits of males in seven animal taxa: barn swallows, humans, sailfin mollies, sticklebacks, swordtails, wolf spiders and zebra finches.

However, based on evidence that notably is still limited, the third prediction, that FA in secondary sexual traits is significantly heritable, appears to fail. Near-zero FA heritability, or lack thereof in many cases, makes it unlikely that FA in secondary sexual traits can reliably reveal heritable genetic quality of mates and thus the potential to transmit "good genes" to offspring (Alatalo et al. 1997; Kirkpatrick and Barton 1997; Houle 1998; Fuller and Houle 2003; Kokko et al. 2003). It therefore seems unlikely that mate preferences for symmetry in secondary sexual traits evolve by good genes sexual selection; indeed, two studies found no significant relationship between FA in sexually selected traits in male parents and offspring viability (Blanckenhorn et al. 1998; Hoikkala et al. 1998; and see Bourguet 2000; Chapman and Goulson 2000).

Perhaps a more likely possibility is that developmental instability is largely trait-specific, and that any, however weak, genetic basis to FA of a trait, or suite of developmentally integrated traits (Leamy 1993; Badyaev and Foresman 2004), results from trait-specific developmental genes (Woods et al. 1998; Klingenberg and Nijhout 1999; Hasson and Rossler 2002; Leamy and Klingenberg 2005). The weak concordance among FAs of developmentally independent traits of individuals (Polak et al. 2003; but see Lens and Van Dongen 1999) supports this view. Klingenberg and Nijhout (1999) showed using a developmental model based on a diffusion-threshold process that low h^2_{FA} values can arise as an epiphenomenon of trait-specific developmental genes. This theoretical insight offers an explanation for the typically weak h^2_{FA} estimates generally observed without invoking genes *for* developmental stability, or a causal link between genetic quality and FA as prescribed by the present hypothesis.

The general lack of significant h^2_{FA} for secondary sexual ornaments makes it unsurprising, therefore, that there is little evidence that FA reveals individual condition, which itself may have a heritable, multi-factorial genetic basis (Andersson 1982; Rowe and Houle 1996; Tomkins et al. 2004). Likewise, given the lack of evidence for heritability and condition-dependence of FA in secondary sexual traits, it is doubly unsurprising that ornament size and FA are not significantly negatively correlated. Even controlled laboratory experiments have generally failed to show that FA is negatively correlated with ornament size, either phenotypically or genetically. Thus, three out of five predictions of developmental instability-sexual selection hypothesis generally appear to fail, indicating that it is unlikely to be viable. This conclusion admittedly may be somewhat premature, in that especially the last two predictions (i.e., condition dependence of FA and negative scaling with size) have attracted very limited good empirical data, so more research in these areas is required for a better assessment of this hypothesis.

How then might mate choice for symmetry be adaptive if symmetry does not reliably reveal genetic quality? A preference for symmetry could arise from *direct* selection on females, if relatively symmetrical males, for example, control better resources, carry fewer contagious parasites, or deliver superior parental care or fertility benefits (Hamilton 1990; Jennions and Møller 2001; Swaddle 2003). As noted by Swaddle (2003), a sexual preference for symmetry evolved via direct benefits could be related to environmental factors (e.g., exposure to parasites and environmental toxins) that perturb developmental stability and individual performance. Alternatively, female preference for symmetry could represent a pre-existing sensory bias that evolved via natural selection for pattern recognition, or it may be merely a by-product of cognition in some cases (Enquist and Arak 1994; Johnstone 1994; Shettleworth 1999; Gangestad and Thornhill 2003; Tomkins and Simmons 2003). Clearly, more research is needed to understand why symmetry is associated with mating success in some species and not in others, and to identify both the proximate and ultimate bases of symmetry preferences.

A Case Study

The aim of this section is to summarize our work with *Drosophila bipectinata* testing the developmental instability-sexual selection hypothesis.

The Study Subject

Drosophila bipectinata Duda is a member of the *ananasssae* subgroup of the *melanogaster* species group, distributed in the Australian and Oriental biogeographic zones (Bock 1978). The focus of our studies has been the male sex combs. The combs are comprised of stout black bristles, or ''teeth,'' arranged in oblique rows on each tarsus of the front legs of males (Fig. 1), but not of females.

In the field, flies aggregate, court and mate on fruit substrates. Females lay eggs into these substrates in which larvae also feed and develop. Pupation occurs in the fruit, or in nearby substrates such as soil. The mating system of these flies is best characterized as scramble competition (Thornhill and Alcock 1983), wherein males do not defend territories or harems of females, but instead chase and court females on the fruits, and engage in agonistic interactions with competitors to position themselves behind females should they signal receptivity.

When a courting male approaches the female from behind, mounts and attempts to copulate, the combs come into contact with the female's abdomen, typically on its lateral, but sometimes dorsal, surface. Contact between the combs and the female's abdomen occurs as the male presses his foretarsi against her body. It is at this stage that the female may be receiving tactile cues concerning features (e.g., size, symmetry, or shape) of the combs. Often males slide off the female, apparently owing to inability to overcome female resistance to mate, allowing for the possibility of female choice on the basis of the sex combs in this system.

The sex comb is present in many *Drosophila* species, but it is not widespread within the genus. Rather, the sex comb occurs only in members of the *melanogaster* and *obscura* species groups of the subgenus *Sophophora* (Kopp and True 2002). Despite its relatively restricted phylogenetic distribution within *Drosophila*, the sex comb is a rapidly evolving secondary sexual trait, exhibiting pronounced variation in size, position, shape, symmetry, and color among populations within species, as well as among sister taxa (Bock 1971; Kopp and True 2002; Polak et al. 2004; Barmina and Kopp 2007; Polak and Taylor 2007).

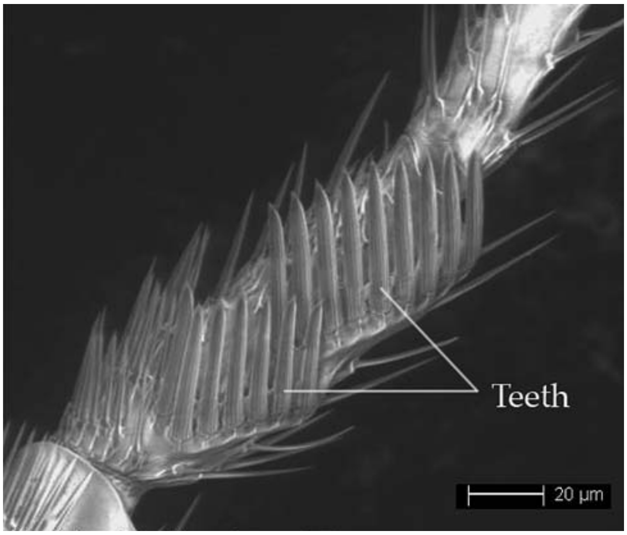

Fig. 1 Scanning electron micrograph (650×) showing the two major segments (C1 and C2) of the male sex comb in *Drosophila bipectinata*. Distal is up

Developmental Instability and Male Reproductive Success

We have been studying the relationship between developmental instability in the sex combs and male reproductive success at Cape Tribulation (northeastern Australia) and in Noumea, New Caledonia (Polak et al. 2004; Polak and Starmer 2005; Polak and Taylor 2007). Importantly, the field and analytic methods used to quantify sexual selection in each population were similar, enabling a direct comparison of selection operating in the wild at these sites. Our field methods consist of sampling copulating and single males directly from the surface of fruits in the field. Copulating pairs are captured as they form, along with a random sample of single males (typically 1–3) in the immediate vicinity of the pair. Sampling is conducted on successive days, and both types of males are then characterized and contrasted in respect to a suite of phenotypic traits of specific interest. The data measure and describe the strength and pattern of pre-copula sexual selection in wild populations, and they are cross-sectional in nature (Arnold and Wade 1984). Multiple logistic regression coefficients (α values, Table 1), which measure the change in the log of the odds of copulating associated with a unit change in the given trait with all other traits in the model held constant, are transformed into estimates of sexual selection gradients (Janzen and Stern 1998). Selection gradients estimate the force of selection on given traits, and can be applied to predict micro-evolutionary change (Lande and Arnold 1983). The results demonstrate strikingly different patterns of sexual selection operating in the Cape Tribulation and Noumea field populations.

Sexual Selection at Cape Tribulation

At Cape Tribulation (left panel, Table 1), the probability of copulation was significantly negatively related to positional FA (Polak et al. 2004). This type of asymmetry captures differences between sides in the *placement* of teeth between the two major sections (C1 and C2) (Polak 1997a). Sexual selection was also detected for increasing size of segment 2 (C2) and thorax length (an estimate of body size). The size of a comb segment is quantified as the number of teeth. Importantly, these significant effects occurred despite statistically accounting for variation in several other potential predictors of copulation success.

Table 1 Results of multiple logistic regression on mating probability in two wild populations of *Drosophila bipectinata* Duda

Trait	Cape Tribulation, Australia (n = 863)[a]				Noumea, New Caledonia (n = 230)[b]			
	α	s.e.	χ^2	P	α	s.e.	χ^2	P
C1	−0.0056	0.054	0.011	0.92	0.0054	0.10	0.0028	0.96
C2	**0.12**	**0.051**	**5.75**	**0.016**	0.092	0.097	0.88	0.35
Thorax length	**3.64**	**1.79**	**4.14**	**0.042**	−0.10	3.11	0.0011	0.97
FA1	0.20	0.14	2.14	0.14	**−0.85**	**0.29**	**8.72**	**0.0032**
FA2	−0.059	0.11	0.29	0.59	−0.24	0.21	1.37	0.24
Positional FA	**−2.070**	**0.91**	**5.13**	**0.024**	0.19	1.94	0.0098	0.92
C1 Phenodeviance	−0.23	0.43	0.30	0.59	**−1.32**	**0.58**	**5.12**	**0.024**
C2 Phenodeviance	−1.63	1.28	1.61	0.20	−0.78	1.41	0.30	0.58
Phenodeviance interaction[c]	−0.53	1.73	0.093	0.76	−0.67	1.52	0.19	0.66
FA1 × C1 Phenodeviance	0.068	.32	0.046	0.83	**1.14**	**0.42**	**7.38**	**0.0066**
FA2 × C2 Phenodeviance	1.06	0.84	1.63	0.20	0.60	0.78	0.59	0.44

Regression coefficients (α), standard errors (s.e.), and χ^2 values testing H_o: $\alpha = 0$, are provided. Significant coefficients are in bold

[a] Reanalyzed data from Polak et al. (2004)

[b] Reanalyzed data from Polak and Taylor (2007)

[c] C1 Phenodeviance × C2 Phenodeviance

Figure 2 presents mean C2 and positional FA in mating and single males at Cape Tribulation.

Sexual Selection in Noumea

None of the traits found to be under sexual selection at Cape Tribulation significantly predicted copulation success in Noumea (Table 1, right panel). Here, both FA and phenodeviance in C1 were significantly negatively selected. Selection gradients that were significant are contrasted between Cape Tribulation and Noumea in Fig. 3. In neither population was the effect of sampling day, or interactions between sampling day and phenotypic predictors of copulation probability, significant.

Conclusions of Sexual Selection Studies

These field results support the first prediction of developmental instability-sexual selection hypothesis, that developmental instability should be negatively associated with mating success. However, strikingly different patterns of selection between these populations exist, consistent with the literature showing heterogeneity among populations and species. Our analyses, which considered the different subunits of the sex comb separately, showed that global developmental instability, even when considered across different subunits of a single compound morphological trait, is not itself under sexual selection. What appears important for driving differential mating success is trait specific developmental instability.

The second prediction, that FA and phenodeviance are the direct targets of female choice or inter-male competition remains unresolved. Tests of this prediction await the development of successful methods for the manipulation of comb size and symmetry.

Heritability

We estimated the heritability of FA traits found to be under sexual selection at Cape Tribulation and in New Caledonia (Polak et al. 2004; Polak and Taylor 2007). For the Cape Tribulation site, heritability was estimated from two laboratory populations, each independently derived from a field population. Estimates for positional FA based on father-offspring ($N = 8$ fathers) and father-grand offspring (N = 15 fathers) did not differ significantly from zero (h^2_{FA} (s.e.): 0.22 (0.38), and −0.073 (0.055)).

For the Noumea population, the heritability of FA and phenodeviance was estimated with a half-sib breeding design, consisting of 80 sires, three dams per sire, and five offspring measured per dam (total N = 1200). Phenodeviance was marginally significant (0.10 (0.056), P = 0.05), indicating an additive genetic basis to comb abnormalitites. Phenodeviance was scored on a binary scale (1,0), and was modeled as a threshold trait (Falconer and Mackay 1996; Roff 1997). The heritability for FA in C1 was 0.044 (0.060, s.e.), but dropped sharply by 85% to 0.0065 (0.055, s.e) when corrected for trait size; neither h^2_{FA} value was significant. This decline suggests that what little genetic variation might exist for FA in C1, it can in large part be attributed to variation in trait size (Klingenberg and Nijhout 1999). The additive genetic correlation between phenodeviance and FA was not significant.

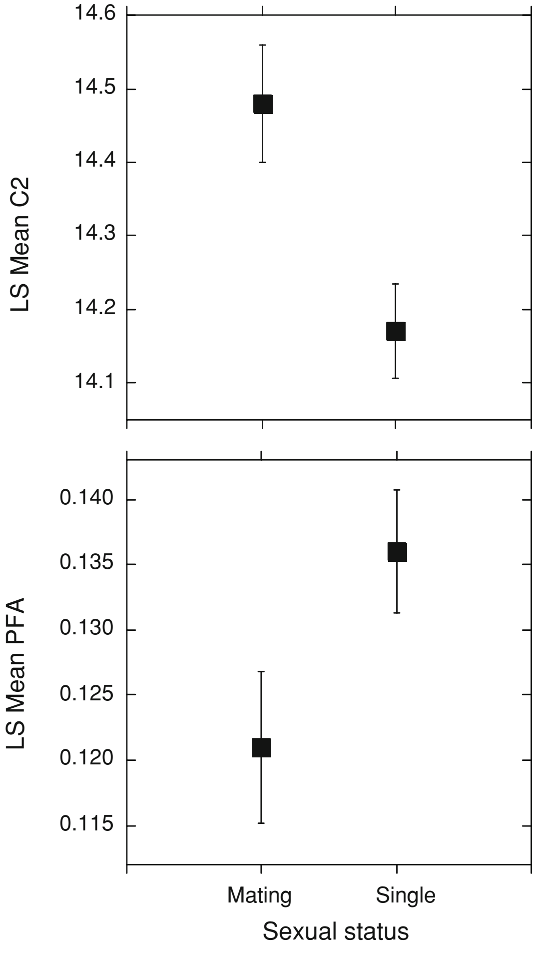

Fig. 2 Ornament size (mean number of teeth in C2, *top panel*) and positional fluctuating asymmetry (PFA, *bottom panel*) in mated ($n = 341$) and single males ($n = 522$). Least squares mean PFA values are corrected for C1 and C2 separately. Errors bars are ±1 s.e. The difference is significant ($P < 0.05$) for both traits

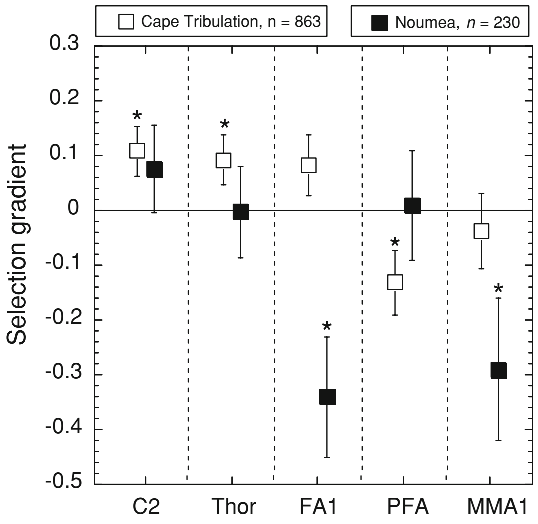

Fig. 3 The strength of sexual selection operating in the wild on various male phenotypic traits at Cape Tribulation and in Noumea, New Caledonia. Asterisks indicate gradients significantly different from zero. The figure illustrates the contrasting patterns of selection operating in these populations. Selection gradients, calculated following Janzen and Stern (1998), are for trait size (C2), male thorax length (Thor), fluctuating asymmetry in C1 (FA1), positional fluctuating asymmetry (PFA), and phenodeviance in C1 scored as minor morphological abnormalities (MMA1; Jones 2006). Error bars are ±1 s.e. Sample sizes for mated and single males are 341 and 522, respectively, for Cape Tribulation, and 100 and 130, respectively, for Noumea

Condition Dependence

To test whether sex comb size and FA are condition dependent, we conducted an experiment to study the response of these variables to temperature stress (Polak and Starmer 2005). If large comb size and symmetry reflect superior body condition, we expected stress exposure to compromise the expression of both these traits. One reason is that induction of protective proteins (e.g., heat-shock proteins, Hsps) within the body (Feder and Hofmann 1999) should channel critical resources toward immediate survival at the expense of other, less-essential traits (Parsons 1995). The fact that sex combs are modified bristles internally constructed of protein (actin) (Tilney et al. 2000) represents a possible physiological basis for a trade-off between stress response and sex comb size.

In the experiment, we performed two independent crosses between pairs of genetic lines recently extracted from nature at two temperatures (25 and 29°C) within the range of values encountered by larvae in the field (Polak and Starmer 2005). Both body size and C2 independently and significantly decreased at the higher temperature. C2 decreased by 9% and 10% in the two crosses (C1 was not significantly affected by the temperature treatment). As predicted, positional FA also responded to the temperature treatment by *increasing* with temperature (independently of body size), but this effect was only significant in one of the two crosses. The results support the conclusion that positional FA, in at least some genotypes, is condition dependent.

Ashley J. R. Carter and David Houle (unpublished manuscript) have criticized this study for failing to properly correct positional FA for trait size, arguing that the increase in positional FA at the higher temperature could merely be an algebraic artifact of the sharp reduction in C2. Indeed, our original analysis (Polak and Starmer 2005) did not control for C1 and C2 individually. Instead, we used overall trait size (C1 + C2) as covariate in an analysis of covariance (ANCOVA) testing for the effect of temperature on positional FA. Thus, for the present article the data were re-analyzed such that C1 and C2 were entered separately into the ANCOVA model, which otherwise was identical to the original analysis criticized by Carter and

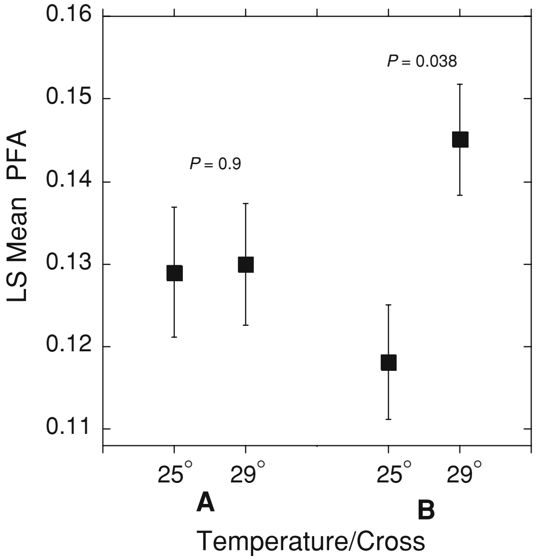

Fig. 4 Least squares mean positional fluctuating asymmetry (PFA) across temperatures in two laboratory crosses (A and B); PFA means are corrected for C1 and C2 separately. The positive effect of temperature stress on positional fluctuating asymmetry (PFA) is restricted to Cross B. *P*-values are from Tukey-Kramer method for post-hoc testing

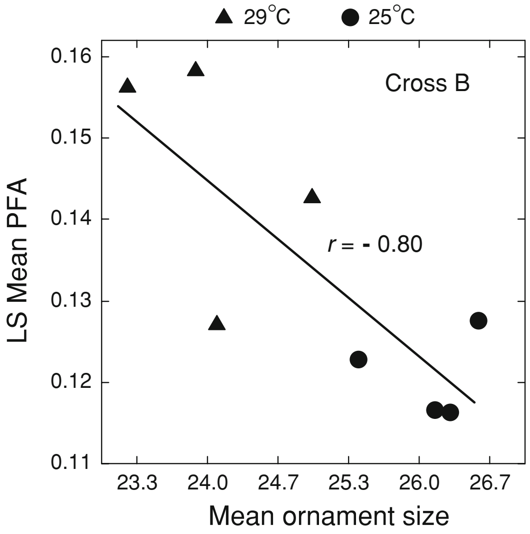

Fig. 5 Least squares mean positional fluctuating asymmetry (PFA) and mean comb size (C1 + C2) of four genotypes raised at two temperatures, demonstrating the "environmental heterogeneity" hypothesis. PFA means are from ANCOVA with C1 and C2 entered separately as covariates. The *r* value is the Pearson product-moment correlation coefficient; the level of significance of *r* was not calculated because the data are not independent

Houle. The effect of temperature on positional FA remained significant (Fig. 4), and remained restricted to one of the two crosses (cross B). This reanalysis affirms the original conclusion that positional FA increases with temperature stress (Polak and Starmer 2005), and supports the prediction that positional FA is condition dependent.

Negative Correlations Between Size and FA

The developmental instability-sexual selection hypothesis predicts a negative phenotypic correlation between secondary sexual trait size and FA because size and FA are expected to reveal overall genetic quality. However, caution has been urged when using negative size–FA correlations to support this prediction, for one because the environmental heterogeneity hypothesis proposes a plausible and arguably more parsimonious alternative to explain these negative correlations in secondary sexual traits from environmentally heterogeneous field samples (Swaddle et al. 1994; Simmons et al. 1995; Polak et al. 2004).

Here I illustrate how the environmental heterogeneity hypothesis can work using data from a reciprocal cross described in Polak and Starmer (2005). Data from one of two replicate crosses (cross B) is used for this purpose because both trait size and positional FA responded in the predicted fashion to the temperature stress (in Cross A, positional FA did not respond). Four lines (parentals, F1 and F1r hybrids) were reared at 25 and 29°C, and emerging adults were scored for phenotypic traits. Pooling data from the different environments yielded the negative relationship between FA and trait size (Fig. 5) predicted by the EH hypothesis. Note that positional FA is corrected for C1 and C2 separately.

This result supports the environmental heterogeneity hypothesis because the same four genotypes were reared at the different temperatures; the negative relationship in Fig. 5 must therefore be the result of the environmental effect and not of differences in genetic quality. Importantly, size–FA correlations in *field samples* collected in two different years at Cape Tribulation were significantly negative (Polak et al. 2004), suggesting that the mechanism depicted in Fig. 5 works in field populations, in fact masking the positive genetic correlation between these traits (see below).

The prediction of negative size–FA scaling should be formulated in terms of a genetic correlation (Polak and Starmer 2005). After all, the original argument of Møller and Pomiankowski (1993) is predicated on the existence of covariation among *genotypes*, and thus implicitly assumes a genetic basis to the covariation. For the many species that cannot be reared under controlled environmental conditions, it will not be feasible to estimate the genetic correlation, so in such cases the phenotypic correlation should be estimated under conditions where environmental effects are minimized (Swaddle et al. 1994; Simmons et al. 1995).

We estimated the genetic correlation between trait size and FA in laboratory populations recently derived from

Cape Tribulation and New Caledonia (Polak et al. 2004; Polak and Starmer 2005). The FA traits were those found to be under sexual selection in the wild. In each population, the genetic correlation between size and FA was *positive*, and weakly significant. No other studies have estimated the genetic correlation coefficient between ornament FA and size, so this result cannot be put into a broader context.

Summary of the Case Study

The conclusions from the research on *D. bipectinata* parallel those of the literature review. Whereas the results demonstrate a role for developmental instability in sexual selection (as FA and phenodeviance in this case), the effect is strongly heterogeneous across populations. Indeed, our most recent work in Taiwan revealed no detectable pre-copulatory sexual selection whatever for any measure of comb FA (M. Polak and Y. Hsu, unpublished manuscript), despite greater sample sizes here than in either of the two previous studies described in the case study (Polak et al. 2004; Polak and Taylor 2007).

We did find evidence that FA in this sexual ornament is condition dependent, at least in terms of positional FA at Cape Tribulation, and this effect was genotype-specific. On the other hand, we found no evidence to indicate that FA in any population is significantly heritable, indicating that FA is unlikely to reveal overall genetic quality of the males, although sample sizes were low in the Cape Tribulation study. Likewise, ornament size and FA were not significantly negatively genetically correlated. The results of this case study fail to support the developmental instability-sexual selection hypothesis as originally formulated.

What May Explain Effect Size Variation?

Variation among populations in the strength of sexual selection for developmental instability has been documented in taxa other than *D. bipectinata*, such as in dung flies, *Scathophaga stercoraria* (Liggett et al. 1993; Blanckenhorn et al. 2003), and black scavenger flies, *Sepsis cinerea* (Allen and Simmons 1996; Blanckenhorn et al. 1998). What might explain such fine-scale heterogeneity (i.e., among populations within species) in the adaptive landscape of developmental instability? For *D. bipectinata*, perhaps variation among populations in the level of DI is a cause of variation in the intensity of sexual selection. For example, FA and phenodeviance in C1 were 16% and 173% higher in Noumea (where intense sexual selection for these traits was detected), respectively, than at Cape Tribulation and Taiwan (where sexual selection for these traits was not detected) (Polak and Taylor 2007; M. Polak and Y. Hsu, unpublished manuscript). This pattern motivates the general hypothesis that variation in the level of developmental instability may in part account for heterogeneity in the effect of developmental instability on sexual selection. In most populations the level of developmental instability may be below a critical threshold and insufficient to propel adaptive processes. Notably, Hewa-Kapuge and Hoffmann (2001) may have identified such a threshold in *Trichogramma* parasitic wasps.

Polak and Taylor (2007) suggested that a recent evolutionary shift toward increased trait size may be responsible for the breakdown of developmental stability in Noumea. That the elevated FA and phenodeviance persisted in the laboratory suggests a genetic basis to this heightened instability, indeed, even despite the very low levels of additive genetic activity for these traits in the population (Polak and Taylor 2007). The relatively smaller combs of putative ancestral populations (Kopp and Barmina 2005) supports the possibility of a recent evolutionary transition toward larger size in New Caledonia. Large-size conferring mutations in specific genes (e.g., that regulate the HOX locus *sex comb reduced*, Barmina and Kopp 2007) could be destabilizing trait-specific developmental networks in the Noumea population (e.g., Clarke and McKenzie 1987), fueling the sexual selection we observed.

Most ornaments, as the *D. bipectinata* sex comb, are likely regulated by a number of signaling pathways, and developmental instability arising from any one of these could simultaneously increase FA/phenodeviance and pleiotropically damage reproductive and other fitness functions, depending on genetic background. Indeed, there are examples of single genes effecting developmental instability in different species (Mitton 1993a; Clarke et al. 2000; Indrasamy et al. 2000), as well as convincing demonstrations of individual genes affecting both symmetry *and* fitness in the Australian sheep blowfly, *Lucilia cuprina* (Clarke and McKenzie 1987; Batterham et al. 1996; Clarke et al. 2000). Random drift or directional selection can be important causes of the increase in frequency of initially rare mutations especially in small, isolated populations (Soulé 1967; Møller 1993d; Templeton 2006). The effect could be breakdown genic co-adaptation and increased FA and phenodeviance of the specific traits in such populations (Lerner 1954; Soulé 1967; Levin 1970; Clarke and McKenzie 1987; Møller 1993d). In general, if the effects of deleterious mutation depend on the genotype of the individual (e.g., Chippindale and Rice 2001), such interaction effects could supply epistatic variance for developmental instability. If this type of genetic variance rises above a critical threshold in the population, sexual selection intensity for reducing developmental instability could spike as a result. The outcome of selection would be to alter the relationship among interacting genes, and may represent a signature of a recent evolutionary shift in trait size.

Sexual selection of this sort may be relatively transient, as the destabilizing effects of new alleles become ameliorated through the evolution of mechanisms that restore genomic co-adaptation and fitness (Bradley 1980; Clarke and McKenzie 1987; Leary and Allendorf 1989; McKenzie and O'Farrell 1993; Møller 1993d). Pélabon et al. (2006) recently conducted artificial selection in opposite directions on the positions of wing veins in *D. melanogaster* and sought correlated responses in developmental instability. Despite significant directional changes in the wing traits in both the up and down directions, FA was not generally affected. The failure to observe a correlated response in developmental instability may be that the selection response in the focal traits did not involve alleles with destabilizing properties, so this result does not necessarily contradict the above ideas. Increasing the frequency of alleles that are already part of a co-adapted genetic network may generally have little consequence for developmental instability.

Conclusions

Based on the available evidence, the developmental instability-sexual selection hypothesis as originally formulated (Møller 1990, 1992a; Møller and Pomiankowski 1993) is in difficulty. A major blow to the hypothesis is that FA in secondary sexual traits is not significantly heritable. This result counters the core concept that FA in such traits reveals heritable differences in genetic quality among males to which females could evolve a preference via 'good genes' processes. Given the failure of this key prediction, it is unsurprising that the two subsequent predictions follow suite in failing to receive convincing support. FA in secondary sexual traits is generally not condition dependent or negatively correlated, phenotypically or genetically, with size in demonstrably condition-dependent secondary sexual traits. But we still have too little information from well-executed studies concerning these predictions for robust conclusions to be made.

In contrast, sexual selection for reducing asymmetry clearly does exist, but by no means is it a general phenomenon. In many species FA is negatively correlated with reproductive success, but many other species and traits do not show a significant relationship. It is also the case that morphological symmetry per se is preferred by females in a small but taxonomically diverse group of species (barn swallows, humans, sailfin mollies, sticklebacks, swordtails, wolf spiders, and zebra finches), suggesting independent cases of the evolution of preference for morphological symmetry among animals. A pressing challenge now is to understand why preferences evolve in some species but not in others. We have no evidence as of yet for a role of direct assessment of FA or phenodeviance in the settlement of intrasexual contests.

Our work with *D. bipectinata* described in the case study uncovered pronounced heterogeneity among populations in the effect of secondary sexual trait FA and phenodeviance on sexual selection. In Noumea, intense sexual selection for reducing FA was detected. Phenodeviance was also negatively sexually selected (though less strongly than FA), confirming the importance of developmental instability for sexual selection in the Noumea population. Although there is some evidence that FA in the male sex comb may be condition dependent, our studies have consistently failed to uncover significant FA heritability and negative size–FA scaling. Comb FA and phenodeviance in *D. bipectinata* appear to reveal trait-specific developmental instability, rather than overall genetic quality.

Theory and empirical data encourage a narrower genetic perspective for predicting a role of developmental instability in sexual selection. Epistatic variance for FA/phenodeviance may be contributed by trait-specific developmental mutations interacting with genetic background, though admittedly this possibility is still purely speculative. Nonetheless, it does appear that the level of developmental instability variation in a population, perhaps largely contributed by nonadditive genetic effects, may need to surpass a critical threshold for selection to operate.

Long-term studies that would simultaneously elucidate the causes of observed associations between sexual trait FA/phenodeviance and mating success, the genetic architecture of these traits, and their genetic associations with trait size and fitness would strengthen our understanding of the role of developmental instability in sexual selection (and see Swaddle 2003, p. 196). Examples of relatively in-depth research efforts that have gone beyond measuring links to mating success involve barn swallows, *Hirundo rustica* (Møller 1992a, 1993b, 1994), black scavenger flies, *Sepsis cynipsea* (Allen and Simmons 1996; Blanckenhorn et al. 1998, 2004), earwigs, *Forficula auricularia* (Tomkins and Simmons 1995, 1998, 1999), and stalk-eyed flies, *Cyrtodiopsis dalmanni* (David et al. 1998; Bjorksten et al. 2000, 2001). Sustained, integrative research with experimentally tractable natural systems promise many more exciting discoveries into this fascinating area of evolutionary biology.

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